Published in Hydrogeology Journal 20, 5-25, 2012
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Review: From multi-scale conceptualization to a classification system for inland groundwater-dependent ecosystems

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Abstract Aquifers provide water, nutrients and energy with various patterns for many aquatic and terrestrial ecosystems. Groundwater-dependent ecosystems (GDEs) are increasingly recognized for their ecological and socio-economic values. The current knowledge of the processes governing the ecohydrological functioning of inland GDEs is reviewed, in order to assess the key drivers constraining their viability. These processes occur both at the watershed and emergence scale. Recharge patterns, geomorphology, internal geometry and geochemistry of aquifers control water availability and nutritive status of groundwater. The interface structure between the groundwater system and the biocenoses may modify the groundwater features by physicochemical or biological processes, for which biocenoses need to adapt. Four major types of aquifer-GDE interface have been described: springs, surface waters, peatlands and terrestrial ecosystems. The ecological roles of groundwater are conditioned by morphological characteristics for spring GDEs, by the hyporheic zone structure for surface waters, by the organic soil structure and volume for peatland GDEs, and by water-table fluctuation and surface floods in terrestrial GDEs. Based on these considerations, an ecohydrological classification system for GDEs is proposed and applied to Central and Western-Central Europe, as a basis for modeling approaches for GDEs and as a tool for groundwater and landscape management.

Keywords Groundwater-dependent ecosystem · Ecology · Western-Central Europe · Conceptual models · Aquifer-biocenosis interface

Introduction

Groundwater flow systems are increasingly recognized for their ecological value as reflected in regulations such as the Swiss Water Protection Ordinance (GSchV 1998), the Western Australian Guidance for the Assessment of Environmental Factors (EPA 2003), the Habitats (92/43/EC, 1992), Water Framework (2000/60/EC) and Groundwater (2006/18/EC) European directives (European Parliament 1992, 2000, 2006), and the Krakow declaration (IAH 2010). In addition, ecosystems requiring groundwater are of special interest from a socio-economic (supply of goods and services) perspective (see Danielopol et al. 2004; Boulton et al. 2008; Tomlinson and Boulton 2010). Ecosystem goods (e.g. production of fishes) and services (e.g. flood controls) are the conditions and processes through which biotopes and biocenoses help sustain and fulfill human life (see Brinson 1993; Daily et al. 1997; Millennium Ecosystem Assessment 2005).

Groundwater has ecological roles within aquifers and in ecosystems located close to the discharge zone or water table, referred as groundwater-dependent ecosystems (GDEs). Dependence can range from obligate to facultative. Obligate dependence means that species presence requires continuous, seasonal or episodic groundwater access, whereas facultative dependence implies that absence does not lead to adverse impacts to the biocenoses (see Eamus et al. 2006). Some reviews dealing with the ecological function, structure and classification of aquifer ecosystems already exist (e.g. Gibert et al. 2005; Goldscheider et al. 2006; Hahn 2009). In contrast, there is a lack of a systematic overview covering the high variability of flow and ecological processes in epigean GDEs with respect to the structuring of landscapes and the

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integration of knowledge from hydrogeology and ecology (Humphreys 2006). From a hydrogeological point of view, groundwater systems are mainly viewed as fluxes of water, heat and chemical compounds. From an ecological point of view, groundwater is a milieu (biotope) featured by environmental conditions (e.g. variability of water temperature and nutrients) in which fauna and flora (biocenoses) adapt and interact. The combination of these two points of view should enable clarification on how biodiversity depends on the extent, source and movement of groundwater and how variations of quality and quantity affect groundwater-dependent biodiversity (Stanford and Ward 1992; Danielopol et al. 2003, 2004, 2008; Hahn 2009; van der Kamp 1995; SKM 2001; Brown et al. 2007, 2010; Younger 2007; Hahn 2009).

To clarify these points, GDEs first need to be delineated in the landscape (Table 1). GDEs may belong to wetlands, which are defined as areas of land saturated with water long enough to promote wetland or aquatic processes. They are featured by poorly drained soils, hydrophytic vegetation or various kinds of biological activity which are adapted to a wet environment (National Wetlands Working Group 1997). In addition, some GDEs may look like terrestrial systems, but groundwater located close to the surface may ensure their viability (Cowardin et al. 1979). These definitions cover numerous morphologic, hydrologic and ecologic types of emergences, i.e. interfaces between aquifers and biocenoses. A given aquifer may sustain several springs, rivers, or peatlands which do not present same ecohydrological processes.

Therefore, the purpose of this review is to evaluate the hydrogeological, morphological and biological factors controlling the ecological roles of groundwater. In a first step, the spatio-temporal variability of aquifer and landscape scale processes affecting groundwater dependence of ecosystems will be synthesized. Secondly, the various kinds of aquifer-biocenosis interfaces, and their functioning will be presented on the basis of both hydrogeology and ecology literature. This permits the development of hydro-ecological conceptual schemes. Finally, on the basis on these schemes, a typology for inland GDEs dealing with relevant aspects of groundwater and ecological heterogeneity is proposed, aiming to help GDE identification and management.

Landscape and aquifer scales: flow systems and ecosystem responses

The location of GDEs within a landscape is influenced by groundwater flow patterns which control the locations of the water table and emergences in the landscape. Groundwater flow patterns are in turn controlled by the topography, the structure of the subsurface, climatic conditions and land uses. Toth (1963) conceptualized groundwater movements as hierarchical flow systems (Fig. 1): local flow systems occur relatively close to the surface, i.e. from a higher elevation recharge area to a directly adjacent discharge area such as a stream or spring (typically at 100 m to 1 km scales). Intermediate (one or more topographic highs and lows may be located between recharge and discharge areas) and regional flows (recharge corresponds to the water divide and the discharge occurs at the bottom of the basin) reach to a greater depth and extend over a greater distance. GDE biocenoses not only depend on the mere emergence of water at a location but also on the temporal variability of the water supply and the quality of discharging groundwater, which are both related to aquifer/landscape processes. In the following, the controlling factors of these two parameters and their effects on GDE characteristics are synthethized.

Supply of water

The main ecological attribute of groundwater is the hydroperiod (Eamus and Froend 2006; Eamus et al. 2006; Hahn 2006), controlled by climate, geology and land use of the catchment (Alfaro and Wallace 1994). Perennial discharge is defined by a year-round continuous

Table 1 Criteria to determine the groundwater dependence of an ecosystem

Target	Criterion	Type of ecosystem	Potential indicators
(1) Ecosystem	Terrain not affected by high water table or excess surface water. If affected, it is only for short periods	Non wetland	Hydrophytic, phreatophytic or aquatic vegetation and processes do not exist
	Terrain affected by high water table at, near or above the land surface	Wetlands and “deepwater habitats” → (2)	Terrain is saturated for sufficient time to promote wetland or aquatic processes
(2) Wetland and “deepwater habitats”	Wetland receiving water exclusively from precipitation and not influenced by groundwater	Ombrotrophic wetlands	Topographically elevatedAcid pH*Sphagnum*-dominated vegetation
	Wetland receiving water rich in dissolved elements	Minerotrophic wetlands and “deepwater habitats” → (3)	Located in topographic depression.Electrical conductivity, pH and/or anion/cation contents
(3) Minerotrophic wetland and “deepwater habitats”	Water source provided uniquely by surface run-off	Surface water dependent ecosystems	Geological settings of watershed
	Water source provided at least partly by groundwater	Groundwater-dependent ecosystems	Geological settings of watershed. Evidence of groundwater arrival (springs, alluvial settings, etc.)

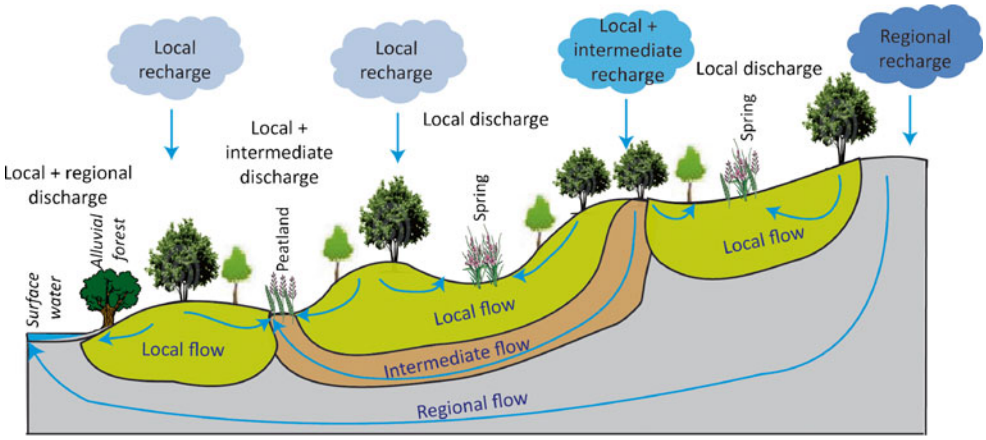

Fig. 1 General description of groundwater flow system (adapted from Toth 1963). Not to scale

source, even during low flow periods. In contrast, non-perennial (intermittent, periodic) outlets dry up, either regularly (climatic control), or irregularly (spates; Meinzer 1923). Variability of groundwater discharge depends on groundwater flow scale, climatic conditions and aquifer type. Granular and fissured aquifers usually show more stable flow conditions than discontinuous (e.g. karst) aquifers (Alfaro and Wallace 1994).

Water regimes constrain abundance and diversity of biocenoses. Morphological and functional plasticity allow some plants to overcome extremes in water regime (e.g. Robe and Griffith 1998; Sraj-Krzic and Gaberscik 2005) and successfully grow in water or on dry land (Nicol et al. 2003). In contrast, submerged and emerged macrophytes were less abundant as they have a lower tolerance to drying out and to prolonged floods, respectively. Benthic communities within temporary aquatic systems have been found to differ from those within nearby perennial systems. Biota with low dispersal abilities and long generation times are expected to be more common in permanently flowing springs (K-strategists, according to Mac Arthur and Wilson 2001), whereas strong dispersal ability (r-strategists) are favored in non-permanent discharge habitats (Erman and Erman 1995; Smith and Wood 2002; Smith et al. 2003). The identification of taxa preferring ephemeral or permanent flow sites can therefore potentially indicate flow permanence (Scarsbrook et al. 2007). However, other site specific conditions such as current and stability of sediments likely intervene (Lenat 1983).

Supply of nutrients and temperature conditions

Variability of flow is particularly important when associated with changes in water quality and temperature (van Der Kamp 1995). Dissolved or suspended elements in groundwater have to be viewed as potential nutrients which impact the productivity in springs (Cantonati et al. 2006), rivers (Vannote et al. 1980), lentic systems (Cooper et al. 1998) or terrestrial GDEs (Sanchez-Perez and Tremolières 2003). The flux of nutrients and heat reaching GDEs varies as a function of the type of groundwater flow systems. In granular and fissured aquifers, usually only dissolved nutrients arrive and concentrations are relatively stable. Sometimes, in some granular aquifers, vegetation and especially wood may be buried, providing a residual source of organic matter. In contrast, in karst aquifers, particulate matter can reach emergence points during high flow events and concentrations and temperature can strongly fluctuate (Goldscheider et al. 2010). Similarly, average temperature and through-year variability are controlled by the geometry of the flow system. Temperature variations result from either shallow flow near the spring or from rapid infiltration and flow. In shallow aquifers, temperature varies close to the mean annual air temperature of the recharge area. Usually GDEs are inhabited by stenotherm species i.e. species adapted to quite narrow ranges of temperature (Van der Kamp 1995).

Bryophytes and macrophytes located at the groundwater emergence constitute good indicators of the long-term nutritive role of groundwater (Cantonati et al. 2006). They are the first to be influenced by the groundwater chemistry and constitute the basis of the trophic chain. Moyle (1945), Hutchinson (1970) and Seddon (1972) exhibited relationships existing between hardness of water and repartition of given plant species. A higher hardness ratio ($([Ca^{2+}]+[Mg^{2+}]/[Na^{+}]+[K^{+}])$ was associated with higher diversity by Seddon (1972) in rivers. Numerous studies (e.g. Garbey et al. 2004) grouped species among dystrophic, oligotrophic, mesotrophic, eutrophic or polytrophic categories. Combining hardness ratio, total dissolved solids and electrical conductivity, Haslam (1987) evaluated the favored nutrient level for broadly spread macrophytes in European rivers. This kind of evaluation is currently refined for various systems, e.g. for springs (Strohbach et al. 2009). Thus, the catchment surface use and the buffering capacity of bedrock and surrounding soils may be considered as drivers controlling the repartition and diversity of plant species in GDEs.

In parallel, Tessier et al. (1981), Chambers et al. (1992), Boar et al. (1995); Schneider and Melzer (2003) and Schneider (2007) indicated that the role of sediments such as sapropel or gyttja (Gobat et al. 2004), in which plant roots settle, is of great importance because they are an additional source of nutrients. Flow velocity, physical stress, nature and texture of a substrate also constrain habitat structures of groundwater emergences (Brinson 1993; Stevens and Springer 2004; Dahl et al. 2007; Springer and Stevens 2009). Consequently, while large-scale groundwater flow patterns and aquifer characteristics control the location of GDEs and some of their features, their characteristics and functioning also depend on the detailed morphology of the aquifer-GDE interface. Therefore, the effect of emergence morphology on the physical and chemical patterns of the interface between the groundwater system and biotopes need to be evaluated to better understand how biocenoses deal with groundwater fluxes.

Role of the aquifer-GDE interfaces

Several types of aquifer-GDE interfaces can be distinguished: groundwater–atmosphere (springs), groundwater–surface water, groundwater–organic soils (peatlands) and groundwater–terrestrial (mineral) interfaces in alluvial systems (Fig. 1). In the following, the main processes shaping the biocenoses of these systems at the local scale are discussed as a basis for classification of GDEs.

Spring ecosystems

The spring habitat structure affects current velocity and substrate texture in the crenon zone, where physicochemical parameters are mainly inherited from the spring (Erman and Erman 1995). Steinmann (1915) and Thienemann (1922) defined limnocrene springs as depressions filled by water, rheocrene springs as rapid current discharge zones and helocrene springs as diffuse discharge zones, often associated with a peaty zone (Cantonati et al. 2006). These interfaces have specific ecological features, similar to those of peatland systems. Springer and Stevens (2009) recently enlarged this typology by including "hillslope springs" and "hanging gardens" where groundwater emerges from hillslopes (30–60° slope) or vertical cliffs.

The variability of spring forms affects physical features such as velocity, turbulence and turn-over time of emerging water, but little information is available about the effect of flow in crenon zones (Janauer and Jolankai 2008). Most available studies were carried out at rivers and assumed that ecological features vary gradually along a continuum between high velocity and low current streams. As the literature on physical conditions in springs is relatively scarce, some terms, concepts and observations provided by such environments can partly be applied to spring ecosystems.

Bornette et al. (2008) hypothesized that species able to survive in high-flow conditions harbor specific phenotypes and/or reproduction ways and provide examples of the effect of physical conditions on biocenoses patterns. Thus, the plant size, form and stand structure, together with the strength of its stems and method of anchoring, constrains its presence to a specific physical environment. For example, species with deep roots and a high root/shoot ratio are expected to have a higher resistance than species with low root/shoot ratio. In addition, "phenoplastic species" are able to adapt their physiology or morphology in response to variations in environmental conditions (Riis and Biggs 2003; Garbey et al. 2006) such as *Myriophyllum spicatum* which is able to adapt to the increase of current by stem elongation (Strand and Weisner 2001). Through a quantitative approach, Chambers et al. (1991) showed that stream velocities>1 m/s would inhibit or prevent macrophyte growths. However, some species can adapt to higher velocities. In mountainous areas, mosses seem to dominate in springs because of their strong attachment on rocks, their limited height (limiting hydraulic forces), and because they tolerate desiccation and low temperature (Cantonati et al. 2006 and references therein). Reproduction mechanisms can also change as a function of flow conditions. Dawson (1976) and Garbey et al. (2004) observed that *Ranunculus sp*. (e.g. *Ranunculus peltatus*) flowers (sexual reproduction) when current velocity is lowest. During high flow, vegetative dispersion through fragmentation dominates.

Spring habitat type also influences the composition of macrozoobenthic assemblages (Cantonati et al. 2006; Mori and Brancelj 2006). Discharge dynamics affect the substrate composition, which influences the diversity and nature of macrozoobenthic communities (ecologic, phenotypic and genotypic adaptations). Von Fumetti et al. (2006) demonstrated that detritivores dominate in low current conditions with abundant leaf litter, whereas mostly grazers are found in high current conditions where periphyton (algae and microorganisms) may grow on exposed substrata.

Sediments are the major source of nutrients to aquatic macrophytes in flowing waters (e.g. Schneider and Melzer 2003). Along the continuum between running (rheocrene) and low gradient (helocrene, limnocrene) springs, the decrease in grain size is also associated with an increase of organic material (Cantonati 1998). Assuming that knowledge about surface water ecosystems can be transferred to springs, a reasonable hypothesis would be that the presence of fine sediments (sand, silts) near low-flow springs favors macrophyte growth because of easier root settlements and higher nutrients availability of primarily nitrate and phosphorus. Biocenoses not only depend on the spring morphology but can also influence it. Vegetation located near the groundwater outlet may reduce water velocity, raise the water level in the channel and on the adjacent land by increase flooding and overland spill and enhance the deposition of suspended sediments (Pitlo and Dawson 1993). Metabolism and life cycle of both producers and consumers are also able to significantly modify the water chemistry, e.g. by uptake of compounds or by concentration due to evapotranspiration leading in some places to the modification of the habitat structure through precipitation of minerals (Schade et al. 2004). During periods of high photosynthetic activity, high pH levels may be reached (Jorga and Weise 1977; Spencer and Bowes 1993;). The magnitude of the impacts on chemistry through biological processes will likely depend on water renewal. Turbulence effects may also favor degassing which impacts the chemical conditions (e.g. pH) of the crenon zone. Cantonati (1998) found that while pCO_2 and $[SiO_2]$ were higher in helocrenes (soil respiration and alteration), pO_2 was lower than in rheocrenes. Investigations on chemical patterns induced by the balance between roots respiration, photosynthesis and water turn-over still need to be carried out in order to be precise about the ranges in which these processes affect spring biodiversity.

Surface water GDEs

Groundwater is important to lotic (flowing waters) or lentic (e.g. lakes) systems if it has a significant contribution during low-flow periods (Brown et al. 2007). Groundwater reaches rivers or lakes through hyporheic or hypolentic zones (HZ), i.e. the space below the surface-water bed and adjacent banks that contain some proportion of channel water (White 1993; Winter 2001). Hyporheic and hypolentic processes are sensitive from hydrological, biochemical and biological points of view (Gibert et al. [1990] used the term of "elasticity").

In HZs, groundwater mixes with surface water in various proportions depending on the hydraulic conditions of the bed material and on the hydrologic situation (loosing, gaining or flow-through water body). Hydraulic conditions are inherited from hydromorphological processes (aggradation, degradation) which shape the bottom and reaches of surface waters into highly complex systems (see Bravard and Gilvear 1996; Huggenberger et al. 1998). High permeability channels may cross low permeability zones favoring high fluxes or allowing more diffuse groundwater discharge (Dahl et al. 2007). In rivers, at the reach scale, up and downwelling of groundwater may be governed by discontinuities such as obstacles which protrude from the river bed (e.g. log jam), changes in the direction of flow, pool-and-riffle sequences, and meanders (Fig. 2) (Brunke and Gonser 1997; Huggenberger et al. 1998; Malard et al. 2002), allowing groundwater discharge even when the channel tends to lose water. In lakes, hypolentic exchanges are usually less favored due to the presence of fine-grained and highly decomposed organic sediment on the bottom. However, groundwater/surface-water interactions may be favored around the lake perimeter where waves can remove fine-grained sediments (USGS 1999).

Groundwater and surface-water mixes provoke sharp changes of chemical concentrations in HZs (Hancock et al. 2005). Surface water is often rich in oxygen and organic matter but contains lower concentrations of inorganic compounds than groundwater. Consequently, the HZ can be considered as a chemical reactor where two reactants meet (Fig. 2) and as a sink for organic nutrients derived from the catchment and the floodplain, as well as a source of nutrients (organic and inorganic) for the river. Much of the subsurface water in a floodplain is repeatedly interacting with the stream and thus is not pure groundwater, but hyporheic water.

Reactions are facilitated by bacteria and geochemically active sediment coatings (see Williams and Hynes 1976; Boulton et al. 2010). Aerobic species may completely use up oxygen at some distance into the streambed, and then may be replaced by organisms adapted to or specialized for hypoxic conditions. These processes affect the movement of nutrients and contaminants between groundwater and surface water. The rate at which organic contaminants biodegrade in the HZ can exceed rates in stream water or groundwater away from the stream (Boulton et al. 1998; Storey et al. 2004; Soulsby et al. 2009). The flux dynamic depends considerably on the porosity and permeability of the sediments (Youngson et al. 2004; Environment Agency 2009) and can be influenced by clogging. Clogging potentially also reduces living space for large invertebrates. Colmation is caused by intensive erosion, linked with landuse at the catchment scale. Even if water quality is good, those waters will never reach the 'good' ecological conditions required by the European Water Framework Directive (2000/60/EC; European Parliament 2000). Consequently, hyporheic processes likely change at the seasonal and inter-annual scale due to hydrologic variability (current conditions, suspended matter content; Malcolm et al. 2004; Steube et al. 2009).

The ecological value of the HZ has been recognized for several decades (e.g. Pollard 1955; Hynes 1983), but the key drivers controlling HZ biodiversity are still being discussed (e.g. Ward et al. 1998; Hayashi and Rosenberry 2002; Datry et al. 2007; Boulton et al. 2010). It seems that these drivers vary in function of implied taxa. The HZ is mainly inhabited by invertebrates (mainly crustaceans and insect larvae), including stygobites (hypogean groundwater specialized), stygophiles (epigean animals preadapted for subsurface life) or stygoxene (accidentally present in the subsurface). Stygobites are readily distinguishable through traits such as reduction of eyes, lack of pigment, small size, elongated shape and reductions of setae in comparison to epigean species (Ward et al. 1998). Some studies (Ward et al. 1998; Storey et al. 2004) indicate that sediment size and morphology of the river bed mainly impact hyporheic assemblages because exchange processes differ strongly when comparing fine- and coarse-sediment stream areas. Accordingly, on the vertical axis, the fauna consists largely of oxyphilous (needing O_2) species (mainly epigean) in superficial sediments, whereas deeper sediments harbor more hypoxic tolerant species. On the horizontal axis, the effect of river-bed morphology is important. An example would be the zones behind dams, where groundwater seepage is favored (see Fig. 2), and where biocenoses should be preferentially dominated by hypoxia tolerant species, particularly stygobites. This results in mosaics of hydrological and ecological patches, each having a particular faunal composition. This was the basis for the qualitative model of Plénet et al. (Plénet et al. 1995) which identifies the areas of groundwater dependence: in downwelling zones, the HZ is dominated by an epigean community, and in upwelling zones (GDEs), hypogean and peculiarly stygobites should dominate. Since the alternation of downwelling and upwelling zones

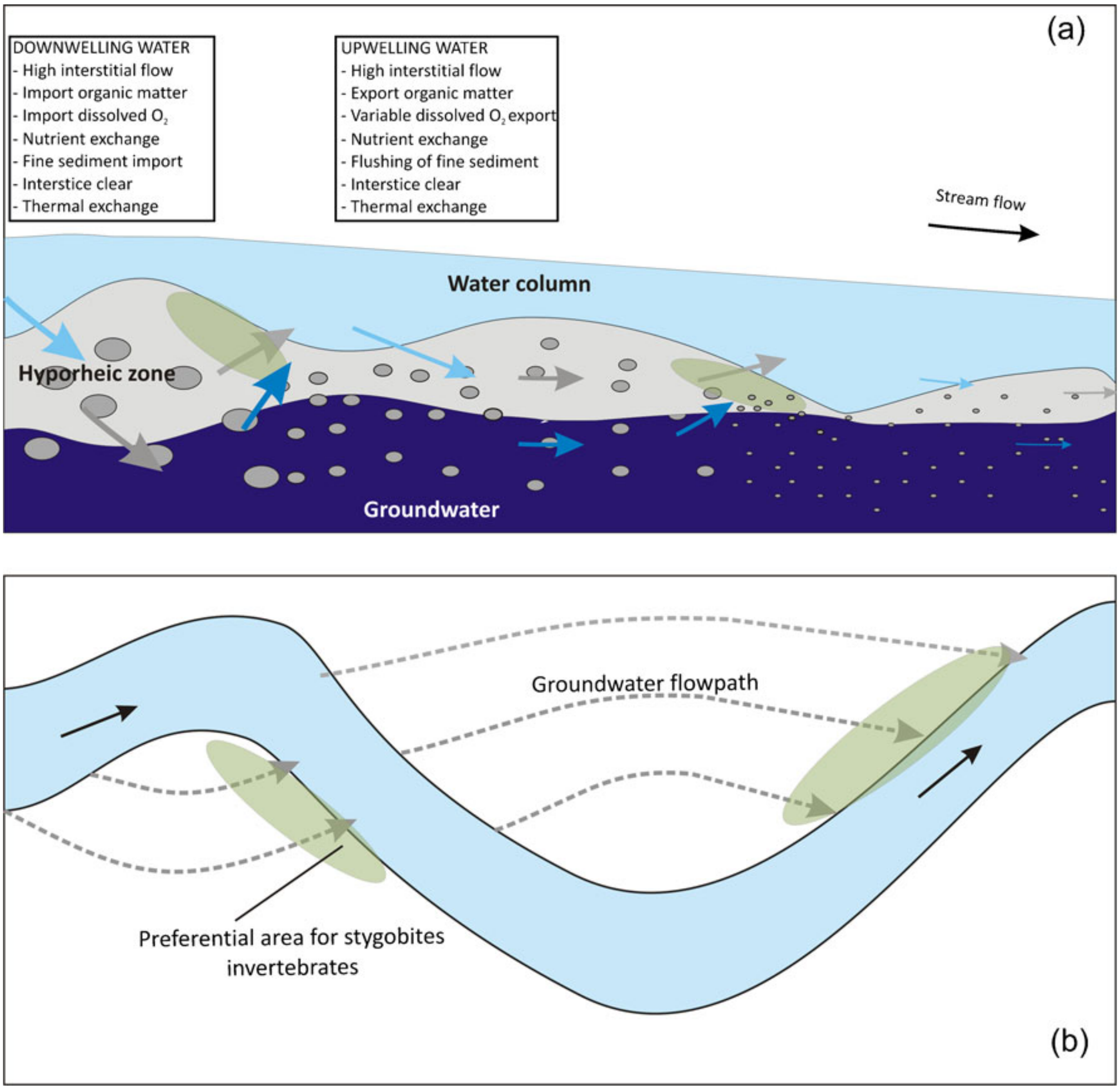

Fig. 2 Conceptual scheme of hyporheic zone (HZ) functioning (adapted from Environment Agency 2009 and Boulton et al. 2010). **a** Lateral view: effect of streambed topography, distribution and size of sediments which influence hydraulic conductivity and extent of vertical hydraulic gradients. *Light blue, grey and dark blue arrows* respectively indicate water flows coming from surface, hyporheic or groundwater compartments. **b** Viewed from above: effect of channel form. *Dashed arrows* represents groundwater flow lines. These patterns impact fluxes of groundwater and chemicals to the HZ

promotes the ecological richness of the whole surface-water systems (Ward et al. 1998), Kasahara et al. (2009) recently provided a practical extension of these considerations by proposing solutions that take account of groundwater/surface-water connectivity, mainly aiming to increase the effect of variability of river-bed morphology (e.g. meanders, dams) and sediment texture.

The HZ is also a preferential location for spawning fish, e.g. salmonids that lay their eggs within gravel. Ova survival is dependent on complex surface-groundwater-metabolism interactions (Environment Agency 2009; Malcolm et al. 2009). It seems that equilibrium between surface water (providing oxygen) and groundwater contributions (providing thermal stability) needs to be reached. In some cases, such thermal stability may be ensured by shading riparian vegetation.

Nilsson et al. 2002 and Jansson et al. 2007 indicate that surface water reaches with a strong groundwater discharge favor an enhanced plant biodiversity. These trends could be explained by (1) a lower drought stress along the hydrological year; (2) higher nitrate concentration in groundwater (e.g. Pinay et al. 1990) due to anthropogenic impacts and aerobic microbiological degradation of organic matter in soils (Sanchez-Perez and Tremolières 2003) or aquifers (Goldscheider et al. 2006). Moreover, even if groundwater has low nitrate concentration, high discharge may imply greater nutrient fluxes due to high fluxes of water. This process may provide a steady source of nutrients for plants (e.g. Jansson et al. 2007). Therefore, considering that the HZ can be viewed as a chemical reactor promoting transformations, rich vegetation should be considered as an indicator of upwelling hyporheic water rather than pure groundwater, i.e. water that has been enriched by nutrients coming from biotransformation of organic material and promoting plant fertilization.

In addition, as mentioned previously, upwelling of groundwater may be enhanced by the increase of current velocity in the HZ through flushing or piston effects (especially behind dams or in meanders). Note that a higher flow velocity becomes a limiting factor due to mechanical stress for anchoring (e.g. Chambers et al. 1991). Hence, surface flow partly controls the nutritive role of groundwater and the availability of habitats (Fig. 3). Moreover, as plants may provide refuge and food for macroinverterbrates, further consumed by fishes, the current velocity impacts the whole trophic web of surface water including areas near groundwater discharges.

The impact of these processes is currently being investigated in detail (Mulholland and Webster 2010; Boulton et al. 2010). The recent technological innovations such as continuous logging sensors for oxygen (Malcolm et al. 2009) and temperature (Hoehn and Cirpka 2006; Vogt et al. 2010) during in situ monitoring of HZs over prolonged periods, and their representation in three dimensions in numerical models (Poole 2010), will probably permit a better understanding of these systems.

Peatland GDEs

Peatlands form where soil-water saturation retards the decomposition of organic matter, allowing it to accumulate. Peatlands may be supplied by rainwater, surface water and groundwater whose proportions depend on their position in the landscape, surrounding geology (terrains permeability) and maturity of the ecosystems (Mitsch and Gosselink 1993; National Wetlands Groups 1997; Euliss et al. 2004). Minerotrophic peatlands (usually referred as fens/marshes, swamps) are mainly fed by surface water or groundwater. Ombrotrophic (rain fed) peatlands (called bogs) are located closer to recharge areas and/or are featured by a sufficient peat accumulation (mature systems), which prevents some groundwater or surface water uses. In the following, hydrologic and chemical variability and the influence of the peaty interface on the ecological roles of groundwater are discussed.

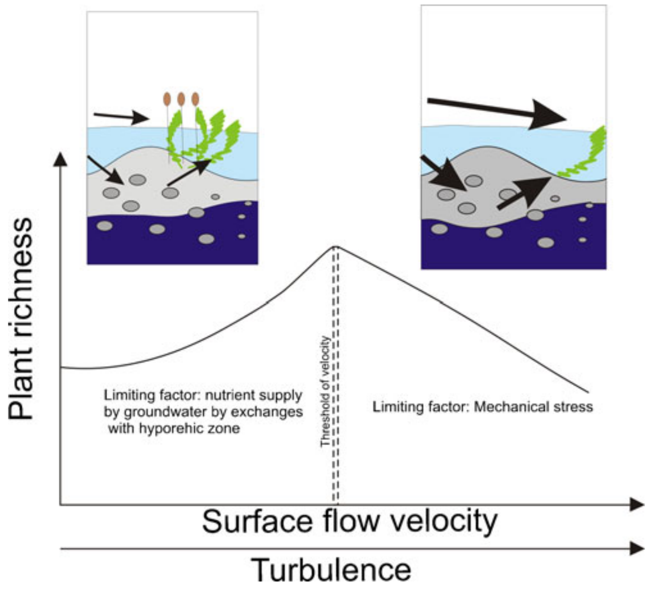

Fig. 3 Conceptual scheme of the impact of current velocity on plant richness in surface-water bodies fed by groundwater (After Chambers et al. 1991; Nilsson et al. 2002; Jansson et al. 2007; Franklin et al. 2008)

Peatlands biocenoses survival depends on the constant humidity that is strongly related to specific hydraulic features of peat. Firstly, organic soils in peatland ecosystems have lower bulk densities and higher water-holding capacities than mineral soils (Price 1992; Mitsch and Gosselink 1993). Secondly, hydraulic conductivities typically decrease with depth from the least decomposed upper layer (acrotelm) to the more decomposed lower zone (catotelm)—Boelter (1965); Fraser et al. (2001); Price et al. (2003); Ronkanen and Klove (2005). Variations in hydraulic structure with depth are due to the progressive decomposition and homogenization of peat through centuries and millennia. Resulting preferential flow is through or over the relatively permeable upper layer of the acrotelm during high flows. The high specific yield in the near-surface layers allows efflux with a relatively small drop in the water table (Mitsch and Gosselink 1993). When low flow occurs, water is retained longer and remains accessible for plants (Fig. 4). This inertia is a key factor for maintaining wet conditions close to surface in case of temporal water level decrease. Therefore, in peatland GDEs, the water availability period may diverge from the supplying groundwater system hydroperiod. It has to be noted that the acrotelm and catotelm can merge because of homogenization of humidity conditions if groundwater frequently saturates all the peat (Gobat et al. 2004).

From a nutritive point of view, the long-term calcium content of water may largely explain the ecology of peatlands (Tahvanainen 2004; Hajek et al. 2006). Focusing on groundwater dependent peatlands, poor to moderately rich systems should be significantly fed by crystalline (igneous, metamorphic) aquifers or may use rainwater. In contrast, extremely rich and calcareous fens are usually fed by calcareous aquifers. These latter are delineated by the fact that *Sphagnum* mosses cannot grow and that carbonate saturation is reached. Beyond the effect of aquifer lithology, calcium richness depends also on aquifer-scale features (recharge, scale of the groundwater system; internal geometry, land use) which influence the degree of groundwater mineralization.

However, intra-annual hydrologic variability of aquifers in addition to high cation exchange capacity and redox processes occurring in the peaty interface may provoke secondary temporal/seasonal changes on the peat-water nutritive status (De Jong 1976; Whigham and Simpson 1976; Verhoeven et al. 1983; Shotyk and Steinmann 1994; Gogo et al. 2010). When the water table is low, precipitation, which is naturally acid (e.g. Bertrand et al. 2008), can saturate exchange sites with

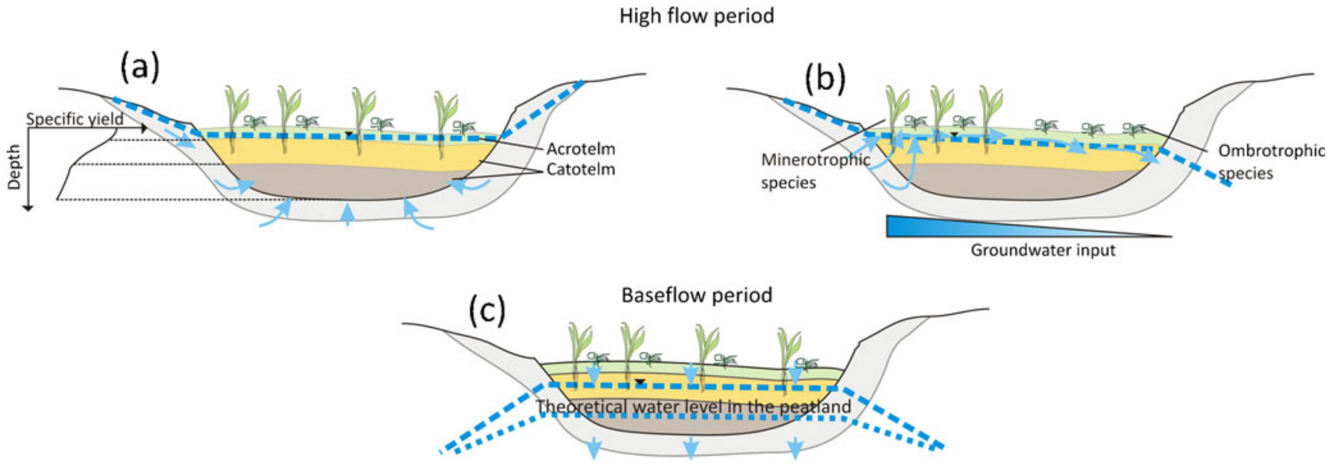

Fig. 4 Conceptual schemes of the hydrologic patterns in the peat-interface fed by groundwater. **a** High flow period for a homogenous groundwater-fed peatland. **b** High flow period for a system locally fed by groundwater; water-table level will vary as a function of hydrological conditions but also as a function of peat material hydrodynamic properties. These heterogeneities may lead to a cohabitation of ombrotrophic and minerotrophic species (see the text). **c** Baseflow period. The high specific yield of peat mat layers may sustain wet conditions and water availability near the surface

hydrogen ions. When the water table rises, the cationic exchanges between groundwater and peat should be significant. After saturation, no more significant exchanges occurs, and the peat water chemistry is likely similar to the groundwater input (Fig. 5a). The effect of cation exchange on peat water chemistry is therefore dependent on the arriving groundwater salinity (Fraser et al. 2001). It could be of primary importance in highlands where arriving groundwater cation concentrations are low, due to short flowpaths. These patterns should also be modified by drying and evaporation as this influences the peatlands' water budget and hence the amount of groundwater influence compared to other sources (e.g. meteoric waters).

In parallel, the prolonged inundations of soil result in anaerobic conditions, which lead to the modification of nutrient bioavailability, especially Fe^{2+}, NO_3^-, SO_4^{2-} and PO_4^{3-} (Fig. 5b). Peatlands can be described as a coupling of redox reactors. An oxidized (aerobic) layer is present near the surface and there is a deeper

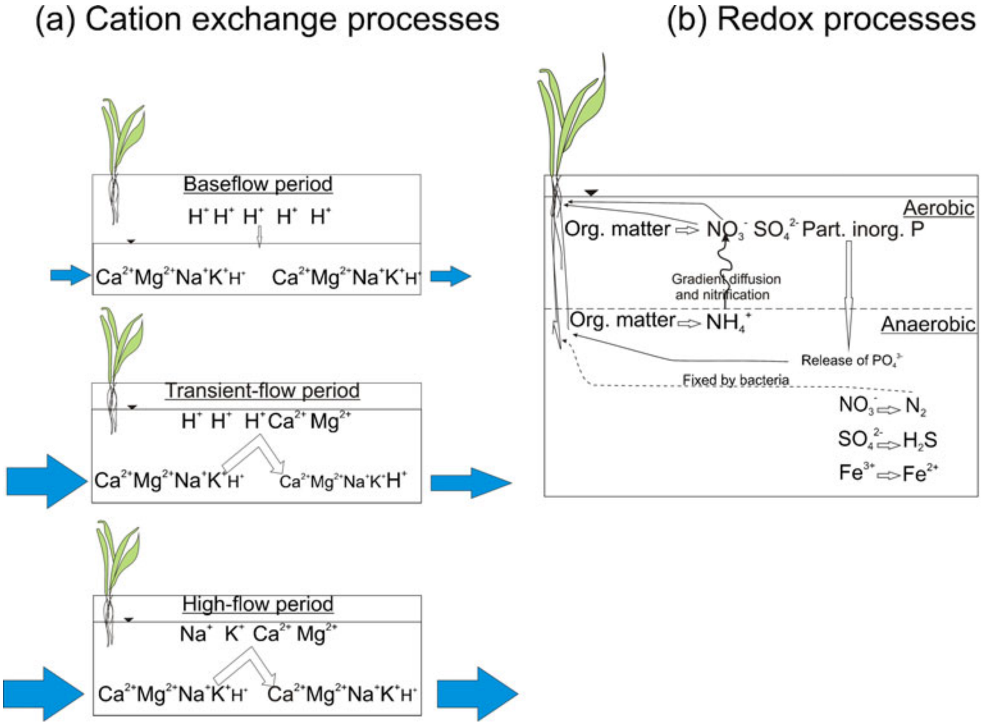

Fig. 5 **a** Conceptual scheme of the effect of cation-exchange capacity of peat on groundwater chemistry during the hydrological year. Character font sizes are related to the concentrations of chemical elements. **b** Effect of redox conditions on the groundwater chemistry and the nutrient bioavailability (adapted from Mitsch and Gosselink 1993 and Jacks and Norrström 2004)

anaerobic layer. After O_2 reduction, further reductions lead to nitrate conversion and then Fe^{2+} forms from Fe^{3+}. As Fe^{3+} is one of the main binding elements for phosphate, this leads to enhanced availability of phosphate ions for plants (Mitsch and Gosselink 1993; van Loon et al. 2009). At the same time, ammonification provokes an increase of NH_4^+ which can reach the surface by upward diffusion, due to concentration gradients between reduced and oxidized layers. NH_4^+ will be further mineralized to nitrate. These patterns are influenced by the aquifer-scale processes constraining groundwater chemistry (in particular initial Eh, pH and ionic contents) prior to peat seepage. The localization of groundwater discharges may also modify the aforementioned abiotic patterns (van Loon et al. 2009) and the uses by adapted plants (Malmer et al. 2003). Peatland forms (in depressions, on slopes) may favor or reduce groundwater circulation (Novitzki 1979; Mitsch and Gosselink 1993; Brinson 1993; National Wetland Working Group 1997) or modify the balance between precipitation and groundwater. These patterns may be modified by anthropogenic activities, e.g. lowering of the water table leads to the oxidation and mineralization of organic soils, which strongly affects vegetation.

Peatland GDEs harbor flora which are adapted to specific redox conditions and which vary along a Ca-poor to Ca-rich gradient. Even if some peatbog specialists (e.g. *Sphagnum* mosses) can be found in moderately rich systems, calcium becomes probably toxic for them over a certain threshold (Andrus 1986; Hajek et al. 2006). Thus *Sphagnum*, where it is dominant, can be used as an indicator of ombrotrophic conditions (Table 1). In contrast, species tolerating higher concentrations (considered in the following section Proposed classification of GDEs) do not show higher calcium bioaccumulation and are able to keep superfluous calcium out (Malmer 1986). In a given peatland, competitive strategies and growth performances may also modify ecological and hydrological features in complex ways (Fig. 4). Malmer et al. (2003) found that by expanding, *Sphagnum* moss structures the plant community by depleting the rhizosphere of nutrients, which tends to increase the peat accumulation. If vascular plants, in obtaining a sufficient supply of mineral nutrients through groundwater, are able to maintain a level of productivity, they may be able to prevent an increase in peat by limiting the growth of *Sphagnum*. This sustains the groundwater-dependence of the system.

These elements show that the term ‘ecohydrology’ is peculiarly adapted with respect to peatlands. Peat is produced by living parts of ecosystems while its production depends on hydrology which in turn is modified by the ecological conditions at the emergence scale. Gobat et al. (2004) pointed out this particularity by using the term “biogeocenose” to describe peatlands. These specificities should be taken into account for classifications and long-term management programs.

Terrestrial GDEs

Terrestrial GDEs are located where groundwater is shallow (root system in contact with the water table), from several centimeters to meters and are mainly found on alluvial systems. Upstream, the root depth tends to be significantly higher than mean groundwater level and in this case riverine forests should be independent from the functioning of river-alluvial aquifer complexes. However, depending on the geology and hydrological regime, the lateral rocky aquifers beside the valley may provide groundwater to riparian forest. Downgradient, with the mean river slope diminishing, the surface is closer to the water table and reaches are periodically flooded. The extent of alluvial plains increases. The periodicity of floods (controlling aggradation and degradation processes), the nature of the alluvium (which depends on erosion process at the catchment scale), the occurrence and form of meanders, dams and cut-off channels, and the groundwater depth, constrain the repartition of vegetation (Vannote et al. 1980; Pinay et al. 1990; Ward et al. 2002; Bornette et al. 2008). Therefore, characterization and conceptualization of terrestrial GDEs should take into account longitudinal, lateral (related to particle-size distribution and geochemistry of the terraces and flood frequency) and vertical dimensions (related to granulometry profile and groundwater level fluctuations) of the fluvial hydrosystem (Amoros and Petts 1993; Ward 1998; Lyon and Gross 2005; Derx et al. 2010).

From a spatial point of view, the combination of general groundwater depth, granulometry and flood frequency gradients leads to a general gradient of humidity and water dependency by riparian vegetation. The combination of the humidity gradient with plant physiology is the basis of a geomorphic-floristic continuum model from riverbeds to floodplains (Kovalchik and Chitwood 1990; Fig. 6). The hydroriparian zone includes the low-flow channel and the main channel where hydrophytes grow. The mesoriparian zone comprises frequently flooded, moist to wet fluvial surfaces (such as stream banks), active floodplains and overflow channels where helophytes (plants whose roots are located in saturated media), including softwood trees (e.g. *Salix sp.*), are located. The xeroriparian zone is located where hardwood trees (e.g. *Fraxinus sp.*) are able to uptake water from deeper within the aquifer. This general and idealized lateral gradient at the floodplain scale is more complicated in the field because depressions, high levees and abandoned channels (oxbows) produce an undulating surface across the floodplain (Lyon and Gross 2005). Lentic systems can occur periodically or perennially, as a function of the groundwater level. From an ecological point of view, along temperate European rivers, depressions are colonized by species adapted to long hydroperiods, whereas the levees and ridges may contain species that also occur in upland areas, even in xeric (i.e. arid) ones. Consequently, woody alluvial species may occupy a broad range of humidity (Reed 1988; Schnitzler 1997).

Flood processes, groundwater level and soil hydrodynamics beneath the alluvial forest influence the vegetation types and nutrient cycles. The lateral and vertical heterogeneity of hydraulic conductivities of the soil

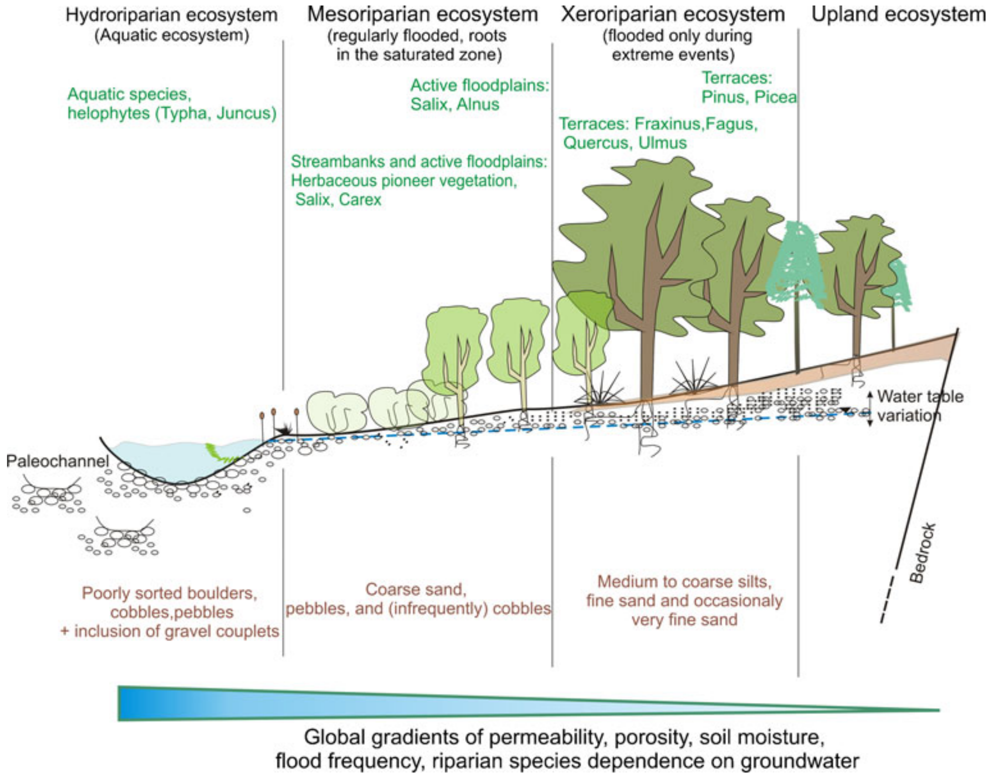

Fig. 6 Lateral and vertical zones of riparian ecosystems. Some characteristic vegetation genera are indicated according to some general phytosociological studies carried out in Europe (e.g. Delarze and Gonseth 2008)

interface should contribute to a patchiness of nutritive conditions (Ward 1998). Conceptually, alluvial floodplains can be considered as pulsed systems (Junk et al. 1989; Tockner et al. 2000; Steiger et al. 2005; Krause et al. 2007; Schnitzer-Lenoble 2007) (Fig. 7a). The main nutrient sources are the litter or the allochthonous organic material brought by surface water during floods (pulse) which then infiltrates vertically. These elements could also be provided through bank filtration during high-flow periods but the trend of groundwater to be reduced tends to limit this phenomenon in its lateral extension (Sophocleous 2002; Sanchez-Perez and Tremolières 2003). The soil texture impacts the rate of water and nutrient transfer from the surface to the groundwater. Nitrification, denitrification, cation and phosphate retention on colloids and calcium phosphate precipitation influence bioavailability (Sanchez-Perez and Tremolières 1997, 2003; Schade et al. 2004; Lyon and Gross 2005). Pinay et al. (2000) showed that below a threshold of 65% content of silt and clay, riparian and floodplain soils do not present significant denitrification rates. This could be related to the oxygen availability during the water's vertical transfer. Long wet periods favor nitrate reduction and limit nitrification. Consequently, as for groundwater-fed peatland, groundwater abstraction may have nutritive impact altering spatio-temporal patterns of reduction and oxidation processes.

The soil structure may favor capillary rise of groundwater and could be a key driver for water usage by plants (Chimner and Cooper 2004). This phenomenon may be accompanied by the hydraulic lift (Caldwell et al. 1998; Fig. 7b). Hydraulic lift occurs in two steps: during the day, transpiration provokes a decrease of root water potentials in comparison to saturated and unsaturated parts of the ground, and the water passes from soil to roots; during the night, reduced transpiration allows xylem water potential to rise above soil water potential in drier soil layers, which leads to a reverse flow from roots to soil. Its effect on groundwater flowpaths has been demonstrated, including in temperate climate areas (Caldwell et al. 1998; Chen 2007). There are many implications of groundwater physical and biotic uplifts, including chemical modification (mixing, change of redox conditions) of the surface water input, nutrient acquisition, facilitation of neighboring plants with shallow roots systems (Dawson 1993) or prolongation of activity (growth and solute uptake) during drought conditions. This means that even when the water table is deep, groundwater may indirectly be used by terrestrial ecosystems if pedological (alluvium capillary potential) and ecological (presence of trees with deep root systems) conditions are favorable.

These long and short-term adaptations have implications at community and ecosystem scales and also from a hydrologic perspective by contributing to water (evapotranspiration) and chemical (uptake) cycling. Groundwater use by terrestrial ecosystems is constrained by (1) dynamics of the adjacent river compartment, (2) stream order, in particular in mountains because riparian ecosystems are not inevitably on alluvium but may be on rocky edges of the river, (3) river style (e.g. braided, anasto-

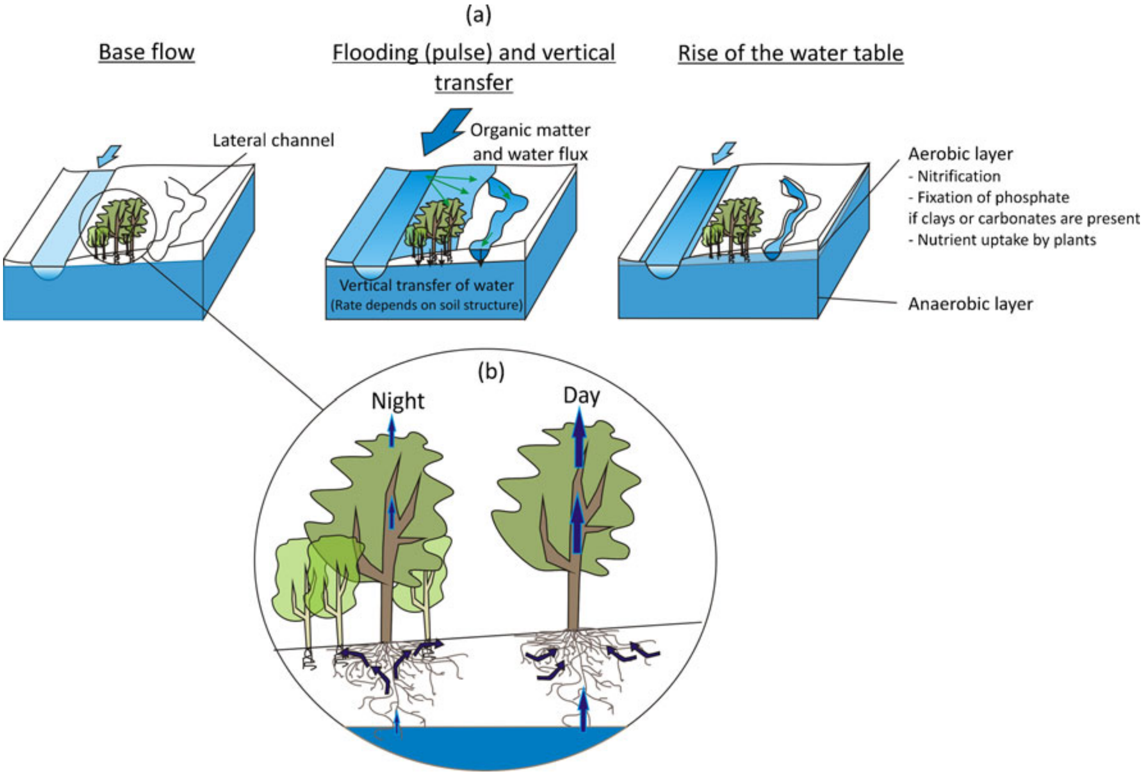

Fig. 7 **a** Conceptual scheme of multiscale water movements in the alluvial plain. At the flood plain scale, the surface water supplies the flood plain with organic matter, water and oxygen, which permit the mineralization of nutrients and the further uptake by plants during the growing season. **b** Patterns of water flow through the root system may lead to a hydraulic lift at the plant scale: during the day, water is absorbed from all depths in which soil moisture is available; at night, when transpiration is reduced and plant water potential rises, water moves from moist soil through the root system to drier soil layers. This hydraulic lift may sustain water supply of neighbor plants (adapted from Schnitzler-Lenoble 2007 and Caldwell et al. 1998)

mosed, meandering; Steiger et al. 2005) and (4) the plant water-use spatio-temporal variability (Krause et al. 2007), depending on the forest stage (pioneer, mature) and type (mesoriparian, xeroriparian).

The knowledge of these processes is useful in assessing the potential groundwater use by other terrestrial ecosystems that are still poorly investigated such as epikarst areas. The epikarst can constitute a perched aquifer which is storing substantial quantities of shallow groundwater (e.g. Perrin et al. 2003; Pronk et al. 2009), sensitive to land use (e.g. Zhao et al. 2010) and harboring rich and diverse subterranean life (Pipan 2005). The ecological role of epikarst water for terrestrial and aquatic ecosystems still needs to be studied in detail.

Proposed classification of GDEs

GDE functioning depends on the dynamics and chemistry of groundwater and the morphology of outlets. These parameters have been proven to be useful in providing a classification scheme for wetlands, of which some examples (although the list is not exhaustive) are summarized in Table 2. Cowardin et al. (1979) focused on salinity regimes, water permanency, pH, and soil material. Brinson (1993), Euliss et al. (2004) and Davies and Anderson (2001) highlighted that the geomorphic settings (type of emergence, position in the watershed), in combination with the hydrological regime and water movement, may help to distinguish a wetland's type and function. The Canadian National Wetlands Working Group (1997) focused on the source of water and on the form of the wetlands (e.g. basin, slope, etc.). Hajek et al. (2006) proposed a typology of fens by using acid-alkaline and fertility gradients determined through indicative species. The proposed classification aims to be a useful complement to the existing typologies.

In this proposed classification, pedological, morphological, hydrological and nutritive factors are combined. The general scheme of the typology is shown in Fig. 8. Water chemistry is simplified to the pH range as it is sensitive to total mineralization, hardness and alkalinity and has been used in the classification of other ecosystems (Moore and Bellamy 1974; Wheeler and Proctor 2000; Tahvanainen 2004; Naqinezhad et al. 2008). At the emergence scale, morphology and/or pedology are generally described, because they give information about the physical environments of GDEs, both on short and long-term scales and may also constrain nutrients availabilities. These distinctions lead to several GDE denominations. Ecosociologies (mainly plant associations) that can be found in European GDEs are presented, including indicative species. It has been argued that lists of "charismatic" species are very useful for answering questions about

Table 2 Parameters used in some published wetland classification schemes and equivalent parameters used in this paper

References cited in the text	Parameter used	Example	Equivalent in this paper for GDEs
Cowardin et al. (1979)	Type of system	Marine, estuarine, riverine	Included as the interface type in Fig. 8
	Type of flooding	Permanent, intertidal	Hydrological conditions or hydroperiod in all tables
	Type of substrate	Unconsolidated bottom	Pedological characteristics (Tables 4 and 6)
	Modifiers	pH, salinity	
Brinson (1993)	Geomorphic settings	Slope, domes	Geomorphological characteristics (Tables 3 and 4)
	Origin of water	Precipitation, surface waters, groundwater	
	Hydrodynamics	Vertical fluctuations, unidirectional flow	
Canadian National Wetlands Working Group (1997)	Type of soil	Mineral/peat	Included as the interface type in Fig. 8 and at a lower scale as pedological characteristics (Tables 4 and 6)
	Origin of water	Ombrotrophic, minerogenous i.e. surface or groundwater sources	
	Form	Slope, basin	Geomorphological characteristics (Tables 3 and 4)
	Type of vegetation	Graminoids, trees	Biotic characteristics (Table 5)
Davies and Anderson (2001)	Geomorphic-hydrologic conditions	Depression, channeled water flow	Included as the interface type in the Fig. 8 and at a lower scale in the Table 4 for HZ
	Origin of water	Ombrotrophic, minerogenous	
	Gross form and topography	Flat, Concave	Geomorphological characteristics (Tables 3 and 4)
	Microtopographic features	Presence of pools	
Euliss et al. (2004)	Hydrologic relation to atmospheric water	Drought, deluge	
	Hydrologic relation to groundwater	Recharge area, discharge area	
Hajek et al. (2006)	Fertility gradient	Bryophytes, nutrient-requiring forbs and grasses	
	pH tolerance gradient	Acid tolerant species, calcicole species	Included in all tables in ecology columns

function and hydrogeological processes (Brinson 1993; Hajek et al. 2006; Pellerin et al. 2009; van Loon et al. 2009) and to assess the effects of hydrochemical changes in ecosystems (Rhode et al. 2004; Brewer and Menzel 2009). Previous ecological studies (Aeschimann et al. 2004; Cantonati et al. 2006; Hajek et al. 2006; Delarze and Gonseth 2008) or databases (Corinne Biotope 1991) were used. Finally, considering the climatic requirements of biocenoses (based on mean temperature and continentality, e.g. Dierkman 1997), the main biogeographic areas (described in the Habitats Directive 92/43/EC, European Parliament 1992) inhabited by ecosociologies are mentioned according to the EUNIS database (European Environment Agency 2010). This mainly considers Western-Central Europe and excludes the Steppic, Black Sea, Anatolian and Arctic biogeographic areas.

Spring habitats (Table 3) are usually colonized by specialized species preferring permanent humidity and

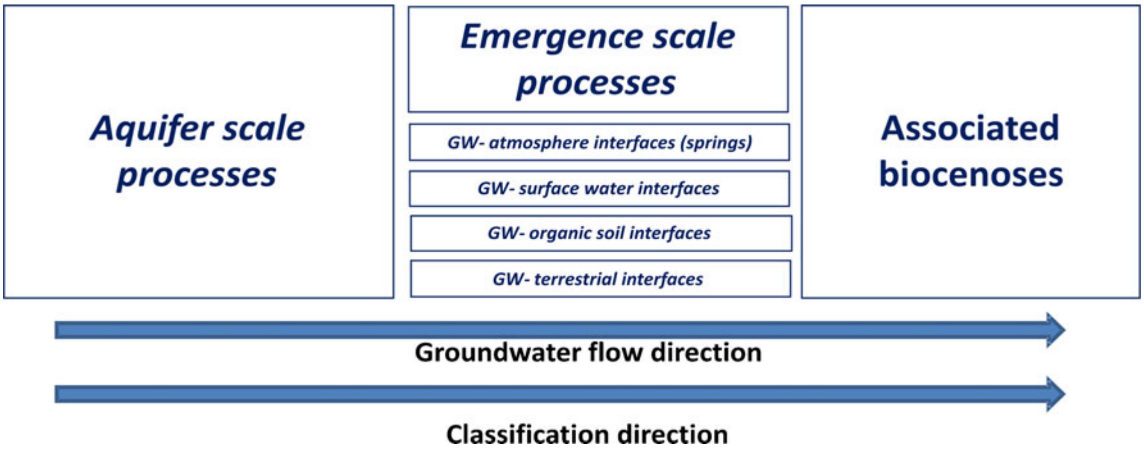

Fig. 8 Conceptual scheme of the proposed classification of GDEs (*GW* groundwater)

stable temperature. Interfaces are defined as helocrene, rheocrene, limnocrene, cliffs and hillslopes. Mosses are often dominant and more useful than higher plants for the ecological classification of spring sites (Cantonati et al. 2006). If the average temperature is sufficient, some specialized ferns may occur. Angiosperms are represented by stenotherm families. The second factor is the calcareous content of water which also constrains pH of water and which is a determinant for plant settlement in springs. The phytosociology of calcareous springs (permanent and non-permanent alkaline spring ecosystems) is featured by *Cratoneuron* alliances. Along the elevation gradient, the mountain association *Cratoneuretum commutati* is replaced by the *Cratoneurion decipiens* alliance (several associations) in the subalpine zone and then the *Cratoneuretum falcati* alliance in the alpine vegetation zone. Plant communities on siliceous substrate (hardwater or acid spring ecosystems) are more variable, and the typical alliance is *Cardamino-Montion*. On cliffs, only humid calcareous rocks (cliff spring ecosystems) with gentle groundwater seepage may be colonized by *Adiantion* alliance. No specific ecosystem has been recognized for siliceous cliffs. *Petasition paradoxi* is often found near the foot of rockslides (colluviosols) or fans (fluvisols; Baize et al. 2009) that can be supplied during glacier or snow melts (Periodic spring ecosystems). These phytosociologies are typical of groundwater emergences. However, one should keep in mind that numerous springs may be inhabited by species also occurring in rivers or lakes. Ecologists usually classify these systems as river, lake or humid meadow ecosystems, because they are adapted to similar conditions (e.g. temperature, presence of water). This situation may occur in karst environments where surface morphology is diverse. In this case, hydrogeologists have to identify the existence of groundwater emergence to rate these systems as GDEs. Phytosociologies possibly associated with these situations are indicated in Table 3.

GDEs of surface water ecosystems (Table 4) are located on the bottom (HZ) or on reaches of rivers and lakes. Accordingly, hyporheic GDEs are everywhere a groundwater seepage occurs, as it is suggested in Fig. 1. This scheme implies that groundwater flow is fairly uniform over a large area. However, on a local scale, flow between groundwater and surface water is often highly variable, as indicated on Fig. 2, because of the textural changes of the riverbeds. The proposal in this paper is to delineate the various kinds of hyporheic GDEs mainly according to the morphology of upwelling zones. Groundwater arrivals are favored by specific reach morphologies. Upwelling GDEs are located where high bed permeability (e.g. paleochannel in lattice-like alluvium) allows a great discharge of groundwater (like a spring). Dam GDEs are located where groundwater is flushed due to a difference in pressure between the upstream and downstream of a dam. Meander GDEs are situated at the end of river elbows, where groundwater seeps preferentially and follows the general hydraulic gradient. No so-called ecosociology GDEs have been defined yet for such areas because HZ fauna is variable in time and space, although some trends can be predicted according to the patchiness model discussed previously. In upwelling conditions, stygobites (e.g. crustaceans such as *Microcharon reginae*, *Salentinella juberthiae*, *Niphargus kochianus*) would tend to dominate epigean species (e.g. *Gammarus* sp., *Candona* sp.; Ward et al. 1998). Accordingly, stygobites tend to dominate in the less flooded part of flood plains. These general trends however have to be viewed with caution, as the mobility (e.g. active vs. passive) of hyporheic fauna is still being researched.

On reaches, the following classification system mainly deals with aquatic and hydrophytic vegetal biocenoses that have settled on mineral interfaces, namely fluvisols, where redoximorphic features are common, or gleysols where influences of groundwater are evident (reddish, brownish and yellowish colours; Baize et al. 2009). These systems are extremely sensitive to hydrological modifications. For lentic ecosystems, a distinction between the circumneutral and alkaline environment is proposed because of the specialization of some plants (e.g. *Chara sp.*) to high water-calcium content. Aquatic plants can be immersed (in *Charion, Potamion*) or floating (*Nymphaeion, Potamion*). Large lakes have a moderate biodiversity, except on their shorelines where *Littorellion* or *Phragmition* alliances are found in the littoral zone.

Peatland GDEs (Table 5) may be described in a different way in comparison to other systems. The groundwater level is dependent on hydrodynamics in the aquifer and peaty interface (histosols; Baize et al. 2009), which also modifies groundwater chemistry. Therefore, aquifer-scale processes and peaty interface roles are not distinguished. The ecological role of groundwater is probably dependent on volumes, hydrodynamics, chemical processes (featuring both aquifer and peat compartments), and the contribution of the meteoric water. The water level and fluctuation are key factors because they directly influence the existence and spatio-temporal extent of anaerobic and aerobic layers. Similarly to some wetlands typologies (e.g. National Wetlands Working Group 1997), ecomorphology is also considered, i.e. the domination by trees (or shrubs) or by graminoids (plant formations). *Caricion fuscae* is mainly characteristic of more or less anoxic systems and rather acid pore water (anoxic acidic groundwater dependent marshes) in contrast to *Salicion cinereae, Alnion glutinosae* (anoxic groundwater dependent swamps) and *Caricion davallianae* where pore water tends to be alkaline (anoxic alkaline groundwater dependent marshes). The redox condition factor is more useful where water-table variation is important because it overlies pH effects (oxygenated circumneutral groundwater-dependent marshes). *Phalaridion* is generally positioned on the edge of lentic systems and can be considered as a transitional system between *Phragmition* and *Magnocaricion*. The latter is inundated during several weeks or months and can support water-table variation of almost 1 m. For higher water-table variations, the typical biocenoses are *Calthion, Molinion* and *Filipendulion*. These systems are similar in their floristic composition, but *Calthion* is more characteristic

Table 3 Classification key of spring ecosystems

Determined by aquifer scale attributes		Determined by emergence scale attributes	GDE's denomination	Ecology		
Hydroperiod	Chemical type	Geomorphological characteristics		Phytosociology	Characteristic species	Biogeographic area
Permanent	Alkaline pH	Helocrene, rheocrene	Permanent alkaline spring ecosystems	*Cratoneurion*	*Cratoneuron filicinum, Saxifraga aizoides*	Atlantic, Continental, Alpine, Mediterranean, Boreal
	Neutral to alkaline pH	Rheocrene	Permanent rheocrene springs	*Ranunculion fluitantis*[a]	*Ranunculus fluitans Potamogeton nodosus,*	Mediterranean, Atlantic, Continental
				Fontinalidion antipyreticae[a]	*Fontanilis antipyretica, Potamogeton nodosus*	Atlantic, Continental, Mediterranean, Boreal
				Scarpanion undulatae[a]	*Brachythecium plumosum, Fontanilis antipyretica*	Atlantic, Continental, Mediterranean, Boreal
				Dermatocarpion rivulorum[a]	*Dermatocarpon rivolurum, Hydrogrimnia mollis*	Atlantic, Continental, Boreal, Alpine
		Helocrene, (limnocrene)	Permanent helocrene springs	*Calthion*[a]	*Caltha palustris, Ranunculus aconitifolius*	Atlantic, Continental, Alpine, Mediterranean, Boreal
		Limnocrene	Permanent limnocrene springs	*Charion*[a]	*Chara fragilis, Chara vulgaris, Nitella batrachosperma*	Atlantic, Continental, Alpine, Mediterranean, Boreal
				Potamion[a]	*Potamogeton crispus, Elodea canadensis*	Atlantic, Continental, Mediterranean, Boreal
				Lemnion[a]	*Lemna minor*	Atlantic, Continental, Mediterranean, Boreal
				Nymphaeion[a]	*Nuphar lutea, Callitriche palustris*	Atlantic, Continental, Mediterranean, Boreal
		On cliffs and hillslopes (colluviosols)	Cliff spring ecosystems	*Adiantion*	*Adiantum capillus-veneris, Eucladium verticillatum*	Mainly Mediterranean
	Acid pH	Helocrene, rheocrene, limnocrene	Acid spring ecosystems	*Cardamino montion*	*Cardamine amara, Montia montana, Sedum villosum*	Atlantic, Continental, Boreal
Periodic	Alkaline pH	Rheocrene	Non permanent alkaline rheocrene springs	*Cratoneurion*	*Cratoneuron filicinum, Saxifraga aizoides*	Atlantic, Continental, Alpine, Mediterranean, Boreal
	Neutral to alkaline pH	Helocrene	Non permanent helocrene springs	*Petasition paradoxi*[a]	*Petasites paradoxus, Adenostyles glabra*	Mainly Alpine
				Calthion[a]	*Caltha palustris, Ranunculus aconitifolius*	Atlantic, Continental, Mediterranean, Alpine

[a] Indicates phytosiociologies that are not necessarily typical of groundwater outflows but are, however, common near springs

of terrains inundated during snow melt and supports larger ranges of temperature.

Terrestrial GDEs (Table 6) are classified as a function of longitudinal and lateral hydrological gradients, related to the upstream-downstream alluvial structure evolution. *Salicenion waldsteinianae, Alnion incanae* (Circumneutral mesoriparian GDEs) and *Salicion elaeagni* (Alkaline mesoriparian GDEs) colonize areas frequently inundated and featured by coarse material (brut and/or juvenile fluvisols, Baize et al. 2009) or rocky substrata if degradation processes did not occur extensively, and a shallow water table. *Salicion albae* is the equivalent for lower elevation of the above-mentioned alliances. Considering the gentler topography, this system is generally characterized by more frequent and longer floods. *Fraxinion* is mainly located on the edge of the largest valleys on brown fluvisols, but can be found on rocky hillslides bordering streams, especially uspstream, if this biocenosis is not inundated for most of the year (Xeroriparian GDEs). This alliance represents the intermediate between terrestrial GDEs and upland ecosystems.

These typologies highlight that groundwater discharge zones support a wide biodiversity and long-term groundwater conditions may be evaluated by knowing representative ecosociology. For management purposes, this inexpensive approach may complement classical hydrological measurements and complete surveys. Therefore, the basis of this classification could be used in other climatic areas, upon condition that it takes into account the regional ecological specificities.

Conclusion

This review highlights that the ecological roles of groundwater are strongly conditioned by both aquifer-scale and GDE-scale processes. The morphological characteristics of spring GDEs, the hyporheic zone (HZ) structure and dynamics for surface waters, organic soil structure and volume for peatland GDEs, and the water-table fluctuation and flood patterns for the terrestrial GDEs influence the groundwater uses by biocenoses.

Biocenoses may adapt to these conditions and sometimes alter the physical and nutritive roles of groundwater, but adaptations are often limited to a certain range (e.g. stenothermy, current conditions adaptability). The use of numerical or statistical tools is currently discussed (Batelaan et al. 2003; Hahn 2009; Steube et al. 2009) to constrain drivers leading the abiotic-biotic interactions in GDEs, but as ecosystems are complex multivariate ensembles exposed to a multitude of influences, the mechanisms and cumulative effects need to be further investigated. Consequently, the underlining key factors shaping biodiversity and the proposed conceptual schemes

Table 4 Classification key of surface-water ecosystems. The hypolentic (in lakes) or hyporheic (in flowing waters) zone (HZ) is mainly characterized by the morphology of the bottom of the surface-water body. Indicated fauna are sensitive to hydrological changes (see text). For reaches, it has to be kept in mind that the mentioned plant associations are mainly determined by chemical concentrations in water, and some plants (e.g. *Phragmition* alliances) may also be found in non-groundwater fed systems, e.g. by surface water flowing over marls which usually contains calcium

Hypolentic/hyporheic zone					
Determined by the aquifer scale attributes		Determined by emergence scale attributes	GDE denomination	Ecology	
Hydrological characteristics	Chemical characteristics	Geomorphological characteristics		Indicative ecosociology	Indicative species
Gaining conditions	Acid to alkaline pH	Upwelling groundwater due to high hydraulic conductivity area	Upwelling hyporheic GDEs	Dominance of hypogean species, in particular stygobites and stygophiles in comparison to epigean species	Stygobites: *Microcharon reginae*; *Salentinella juberthiae*; *Niphargus kochianus*; *Niphargus rhenorhodanensis* Epigean: *Gammarus* sp.; *Candona* sp.
		Groundwater arrival at a river elbow	Meander hyporheic GDEs		
		Flushing of groundwater due to river bed morphology (behind a dam)	Dam hyporheic GDEs		

Reach zone						
Hydrological characteristics	Chemical characteristics	Geomorphological and pedological characteristics		Indicative ecosociology	Indicatives species	Biogeographic area
Possibly periodic groundwater discharge	Acid to alkaline pH	Lotic systems (brut fluvisols and/or gleysols)	Lotic reach GDEs	*Glycerio-sparganion*	*Glyceria flutans, Berula erecta, Nasturtium offcinale*	Atlantic, Continental, Boreal, Pannonian,
				Caricion bicolori-atrofuscae	*Carex bicolor, Juncus articus*	Alpine
Probably permanent groundwater discharge	Neutral to alkaline pH	Lentic systems (brut fluvisols and/or gleysols)	Alkaline lentic reach GDEs	*Potamion*	*Potamogeton crispus, Myriophyllum spicatum*	Atlantic, Continental, Boreal, Pannonian,
				Charion	*Chara fragilis, Nitella batrachosperma*	Atlantic, Continental, Alpine
				Phragmition	*Phragmites australis, Equisetum fluviatile, Typha latifolia, Typha angustifolia*	Atlantic, Continental, Mediterranean, Boreal,
	Acid to neutral pH		Circumneutral lentic reach GDEs	*Nymphaeion*	*Nuphar lutea, Ranunculus peltatus*	Atlantic, Continental, Boreal, Pannonian, Alpine
				Littorellion	*Littorella uniflora, Sparganium angustifolium*	Atlantic, Continental, Mediterranean, Alpine

Table 5 Classification key of peatland GDEs (on histosols)

Determined by aquifer scale and emergence scale attributes			Ecological feature	GDE denomination	Ecology		
Hydrologic characteristics	Redox characteristics	Chemical characteristics	Biotic characteristics		Characteristic phytosociology	Characteristic species	Biogeographic area
High groundwater level and low fluctuations	Anoxic groundwater-dependent peatland	Acidic pore water	Dominated by graminoids	Anoxic acidic groundwater-dependent marshes	*Caricion fuscea*	*Carex canescens, Eriophorum scheuchzeri*	Atlantic, Continental, Alpine
		Neutral to alkaline pore water	Dominated by trees	Anoxic groundwater-dependent swamps	*Salicion cinereae*	*Salix cinerea, Salix aurita*	(Atlantic, Continental, Boreal, Pannonian Mediterranean)
					Alnion glutinosae	*Alnus glutinosa*	Atlantic, Continental, Alpine, Mediterranean (Pannonian),
			Dominated by graminoids	Anoxic alkaline groundwater-dependent marshes	*Caricion davallianae*	*Carex davalliana, Schoenus ferrigineus*	Atlantic, Continental, Alpine, Boreal
Higher groundwater fluctuations	Temporarily oxygenated groundwater-dependent peatland	Acidic to alkaline pore water	Dominated by graminoids	Oxygenated groundwater-dependent marshes	*Phalaridion*	*Phalaris arundinacea, Phragmites australis*	Atlantic, Alpine, Continental
					Magnocaricion	*Carex riparia, Carex elata*	Atlantic, Continental
					Calthion	*Caltha palustris*	Atlantic, Continental, Mediterranean, Alpine
					Molinion	*Molinia caerulea, Juncus conglomeratus*	Atlantic, Continental
					Filipendulion	*Filipendula ulmaria*	Continental, Alpine, Mediterranean (Atlantic)

Table 6 Classification key of groundwater-dependent terrestrial ecosystems

Determined by aquifer scale attributes		Determined by emergence scale attributes	GDE denomination	Ecology		
Hydrological characteristics	Chemical characteristics	Pedological characteristics		Characteristic phytosociology	Characteristic species	Biogeographic area
Shallow water table	Slightly acid to alkaline pH	Upstream: On rocky substratum bordering streams. Downstream: On large alluvial sediments (frequently removed: brut and/or juvenile fluvisols)	Circumneutral mesoriparian GDEs	*Salicenion waldsteinianae*	*Salix waldsteinniana, Salix helvetica*	Alpine
				Alnion incanae	*Alnus incana, Equisetum hyemale*	Continental
				Salicion albae	*Salix alba, Populus alba, Populus nigra*	Alpine, Atlantic, Continental, Boreal, Pannonian Mediterranean
	Neutral to alkaline pH		Alkaline mesoriparian GDEs	*Salicion elaeagni*	*Salix elaegnos, Salix daphnoides*	Alpine, Continental
Periodically deep water table	Slightly acid to alkaline pH	Upstream: On rocky substratum bordering streams. Downstream: On fine alluvial sediments (infrequently renewed by floods: brown fluvisols)	Xeroriparian GDEs	*Fraxinion excelsioris*	*Fraxinus excelsior*	Atlantic, Continental, Boreal, Pannonian Mediterranean

could be used as a basis for the modeling of GDEs under various hydrological conditions.

The proposed classification aims at considering these multiscale processes and covers broad ranges of hydrological and physico-chemical conditions as well as biocenoses types to obtain an overview of epigean GDEs found in European landscapes. This typology harbours a similar philosophy to previous classification schemes, which are discussed comprehensively by Cowardin et al. (1979). To be applicable to large areas, the used parameters are mainly qualitative, which could be viewed as the main limitation of this classification scheme. However, such an approach could be sufficient for European or national mapping of GDEs, for example, because it permits the inclusion of a wide range of ecohydrological situations. From the identification of some typical species, long-term hydrological situations could be clarified. Reciprocally, the knowledge of groundwater patterns should allow characterization of potential ecological conditions close to the emergences. For local or specific applications aiming to take into account regional specificities or to focus on one GDE type (e.g. only peatlands), the proposed classification should be considered as a framework in which the parameters could be used once subdivided (e.g. by increasing the number of pH classes or by indicating the elevation ranges in mountainous areas). This should improve the increasing amount of field work dealing with both biological and hydrogeological approaches (e.g. Goldscheider et al. 2006 and references therein) and tracers (e.g. stable isotopes) in the study of short-term relationships between different compartments (including biocenoses) of the water cycle.

Finally, one should keep in mind that most of the presented ecohydrological concepts in both the review and the classification deal with the relationship between abiotic conditions and primary producers or sometimes primary consumers or detritivores. One challenge for the future should be to integrate the higher trophic chain members. Since humans are the last link in many of these trophic chains, these approaches should further connect hydrogeologic and hydroeconomic models in order to adapt/improve groundwater and landscape management policies from the international to ecosystem levels.

Acknowledgements The work was carried out as part of the GENESIS project on groundwater systems (http:/www.thegenesisproject.eu) financed by the European Commission 7FP large scale project contract 226536. The authors are grateful to Dr. Jari Ilmonen for his comments on this work and to Jessica Meeks for her assistance in improving the quality of the text. We also thank Dr. Hans Jürgen Hahn and one anonymous reviewer for their remarks which allowed enrichment of this work.

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