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A proposal for a groundwater habitat classification at local scale

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Abstract

Distribution of groundwater invertebrate communities in porous aquifers (and their habitats) varies on spatial scales and many attempts have been made to classify these on various scales. The new data-based approach, presented here, classifies the complex distribution of groundwater habitats on a local scale (i.e. along transects of < 100 m) and merges the latest classification approaches at this scale. Data from a regional (i.e. approximately 100 km^2) biogeographic groundwater survey was analysed in terms of stability of: community structure, different intensities of surface water influence, and occurrence, together with the distribution of stygobites within those groundwater ecosystems. On the investigated local scale, the faunistic communities' composition is mainly depending on surface water influence, coupled with immision of dissolved oxygen and organic matter. Derived from this finding, five types of faunistic habitats are proposed: (I) Stressed groundwater habitats, (II) Stable groundwater habitats, (III) Rain fed groundwater habitats , (IV) Surface water fed groundwater habitats, and (V) Hyporheic habitats.

Keywords

Groundwater ecosystems, classification, sampling efficiency, groundwater invertebrates

Introduction

According to their occurrence in groundwater or surface water, invertebrates can basically be classified as stygobites, stygophiles and stygoxenes (Thienemann 1926). Stygobites spend their whole life-cycle completely in groundwater and are well-adapted to low food and oxygen supply (Culver 1982, Hervant et al. 1997, Malard and Hervant 1999, Mösslacher and Hahn 2003). In contrast to stygobites, stygophilic invertebrates commonly occur in well food- and oxygen supplied surface waters. However, they can immigrate into groundwater actively, if the conditions there are favourable (Malard et al. 1996, Malard and Hervant 1999, Sket 1999). Invertebrates that are carried passively into groundwater (for example by pulse-like surface water intrusion into groundwater) are called stygoxenes. Stygoxenes cannot endure the specific living conditions in groundwater for long periods of time. This classification, based on autecological data of species is well known. However does not represent a description of groundwater habitats.

In this paper "habitat" as the living space of a particular species (sensu Abercrombie et al. 1966) is used synonymously with "biotope" as the living space of a community (Schaefer 2012).

Groundwater invertebrate communities and the habitats in which they occur, show different patterns depending on the spatial scale regarded. Many independent attempts have been made in the past to classify groundwater communities and habitats, each focusing on different combinations of scales. With the exception of the classification based on faunal communities from groundwater wells in the federal state of Baden-Wuerttemberg (South-Western Germany) by Hahn and Fuchs (2009), most classifications in the past were based purely on theoretical considerations. Galassi et al. (2009a) did not intend to develop a new classification of groundwater habitats, yet they described the occurrence of species and faunistic composition in the investigated area. Other studies were mainly focussing on certain sub-classes, like copepods (Galassi et al. 2009b), or disregarded areas besides alluvial plains (Datry et al. 2008) where different faunistic composition patterns and habitats were dominating, or dealt with biodiversity patterns among different types of aquifers (Malard et al. 2009). Because of those restrictions, the findings of these studies are not easily transferable to other regions. Here, we develop a multi-scale classification scheme that is based on data from a ca. 100 km^2 region in Southern Germany, which also considers previous theoretical attempts.

For clarification purposes, we summarise the most important classification attempts to date:

(i) Husmann (1966, 1967) proposed a typological system which was closely linked to the latitudinal zonation of running waters, based on the hydrological understanding of surface water flow, ignoring that fundamentally different flow patterns below the surface.

(ii) Illies (1967) explained the distribution and diversity of surface-water species by connecting species to a list of habitats and regions, which he called bioregions. Since it has recently been shown that the surface bioregions do not mirror groundwater regions (Hahn and Fuchs 2009, Stein et al. 2012), this classification does not offer much help or assistance in classifying groundwater habitats.

(iii) Illies' (1967) concept was modified by Botoşăneanu (1986) by adding groundwater habitats which were affiliated to different types of subterranean biotopes or by the hydraulic conductivity of the aquifers.

(iv) Ecological issues, the hydraulic conductivity as well as the type of aquifer, were the basis of the typology by Gibert et al. (1997) and Gibert (2001).

(v) Schmidt and Hahn (2012) stressed the heterogeneity within groundwater habitats and suggested a classification of groundwater habitats accordingto the degree with which they were characterised by surface water ingressions.

(vi) Another attempt to classify groundwater habitats on different spatial scales (i.e. macroscale, continent; landscape scale, km; local scale; dm to m) was proposed by Hahn (2009).

(vii) Stein et al. (2012) developed a data-based approach for classifying groundwater habitats into stygoregions at large scales.

(viii) Based on heterogeneous data, Gutjahr et al. (2013a) classified groundwater habitat types on a local scale, depending on the degree to which they were stressed by diffuse effects, such as hypoxia, silt or iron ochre.

On a local scale (i.e. from decimetres to metres), another recent classification approach for groundwater habitats was suggested by Hahn (2006). It is based on the estimation of alimony (availability of organic nutrients) and oxygen supply, expressed by the groundwater-fauna-index (GFI). Except for the last three, none of the aforementioned typologies were tested using faunistic datasets. Moreover, only the classifications (vii) and (viii) are based on the identified faunistic assemblage. The approach by Stein et al. (2012) is on an almost continental scale and differs from the approach by Hahn and Fuchs (2009), which was developed only on samples from South-Western Germany on a landscape scale.

Gutjahr et al. (2013a) identified three groups of habitats according to the level of resilience to stress: (1) stressed habitats with low numbers of taxa and individuals, (2) intermediate habitats with highest numbers of taxa and individuals, and (3) stable habitats with intermediate numbers of taxa and individuals. This classification enables the evaluation of faunistic stability of communities and the evaluation of sampling efficiency at a sampling site (e.g. how many samples are needed to catch 95% of the species occurring at the investigated site).

The degree of surface water intrusion drives faunistic composition to a great extent. In order to assess the influence of surface water on groundwater environments at landscape level, the GFI was proposed by Hahn (2006). It distinguishes three groups of ecological groundwater habitats, based on the availability of organic nutrients. He classified oligo-alimonic habitats as those with weak hydrological exchange, a poor food and oxygen supply and often an absence of groundwater invertebrates. Meso-alimonic habitats have a moderate hydrological exchange and food supply with moderate to high oxygen concentrations and are dominated by a stygobiotic fauna. A strong influence of surface water accompanied by moderate to high oxygen and nutrient supply is considered to be characteristic for eu-alimonic habitats. Those habitats often harbour an abundant and species-rich fauna which is a mixture of stygoxenes and stygophiles.

Schmidt and Hahn's (2012) theoretical approach clearly distinguishes between rain fed groundwater ecosystems and surface water fed groundwater ecosystems. The former are recharged by precipitation infiltrating into groundwater through the soil and the latter are recharged by water infiltrating into groundwater from surface water bodies. Local conditions have varying degrees of groundwater and surface water interfusion and the scale might range from dm in low conducive sediments to km in highly conducive sediments.

For the classification of groundwater habitats within a landscape, a characterisation of groundwater invertebrate communities is required (Tomlinson and Boulton 2010, Larned 2012) at regional and local scale. In order to reach this goal, the latest regional / local concepts are used (Hahn 2006, Schmidt and Hahn 2012, Gutjahr et al. 2013a) and tested on a dataset which comprised different spatial scales but was mainly focussed on the local scale (i.e. from decimetres to metres). With this background, data from 30 traps in groundwater wells situated in four catchments in Rhineland-Palatinate (Germany) were analysed and the results were compared with findings of the aforementioned concepts (Hahn 2006, Schmidt and Hahn 2012, Gutjahr et al. 2013). This study aims to check an empiric groundwater faunistic dataset on the background of previously available classification approaches (Hahn 2006, Schmidt and Hahn 2012, Gutjahr et al. 2013a) and to merge them, where appropriate.

Material and methods

Study area

The study area is situated in the federal state Rhineland-Palatinate, South-Western Germany. It comprises three different natural geographic regions, the Pfälzerwald Mountains, the Haardtrand and the Upper Rhine Plateau. Groundwater wells were located in transects in four alluvial floodplains, the Kolbental [KT], Klammtal [HB] (both in the Pfälzerwald Mountains), the Modenbachtal [MB] (Haardtrand) and the Offenbacher Wald [OW] (Upper Rhine Plateau) (Table 1, Fig. 1).

The Pfälzerwald Mountains have unfertile and sandy soils in conjunction with a high rate of groundwater recharge (~ 25% of precipitation, i.e. 200–300 mm y^{-1}) (LUWG 2005). The groundwater is characterised by high oxygen concentrations and low conductivity values (mean ~ 103 µS cm^{-1}). The Haardtrand is the Western fault belt of the Upper Rhine Plateau, which encompasses a fractured geology, intensive steep slope viticulture and intermediate conductive groundwater (mean ~250 µS cm^{-1}). Soils in the Upper Rhine Plateau are fertile in most instances, thus intensive agricultural use dominates (Geiger et al. 2008) and groundwater is featured by high conductivities (mean ~ 590 µS cm^{-1}).

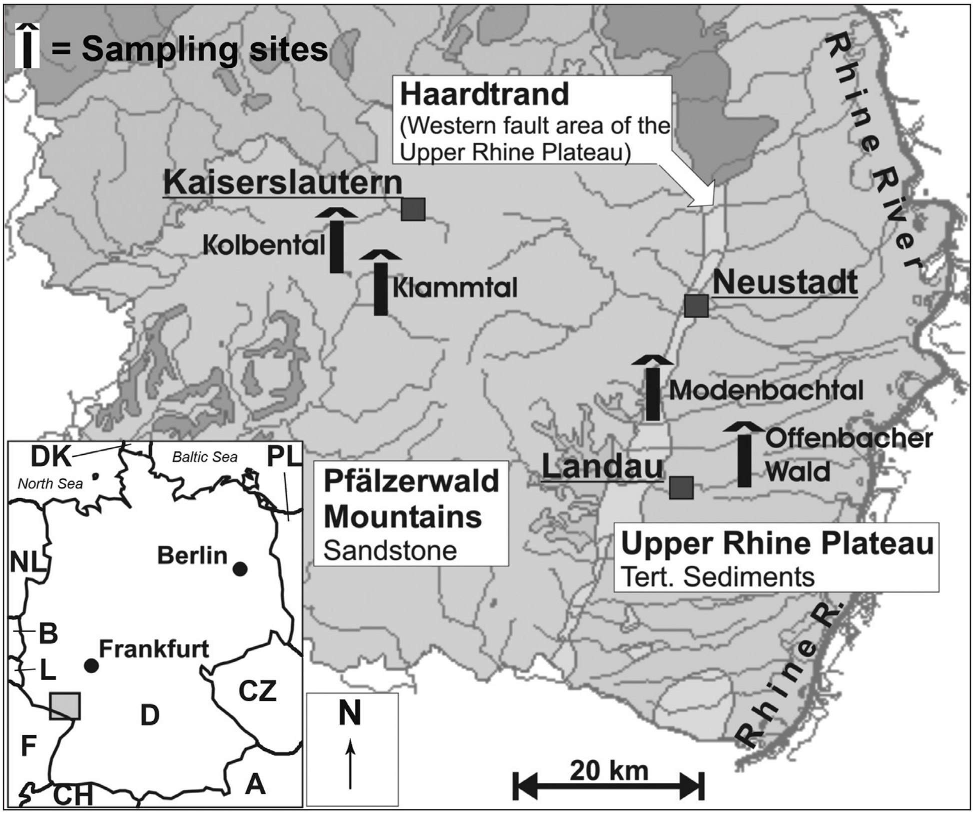

Figure 1. Map of the study area (from Hahn 2006, modified). All sites were equipped with 4–5 transsectional groundwater wells. Boxes: The respective natural regions [Pfälzerwald Mountains = Central Uplands; Haardtrand and the Upper Rhine Plateau = South-Western Uplands (according to Stein et al. 2012)]. Abbreviations on overview map: A = Austria, B = Belgium, CH = Switzerland, CZ = Czech Republic, D = Germany, DK = Denmark, F = France, L = Luxembourg, NL = Netherlands, PL = Poland.

The sandy and unfertile soils of the Offenbacher Wald are completely covered by forests.

Annual mean temperatures decrease from the Offenbacher Wald (10.1 °C) over the Haardtrand (9.7 °C) to the Pfälzerwald Mountains with 8.6 °C by mean (for details see Hahn 2005, 2006).

Sampling methods

To sample invertebrates, unbaited stratified trap systems (Table 1) were installed in wells (Hahn 2005, 2006, Bork et al. 2008). The wells were arranged in transects from the slope of the hill towards the brook in intervals of approximately 50 meters, ending up with the last well directly next to the brook. Thus 13 wells including stratified trap systems in four regions and additionally two hyporheic traps were sampled (Table 1).

Table 1. Sampling sites.

Landscape	Site	Trap	Valley	Lat. (N.)	Lon. (E.)	altitude of terrain surface above sea level [m]	depth [m] below terrain surface	Recharge from	groundwater-fauna-index (GFI) (mean)
Pfälzerwald	KT1	KT1/A	Kolbental	49°23'57.2"	7°40'50.61"	289.0	1.70	lateral groundwater instream from the adjacent fractured rock sand-stone aquifer	2.13
Pfälzerwald	KT1	KT1/B		49°23'57.2"	7°40'50.61"		2.90		1.54
Pfälzerwald	KT1	KT1/C		49°23'57.2"	7°40'50.61"		6.90		1.43
Pfälzerwald	KT2	KT2/A		49°23'55.94"	7°40'51.73"	288.5	1.61	deep alluvial groundwater	2.38
Pfälzerwald	KT2	KT2/B		49°23'55.94"	7°40'51.73"	296.0	2.81		2.09
Pfälzerwald	KT2	KT2/C		49°23'55.94"	7°40'51.73"	296.0	6.81		0.47
Pfälzerwald	KT3	KT3/A		49°23'55.21"	7°40'50.56"	288.0	1.19	lateral groundwater instream from the adjacent fractured rock sandstone aquifer	1.62
Pfälzerwald	KT4	KT4/A		49°23'55.4"	7°40'49.52"	288.3	1.51		5.11
Pfälzerwald	KT4	KT4/B		49°23'55.4"	7°40'49.52"		3.81		4.02
Pfälzerwald	HB1	HB1/A	Klammtal	49°20'8.95"	7°40'33.97"	270.0	1.52	lateral groundwater instream from the adjacent fractured rock sandstone aquifer	3.72
Pfälzerwald	HB1	HB1/B		49°20'8.95"	7°40'33.97"	291.0	2.72		2.74
Pfälzerwald	HB1	HB1/C		49°20'8.95"	7°40'33.97"	291.0	3.42		2.27
Pfälzerwald	HB2/HZ	HB2/HZ		49°20'9.23"	7°40'33.27"	268.7	0.72	deep alluvial groundwater	3.58
Pfälzerwald	HB2	HB2/A		49°20'9.20"	7°40'33.27"	269.0	1.46		1.69
Pfälzerwald	HB3	HB3/A		49°20'9.64"	7°40'32.42"	270.0	1.62	lateral groundwater instream from the adjacent fractured rock sandstone aquifer	7.72
Pfälzerwald	HB3	HB3/B		49°20'9.64"	7°40'32.42"		2.82		4.06
Pfälzerwald	HB3	HB3/C		49°20'9.64"	7°40'32.42"		3.82		2.52
Haardtrand	MB3	MB3/B	Modenbachtal	49°15'29.48"	8°4'54.79"	197.0	3.75	surface water / brook	3.52
Haardtrand	MB4	MB4/A		49°15'29.74"	8°4'54.64"	197.0	2.20		8.77
Haardtrand	MB4	MB4/B		49°15'29.74"	8°4'54.64"		3.40		3.58
Haardtrand	MB4	MB4/C		49°15'29.74"	8°4'54.64"		7.40	mainly deep groundwater / little surface water influence	1.83
Upper Rhine Plateau	OW1	OW1/A	Offenbacher Wald	49°12'52.50"	8°11'45.41"	128.0	2.09	surface water impact from gully	2.12
Upper Rhine Plateau	OW1	OW1/B		49°12'52.50"	8°11'45.41"		3.29		0.20
Upper Rhine Plateau	OW2	OW2/A		49°12'50.63"	8°11'45.49"	127.5	1.49	alluvial forest, periodically flooded	3.94
Upper Rhine Plateau	OW2	OW2/B		49°12'50.63"	8°11'45.49"		2.69	occasional surface water impact	1.48
Upper Rhine Plateau	OW3/HZ	OW3/HZ		49°12'47.88"	8°11'45.98"	127.0	0.87	surface water impact from brook	11.93

Landscape	Site	Trap	Valley	Lat. (N.)	Lon. (E.)	altitude of terrain surface above sea level [m]	depth [m] below terrain surface	Recharge from	groundwater-fauna-index (GFI) (mean)
Upper Rhine Plateau	OW3	OW3/A		49°12'47.85"	8°11'45.98"	127.5	2.20		1.36
Upper Rhine Plateau	OW4	OW4/A		49°12'47.33"	8°11'46.33"		1.54	occasional surface water impact, otherwise alluvial groundwater	1.15
Upper Rhine Plateau	OW4	OW4/B		49°12'47.33"	8°11'46.33"	127.5	2.74		0.79
Upper Rhine Plateau	OW4	OW4/C		49°12'47.33"	8°11'46.33"		6.74		0.35

To sample the fauna, the contents of the traps (0.9 L) were pumped and an additional 2 L were sampled afterwards for hydro-chemical analyses. Physical and chemical properties of groundwater, such as temperature, dissolved oxygen (DO), pH-value and electric conductivity (EC) were measured using a WTW multi-meter Multiline P4 directly after pumping out the water. Total dissolved iron was measured using a Merck Reflectoquant reflectometer. Organic matter (OM) was estimated and scaled into four categories: absent, little, much, very much according to Hahn (2006).

The mean depths (below surface) of the investigated groundwater wells were 5.0 m (1 well) and 7.5 m (12 wells) and all tapped into the shallow local aquifer. The traps were installed in triplicates: the first trap (A) was always installed just below groundwater table, the second trap (B) in the middle of the water column and the third trap (C) at 0.5 m above the bottom of the wells (Table 1). The two hyporheic wells [HZ] (Table 1) contained one trap each, which was installed 0.3 m below the sediment surface. Faunistic samples were taken and then brought back to the laboratory within 24 hours and sorted alive. For more detailed information on the processing of the samples see Hahn (2005).

Fauna was determined to species level and ecological information given on species was derived from Einsle (1993), Janetzky et al. (1996), Meisch (2000), Wägele (2007) and Schminke (2007 a–c).

For this study, data were analysed from 30 traps containing fauna and which had been sampled on 13-15 occasions over an eighteen month period (2001–2002) (Tables 1 and 2). Due to seasonal fluctuations in water levels, one trap fell dry repeatedly and was not taken into account for this analysis.

Statistical analysis

Faunal data were not normally distributed (Shapiro-Wilk-test) even after log (x+1) transformation ($p < 0.05$) and non-parametric tests were performed. SIMPER analyses were applied to taxonomic data, which was available at species level (Clarke 1993). This process was developed specifically for the comparison of faunal samples in which typical or dominant species are identified, and pairs of species that do occur together more frequently are considered. Based on a matrix of presence-absence of taxa (or pairs of species) a similarity percentage can be calculated to express faunistic similarities between samples of a certain sampling site or sampled trap. False-negative rates were calculated for each trap in order to draw conclusions on the aspects of sampling efficiency (Eberhard et al. 2009, Gutjahr et al. 2013a). The GFI was calculated according to Hahn (2006).

Faunal communities' abundances were fourth rooted after incorporating a dummy variable to overcome bias from extremely heterogeneous faunistic data among traps. Bray-Curtis dissimilarities among traps were then calculated based on faunistic data at species level. This dissimilarity matrix was plotted in the multi-dimensional scaling method (MDS). Vectors of physical and chemical characteristics of groundwater, explaining the distribution of the traps by multiple correlation, were integrated to the MDS to indicate possible influences of the physical and chemical characteristics of groundwater to the faunistic assemblages. To test whether scaled groups were statistically distinguishable, a one-way ANOSIM analysis (Clarke 1993) and a distribution-free discriminance analysis (DA; 10,000 permutations) were performed. The MDS, ANOSIM and DA were carried out by PRIMER v6 with PERMANOVA+ -Addon (Primer E Ltd.). All other processing was performed using Excel 2007 (Microsoft Corporation) or SPSS 15.0 (SPSS Inc.).

Results

Five distinct ecological groups were identified, mainly based on a MDS (Fig. 2), but also on a cluster analysis (single linkage, see Suppl. material 1) as well as the site particularities (Table 1):

(I) stressed groundwater habitats [Stressed]
(II) habitats where groundwater was secluded from all surface water influences, thus was comparably stable in faunistic composition [GWstable]
(III) rainwaterfed groundwater habitats [GWrainfed]
(IV) surface waterfed groundwater habitats [GWswb], and
(V) Hyporheic habitats [Hyporheic].

The KT1/A and KT2/A traps (Table 2) were defined to be "GWstable" and "GWrainfed", according to the MDS plot (Fig. 2), though the cluster analysis would have categorised them as "Stressed". The separation of all groups was significantly and strongly distinct (one way ANOSIM: global $R = 0.608$, $p=0.001$). The pair-wise comparisons for the groups within this ANOSIM GWstable to GWrainfed ($R = 0.006$, $p = 0.4$) as well as GWstable to Stressed ($R = 0.02$, $p = 0.438$) were not significant. Using a DA, a total of 90% ($p = 0.0001$) of the samples were correctly classified to one of the identified habitats.

The MDS ordination (Fig. 2) revealed a separation at landscape level on the y-axis with sampling sites from the Pfälzerwald Mountains at the higher end, the Upper Rhine sampling sites at the lower end and the Haardtrand region with an intermediary position. The distribution of the sampling sites on the x-axis shows an increase in (from the left to the right) surface water influence. This is indicated by faunistic communities' composition as the proportions of stygobiotic fauna decrease and GFI (Fig. 2) values rise.

Stressed habitats (I) were found in all natural investigated regions and constituted a heterogeneous group (about 50% of all the traps). This type of habitats was characterised by a low average of standard deviation of temperature, DO and OM and a high amplitude of measured values (Fig. 3). Stressed habitats always harboured populations of low abundances (mean = 1.08 individuals/sample) and a broad fluctuation of

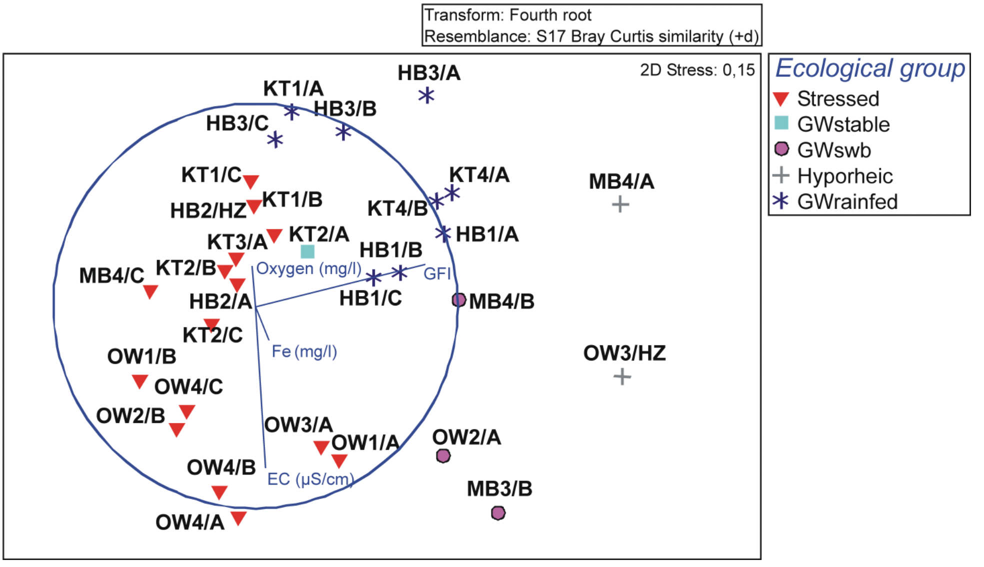

Figure 2. MDS (Multi-dimensional scaling) ordination of invertebrate assemblages of each trap (faunal data aggregated by mean for traps having 13–15 samplings). Vectors show physical and chemical parameters of groundwater explaining the distribution of traps within the MDS best (Fe = Total dissolved iron [mg l^{-1}]). Naming of the traps in accordance with Table 1.

proportions of stygobites (mean = 52.18%) accompanied by low SIMPER similarity values (Table 3 and Fig. 4d). The average group SIMPER similarity was 6.76%, with the cyclopoids *Diacyclops* cf. *languidoides* and *Paracyclops fimbriatus* (Fischer, 1853) being the characteristic species.

Table 2 and Figure 4c show different distributions of abundances between the scaled groups. Derived from this data low abundances are less than 12 individuals/sample, intermediate abundances are 12 to 79 individuals/sample and high abundances are more than 80 individuals/sample.

One trap (KT2/A), situated in the Kolbental (Pfälzerwald Mountains), was classified as GWstable (II). This trap was featured by groundwater, which was well-shielded from surface water and characterized by very low standard deviation of temperature (mean = 1.45 °C) and low GFI-values (mean = 2.38). KT2/A displayed the highest percentages of stygobites (mean = 99.49%) in low abundances (mean = 11.6 individuals/sample), stable faunal communities (Fig. 4b-d) and low standard deviations of temperature (Fig. 3a). GFI values were low, indicating oligo-alimonic conditions (lower dashed line in Fig. 4a). The SIMPER test (as there was only one site in the group, a SIMPER test was performed for all the sampling occasions) generated *Diacyclops* cf. *languidoides* as a characteristic species at this habitat. The similarity of the 15 samples was 78.44% by SIMPER, indicating very stable communities (Table 3).

GWrainfed (III) habitats were situated mainly at the edges of valleys and only in the Pfälzerwald Mountains. They were characterised by groundwater from adjacent fractured rock aquifers. The standard deviation of temperature of 1.52 °C (Fig. 3a)

Table 2. Taxa vs. site matrix for the samples of the traps investigated (faunal data aggregated by sum over 13 – 15 samples). Marked taxa (grey) proved to be most important in differentiating between habitats by SIMPER analysis (Table 3).

Sampling sites	Number of samples	*Niphargus aquilex* SCHIOEDTE, 1855	*Acanthocyclops robustus* (SARS, 1863)	*Acanthocyclops vernalis* (FISCHER, 1853)	*Diacyclops bisetosus* (REHBERG, 1880)	*Diacyclops crassicaudis* (SARS, 1863)	*Diacyclops cf. languidoides*	*Diacyclops languidus* (SARS, 1863)	*Eucyclops serrulatus* (FISCHER, 1851)	*Graeteriella unisetigera* (GRAETER, 1908)	*Macrocyclops albidus* (JURINE, 1820)	*Megacyclops viridis* (JURINE, 1820)	*Paracyclops fimbriatus* (FISCHER, 1853)	*Thermocyclops dybowskii* (LANDÉ, 1890)	*Tropocyclops prasinus* (FISCHER, 1860)	*Attheyella crassa* (SARS, 1863)	*Bryocamptus minutus* (CLAUS, 1863)	*Bryocamptus pygmaeus* (SARS, 1863)	*Bryocamptus typhlops* (MRÁZEK, 1893)	*Canthocamptus staphylinus* (JURINE, 1820)	*Moraria (Moraria) brevipes* (SARS, 1863)	*Parastenocaris brevipes* KESSLER, 1913	*Parastenocaris germanica* KIEFER, 1936	*Parastenocaris fontinalis borea* KIEFER, 1960	*Parastenocaris psammica* SONGEUR, 1961	*Candona candida* (MÜLLER, 1776)	*Candonopsis kingsleii* BRADY & ROBERTSON, 1870	*Cryptocandona reducta* (ALM, 1914)	*Cryptocandona vavrai* KAUFMANN, 1900	*Fabaeformiscandona latens* (KLIE, 1940)	*Fabaeformiscandona wegelini* (PETKOVSKI, 1962)	*Heterocypris reptans* (KAUFMANN, 1900)	*Pseudocandona albicans* (BRADY, 1864)	*Troglochaetus beranecki* DELACHAUX, 1921	*Antrobathynella stammeri* (JAKOBI, 1954)	Type of habitat
KT1/B	15						18					1	4								1															Stressed
KT1/C	15						8					1	30								1		2													Stressed
KT2/B	15						8																1													Stressed
KT2/C	15						1																													Stressed
KT3/A	15						21												1																	Stressed
HB2/HZ	15	1					5						34																							Stressed
HB2/A	15						1						2																							Stressed
MB4/C	14					1							3																				1			Stressed
OW1/A	15				12			1																10				1								Stressed
OW1/B	15																															1				Stressed
OW2/B	15							21																												Stressed
OW3/A	15				9																	1		1												Stressed
OW4/A	15																					6	4	19	2											Stressed
OW4/B	15							1														1		3	1											Stressed

Sampling sites	Number of samples	*Niphargus aquilex* SCHIOEDTE, 1855	*Acanthocyclops robustus* (SARS, 1863)	*Acanthocyclops vernalis* (FISCHER, 1853)	*Diacyclops bisetosus* (REHBERG, 1880)	*Diacyclops crassicaudis* (SARS, 1863)	*Diacyclops cf. languidoides*	*Diacyclops languidus* (SARS, 1863)	*Eucyclops serrulatus* (FISCHER, 1851)	*Graeteriella unisetigera* (GRAETER, 1908)	*Macrocyclops albidus* (JURINE, 1820)	*Megacyclops viridis* (JURINE, 1820)	*Paracyclops fimbriatus* (FISCHER, 1853)	*Thermocyclops dybowskii* (LANDÉ, 1890)	*Tropocyclops prasinus* (FISCHER, 1860)	*Attheyella crassa* (SARS, 1863)	*Bryocamptus minutus* (CLAUS, 1863)	*Bryocamptus pygmaeus* (SARS, 1863)	*Bryocamptus typhlops* (MRÁZEK, 1893)	*Canthocamptus staphylinus* (JURINE, 1820)	*Moraria (Moraria) brevipes* (SARS, 1863)	*Parastenocaris brevipes* KESSLER, 1913	*Parastenocaris germanica* KIEFER, 1936	*Parastenocaris fontinalis borea* KIEFER, 1960	*Parastenocaris psammica* SONGEUR, 1961	*Candona candida* (MÜLLER, 1776)	*Candonopsis kingsleii* BRADY & ROBERTSON, 1870	*Cryptocandona reducta* (ALM, 1914)	*Cryptocandona vavrai* KAUFMANN, 1900	*Fabaeformiscandona latens* (KLIE, 1940)	*Fabaeformiscandona wegelini* (PETKOVSKI, 1962)	*Heterocypris reptans* (KAUFMANN, 1900)	*Pseudocandona albicans* (BRADY, 1864)	*Troglochaetus beranecki* DELACHAUX, 1921	*Anthrobathynella stammeri* (JAKOBI, 1954)	Type of habitat
OW4/C	15							1																												Stressed
KT2/A	15						165	7					1																	1						GWstable
KT1/A	15						147					33	44								2		1							45				4		GWrainfed
KT4/A	15	99			220		2206		5				2																							GWrainfed
KT4/B	15	186			103		1077		4				3																							GWrainfed
HB1/A	15	8			521		669																						2							GWrainfed
HB1/B	15	33			35		52																					1						1		GWrainfed
HB1/C	15	1			53		82																											4		GWrainfed
HB3/A	15			10	13		922						80					10			607		194	12											22	GWrainfed
HB3/B	15				1		339						3					1	2		24		5												9	GWrainfed
HB3/C	15						57						1						2		10		1												27	GWrainfed
MB3/B	14		10		20	39				20														1806												GWswb
MB4/B	14				70	44	4						12			4	5																1			GWswb
OW2/A	15				106			698		2																										GWswb
MB4/A	13		198		3301	80	40		84				1529			93	32			1						5							347			Hyporheic
OW3/HZ	13		714		164			2			10		9	1	1	87				110							7				89					Hyporheic

Table 3. Results of a SIMPER similarity test (for aggregated data of 13-15 sampling events per trap). SIMPER similarity for stressed sites calculated from all data of trap KT2/A. Key species cumulating to inner group similarity to > 60%.

Ecological group	Average faunistic similarity per sampling site	Index species	Contribution to groups inner similarity [%]
Stressed	6.76	*Diacyclops* cf. *languidoides* *Paracyclops fimbriatus* (FISCHER, 1853)	47.1 18.7
GWstable	78.44	*Diacyclops* cf. *languidoides* None	98.8 -
GWrainfed	58.02	*Diacyclops* cf. *languidoides* *Diacyclops bisetosus* (REHBERG, 1880)	55.3 19.8
GWswb	29.48	*Diacyclops bisetosus* (REHBERG, 1880) *Diacyclops crassicaudis* (SARS, 1863)	68.1 20.9
Hyporheic	43.69	*Acanthocyclops robustus* (SARS, 1863) *Diacyclops bisetosus* (REHBERG, 1880) *Attheyella crassa* (SARS, 1863)	28.6 27.3 23.3

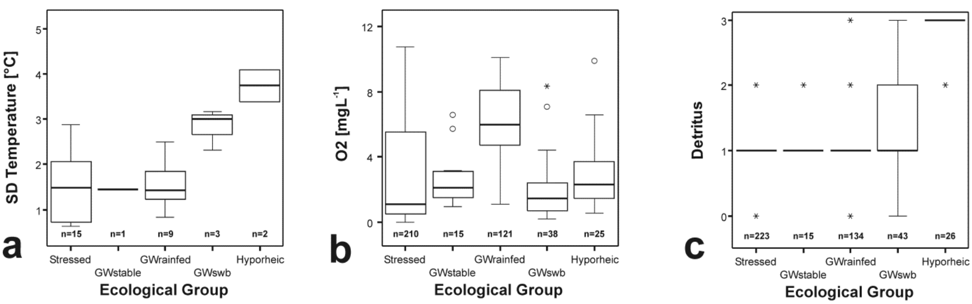

Figure 3. Standard deviations of environmental factors for each of the ecological groups. **a** Temperature [I =Stressed, II = GWstable, III = GWrainfed (recharged by precipitation), IV = GWswb (surface water body-recharged), V = Hyporheic] **b** DO-concentration, and c) detritus contents (estimated). Box = Inter-quartile range, vertical black bar = median; whiskers showing the lowest and highest non-outlier. Circles showing outliers and stars extreme outliers.

was in the same low range as groups (I) and (II). The percentage of stygobites was high (mean = 77.23%), with intermediate abundances (mean = 59.2 individuals/sample; Fig. 4b, c). The average SIMPER similarity was 58.02% and *Diacyclops* cf. *languidoides* was again the characteristic species, contributing with 55.31% to the inner similarity of this group. Only in this group – but not in all traps - amphipods (Table 2) were found in appreciable numbers.

GWswb habitats (IV) were found in the Haardtrand and in the Upper-Rhine-Plateau. These habitats were situated within only a few meters from a brook. This special vicinity was reflected by higher variances in GFI values (mean = 3.68, SD GFI = 3.52) and declining proportions of stygobites (mean = 61.14%; Fig. 4a, b) in comparison to groups (II) and (III) abundances that were found to be lower (mean = 66.4 individuals/sample) (median, Fig. 4c) than for group (III). The average SIMPER similarity (Table 3, Fig. 4d) for faunistic communities was 29.48% and the taxon contributing

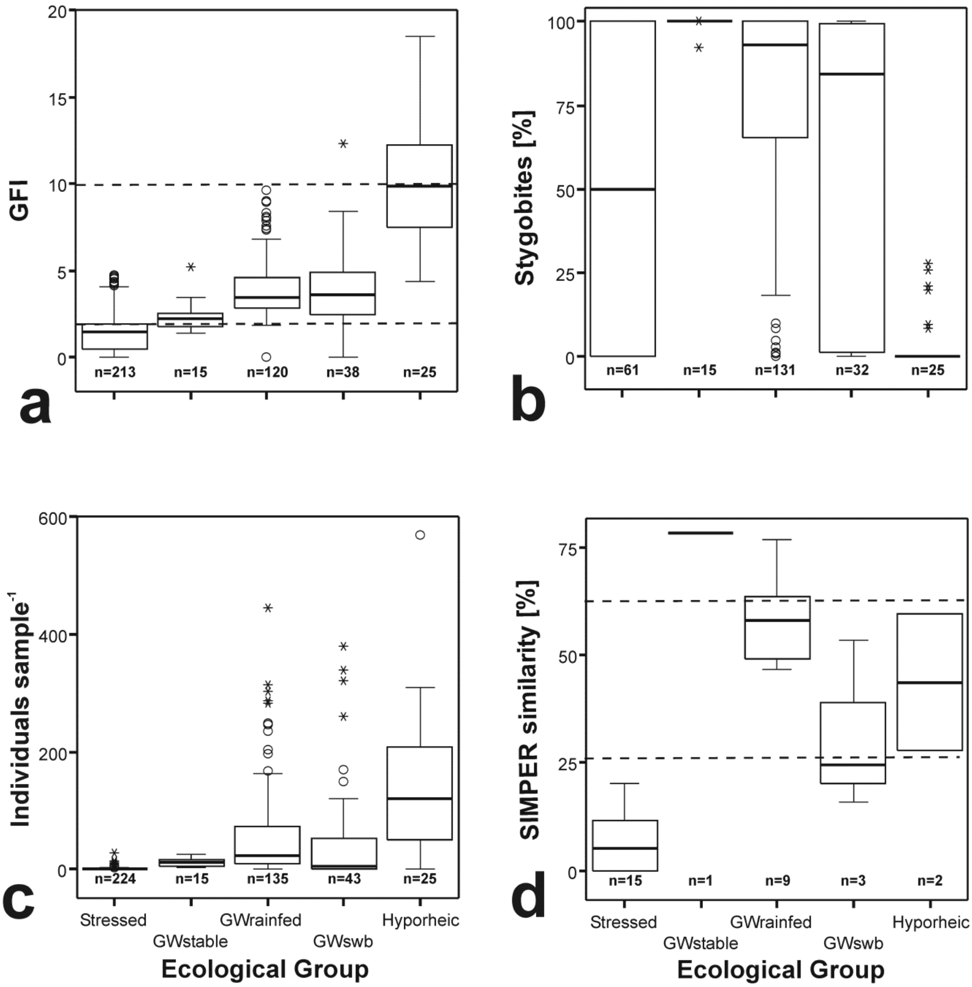

Figure 4. Boxplots on **a** Groundwater-Fauna-Index-values **b** percentage of stygobiotic species **c** Individuals per sample (one outlier omitted each in the groups GWrainfed, GWswb and Hyporheic) and **d** similarity [%] of faunistic communities in scaled ecological groups. Thresholds for alimony are marked by dashed lines (after Hahn 2006) in Fig. 4a and for faunistic stability (according to Gutjahr et al. 2013a) in Fig. 4d; n = number of samples, box = Interquartile range, vertical black bar = median; whiskers showing the lowest and highest non-outlier; circles showing outliers and stars extreme outliers.

most to the group's inner similarity was the cyclopoid *Diacyclops bisetosus* (Rehberg, 1880) (68.05%). The previous two types of habitats (III and IV) were characterised by a higher alimony (Fig. 4a).

Hyporheic habitats (V) were identified only in the Haardtrand and the Upper-Rhine-Plateau. The sampling sites were situated in the hyporheic zone of the brook. The influence of the flowing waters was reflected by the highest GFI values (mean = 10.41; Fig. 4a), by the highest numbers of individuals (mean = 265.5 individuals/sample) as well as by the lowest proportions of stygobites in all groups (mean = 4.49%;

Fig. 4b, c). The average SIMPER similarity here was 43.69% (Fig. 4d) and the most formative species for this group was the stygophilic cyclopoid *Acanthocyclops robustus* (Sars, 1863) with 28.60% contribution to the group's inner similarity (Table 3).

Discussion

Aquifers are an assemblage of habitats, where life is limited mainly by the supply of oxygen and organic carbon (Schwoerbel 1961, Husmann 1966, Williams and Hynes 1974, Strayer et al. 1997, Pospisil 1999, Datry et al. 2005, Schmidt and Hahn 2012). These characteristics could be reflected by the subterranean invertebrate communities, well described by the GFI and the SIMPER similarity in this survey. The SIMPER similarity calculated over samples per site or trap describes, in the broadest sense, the variability of faunal communities. High variability may be an indicator for stressors within a habitat (Gutjahr et al. 2013a). To simplify matters, other potentially important factors such as community assembly rules, biotic interactions and stochastic effects, are not considered here.

The distribution on the MDS ordination corresponds to the altitude of the sampling sites with the Pfälzerwald Mountains on top, and by the faunistic communities' composition as the proportions of stygobiotic fauna decrease and GFI values rise. Furthermore, GWrainfed habitats were found predominantly in the Pfälzerwald Mountains and GWswb habitats in the Upper Rhine Plateau. Species like *Niphargus aquilex* (Schioedte, 1855) do not indicate GWrainfed, but groundwater from adjacent fractured rock. *Diacyclops* cf. *languidoides* and *Diacyclops languidoides* (Lilljeborg, 1901) are considered to be typical of the Pfälzerwald Mountains and the Upper Rhine Plateau respectively (Hahn 2004, 2006), though the taxonomy of this group is still questionable. An overlapping of species, some of which typical for the Pfälzerwald and others which are typical for the Upper Rhine Plateau at the sampling sites of the Haardtrand, pointed towards a transition zone between two stygoregions: the Central Uplands and the South-Western Uplands (Stein et al. 2012). This posed the question as to whether a landscape effect or an aquifer-related effect is observed here, rather than general ecological patterns.

At the Haardtrand, all habitat types described in this study, with the exception of the rare GWstable, were found. However, GWrainfed site MB1 was not considered here due to low sampling frequency (four sampling occasions only). This site however, situated at the edge of the valley, was similar with respect to invertebrate assemblage to the GWrainfed habitats, situated 50 km apart.

Stressed habitats were observed all over the study area, which negated the assumption of an effect caused only by a transition between two stygoregions. Aquifer-related effects could be neglected, as all traps were situated in porous aquifers. However, the GWrainfed habitats of the Pfälzerwald were influenced by groundwater from the adjacent fractured rock aquifers (Hahn 2004). At the Haardtrand [MB] most types of habitats - excluding GWstable and GWsoilrech - were represented within an area of one hectare. This area constituted a small-scale example of the variability across all types of groundwater habitats of the whole investigated area. Having most types of habitats within the transition zone between two stygoregions (as delineated by Stein et al. 2012) indicated rather ecological and functional patterns than bioregional ones.

The five types of habitats identified here are considered distinct groundwater habitats. It was challenging to assess the ecological appartenance to a definite category for some of the traps. The MDS ordination clustered some of the traps as being "Stressed", whereas actually did comprise of stressed traps and GWswb traps (i.e. OW1/A and OW3/A). Since those traps were characterised by depleted faunal assemblages, with low SIMPER similarities (Gutjahr et al. 2013a) and surface water recharge (Hahn 2006) most seemed to take place as occasional pulse-like water intrusion from the surface. These two traps were also categorised as "Stressed". The proposed classification implies definitive parameters and may be categorised as an organisational indicator, but it cannot be assumed that each trap fits into one definitive category; there are gradients that could in fact delineate cryptic transitions between the idealised ecological groups characterised here. In accordance with former classification systems, a habitat synopsis is proposed here (Table 4).

Stressed habitats (I) were found in all natural investigated regions and constituted a heterogeneous group, comprising about 50 percent of all traps and were characterised by very harsh living conditions. Low oxygen concentrations and small pore spaces (compact aquifers), caused by iron ochre (e.g. KT3/A) or silt (e.g. MB4/C), as well as low amounts of OM acted as natural stressors in these traps (Fišer et al. 2012). The heterogeneity of this group was expressed by faunal communities as well as by abiotic parameters. Stressed habitats comprised two sub-types, indicating two different stressors. The first subtype was characterised by low OM availability at well-shielded locations mainly in the Pfälzerwald Mountains with very constant conditions, and secluded oligo-alimonic groundwater with low impact from the surface. However, there were sufficient DO-concentrations of > 1 mg L^{-1} for invertebrates, but there was virtually no stygobiotic fauna (e.g. KT2/B). This was indicated for example by the presence of species like *Diacyclops* cf. *languidoides*

Table 4. Proposal of a classification scheme of groundwater habitats by integrating former classifications on a local scale.

<table>
<tr><td>New classification approach</td><td>Stressed</td><td>GWstable</td><td>GWrainfed</td><td>GWswb</td><td>Hyporheic</td></tr>
<tr><td>Hahn (2006)</td><td colspan="2">Oligoalimonic</td><td colspan="2">Mesoalimonic</td><td>Eualimonic</td></tr>
<tr><td>GFI-value</td><td colspan="2">< 2</td><td colspan="2">2–10</td><td>> 10</td></tr>
<tr><td rowspan="2">Schmidt & Hahn (2012)</td><td colspan="2" rowspan="2">Old groundwater recharged by precipitation or surface water</td><td rowspan="2">Rainfed recharged by precipitation</td><td rowspan="2"></td><td>Surface water recharged</td></tr>
<tr><td>Groundwater / surfacewater ecotone</td></tr>
<tr><td>Gutjahr et al. (2013a)</td><td>Stressed sites</td><td>Stable sites</td><td colspan="3">Intermediate sites</td></tr>
<tr><td>Samples needed to catch 95% of occurring species</td><td>11.55</td><td>4.27</td><td colspan="3">5.79</td></tr>
<tr><td>SIMPER-similarity [%] (mean)</td><td>10.50</td><td>71.05</td><td colspan="3">46.23</td></tr>
</table>

or, especially for compact aquifers, by species of the genus *Parastenocaris* in low abundances. The second sub-type comprised traps which were almost permanently hypoxic (e.g. OW4/A) or affected by silt or iron ochre. Presumably, only occasional pulse-like surface water ingresses promoted significant supplies with DO, as for OM (e.g. OW1/A, situated directly at a gully) and ubiquistic invertebrates (e.g. the stygophilic cyclopoid *Diacyclops bisetosus*). Apart from these events, the impoverished fauna was dominated by tolerant *Parastenocaris* species (Hahn 1996, Matzke 2006). This statement was supported by the fluctuating proportions of stygobites and ubiquists at these sampling sites, as well as fluctuating standard deviations of temperature, low numbers of species and individuals. For such habitats Gutjahr et al. (2013a) proposed the term "Stressed", as they often exhibited low pore spaces, caused by ochry or silty sediments and harboured a depleted invertebrate fauna [see Hahn (2009), who named these "compact" sites]. These habitats required a high sampling effort (18.46 samplings) to collect 95% of the occurring species. Furthermore, the SIMPER similarities were comparatively low, indicating heavily fluctuating communities and a very high potential for stress. Sampling sites with GFI values lower than 2 are oligo-alimonic, according to Hahn (2006). A part of the stressed habitats would be interpreted as being "old groundwater", according to Schmidt and Hahn (2012), as they exhibited only low amounts of DO and/or OM, indicated by the lowest GFI within the study. In contrast to Gutjahr et al. (2013a) the latter two approaches did not distinguish stressed from stable habitats.

Gutjahr et al. (2013a) found faunistically and hydrologically stable habitats with little surface water influence at various depths all over the study area in Baden-Wuerttemberg, South-Western Germany. Within this study one stable trap was identified (KT2/A) in the group GWstable (II). For this habitat, the highest SIMPER similarity (78.4%), indicated very stable faunistic communities and it is assumed, that abiotic conditions are also stable here. Constantly low GFI-values (~2) indicated the upper boundary of the oligo-alimonium category. The stability was confirmed by a constantly low population and low numbers of species, but characterised by the highest percentages of stygobites. Stable habitats were characterised by a poor supply with OM and intermediate OM-values. However, they still offered enough OM and DO for the uncompetitive though tolerant stygobites, but not for ubiquists (Schmidt & Hahn 2012). DO concentrations were uniformly above the critical threshold for a permanent invertebrate colonisation (1 mg L^{-1}, Hahn 2006) and OM amounts are low, but still high enough to maintain stable invertebrate communities (Hahn 2006). These parameters indicate well-shielded groundwater with little influence from the surface. After Hahn (2006), it is believed that OM quality is lowest within GWstable habitats (with the exception of oligo-alimonic stressed habitats). Within the sampling period of fifteen months, a moderate surface water impact occurred only once. This statement was supported by one individual of the ubiquistic *Paracyclops fimbriatus* (Fischer, 1853) found in the trap. According to Schmidt and Hahn (2012), GWstable habitats (II) correspond to the "old groundwater ecosystem" with a very low influence of surface water. These ecosystems are secluded in depth and have low or almost no connectivity to the epigean environment.

While they were different in terms of the origin of the infiltrating water, the next two described habitat types (III and IV) shared some characteristics: since both were moderately influenced by surface water, well-supplied with OM and intermediately supplied with DO. The groups GWrainfed (III) and GWswb (IV) were both characterised by medium GFI values, with quite high proportions of stygobites and intermediate invertebrate abundances. With increasing surface water influence, the faunistic communities were replaced by ubiquitous species. One species characteristic of both groups and in all landscapes investigated was the ubiquistic *Diacyclops bisetosus*.

Habitats recharged by precipitation and water percolation through the soil profile (Schmidt and Hahn 2012) were grouped as GWrainfed (III), which comprised only of habitats recharged by groundwater from adjacent fractured rock, situated at the edge of the valleys and with moderate influence of intruding surface water. This was indicated by high amounts of DO (mean = 6.20 mg L^{-1}, which are typical for the Pfälzerwald Mountains) and typical species, such as the stygobiotic *Niphargus aquilex*. This species is a typical representative of the fractured aquifers in sandstones recharged by percolation water (Hahn 2006). GFI values between two and ten indicate meso-alimonic conditions (Hahn 2006). This group featured intermediate to high species richness and densities, intermediately stable habitats (in terms of DO and nutrient supply) and the strong dominance of stygobites. In terms of faunistic stability (i.e. SIMPER similarity, 58%) those habitats were found to be intermediately stable (Gutjahr et al. 2013a). This was also reflected by a high sampling efficiency of 4.13 samples necessary to collect 95% of the occurring species (Gutjahr et al. 2013a). Due to this, it is assumed that there are very few ingressions of surface water containing ubiquistic fauna, and subsequently no influence on the occurring faunal communities.

Unlike the abiotic conditions characteristic to GWrainfed, the group GWswb (IV) suggested surface water inputs from brooks, gullies and transient ponds, but not of soil water. The intrusion of surface water could take place much faster at these habitats than at GWrainfed, as higher standard deviations of temperature (mean = 1.52 °C for GWrainfed, mean = 2.84 °C for GWswb) and showed a subsequent immigration of epigean invertebrates. These habitats were less stable faunistically than those in group GWrainfed. The characteristic species to this group were the stygobiotic *Graeteriella unisetigera* (Graeter, 1910) and the ubiquistic *Diacyclops crassicaudis* (Sars, 1863), the latter known to be a riparian species (Dole-Olivier et al. 2000). However, *G. unisetigera* is not to be considered as an indicator of GWswb, but as a typical species of the Upper Rhine Valley (unpublished data). With GFI values from two to five GWswb, habitats have to be regarded as meso-alimonic habitats according to Hahn (2006). As GWswb habitats were all situated in the vicinity of surface waters, they were heavily influenced by epigean ecosystems (Schmidt and Hahn 2012). Sampling efficiency was, compared to GWstable and GWrainfed, relatively low (7.9 sampling events necessary to collect 95% of the occurring species, Gutjahr et al. 2013a). According to Gutjahr et al. (2013a) GWswb habitats should be classified as intermediately stable habitats with SIMPER similarities of roughly 29.5%.

The hyporheic (V) habitats exhibited the highest surface water influence and were regarded as being well-supplied with OM and intermediate DO-values (suggested by the highest registered scores of GFI, mean = 10.41) in combination with highest abundances (mean = 265.5 individuals /sample) and species diversity (Griebler and Mösslacher 2003). Despite being supplied in sufficient amounts of OM from the surface water, DO values were very intermediate here (as well as in GWswb), presumably due to respiration processes. Highest standard deviations of temperature (mean = 3.74 °C) indicated vast influences of surface waters. This epigean vicinity was also reflected by the faunal assemblages, which displayed the highest percentage of ubiquistic invertebrates (mean = 95.51%). Key species for this group were the ubiquistic epigean *Canthocamptus staphylinus* (Jurine, 1820), *Acanthocyclops robustus* (Sars, 1863), *Attheyella crassa* (Sars, 1863), *P. fimbriatus* and *Fabaeformiscandona wegelini* (Petkovski, 1962). With regard to alimonic conditions, ecotonal habitats have to be classified eu-alimonic according to Hahn (2006) with GFI values higher or equal to ten. According to Schmidt and Hahn (2012) these habitats have to be considered surface water recharged with an ecotonal character. As no drying out or sediment runoff events took place, there were intermediately stable faunistic communities in the hyporheos (SIMPER similarity 43.7%). 5.4 sampling occasions would have been necessary to collect 95% of the occurring species within this type of habitat. Although the trap HB2/HZ was situated in the hyporheic zone, it was supplied by deep, upwelling groundwater of the valley (Hahn 2005), similar to the nearby HB2/A (distance < 1m).

Different habitats can occur in a vertical stratification within wells. This is true for MB4, where the upper trap MB4/A was classified as hyporheic (V) due to surface water influence by the nearby brook. MB4/B in the middle was influenced faunistically by both groundwater and surface water and it was thus classified as GWswb. MB4/C was influenced by deep and predominantly hypoxic groundwater with sporadic pulses of surface water. This was indicated by low numbers of individuals and the occurance of the ubiquistic *P. fimbriatus*.

Vertical stratification is also true for KT1 and KT2. KT1/A was classified as GWrainfed, faunistically indicating the underground runoff from the hills slopes. KT2/A was found to be a trap with very constant abiotic conditions and very stable faunistic communities. KT1/B /C and KT2/B /C were traps with constant conditions, well DO supply but OM was lacking. These traps were classified as stressed habitats and due to the absence of food only low numbers of species and individuals could be found.

From these findings abiotic characteristics and community traits of the habitat types are proposed (Table 5).

Previous classification schemes of GW habitats by Hahn (2006), Schmidt and Hahn (2012) as well as by Gutjahr et al. (2013a) are convergent and can be combined to reflect a wider range of characteristics within the described habitats. Compared to other classification approaches, the approach presented here includes alimony as well as surface water connection and stress related parameters. At a landscape scale, the type of aquifer seems to drive the groundwater habitats (Gibert et al. 1997, Hahn and Fuchs 2009). However, all traps analyzed here are situated within porous aquifers, so that consequently statements on the aquifers influence on these communities are not

Table 5. Characteristics of the groundwater habitats proposed (- = low/little; o = intermediate; + = high/much); SIMPER similarity for stable sites calculated from all data of trap KT2/A. The table has orientational character; there may be gradients and smooth transitions. The columns are in accordance to those in Table 4.

	Type of habitat				
Traits	**Stressed**	**GWstable**	**GWrainfed**	**GWswb**	**Hyporheic**
metazoan abundance	-	-	o	o	+
number of species	-	-	+	+	+
% stygobites	variable, depending on site	+	o	o	-
alimony	variable, depending on site	-	o	o	+
oxygen	variable, depending on site	o	o	o	+
OM	variable, depending on site	-	o	o	+
stability	-	+	o	-	o
Samples needed to catch 95% of occurring species	18.46	5.4	4.13	7.9	5.4
SIMPER similarity [%] (mean)	15.75	78.44	46.73	28.84	40.45

possible – with one exception: the influence of fractured rock aquifers in the Pfälzerwald Mountains. Differences between two of the stygoregions described by Stein et al. (2012) were detected, but could not explain the groundwater invertebrates' distribution all over the investigated area. In particular, samples from the Haardtrand, the transition zone between the stygoregions Central Uplands and South-Western Uplands (Stein et al. 2012), harboured (with the exception of GWstable) all groups identified within this classification concept.

The groundwater habitats derived from faunistic data yielded in a five-class system provided valuable information for understanding patterns in the sampled region of the Palatinate, South-Western Germany and allowed the incorporation of former classification approaches. Gutjahr et al. (2013b) transferred the findings of this study to another local scale groundwater survey in Baden-Wuerttemberg, South-Western Germany, where four of the five habitats proposed here were identified. While limited to a comparatively moderate dataset from a specific region, we propose that this concept describes general patterns. Hence, it will be exciting to see whether this approach can be supported by further studies and study areas, including karstic regions.

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Supplementary material 1

Graphic output of a hierarchical cluster analysis (single linkage) of faunistic data.
Authors: Simon Gutjahr, Susanne I. Schmidt, Hans Jürgen Hahn
Data type: Statistical data.
Explanation note: Cluster analysis of the ecological goups' faunistic data based on a Bray-Curtis-similarity-matrix (calculated using a dummy variable).

Supplementary material 2

Output of the one-way ANOSIMS' pairwise test.
Authors: Simon Gutjahr, Susanne I. Schmidt, Hans Jürgen Hahn
Data type: Statistical data.

Supplementary material 3

Output of a Canonical Analysis of Principal Coordinates (CAP).
Authors: Simon Gutjahr, Susanne I. Schmidt, Hans Jürgen Hahn
Data type: Statistical data.