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Ecohydrogeology: The interdisciplinary convergence needed to improve the study and stewardship of springs and other groundwater-dependent habitats, biota, and ecosystems

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ABSTRACT

This essay discusses the need for, advantages and challenges of integrating the scientific disciplines of ecology and hydrogeology in the study of groundwater-dependent ecosystems (GDEs). We provide a definition for ecohydrogeology as “a unifying, synthetic field of study integrating the approaches from the ecological and hydrogeological sciences in the study of groundwater (GW)-related ecosystems, habitats, and organisms to advance science, stewardship, and policy”. We selected specific case studies to illustrate first how hydrogeological approaches can favour in-depth understanding and modelling of springs and crenobiontic (spring-dependent) species distribution, assemblage composition and organization. Second, this essay also examines how taxa and assemblages serve as bioassays and ecosystem indicators to infer hydrogeological aspects of GW flow and discharge, as well as quantitative and qualitative human impacts. We consider both types of features and parameters as ecohydrogeological indicators. The examples presented include topics related to springs and other GDE geomorphological types and classification, GW quality influences on crenobiont distribution, phreatophyte (= plant species the roots of which reach to and into the water table) ecophysiology in relation to water table depth, and flow variability in karstic systems, to nutrient dynamics in relation to dinoflagellate blooms in GDE montane lakes. Conceptual approaches that integrate ecology with hydrogeology include the investigation of GDE distribution and ecology, groundwater-surface water (GW-SW) interactions, and the development of the discipline of ecohydrology. Despite widespread applications, the scientific community still lacks a complete or effective integration of the principles described in the fields of groundwater hydrogeology with ecology, ecophysiology, and environmental biology. Springs are aquatic-wetland-riparian habitats that link shallow subsurface-surface processes and assemblages, often functioning as biodiversity hotspots, ecotones, keystone, and refugial ecosystems, for which coordination between studies of hydrogeology and ecology are both obvious and essential. Over the past century, springs ecosystem ecology has been largely ignored by hydrologists, and, conversely, hydrogeology has been under-emphasized by ecologists. Recent global recognition of the extraordinary biodiversity and socio-cultural significance of springs, coupled with their globally highly threatened conservation status, stimulated this inquiry into how to better integrate hydrogeology with springs ecosystem ecology. Acknowledging the highly threatened status of springs ecosystems around the world, there is an urgent need to integrate and invigorate the union of these disciplines into ecohydrogeology, the study of groundwater-dependent organisms, habitats, ecosystems, and management policy.

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1. Introduction

Fresh water represents only 2.5% of the Earth's water volume, but approximately two thirds of that fresh water is stored as glacial or permafrost ice (e.g., Oki and Kanae, 2006). Groundwater (GW) represents 96.3% of the unfrozen global fresh water (Downing, 2014; Stevens et al., 2019a). GW-sourced ecosystems provide goods and services that have enormous ecological and socio-economic value, such as purification of water, degradation of contaminants, nutrient recycling, mitigation of floods and droughts, and refugia for many species, including early human ancestors (Griebler and Avramov, 2015; Cuthbert and Ashley, 2014; Mueller et al., 2017). Modern humans have now appropriated more than half of the renewable and accessible freshwater flows on Earth for the purposes of urban, agricultural, industrial uses (Postel et al., 1996), but nearly 80% of the world population suffers from highly threatened water security (Vörösmarty et al., 2010). Although springs are the ecosystem on which the science of ecosystem ecology was founded (Odum, 1957), and though most subsequent research on springs ecology identifies dire anthropogenic threats to natural and human-dominated groundwater-dependent ecosystems (GDEs), springs have been widely neglected in research and targeted conservation studies (e.g., Baron et al., 2002).

The Anthropocene epoch heralds humanity's overwhelming influence on planetary ecology, and we face new levels of regional, national, and global concern over freshwater availability (e.g., Rockström et al., 2014). Springs, streams, rivers, and lakes are among the most heavily modified GDEs on Earth, with primary alterations through changes in land use and climate influencing water feature morphology, hydrology, and ecosystem ecology (e.g., Carpenter et al., 2011). Climate change is predicted to affect all aspects of freshwater ecosystems because altered temperature and precipitation patterns influence geomorphology, infiltration, flow, flood intensity, sedimentation, nutrient dynamics, and detoxification, as well as ecosystem characteristics, structure, and function (Carpenter et al., 2011). To protect the world's freshwater resources, human and biodiversity perspectives on water security need to be considered jointly (Vörösmarty et al., 2010). Growing recognition of the need to preserve freshwater GDE integrity, functionality, and biological complexity has stimulated initiatives for safeguarding the many services and benefits freshwater ecosystems provide to society (e.g., Baron et al., 2002; Kremer et al., 2015).

Satisfying the demand for balance between ecological sustainability with a global population of nine billion people by 2050 (Rockström et al., 2014) requires new approaches in the use and management of freshwater resources (Postel, 2000). A shift in conceptualization and practice is required, acknowledging the central role of water in ecosystems and societal integrity. Emphasis is needed to managing water for social-ecological resilience and sustainability (Rockström et al., 2014). Freshwater ecosystem integrity depends on adequate quantity, quality, timing, and temporal variability of flow within a natural range of variation (e.g., Baron et al., 2002). Thus, there is urgent need to develop basic understanding, technology, and policy to maintain and preserve related ecosystem services. Mitigation and restoration efforts must be based on well-grounded understanding of both hydrogeological and ecological principles (Baron et al., 2002; Carpenter et al., 2011).

Among the factors contributing to good GW policy and management, Alley et al. (2016) list the following: recognizing surface water and GW as a single resource; public education on GW and its importance; consideration of GW role within other policy areas, such as agriculture, energy, and land use; adequate laws and enforcement; fully funded and properly staffed GW management agencies; characterization of major aquifer systems; effective and independent monitoring of GW status and trends; recognizing the long-term response of GW systems; and accounting for interactions between GW and climate. However, such recognition is rare to non-existent among both developed and developing nations, and few are sustainably managing their GW supplies.

Ecohydrology integrates GDE ecological and hydrological disciplines. Over the past century, studies have been focused at the basin and sub-basin scale, as well as on applied issues, such as ecosystem remediation and improvement of resilience (Zalewski et al., 1997; Rodríguez-Iturbe, 2000; Zalewski, 2002; Cartwright et al., 2019). The intensity of interest in the intersection of hydrogeology and ecology has led to the publication of several specialised journals, including *Ecohydrology* and *Ecohydrology & Hydrobiology*. Another result of this integration has been the conceptualization and practice of environmental flow management, as evidenced by Mott LaCroix et al. (2017).

Several specific areas of hydrogeological study remain under-integrated with GDE ecology research. The term groundwater-dependent ecosystem is widely used and refers to the linkage between aquifers and associated subterranean and surface water bodies, relationships that require a more fully integrated, multidisciplinary research (e.g., Eamus and Froend, 2006; US Forest Service, 2012). Phreatology is a field of interdisciplinary research focusing on the geological, hydrological, biological and chemical processes at the interface of the phreatic water with the vadose or surface waters (Batelaan, 2006). This field is restricted to unconfined, phreatic GW. While leaky-confined or confined aquifers are sometimes ecohydrogeologically important when close to the surface, these cases are not included in phreatology. Reiss and Chiffard (2017) discuss an integrative approach for spring habitats within the Earth's Critical Zone (Brantley et al., 2007), seeking coupling of perspectives between ecohydrology and hypopedology. Steube et al. (2009) note that legislation has started to consider groundwater not only as a resource but also as an ecosystem, and discuss attempts for an integrative concept of the ecological assessment of groundwater systems. Limnogeology (Gierlowski-Kordesch, 2003) is a branch of paleolimnology devoted to the study of lake systems and their deposits. Paleolimnology sometimes requires combining hydrogeological and ecological parameters. Zheng et al. (2019), for instance, reconstructed peatland hydrology (mire water-table depth) using testate-amoeba assemblages. Research on groundwater-surface-water (GW-SW) interactions examines the interface between aquifers and rivers, and emphasizes relationships among spatial and temporal variation in hydrological, physical, biogeochemical, and ecological factors (Larned et al., 2015). Stevens et al. (2019a) review GW-SW interactions influencing the hydrologic cycle at the watershed scale, noting that springs and (often GW-fed) lakes provide base flow for virtually all the rivers in non-ice-dominated portions of Earth. They also conclude that the role of GW in fluvial ecology has been considerably underestimated and underappreciated. Geobotanical survey techniques have been used since the late 1950s for mineral prospecting and complement field-based studies in several disciplines (Brooks, 1988; Ustin et al., 1999). Such investigations also involve land management and monitoring, and their importance is becoming progressively more evident.

In contrast to the above concepts, the term "ecohydrogeology" has only occasionally been used in the literature (e.g., Kimberley and Coxon, 2015; Wang et al., 2015), without discussion of its utility and novelty and without attempting a clear, unambiguous definition. We propose the following definition for this term: "Ecohydrogeology is a unifying, synthetic field of study integrating the approaches from the ecological and hydrogeological sciences in the study of groundwater-related ecosystems, habitats, and organisms to advance science, stewardship, and policy". Etymologically, ecohydrogeology is built on a foundation of geology, which largely controls aquifer hydrology, and which in combination permit development of GW and GW-SW aquatic and riparian ecosystems. GDEs include fully subterranean microbial and invertebrate aquifer ecosystems, as well as aquifer-surface water linked ecosystems, such as submarine and surface springs and GW-fed streams, lakes, and oceans. Expanding the concept of GDE ecology by adding the physical-process underpinnings of geology and hydrology, ecohydrogeology emphasizes the linkage between the intrinsic geological heterogeneity of the subsurface with GW occurrence, emergence, geomorphology, and biology. This multidisciplinary interaction has

Sharaky, 2019). This indicates that this multidisciplinary integration not yet gained the attention of the scientific community. Also, the terms geology, evolution, and conservation were inconspicuous in the word cloud, indicating that the temporal scaling that so strongly influences those fields has not been integrated into freshwater ecology. We discuss these and other issues throughout the rest of this paper.

3. Springs and crenoeology

3.1. Spring sources as a central focus for the converging fields of ecology and hydrogeology

Springs are ecotones in which aquifer-surface components are linked across aquatic, wetland, and riparian systems where GW emerges. These usually flow from the Earth's surface and include sub-aqueous (e.g., submarine) as well as subaerial settings (Springer et al., 2008). Among the world's most socio-ecologically interactive, intriguing, diverse, and threatened ecosystems, spring ecohydrogeology has been insufficiently-studied by the scientific, and insufficiently recognized as worthy of protection by the public and the management/governance communities. The study of springs has been hindered by the highly incomplete knowledge of their distribution, density, and types across landscapes. An accumulation curve analysis of Death Valley National Park, one of the landscapes with the best known distribution and densities of springs in N. America determined that there were likely many more undiscovered springs on the landscape (Junghans et al., 2016). Illies and Botosaneanu (1963) formally defined 'crenobiology' as the study of the biological properties of springs, and the term 'crenoecology' has been used sporadically in the literature over the last two decades (e.g., Cantonati et al., 2012). Springs are widely recognized as important habitats (Cantonati et al., 2012, 2015), creating complex ecotones and biodiversity hotspots (Cantonati and Lange-Bertalot, 2010; Cantonati et al., 2016; Taxböck et al., 2017), and thus also are ideal sites for long-term ecological research (Cantonati and Ortler, 1998).

Hydrogeologists and ecosystem ecologists converge at springs sources, but work in opposite directions. Hydrogeologists often conclude their studies at the point of emergence, while ecologists often initiate their research at that point. Thus, for hydrogeologists the source is the final point of interest in the aquifer, while for ecologists the source is the starting point of their study of GDE flow, habitats, and species in fens, *ciénegas*, or mires, hanging gardens, lakes, and associated lacustrine, palustrine, or fluvial riparian wetland zones (Fig. 2).

In many settings, GW discharge and surface water runoff intermingle, e.g.: hard-rock-aquifer mountain-stream reaches that directly receive GW discharge, and are fed only by GW during periods of hydrological recession without quick flow (overland flow + interflow), actually show a combination of GW-discharge and surface-water body features (e.g., Miller et al., 2016).

3.2. Springs and other GDE classification

As mentioned above, springs represent a water-dominated critical (=because it is essential to sustain life) zone at the interface between lithosphere, hydrosphere, and biosphere, but none of these fields of science by itself can fully embrace the phenomenology of physical, biological, and cultural interactions over time that constitute a spring ecosystem. On the geological side of springs research, hydrogeology is multidisciplinary among earth sciences and hydrological sciences, whereas ecosystem ecology also is strongly multidisciplinary but emphasizes a much different lexicon, suite of concepts, variables, and study approaches. Bryan (1919), Meinzer (1923), Alfaro and Wallace (1994), Springer et al. (2008), and Glazier (2009) review the many spring classification topics and approaches that have been proposed.

Springs ecology is focused on the point of discharge of the GW, which is not considered SW or GW by some rules, regulations, or

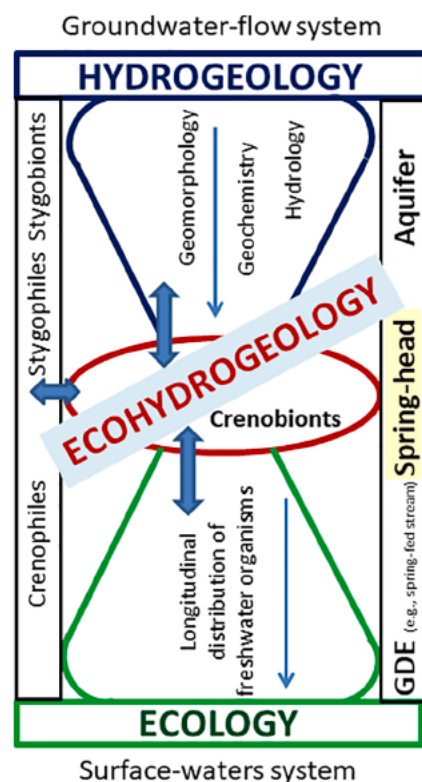


Fig. 2. Hourglass model of springs GW-SW ecotonal transitions (double arrows) as an emblematic example of synergistic ecological and hydrogeological approaches. Spring ecosystems are thus the iconic environment of ecohydrogeology (revised and redrawn from Cantonati et al., 2012).

policies. However, a growing body of literature identifies a suite of species not only dependent on springs, but restricted to discrete spheres of discharge and springs microhabitats (Springer and Stevens, 2009; Sinclair, 2018).

Nonetheless, springs are complex composite hydrogeological and ecological ecosystems and deserve a dedicated classification in order to provide a systematic framework necessary to study them. A variety of classifications have been presented in the literature from the hydrogeological stand-point, as well as from the ecological, crenobiological, and ecosystem-services perspectives. These two groups of classifications are useful and are utilized in an intra-disciplinary fashion by hydrogeologists or ecologists. However, they are rarely considered or taught to students outside of the individual disciplines. Table 1 provides a synthetic review of the main classification approaches that have been proposed, along with examples of references, some of which present additional literature compilations.

From the hydrogeological standpoint, basic classifications rely primarily upon: parent rock geology (lithology, stratigraphy) and structural geology of the groundwater basin; driving force mechanism (gravity, pressure or density/temperature dominated discharge), GW quality including water temperature and/or geochemistry; discharge quantity (magnitude, variability, and recession); or the geomorphology of the discharge point of the spring (the "sphere of discharge" as landform pattern at the springs source; Meinzer, 1923). Stevens et al. (2019b) emphasize that of the proposed classification factors, only geomorphology clearly and unambiguously distinguishes springs types.

From ecological and anthropogenic perspectives, the focus of springs classification may be physical and/or biological, depending on taxonomic composition, in addition to the structural or functional properties of the associated biota and assemblages. Early attempts to identify features determining spring characteristics particularly relevant for the colonizing biota are attributable to van der Kamp (1995),

Table 1
Selected spring classification systems according to hydrogeological and ecological criteria.

Field of research		Classification property	Examples of descriptors/indicators	Selected references (e.g.)
Hydrogeology	Geomorphology	Location of spring	Subaerial/subaqueous/subglacial/subterranean	Alfaro and Wallace, 1994; Springer et al., 2008
	Geology	Shape of spring outlet	Conduit/fracture/seepage	Meinzer, 1923; Kresic, 2010
		Aquifer lithology	Limestone/volcanic/hard rock/alluvium	Meinzer, 1923; Kresic, 2010
		Discharge hydrostructure	Contact/barrier/vaclusian	Bryan, 1919; Meinzer, 1923; Civita, 1973; Alfaro and Wallace, 1994
	Hydrology	Flow forcing mechanism	Gravity/artesian/geothermal	Meinzer, 1923; LaMoreaux and Tanner, 2001; Springer et al., 2008
		Discharge pattern	Perennial/seasonal/intermittent/ebb-and-flow	Meinzer, 1923; Springer et al., 2008; Kresic, 2010
		Discharge flow rate	Flowrate magnitude	Meinzer, 1923, 1927
	Geochemistry	Flow rate variability	Indexes of flow variability	Meinzer, 1923; Alfaro and Wallace, 1994
		Hydrologic recession	Classes based on recession coefficient	Gargini et al., 2008
		Water temperature	Cold/warm/thermal	Meinzer, 1927; Alfaro and Wallace, 1994; Springer et al., 2008
Ecology	Habitat	Water pH	pH ranges	Springer et al., 2008
		Water salinity	Total Dissolved Solids/Electrical Conductivity ranges	Springer et al., 2008
		Major-ions concentration	Chloride/sulphate/bicarbonate/alkaline	Fetter, 2001
				Clarke, 1924
		Current-velocity conditions at the spring outlet	Rheochrene/helocrene/limnocrene/hypocrene	Steinmann, 1915; Thienemann, 1922; Springer et al., 2008
	Biology	Ecomorphological types & associated invertebrate fauna	Rock-face, boulder, cobble, gravel, debris spring, limnocrene (fine grained)	Schröder et al., 2006
		Sphere of discharge	Cave/exposure spring/fountain (artesian)/hillslope/gusher/hanging garden	Springer and Stevens, 2009
		Microhabitat type	Aquatic/wetland/riparian/barren rock	Springer et al., 2008; Glazier, 2009
		Habitat size	Areal extension of spring habitat	Springer et al., 2008
		Plant, invertebrate, vertebrate richness	Number and species observed	Shannon, 1948
Human ecology	Human use	Biotic diversity	Diversity index	Springer et al., 2008
		Biota (algae based) classification	Taxonomic groups (diatoms, benthic algae)	Cantonati et al., 2012a,b
		Faunal (invertebrate) assemblages	Species composition of Hydrachnidia, Trichoptera, Coleoptera, and Gastropoda Macroinvertebrate functional feeding groups (scrapers, filtering collectors etc.)	Martin and Brunko, 2012
		Feeding groups		Cummins and Klug 1979; Von Fumetti and Nagel, 2011
		Phytosociological classification	Crenic vegetation types	Tomasselli et al., 2011
		Biota (multi-taxon) based classification	Consistency of classification tested using diatoms, bryophytes, vascular plants, nematodes, mollusks, oligochaetes, water mites, copepods, ostracods, chironomids, stoneflies, caddisflies	Spitale et al., 2012
		Human use	Drinking/household/irrigation/industrial	LaMoreaux and Tanner, 2001; Springer et al., 2008
		Spring diversion/spring enhancement	Spring diversion/aquifer diversion	Civita, 1973; Stevens et al., 2016; Swistock and Sharpe 2017

who demonstrated that the hydrological stability of many springs and springs-associated biota is determined by the hydrogeological features of the parent aquifer. The proposed classifications are generally related to natural GDE conditions, not to springs that have been diverted for human use or created by anthropogenic activities. However, the majority of springs in many landscapes have been dominated by human activities for millennia (e.g., Haynes, 2008 in North America; Cuthbert and Ashley, 2014 in the Old World), and are today partially or fully diverted, ecologically impaired, or obliterated (Stevens and Meretsky, 2008; e.g., Ledbetter et al., 2019). Because humans have relied on and altered springs throughout our evolution and history, our impacts must be taken into account in both research and stewardship (Stevens et al., 2016).

3.3. Freshwater springs lithology/geology and biota

The physical and chemical characteristics of emerging groundwater are determined by the geological settings and regional climate features, and often are modified by the indirect and direct impacts of human activity elsewhere (in Fig. 2 all environmental influences and impacts on the aquifer-spring-surface-water system can be influenced by anthropogenic activities). Such water quality interactions directly influence algal, macrophyte, invertebrate, vertebrate biodiversity, assemblage structure, and trophic dynamics.

3.3.1. Algae

Spring algal assemblages often largely constitute the aquatic food-base of spring sources. These assemblages include both generalists and species that preferentially occur at spring sources and in comparable habitats (e.g., Cantonati et al., 2010, 2012c). Springs are often subjected to severe anthropogenic impacts, particularly alteration of the morphology of the springhead and contamination from increased nitrate concentrations. These impacts are clearly identifiable using diatom assemblages (e.g., Angeli et al., 2010). Werum and Lange-Bertalot (2004) studied the geologically-heterogeneous region around the city of Frankfurt (central Germany, Hessen). On the basis of hydrogeological criteria and hydrochemical analyses, eight spring groups could be recognized, and each of these was found to host its characteristic diatom assemblage. For epilithic (those living on stony and rocky substratum) algae and lichens, the lithology determining the hydrochemistry of the aquifer is generally more important than the petrography of the rocky material on which they grow. This was evident for calciphile species, such as the red alga *Hildenbrandia rivularis* and the aquatic lichen *Verrucaria eleomelaena*, thriving on igneous (granites, granodiorites, tonalities etc.) boulders and cobbles (covered by glacial quaternary deposits) at the site of emergence of springs with typical calcium-bicarbonate chemistry (limestone-dolomite aquifers) (M. Cantonati, unpublished data). Contrary to what is known for several groups of invertebrates, in particular water mites (e.g., Cantonati et al., 2012), few diatom species occur exclusively in springs (crenobiotic taxa; one exception may be *Gomphonema montezumense* Czarnecki and Blinn, 1979). However, there are diatom species that occur preferentially in springheads + spring-fed streams, and comparable habitats. For example, *Cymbella tridentina* is characteristic of springs and the upper part of spring-fed streams in the Dolomites and calcareous Alps (Cantonati et al., 2010). Algae and cyanobacteria turnover can occur when the geological substratum changes, and so called 'vicariant species' replace each other. For instance, the cyanoprokaryote genera *Chamaesiphon* and *Tapinothrix* are particularly common in mountain, relatively pristine waters but *Chamaesiphon fuscus* occurs in the low-conductivity waters of igneous rocks and is replaced by *C. geitleri* in the more mineralized waters on limestones and dolostones. Analogously, *Tapinothrix janthina* occurs in low alkalinity waters on hard rocks, to be replaced by *T. varians* on carbonate rocks (e.g., Cantonati et al., 2015). The diatom *Achnanthes dolomitica* (Cantonati and Lange-Bertalot, 2006) was described from the Dolomites

(Dolomiti Bellunesi, eastern Alps, Italy) as a typical for aquatic habitats characterized by dolostone influence on their GW-flow system. The species could also be characterized as epiphytic (living on plant-like substratum, for instance on bryophytes in springs, or on vascular plants in lakes), and typically inhabiting the depth zone influenced by water-level fluctuations in lakes and springs affected by discharge fluctuations (Cantonati et al., 2012). More recently, *A. dolomitica* was found also in springs emerging from ophiolitic rocks, mainly peridotite and serpentinite (Kamberović et al., 2019), and this confirmed a supposed preference of the species for above-average magnesium concentrations.

3.3.2. Vascular plants

Some aquatic and terrestrial vascular plant species are nearly or entirely restricted to springs. For example, aquatic Texas wild rice (*Zizania texana*) occurs only along the spring-fed headwaters of the San Marcos River in Texas (Poole and Bowles, 1999). Spring-supported alkaline meadows in Ash Meadows, Nevada support several endemic plant species (i.e., *Nitrophila mohavensis* and *Zeltnera namophilum*; Beatley, 1977). Floating-mat and iron-precipitating fens in central Rocky Mountains support populations of the rare roundleaf sundew plants (*Drosera rotundifolia*; Wolf et al., 2006).

3.3.3. Invertebrates

The global list of crenobiotic invertebrates is enormous, but no comprehensive global list has, to our knowledge, yet been developed. Synopses of regional springs-dependent invertebrates include those of Williams and Danks (1991), Erman and Erman (1990), Botosaneanu (1998), Spitaler et al. (2012), and Springs Online (Springs Stewardship Institute, 2019), as well as other reviews. Among the most comprehensive analyses of crenobiont endemism and evolution is the work by Robert Hershler and his colleagues on North American Hydrobiidae springsnails (summarized in Hershler and Liu, 2017). Why the diversity of crenobiotic invertebrates so vastly outnumbers that of crenobiotic vascular plants remains unexplained.

3.3.4. Vertebrates

Rather many fish and amphibian species are springs-dependent, while numbers of reptilomorphs and higher vertebrates are relatively few. Springs dependence is abundantly evident among fish in arid regions, such as the American Southwest and central Australia (e.g., Minckley and Deacon, 1991; Unmack, 2001; Stevens et al., 2019b), but has been less intensively studied in mesic and tropical regions. Also, the role of springs in imprinting and homing of riverine and anadromous fish may be important but has received insufficient attention. Amphibians, such as the Amargosa toad, ranid frogs, and cryptobranchid hellbender salamanders often are endemic to springs or spring-fed reaches of headwater streams, and several species of garter snakes (*Thamnophis* spp.) are springs-dependent in the American Southwest (Stevens et al., 2019b). Only one bird population to our knowledge can be clearly described as springs-dependent: the southwestern USA population of American Dippers (*Cinclus mexicanus*), which nest exclusively near or behind madicolous flows in spring-fed headwater streams. In other portions of its range it nests in such habitats along higher order streams and rivers. Only a few North American mammal species can be considered crenophilic or crenobiotic, including Florida manatees (*Trichechus manatus latirostris*), which winter in the warmer waters of inland springs, and water shrews (*Sorex palustris*), which routinely forage in high elevation, high latitude spring-fed headwater streams.

3.4. Karst ecohydrogeology, limestone precipitating springs (LPS), and biocalcification

The water demands of approximately one quarter of global human population are met using GW obtained from karst aquifers (Ford and Williams, 2007). The huge practical relevance of karst aquifers, of

which decision makers and the public need to recognize, ignited, among other initiatives, the World Karst Aquifer Mapping (WOKAM) project (Chen et al., 2017). WOKAM produced a world map and data-base of karst aquifers, also including selected karst springs and caves, acknowledging that karst springs are the “entrance” to karst conduits and caves. We regard this as a prominent example of how enhanced collaboration among disciplines can improve understanding and management of karst ecohydrogeology and water supplies.

Karst aquifers and associated habitats also are relevant to regional biodiversity and ecology (e.g., Goldscheider, 2019). Species in the genus *Niphargus* (Amphipoda) are crustaceans that are endemic to individual karst springs/aquifers; e.g., Fišer, 2012). For example, the amphipod *Niphargus poianoi* was described from the evaporitic karst springs of Poiano in northern Italy (Karaman, 1988). Not only small invertebrates, but also large species can be endemic of karst aquifers (e.g., large fish in karst inland desert springs in the Arabian Peninsula; Krupp, 1992).

The structural-stratigraphic framework of the subsurface influences the hydrologic system by compartmentalizing GW flow pathways and water quality, and consequently the surface expressions of mineral spring deposits, the accumulation of which often are mediated by bio-logical activity (see e.g. Pedley, 2009; Jones and Renaut, 2010 and references therein). In this framework, calcium carbonate accumulation in Limestone-Precipitating Springs (LPS; see Cantonati et al., 2016) represents the vast majority of cases, with deposits from thermal springs commonly termed as “travertines”, and the ones originated from non-thermal springs commonly termed as “tufas” (e.g., Golubić et al., 2008; Cantonati et al., 2016).

For such situations the necessary CO₂ commonly is derived from the atmosphere and/or the soil cover (e.g., Celico et al., 2010). Nonetheless, deeper sources related for instance to hypogenic processes such as anaerobic degradation of hydrocarbons (e.g., Chakraborty and Coates, 2004) and metamorphism of carbonate rocks (e.g., Ague, 2000; Bissig et al., 2006), also represent important contributions to the development of such deposits, in which the role of the geological background appears to be even more important. A showcase example of such deep surface-subsurface interaction is represented by HC-related cold seeps detected on modern sea floor (Laming et al., 2018).

The approach used in the hydrocarbon industry for the characterisation of dual porosity-permeability reservoir systems (e.g., Spence et al., 2014), can be used to describe GW permeation in terrestrial settings. Subsurface structural-stratigraphic heterogeneity, in fact, controls the distribution and efficiency of GW flow pathways, given favourable biological, physical, and chemical boundary conditions for LPS formation at their emergence (see e.g. Pedley, 1990; Ford and Pedley, 1996; Pentecost, 2005; Pedley, 2009; Jones and Renaut, 2010, and references therein). Recently, a general, comprehensive model has been developed by Cantonati et al. (2016), by subdividing LPS on the basis of their integrated geological background. According to this classification, fracture-related contribution to permeability-porosity appears crucial, with a continuum of processes-products from gravitational to tectonic end members. In this framework, vertically persistent (deep-reaching) tectonic faults and large-scale fracture corridor systems may promote rise of hypogenic CO₂-charged GW, related or unrelated to magmatic/hydrothermal activity (thermal and non-thermal), with CO₂ likely provided by oxidation of thermogenic methane or metamorphism of deeply buried carbonate rocks (e.g., Frery et al., 2015).

From a practical standpoint, hydrogeology helps predict LPS location (Cantonati et al., 2016). This is a crucial factor considering that LPS are the only widespread spring type included in the Annex I of the Habitat Directive (EU-HD, 1992). LPSs harbour unique biota, including calcifying mosses (e.g., *Eucladium verticillatum* and *Palustriella commutata*), cyanoprokaryotes and diatoms, and, in particular, the peculiar and habitat-specific desmid microalga *Oocardium stratum*, as well as vascular plants (*Cochlearia bavarica*, Brassicaceae), midges (“chironomid tufa” inhabited by *Tanytarsus*

reissi), caddisflies (*Rhyacophila pubescens*), and even a calcium-carbonate encrusted moth fly (*Pericoma trifasciata* gr., Diptera Psychodidae) (Cantonati et al., 2016).

In light of these close relationships, LPS studies on both the modern (actual ecosystem) and ancient (paleo-spring ecosystem) counterparts, can provide insight into short-term and long-term behaviour of subsurface fluid flow. Specifically, high-resolution stratigraphy coupled with geochemical fingerprinting (major and trace elements) and stable isotope analyses (e.g., C, O, Sr) can provide crucial information when matched with other archives. By isolating “normal” baseline trends, the punctuated signal of extreme climatic and/or tectonic events (e.g., floods, earthquakes) inferred to influence GW geochemistry (e.g., mixing of different fluid sources) and flow regime (e.g., variations in transmissivity-interconnectivity of the matrix-fracture network) can be recognized and used to validate modeling of combined tectonic-climatic events in the recent geological record (Cantonati et al., 2016 and citations of examples therein).

The peculiar photoautotrophic component of LPS biota (calcifying cyanobacteria, algae-especially the desmid *Oocardium stratum*, and mosses) also offers a unique opportunity to study the complex process of biocalcification. Hydrogeology is necessary for a correct understanding of *O. stratum* occurrence in springs and spring-fed streams (mineralization level of the water), and the longitudinal development of its niche in the spring-fed streams (governed by carbon dioxide degassing) (Rott et al., 2012).

To test Pfister’s (1976) hypothesis that *Oocardium stratum* is often overlooked because it develops in a habitat type rarely visited by phycologists, Trobej et al. (2017) studied algal communities only in springs with spring-associated limestone (SAL) deposits. They found the species in 50% of the sites studied, supporting the hypothesis that this species is more common than supposed, but that it occurs exclusively in habitats with very specific hydrogeological characteristics, as described above for LPS (see e.g., Cantonati et al., 2016). This is a typical example of a biogeographic pattern that needs an ecohydrogeological perspective for correct interpretation.

4. Groundwater and GDE ecology

4.1. Groundwater-dependent ecosystems: classification

Acknowledging that the role of GW in surface ecosystems is still insufficiently understood, Kløve et al. (2011) stress the importance of developing conceptual models to explain GW-environment interactions, and identifying hydrogeology and biodiversity as key aspects of GDEs. Bertrand et al. (2011) point out that GDE classification should be primarily achieved by highlighting the ecological roles of GW, with a focus on aquifer-scale processes, emergence-scale processes, and associated biocoenoses. Eamus et al. (2016) list hydrogeological indicators and biotic assemblages among the main techniques for identifying the location of GDEs in the landscape. Stevens et al. (2019b) emphasize that the utility and disambiguation of GDE classification can be greatly improved by employing an ecohydrogeological approach.

4.2. GDEs and primary anthropogenic impacts

The dependence of GDE on aquifer status relates quantitative or qualitative impairment of the aquifer to the geochemical and ecological integrity of the associated GW, springs, and other GDEs. Kløve et al. (2011) note that GDEs also are highly threatened by a plethora of different land-use activities, as well as land use changes and climate change. Groundwater pumping often is regarded as having a direct local impact on the aquifer; however, regional impacts also may occur. If not properly designed the construction of tunnels for large-scale transportation, energy schemes (high speed railways, motorways) and subterranean hydroelectric canals can generate irreversible regional impacts on GW discharge and GDEs (Cantonati et al., 2016).

A recent and well documented case study concerns the High Speed Train line between Bologna and Florence through the northern Apennines (Italy). Between 1996 and 2009 a series of tunnels were drilled through sedimentary hard-rock aquifers, mainly represented by fractured turbiditic sandstones (Gargini et al., 2014). The tunnels, designed to lower the hydrostatic head, induced a water table drawdown over a radius of influence of up to 6 km, causing the permanent or seasonal desiccation of a number of springs and spring-dominated stream reaches. The impacts were spread throughout fault and fracture zones connecting the tunnels to the surficial discharge points (Gargini et al., 2008). Hydraulic connectivity was convincingly demonstrated through tracer tests (Vincenzi et al., 2009; 2014). Now, 10 years after completion of the railway line, tunnel drainage has reached a steady state condition, and currently acts as a large spring, showing a discharge regime consistent with the local spring outflow regime. It has been estimated that 53% of the total amount of stream base flow (700 L/s) was subtracted from natural runoff and is now discharged at a lower base level at the tunnel main portals (Vincenzi et al., 2014).

Other documented references about the impacts of tunnels against groundwater flow systems are presented in: Massoli-Novelli and Petitta, 1997; Petitta and Tallini, 2002; Masset and Loew, 2010. The first two refer to the highway tunnel through the Gran Sasso karst massif in Central Italy, while the latter refer to the hydrological effects of various tunnels drilled through crystalline and metamorphic hard rock aquifers in the Aar and Gotthard massifs (Switzerland).

These case studies emphasize that groundwater issues must not only be considered at local scales in relation to safety of drilling procedures and consolidation measures at the drilling face of the tunnel, but also at a broader spatial scale to minimize potential negative impacts on GDEs (Bertrand et al., 2011). Broader consideration and planning will provide protection and mitigation measures, such as more effective sealing of tunnels, and identify options such as sealing losing reaches of streams or creating small reservoirs to guarantee environmental flows.

4.3. Ecohydrogeological indicators and GW flow systems (indicators of hydrological discharge)

Spring-discharge changes reflected by shifts in electrical conductivity can influence spring biota. The appearance of *Niphargus* species (amphipod crustaceans) was examined in two studies in the northern Apennines (Italy): the Mt. Zirone and Mt. Prinzera ophiolite hard-rock aquifers (HRAs; Fig. SS1 in supplementary material). These isolated, km-sized ultramafite bedrock bodies are bordered and underlain by aquitard units, predominantly characterized by polygenic breccias having a fine-grained matrix (Fig. SS2 in supplementary material). Spring flow and geochemistry was monitored daily to weekly for 16 months (Segadelli et al., 2017a,b). Electrical Conductivity at 25 °C (EC) was positively related to the flow of perennial basal springs, located along the contact between ophiolite HRA and underlying aquitard (Segadelli et al., 2017a,b): EC increased with increasing flow during the charging phase (Fig. 3). In addition, depigmented, stygobiontic living specimens of niphargid amphipods, identified as *Niphargus* sp. aff. *puteanus* (Fig. SS3 in supplementary material; Bottazzi et al., 2011) appeared during discharge peaks. Correspondence between main precipitation peaks, flow-rate increases, and occurrence of niphargids is clearly recognizable in Fig. 4. Similar observations were made at a spring on Mt. Prinzera (P10 in Segadelli et al., 2017), but only during the autumnal recharge phase (Fig. 5). Segadelli et al. (2017a,b) developed a conceptual hydrogeological model (briefly summarized in SM), through which we hypothesize that links between increased *Niphargus* sp. aff. *puteanus* occurrences and EC values are due to enhanced spring flow rates, mainly caused by the arrival in the feeding aquifer of newly infiltrated waters with the consequent sudden increase in the hydraulic head. This abrupt increment and the subsequent pressure wave likely favoured mobilization of large volumes of deeper and more mineralized waters, along with the displacement of the hypogean

organisms that live in the immediate vicinity of the spring (Fig. 6).

Among the possible practical implications, this approach can provide important benefits such as: – optimization of detection, monitoring and sampling activities of hypogean fauna; – use of the measured *Niphargus* dimensions (ranging from a minimum of a few millimeters to a maximum of 8 mm) as a proxy for pore/fracture dimensions; – fast tracking of intense pulses of concentration of chemical and physical parameters that may have a significant effect on spring biota.

Based on the conceptual hydrogeological scheme outlined (Segadelli et al., 2017a,b), it is possible to assume that deep GW circulation over a hydrological year can influence the seasonal behaviour of the hypogean organisms living in the feeding aquifer, along with controlling the EC fluctuations in the associated spring waters and the possible concentrations of other chemical components present in spring waters. Such effects suggest a strong control of the subsurface structural-stratigraphic architecture on directional preferential pathways of GW flow and aquifer compartmentalization, in a way conceptually similar to the “plumbing” system developed for karst settings (see below).

4.4. Flow in karstic systems: nutrients & scenic red dinoflagellate blooms (Lake Tovel)

Lake Tovel in the Brenta Dolomites (Italy, southeastern Alps, Unesco World Heritage site) was known as being affected by red dinoflagellate blooms which ceased in 1964. This lake is characterized by a karstic drainage in the upper part of the drainage basin, and by a pseudokarstic circulation around the lake, due to the presence of a thick glacial deposit (Ferretti and Borsato, 2006). The porous nature of the upper part of the glacial rim is also the cause of marked seasonal water-level fluctuations (WLFs), and the lake has been used also as a model system for lakes affected by relevant natural WLFs (e.g., Cantonati et al., 2014a,b). Also planktic rotifer-crustacean interactions could be shown to be mainly driven by water-residence-time (Oberegger et al., 2009). This ecohydrogeological approach *ante litteram* has provided definitive confirmation that the red discolouring was due to localized inputs of nutrient-enriched GW. The spatial distribution of the bloom within the lake, and its correlation with the points of GW input into the lake (perilacustrine, mostly submerged springs), and identified using the tracers uranine and tinopal CBS-X, confirmed that the mass dinoflagellate proliferation was a localized reaction to nutrient input. This inflowing water was affected by sewage generated by cow cattle-barn management practices before 1965 (Borghi et al., 2006). The use of tracers also showed that the hydrology of the lake was dominated by GW input and flow through the lake (Ferretti and Borsato, 2006). This inspires us to reconsider this classical study site using an ecohydrogeological perspective, considering it primarily in relation to GDE interactions.

5. Phreatophytes and phytoscreening

5.1. Ecophysiology of phreatophytes and water-table depth and fluctuations

The clear relationship between phreatophytes and GW depth and discharge has long been known in arid and semi-arid regions (e.g., Nichols, 1994; Stevens et al., 2019a). For regions with more humid climate such relationships are less obvious and have been studied more recently. Several studies bear mention. Batelaan et al. (2003) used phreatophytic vegetation to calibrate numerical GW models and Loheide et al. (2005) investigated the methods of White (1932) to analyze well hydrographs to estimate GW consumption by phreatophytes. The roots of these species reach to and into the water table, and can cause daily oscillations of the water-table depth, data on which can be used to estimate water consumption. Study of a Kansas riparian system demonstrated that maximum depth of phreatophyte roots depends on maximum water-table depth, confirming the value of a GW hydrology perspective (Butler et al., 2007; Nippert et al., 2010). At

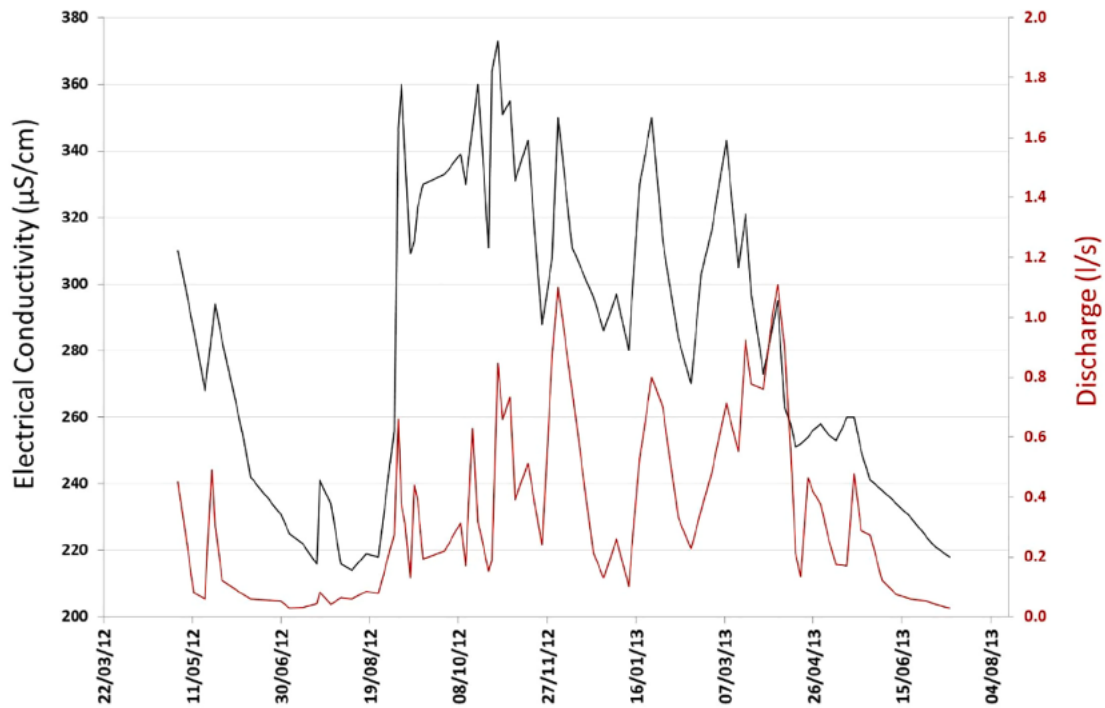


Fig. 3. Example of flow hydrograph (red line) of a basal perennial spring monitored in the Mt. Prinzeria area (P03 in Segadelli et al., 2017a,b) showing discharge rates vs. time variations of the electrical conductivity (black line).

some sites, subsurface strata with water-retaining capability ensured the permanence of water in the vadose zone during water table subsidence, while shallow aquifers dominated by sand and gravel could be entirely drained by phreatophyte water uptake. The hydrogeology of those sites thus is crucial for understanding of phreatophyte distribution and development. Surprisingly not only plant-physiologists but

also ecohydrologists have not given much attention to daily water-table oscillations, which are an excellent proxy of phreatophyte activity (Butler et al., 2007). Also, invasive plant species, such as the salt cedar (*Tamarix ramosissima* × *chinensis* hybrids), in the American Southwest can rapidly shift water sources in response to water-table declines, and thus minimize water stress during drought periods. Unfortunately,

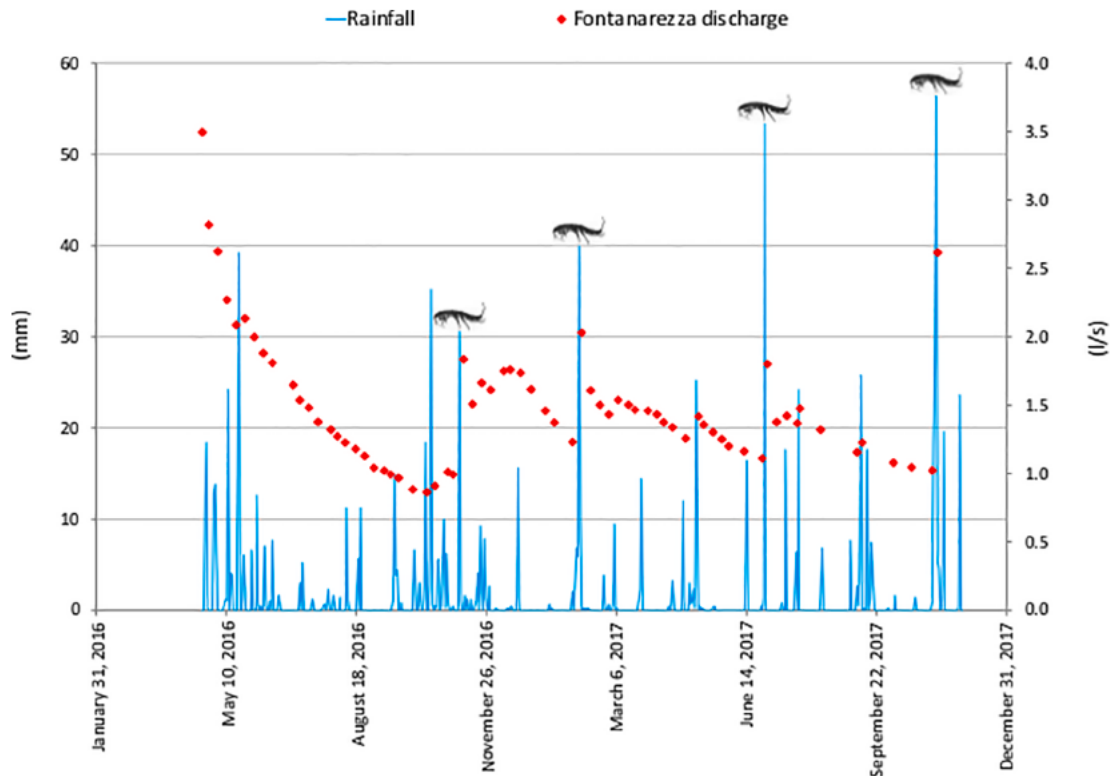


Fig. 4. Flow rate (red dotted line), *Niphargus* occurrences, and precipitation data (blue bar histogram) obtained from the basal spring (Z04), monitored in the Mt. Zirone area (Fig. SS4 in supplementary material).

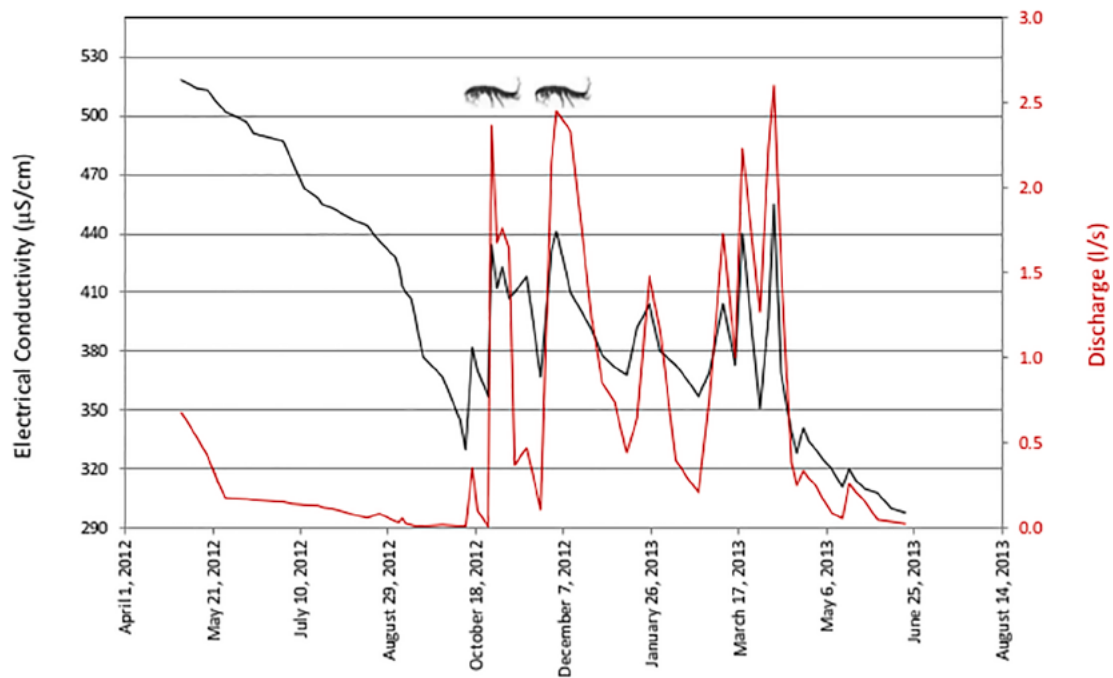


Fig. 5. Flow-discharge rate (red line) and electrical conductivity (black line) temporal variations in a basal perennial spring monitored in the Mt. Prinzera area (P10 in Segadelli et al., 2017a,b) and *Niphargus* occurrences.

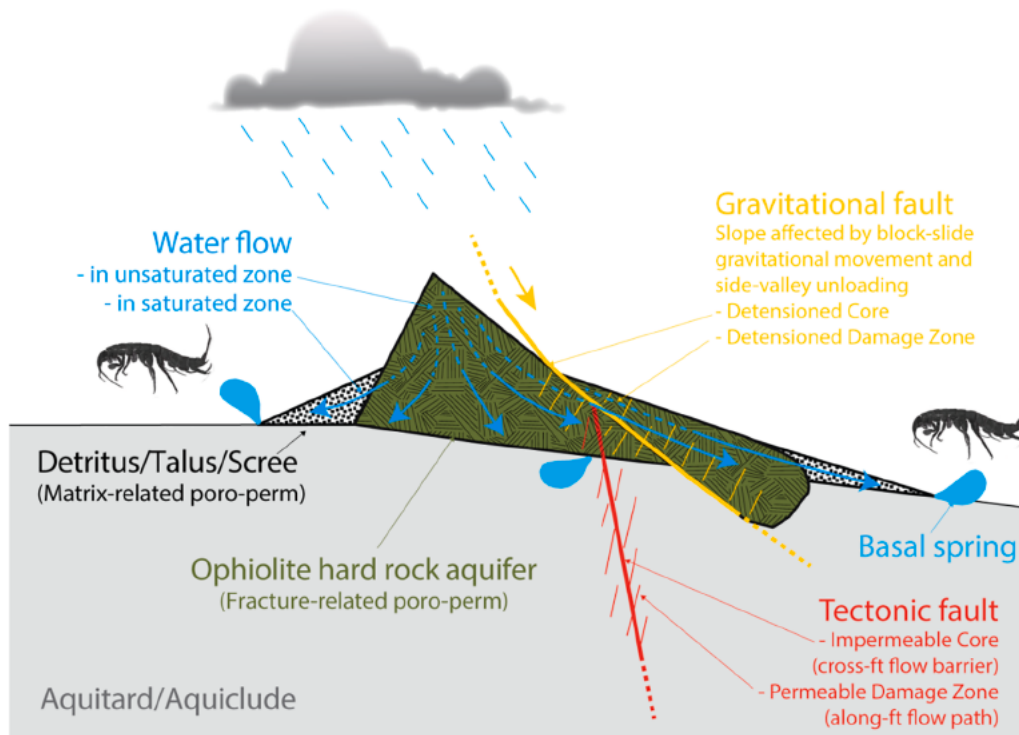


Fig. 6. Conceptual representation of the hydrostructure of a faulted and fractured hard-rock aquifer with location of the springs discussed for the *Niphargus* case study (Segadelli et al., 2017a,b).

many native southwestern Salicaceae and other riparian tree and shrub species have little capacity for such changes.

Stevens et al. (2019b) reported that fluvial southwestern riparian plant species were stratified by stage due to xylem water potential (Ψ_p) physiology and the depth to the riverine water table. Wetland species consistently had higher midnight and mid-day Ψ_p , while riparian species except *Tamarix* spp. had somewhat lower Ψ_p , upper riparian zone *Prosopis* and *Senegalia* had low Ψ_p , and adjacent desert upland taxa had

the lowest Ψ_p values. Such findings indicate that the ecophysiology of phreatophyte assemblages can serve as accurate indicators of shallow aquifer depth and change.

5.2. Phytoscreening as an indicator GW quality

In the past few decades, trees have been used as biondicators of environmental pollution (Vroblesky, 2008). As trees transpire GW,

many dissolved constituents are translocated, thus the plant works as a passive sampler of GW chemistry and contamination (Burken et al., 2011; Limmer et al., 2014). A variety of compounds from subsurface contamination can be taken up by plant roots, including heavy metals and volatile organic compounds (VOCs), such as BTEX and chlorinated hydrocarbons (e.g., Algreen et al., 2014; Algreen et al., 2015a; Vroblesky, 2008). Besides the well-known application of phytoremediation, the ability of trees to assimilate pollutants also is exploited for GW quality screening or monitoring (i.e. phytoscreening and phytomonitoring; Sorek et al., 2008). Underground contaminants transferred into trees are generally detected using minimally invasive techniques, such as trunk core samples or, less frequently, branch or leaf samples (e.g. Duncan et al., 2017; Gopalakrishnan et al., 2007).

Duncan and Brusseau (2018) reviewed a large number of previous studies on phytoscreening in sites contaminated by chlorinated ethenes (CEs) and reported a linear correlation between tree and shallow GW contaminant concentrations where the roots interact directly with contaminated GW. A much poorer correlation was found for deep GW contamination, even though CEs in trees were associated with GW contamination down to 19 m below the surface (e.g., Vroblesky et al., 2004; Sorek et al., 2008; Duncan et al., 2017). Recent work shows better correlation between tree and soil (Struckhoff et al., 2005), as well as between trees and soil CEs gas concentrations (Yung et al., 2017; Wilson et al., 2018), suggesting a new potential application of phyto-screening for vapour intrusion risk assessment (Burken et al., 2011; Algreen et al., 2015b; Wilson et al., 2018). The literature about phyto-screening in sites contaminated by metals and BTEX is sparse compared to that for CEs. Algreen et al. (2014) suggested that a linear correlation between metal concentrations in soil and trees may exist above a certain concentration threshold. To the best of our knowledge, correlations between GW and tree concentrations of metals or BTEX have yet to be investigated. Further research is needed to improve prediction on the use of phytoscreening for quantitative assessment of GW contamination. However, the technique has been proven effective on a qualitative level.

Among major applications from the literature, phytoscreening was used to: (1) detect unknown GW contamination (e.g., Sorek et al., 2008); (2) integrate the information from traditional hydrogeological investigations in remote locations (e.g. Holm and Rotard, 2011; Wilcox and Johnson, 2016); (3) date contamination events (e.g. Yanosky et al., 2001); (4) perform long term GW monitoring in sites of monitored natural attenuation or phytoremediation (e.g. Gopalakrishnan et al., 2007; Larsen et al., 2008); (5) detect contaminant degradation based on the concentration ratio between parent and daughter compounds (e.g., Limmer et al., 2011; Vroblesky et al., 2004).

6. Mutual gains and challenges in combining ecological and hydrogeological approaches

The existing terminology in ecohydrogeology already is too complex and divisive (e.g., hydro-geo-ecology, Zanini et al., 2018; hydroecology, ecohydraulics, limnogeology, etc.).

Reviewing palaeolimnology, Juggins (2013) appropriately asked if reconstructed variables are also ecologically important. GW-SW interactions science has focused on the interfaces between rivers and aquifers.

However, we think that combining hydrogeology with ecology, and choosing the most straightforward term to define those interactions are worthwhile. If these disciplines can agree on the definition of ecohydrogeology we recommend here, this broad field of research should be offering a promising theoretical framework for dealing with GW-associated ecosystems, habitats, and organisms (Fig. 7).

To further exemplify what we consider an ecohydrogeological approach, we provide two recent examples from the literature. Grover (2019) studied the relationships between GW levels, SW levels, and the distribution and habitat use of cyprinid fishes in a large spring complex,

and found that temporal variation of SW levels was almost completely (97%) explained by GW levels, that populations of both species studied became more fragmented as GW and SW levels declined, and that long-term reductions of shallow GW levels exceeding 40 cm eliminated most spawning and juvenile habitats. Similarly, Fuchs et al. (2019) compared ponderosa pine (*Pinus ponderosa*) dendrochronology between paired trees growing at or away from northern Arizona springs. They reported faster growth and greater ring complacency among trees living at springs as compared to those occurring in nearby upland habitats, and suggested that such relationships could be used to more closely examine and model climate-GW relationships and springs perennality in relation to this economically-relevant forest conifer.

Among the mutual gains to be obtained by combining ecological and hydrogeological approaches, we identify the following:

- Unique opportunities to identify and determine ultimate determinants of ecological and ecosystem patterns, processes, and constituent elements;
- Hydrogeology can provide GDE ecology with a more deeply grounded understanding and predictive modeling of habitat resilience;
- Biology can provide new indicators (“tracers”, “bio-assays”) for and from hydrogeology.

Among the main challenges to this physical and biological discipline integration, we recognize:

- Barriers due to disciplinary attitudes, habits, lexicons, and networking;
- The tendency to work in disciplinary isolation (e.g., SW versus GW sciences);
- Funding for multi-disciplinary research requires multi-disciplinary review panels;
- Difficulties in collaboration among non-multi-disciplinary fields;
- More complex education, skill sets, and working attitudes needed for more effective physical-biotic ecosystem integration and synthesis.

7. Conclusions: it is time for integrated ecohydrogeology

We demonstrate here that ecohydrogeology represents an important new form of integrated research, that springs ecosystem and socio-cultural functions are fundamental to societal well-being, and that springs ecosystem ecology is too complex to be understood from a single-discipline context. Thus, we propose here a strongly integrated, interdisciplinary approach, one based on synergistic hydrogeological and ecological principles, one that is needed to study the environmental interactions of GW-dependent organisms, assemblages, habitats, and socio-cultural systems. Deeper understanding of GDEs will only be possible with due consideration given to collaborative interactions among the fields of hydrogeology and ecology.

It is our opinion that the integrated approach represented by the term ecohydrogeology has so far been only been used timidly in GDE research, in particular without a clear, formal definition. This concept holds great promise for many useful future applications, as we have demonstrated with emblematic case studies and emphasized the following explicit definitions:

Ecohydrogeology: The unifying, synthetic scientific field integrating the approaches of ecology and hydrogeology in the study of groundwater-related ecosystems, habitats, organisms, and socio-cultural processes to advance understanding, stewardship, and policy.

Ecohydrogeological indicator: 1) a hydrogeological parameter that may greatly enhance in-depth understanding and modelling of species distribution and autecology, as well as assemblage

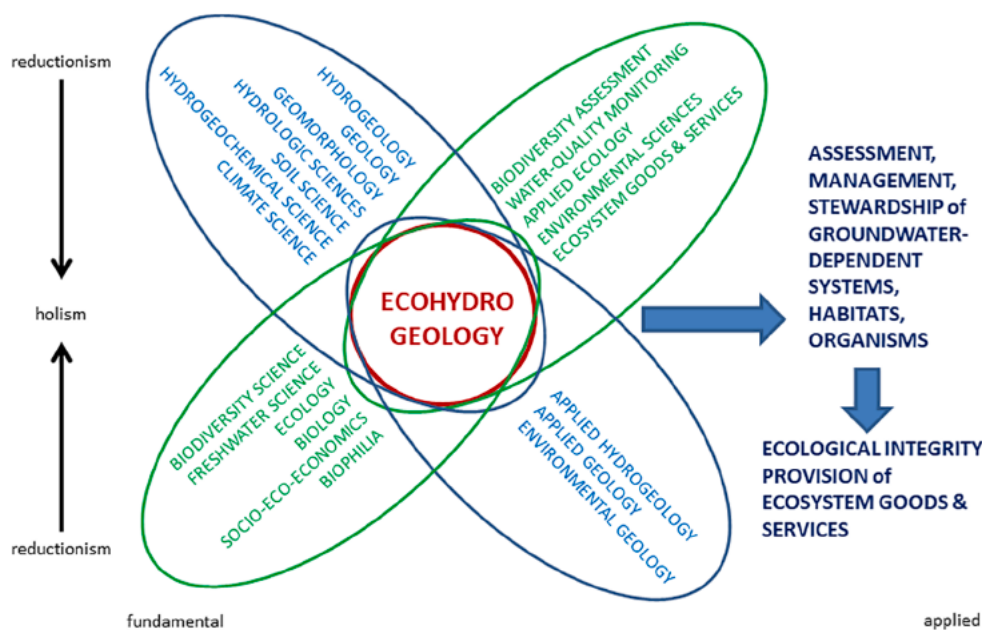


Fig. 7. The scientific domain of the unifying, integrative, multi-disciplinary field of ecohydrogeology and its applied consequences.

composition and drivers; and 2) a taxonomic or biocenotic parameter that may serve as a strong indicator, and even a tracer, to infer variables and parameters of hydrogeological interest.

The key topics we identified in ecohydrogeology overlap with many EU, Australian, and USA environmental high priority topics, policies, and socio-cultural issues, including at least two United Nations Sustainable Development Goals.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.105803>.

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