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Impact of Hydromorphology and Spatial Scale on Macroinvertebrate Assemblage Composition in Streams

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EDITOR'S NOTE:

This is 1 of 12 papers prepared by participants attending the workshop "Risk Assessment in European River Basins—State of the Art and Future Challenges" held in Liepzig, Germany on 12–14 November 2007. The meeting was organized within the framework of the European Commission's Coordination Action RISKBASE program. The objective of RISKBASE is to review and synthesize the outcome of European Commission FP4–FP6 projects, and other major initiatives, related to integrated risk assessment–based management of the water/sediment/soil environment at the river basin scale.

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ABSTRACT

Stream risk assessment and restoration requires understanding of the controlling factors and the scale at which they act. The role of hydromorphology, along with physicochemistry, was for a long time neglected, and scale issues were barely tackled. In this study, both the role of hydromorphology and the relevance of scale are studied. For this purpose, the macroinvertebrate community of the stream is used as the scale of the target biota. Next, the following research question is dealt with: At which scale, and to what extent, do hydrology and morphology along with physicochemistry explain stream macroinvertebrate distribution? Three data sets were used: The European AQEM study, the Dutch streams study, and an extensive habitat-preference study. Ordination was used to relate the macroinvertebrate species composition to the (hydromorphological) environment for both the European study and the Dutch stream study data. To explore the strength of one or more variables in explaining the macroinvertebrate distribution over the sampling sites, the fraction of the sum of canonical eigenvalues was used as a measure. To determine the preference for a specific habitat type of each macroinvertebrate species in the habitat preference study, the index of representation was calculated. The European study showed that streams within a more limited geographic area tend to carry macroinvertebrates whose distribution is better explained by stream stretch and in-stream variables. However, even within stream type catchment and stream valley, variables almost equally add to the explanation of the macroinvertebrates distribution. The explanatory power of hydrological and physicochemical variables increased toward smaller scales, and morphological variables showed an equal explanatory power over the different scales. In the Dutch streams study, stream level was much better explained in comparison to the habitat level. Geographical, morphological, and physicochemical variables were strong explanatory variables. For both habitat and stream, the stream stretch variables contributed most to the explanation of macroinvertebrate distribution, whereas microhabitat variables were less explanatory. The habitat preference study supported the observation that habitat provided less explanation than stream stretch. Only 15% of the macroinvertebrate species showed a clear habitat preference; none showed an obligatory one. In conclusion, stream macroinvertebrates distribution is best explained by local stream–stretch variables, provided those variables are contained within a catchment and stream valley context. Differences in vulnerability and biotic capacity between macroinvertebrate species determine the assemblage present. Applying this knowledge in water management means that any risk assessment and restoration effort needs a hydromorphological context.

Keywords: Risk assessment Restoration Management Key factor Macroinvertebrate distribution

INTRODUCTION

Stream risk assessment and restoration requires understanding of the controlling factors and the scale at which those factors act. The role of hydromorphology, along with physicochemistry, was for a long time neglected, and scale issues were barely tackled. In this study, both the role of hydromorphology and the relevance of scale are studied.

The extensive degradation of stream hydromorphology and concurrent loss of biological diversity resulting from human activities are of great concern in conservation and restoration (Karr et al. 1985; Williams et al. 1996). Losses of stream length, erosion of streambeds and banks, incision leading to valley droughts, groundwater depletion, intense flooding, and extinction of indicative and rare species are consequences of current stream management and policies (Naiman et al. 1995; Poff et al. 1997). The European Water Framework Directive (European Commission 2000) and Natura 2000 (European Commission 1997) strive to maintain and restore the self-sustaining functioning and ecosystem services of stream ecosystems. During the past decades, conservation and management actions have already been undertaken in different European countries to improve stream ecosystems (Verdonschot et al. 1994; Malmqvist and Rundle 2002; Newson and Large 2006). At the same time, risk assessment methods were being developed to evaluate success or failure of these programs.

Stream restoration began with a focus on healthy rivers, although the multiple targets and measures were often out of balance (Ormerod 2003). Restoration included cosmetic operations, aiming simultaneously at all aspects of ecosystem functioning. Many more-recent restoration practices were

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successful in terms of enhancing certain hydromorphological features, but nevertheless, they did not have an effect on the in-stream macroinvertebrate and fish community (Poff et al. 1997, Verdonschot and Nijboer 2002). Causes for these failures include that, among others, 1) the focus was often directed at only one set of pressures, either physicochemical water-quality properties or morphology; 2) the importance of the (catchment) hydrology was often underestimated; 3) the lack of scientific understanding about the basic ecosystem properties inherent in the management actions meant that a catchment-embedded ecosystem approach was not (fully) understood or implemented; and 4) the issues of scale were neglected.

Proper choices in stream and catchment management (risk assessment and restoration) require knowledge about the functions and interactions of the controlling factors. The baseline starts with the understanding that the catchment is part of the stream ecosystem (Hynes 1975). Within the catchment, the concept of the 4-dimensional nature of stream ecosystems, with a longitudinal, lateral, vertical, and temporal components, are a later focus (Ward 1989). the Ward (1989) concept identifies all interactions and functionings of a stream as an integral part of the whole catchment, and as such, this concept can be used as a frame for stream management. From a stream-restoration perspective, the 4 dimensional catchment concept must be broadened by including, among others, biotic interactions, dispersal, and ecological connectivity (Verdonschot 2000). All these considerations provide a conceptual basis for an understanding of catchment ecology, which Verdonschot (2000) defined as stream ecology embedded into a landscape ecological frame. To implement catchment ecology in stream management, the 5-S-Model was formulated (Verdonschot et al. 1998). This conceptual model provides guidelines for both stream restoration and stream assessment. It implies knowledge of hydrology–morphology–biota interactions, of spatial and temporal scales and their hierarchy (Frissell et al. 1986), and of the functioning of reference streams. Such and ecosystem approach to stream restoration and assessment is both complex and necessary in anticipating stream-restoration failure.

Large watersheds are composed of tributaries and their catchments. Tributaries contain multiple stream reaches; each reach, potentially, includes riffles, pools, and other habitat units; and these habitat units each contain multiple microhabitats (Sedell et al. 1990; Thomson et al. 2001). The multitude of processes that form stream systems exist within a hierarchical framework (Allan and Starr 1982; Frissell et al. 1986). The hierarchy theory provides a framework for describing the components of an ecosystem and their scaled relations (O'Niell et al. 1986; Jensen et al. 1996). The 2 key issues of scale and hierarchy are most crucial in stream restoration and assessment. The implementation of scale and hierarchy in the description of stream ecosystems involves explicitly characterizing the scaled relations between the patterns of interest, the ecological factors (processes) that determine those patterns, the spatial and temporal bounds of each, and the order in which they are nested.

The smallest resolvable area (grain), the area influenced by the phenomenon under study (extent), and the boundaries of the respective system decide the scale of observation in stream restoration and risk assessment. From the concepts of scale and hierarchy, it becomes clear that the stream ecosystem functioning depends largely on the natural flow regime. Stream flow can be seen as a master variable in the stream ecosystem (Power et al. 1995; Bunn and Arthington 2002). Stream flow is strongly correlated with the morphological characteristics of a stream, such as bed load, channel morphology, and substratum pattern. Because of their mutual dependence, hydrology and morphology are more often discussed together under the term "hydromorphology."

Still, what roles hydrology and morphology play, at which scale, in stream ecosystems can be questioned because morphology, especially, is often based on a human (visual) perspective. To answer that question, the scale of the ecosystem must first be set. Macroinvertebrates are one of the most important and indicative organismal groups in lowland streams. In a natural lowland stream, they comprise the larger part of the ecosystem and include both generalists and specialists (e.g., Allan and Johnson 1997). High numbers of taxa inhabit streams, and they all differ in sensitivity to different ecosystem components (e.g., Cummins and Lauff 1969) and to different temporal and spatial scales (e.g., Feld and Hering 2007). This makes macroinvertebrates well suited as indicators of hydromorphological conditions over different scales and, thus, of the success or failure of restoration efforts.

Next, the following research question was dealt with in this study: At which scale (European, regional, habitat) and to what extent do hydrological and morphological variables explain stream macroinvertebrate distribution?

MATERIALS AND METHODS

Data sources

To answer the research question, data collected in 3 different field studies were used:

- The project for the development and testing of an integrated Assessment system for the ecological Quality of streams and rivers throughout Europe using benthic Macroinvertebrates (AQEM) (Hering et al. 2004): A research project on the development and testing of an integrated assessment system for the ecological quality of streams and rivers throughout Europe using benthic macroinvertebrates.
- The Dutch streams study (van Walsum et al. 2001): A research project on the effects of climate change on lowland stream catchments and their macroinvertebrate inhabitants.
- A habitat-preference study: An inventory of the substratum/habitat binding of lowland stream macroinvertebrates in the Netherlands.

Macroinvertebrate data collection and elaboration—The macroinvertebrate samples within the European AQEM study were taken in 2000 and 2001 from 889 streams, distributed over the 29 stream types of different quality classes and 8 countries (Hering et al. 2004). Sampling followed the guidelines described in the AQEM manual, which included site selection, sampling strategy, and processing (AQEM consortium 2002; Hering et al. 2004).

The macroinvertebrate samples within the Dutch stream study were collected 3 times in 1998 to 1999 from 9 upper watercourses of near-natural, soft-bottomed, lowland streams (van Walsum et al. 2001). The selected streams were distributed throughout the country and represented different hydrological regimes. The subsamples were taken by means of a 10- $\times$ 15-cm macrofauna shovel (sampled surface area: 150

Table 1. Number of samples per major region, region, and stream type in Europe. (ME = middle-eastern, SW = south-western)

Major region	Region	Stream type[a]	Nr of samples
Mountains	Low alpine	A01	24
Mountains	High alpine	A02	26
Mountains	High alpine	A03	26
Mountains	Low alpine	A04	24
Mountains	Low alpine	C14	24
Mountains	Low alpine	C15	28
Mountains	Low alpine	C16	22
Lowland	Central lowlands	D01	24
Lowland	Western lowlands	D02	15
Lowland	Central lowlands	D03	54
Mountains	Low alpine	D04	58
Mountains	Low alpine	D05	40
Mediterranean	ME Mediterranean	H01	25
Mediterranean	ME Mediterranean	H02	25
Mediterranean	ME Mediterranean	H03	29
Mountains	High alpine	I01	33
Mediterranean	ME Mediterranean	I22	22
Mediterranean	ME Mediterranean	I23	23
Mediterranean	ME Mediterranean	I24	22
Lowland	Western lowlands	N13	63
Lowland	Western lowlands	N14	93
Mediterranean	SW Mediterranean	P01	15
Mediterranean	SW Mediterranean	P02	11
Mediterranean	SW Mediterranean	P03	13
Mountains	Northern Scandinavia	S01	30
Mountains	Northern Scandinavia	S02	30
Mountains	Northern Scandinavia	S03	30
Mountains	Northern Scandinavia	S04	30
Lowland	Central lowlands	S05	30

[a] A = Austria; C = Czech Republic; D = Germany; H = Greece; I = Italy; N = The Netherlands; P = Portugal; S = Sweden. The numbers are national stream type number codes.

cm^2). At each site, the 5 major substratum types were subsampled, and subsamples were aggregated. This resulted in a total of 27 samples.

A total of 604 habitat-specific macroinvertebrate samples were taken from 16 different Dutch lowland streams between 1995 and 2002, within the habitat preference study. The habitat samples were taken by using a 10- × 15-cm macrofauna shovel (sampled surface area: 150 cm^2). The resulting taxa abundances were treated as such.

In all studies, identification took place to the species level, whenever possible. Before analysis, it was necessary to conduct a taxonomic adjustment on the macroinvertebrate data to ensure unambiguous data processing. Otherwise, differences in taxonomic level could later prove to be the cause of differences between species groups and samples. We used a weighted taxonomic adjustment according to the criteria listed by Nijboer and Verdonschot (2000) and Vlek et al. (2004). All macroinvertebrate data were $\log_2$-transformed before analysis.

Environmental data collection—In the European study, a large number of parameters describing the stream and its surroundings were recorded at each sampling site using a standardized site protocol. The site protocol included 222 parameters and covered characteristics of the (supra)catchment, the stream stretch and its surroundings, and the in-stream environment (AQEM consortium 2002). Some physicochemical parameters were analyzed at the respective laboratories according international (International Standards Organization [ISO]) or European (Centre Européen pour la Normalisation [CEN]) standards.

In the Dutch streams study, 113 variables describing the stream stretch and its habitats were recorded at each sampling site using a standardized field protocol. The discharge was registered continuously throughout a 15-month period. In each 5th week, the percentages of cover for major substrata were estimated throughout a 30-m stretch of each stream. Samples for grain-size analysis and organic matter content were taken from the major substratum types. The chemical variables were analyzed in the laboratory according to ISO standards.

From the habitat preference study, only the 8 predefined habitat types (macrophyte vegetation, wood/branches, leaves, detritus, mud, clay, sand, and gravel) were used in the analysis. The habitat types were directly recorded in the field during sampling.

All environmental variables were $\log_{10}$-transformed to avoid effects of a skewed parameter distribution.

Ordination analyses

The European study data were split into 4 geographical levels of data sets. All data together composed the European data set. Next, the European data set was split into the 3 major regions: lowlands, Mediterranean areas, and mountains (Table 1). Each of these 3 major regions was thereafter split into regions. The lowlands were split into the western and the central lowlands, the Mediterranean data were split into the middle-eastern and the southwestern Mediterranean data, and the mountain data were split into the low alpine, high alpine, and northern Scandinavia regions. Finally, these 7 regions were split according to stream type for a total of 29 types (see Table 1 and further details in Verdonschot and Nijboer 2004).

Table 2. Classification of the European study data according to the spatial scale at which they act and the variable group to which they belong to

Category of variables	Group name	Nr of variables included
Scale	Supracatchment	29
	Catchment	31
	Stream valley	35
	Stream stretch	55
	In-stream	43
Variable group	Climate	7
	Geography	22
	Geology	10
	Hydrology	13
	Morphology	79
	Physicochemistry	27

Next, all data sets within the European study were used to test the importance of scale and of groups of variable. For that, all environmental variables were either classified according to 5 scale levels: supracatchment, catchment, stream valley, stream stretch, and in-stream; or to 6 variable groups: geography, climate, hydrology, morphology, and physicochemistry. Thus, the environmental variables were classified according to the spatial scale at which they act and the variable group to which they belong (Table 2). For example, stream density is a hydrological variable at the catchment level, and phosphate concentration is a physicochemical variable at the in-stream level.

Ordination was used to relate the composition of macroinvertebrate species to the (hydromorphological) environment for both the European study and the Dutch stream study data, separately. Ordination was carried out using canonical correspondence analysis (CCA; ter Braak 1987), as part of the program CANOCO for Windows, version 4.0 (ter Braak and Šmilauer 1998). Canonical correspondence analysis is a direct ordination technique, which means that the environmental variables are directly related to the species composition at the sites. The ordination axes in CCA are chosen as linear combinations of the environmental variables. The option to down-weight rare species was used because emphasis was given to more commonly distributed species. Hill scaling was performed and focused to intersample distances (ter Braak and Šmilaur 1998).

To explore the strength of one or more variables in explaining the macroinvertebrate distribution over the sampling sites, the sum of canonical eigenvalues (SCE) was used as a measure. This measure expresses the total contribution of environmental variables included in an analysis to the explanation of the macroinvertebrate distribution. Only those variables that significantly contributed ($p > 0.05$ in an unrestricted Monte Carlo permutation test with 499 runs) to the explanation of the ordination diagram of axis 1 and 2 were included in the analysis. In other words, those variables that explained the macroinvertebrate distribution over the samples were included.

To investigate the contribution of one (or of each of the variable and scale groups) variable to the explanation of the macroinvertebrate distribution, the SCE of the one-variable–based analysis was divided by the SCE of the same analysis using all variables and expressed as the fraction of SCE. Because the SCE of the analysis using all variables is always higher than

Table 3. Number of habitat samples per habitat type in the habitat preference study

Habitat type	Nr of samples
Branches/wood	11
Leaves	93
Detritus	113
Mud	75
Clay	3
Sand	128
Gravel	113
Vegetation	68

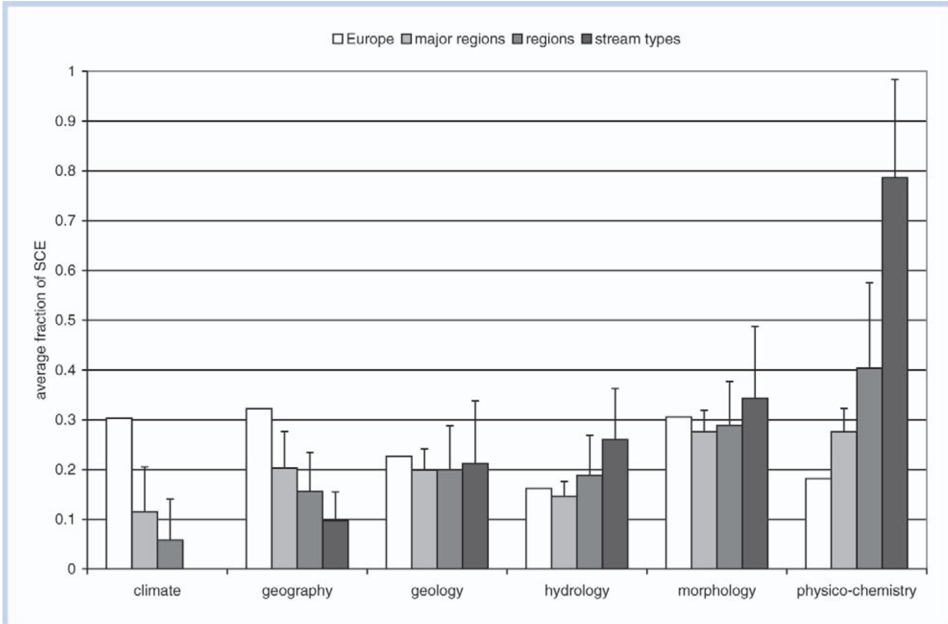

Figure 1. The explanatory strength of groups of environmental variables, expressed as the average fraction of the sum of canonical eigenvalues (SCE), for the scale of Europe, the major regions, the regions, and the stream types.

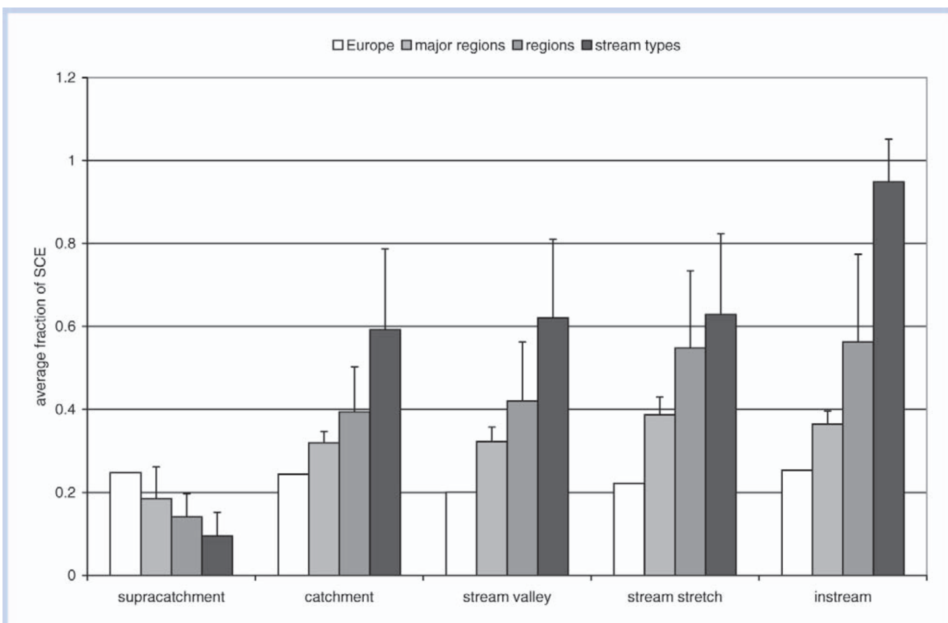

Figure 2. The explanatory strength of environmental variables grouped according to their spatial scale of impact, expressed as the average fraction of the sum of canonical eigenvalues (SCE), for the scale of Europe, the major regions, the regions, and the stream types.

one-variable–based analysis, the fraction of SCE is a number between 0 and 1. If the fraction of SCE is close to 0, the variable (group) explains only part of the macroinvertebrate distribution; if the fraction of SCE is close to 1, the variable (group) strongly explains the macroinvertebrate distribution.

Habitat preference analyses

To investigate taxon-specific habitat preferences, the habitat-preference study data were used. First, the species distribution over 8 habitat types (Table 3) was tested against random distribution with chi-squared analyses. Next, to determine the preference of each macroinvertebrate species for a specific habitat type, the index of representation (IR) was calculated, according to Hildrew and Townsend (1976). As some taxa occurred in low numbers or were not identified to the species level, the results would not be a reliable interpretation of habitat preferences. Therefore, only those taxa that met the following criteria were included in the analyses:

- More than 5 total specimens were found,
- The distribution throughout the 8 habitat types significantly deviated from a random distribution, and
- Taxa were identified to the species level unless all taxa within a higher taxonomical group could be assumed to have similar habitat requirements.

Table 4. Canonical correspondence analysis (CCA) ordination characteristics of the stream data within the Dutch streams study

Axes	1	2	3	4	Total
Eigenvalues	0.403	0.263	0.223	0.192	—
Species–environment correlations	0.994	0.991	0.995	0.995	—
Cumulative % variance of species data	15.1	25	33.4	40.6	—
Cumulative % variance of species–environment relation	19.5	32.2	43	52.2	—
Sum of all eigenvalues	—	—	—	—	2.663
Sum of all canonical eigenvalues	—	—	—	—	2.069

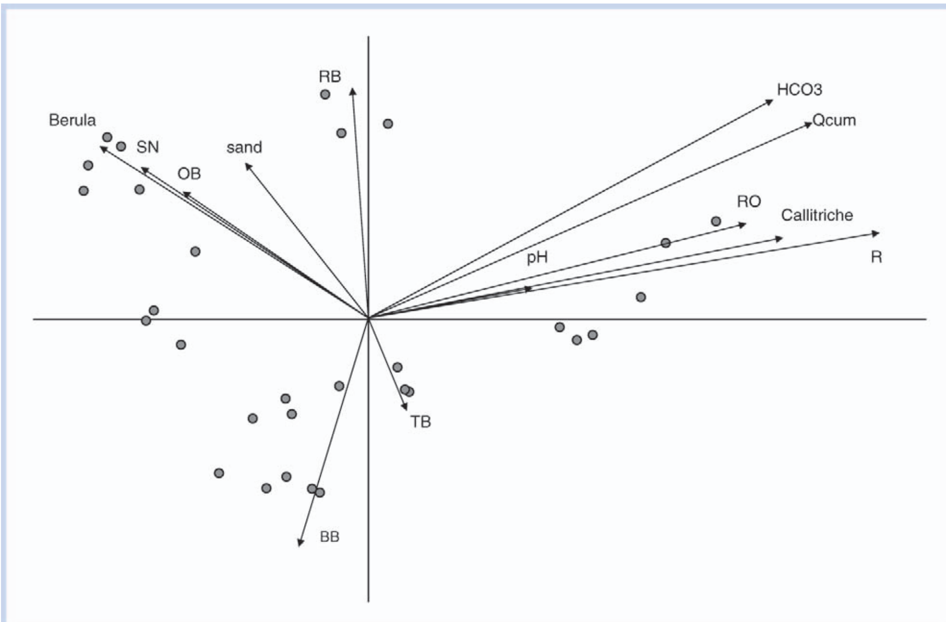

Figure 3. Canonical correspondence analysis (CCA) ordination diagram of axis 1 and 2 of the stream samples from the Dutch stream-study data. Arrows show the significant explanatory variables. Labels indicate the samples (●). Codes SN, OB, RO, TB, and BB refer to individual streams, Qcum = cumulative discharge (m^3/s), Berula = *Berula erecta* vegetation, Callitriche = *Callitriche* spp. vegetation, sand = sand substrate.

Table 5. Canonical correspondence analysis (CCA) ordination characteristics of the habitat data within the Dutch streams study

Axes	1	2	3	4	Total
Eigenvalues	0.391	0.266	0.221	0.176	—
Species–environment correlations	0.955	0.898	0.893	0.912	—
Cumulative % variance of species data	6.6	11	14.8	17.7	—
Cumulative % variance of species–environment show relation	19.6	32.9	44	52.8	—
Sum of all eigenvalues	—	—	—	—	5.958
Sum of all canonical eigenvalues	—	—	—	—	2

RESULTS

European study

Climate and geography both strongly explained the variable groups in the macroinvertebrate distribution within the overall European data set, but their explanatory power decreased going from major region to region to stream-type data sets (Figure 1). Geology showed an equal explanatory score for each set of data. Hydrology increased in explanatory power in regional data sets and increased even more in stream-type data sets. Morphology showed an equal explanatory power throughout the different data sets, although in

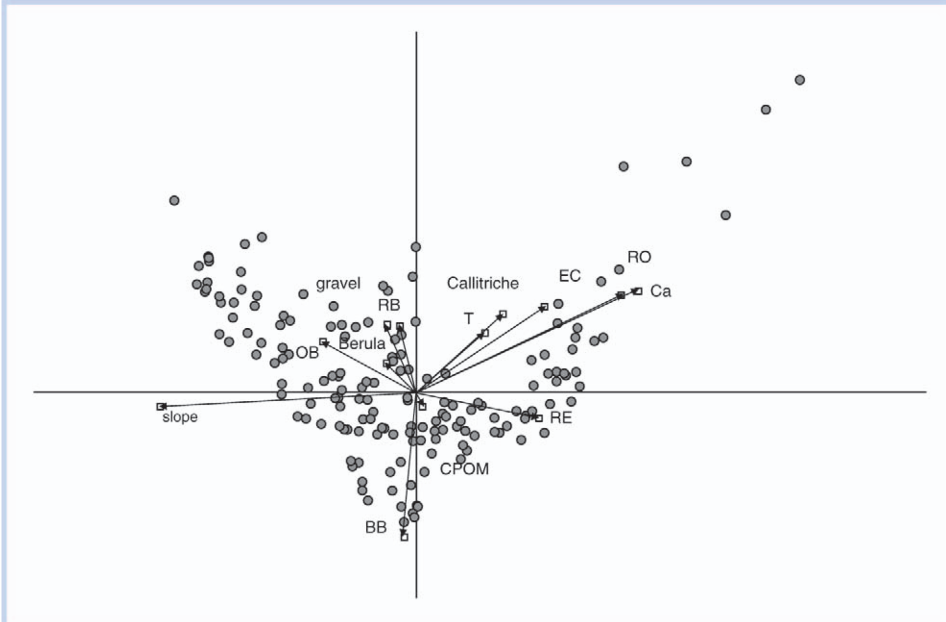

Figure 4. Canonical correspondence analysis (CCA) ordination diagram of axis 1 and 2 of the habitat samples from the Dutch stream-study data. Arrows show the significant explanatory variables. Labels indicate the samples (●). Codes OB, RB, RO, and BB refer to individual streams, EC = electric conductivity, Berula = *Berula erecta* vegetation, Callitriche = *Callitriche* spp. vegetation, gravel = gravel substrate, T = temperature (°C), CPOM = coarse particulate organic matter.

absolute terms, it explained more, in comparison to climate, geography, geology, and hydrology. Physicochemistry had a low explanatory power for the European data set, but its explanatory power increased strongly in stream-type data sets. For the latter, its average fraction of SCE reached as high as 0.8, explaining most of the variation.

Ordering the environmental variables according to scale shows that the supracatchment variables decreased in explanatory power going from the European data set toward the stream-type data sets (Figure 2). All 4 of the other scale levels showed a comparable tendency of increasing explanatory power going from the European data set toward the stream-type data sets. Thus, streams within a more limited geographic area tend to carry macroinvertebrates whose distribution is better explained by stream stretch and in-stream variables. However, even within stream type, catchments and stream-valley variables almost equally added to the explanation of the macroinvertebrates distribution.

Dutch stream study

The Dutch stream study resulted in 2 CCA–ordination diagrams that showed the relationship between macroinvertebrate distribution and both the stream (Table 4 and Figure 3) and habitat variables (Table 5 and Figure 4). The variables shown are significant explanatory variables and were selected using forward selection ($p = 0.05$; unrestricted Monte Carlo permutation test).

Each stream was defined as a nominal variable and was used as a geographical variable. Out of 10 streams, 6 appeared to have significant explanatory variables at the stream-level analysis. The first axis is explained by the hydraulic radius (R) and by the cumulative yearly discharge (Qcum). The larger streams, like the Rosep stream (RO), point to the right of the diagram, and the smaller ones, like the Springendal stream (SN) and the Old stream (OB), point to the left. The larger streams have a higher pH and bicarbonate concentration and are occupied by *Callitriche* sp. vegetation. The smaller streams are occupied by *Berula* sp. vegetation and are more sandy. The second axis mainly shows the gravel dominated Red stream (RB) versus the organic material–dominated Forest stream (BB) and, to a much lesser extent, the Tongerense stream (TB). In conclusion, at the stream level, the major characteristics of the stream (discharge, size, major bottom composition) strongly influenced the macroinvertebrate composition.

Out of 10 streams, 5 appeared to have significant explanatory variables at the habitat level of analysis. The first axis is explained by slope, conductivity, and calcium concentration, which were high in stream RO. The streams with a higher slope, like the SN and OB streams neither shown in the diagram), are situated in the left of the diagram, and the more flat, valley streams, which were also larger, like the RO and the Reusel stream (RE), are situated in the right. The larger streams with a gradual slope are occupied by *Callitriche* sp. vegetation and showed higher water temperatures. The smaller streams with a steeper slope are occupied by *Berula* sp. vegetation. The

Table 6. Classification of the Dutch stream study data according to the spatial scale at which they act and the variable group to which they belong

Category of variables	Group name	Nr of variables included
Scale	Stream stretch	34
	Habitat	46
	Microhabitat	30
Variable group	Geography	10
	Hydrology	3
	Hydromorphology	6
	Morphology	66
	Physicochemistry	25

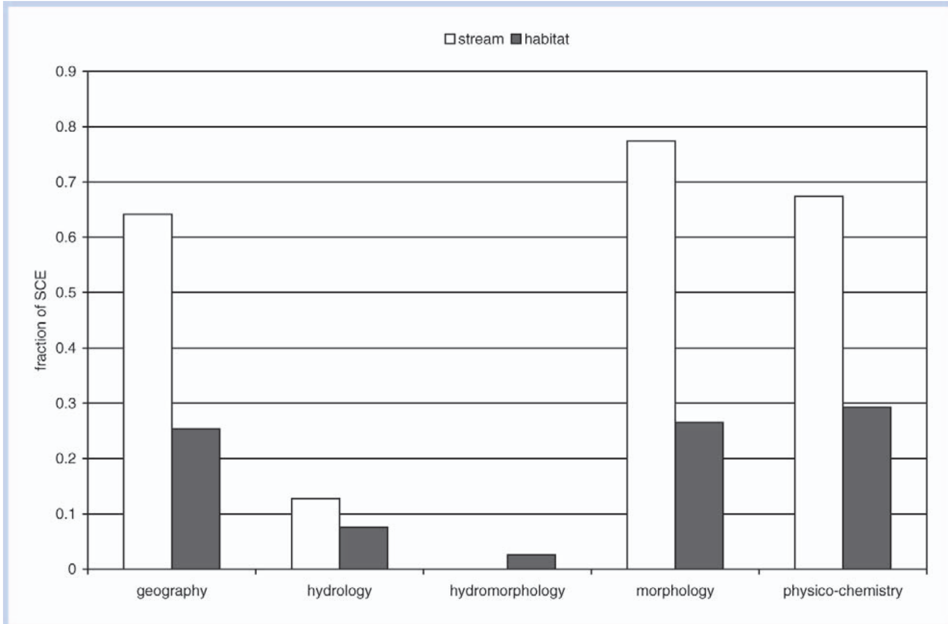

Figure 5. The explanatory strength of groups of environmental variables, expressed as the average fraction of the sum of canonical eigenvalues (SCE), for the stream and habitat samples of the Dutch streams study.

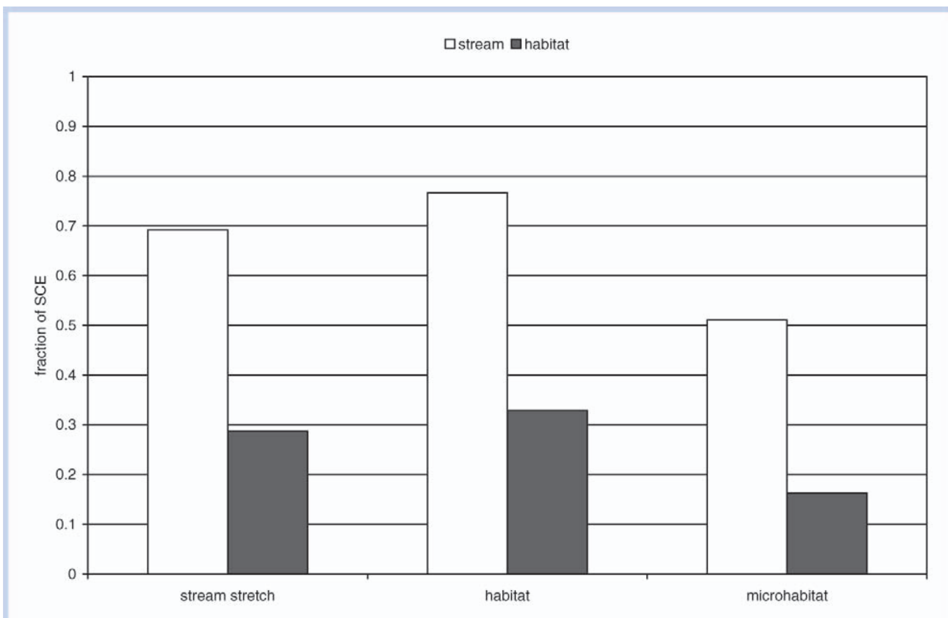

Figure 6. The explanatory strength of environmental variables grouped according to their spatial scale of impact, expressed as the average fraction of sum of canonical eigenvalues (SCE), for the stream and habitat samples of the Dutch streams study.

second axis mainly showed the gravel-dominated RB versus the organic material–dominated BB stream with a high course particulate organic mater (CPOM) content.

Although some explanatory variables differed between the stream-level and habitat-level analysis, the general pattern, as well as most variables, was the same.

Both stream and habitat data sets were also used to test the importance of scale and variable group. Therefore, all environmental variables were classified into 3 scale levels: Stream stretch, habitat, and microhabitat; and into 5 variable groups: Geography, hydrology, hydromorphology, morphology, and physicochemistry. Thus, the environmental variables were classified according to the spatial scale at which they acted and the variable group to which they belonged (Table 6). For example, cumulative discharge is a hydrological variable at the stream-stretch scale, and grain-size class gravel is a morphological variable at the micro-habitat level. The importance of each of the variable groups, in terms of the fraction of SCE, and the relevant scales were calculated using CCA.

The aggregated data at stream level provided much better explanations than the habitat-level data (Figure 5). Geography, morphology, and physicochemistry variables were strongly explanatory variable groups, and the morphology variables were most explanatory. Surprisingly, the hydro-morphology variables did not explain any of the variation in the macroinvertebrate data. Almost the same pattern was seen in the habitat data set. Again, geography, morphology, and physicochemistry variables contributed the most to the explanation, although 3 times less in comparison to the stream-level data, whereas the physicochemistry variables explained the most.

Concerning scale, Figure 6 shows that, again, the explanatory power of the environmental variables is 3 times higher in the stream-level data than in the habitat-level data. Habitat-level data seem to be much more heterogeneous in comparison to the data aggregation at stream level. For both habitat and streams, the stream-stretch variables contribute the most to the explanation of macroinvertebrate distribution. Microhabitat variables contribute less to the explanation.

Habitat preference study

From the total number of 547 taxa, 192 taxa (35%) were distributed in a manner that significantly deviated from random ($p < 0.05$). No Bonferroni correction was used, and it can, therefore, be expected that, with 547 significance tests, significant nonrandom distributions should occur in 27 taxa based on random expectations (i.e., 27 of the 192 significant chi-square results may have occurred randomly). Of the 192 nonrandomly distributed taxa, 128 taxa met the criteria to be useful in a habitat-preference analysis. Table 7 summarizes the results of the chi-square and IR analyses for the 128 nonrandomly distributed species. According to Tolkamp (1980), IR values are especially meaningful when they deviate more than 2 from 0, with positive values indicating a preference for the habitat type and negative values indicating aversion. Each habitat type had a substantial number of species representing either preference or aversion (Table 8), except for the clay habitat type, which had only 4. However, this result should be interpreted with caution because the low number of representative taxa for clay could be caused by the low number of samples for that habitat type (Table 3).

Taxa can not only show a preference for a particular habitat type but also a preference or aversion for other habitat types. For example, Figure 7 shows the taxa with a preference for leaves and a preference or aversion for the other habitat types. It becomes clear that taxa with a leaf preference often have an aversion for sand or gravel. On the other hand, they may also prefer detritus, branches/wood, and vegetation.

To determine whether habitat preferences differed uniquely, the IR scores of pairs of habitat types were correlated. Table 9 shows only the significant differences. The mineral habitat types (sand, gravel) often differed significantly from the organic ones (branches/wood, leaves, detritus, mud). Gravel differs the most from the other habitat types. Branches/wood and vegetation are the most different. Thus, the hard substrata were more often are inhabited by a preferent fauna. More than half of the habitat-type combinations did not differ significantly. In total, 84 taxa (66%) of the 128 taxa with a habitat preference preferred only one habitat type, either with or without an aversion to one or more other habitat types (Figure 8 and Table 8).

Table 7. Total number of taxa with a habitat preference (index of representation [IR] > 2.0) or aversion (IR < -2.0) per habitat type

Habitat type	Preference	Aversion
Branches/wood	26	0
Leaves	25	6
Detritus	26	3
Mud	5	4
Clay	4	0
Sand	5	36
Gravel	16	30
Vegetation	65	2

Table 8. Number of taxa and the number of habitat type preferences or aversions

	Nr of habitat types	
Nr of taxa (%)	Preferences	Aversions
2 (2)	3	2
2 (2)	3	1
9 (7)	2	2
14 (11)	2	1
14 (11)	2	0
1 (1)	1	3
8 (6)	1	2
23 (18)	1	1
52 (41)	1	0
2 (2)	0	1

DISCUSSION

Hydromorphology gets more and more attention in stream (risk) assessment and restoration. This is partly due to the number of stream restoration projects that fail to succeed after physicochemical measures have been taken (e.g., Verdonschot and Nijboer 2002). Besides, the inclusion of hydromorphology in several European directives also adds to this attention. Finally, physical features of steams are easy for the human eye to recognize and classify. Visual features are easy to detect and are often linked to ecological structure and functioning without testing correlative or causal relations.

Hydromorphological risk assessment implies knowledge of the significant ecological differences between the natural and the degraded hydromorphological state of a stream. A high number of morphology-based assessment systems were developed during the past decades (e.g., US Fish and Wildlife Service 1981; Werth 1987; Ohio EPA 1989; Plafkin et al. 1989; NRA 1992; Petersen 1992; Friedrich et al. 1993; Raven et al. 1997; Agences de l'Eau & Ministère de l'Environnement 1998; Muhar et al. 1998; Siligardi et al. 2000; Braioni et al. 2001; Feld 2004). These indices include a high number of metrics, most often based on stream valley, stream stretch, or in-stream variables. Morphology-based quality assessment evaluates physical stream characteristics that are controlled by fluvial processes and human interference. Until now, hydrology played a minor role, and most hydrology-based metrics oversimplify the complexity of stream ecosystems by

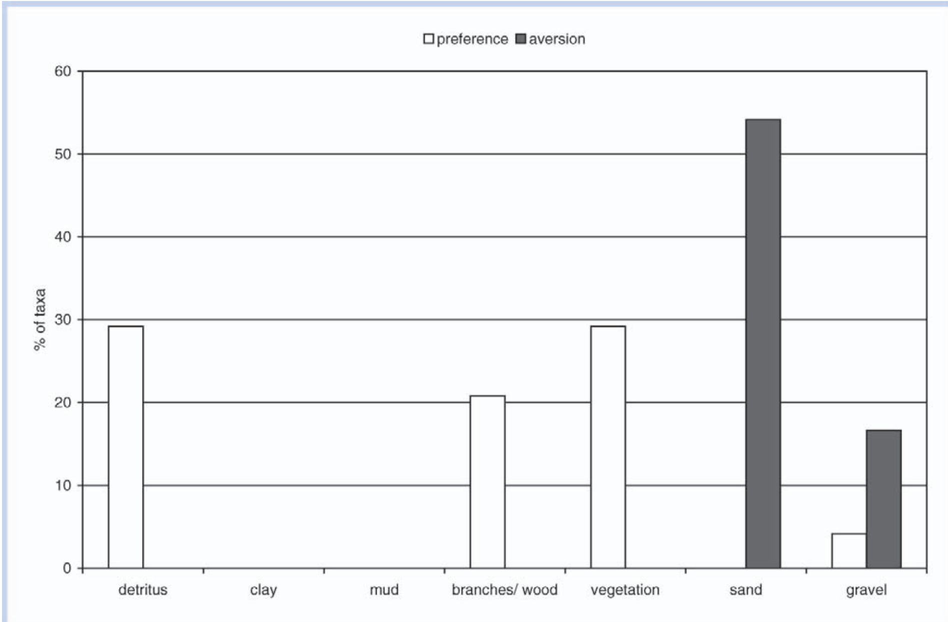

Figure 7. The percentage of taxa with a significant preference for leaves ($n = 24$), which also indicated a preference or aversion for other habitat types.

Table 9. The significant correlations ($n_{taxa} = 128$, $p > 0.05$) between the 8 habitat types in the habitat-preference study

Habitat type	Branches/wood	Leaves	Detritus	Mud	Clay	Sand	Gravel	Vegetation
Branches/wood	—	—	−0.42	0.25	—	−0.18	—	—
Leaves	—	—	—	—	—	−0.62	−0.32	—
Detritus	—	—	—	—	—	—	−0.53	−0.2
Mud	—	—	—	—	—	—	−0.38	−0.19
Clay	—	—	—	—	—	—	—	—
Sand	—	—	—	—	—	—	—	—
Gravel	—	—	—	—	—	—	—	−0.25
Vegetation	—	—	—	—	—	—	—	—

describing flow regimes based on the average daily discharge or the mean annual flow (Gordon et al. 1992), except for a few that characterized more ecologically relevant attributes of a flow regime (e.g., Bovee 1982; Nestler et al. 1989; Richter et al. 1996, 1997). Still, one might ask to what extent hydrological and morphological assessments are based on human perspectives and not the needs of the benthic invertebrate fauna.

Raven et al. (2002) compared 3 major hydromorphological stream-assessment methods, and Parsons et al. (2002) compared 7. The Parsons et al. (2002) results are summarized in Table 10. Parsons et al. (2002) and Raven et al. (2002) also each summarized the major problems encountered in the current hydromorphological assessment systems and indicated necessary improvements by including:

- A meaningful stream typology with (quantified) reference conditions (see also Nijboer et al. 2004),
- Catchment, mesohabitat, and microhabitat features (see also Tickner et al. 2000),
- Only those hydromorphological features that link to aquatic biota (see also Harper et al. 1995),
- Geomorphological characters that help to predict hydrological and hydraulic behavior in the channel (see also Newson et al. 1998), and
- Temporal scale.

Both the European study and the Dutch stream study showed the ecological importance of hydrology, especially at the larger scale in the European study, and morphology in explaining the macroinvertebrate distribution. Both studies also stressed the importance of physicochemical parameters. Thus, no stream restoration or stream risk assessment and management can be focused exclusively on hydrology, morphology, or physicochemistry, but must deal with all 3 groups of variables. Furthermore, not all variables contributed equally to the macroinvertebrate distribution. In most cases a limited number of explanatory variables (about 10) were sufficient to explain the distribution.

Frequently, a hierarchy has been described (Hart and Fonseka 1996) in which, in polluted rivers, hydromorphological variables are less important for macroinvertebrate assemblages than in unpolluted streams. However, understanding of the role played by human-related individual stressors under multiple stress conditions, often referred to as "general

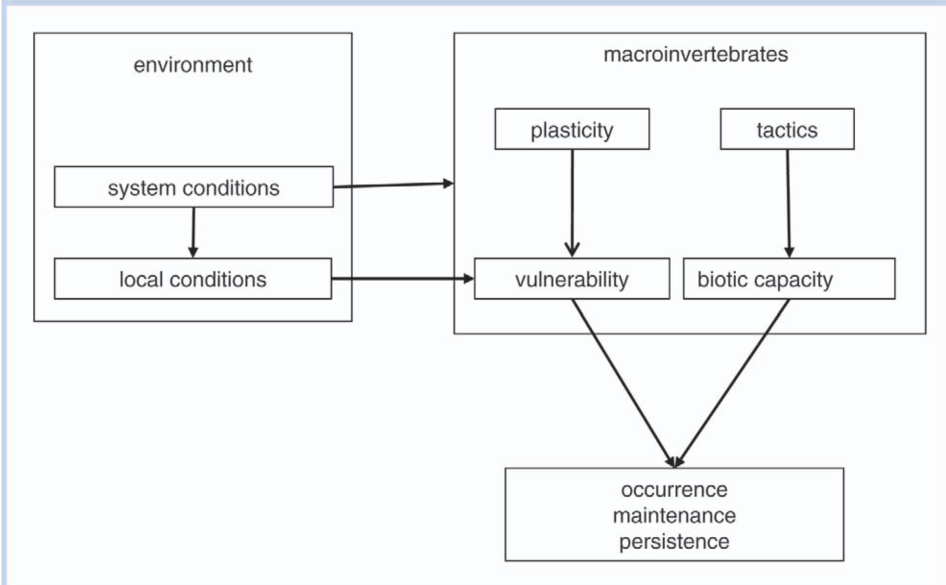

Figure 8. General scheme of selective forces determining a local macroinvertebrate assemblage.

Table 10. Evaluation of 7 river assessment methods against scale, ecological relevancy, link to a reference state, and inclusion of processes. The representation of each of the features by the methods is designated as yes (Y), no (N), potentially (P), or indirectly (I)[a]

Method, link to	AUS-RIVAS	HAB-SCORE	Index of stream condition	Geomorphic river styles	State of the rivers survey	Habitat predictive modeling	River habitat survey
Scale	Y	Y	N	P	P	Y	P
Reference state	Y	Y	Y	I	Y	Y	I
Biota (fauna)	Y	Y	Y	P	P	Y	P
(Habitat) processes	N	N	N	Y	I	P	Y

[a] AUS-RIVAS = Australian River Assessment System; HAB-SCORE = USEPA rapid habitat assessment. Adapted from Parsons et al. (2002).

degradation," in changes to macroinvertebrate assemblages is still fragmentary and hard to untangle, despite the importance of applied issues, such as assessment (Riis and Sand-Jensen 2001). In both the Dutch and the habitat study, there was only a small pollution gradient upon which to draw conclusions. The European data showed that hydromorphology became more pronounced without severe pollution. A trait or functional approach is needed to deal further with this issue.

The role of spatial scale in hydromorphological assessment was stressed by Turner (1990), Allan et al. (1997), Davies et al. (2000), Sponseller et al. (2001), Sandin and Johnson (2004), and Chaves et al. (2005). Analyses of German, Dutch, and Swedish stream data showed that hydromorphological variables were dependent on scale and changed from catchment scale to reach or site scale (Feld 2004; Mykra et al. 2004). On the other hand, Verdonschot and Nijboer (2004) showed that variables are more or less independent of spatial scale. Frissell et al. (1986) and Rabeni (2000) argued for a distinct spatial hierarchy in hydromorphological stream habitats. Although some in-stream variables (morphological and physicochemical) better explained the macroinvertebrate distribution in local regions and stream types, a hierarchy that was lacking in the European stream typology presented by Verdonschot and Nijboer (2004). A clear understanding of spatial and temporal scale of objectives is needed to define risk assessment criteria or to prioritize restoration activities (Verdonschot 2000). Large-scale constraints, like nutrient-rich sewage discharges or dams, can set back single stream-stretch restoration (Verdonschot and Nijboer 2002). However, more often, pressures are multiple and act at different scales.

The European study clearly showed the importance of in-stream variables in explaining macroinvertebrate distribution at the stream level but, at the same time, stressed the explanatory strength of catchment, stream-valley, and stream-stretch variables. Stream restoration and risk assessment are practiced at the local scale of the stream stretch, but even in this perspective, the results of the European study showed the role of catchment to in-stream scale variables, pleading for a multiple-scale approach. The Dutch stream study added the importance of habitat when looking at stream stretch or site level. But both the Dutch stream study and the habitat-preference study showed the lesser importance of micro-habitat. In the habitat-preference study, it became clear that only 84 out of 547 taxa (15%) preferred a single habitat. Furthermore, no taxa were obligate-related to a specific habitat. In this respect, it is an interesting question whether an underlying substrate type affects the preference of a macroinvertebrate for an overlying one. For example, there might be a fauna that prefers detritus on top of gravel versus detritus on top of sand, which could partly explain why there was less often a preferent fauna for the organic substratum. Such interactions need further research.

These results provided several answers to the research question: At which scale, and to what extent, do hydrology and morphology explain stream macroinvertebrate distribution? Stream macroinvertebrate distribution can be explained, and is driven by, hydrological, morphological, and physicochemical variables. One must not tackle 1 or 2 variables and neglect the 3rd when striving for ecological restoration or for risk assessment. This study showed that the spatial scale depended on the objective. Dealing with macroinvertebrate distribution on a European scale, conditional variables, like climate and geology, strongly contributed to the explanation. Going down to stream stretch, operational variables (hydrology, morphology, physicochemistry) became important. On the other hand, microhabitat seemed to be too small of a scale to explain macroinvertebrate distribution. In general, geography was, in both the European and the Dutch stream study, a strong explanatory variable because the stream summarizes all environmental conditions for a site, and apparently, sites reflect the unique combination of site-specific conditions. The habitat-preference study supported the observation that habitat explained less than did stream stretch.

In conclusion, stream macroinvertebrate distribution is best explained by local stream-stretch variables, provided they are dealt within a catchment and stream valley context, conforming to the findings of Johnson et al. (2004). Both the European and Dutch stream study showed that a number of variables are exchangeable. Such variables point in the same direction of an ordination diagram, representing about the same overall environmental constraint, for example, catchment area, distance to source and stream order, or geology and calcium content, which means that overall system conditions (the combination of climate and geomorphology) set the scene for the overall macroinvertebrate pool (the ecoregional pool), and local conditions determine the macroinvertebrate assemblages present. Most macroinvertebrates are flexible, depending on its tactics and plasticity and thus can occur under a wide range of circumstances. On the one hand, small differences in vulnerability between macroinvertebrate species can make local conditions become too harsh (the limits of plasticity) for some. On the other hand, differences in biotic capacity (e.g., tactics such as life-cycle strategies, dispersion, colonization, and competition) is the other, equal, selective force. In combination, these factors determine macroinvertebrates occurrence in space and their maintenance and persistence in time.

Applying this knowledge to water management means that any risk assessment and restoration effort needs a hydromorphological context. Furthermore, risk assessment must

- Be based on an ecological stream typology defined at a regional or local scale,
- Be linked directly to an organism group,
- Include hydrological and hydraulic, morphological and habitat, and physicochemical variables, and
- Include both multiple spatial (catchment, stream valley and stretch, and habitat) and temporal (diel to multiannual) scale variables.

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