Hydrogeology Journal (2023) 31:2231–2249
https://doi.org/10.1007/s10040-023-02711-9

REPORT

Distribution, threats and protection of selected karst groundwater-dependent ecosystems in the Mediterranean region

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Received: 13 January 2023 / Accepted: 31 August 2023 / Published online: 22 September 2023

Abstract
Karst groundwater-dependent ecosystems (KGDEs) in the Mediterranean region are important in terms of ecosystem services and biodiversity but are increasingly under anthropogenic pressures and climate-change constraints. For this study, the eco-hydrological characteristics, threats, and protection status of 112 selected KGDEs around the Mediterranean Sea, including caves, springs, rivers and wetlands, were evaluated, based on local expert knowledge and scientific literature. Results demonstrate that KGDEs contribute considerably to regional biodiversity. The diversity of karst landscapes, combined with the groundwater emergence at springs, leads to exceptional habitat diversity, particularly in arid climates, where KGDEs serve as a refuge for species that could not thrive in the surrounding environment. The most common threats identified among the selected sites are direct human disturbances, such as mass tourism or overfishing, water-quality deterioration and water shortage from aquifer overdraft and/or climate change. Although most of the selected sites are under protection, conservation measures are frequently insufficient. Such shortcomings are often caused by poor data availability, little knowledge on conservation needs of invertebrate species, and conflicts of interest with the local population. For this purpose, it is necessary to raise environmental awareness and promote interdisciplinary research, in order to monitor water quality and quantity in addition to the status of the biocenoses.

Keywords Karst · Ecology · Springs · Groundwater-dependent ecosystem · Mediterranean region

Introduction

Mediterranean karst aquifers are important resources for water supply but also associated with valuable karst groundwater-dependent ecosystems (KGDE's). Groundwater-dependent ecosystems (GDE) are defined as ecosystems whose composition, structure, and functioning rely essentially on groundwater (Kløve et al. 2011a). Karst groundwater-dependent ecosystems are therefore GDE that rely on groundwater that is derived either directly or indirectly from a karst aquifer. The diverse geomorphology and hydrogeology of karst systems within the Mediterranean area enhance the development of diverse KGDEs situated both under- and above ground (Bonacci et al. 2009).

Karst springs are prime examples of KGDEs at the interface of aquifers and surface waters. According to Cantonati et al. (2020), springs are diverse, endangered, and socio-ecological interacting ecosystems that are still insufficiently studied and appreciated by the public. The biocenoses of many spring ecosystems show adaptations to the respective spring characteristics such as water regime and water quality. Spring-dependent species are called crenobionts, which are mostly restricted in their distribution (Kløve et al. 2011a; Stevens et al. 2022). Several habitats can coexist at one spring system, which enhances the biodiversity of the entire ecosystem (Stevens et al. 2021). In arid regions, springs and their surroundings can also serve as a refuge for species during droughts (Cartwright et al. 2020; Kløve et al. 2011a). Furthermore, springs support the biodiversity of associated wetlands, rivers and lakes (Eamus et al. 2016); however, the importance of groundwater contributions to these waterbodies in regards to the ecological benefits is not yet fully understood (Kløve et al. 2011a).

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Underground habitats such as caves, are associated with special environmental conditions (e.g. darkness, limited nutrient supply, almost constant temperature) to which species have to adapt (Culver and Pipan 2013; Gunn 2004). Highly adapted, exclusively subterranean terrestrial species are called troglobionts; stygobionts are aquatic species that are obligate and permanent residents of subterranean habitats (Culver and Pipan 2019; Gunn 2004). Due to the physical isolation in cave systems, such species often show a limited distribution (Howarth and Moldovan 2018a), and many subterranean species are endemic vulnerable (Mammola et al. 2019). Different microhabitats in caves promote a diverse composition of species (Bonacci et al. 2009; Howarth and Moldovan 2018b). The *Encyclopedia Biospeleologica* represents an extensive collection on cave species worldwide, including the Mediterranean, and illustrates the high biodiversity of underground habitats (Juberthie and Decu 1994). However, only a small percentage of caves and other subterranean habitats are protected with proper legislation (Culver and Pipan 2019; Mammola et al. 2019; Niemiller et al. 2018).

Nevertheless, appropriate conservation management is important, because KGDEs are exposed to several threats. Point recharge via swallow holes, fast infiltration and transport of pollutants make karst aquifers particularly vulnerable to contamination (Ford and Williams 2007). Depending on the type of pollution, groundwater species are affected by pollutants or lack of oxygen. Also, changes in water temperature and chemical composition can impact population dynamics and species assemblages (Chapin et al. 2011; Kløve et al. 2011a). Declining groundwater levels can impair ecosystem functions and lead to a loss of habitats and species (Griebler et al. 2019; Mammola et al. 2019). When the KGDE is disconnected from the aquifer, its groundwater-dependent vegetation is replaced by terrestrial vegetation. Habitat destruction is another threat for KGDEs, e.g., draining wetlands to account for development needs (Erostate et al. 2020). Population growth and tourism depict increasing pressures on Mediterranean ecosystems, with climate change intensifying the existing pressures on KGDEs (Erostate et al. 2020; Fosse et al. 2021).

Systematic ecohydrological information on KGDEs is rare, scattered and inhomogeneous. The data situation varies greatly within the study area. Available information often covers only one subject area without addressing interdisciplinary relationships (De Harveng et al. 2009). Stevens et al. (2022) point out similar issues for global data on springs' ecological integrity. Progress on the combined hydrogeological and ecological understanding of KGDEs in a socioeconomic context is relevant to designing appropriate management strategies that allow sustainable use of groundwater and the proper conservation of ecosystems (European Commission 2012; Mammola et al. 2019). KGDEs in the Mediterranean region are essential to consider, as this area is generally referred to as a conservation priority and biodiversity hotspot (Cowling et al. 1996; Myers et al. 2000). Nevertheless, no specific protection procedure targeting GDE has been established at either the European or international level. Their protection is currently ascribed to biological and environmental networks (e.g. Ramsar and Natura 2000 lists), and rarely to groundwater withdrawal limitations.

This study aims to present a multidisciplinary characterization of selected KGDEs in the Mediterranean region which could serve as a basis for further investigations and increase general awareness for KGDE conservation. Based on the collected data, the following questions were answered: (1) How are KGDEs distributed in the Mediterranean area and which ones stand out in terms of ecological value and ecosystem services? (2) What are the major threats to KGDEs in the study area? (3) Which actions are necessary for their appropriate conservation? Despite not being fully exhaustive, the list of KGDEs collected and evaluated for this study demonstrates the general characteristics, ecological values, threats and protection status of Mediterranean KGDEs.

Data collection and methods

Study area

The Mediterranean region can be defined and delineated in different ways (Fig. 1). Both the Mediterranean climate classification by Köppen-Geiger (according to Beck et al. 2018) and the biogeographical definition of the Mediterranean biome (Olson et al. 2001) were deemed not suitable for this study, because large parts along the Mediterranean coastline are not covered, while areas far away from the Mediterranean Sea belong to the respective climate or biome. Using the surface basin of the Mediterranean Sea to delineate the study area is equally inappropriate due to the large basin of the Nile, which reaches far into the African continent. A similar issue exists with the fourth concept of taking all littoral states of the Mediterranean Sea as part of the study area. As an alternative, a buffer zone of 250 km width along the coastline of the Mediterranean Sea was applied, which, although arbitrary to some degree, covers large parts of the region that is typically referred to as Mediterranean. It serves as a focus area for the KGDE collection but does not depict a definite limitation. Relevant KGDEs outside this zone can still be included in the collection.

This buffer zone corresponds roughly to the Mediterranean coastal belt that was affected by the Messinian Salinity Crisis (MSC) at the end of the Miocene. The MSC describes the event of the closure of the Strait of Gibraltar and consequently the almost entire desiccation of the Mediterranean Sea (Rouchy et al. 2006). The MSC has shaped

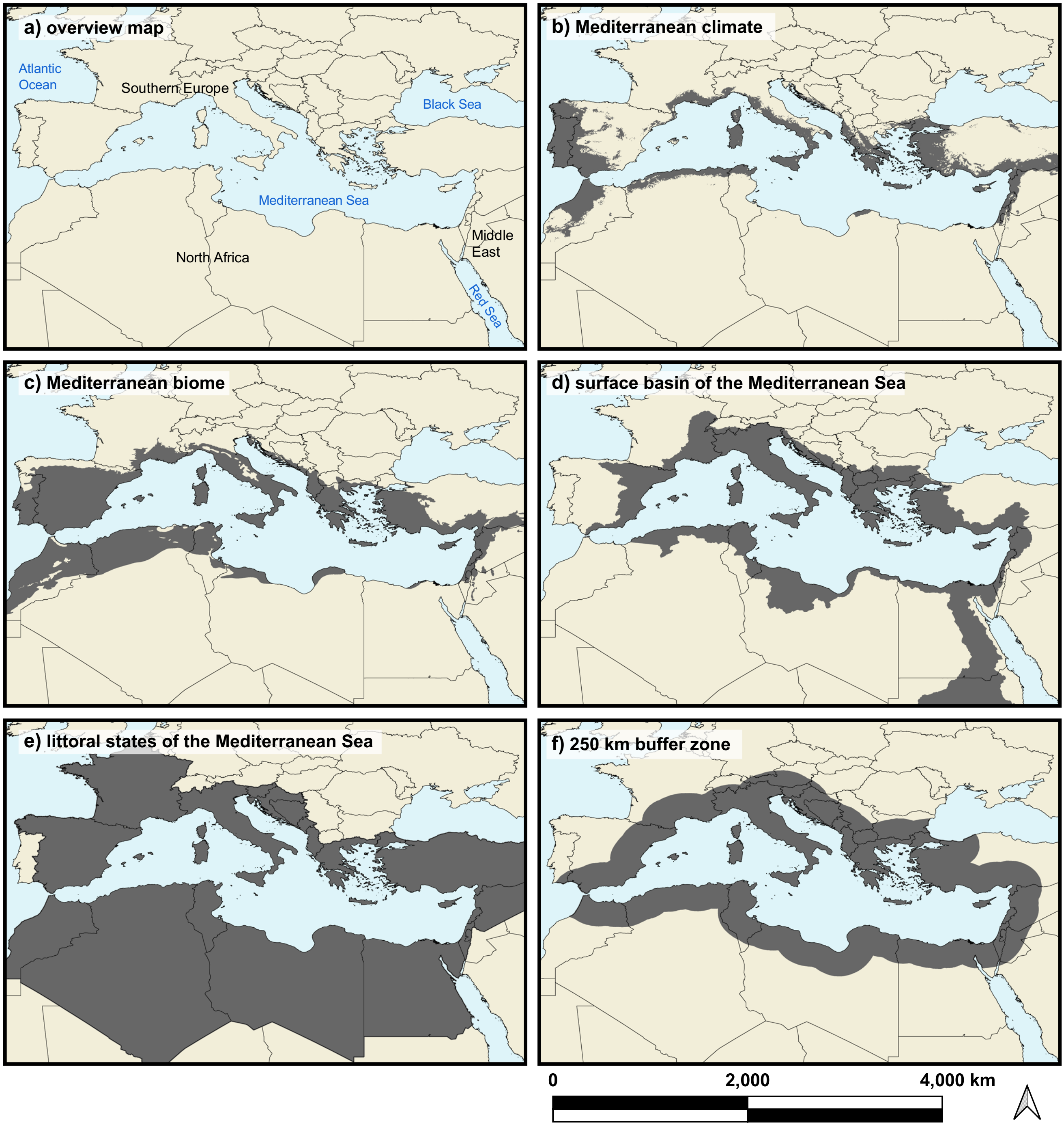

Fig. 1 Concepts of the Mediterranean region (dark grey). **a** Overview of the Mediterranean region; **b** area of Mediterranean climate, i.e., temperate climate with dry and hot summers (Csa) or warm summers (Csb), according to the Köppen-Geiger classification (Beck et al. 2018); **c** area with a biome of "Mediterranean Forests, Woodlands and Scrubs" (Olson et al. 2001); **d** surface basin of the Mediterranean Sea; **e** littoral states of the Mediterranean Sea; **f** buffer zone of 250 km width

the Mediterranean basin significantly. Geologically, isostatic movements caused fracturing of the rocks up to 200 km inland from the present coast (Jolivet et al. 2006). Karstification and fluvial erosion occurred far below the current sea level, explaining the complexity of the functioning of the Mediterranean coastal karst aquifers, which have numerous off-shore outlets, but also marine intrusion inlets (Fleury et al. 2007). Regarding groundwater ecology, the intrusion of oceanic waters into the deep and well-developed coastal karst systems likely affects the subterranean biodiversity. However, the possible introduction of marine species into karst systems has not been fully considered yet (Fleury et al. 2023). For a long time, it was assumed that groundwater fauna originates from the surface (Rouch and Danielopol 1987), but De Harveng et al. (2009) show that Mediterranean karst aquifers are inhabited by a more abundant and diverse aquatic fauna of hypogean origin compared to other regions.

Expert consultation and literature research

Numerous experts from the Mediterranean area (co-authors and colleagues mentioned in the 'Acknowledgements') were asked to contribute information on KGDEs by completing a data collection template. The received data served as the basis for this work. Additional literature research helped to close identified gaps of regional coverage. Springs and caves registered in the WOKAM database (Chen et al. 2017; Goldscheider et al. 2020) were checked and complemented in terms of ecosystem properties.

Furthermore, the open-access databases Natura 2000 network viewer (European Environment Agency 2021) and the Ramsar Sites Information Service (Ramsar Convention Secretariat 2022) are also used as data sources. Ramsar Sites are protected by an intergovernmental convention on wetlands of international importance enforced in 1971. Natura 2000 Sites are protected areas based on two important directives of the European Union (EU) in terms of nature conservation, the Habitats directive (92/43/EEC) and the Birds directive (2009/147/EC; European Commission 1992, 2009). Additionally, international biodiversity programmes that designate hotspot areas like the Important Plant Area (IPA) programme from Plantlife International (Radford and Odé 2009) or the Freshwater Key Biodiversity Area (KBA) in the Mediterranean, which are identified and published by the International Union for Conservation of Nature (IUCN; Darwall et al. 2015; Máiz-Tomé et al. 2017), are helpful for finding KGDEs.

To characterize KGDEs, global datasets containing spatial information on terrain data (GMTED 2010 by Danielson and Gesch 2011), the Köppen-Geiger climate classification (Beck et al. 2018) and a biogeographical classification into biomes (Olson et al. 2001) are applied. Moreover, the database of protected areas worldwide by UNEP-WCMC and IUCN (2022) is used to check if KGDEs are situated in a protected area. The database also contains the spatial level of designation of a protected area, distinguishing between national, regional (EU), or international levels (Dudley 2013). The spatial data are processed with the QGIS application (version 3.16.12 Hannover).

Compilation of a dataset

Based on the aforementioned data, a descriptive dataset is derived, which allows a basic evaluation of the distribution and properties of KGDEs. Each KGDE is assigned to one principal ecosystem type. Since many KGDEs consist of more than one component, the allocation to one specific ecosystem type was based on the availability of data and the ecological importance of each component. Consequently, when evaluating differences between ecosystem types, only information from the respective component of a KGDE is used.

Furthermore, the occurrence of endemic species, stygo- and troglobionts is evaluated, since the spatial concept to which a species is described as "endemic" is crucial. Four possibilities were distinguished. The narrowest concept relates to species that only inhabit one site or ecosystem (e.g., a single cave). Endemic species that are distributed at a given KGDE and the surrounding area including rather small geographical units are allocated to local endemism. The third category comprises national endemic species and the last one regional endemic species. Regional describes any transboundary geographical unit like the Atlas Mountains or the Balkan. Another variable dealing with endemism comprises the taxonomic group of the present endemic species of each KGDE. For reasons of practicality, the groups do not cover the entire animal and plant kingdom systematically. Instead, groups that are regularly mentioned in the reviewed literature are selected. Plant taxa are not subdivided any further. Vertebrates are divided into reptile, fish, amphibian, mammal and bird, and invertebrate taxa are included based on the occurrence in the literature. Regarding hydrological properties, a distinction is made between KGDEs with permanent and nonpermanent water flow (river or springs), or water occurrence (wetlands, lakes, and caves).

Evaluation of selected KGDEs

Spatial distribution

In total, 112 KGDEs in the Mediterranean region are considered in this study (Table 1; Fig. 2). Their distribution is partly influenced by the selection of KGDEs and also reflects the different degrees of research within the study area. The Dinarides are a core area and prime example for research on karst and associated ecosystems (Stevanović et al. 2021), whereas there is much less research in other regions such as North Africa. Still, the Balkan Peninsula with the Dinarides and the Iberian Peninsula show an abundance of KGDEs, which indicate their higher importance and frequency in these regions. Moreover, several studies describe northern

Table 1 List of all selected KGDEs and basic information

ID	Site name	Country	com.	end.	pro.
1	Butrint	Albania	L	+	+
2	Drilon	Albania	S	+	+
3	Rhar Bou Ma'za	Algeria	C, R	-	+
4	Lappenbach tufa springs	Austria	S	+	+
5	Nassköhr bogs	Austria	W, S	-	+
6	Vjetrenica Cave, Popovo Polje	Bosnia and Herzegovina	C	+	+
7	Yagodinska	Bulgaria	C	-	+
8	Lepenitsa	Bulgaria	C, R	-	+
9	Duhlata	Bulgaria	C	-	+
10	Plitvice Lakes	Croatia	R, L	+	+
11	Krka River, Skradinski Buk	Croatia	R	+	+
12	Ombla spring	Croatia	S, R	+	+
13	Jadro spring	Croatia	S, R	+	+
14	Vruljas of Velebit channel	Croatia	SS	-	+
15	Cetina	Croatia	S, R	+	+
16	Siwa Oasis	Egypt	S	-	-
17	Lez	France	R, S	+	+
18	Fontaine-de-Vaucluse, Sorgue	France	S, R	+	+
19	Touvre	France	R	+	+
20	Aube	France	R	-	+
21	Argens	France	R	-	+
22	Loue	France	R	-	+
23	Langres Plateau peat swamp	France	W	-	+
24	Dessoubre	France	R, S	-	+
25	Foux de la Vis	France	R, S	-	+
26	Bernadouze bog	France	W	+	+
27	Baget-Sainte Catherine system	France	C	+	+
28	Cent-fonts	France	C, S	+	+
29	Aggitis River	Greece	R	+	+
30	Stymfalia Lake	Greece	L	+	+
31	Agyia springs	Greece	S, L	+	+
32	Dan	Israel	R, S	-	+
33	Banyas	Israel	R, S	-	+
34	Ein Feshkha, Tsukim, West Bank	Palestine	S, W	+	+
35	Ein Gedi	Israel	S, R	-	+
36	Ayalon	Israel	C	+	-
37	Capo Pescara springs	Italy	S	+	+
38	Presciano springs	Italy	S	+	+
39	Chiarino springs	Italy	S	+	+
40	Frasassi Caves	Italy	C	+	+
41	Su Gologone	Italy	S	+	+
42	Buso della Rana	Italy	C	+	+
43	Grotta Zinzulusa	Italy	C		
44	Ammiq wetland	Lebanon	W, S	+	+
45	Safa and Barouk springs	Lebanon	S	+	+
46	Ain Elshakika	Libya	W	-	+
47	Ayn Zayanah	Libya	LG	-	+
48	Wadi Derna	Libya	R	+	-
49	Afennourir Lake	Morocco	L	-	+
50	Lacs d'Imouzzer du Kandar	Morocco	L	+	+
51	Aguelmam Azegza	Morocco	L	-	+

Table 1 (continued)

ID	Site name	Country	com.	end.	pro.
52	Aguelmam Sidi Ali - Tifounassine	Morocco	W	+	+
53	Friouatto	Morocco	C	+	+
54	Oued Chaara	Morocco	C	+	-
55	Piva and Tara river (Durmitor)	Montenegro	R	+	+
56	St. Naum	North Macedonia	S	+	+
57	Biljanini springs	North Macedonia	S	+	+
58	Studenchishte marsh	North Macedonia	W	+	+
59	Veli Dab	North Macedonia	SLS	+	+
60	Matka Canyon	North Macedonia	R	+	+
61	Alviela spring and Mira Minde polje	Portugal	S, L	+	+
62	Nascente do Rio Ancos	Portugal	R, S	-	-
63	Fontes do Lis	Portugal	R, S	-	-
64	Nascente do Rio Nabao	Portugal	S, R	+	+
65	Fontes de Estombar	Portugal	S, R	+	+
66	Olhos des Água	Portugal	SS	-	-
67	Sistema Espeleológico do Dueça	Portugal	C, S	+	-
68	Moinhos Velhos Cave system	Portugal	C	+	-
69	Pester polje	Serbia	W	+	+
70	Djerdap Gorge	Serbia	R	+	+
71	Postojna-Planina cave system	Slovenia	C	+	+
72	Škocjan Caves	Slovenia	C, W	+	+
73	Cerkniško polje	Slovenia	L	+	+
74	Planinsko polje	Slovenia	L	+	+
75	Pivka lakes	Slovenia	L	+	+
76	Dobličica, Jelševnik	Slovenia	S	+	+
77	Vir pri Stični	Slovenia	S	+	+
78	Cuevas del Drach	Spain	C	+	+
79	Lagunas de Ruidera	Spain	W, L	+	+
80	Lago de Bañolas	Spain	L	+	+
81	Laguna de Fuente de Piedra	Spain	W	-	+
82	Complejo lagunar del Trías de Antequera (Lagunas de Archidona)	Spain	W	-	+
83	Lagos de Covadonga	Spain	L	-	+
84	Cueva de Nerja	Spain	C	+	-
85	Karst en yesos de Sorbas	Spain	C	+	+
86	Nacimiento del rio Guadalquivir	Spain	R, S	+	+
87	Nacimiento del rio Segura	Spain	R, S	+	+
88	Manantial de Alcossebre	Spain	SS	-	+
89	Nacimiento del rio Ebro	Spain	R, S	-	+
90	Nacimiento del rio Tajo	Spain	S, R	-	+
91	Manantial de Sa Costera o Font des Verger	Spain	S	-	+
92	Ojo Guarena	Spain	C, R	+	+
93	Nacimiento del rio Mundo	Spain	R, S	+	+
94	Manantial de Arteta	Spain	R, S	-	+
95	Cueva del Gato	Spain	C	-	+
96	Torcas de los Palancares	Spain	L	-	+
97	Manantiales del Monasterio de la Piedra	Spain	S, R	-	-
98	Laguna del Padul	Spain	W	-	+
99	Nahr al Marqiyah	Syria	R	+	-
100	Springs of Jebel Zaghouan	Tunisia	S	-	+
101	Lac Ichkeul	Tunisia	L	-	+

Table 1 (continued)

ID	Site name	Country	com.	end.	pro.
102	Ain Charchara, Hammam Haddej	Tunisia	S, R	-	+
103	Grotte ain Dhab	Tunisia	C, S	-	+
104	Kizören Obrouk	Türkiye	L	+	+
105	Güllük Lagoon	Türkiye	LG	-	+
106	Düden	Türkiye	R	+	-
107	Egirdir	Türkiye	L	+	+
108	Köprücay River	Türkiye	R	+	+
109	Lake Skadar	Albania, Montenegro	L	+	+
110	Lake Ohrid	Albania, North Macedonia	L	+	+
111	Lake Prespa	Albania, North Macedonia, Greece	L	+	+
112	Una	Bosnia and Herzegovina and Croatia	R	+	+

ID refers to the numbers on the map in Fig. 2; the components (*com.*) the ecosystem is composed of, the first mentioned is the considered and evaluated one (*C* cave, *S* springs, *R* river, *L* lake, *W* wetland, *SS* submarine springs, *SLS* sublacustrine springs, *LG* lagoon); information about endemic species occurrence (*end.*) distinguishing between KGDEs with (+) or without (-) endemics; information on the protection status (*pro.*) distinguishing if KGDEs are located in designated protection areas (+) or not (-)

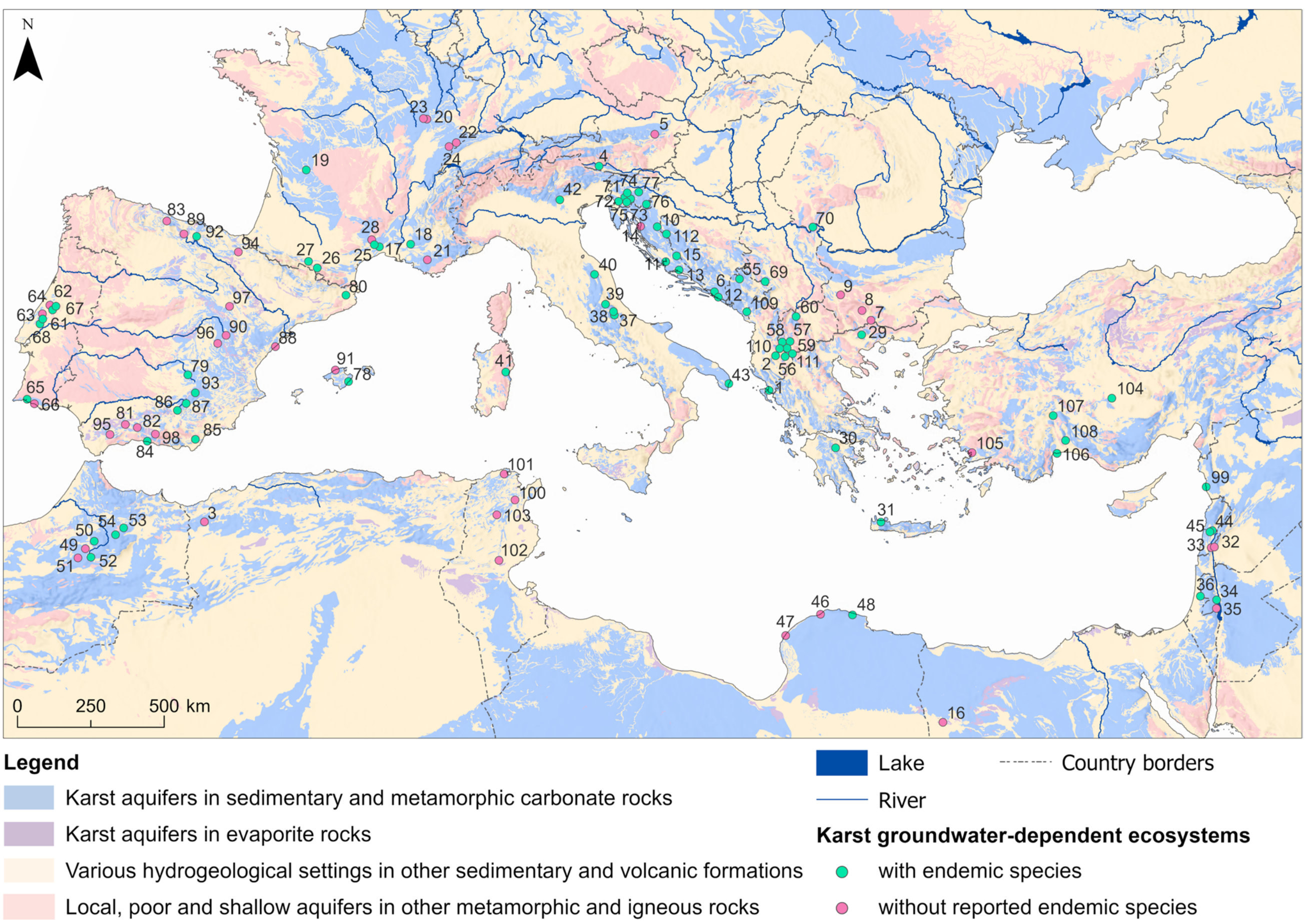

Fig. 2 Locations of the 112 selected KGDEs on the Mediterranean Karst Aquifer Map (MEDKAM, modified from Xanke et al. 2022). The given numbers refer to the ecosystem names in Table 1. Countries are represented in accordance with UN (2023)

Spain and the Dinaric karst as subterranean biodiversity hotspots (Culver et al. 2021; Iannella et al. 2020).

The predominant biome in the study area is the "Mediterranean forests, woodlands and scrub", as 71 of the selected KGDEs are located in this biome (cf. Fig. 3). "Temperate Broadleaf and Mixed Forests" is the second most represented biome with 28 KGDEs. In contrast, the oases of Ein Feshkha (ID 34, cf. Table 1; Fig. 2) and Ein Gedi (ID 35) are situated in Desert and Xeric Shrubland environment, which is scarcely represented in the Mediterranean area. These oases demonstrate how emerging groundwater converts the otherwise desert environments to "green islands" and forms habitats that differ from the biome of the surrounding region (Fig. 4). Thus, KGDEs can serve as a refuge for species that could not survive in the surrounding landscape (Cartwright et al. 2020) and, therefore, enhance regional biodiversity.

Regarding climate, the Köppen-Geiger classification as presented by Beck et al. (2018) is applied. The typical Mediterranean and predominant climatic type is temperate climate with dry and hot summers (Csa) and is found at 40 KGDEs; 8 KGDEs are located in temperate climate with dry and warm summers (Csb) (Fig. 3). Many KGDEs are located in mountain ranges, which affects the climate and might explain the occurrence of a larger number of KGDEs in colder and wetter climates than one might assume in the Mediterranean context of the study area. Examples of mountainous KGDEs that show colder climate conditions are the

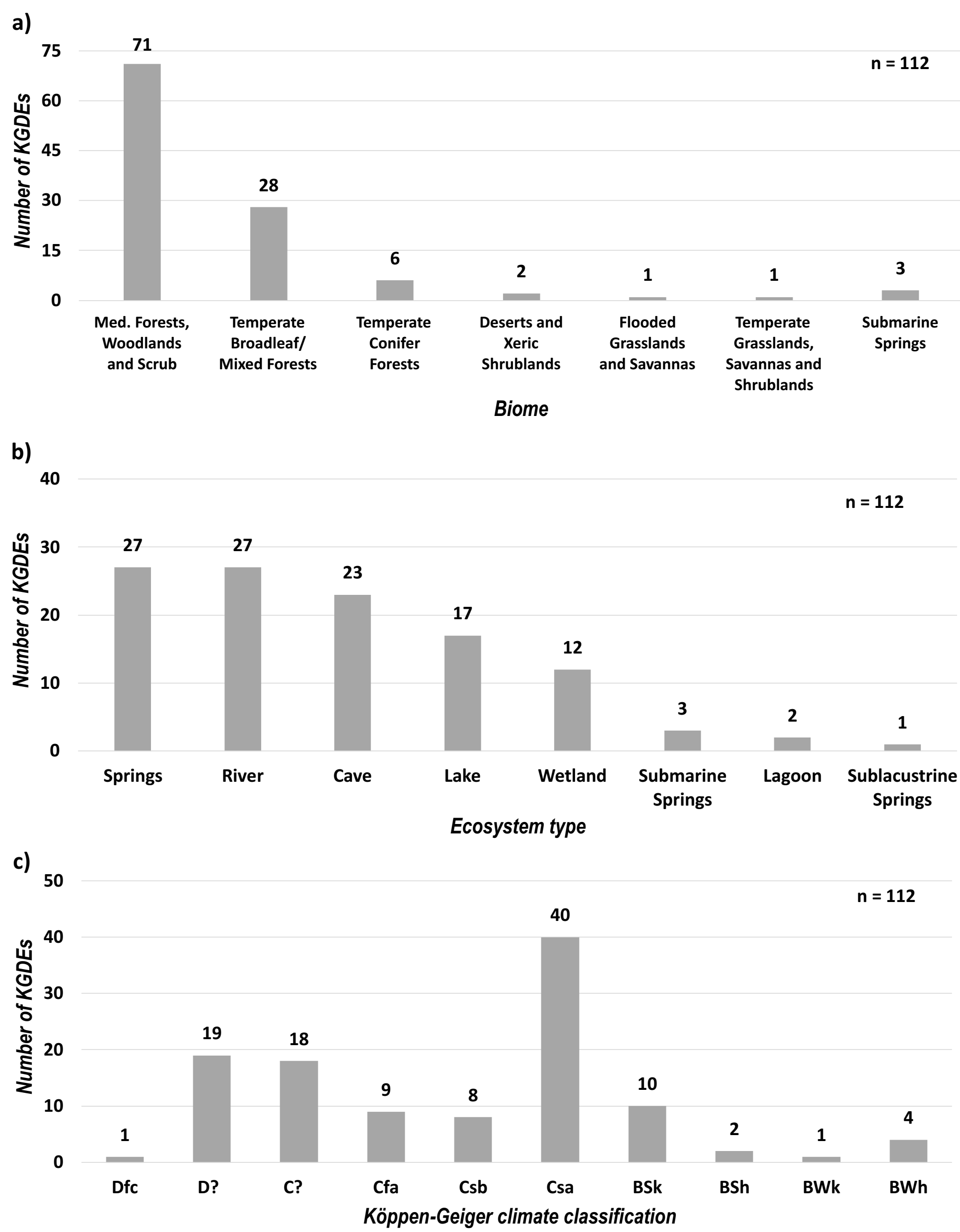

Fig. 3 Distribution of the KGDEs included in the data collection ($n = 112$) among **a** biomes, **b** ecosystem types and **c** Köppen-Geiger climate classes that occur in the study area. BWk cold desert; BSh hot semi=arid; Bsk cold semi-arid; Bsk cold semi-arid; Csa dry and hot summers; Csb warm-summer; Cfa humid subtropical; Cfb temperate oceanic, Dfb warm summer humid; Dfc subarctic

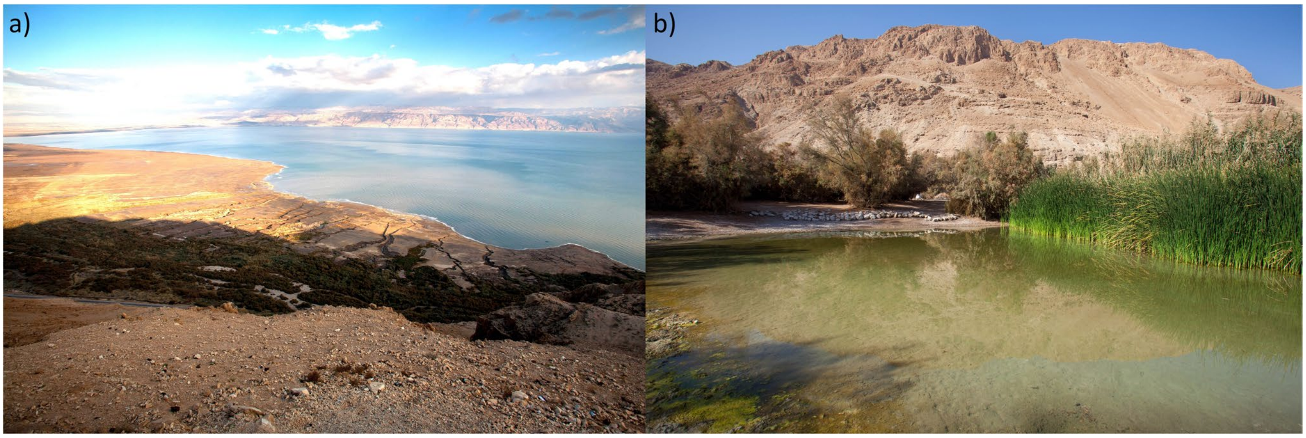

Fig. 4 Impression of Ein Feshkha oasis: **a** View from the top of the escarpment, showing the wet area of the oasis with vegetation in the desert environment adjacent the Dead Sea. Between the shoreline and the main area of the reserve, gullies cut through the salty clay plains and carry water from the wet area towards the receding Dead Sea. **b** One of the pools of the oasis, with aquatic vegetation on the right and several tamarisk trees typical of salty dry areas on the left shore (photos: Doron Nissim, Israel Nature and Parks Authority, with permission)

Bernadouze bog (ID 26) in the French Pyrenees or the Tajo spring (ID 90) in the Sierra de Albarracín in Spain.

Ecosystem properties

The first step for characterizing a KGDE is the allocation to a main ecosystem type. Springs (27), rivers (27) and caves (23) are the most common types in the presented collection. Lakes follow with 17 examples, and 12 karst groundwater-dependent wetlands were included (Fig. 3). Among these types, there are special habitat forms such as anchialine habitats in caves close to a coastline. Anchialine habitats, like the Cuevas del Drach (ID 78, Fig. 2) and Grotta Zinzulusa (ID 43), are under marine influence which is demonstrated by a variable salinity of the water and the presence of stygobionts along with species of marine origin (Gunn 2004). Other special habitats are created by limestone precipitating springs (LPS) (Cantonati et al. 2016), e.g., at the prominent Plitvice Lakes (ID 10; Fig. 5) but also in similar ecosystems such as the Lagunas de Ruidera (ID 79) or the Monasterio de Piedra system (ID 97) in Spain, or the Düden Waterfalls (ID 106) in Turkey. Also, the Lappenbach tufa springs (ID 4) in Austria relates to this typical karst feature and constitutes a special spring habitat. Other ecosystem types are represented by the two lagoons, the Güllük lagoon (ID 105) in Türkiye and the Ayn Zayanah (ID 47) in Libya, and the sublacustrine springs of Veli Dab (ID 59) in Lake Ohrid. Furthermore, there are the submarine springs “Vruljas” in the Velebit channel (ID 14) of Croatia, the submarine springs of Alcossebre (ID 88) in Spain and the Olhos de Água (ID 66) in Portugal.

Within the data collection, 73 KGDEs are assigned to the hydroperiod of permanent discharge or water occurrence. Among those, many KGDEs still show a highly variable

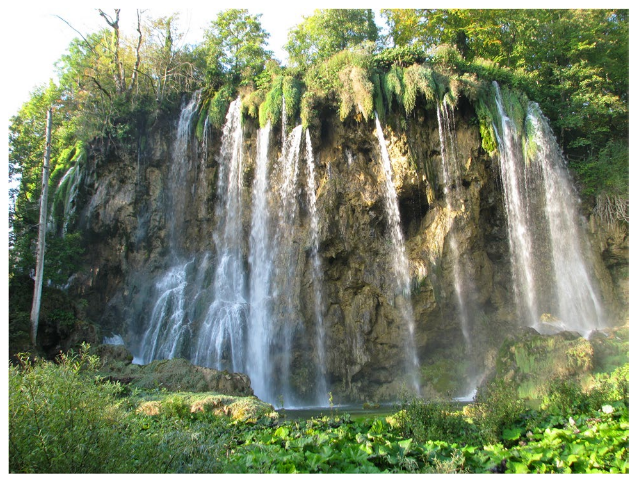

Fig. 5 One of many waterfalls with active limestone precipitation at Plitvice Lakes National Park and UNESCO World Natural Heritage, Croatia. The lakes and their ecosystem are supplied by groundwater from several karst springs (photo: N. Goldscheider)

water regime as it is typical for karst. Conversely, there are also some KGDEs showing a steady regime, especially springs with a relatively high discharge, like Capo Pescara (ID 37; Stoch et al. 2015). For 14 KGDEs, a nonpermanent hydroperiod is recorded, which is related to the hydrologic variability of karst systems and/or the low water availability in some parts of the study area. The first is illustrated, for example, at several intermittent lakes in Slovenia, like the Pivka lakes (ID 75), or in Planinsko (ID 74) and Cerkniško Polje (ID 73; Fig. 6). After prolonged or intense precipitation events, the water level in the karst aquifer rises and leads to flooding, often along the stream channels of the polje, because the water inflow exceeds the capacity of drainage

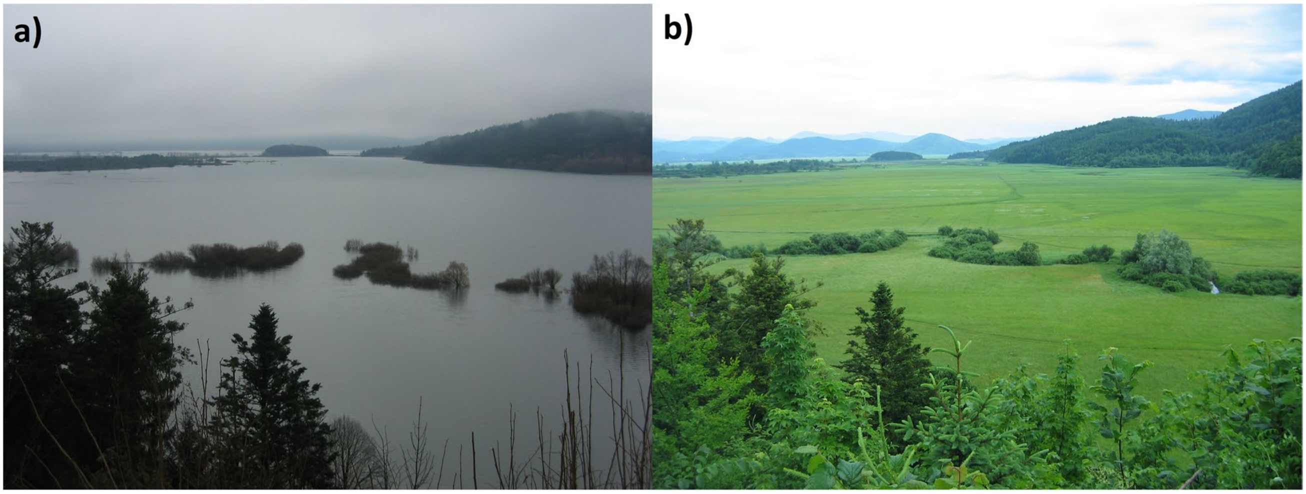

Fig. 6 Cerkniško Polje, the largest polje in Slovenia, during **a** flooded and **b** dry conditions. On average, the polje is flooded three-quarters of the year, but in some years, it does not dry up at all (Ravbar et al. 2021; photos: N. Ravbar)

channels (Ravbar et al. 2021). The changing hydrological conditions induce the presence of several plant communities according to the different hydrologic conditions of the intermittent lakes (Gaberščik et al. 2018). The KGDEs of the Popovo Polje and Vjetrenica cave (ID 6) used to show a similar pattern, but the river regulations stopped the regular flooding and therefore threatens the species which are adapted to changing water table (Gunn 2004; Lučić 2007). A nonpermanent waterbody of the KGDE selection that is related to water scarcity is represented by Lake Aoua, which belongs to the Imouzzer du Kandar lake complex (ID 50) in Morocco. Formerly known as permanent waterbody, Lake Aoua and Lake Hachlaf dried out several times in the last decades due to droughts and overexploitation (Nogueira et al. 2021; Sayad et al. 2020). Since there is no consistent and complete data source for the hydroperiod, a total number of 25 KGDEs could not be allocated clearly. The limited research poses a problem regarding classification of KGDEs, especially for the ones that are threatened to dry out due to climate change and/or overexploitation.

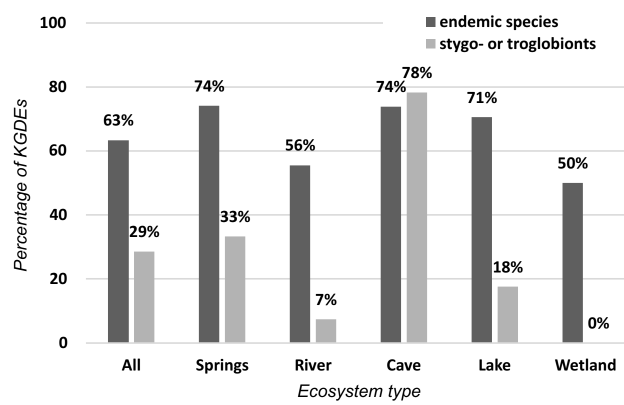

Fig. 7 Percentage of selected KGDEs of the different ecosystem types that are inhabited by endemic species (dark grey) and stygo- or troglobionts (light grey). By definition, stygo- and troglobionts should only occur underground, but they are also found in KGDEs that primarily belong to another type but include underground habitats

Species in KGDEs

This study focuses on endemic species because entire species inventories are not available in most of the cases, whereas the presence of endemic species is mostly reported (if investigated) for the ecosystems. Because underground ecosystems are part of this study, the presence of troglobionts and stygobionts is also considered. In all, 63% of selected KGDEs harbour at least one reported endemic species (Fig. 7). Caves (74%), springs (74%) and lakes (71%) have the highest frequency of endemic species occurrence within the considered KGDE selection (Fig. 7). Regarding stygo- and troglobionts, 29% of all considered KGDEs are inhabited by such species. Caves contribute greatly to that result, as stygo- and/or troglobionts are recorded for 78% of the evaluated caves; however, stygo- and troglobionts are also reported from other ecosystem types that are closely connected to underground habitats and/or include caves as part of the overall KGDEs (e.g., springs emerging from caves, lakes with caves along the shoreline). Such species occur at 33% of the springs, 18% of the lakes and 7% of the rivers within the selected KGDEs evaluated for this study (Fig. 7).

Springs often form relatively isolated ecosystems and harbour spring-dependent taxa adapted to the specific condition of a spring, such as relatively stable water temperatures (Cartwright et al. 2020; Stevens et al. 2022). This relates to the observed high frequency of endemic species at springs. For lakes, the isolation and old age of some lake ecosystems, such as Lake Ohrid (ID 110) and Lake Prespa (ID 111), also explain the frequent occurrence of endemics (Albrecht and Wilke 2008; Neubauer et al. 2015). Lake ecosystems are relatively well studied and supported with good data availability, which could lead to a bias induced by the advanced research. The high percentage of caves with reported endemic species can be attributed to their isolation and unique habitats (Goldscheider 2019; Lauritzen 2018). The two caves with the highest reported biodiversity in the world are the Postojna-Planina Cave system (ID 71) and the Vjetrenica Cave (ID 6), both located in the Dinaric Karst (Culver and Pipan 2013; Culver and Sket 2000; Niemiller et al. 2018). The Postojna-Planina Cave system (cf. Fig. 8) is referred to as the cradle of speleobiology, because research on its fauna already started in the 19th century. The cave system is the type locality for the first troglobitic cave beetle (*Leptodirus hochenwartii*) and more than 60 other invertebrate species (Culver and Sket 2000; Gunn 2004; Zagmajster et al. 2021). The epikarst of this system depicts another habitat from which 23 copepod species are recorded (Culver and Pipan 2013). Zagmajster et al. (2021) recently revised data on the Postojna-Planina Cave fauna and updated the number of troglobionts to 45 and of stygobionts to 71 species illustrating the enormous biodiversity. Since the cave system is fed by two sinking rivers, a rich species diversity from stygobionts to surface species can be detected in the underground rivers (Culver and Sket 2000). The large amounts of organic matter that enter the cave via sinking rivers are utilized as nutrient source (Simon et al. 2010; Zagmajster et al. 2021). Particularly interesting are populations of stygophilic species that show an increase in troglomorphic adaptations between the sinking point towards the resurgence of the underground river (Gunn 2004).

The level of endemism, i.e., the spatial extent to which the species are restricted to, is also evaluated. For each KGDE, the endemic species with the narrowest distribution is taken as the reference. In all, 32 KGDEs harbour at least one species that is restricted to the respective site. One example is the fish species *Cottus petiti* (Lez sculpin), which only occurs in the upstream part of the Lez River (ID 17) and its tributary (Lefebvre et al. 2019). At additional 21 KGDEs, endemic species with local distribution were found. National and regional endemics were recorded for 12 and 6 KGDEs, respectively.

As far as the available data allows, the taxonomy of the endemic species is considered as well. The most frequent species group with endemic representatives are fish, as 25 of the 112 KGDEs harbour at least one endemic fish. Amphibians follow with endemic species at 19 KGDEs. The occurrence of *Proteus anguinus* (Fig. 8) in several KGDEs of the Dinaric Karst contributes substantially to this result. Crustaceans and plants are represented with at least one endemic species at 18 KGDEs, followed by Mollusca at 17 KGDEs (Table 2). Among the endemic Mollusca species, Gastropods dominate. This is in accordance with the representative groundwater taxa for KGDEs stated by Ravbar and Pipan (2022). Table 2 additionally shows the frequency of species groups with endemic representatives among the ecosystem types. In caves, Crustaceans are the prevailing taxonomic group. Endemic Crustaceans are also described at five spring ecosystems. The frequent presence of endemic Crustaceans in caves and springs is consistent with the fact that Crustacea are considered the most diverse group among the stygobionts (Moldovan 2018). However, these results are likely biased due to the limited information available on invertebrate fauna for several ecosystems. Moreover, individual studies often focus on single taxa, such as Mollusca

Fig. 8 **a** The Postojna-Planina cave system hosts various habitats including seeps (sampling point on the left side), an underground river, and other aquatic and terrestrial habitats (photo: Blaž Kogovšek, with permission) **b** An endemic species of the Dinaric Karst, *Proteus anguinus*, the first described cave animal in the world, also known as "human fish". The photo shows a young animal with eyes still visible, later covered with skin (photo: T. Pipan)

Table 2 Number of KGDE examples that host at least one endemic species of the given taxonomic groups

Type	Fish	Amphibian	Reptile	Mammal	Crustacea	Hexapoda	Mollusca	Plant	Other
All KGDEs	25	19	5	1	18	14	17	18	10
Springs	8	4	2	0	5	2	4	2	4
Rivers	7	5	1	0	0	2	3	6	0
Caves	2	5	0	1	10	6	3	3	3
Lakes	5	3	2	0	2	2	5	5	1
Wetlands	3	2	0	0	1	2	1	2	2
Sublacustrine springs	0	0	0	0	0	0	1	0	0

The first row contains the data for all KGDEs, while the following rows present endemic species in the individual ecosystem types

or diatoms (e.g. in Cvetkoska et al. 2018; Hauffe et al. 2011; Lai et al. 2020; Prié 2008), allowing them to be better known and classified, while other species remain undetermined or undiscovered.

Human utilization, threats and impacts

For 101 out of the 112 selected KGDEs, utilisation by humans is documented. Many of them serve multiple purposes, demonstrating their high value. In all, 64% of the selected KGDEs provide recreational and cultural services. Water supply as service was recorded for 37% of the KGDEs, with one example being the Lez spring (ID 17) which provides water for 350,000 people by pumping directly from the aquifer (Fig. 9) with a maximum rate of 1,700 L/s (Dausse et al. 2019; Hérivaux and Maréchal 2019). To account for the ecological water demand of the river ecosystem, a continuous reserved flow compensates for the pumping (SYBLE 2017). Other biological resources, including food provision or production (e.g., fishing, grazing, mussel farms), are provided by 24% of the listed KGDEs. Hydropower, quarrying or salt extraction, take place at 8% of the KGDEs.

Regarding threats, human disturbances present the most frequent type (48%), including fishing, hunting, tourism and other recreational activities. Intense boat traffic and other sport activities as well as overfishing of two native fish species in Lake Ohrid (ID 110), which is characterized by exceptionally high biodiversity and endemicity, are examples for this problem (Albrecht and Wilke 2008; Kostoski et al. 2010). The touristic popularity of the Mediterranean might explain the substantial role of human disturbances as threat for KGDEs. Excessive tourism is associated with high interference with the ecosystem such as damaging sensitive vegetation, as well as the construction of hotels or other facilities that lead to habitat destruction (Fosse et al. 2021). For Vjetrenica Cave (ID 6), Lučić (2019) states impacts of the visitor development including the defragmentation of cave habitats, the generation of lampenflora, and the toxic effect of a discarded camera battery harming the crustacean community. To address this problem, it becomes necessary to raise the environmental awareness among visitors and to restrict development in such vulnerable areas (Kostoski et al. 2010).

Altogether, 31% of the considered KGDEs are subject to habitat destruction, which besides touristic infrastructure, includes all other types of industrial development and urbanization as well as the construction of dams and hydropower plants. The Ayalon Cave (ID 36) in Israel, known for the chemoautotrophic ecosystem with several endemic species (Por et al. 2013), is at immediate and severe risk due to extensive infrastructure development plans.

Water quality deterioration is a major threat for 40% of the ecosystems in the data collection. The Dinaric Karst is a region where improper waste management and a lack of wastewater treatment plants is the main threat causing water quality deterioration (Stevanović et al. 2021). Stevanović et al. (2021) advise the construction of sanitary landfills and wastewater treatment plants to better manage solid and liquid waste. Lake Ohrid, originally oligotrophic, shows signs of eutrophication caused by nutrient inputs from agricultural and forestry practices and a lack of appropriate sewage systems (Cvetkoska et al. 2018; Kostoski et al. 2010). Eutrophication of Lake Ohrid is evident in the more populated northern part of the lake, where total phosphorus levels are 10 times higher than in the eastern parts (Cvetkoska et al. 2018). In total, 41% of the considered KGDEs are threatened by agricultural activities, including excessive groundwater extraction, contamination, habitat and soil degradation (Eamus et al. 2016; Erostate et al. 2020; Kløve et al. 2011b).

Water shortage is threatening 37% of the studied KGDEs, predominantly in arid regions. Two of the three lakes of the Imouzzer du Kandar complex (ID 50) developed from a permanent to a temporary lake, severely affecting the aquatic habitats and species. Groundwater is pumped increasingly to irrigate agricultural lands and tree plantations leading to a decline of the water table. Although the lakes are part of a Ramsar Site and National Park, effective protection and groundwater management are missing because of conflicts

Fig. 9 Human utilization of and threats to KGDEs: **a** Pathway for visitors of Plitvice Lakes; more than 1 million tourists visit this National Park per year; **b** Former infrastructure to pump groundwater at the Lez spring for Montpellier water supply; **c** Flamingos at Laguna de Fuente de Piedra, which suffers from declining water tables caused by aquifer overdraft; urban development adjacent to the wetland is visible in the background; **d** illegal dumping of waste in a karst shaft in Slovenia; **e** Fire incident at Ein Feshkha area in 2008; **f** Burnt vegetation of Ein Feshkha after the fire (photos: **a**–**c** N. Goldscheider, **d** J. Tičar, with permission, **d**–**e** Doron Nissim, Israel Nature and Parks Authority, with permission)

with the local population (Ichen et al. 2021; Nogueira et al. 2021; Sayad et al. 2020). In Spain, the natural status of Laguna de Fuente de Piedra (ID 81) is also affected by groundwater pumping and the inflow of insufficiently treated wastewater effluents and residuals from intensive agriculture (de-los-Ríos-Mérida et al. 2021; Heredia-Díaz et al. 2007; Rodriguez-Rodriguez et al. 2016b). A trade-off between water consumption by humans and the conservation of the ecosystem and associated services is necessary but extremely difficult (Kløve et al. 2011b). The implementation of groundwater management strategies, reforestation with native trees and subsidies for suitable agricultural practices are recommended for the Imouzzer du Kandar lake complex in Morocco (Ichen et al. 2021). Environmental awareness and the recognition of limited water resources among the local population are critically important to successfully implement management strategies (Stevanović et al. 2021).

About 10% of the selected KGDEs are threatened by the introduction of invasive species that can replace the native species composition, change habitats and reduce biodiversity and ecosystem functioning in the long term (Mollot et al. 2017). One example is the intermittent lake of Cerkniško Polje (ID 73) where a distinct carnivore fish (perch) was introduced in the 1990s which attacks the native fish populations (Ravbar and Pipan 2022). Another peculiar threat for KGDEs is due to hydrological changes related to earthquakes, as occurred in Central Italy to Presciano spring (ID 38), where a dramatic decrease in subterranean species abundance was recorded after the seismic crisis of 2009 (Galassi et al. 2014). A unique type of threat occurs at Ein Feshkha oasis (ID 34) where springs are moving to a lower level as a response to the rapidly receding Dead Sea. This shift of the springs' locations and eventually their drying up at their current location will cause dramatic damage to the ecosystem (Levy et al. 2020). Several uncontrolled fires have also damaged the oasis (Fig. 9).

Protection status

Evaluation of the protection status, mainly based on the IUCN database, has revealed that either 13% of the selected KGDEs are not protected or no respective information was found (Fig. 10). The data collection shows that caves are the least protected KGDE type, with 26% of the respective sites without any protection. Previous studies on subterranean ecosystems also report a lack of conservation (Culver and Pipan 2013; Mammola et al. 2019), probably because caves were not recognized as species-rich ecosystems for a long time. Only in the last two decades, research has revealed their actual species richness (Niemiller et al. 2018). The Škocjan caves (ID 72) are a positive example, as they are protected by national and EU programmes, recognized as UNESCO Natural World Heritage Site and designated as Ramsar Wetland of International Importance.

Unlike caves, all selected lake and wetland KGDEs are protected. A large share of the lake (65%) and wetland (75%) ecosystems is protected by international conventions. Due to bird migration, the protection of these ecosystems is a global-scale responsibility (Ramsar Convention Secretariat 2016). Lake Skadar (ID 109), Lac Ichkeul (ID 101) and the Laguna de Fuente de Piedra (ID 81) are examples of KGDEs that are important for waterfowl populations. The Laguna de Fuente de Piedra presents the second most important breeding area for flamingos (*Phoenicopterus ruber roseus*) in the Western Mediterranean (Fig. 9), harbours a stable population of the endangered summer-breeding gull-billed tern (*Gelochelidon nilotica*) and is inhabited by more than 170 bird species in total (Heredia-Díaz et al. 2007; Rendón et al. 2001; Rodriguez-Rodriguez et al. 2016a).

Although the majority of KGDEs are considered in conservation programmes, many are still under pressure, demonstrating the relatively negligible protective effect of conservation programmes—for example, Nogueira et al. (2021) identified several shortcomings concerning the delineation of freshwater key biodiversity areas initiated by the IUCN due to outdated or lacking species distribution data. Knowledge gaps on species occurrence, particularly about invertebrates, and the ecosystem ecology remain a problem (Albrecht and Wilke 2008; Nogueira et al. 2021). Moreover, invertebrates are regularly under-represented in conservation legislations and projects on invertebrate protection cannot be funded (Niemiller et al. 2018).

More investigations about the ecosystem's dependency on the quantity and chemical status of the groundwater supply are important for designing appropriate conservation strategies (European Commission 2015). When groundwater is extracted, the concept of reserving an ecological flow that describes the minimum required contribution of groundwater to ensure KGDE functioning and ecosystem survival should be implemented. Different hydrological approaches to determine the water demand and consequently the required ecological flow rate are

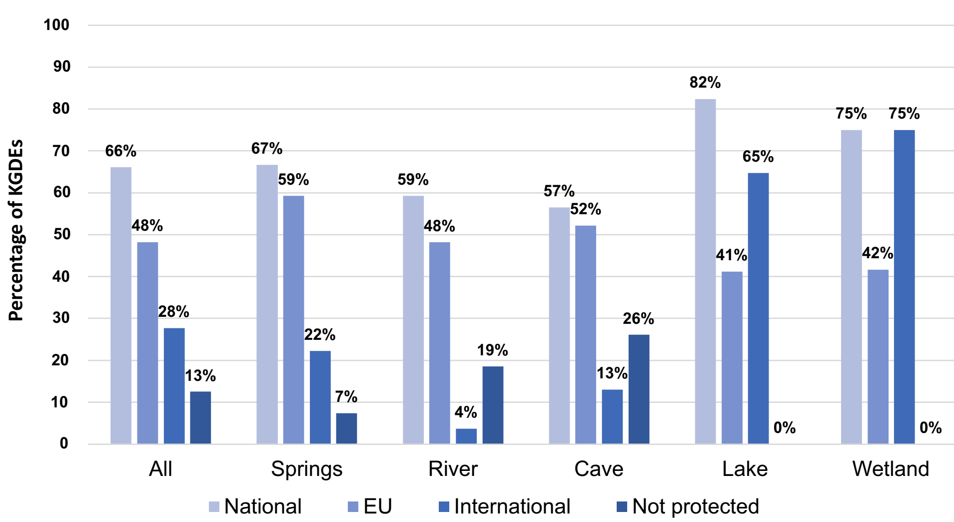

Fig. 10 Percentage of the selected KGDEs that are protected by national, EU and international agreements, grouped by ecosystem types (all KGDEs, springs, rivers, caves, lakes, wetlands)

reviewed by Stevanović et al. (2022). Complementing the hydrological approach with biological methods to define the water demand is recommended to improve the minimal flow for sustaining the ecosystems (Stevanović et al. 2022). Ecosystem damages related to water quality deterioration can be prevented by the designation of protected areas; however, due to the high flow velocities in karst conduits, contaminants can be transported over long distances (Goldscheider 2005), polluting KGDEs far away from the contaminant source. Consequently, exhaustive groundwater protection by constructing appropriate landfills and treatment plants and raising awareness on the issue of groundwater pollution are further needed (Stevanović et al. 2022). The need to protect KGDEs is clear and urgent: Current actions are under development worldwide and regardless of boundaries (IAH, 2016), by different approaches adopted in developing countries, where local stakeholder engagement and bottom-up governance is recommended; conversely, in developed countries, social awareness is currently increasing and international policy actions (e.g. EU Green Deal) have been launched for environmental preservations.

Limitations and perspectives for research

The evaluation of KGDEs is complicated as they differ highly in phenotypes and characteristics. The biogeographical and other spatial differences in the Mediterranean region are high and therefore influence the shape and expression of KGDEs. Climate characteristics, biomes and altitude data are relevant for a first categorisation of KGDEs. The applied criteria in this study remain general and are adapted to the available information at this spatial scale. In many cases, varying availability and quality of data has hampered more in-depth analysis. Criteria such as the degree of groundwater dependency, holistic species assemblages and biodiversity indices are interesting aspects for future research. Also, accurate hydrological information on the discharge pattern and flow rate as well as the chemical water quality could supplement the given criteria (Cantonati et al. 2020). Ravbar and Pipan (2022) suggest that habitat types, groundwater taxa and ecohydrogeological processes should be used to characterize KGDEs. In this context, it would be interesting to further evaluate the differences between karst systems with autogenic and allogenic recharge and systems with exclusively autogenic recharge, as this influences water chemistry, nutrient supply and species assemblage (Gunn 2004; Ravbar and Pipan 2022). The comprehensive online springs database hosted by the Springs Stewardship Institute (Stevens et al. 2016) and the World Karst Spring hydrograph (WoKaS) database (Olarinoye et al. 2020) are helpful tools for such future investigations.

Conclusions

In this study, a selection of 112 karst groundwater-dependent ecosystems (KGDEs) in the Mediterranean region is considered and evaluated by using multidisciplinary criteria, including climatic, hydrogeological and ecological properties, as well as information on the socio-economic context of the ecosystems related to protection, threats and human impacts. The provided representative list intends to illustrate the variety and importance of KGDEs throughout the Mediterranean and is not meant to represent a complete collection.

Although such ecosystems are widespread in the entire study area, two clusters in Spain and the Dinaric Karst stand out in particular. In terms of ecological value, the Dinaric Karst is characterized by a high frequency of endemic species and a great diversity in species and in habitats. Yet, the Dinaric Karst is a core area for karst research, while other regions are not that deeply studied and might harbour undetected biodiversity, thus implying a possible research bias. In arid regions, KGDEs are particularly important, because emerging groundwater often serves as the only water source and creates valuable habitats in the otherwise dry surroundings.

Increasing anthropogenic pressures endanger many KGDEs. Direct human intrusions prevail and need to be addressed by enforced restrictions and promotion of public environmental awareness. Increasing tourism and population growth enhance these impacts in many Mediterranean regions. In large parts of the study area, water shortage poses a threat to KGDEs as a consequence of increasing droughts and overexploitation for irrigation agriculture.

Therefore, appropriate management strategies coupled with efficient hydrological and ecological monitoring activities are necessary. A sustainable development is needed in order to tackle declining groundwater levels and water quality degradation. Innovation in groundwater knowledge and management has been recognized to be based not only on scientific or technical improvements. A modern approach requires an engagement strategy of stakeholders for obtaining effective guiding policies and practices, involving international agreements, governments, basin agencies and final users (Petitta et al. 2023). This condition is particularly appropriate for KGDEs, having so many different sizes and characteristics, from local basins to transboundary aquifers.

Furthermore, the shortage of studies and conservation programmes, covering invertebrate taxa, leads to additional conservation guidelines when funding for habitat protection of invertebrates is not sufficiently provided. Moreover, cave and spring KGDEs, which have an outstanding valuable invertebrate diversity, suffer under these circumstances the most. To conclude, projects on species monitoring, as well as individual studies evaluating the dependency on the quantity and quality of the groundwater supply are necessary, in order to ensure suitable ecosystem management and conservation.

Acknowledgements We thank Diana Galassi, Barbara Fiasca, Želimir Pekaš, Romeo Eftimi, Daniel Scarry, Konstantinos Voudouris, John Gunn, Carlos Almeida and Sebastian Schmidtlein who contributed to this study by providing additional data and/or by scientific discussions.

Funding Open Access funding enabled and organized by Projekt DEAL. This study is a contribution to the project "Karst Aquifer Resources availability and quality in the Mediterranean Area" (KARMA). Financial support of KIT researchers through the German Federal Ministry of Education and Research (BMBF) and the European Commission through the Partnership for Research and Innovation in the Mediterranean Area (PRIMA) program under Horizon 2020 (grant agreement no. 01DH19022A) is greatly appreciated, as well as funding of our KARMA project partners by their respective national funding agencies (MITECO for Spain, oANR for France, MIUR for Italy, CNRS-L for Lebanon, ANPR for Tunisia).

The study is also a contribution to the Spanish project of the "Acción Conjunta Internacional" (ref. PCI2019-103675) of the Ministry of Science, Innovation and Universities (MITECO), and the Research Group RNM-308 of the Junta de Andalucía, funded by the Autonomous Government of Andalusia. The Slovenian contributions were funded by the research programme Karst Research, No. P6-0119, and project Ecohydrological study of spatio-temporal dynamics in karst critical zones under different climate conditions, NK-0002, financially supported by the Slovenian Research Agency and the EU H2020 projects: eLTER Preparatory Phase Project (eLTER PPP), eLTER Advanced Community Project (eLTER PLUS), LifeWatch ERIC (e-Science and Technology European Infrastructure for Biodiversity and Ecosystem Research), ENVRI FAIR and Development of research infrastructure for the international competitiveness of the Slovenian RRI space – RI-SI-LifeWatch, supported by the Republic of Slovenia, Ministry of Education, Science and Sport and the European Union from the European Regional Development Fund.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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