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INVITED REVIEW

Mediterranean springs: Keystone ecosystems and biodiversity refugia threatened by global change

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Abstract

Mediterranean spring ecosystems are unique habitats at the interface between surface water and groundwater. These ecosystems support a remarkable array of biodiversity and provide important ecological functions and ecosystem services. Spring ecosystems are influenced by abiotic, biotic, and anthropogenic factors such as the lithology of their draining aquifers, their climate, and the land use of their recharge area, all of which affect the water chemistry of the aquifer and the spring discharges. One of the most relevant characteristics of spring ecosystems is the temporal stability of environmental conditions, including physicochemical features of the spring water, across seasons and years. This stability allows a wide range of species to benefit from these ecosystems (particularly during dry periods), fostering an unusually high number of endemic species. However, global change poses important threats to these freshwater ecosystems. Changes in temperature, evapotranspiration, and precipitation patterns can alter the water balance and chemistry of spring water. Eutrophication due to agricultural practices and emergent pollutants, such as pharmaceuticals, personal care products, and pesticides, is also a growing concern for the preservation of spring biodiversity. Here, we provide a synthesis of the main characteristics and functioning of Mediterranean spring ecosystems. We then describe their ecological value and biodiversity patterns and highlight the main risks these ecosystems face. Moreover, we identify existing knowledge gaps to guide future research in order to fully uncover the hidden biodiversity within these habitats and understand the main drivers that govern them. Finally, we provide a brief summary of recommended actions that should be taken to effectively manage and preserve Mediterranean spring ecosystems for future generations. Even though studies on Mediterranean spring ecosystems are still scarce, our review shows there are sufficient data to conclude that their future viability as functional ecosystems is under severe threat.

For Affiliation refer page on 15

KEYWORDS
biodiversity conservation, freshwater ecosystems, groundwater, semiarid regions, sources

1 | INTRODUCTION

The Mediterranean climate is characterized by warm, dry summers, mild winters, and a high degree of temporal variability, both within (i.e., seasonally) and between years (Rundel et al., 2016). Worldwide, Mediterranean climate regions are among the ecosystems most threatened by global change due to the expected decreases in water availability and intensive human impacts (Cramer et al., 2018; Mekonnen & Hoekstra, 2016). These regions often align with arid or semiarid conditions and can be found around the Mediterranean basin, California, central Chile, the Western Cape Region (South Africa), and southwestern Australia (Blondel & Aronson, 1999; Rundel et al., 2016). The characteristics of these regions make their springs, and spring ecosystems, of paramount importance for human development and biodiversity conservation. Spring ecosystems from these regions (hereafter, Mediterranean spring ecosystems) have been described as refugia for a wide array of organisms, including a large number of endemic species found only in one single spring (Fensham, Ponder, et al., 2023; Freyhof et al., 2017). Spring ecosystems have been reported to support high values of both freshwater (Bes et al., 2018; Cantonati, Füreder, et al., 2012; Fernández-Martínez et al., 2021; Sabatino et al., 2003) and terrestrial biodiversity (Votto et al., 2020; Zamora-Marín, Zamora-López, et al., 2021).

Mediterranean springs can be natural (lacking any human intervention) or seminatural (i.e., human modified), the latter consisting of a small construction, usually of local rock and concrete, with a spout that drains the water from the aquifer to a sink or cistern, maintaining a pool of water before it runs off. These ecosystems are usually small in size (sometimes even less than $1\,m^2$) but nonetheless complex, representing ecotones linking surface and underground water bodies (Cantonati & Ortler, 1998). Spring ecosystems are characterized by a mosaic of numerous microhabitats (Illies & Botosaneanu, 1963), and such features could explain the high number of taxa coexisting in just a few square meters (Lencioni et al., 2018; Mezquita et al., 2000). This spatial heterogeneity also influences the distribution of plant and animal species, the interactions between species, and the trophic structure of biological communities. Even though spring ecosystems and their biodiversity are threatened worldwide, those from Mediterranean-type regions suffer the consequences of global change more strongly because their intrinsic water limitation exacerbates other potential problems, such as eutrophication (Fernández-Martínez et al., 2020; Martín et al., 2024). Furthermore, it is in these regions where spring ecosystems play an important role in sustaining biodiversity because they represent isolated habitats with permanent water availability surrounded by habitats where water is not typically available (Fernández-Martínez, Berloso, et al., 2019; Zamora-Marín, Ilg, et al., 2021).

Spring ecosystems are also of great interest from the viewpoint of freshwater quality monitoring because their particular biodiversity and limited size make them extremely sensitive to any disturbance (Cantonati et al., 2006; Lencioni et al., 2018; Williams, 1991), thus allowing the effects of different environmental stressors (e.g., water pollution or groundwater depletion) to be assessed within river basins. Pollution from diffuse sources is difficult to track—particularly in aquifers—but this is essential for assessing nutrient legacy effects and safeguarding freshwater resources (Goyette et al., 2018; Van Meter et al., 2018).

Currently, the main threats to the conservation of spring ecosystems (Stevens et al., 2021) can be summarized as: (i) habitat modification for anthropogenic uses, including the overexploitation of water from the source or its related aquifer (Barquín & Scarsbrook, 2008); (ii) eutrophication, mainly related to the disruption of regional and global N and P biogeochemical cycles due to intensive livestock farming and agriculture, as well as leakages from urbanized areas (Fernández-Martínez et al., 2020; Martín et al., 2024); and (iii) climate change, through several processes: (a) Increases in temperature lead to increases in evapotranspiration (ETR) by the vegetation, which has largely expanded in many regions of the planet, reducing water in aquifers (Gallart & Llorens, 2003; García-Ruiz et al., 2011); (b) an increase in torrentiality also reduces infiltration and groundwater recharge; and (c) if total precipitation also decreases (−5% to −30% is expected for the Mediterranean basin, Cramer et al., 2018), this will also reduce the water available for aquifers and springs. In fact, water demand for human and industrial uses is expected to increase in the near future in Mediterranean climate regions as a consequence of global warming (Mekonnen & Hoekstra, 2016), exacerbating the effects of all these threats on spring ecosystems.

Hence, this review aims to first provide a synthesis of the functioning of Mediterranean spring ecosystems, focusing on their main features, geomorphology, and the determinants of their water chemistry. Second, we synthesize the current knowledge regarding general biodiversity patterns in Mediterranean spring ecosystems. Third, current and future threats to these vulnerable ecosystems are discussed. Finally, we provide a roadmap for enhancing spring conservation and management efforts, offering practical recommendations to safeguard spring ecosystem integrity.

2 | FUNCTIONING AND GEOLOGICAL FEATURES OF SPRING ECOSYSTEMS

2.1 | Hydrogeological features

Springs constitute discrete points of groundwater discharge in the landscape (van der Kamp, 1995), and their characteristics are determined by geomorphological (relief) and geological (lithology, tectonics) attributes (Figure 1). For example, high reliefs favor the presence of springs because water discharge can occur when the topography intersects the water table (depression springs). Faults also play an

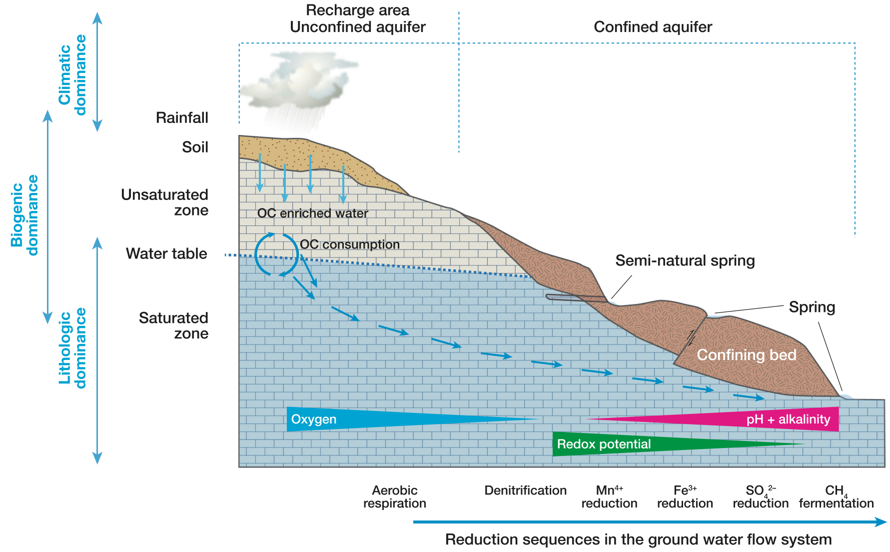

FIGURE 1 Spring hydrogeological characteristics, processes, and physical and chemical features of groundwater. On the left, in blue, are the processes dominating the water chemistry of the aquifer. OC, organic carbon.

important role in the occurrence of springs: They displace materials and generate conduits that allow groundwater to flow. Contact or lateral springs, which occur because of the lateral contact between the aquifer and a poorly permeable unit, are also often related to faults, as are most thermal springs (i.e., those that discharge water at a temperature higher than the average air temperature). Geological characteristics also determine the difference between the elevation or pressure of the hydraulic head in the aquifer and the discharge, resulting in either gravity (descending) or artesian (ascending) springs.

Springs located in karst systems, or in extrusive volcanic rocks, show larger drainage flows compared to other lithologies (e.g., granites). In particular, karstified rocks rapidly transmit a large percentage of precipitation events as newly infiltrated water. Karst aquifers have primary porosity, common rock discontinuities such as fractures or secondary porosity, and enlarged voids, such as channels and waterways, developed from initial discontinuities (Kresic, 2010). The drainage or catchment areas of karst springs often extend beyond topographic divides. This is why karst aquifers give rise to the largest springs in the world. Given their strong dependence on hydrogeological features, the density of springs can vary widely across geographical areas (see Supporting Information, Section S1; Table S1).

2.2 | Water chemistry

The chemistry of spring water is mainly determined by the natural characteristics of the parental aquifer and the organic and inorganic processes that occur along the aquifer (Figure 1). The concentration of ions in water depends on the solubilization and re-precipitation of bedrock minerals and is thus related to the composition of the rocks. For example, it has been shown that the Ca/Mg ratio in spring water is indicative of the type of carbonate rock (dolomite vs. limestone) that forms the aquifer (Cantonati et al., 2007). The hydrogeological properties of the parent material (porosity, hydraulic conductivity, transmissivity) determine the length of flow paths, the volume of aquifer recharge and the residence time of the water, and these properties influence ion exchange and biogeochemical transformations (Welch & Allen, 2014). Longer residence time in the aquifer, often accompanied by increased weathering, leads to an increase in the ion content of the water and determines factors such as alkalinity, and sulfate and chloride ratios (Morell, 1992; Roca, 1990), all of them very influential for spring flora and fauna. In deeper aquifer springs, the water chemistry is highly dependent on temperature and pressure conditions. Water from such springs is usually rich in CO_2, Fe, and H_2S (Lachassagne et al., 2021), leading to naturally occurring sparkling water springs.

Climate characteristics also influence spring water chemistry. Temperature affects weathering rates: the higher the temperature, the higher the reactivity and the greater the weathering. Precipitation may also facilitate weathering by accelerating chemical reactions when water is flowing through dry soils, but it eventually tends to dilute the concentration of ions in the water. Proximity to the coast mainly increases the concentration of Na^+ and Cl^- due to continuous deposition of sea spray (Fernández-Martínez, Margalef, et al., 2019). On top of lithology and climate, vegetation and soil properties can also affect the water chemistry of the aquifer. Vegetated and well-structured soils favor water infiltration, and as it flows through the soil, the water is enriched in organic matter. Additionally, soil properties can also buffer the pH of the infiltrated water. Connectivity between shallow and deep soil layers due to biological factors such as root structure and root exudation, or soil fauna and the microbiome may also interact with the chemistry of the infiltrated water (Neary et al., 2009; Scanlon et al., 2005). The importance of these factors affecting the chemistry of spring water, however, remains unknown.

2.3 | Hydrogeomorphology

Two zones are usually distinguished in springs: the eucrenon (i.e., the source area) and the hypocrenon (i.e., spring brooks running down from the outlet) (Illies & Botosaneanu, 1963), but the threshold between both is hard to delimit in Mediterranean springs because it varies widely throughout the different periods (i.e., wet and dry seasons). Especially during the dry season, the extension of the spring outlets (eucrenon) is vague because the running flow is significantly reduced. Temperature differences and bryophyte coverage have been some criteria suggested to establish the extension limits of the eucrenon (Crema et al., 1996; Erman & Erman, 1995; Illies, 1961; von Fumetti et al., 2007), but there is still no general consensus. Alternatively, the hydrogeomorphological approach is particularly suitable for defining the limits of Mediterranean springs. It has been long recognized that springs are composed of a particular mosaic of microhabitats, each one characterized by size, water dynamics and type of substratum (Gerecke et al., 1998; Myers & Resh, 2002; Stoch et al., 2011; White & Pickett, 1985). Consequently, we could define the spring limits as the border of the area filled by these eucrenon microhabitats. The latter can be identified by the influence of the spring water on the community of hygrophytes (i.e., aquatic or semi-aquatic organisms). This approach was proposed by Stevens et al. (2011) and is easily applicable to Mediterranean environments because of the typical lack of hygrophytes outside of the spring domain, unless the spring is located on a riverbank.

Typically, Mediterranean springs from arid and semiarid areas (annual precipitation below 500 mm per year) have low-discharge flow, their influence area (eucrenic or crenic ecosystem) is relatively small (usually in the metric or decametric range), and the hypocrenon is poorly developed or nonexistent. Consequently, in these springs, the most frequent situation is the lack of connection between springs and the river network, except for short periods of heavy rainfall. In these semiarid regions, springs are typically isolated freshwater habitats that predominantly act as biodiversity refuges during drought periods, when the fluvial network is dry. In contrast, during hyper-humid periods (which may occur only a few days a year), they can aid in the dispersion of organisms that live in the spring, thus contributing to maintaining biological communities in adjacent rivers and freshwater habitats.

2.4 | Spring classifications

Springs are usually classified according to their morphology, size, or hydrological regime (Stevens et al., 2021). The first spring classification systems (Steinmann et al., 1915; Thienemann, 1926) distinguished three main types according to hydromorphological criteria: (1) *rheocrenes* or flowing springs, in which water flow feeds small streams; (2) *limnocrenes* or pool springs, where the flow is low and creates lentic habitats; and (3) *helocrenes* or seepages that generate shallow or soggy wet zones. This basic classification remains accepted today, but modern approaches also distinguish them according to their geology, hydrology, water chemistry, water temperature, ecology, and human use (Glazier, 2014). For instance, Stevens et al. (2021) used site-specific source geomorphology to define 13 types of springs. Cantonati (2022), instead, used a multicriteria approach to distinguish seven macrotypes of springs. The high spring diversity resulting from the great variety of geological and morphological features in regions with Mediterranean climate implies that almost all types of both Stevens' and Cantonati's classification are present (except for geysers and desert springs).

However, most Mediterranean springs have been *domesticated*, so their current status is seminatural. In fact, a great proportion of small springs, the most widespread representatives (Cantonati, 2022), which had been originally helocrenes or rheo-helocrenes, have been transformed to rheocrenes by digging a hole in the ground to reach the subterranean aquifer, or through water mines or wells to concentrate the flow through a spout, a pipe, or a channel. In addition, other artificial elements are sometimes present, such as cisterns or small ditches to transport the water. Nevertheless, unless water abstraction is very high, these artificial elements do not generate strong negative impacts on the biodiversity of springs and they can still support relevant populations of threatened species (e.g., when a sink is created, it can be used by amphibians for reproduction) (Buono et al., 2019; Egea-Serrano, Oliva-Paterna, Tejedo, et al., 2006; Egea-Serrano, Oliva-Paterna, & Torralva, 2006).

3 | BIODIVERSITY OF MEDITERRANEAN SPRING ECOSYSTEMS

3.1 | General patterns of spring biodiversity

The characteristics of spring ecosystems are determinant in providing refugia or structuring freshwater biotic assemblages in the landscape. When the springs are stable and isolated, the environmental conditions can favor the development of a highly specialized flora and fauna. These specialized spring-dwelling organisms are often called *crenobionts* and correspond to species that have necessarily adapted to these spring habitats to survive and complete their life cycles. Some authors also consider springs as potential refuges for relict species (Botosaneanu, 1995; Cantonati, Füreder, et al., 2012; Taxböck et al., 2017). In contrast, in densely populated landscapes with heavily exploited aquifers, most of these species have already disappeared.

The biodiversity of spring ecosystems is strongly linked to the ecohydrogeological characteristics of the aquifer (Cantonati, Stevens, et al., 2020). The climate, hydrostructure, and lithology of the aquifers determine whether a spring has permanent or intermittent flow (Cantonati, Segadelli, et al., 2020, see also Section 2). In some regions, springs fed by large karst systems become even more vital as stable hydrological refuges for biodiversity as climate change advances (Cartwright et al., 2020). For example, larger and more permanent springs might have a higher contribution as freshwater refuges in arid and semiarid regions (Davis et al., 2013; Work, 2023), while the role of smaller and more temporary springs might be critical as stepping stones in metapopulation and metacommunity dynamics (Collier & Smith, 2006), with an influence on alpha, beta, and gamma diversity. Data from a survey of springs in the NE Iberian Peninsula using bryophytes (Fernández-Martínez et al., 2021) were used here to calculate diversity measures through the R packages *vegan* and *betapart* (Baselga, 2010; Oksanen et al., 2018; R Core Team, 2023). The results confirm that alpha and gamma diversity are higher in springs under wetter climates compared to those from drier climates (Figure 2a). Beta diversity, instead, is higher among springs located in drier regions, since they are generally more isolated environments as compared to springs from more humid regions. Hence, the relative contribution of species turnover to their community composition is also higher compared to that in wetter areas (Figure 2b,c). This highlights the high degree of uniqueness of spring community composition in drier areas. In this regard, the degree of connectivity or isolation of a spring habitat to other surface waters could be determinant to prevent the colonization of invasive species or to conserve their unique biota.

Despite most Mediterranean springs being small in size, the structure of microhabitats can always be recognized. Biological richness (or biodiversity) in springs has been shown to increase with the diversity of hydrogeomorphological microhabitats (Reiss & Chifflard, 2015; Taxböck et al., 2020). Distinct organisms occupy different microhabitats of the crenic environment as depicted in Figure 3. Those organisms living in the actual source of spring water are referred to as crenobionts (e.g., springsnails), while those being associated with the spring sink during a given phase of their life cycle are called crenophiles (e.g., amphibians or emerging insects). Several plant and animal species (e.g., ferns or terrestrial vertebrates) that do not inhabit spring ecosystems (crenoxens) may also routinely benefit from many ecological functions provided by springs, such as food, habitat, or water supply (Zamora-Marín et al., 2023). With regard to the microhabitat selected within the springscape (i.e., the natural spatial unit of springs encompassing abiotic and biotic factors), species may be classified as stygobionts when they inhabit the groundwater ecosystem, stygophiles when they mostly inhabit the spring sink, and rheophiles when they use spring downstream waters. This water continuum from aquifer to spring and to streams may be severed in periods of intense drought. Therefore, the degree of endemicity is more likely to occur among stygophile and crenophile taxa, often mites and mollusks (see Section 3.3), than among

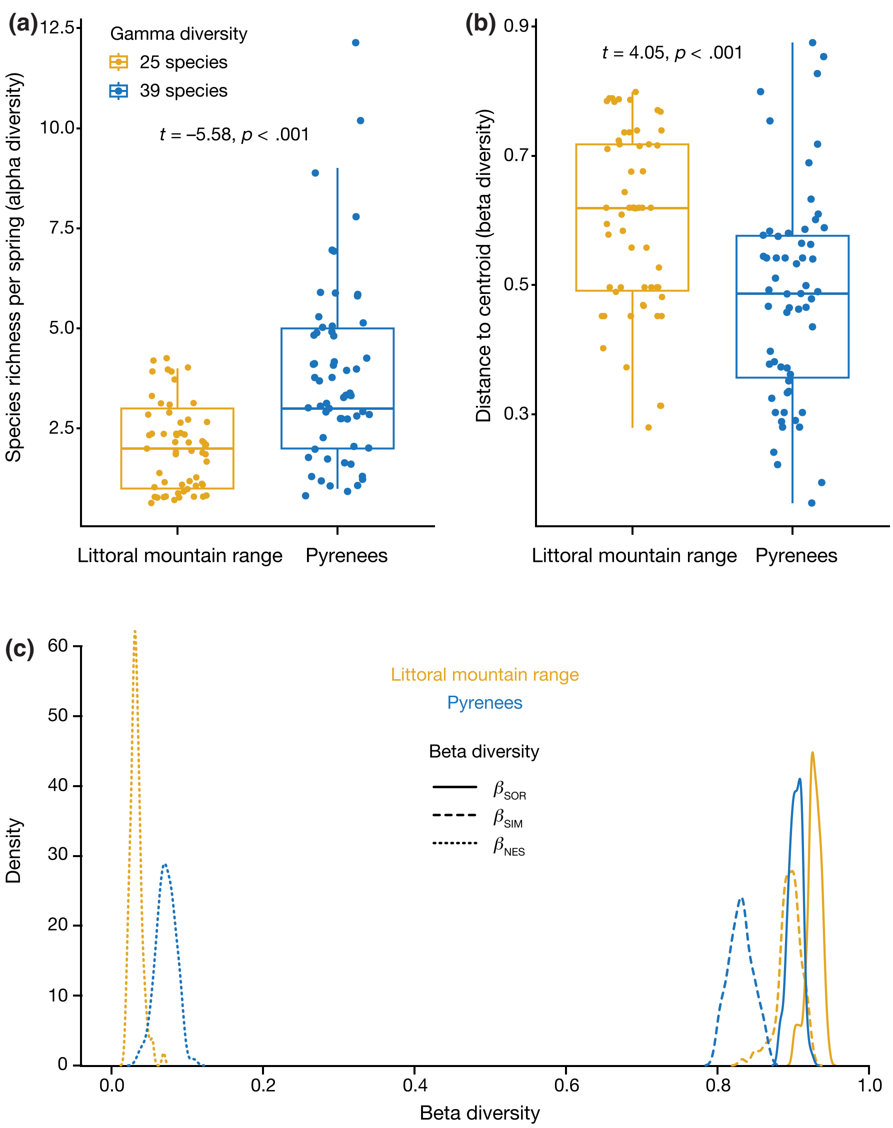

FIGURE 2 Alpha, beta, and gamma diversity of bryophytes in 58 and 59 springs (~1 m^2) for the Littoral mountain range and the Catalan Pyrenees regions, respectively. Temperature and water availability differ between these two regions, with the Littoral mountain range being warmer and drier than the Pyrenees (respectively [mean ± standard deviation], mean annual temperature: 14.0 ± 0.8, 11.7 ± 2.0°C; annual precipitation: 726 ± 67, 1060 ± 64 mm year^{-1}). Panel (a) shows alpha diversity, with the inset stating the gamma diversity in the two regions. Springs from more arid regions are more important as biodiversity refugia. Panel (b) shows total beta diversity and panel (c) shows the different components of beta diversity. B_{SOR} stands for Sorensen's beta diversity (total beta diversity), B_{SIM} stands for Simpsons' beta diversity (species turnover), and B_{NES} stands for nestedness ($B_{SOR} - B_{SIM}$). These analyses were performed using freely available data published in Fernández-Martínez et al. (2021) and the experimental design can be found therein. Calculations of diversity were performed using packages *vegan* and *betapart* in R (Baselga, 2010; Oksanen et al., 2018; R Core Team, 2023). See Data Availability Statement to access data and code to generate these results.

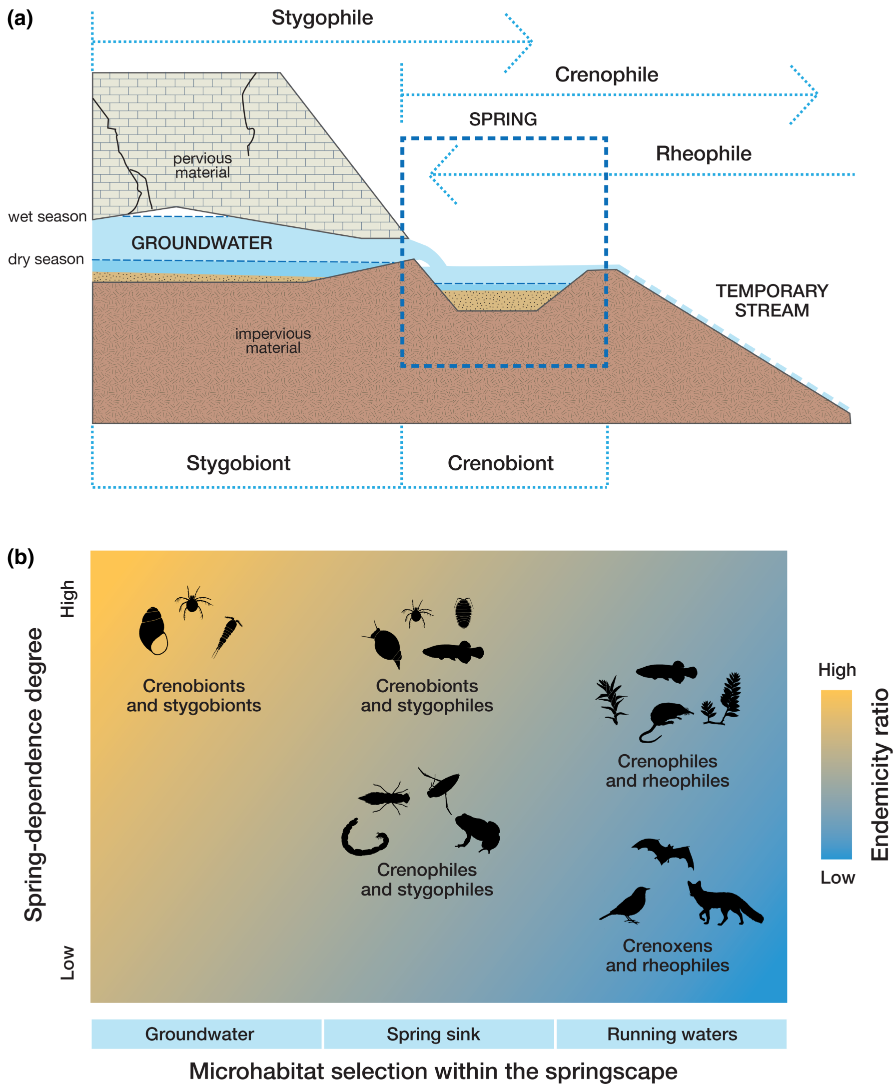

FIGURE 3 Conceptual models representing the geomorphological structure of a typical spring ecosystem (a) and the distribution of different spring-associated biotic groups across the springscape (b). Panel (a) shows the main geomorphological elements composing a Mediterranean spring ecosystem, and terms for spring-associated biodiversity are also depicted. Panel (b) displays the distribution of typical spring-associated biotic groups across the springscape in relation to their spring dependence degree and the expected endemicity ratio.

rheophile taxa which are much more connected to downstream waters. Overall, the list of taxa that has been described to inhabit spring ecosystems is very large (Figure 4; Table S2; Sections 3.2 and 3.3), even though they have received far less attention compared to many other freshwater ecosystems.

3.2 | Plants, algae, and microorganisms

Autotrophs form the basis of the food webs in spring ecosystems as primary producers (Cantonati et al., 2015; Cantonati, Rott, et al., 2012). Vascular plants, bryophytes, algae, and microbial mats can all be found in Mediterranean spring ecosystems and provide important functions, such as stabilizing soils, retaining water, and offering food and shelter to aquatic invertebrates (Cantonati, Füreder, et al., 2012; Žutinić et al., 2018). Spring vegetation contributes significantly to habitat structure and plays a central role in various physicochemical processes (e.g., limestone precipitation). Generally, European springs are known to harbor high plant diversity (e.g., see Cantonati & Ortler, 1998; Seiler et al., 2021), including numerous specialized and rare plant species, especially bryophytes (Cantonati et al., 2006; Geissler, 1976). Spring bryophyte communities can also sustain large communities of associated microflora (e.g., diatoms, green algae) and fauna (e.g., nematodes, tardigrades, and arthropods, Cantonati, 2022; see Section 3.3). However, in contrast to other regions (e.g., the Alps), there are very few studies on the vegetation of Mediterranean spring ecosystems. For example, Pascual et al. (2020) found similar plant species richness in springs in the mountains of Mallorca and Catalan pre-littoral mountains compared to springs in the Alps.

Further studies with bryophytes carried out in Catalonia (NW Mediterranean) indicate that these habitats play an important role in semiarid regions as shelters where water is constantly available, representing important biodiversity refuges for these species (Bes et al., 2018; Fernández-Martínez, Berloso, et al., 2019). Some typical plant species associated with Mediterranean spring ecosystems are currently considered near-threatened or endangered in Europe (e.g., Christenhusz et al., 2017; de Foucault, 2015), as well as many other narrow-ranging or endemic plant and animal species (Deleuil, 1974; Jiménez-Alfaro et al., 2013; Jiménez-Mejías &

FIGURE 4 Simplified representation of the Mediterranean spring biodiversity, showing most of the taxonomic groups related to this ecosystem and their microhabitat preferences in a seminatural spring. 1, Odonata, *Ischnura graellsii*; 2, Diptera, *Culex*; 3, Rotifera, *Cephalodella forficula*; 4, Ostracoda, *Notodromas*; 5, Acari, Hydrachnidia; 6, Tardigrada; 7, Bacillariophyceae, *Navicula*; 8, Cyanobacteria, *Phormidium*; 9, Nematoda; 10, Aves, *Turdus merula*; 11, Magnoliophyta, *Carex pendula*; 12, Mammalia, *Capreolus*; 13, Bryophyta, *Apopellia endiviifolia*; 14, Bryophyta, *Eucladium verticillatum*; 15, Fungi, *Scutellinia* sp.; 16, Pteridophyta, *Adiantum capillus-veneris*; 17, Amphibia, *Salamandra*; 18, Copepoda, *Cyclops*; 19, Cladocera, *Daphnia*; 20, Amphipoda, *Echinogammarus*; 21, Pteridophyta, *Equisetum telmateia*; 22, Amphibia, *Alytes obstetricans*; 23 Amphibia (larva), *Alytes obstetricans*; 24, Gastropoda, *Physa*; 25, Odonata (nymph), *Chalcolestes viridis*; 26, Lepidoptera, *Celastrina argiolus*; 27, Magnoliophyta, *Carex remota*.

Luceño, 2009; Rivas-Martínez et al., 2011). Although only a few lichen species are known from freshwater habitats, they may offer valuable information about the quality and integrity of spring ecosystems (Cantonati, 2022). There are indications that Mediterranean freshwater habitats contain lichen communities that differ in their taxonomic and functional composition from other European regions and likely host yet-undiscovered species (Nascimbene et al., 2023), which deserves further research.

Diatoms and cyanobacteria (accompanied by bacteria and fungi) are the dominant autotrophs found in microbial mats (Cantonati et al., 2015; Kolda et al., 2019). Diatom diversity has been shown to increase from 0 to 25°C and starts to decrease at temperatures above 25 or 30°C, mainly in thermal springs (Dallas, 2008; Delgado et al., 2020; Kishi et al., 2005; Patrick et al., 1969). Hence, climate warming will likely change diatom communities of springs. Springs are indeed important habitats for diatoms with unique environmental requirements, and this may explain why new species are regularly discovered in spring ecosystems (Cantonati, Angeli, et al., 2016; Cantonati & Lange-Bertalot, 2006; Delgado et al., 2013; Sabater & Roca, 1990). From the 22 taxonomic orders of Cyanobacteria, only four (Oscillatoriales, Chroococcales, Leptolyngbyales and Gomontiellales) are mainly present in freshwater springs. Many of the identified taxa, however, comprise a plethora of poorly reported and uncommon species (Cantonati, 2008; Cantonati, Rott, et al., 2012; Nowicka-Krawczyk & Żelazna-Wieczorek, 2013, 2017). Unlike hot springs where cyanobacteria diversity is well characterized, little is known about species composition in ambient springs (Cantonati et al., 2015; Jasser et al., 2022).

3.3 | Animals: Aquatic and terrestrial fauna

Mediterranean spring ecosystems show an extremely high environmental heterogeneity, promoting the uniqueness of individual spring assemblages (Cantonati, Segadelli, et al., 2020) and leading to increased values of faunistic dissimilarity (i.e., higher beta diversity mediated by greater contribution of species turnover as compared to more humid environments; see Figure 2) and ultimately enabling higher levels of gamma diversity (Pascual et al., 2020; Pešić et al., 2017; Płóciennik et al., 2016). Mediterranean spring ecosystems support outstanding ratios of endemic and rare freshwater fauna as a result of their role as biodiversity paleorefugia, but also provide key ecological functions to associated terrestrial species and adjacent ecosystems. Even though previous studies on animal communities in Mediterranean spring ecosystems are notably scarce, the available information points toward disproportionately high values of richness for several animal groups (Fensham et al., 2011; Rossini et al., 2018), including spring-dwelling and spring-associated taxa.

Several genera of spring-dwelling invertebrates evolved strong ecological links to spring habitats, such as in the case of water mites (Hydrachnidia), rotifers and springsnails (Cantonati, Segadelli, et al., 2020; Miracle et al., 1995), all being considered representative components of spring ecosystems and showing high levels of spring-specific endemicity. For instance, Italian spring ecosystems host up to 18 endemic species of water mites and provide habitat for a total of 163 water mite species, which represent about 43% of the total water mite diversity recorded in Italian inland waters (Sabatino et al., 2003). Likewise, Mediterranean spring ecosystems placed in the eastern Iberian Peninsula support a non-negligible proportion (32%) of the total diversity of non-marine ostracods inhabiting Iberian inland waters (Mezquita et al., 1999). High values of endemicity have also been found in outcrop and discharge springs from the Eastern Lake Eyre Basin (Australia), which support at least 18 endemic mollusk species (Fensham et al., 2011), most of them belonging to a single genus (*Jardinella*). In turn, these spring ecosystems support a higher number of endemic and narrow-ranging mollusk species as compared to other freshwater habitats within the same region. In this context, three new genera of gastropods have also been recently described as endemic from Tunisian spring ecosystems (Khalloufi et al., 2020), and two new species of ostracods have recently been found in Italian spring ecosystems (Rossetti et al., 2022). Also among crustaceans, the amphipod genus *Echinogammarus* is a paradigmatic case. It has more than 20 species inhabiting springs and upper zones of small rivers in the Mediterranean Basin. The distribution of most of these species is very restricted, and a few of them are only found in a single location (Pinkster, 1993). However, the highest values of spring-specific species endemicity worldwide are found in Australian springs from the Great Artesian Basin, with at least 51 mollusk and 24 crustacean species known as being endemic from this spring biodiversity hotspot (Rossini et al., 2018).

Although the vast majority of mollusks inhabiting spring ecosystems correspond to snails (Gastropoda), some clam species (e.g., taxa from the Sphaeriidae or Lasaeidae families) may also occur in these singular environments and even show clear spring-habitat preferences (Rassam et al., 2021; Rossini et al., 2018). In addition to passively dispersing organisms (e.g., crustaceans, mollusks, and water mites), Mediterranean spring ecosystems also host a high diversity of actively dispersing invertebrates and even comprise the main habitat for several threatened taxa, such as some conservation concern and spring-dependent Odonata species (Assandri et al., 2020; Vilenica et al., 2021). In fact, about 60% of the total Odonata species occurring in Montenegro have been recorded at spring ecosystems (Pešić et al., 2017). In the same country, spring surveys targeting water bugs (Heteroptera) found 13 new species previously unrecorded at national scale (Gligorović et al., 2016). In line with the above studies, spring ecosystems from the Rif region (North of Morocco) have been identified as priority conservation habitats to ensure the effective protection of threatened water beetle species (Bennas et al., 2009).

Mediterranean spring ecosystems, and those from more arid regions, also support vertebrate species including endemic or conservation concern species. For instance, outcrop and discharge springs from the Eastern Lake Eyre Basin (Australia) host three fish species which are endemic from a single site or highly concentrated to a local area (Fensham et al., 2011). Likewise, the Australian Artesian springs harbor up to eight fish species endemic to single spring sites or confined to extremely restricted areas (Rossini et al., 2018). Spring ecosystems from some Mediterranean countries also support endemic or narrow-ranging fish species, mostly killifishes (i.e., genus *Aphanius*). For instance, *Aphanius sirhani* is endemic to the Azraq Oasis in Jordan, whereas *A. kruppi*, *A. dispar*, and *A. richardsoni* are highly concentrated to spring ecosystems in Oman, Sinai, and Israel, respectively (Freyhof et al., 2017). Mediterranean spring ecosystems also comprise critical habitats for amphibians and several aquatic reptiles, as populations of many species appear highly concentrated to springscapes or are even spring dependent. For instance, threatened populations of the Betic midwife toad (*Alytes dickhilleni*) and the fire salamander (*Salamandra salamandra morenica)* from the south of the Iberian Peninsula mostly rely on spring-fed drinking troughs and artificial pools as breeding habitats (Egea-Serrano, Oliva-Paterna, Tejedo, et al., 2006; Egea-Serrano, Oliva-Paterna, & Torralva, 2006). Springs also deliver important ecological services to terrestrial wildlife and may largely contribute to ecosystem functioning in adjacent landscapes. In this context, Mediterranean spring-fed small water bodies act as key landscape elements for about 70% of the breeding bird species inhabiting adjacent ecosystems (Zamora-Marín et al., 2022), performing pivotal cross-system functions such as the provision of drinking, bathing, and foraging sites (Zamora-Marín et al., 2024). In fact, spring ecosystems may play a key role in nutrient exchange with the adjacent terrestrial ecosystems through the provision of emerging insects (e.g., in the form of chironomids or mayflies) to both aerial (e.g., bats and swifts) and terrestrial (e.g., spiders and lizards) consumers, as reported for other small water bodies (Lewis-Phillips et al., 2020). However, quantitative assessments have not yet been conducted in spring ecosystems.

3.4 | Temporal dynamics of biodiversity in Mediterranean springs

As highlighted in the previous sections, the importance of perennial springs as biodiversity refuges for Mediterranean flora and fauna is largely due to the fact that they are shelters where water

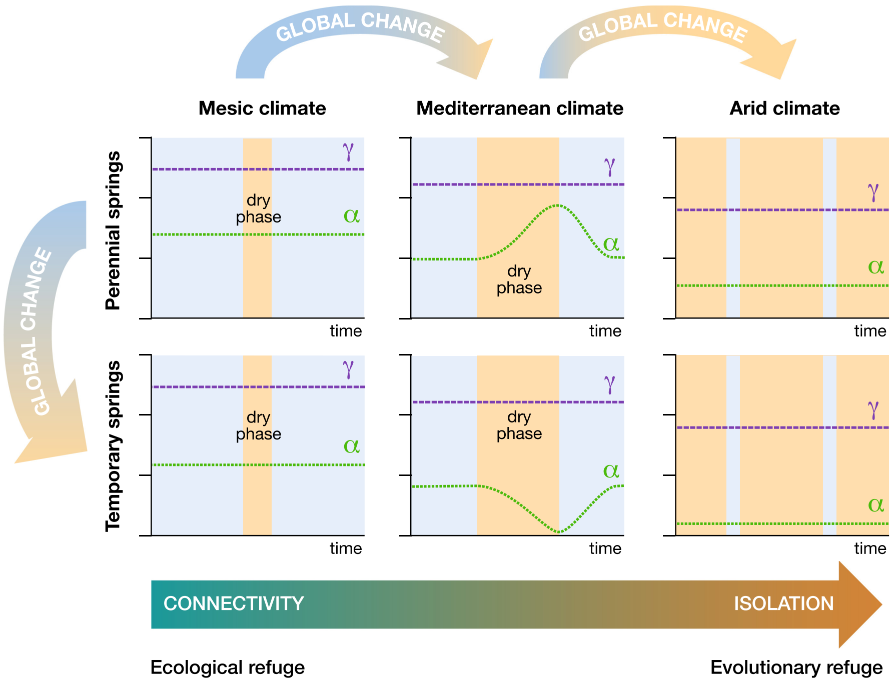

FIGURE 5 Hypothetical temporal dynamics (i.e., seasonal and interannual) of biodiversity in perennial and temporary spring ecosystems under the effects of global change (e.g., drought). Spring ecosystems from more mesic climates (i.e., temperate) are more likely to be better connected than those from arid regions, which are more isolated and may represent an evolutionary refuge for endemic species. The increase/drop in alpha diversity is only shown in Mediterranean climates to highlight that seasonal and interannual hydrological differences are more pronounced in these regions. This potential fluctuation in alpha diversity is also related to differences in connectivity, which in Mediterranean regions lies between that of mesic and arid regions. In mesic climates, even if the springs are temporary, the dry phase is usually short and there is high connectivity in the hydrological network, so we would expect variations in alpha diversity to be low. In arid climates, weather is predominantly dry, perennial springs have a high degree of isolation, and the hydrological disconnection is even greater in temporary springs, but again, we would expect low seasonal and interannual differences.

is constantly available in the midst of often dry environments. However, temporary springs are also common in the Mediterranean as a result of the high seasonality and interannual variability imposed by the climate (Bonada & Resh, 2013). The effect of global change, as described below (Section 4), could displace the environmental conditions of mesic (i.e., temperate) springs (and their surrounding regions) into Mediterranean-like or arid conditions (Figure 5). Similarly, perennial springs under any type of climate may become temporary due to the effects of global change. We predict that those changes could have profound impacts on spring biodiversity. As previously shown (Section 3.1; Figure 2), spring ecosystems from wetter regions tend to have higher diversity per spring (alpha diversity) and a higher pool of species (gamma diversity) because springs have a higher connectivity locally (e.g., downstream reaches) and regionally (e.g., a larger set of potential habitats and larger colonizable areas for crenophillic biodiversity). Hence, we would expect alpha and gamma diversity to decrease as we move from mesic, to Mediterranean and arid climates, as the latter ones are much more isolated (i.e., drying results in a decrease of richness and a loss of connectivity) (Soria et al., 2017).

In mesic springs, changes in gamma diversity should not be evident when perennial springs become temporary, as other surrounding habitats with available water should still preserve the overall pool of species. Nonetheless, given the high number of spring endemisms, the disappearance of species cannot be disregarded. Alpha diversity (at the spring scale), however, should be more sensitive to shifts in the environmental conditions. While mesic spring ecosystems should keep their alpha diversity more or less steady with time, Mediterranean springs should experience variations in their alpha diversity due to the occurrence of drought periods, either seasonal (i.e., summer droughts) or meteorological (i.e., prolonged periods of unusual drought conditions). In perennial Mediterranean springs, drought periods can actually increase alpha diversity. This is because organisms that typically do not rely on spring ecosystems, both spring-dwelling (e.g., those depending on the springs, such as invertebrates and amphibians) and spring-subsidized species (e.g., those that visit them, such as mammals and birds), may be drawn to these springs in order to survive. Conversely, in temporary Mediterranean springs, drought periods are likely to coincide with the dry phase when the springs have the potential to run dry. This is expected to reduce alpha diversity because several species that rely on these springs may temporarily disappear. In mesic climates, dry periods may not be long enough to significantly impact the alpha diversity of temporary springs in most cases. Even if the spring does not flow, ponds and high humidity may persist, providing sustenance for all species. However, in arid climates, the dry conditions may be the norm. In such environments, alpha diversity will likely only decrease when a spring becomes temporary. The extended dry phases in arid climates require all present species to be adapted to tolerate the lack of water, preventing a significant decrease in alpha diversity. In arid regions, springs function as oases and are highly isolated habitats regionally, with low alpha and gamma diversity, and a high number of endemic species (Souza et al., 2006). Therefore, the importance of springs as refuges increases as we move away from mesic conditions, where they act as ecological refuges, to more arid conditions where they act as evolutionary refuges (hence the large number of endemisms, see sections above).

4 | CURRENT AND FUTURE RISKS OF SPRING ECOSYSTEMS

4.1 | Reduction of water availability

In Mediterranean regions, climate change is expected to severely affect freshwater availability (Ali et al., 2022; Cramer et al., 2018), due to more frequent, longer and intense droughts and heat waves (Hartmann et al., 2014), leading to drier conditions in the coming years (Dubrovský et al., 2014). Heat waves and droughts will reduce water availability in aquifers and springs through various mechanisms: (i) lack of precipitation and therefore direct declines in soil water content and groundwater (Barros et al., 2014); (ii) higher temperatures, with higher ETR rates by vegetation; (iii) higher water demand for agriculture and livestock, as well as for the population, and thus increased groundwater abstraction (Sivelle et al., 2021). Together with longer drought and the general decrease in precipitation, future scenarios indicate a trend toward extreme precipitation events and flash floods (Dubrovský et al., 2014; Llasat et al., 2016), which would further decrease infiltration rates and limit groundwater recharge (Hartmann et al., 2014; Nerantzaki & Nikolaidis, 2020).

In addition, climate change interacts with other environmental issues that can exacerbate water scarcity in spring ecosystems, such as increased urbanization and land use changes. Increased urbanization entails an increase in impermeable surfaces and reduced infiltration rates. The increase in forests following cropland abandonment has increased ETR and reduced water availability, with numerous examples from European Mediterranean countries (Gallart & Llorens, 2003; García-Ruiz et al., 2011; Teuling et al., 2019) and other arid and semiarid regions (Farley et al., 2005; Filoso et al., 2017). Degraded and compacted soils, along with desertification, can also lead to lower infiltration rates and a decrease in the water recharge of the aquifers (Ferreira et al., 2022).

A clear example of how global change may affect spring water quantity can be found in a recent regional study (Figure 6). In January–February 2013, we measured water runoff from a total of 60 springs across the Littoral mountain range (NE of the Iberian Peninsula). Ten years later, in January–February 2023, we resampled 31 of them (selected randomly) and found an overall 92% reduction in water runoff, with 45% of the springs being completely dry. These

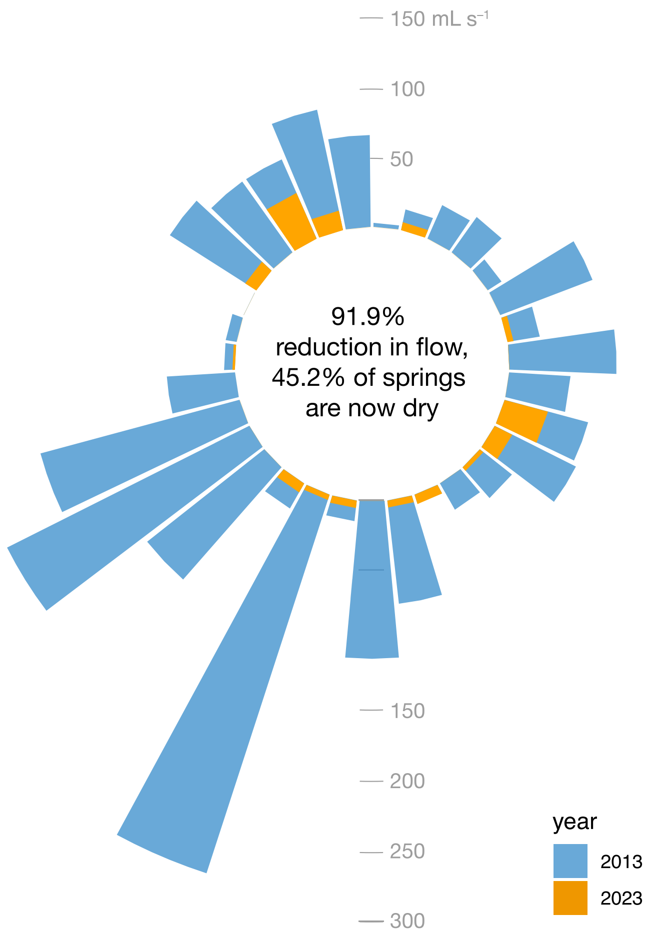

FIGURE 6 Water flow differences (10-year period) recorded at 31 springs located in the Littoral mountain range, in Catalonia. More than 45% of the springs surveyed in 2013 had dried up by 2023, and a reduction in 92% of total flow was observed.

changes are fully consistent with changes in piezometric levels from four wells located around the same area, recording a reduction of 1.1 ± 0.4 m in the water table from January 2013 to January 2023 (p = .001; Figure S1). The most likely factors affecting the decrease in water runoff of these springs are: (1) lack of management, (2) a 2-year persistent drought in the region, accounting for around 30% less precipitation during the 2021–2022 period, compared to the 2011–2012 period, and (3) an increase in mean temperature of 0.6°C during the latter period compared to the first one. In this area, monthly and annual real ETR derived from MODIS (product MOD16A2GF, Running et al., 2019) is positively related to precipitation and temperature (Figure 7). We found that for every increase of 1°C, ETR increases from 3.8% ± 0.4% during the spring season, to 15.1% ± 0.9% in winter, with an annual average of 7.2% ± 1.6% increase per °C. Since 2003 (when data were available), there have been considerable increases in both mean annual temperature (0.49 ± 0.11°C per decade, p < .001) and ETR (6.8 ± 1.0% per decade, p < .001). In this case study, an increase in water abstraction from these springs seems very unlikely because they are mainly located in mountainous regions with very little human influence. The data presented here clearly show that Mediterranean spring ecosystems

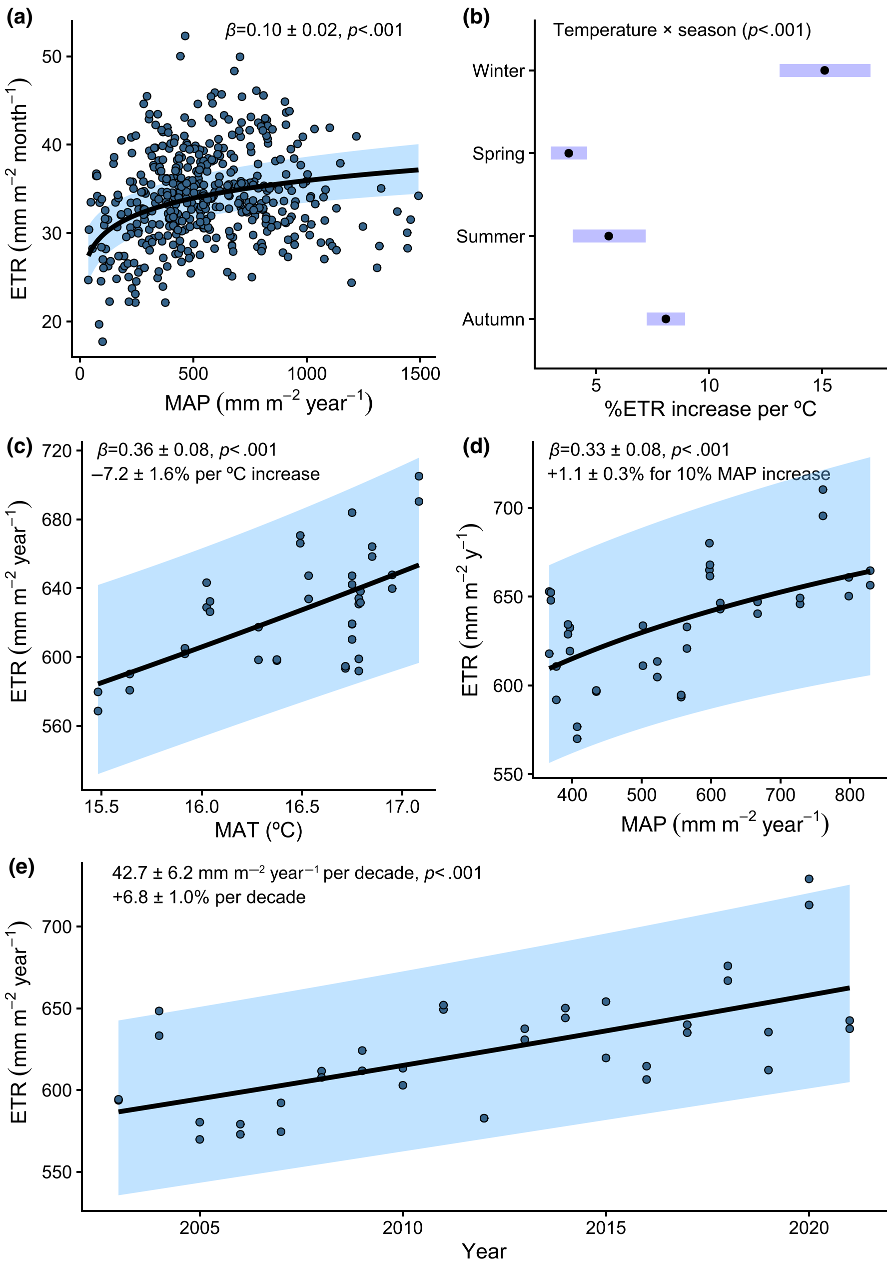

FIGURE 7 Partial residual plots showing effect of temperature and precipitation on real evapotranspiration (ETR) of the studied region (Littoral mountain range, Catalonia). Panel (a) shows a positive but saturating relationship between monthly ETR and precipitation (MAP, here precipitation of the last 12 months). Panel (b) shows how the effect of monthly temperature on monthly ETR depends on the season. Panels (c, d) show, respectively, the effect of mean annual temperature, and precipitation, on annual ETR. Finally, panel (e) shows the temporal trend of ETR from 2003 to 2022. During this same period, MAT increased by 0.49 ± 0.07°C per decade ($p<.001$, weather data from the town of Mataró 41°33′23″ N to 2°26′10″ E: www.meteomataro.com). We used ETR data from MODIS [product MOD16A2GF (Running et al., 2019)] for central coordinates for the two main massifs of the study region (Cèllecs and Montnegre, respective coordinates: 41.67831 N, 2.57941 E; and 41.56768 N, 2.36892 E) covering an area of 20.5 × 20.5 km. Results from panels (a, b) were obtained using a mixed effects model in which the response variable was monthly ETR (ln-transformed) and the fixed predictors were mean monthly temperature, season, their interaction, and monthly precipitation of the last 12 months (ln-transformed). We included the massif as the random factor (Cèllecs or Montnegre) and an AR1 (auto-regressive function for lag 1) temporal autocorrelation structure. Results in panels (c, d) followed the same approach for annual values, but excluding the season. Results in panel (e) followed the same procedure but including only year as a fixed predictor. Shaded areas represent 95% confidence intervals. See the data availability statement to access data and code to reproduce these results.

are under threat due to global change. If the climate continues to become warmer and drier, as expected, many of these ecosystems will likely be lost in the near future.

Moreover, Mediterranean springs will become increasingly disconnected from downstream areas, which will shift from perennial to intermittent conditions. This change will lead to substantial alterations in biological communities. While this shift will impact spring biodiversity and its temporal dynamics (as depicted in Figure 5), it will also serve to reduce the risk of downstream colonization by non-native species (Costello et al., 2011). Additionally, a decrease in water quantity will affect the water quality of aquifers and springs. This reduction diminishes the potential for pollutant dilution, as discussed in Section 4.2 (e.g., Mas-Pla & Menció, 2019; Van Vliet et al., 2017). The higher concentrations of pollutants in spring water are likely to result in a reduction in spring biodiversity (Fernández-Martínez et al., 2020).

4.2 | Water quality

4.2.1 | Eutrophication

Intensive agricultural practices have relied for decades on the overfertilization of crops with synthetic fertilizers and manure, and much of the excess nutrients applied are carried by runoff into surface watercourses and through infiltrated water into aquifers (Galloway et al., 2008; Sutton et al., 2011). Intensive livestock farming is also responsible for much of the N and P leaching into freshwater systems (Bouwman et al., 2013). Once produced, the removal of nutrient pollution (mainly nitrates) in groundwater is difficult to achieve (Mas-Pla & Menció, 2019), and given that the residence time in aquifers can be long, sometimes the pollution detected in springs lags years behind the time when pollution occurred (Alley et al., 2002).

Intensive agricultural practices have already compromised groundwater quality in Mediterranean areas of southern Europe and North African countries (Morocco, Algeria, Tunisia). In Spain, Italy, France, Greece, Croatia and Malta, both nitrogen surpluses and high abstraction pressures have been identified (European Environment Agency, 2022; Psomas et al., 2021), and many of their aquifers are in nitrate vulnerable zones. High concentrations of nutrients in the groundwater that feed springs can lead to eutrophication and drastic changes in the flora and fauna of the spring ecosystems (Fernández-Martínez et al., 2020; Jacoby et al., 2008; Martín et al., 2024). Some studies have reported plant community shifts from adapted submerged aquatic plants to systems dominated by benthic and attached filamentous algae, while some others link elevated nitrate concentrations with alterations in the reproductive functioning of amphibians and fish (Jacoby et al., 2008).

4.2.2 | Wastewater

Human activities, such as intensive livestock farming and wastewater discharges, have also contributed to the degradation of the microbiological quality of groundwater, aquifers, and springs (Savio et al., 2018; Stevens et al., 2022; Takuissu et al., 2022). Fecal contamination infiltrates soils and reaches groundwater and aquifers, even at great depths. The extent of contamination depends on several factors, including soil type, vegetation, terrain and bedrock fracture, precipitation, and land use (Aqso et al., 2014; Davidson et al., 2016; Murphy et al., 2017; Savio et al., 2018). Recent studies have indicated a general underestimation of aquifer contamination through enlarged cracks and fissures (Hartmann et al., 2021). Pathogenic bacteria, such as *Escherichia coli* and other coliforms, and enteric viruses like *Norovirus*, *Rotavirus*, hepatitis A and E viruses, as well as protozoa like *Cryptosporidium* and *Giardia*, are increasing, compromising springs as secure freshwater resources (An & Breindenbach, 2005; Aqso et al., 2014; Blanco et al., 2017; Davidson et al., 2016; Murphy et al., 2017; Ryu et al., 2019; Takuissu et al., 2022).

4.2.3 | Emergent pollutants: Synthetic chemicals, drugs, and microplastics

Soils act as a sink of organic pollutants; however, organic contaminants can also leach from soils to groundwater (Burri et al., 2019), especially in karst systems (Chen et al., 2022). Diffuse pollution from agriculture is the most common pressure to the quality of groundwater, affecting 19% of the total groundwater body area in the EU (European Environment Agency, 2022). Pesticides can migrate through soil or surface water to streams and groundwater, where they can have unintended ecological impacts such as accumulation in aquatic organisms and loss of ecosystem biodiversity (McGinley et al., 2023). Among pesticides, triazine herbicides have been highlighted as being one of the most widespread pesticides in European groundwaters (Loos et al., 2010), and the most frequently detected herbicides in water resources in Spain (Herrero-Hernández et al., 2017; Llamas et al., 2022). The impact of pesticides on groundwater can last for long periods due to the slow renewal rate of groundwater and the slow release of retained pesticides and their metabolites in the soil (Baran et al., 2022).

Pharmaceuticals may enter the aqueous environment through anthropogenic activities such as sewage discharge, livestock, fertilizing and landfill leachate, resulting in their presence in groundwater at high concentration levels of $ng\,L^{-1}$ to $\mu g\,L^{-1}$ (Sui et al., 2015). Recently, awareness has grown about the presence of antibiotic residues in groundwaters related to the presence of antibiotic-resistant bacteria (ARB) (Andrade et al., 2020; Kaiser et al., 2022; Kampouris et al., 2022; Singh et al., 2022). The incorrect usage and overuse of antibiotics in human and veterinary health treatments has created an anthropogenic selective pressure on environmental bacteria, and the emergence of multidrug-resistant "superbugs" is now a reality (Andrade et al., 2020; Huang et al., 2023). A recent review by Andrade et al. (2020) states that groundwater represents a major global reservoir for ARB. Several recent studies have reported high amounts of ARB, antibiotic-resistant genes, and mobile genetic elements in groundwater and springs (Gros et al., 2023; Huang et al., 2023; Kaiser et al., 2022; Kampouris et al., 2022).

Nonsteroidal anti-inflammatory drugs (NSAIDs) are other pharmaceuticals frequently detected in water resources due to their widespread use. The main source of contamination is excretion through urine and feces in wastewater, which contain unmetabolized or conjugated and transformed forms (Singh et al., 2014). Jurado et al. (2021) studied 13 groundwater samples in an urban aquifer in Barcelona and concluded that individual NSAIDs and their mixtures posed minimal risk to human health. However, the risk posed by the sum of different pharmaceuticals that can simultaneously be detected in groundwater remains elusive. Additionally, polycyclic aromatic hydrocarbons (PAHs) are concerning compounds for wildlife and human health due to their carcinogenic, mutagenic, and endocrine disruptor potential (Wallace et al., 2020). Forest fires are a well-known natural source of PAHs that play an important role in their distribution in both terrestrial and aquatic compartments (Campos & Abrantes, 2021). Mansilha et al. (2019) studied the impact of wildfires and posterior precipitation to water from springs and streams from Caramulo Mountain (Portugal) indicating that burnt areas presented from 1.2 to 4 times higher concentrations of PAHs compared to unburned areas.

Among emerging pollutants, microplastics (MPs, plastic particles smaller than 5 mm) are becoming important due to their persistence in aquatic environments (Viaroli et al., 2022). The penetration of MPs through pores and fractures, as well as interaction with colloidal aggregates, can partially affect the dynamics of MPs in the subsoil, making their detection difficult in groundwater systems and springs. MPs in groundwater may have several sources, including the atmosphere, the interaction with surface water bodies, urban infrastructures, or agricultural soils (Viaroli et al., 2022). The characterization and quantification of MPs in groundwater are challenging due to the wide variety of sizes and compositions (Alfonso et al., 2021). Some studies focused on aquifer and spring water MP pollution have been performed in the USA, Europe, and South Africa (Mintenig et al., 2018; Panno et al., 2019). Despite the low number of studies, most of them have found the presence of MPs in groundwater (Boyle & Örmeci, 2020), highlighting the fact that MP contamination of groundwater is a problem that deserves further attention.

4.3 | Biological invasions

The introduction of alien species is an ongoing and widespread conservation issue for spring ecosystems, especially because of the constant conditions of these freshwater habitats (Fensham et al., 2011; Kodric-Brown & Brown, 2007). Although the magnitude of this threat has not yet been quantified for these freshwater environments, several alien plant and animal species have been widely introduced in Mediterranean springs, where they became established and now maintain self-sustaining populations (e.g., Aksu et al., 2021; Emiroğlu et al., 2016; Saber et al., 2022).

For instance, invasive diatoms have been introduced into an oasis mineral spring in Egypt, with potential impacts on native diatom assemblages (Saber et al., 2022). The occurrence of alien plant species in springs has been associated with increased anthropogenic disturbance, ultimately being correlated with decreased richness of native flora (Nielson et al., 2019). Cases of animal introductions in Mediterranean spring ecosystems are comparatively much more abundant, particularly concerning exotic fish and crayfish (Kodric-Brown & Brown, 2007). Mediterranean spring ecosystems are particularly prone to biological invasions due to the scarce representation of native spring-dwelling predators (e.g., fish) and the high popularity of springs among local people, which acts as an intentional (e.g., releases for aesthetic or recreational purposes) or unintentional vector for alien species introduction. In fact, the establishment of alien species in spring ecosystems likely involves greater impacts on native spring-dwelling biodiversity as compared to other larger freshwater ecosystems, because their limited size and delicate ecological balance magnify the ecological impacts of introduced alien species. Conversely, the high degree of isolation that characterizes Mediterranean spring ecosystems could reduce the propagule pressure of alien species and the invasion risk through natural spread mechanisms (Stevens et al., 2021).

4.4 | Changes in local culture and traditions: Spring abandonment

In Mediterranean regions, the presence of natural springs has been a key part of the culture since the earliest civilizations. The location of the Acropolis in Athens was likely selected not only for its defensive capacity but also because an aquifer and a spring were located there, and the aqueduct system of Ancient Rome was predominantly supplied with water taken from springs (Mays et al., 2007). The influence of springs in Mediterranean culture is also evident in numerous ancient literary works, often highlighting their spiritual and biodiversity importance as shown in the book “Llibre de meravelles” by Ramón Llull (1287–1289 AD), in a fragment that translates as: “The philosopher was sitting under a tree, full of leaves and flowers. The tree was watered by a spring, in which there were lots of sweetly singing birds. The philosopher was contemplating the greatness and goodness of God in the arrangement of the tree, the spring and the birds” (see original text in Section S2 of Supporting Information). This short text exemplifies how deeply ingrained these ecosystems are within Mediterranean culture.

Large technological advances and important lifestyle changes occurred during the 20th century in many countries, leading to the abandonment of rural areas and increasing human population density in cities. This has consequently led to the abandonment of traditional practices as well, even though they may have been crucial for human livelihoods just a few decades before. Some of these activities were strongly related to spring ecosystems, particularly in Mediterranean and arid regions. The management of human-modified springs for providing both humans and livestock with drinking water, but also for supporting irrigated crops and other uses, has sharply decreased in just a few decades. The abandonment of traditional croplands or farmhouses has been directly related to the loss of human-modified springs and their related ecosystems. For instance, the decline of livestock transhumance and other regimes of extensive pastoralism across the Mediterranean basin is leading to the abandonment and consequent collapse of spring-fed drinking troughs (Manenti et al., 2017), particularly in the Iberian southeast (Zamora-Marín et al., 2022).

In addition to land abandonment, changes in lifestyle and beliefs have further affected the conservation of springs. Religious celebrations associated with springs went from being very popular and common to becoming almost completely extinct. Since the second half of the 19th century, spring-mediated tourism to drink naturally occurring sparkling water, which was believed to have curative properties, was also very popular among wealthy people. Again, social changes have almost completely put an end to both activities and left spring-based health resorts and their saints as anecdotes from old times, thus causing the progressive loss of springs caused by vegetation encroachment. These cultural manifestations, based on traditions, legends, customs, and habits occurring in the surroundings of springs, have been previously referred to as "spring culture" (Fernández-Martínez et al., 2017). Losing these springs implies not only losing the biodiversity linked to those ecosystems, but sometimes also losing ancient local knowledge and rich cultural legacy often only preserved through oral transmission (Table S3 provides a list of cultural events linked to spring ecosystems in Mediterranean and arid regions around the world).

In spite of the general trend of spring cultural abandonment, new social trends are emerging with an increasing interest in protecting nature, including movements in several Mediterranean regions to study and protect spring ecosystems. In Catalonia, several local groups have engaged different projects to study and protect springs (e.g., *Grup de Fonts d'Argentona*; *Projecte Fonts* by several of the signing authors; *Grup de Defensa del Ter*; *Fonts del Montseny*; or the *CercaFonts*, a mobile app with information on 5000 springs). In Andalusia, the *Asociación Proyecto Conoce Tus Fuentes* manages the first participatory online catalog of springs in Andalusia, with more than 13,000 springs inventoried to date. Likewise, in Mallorca (Balearic Islands), an exhaustive survey of springs was performed across the Tramuntana mountain range. In Castilla-La Mancha, the project *Apadrina una Fuente* aims to find, signpost, and restore all the springs in the municipality of Cifuentes (whose name means "one hundred springs"). Some other initiatives of international relevance have emerged in order to put springs and their conservation into the spotlight, such as the Fellowship of the Spring (Fensham, Adinehvand, et al., 2023), or the Springs Stewardship Institute. Whether the spring culture will remain alive for future generations or not depends mostly on our ability to preserve spring ecosystems.

5 | CONSERVATION AND MANAGEMENT

Most Mediterranean spring ecosystems are managed in order to provide water for human activities, thus mostly ignoring the conservation of their biodiversity and ecological functions. Hence, it should be a top priority for biodiversity conservation to preserve, as intact as possible, those few natural springs that have not yet been disturbed. However, as mentioned above, most Mediterranean spring ecosystems are now seminatural ecosystems. In these cases, managers should oversee a trade-off between conserving or restoring (fully naturalizing) those ecosystems. In cases where the spring remains in active use, we strongly recommend maintaining its current utilization. This approach is advisable because the existing biota should already be in equilibrium with the spring's current conditions, as well as the social services these ecosystems offer (see Section 4.4). Preserving springs that are still in use can be achieved at a very low cost, and the benefits for biodiversity conservation can be substantial, particularly in arid regions and in springs inhabited by endemic species. However, if the spring is no longer in use or has dried up, certain actions should be taken: (i) To restore the spring to a previous state: This involves rejuvenating the spring to a condition where it can sustain a more or less constant flow of water. Sometimes, issues like collapsed water mines or obstructed pipes due to plant roots can be addressed to revive spring biodiversity. (ii) Fully re-naturalize the spring: In this approach, any artificial construction or modifications are removed to return the spring to its natural state. The choice between these two options depends on the specific circumstances. The first option is more likely to successfully recover the spring ecosystem. However, the latter solution may not be practical for preserving spring ecosystems that have been significantly altered by human intervention, especially those fed through water mines, because restoring them to a state before any human intervention would imply irreversibly losing any potential water flow. Nonetheless, in humid regions, the second option could be a valuable approach in order to increase the number of natural springs. Furthermore, in human-modified springs, conservation actions should also promote environmental heterogeneity at spring scale (i.e., microhabitats), thus boosting diversified biotic communities (Zamora-Marin et al., 2024). For that purpose, management actions could be focused on promoting adjacent terrestrial vegetation, allowing the occurrence of ground-level puddles from water leakages or overflow, and providing structural refuges (e.g., stone walls) for crenophilic wildlife, among others. In this regard, regional authorities should provide management guidelines to promote a more nature-friendly management from stakeholders and spring users, some of which are currently subjected to extensive livestock or farming purposes.

Legislation to protect spring ecosystems, however, is somewhat scarce. The Habitats Directive of the EU, which forms part of the legal basis for the Natura 2000 Network, includes in its list of protected habitats only limestone-precipitating springs, leading to a situation in which many spring habitats remain unprotected (Cantonati, Segadelli, et al., 2016). For example, Spampinato et al. (2023) listed soft water springs and crenel brooks of southern Italy as habitats deserving protection but neglected by the Habitats Directive. Indirect protection of spring ecosystems may be afforded by the protection of, for instance, calcareous spring mires and other wetlands, given that these habitats often include springs within their heterogeneous structure. However, although spring ecosystems are meaningful for regional biodiversity and threatened in many regions by human activity, few nations bear a legal framework explicitly protecting spring habitats. Comprehensive legislation for the conservation of spring ecosystems worldwide is urgently required (Cantonati et al., 2021).

An important step toward the large-scale protection of the biodiversity of springs is the comprehensive research on their ecological integrity. Stevens et al. (2022) found in their global review that studies of spring ecosystems are sparse, erratic, and widely scattered. Contributing scientists of Mediterranean biogeographical regions generally reported both insufficient data on springs as well as high estimated endangerment levels (e.g., for the Iberian Peninsula, South Africa, Greece, and Morocco). National or regional spring studies such as those underway in Andalusia and Catalonia (Section 4.4) can help to close this gap.

6 | CONCLUSIONS

Spring ecosystems are interface habitats between subterranean and surface freshwater environments, and they harbor unique biodiversity favored by both surface and groundwater organism populations providing important ecological functions. However, they probably constitute one of the rarest, most fragile ecosystems threatened by the effects of global change and the overexploitation of water, which might impair their capability to function as "time capsules of biodiversity" (Beasley-Hall et al., 2023). This is particularly critical for Mediterranean springs where the combination of natural (drying) and anthropogenic disturbances jeopardize their biodiversity and the ecological functions and ecosystem services they provide. Given that future scenarios for Mediterranean climate regions suggest an increase in aridity, it is imperative to prioritize the conservation of Mediterranean springs and develop specific management plans for these ecosystems. Our review demonstrates the urgent need for immediate action to preserve these ecosystems ensuring the retention or restoration of their ecological and cultural value.

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Marcos Fernández-Martínez: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **José Barquín:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Nuria Bonada:** Data curation; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Marco Cantonati:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Catarina Churro:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Jordi Corbera:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; validation; visualization; writing – original draft; writing – review and editing. **Cristina Delgado:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Maria Dulsat-Masvidal:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Guillermo Garcia:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Olga Margalef:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Roger Pascual:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Josep Peñuelas:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Catherine Preece:** Conceptualization; investigation; methodology; resources; validation; visualization; writing – original draft; writing – review and editing. **Francesc Sabater:** Conceptualization; investigation; methodology; resources; validation; visualization; writing – original draft; writing – review and editing. **Hallie Seiler:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **José Manuel Zamora-Marín:** Conceptualization; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Estela Romero:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

All signing authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code to perform analyses presented in this study can be openly found at Figshare: https://doi.org/10.6084/m9.figshare.23220998.v1, reference number 23220998.

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