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# Using discharge dynamics characteristics to predict the effects of climate change on macroinvertebrates in lowland streams

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**Abstract.** Despite the uncertainties in the rate of climate change, the Atlantic zone of northwestern Europe is expected to experience warmer, wetter winters and wetter summers than at present. Summer precipitation probably will depend on short, heavy rain showers between dry periods. Changes in the amount, frequency, and intensity of precipitation are expected to change stream discharge patterns, especially in rainwater-fed lowland streams, which will shift toward more dynamic flow regimes. Indices of discharge dynamics were used to assess the effect of changes in climate through changes in hydrology and land and water use on natural lowland stream macroinvertebrate communities. Discharge dynamics were significantly correlated with macroinvertebrate community structure, current velocity, and organic material preference. Our results demonstrate important influences of dynamic discharge regimes and extreme flows on macroinvertebrate community structure. Predictions of the ecological effects of climate change and of changes in land and water use indicate impaired ecological conditions in lowland streams of the Atlantic zone of northwestern Europe. Scenario tests involving different climate and landuse options suggest that current restoration practices and planned restoration activities can positively interact to reduce negative effects of climate change on lowland stream ecosystems.

**Key words:** macroinvertebrate, climate change, discharge prediction, stream.

Global climate change will result in a more variable hydrological cycle expressed as a substantial increase in precipitation and a greater evaporation rate (IPCC 2001). For Europe as a whole, models predict an increased chance of prolonged heavy precipitation and short intense showers (KNMI 2006). In the Atlantic zone of northwestern Europe, the more extreme climate events are likely to include heavy rainfall over short periods of time resulting in spates and dry periods, with high air temperatures and high evapotranspiration rates leading to drought. These environmental changes will affect streams and rivers. Higher precipitation will result in more surface runoff to streams and higher spates in rivers (Poff 1992, George et al. 2004). Under predicted future climates, further stresses on streams and rivers will be introduced, including the combined effect of direct changes in precipitation and indirect climate-induced changes in landuse patterns. These shifts, in turn, might cause changes in catchment hydrology that will affect runoff and discharge regimes, sediment transport and channel morphology, and inundation frequency and extent, all of which will affect stream and river ecosystems.

Climate change has had, and to a greater extent will have, a direct effect on stream water temperature (Hari et al. 2006). Temperature is one of the most important factors affecting life-history characteristics; bioenergetics; physiological, developmental, behavioral mechanisms; and biogeography of stream macroinvertebrates (Ward and Stanford 1982, Sweeney 1984). Therefore, climate change will directly affect the stream communities.

The flow regime of a natural stream also is regarded as a key driver of biodiversity, ecological integrity, and the supply of ecological goods and services (Naiman et al. 2002). Changes in the natural flow regime frequently impair these variables (Bunn and Arthington 2002), but ecologists often fail to provide prescriptions for water-flow management because of a lack of empirical information on flow regime–ecosystem relationships. This difficulty is likely to be exacerbated by the effects of climate change on stream-flow regimes (Arthington et al. 2006, Dudgeon et al. 2007).

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Water managers have expressed the need to assess the effects of climate change through changes in hydrology on lowland stream communities. The European Water Framework Directive requires that all streams in Europe must meet 'good ecological status' by the year 2015 (European Commission 2000). Several restoration measures, including remeandering, water retention, and rehabilitation of riparian zones, will be undertaken to achieve this objective. Climate and the use of land and water will change over time, and these changes could affect the ecological outcomes of restoration. For example, new environmental conditions might lead to more dynamic flow regimes than anticipated before the restoration.

Flow regime and discharge patterns have a major influence on stream ecosystems, e.g., on geomorphology, species diversity, foodweb structure, and ecological processes (Jowett and Duncan 1990). Streamflow variability is one of the most important factors governing the structure and processes of stream ecosystems (Poff et al. 1997), but our understanding of biologically relevant hydrograph parameters is still in its infancy. Richter et al. (1996) distinguished 5 groups of characteristics of the flow regime (magnitude, frequency, duration, timing, and rate of change of flow conditions) over different time periods, such as monthly or annual periods. Puckridge et al. (1998) identified 11 relatively independent measures of flow variability that were associated with aspects of fish biology. Stream organisms are generally adapted to a wide range of variability in stream discharge (Allan 1995, Petts 2000, Lytle and Poff 2004, Herbst and Cooper 2010), but whether stream biota and communities respond to the overall flow regime or are selected on the basis of their responses to individual variables is unknown. Authors of many hydroecological studies have assumed that monthly or daily mean flows, which are often readily available, are sufficient to characterize flow regimes (e.g., Clausen and Biggs 2000, Olden and Poff 2003). However, even single events, such as an extreme peak flow or, at a smaller scale, a fallen tree, can cause temporary, but substantial, changes in the physical habitat and affect ecological functioning (Schlosser 1995, Arndt et al. 2002). Thus, analytical approaches are needed that focus on the temporal resolution of stream hydrographs in relation to stream biota and community structure. We explored the influence of flow variables over time periods ranging from 1 to 365 d before biological sampling.

Macroinvertebrates are an important and indicative group of organisms in lowland streams. This important group of organisms includes many taxa, both generalists and specialists (Tolkamp 1980, Verdonschot 1995), that differ in their sensitivity to different ecosystem components (Cummins and Lauff 1969). Thus, macroinvertebrates are useful indicators of stream quality, and they might also be useful indicators of hydrological conditions or overall patterns of discharge. Many macroinvertebrate indicator metrics are available (e.g., Hering et al. 2004), but few other than the Lotic-invertebrate Index for Flow Evaluation (LIFE) score (Monk et al. 2006) include aspects of stream hydrology. However, such summary variables could be valuable tools for linking characteristics of the flow regime to macroinvertebrate responses. Such relationships might be useful for predicting effects of climate-induced changes in hydrology and landuse on stream condition.

Climate change is a global phenomenon, whereas agricultural land use and urbanization both act at the catchment scale. During its aquatic life stage, a stream macroinvertebrate might be limited to a few square meters of the stream bed, i.e., the habitat scale (Boon 1998, Gordon et al. 2004), except when it is drifting. Habitat availability and dispersal–migration processes affect distribution patterns of macroinvertebrates (Downes et al. 1993, Parsons et al. 2003). Therefore, climatic and hydrological processes induced at the global scale and acting at the catchment scale have to be related to their effects on stream inhabitants living at the much smaller and more local habitat scale.

Responses of macroinvertebrates to flow characteristics have been described in many studies (Bunn and Arthington 2002, Acreman and Dunbar 2004), but attempts to predict macroinvertebrate community composition or diversity based on flow variables are scarce. Macroinvertebrate-relevant flow variables must be identified and related to macroinvertebrate characteristics (indices or metrics) so that expected future flow conditions can be used to predict future community composition or diversity.

Our goal was to relate the characteristics of flow regimes in lowland streams to macroinvertebrate community structure and to use such relationships to predict the effects of future changes in climate, and land and water use. First, we undertook a field study to monitor stream flow and extract ecologically relevant discharge variables in streams with flow regimes that reflected a wide range of groundwater–rainwater dependence (Sear et al. 1999, Boulton and Hancock 2006). Second, we modeled climate, landuse, and water-use scenarios that included a wide range of flow conditions and related these scenarios to discharge variables via a hydrological model of a representative catchment. Third, we parameterized our time series of discharge data and implemented them in the hydrological model to predict macroinvertebrate responses to climate and landuse change scenarios.

Our 4 major objectives were to: 1) select a suitable variable or suite of variables that describe(s) a biologically relevant stream-flow regime, 2) identify the antecedent time period explaining the most variance in macroinvertebrate community characteristics, 3) define a community variable that is directly linked to the best explanatory flow variable(s), and 4) apply this knowledge to predict the effects of changes in climate, and land and water use on stream hydrology and consequent changes in stream macroinvertebrate communities.

## Methods

### *Field study*

We collected data from the upper reaches of 9 free-flowing, soft-bottomed, lowland streams. The streams were distributed over the eastern and southern part of The Netherlands. The Netherlands has a temperate climate with a precipitation surplus (difference between precipitation and evapotranspiration) of ~300 mm/y. We selected sites with similar morphological and physicochemical features. The study streams were 0.5 to 4.0 m wide, 0 to 50 cm deep (on average ~10 cm), with current velocities between 20 and 30 cm/s (with extremes of 0–>60 cm/s) and slopes of ~0.5 to 5 m/km. Stream-water temperature ranged between 0 and 18°C. All stream beds were heterogeneous with mosaics of several substratum types. Important physicochemical variables for each study site are presented in Table 1.

We selected sampling sites based on low level of human effects, near-natural morphology, high water quality, and discharge regime. Natural lowland streams have a high retention capacity (the catchment is capable of absorbing rain water and releasing it slowly to the stream) and fairly constant discharge patterns without high peaks or low-flow spells. Drainage, forest clearance, and paved surfaces reduce retention capacity and increase a stream's response to rainfall. The faster rainwater enters a stream, the more dynamic the discharge pattern becomes. The streams ranged from primarily groundwater-fed by helocrene springs (constant discharge) to primarily rainwater-fed in anthropogenically altered catchments (variable discharge). Thus, the sites represented different hydrological regimes along a gradient from constant to dynamic flow.

We sampled macroinvertebrates in spring (March–April) and autumn (October–November) of 1998. At each site, we recorded the percentage of all substratum types contributing ≥5% of coverage in a 50-m reach and used a standardized site protocol to measure a number of variables (Table 1) describing the stream and its surroundings. Chemical variables (Table 1) were analyzed according to international (ISO) standards. We collected 1 macroinvertebrate sample with a 10 × 15-cm (mesh size = 0.5 mm) micro–macrofauna shovel (Tolkamp 1980) from each of 5 major substratum types (silt, sand, gravel, macrophytes, detritus) at each site. Samples were kept separate, brought to the laboratory, and sorted. We preserved invertebrates in 70% alcohol, except oligochaetes (4% formalin) and water mites (Koenike's fluid). We identified individuals to species level whenever possible. We combined data from the 5 substratum types within each stream for each sampling date to yield 18 samples (9 streams on 2 dates).

Identification to different taxonomic levels can cause inconsistencies within a data set. Our analysis required consistent data sets, so we taxonomically adjusted macroinvertebrate data before statistical analyses. We used 2 methods of weighted taxonomic adjustment: 1) we removed genera or higher taxonomic levels from the data set if species occurred within the genus or higher level, and 2) we aggregated species to genus or higher taxonomic level if both species and the higher level occurred (Nijboer and Verdonschot 2000, Vlek et al. 2004).

### *Discharge variables and variable groups*

We collected hydrologic data over a 15-mo period from July 1997 to October 1998. We recorded water level continuously throughout this period at 15-min intervals. We used a stage–discharge relationship to transform water level into discharge ($m^3/s$). We calculated the median discharge ($Q_{50}$ or base flow) based on 1 hydrological year (the 12-mo period before the last macroinvertebrate sample was taken).

We distinguished 3 major groups of discharge variables: 1) quantitative discharge variables (Q), 2) variables composed of discharge percentiles (P), and 3) variables based on discharge exceedance levels (E) (Table 2). Discharge exceedance refers to the number of exceedances of a predefined discharge within a specified time period. We classified Q variables into a group composed of the quantitative discharge values (Qvalue) and a group with the same values divided by the median discharge based on 1 hydrological year (Qvalue/med). This procedure corrected for differences in $Q_{50}$ between streams that were related to differences in the size of the catchment and the wetted area of the stream and made the 9 streams compara-

TABLE 1. Mean (SE) values for physicochemical variables in the 9 lowland study streams (SN = Springendal North, SZ = Springendal South, RO = Rosep, RE = Reusel, RB = Red Stream, BB = Forest Stream, TB = Tongerense Stream, OB = Old Stream, KB = Cold Stream). Flow characteristic is described by the rank order among study streams in terms of inflow pattern: 1 = constant flow to 9 = dynamic flow.

| Variable | SN | SZ | RO | RE | RB | BB | TB | OB | KB |
|---|---|---|---|---|---|---|---|---|---|
| Catchment area (ha) | 60 | 48 | 1895 | 15874 | 1890 | 1901 | 238 | 455 | 243 |
| Cumulative discharge ($m^3/y$) | 979 | 194 | 19498 | 13081 | 13963 | 648 | 2369 | 1955 | 1087 |
| Flow characteristic (rank order) | 2 | 8 | 7 | 9 | 6 | 3 | 4 | 1 | 5 |
| Width (m) | 0.85 ± 0.00 | 0.71 ± 0.00 | 3.60 ± 0.00 | 3.38 ± 0.00 | 2.95 ± 0.00 | 1.46 ± 0.00 | 2.25 ± 0.00 | 1.21 ± 0.00 | 1.16 ± 0.00 |
| Depth (cm) | 6.6 ± 1.1 | 6.1 ± 0.7 | 14.8 ± 1.8 | 17.8 ± 2.6 | 13.8 ± 2.5 | 9.6 ± 1.5 | 12.0 ± 1.1 | 6.7 ± 0.4 | 8.2 ± 1.4 |
| $O_2$ (mg/L) | 9.2 ± 0.1 | 8.8 ± 0.4 | 8.6 ± 0.5 | 9.3 ± 0.4 | 10.8 ± 0.4 | 11.2 ± 0.4 |  |  | 11.2 ± 0.6 |
| pH | 6.5 ± 0.1 | 6.6 ± 0.1 | 7.2 ± 0.1 | 6.6 ± 0.0 | 7.6 ± 0.1 | 7.0 ± 0.1 | 7.3 ± 0.1 | 6.9 ± 0.1 | 7.3 ± 0.0 |
| Total P (mg/L) | 0.08 ± 0.002 | 0.17 ± 0.07 | 0.19 ± 0.03 | 0.13 ± 0.04 | 0.24 ± 0.03 | 0.10 ± 0.00 | 0.08 ± 0.02 | 0.07 ± 0.03 | 0.07 ± 0.01 |
| $NH_4$-N (mg/L) | 0.11 ± 0.02 | 0.10 ± 0.02 | 0.19 ± 0.03 | 0.53 ± 0.07 | 2.10 ± 0.29 | 0.34 ± 0.03 | 0.04 ± 0.01 | 0.04 ± 0.00 | 0.08 ± 0.02 |
| $NO_3$-N (mg/L) | 11.08 ± 0.04 | 7.35 ± 0.38 | 2.98 ± 0.60 | 7.91 ± 1.04 | 1.34 ± 0.09 | 0.43 ± 0.03 | 0.62 ± 0.05 | 5.85 ± 0.80 | 5.68 ± 0.21 |
| Electrical conductivity (µs/cm) | 247 ± 7 | 209 ± 14 | 315 ± 59 | 492 ± 27 | 323 ± 15 | 126 ± 6 | 131 ± 8 | 174 ± 6 | 244 ± 5 |
| % gravel | 11 ± 1 | 29 ± 2 | 0 ± 0 | 15 ± 2 | 38 ± 1 | 0 ± 0 | 8 ± 0 | 19 ± 3 | 3 ± 0 |
| % sand | 41 ± 1 | 10 ± 0 | 19 ± 4 | 17 ± 3 | 43 ± 1 | 1 ± 0 | 23 ± 1 | 48 ± 5 | 47 ± 5 |
| % silt | 10 ± 1 | 28 ± 1 | 28 ± 3 | 31 ± 4 | 12 ± 1 | 29 ± 5 | 37 ± 2 | 13 ± 1 | 6 ± 1 |
| % detritus | 26 ± 2 | 23 ± 3 | 6 ± 1 | 20 ± 1 | 6 ± 0 | 68 ± 5 | 18 ± 2 | 13 ± 1 | 44 ± 5 |
| % plants | 11 ± 1 | 9 ± 1 | 46 ± 4 | 9 ± 1 | 0 ± 0 | 2 ± 0 | 14 ± 1 | 6 ± 1 | 0 ± 0 |

TABLE 2. Discharge variables in 3 major discharge variable groups: 1) quantitative discharge variables (Q) (Qvalue = quantitative discharge values, Qvalue/med = Qvalue divided by the $Q_{50}$ based on 1 hydrological year), 2) discharge percentiles (P) (Pclass = occurrences of percentile classes, Pexceed = ranges of percentile exceedances), and 3) discharge exceedances (E; number of exceedances of a predefined discharge within a specified time period) (Ecombi = combined number of over and under exceedance occurrences, Eexceed = ranges of percentile exceedances). min = minimum, med = median, max = maximum, cum = cumulative, ave = average, sd = standard deviation, Qnumber = discharge percentile indicated by the number, C = combined over and under exceedance, O = over exceedance, U = under exceedance, r = range, c = class. For C(r or c)number, O(r or c)number, or U(r or c)number, the range or class number indicates the over or under exceedance range or class value, respectively.

| Qvalue | Qvalue/med | Pclass | Pexceed | Ecombi | Eclass | Eexceed |
|---|---|---|---|---|---|---|
| Qmin | Qmin/med | <Q10 | <Q5 | C1 | O5 | O5 |
| Q10 | Q10/med | <Q30 | <Q10 | C2 | Oc45 | O4 |
| Q30 | Q30/med | Q10–Q30 | <Q30 | C3 | Oc34 | O3 |
| Q50 | sd of Q/med | Q30–Q50 | <med | C4 | Oc23 | O2 |
| Q70 | Q70/med | Q50–Q70 | Q30–Q70 | C5 | Oc12+Uc12 | O1+U1 |
| Q90 | Q90/med | Q30–Q70 | >med | Cr11 | Uc23 | U2 |
| Qmax | Qmax/med | Q70–Q90 | >Q70 | Cr22 | Uc34 | U3 |
| Qcum | Qcum/med | >Q70 | >Q90 | Cr33 | Uc45 | U4 |
| Qave | Qave/med | >Q90 | >Q95 | Cr44 | U5 | U5 |

ble. We classified P variables into a group based on occurrences of percentile classes (Pclass) and a group based on ranges of percentile exceedances (Pexceed) (Table 2). We classified E variables into a group based on the combined number of over and under exceedance occurrences (Ecombi), number of occurrences in separate over and under exceedance classes (Eclass), and separate ranges of over and under exceedances (Eexceed) (Table 2). We defined over and under exceedance boundaries in terms of a factor × $Q_{50}$. This factor was an exponential function of increase and decrease: 1, 2, 4, 8, or 16 for over exceedances and 1, 0.5, 0.25, 0.125 or 0.0625 for under exceedances, respectively (van Walsum et al. 2001). We determined the percentage of discharges that fell within the interval defined by the upper and lower bounds for each exceedance class.

The extremes at the low and high end of the discharge spectrum (i.e., droughts and floods) are called discharge dynamics groups. We gave special emphasis to these extremes. We multiplied the class assignment as indicative weight of each exceedance class by a factor of 1 (D group indicated by D1), by a linearly increasing weight class of 1 to 5 (1, 2, 3, 4, and 5 at both the high and low ends of the D group; D5), and by an exponentially increasing weight class of 1 to 16 (1, 2, 4, 8, and 16 at both the high and low ends of the D group; D16). As for E-based variables (see Table 2 last 3 columns), we classified all 3 D groups in combined over and under exceedance classes (D*x*combi = Ecombi), in separate over and under exceedance classes (D*x*class), and in separate ranges of over and under exceedance classes (D*x*exceed).

Each discharge dynamics group was composed of 9 variables. We calculated all discharge variables for periods of 1, 3, 6, 11, 23, 46, 92, 182, and 365 d before the respective macroinvertebrate sample was taken to identify the antecedent time period that explained the most variance in macroinvertebrate community characteristics.

### *Multivariate analysis*

We log($x$)-transformed all variables to avoid effects of a skewed variable distribution. We used ordination to analyze macroinvertebrate community structure in relation to environmental factors. First, we used detrended correspondence analysis (DCA) (Hill 1979) with the option 'detrending-by-segments' to measure the length of gradient along the axis. A gradient length >3 standard deviation units (SD) of species turnover implies a unimodal response (ter Braak and Šmilauer 2002). We used canonical correspondence analysis (CCA; ter Braak 1987) for further ordination (CANOCO for Windows, version 4.5; ter Braak and Šmilauer 2002). CCA is a direct ordination technique, so environmental variables are related directly to the species composition at the sampling sites. Ordination axes in CCA are chosen as linear combinations of the environmental variables. We used the option 'down weighting of rare species' to give more emphasis to more commonly distributed species.

We used the 'Sum of Eigenvalues' (SE) and the 'Sum of Canonical Eigenvalues' (SCE) from the CCA analysis done with only significant discharge variables to explore the ability of each variable group to explain the relationship of macroinvertebrate data to discharge gradients. The eigenvalue is a measure of the importance of an axis. The sum of eigenvalues or total inertia is a measure of the total variance explained in species data. The sum of all canonical eigenvalues expresses the total contribution of environmental variables included in an analysis to the explanation of patterns in the macroinvertebrate assemblages. We divided the SCE of each discharge variable group analysis by the SE of the macroinvertebrate analysis alone to investigate the contribution of each discharge variable group to the explanation of variation in macroinvertebrate community structure. SCE/SE ranges from 0 to 1, where 0 indicates that the variable (group) explains little and 1 indicates that the variable (group) explains most of the variation in the macroinvertebrate data.

We used the 'forward selection' option in CCA to explore the importance of single discharge variables within each discharge variable group. We tested variables with 499 Monte Carlo permutations. In forward selection, the program orders the variables by their explanatory strength (conditional effects). It starts by selecting the most important variable and adds the remaining variable that explains most of the remaining variation in community structure. Thus, the 2nd variable explains part of the variation that is independent of the part explained by the 1st variable. This process continues until additional variables no longer contribute significantly ($p < 0.05$) to the model. Forward selection results are expressed as LambdaA (the higher the LambdaA, the more important the variable). We added all LambdaAs from the conditional tests (for all discharge variables tested) and used LambdaAs to order the discharge variables according to their importance in explaining macroinvertebrate patterns. Last, we ran CCAs using only the significant discharge variables for each discharge variable group. We did marginal tests (the contribution to the explanation of the data by a variable on its own) to provide information about interchangeability of variables in the model. Marginal and conditional significance can differ because of colinearity among variables.

### Macroinvertebrate metrics

We used macroinvertebrate metrics to identify the discharge variables that best explained and were useful predictors of macroinvertebrate community composition. We used a metric as a summary variable if it made interpretation and communication of hydrology–macroinvertebrate community relationships more straightforward and easier to explain.

We considered 5 indices: LIFE, current velocity index, saprobity index, Shannon diversity, and rarity. LIFE links qualitative and semiquantitative change in riverine benthic macroinvertebrate communities to prevailing flow regimes (Extence et al. 1999). The index is calculated by assigning each taxon to 1 of 6 categories ranging from a group primarily associated with rapid flows to a group frequently associated with drying or drought-affected sites. Each taxon is then placed in a 2nd category related to its abundance. These 2 values are used to assign an index score. Higher flows give higher index scores.

The current velocity index (v-index; Tolkamp and Gardeniers 1977) represents the extent of rheophily of the taxa in a sample. Taxa are assigned to 1 of 5 classes. Class 1 includes taxa found in stagnant water (limnetic taxa), and class 5 includes taxa that occur only in fast-running water (rheobionts). Natural lowland streams in northwestern Europe have high proportions of rheophilic taxa and high v-index scores (AQEM Consortium 2002).

The saprobity index (s-index; Sládeček 1973) represents the saprobity rate (the level of enrichment with organic material) indicated by the macroinvertebrate taxa in a sample. The saprobity rate is expressed in 5 classes. Class 5 includes oligosaprobic taxa, whereas class 1 includes taxa that occur only in polysaprobic waters (saprobionts). Natural lowland streams in northwestern Europe have high proportions of taxa indicating oligosaprobic conditions and low s-index scores.

The diversity index (H-index; Shannon and Weaver 1949) represents the diversity in taxonomic composition of a sample. In general, high H-index values are expected in natural streams. A slight disturbance in a pristine stream increases diversity, but further disturbance causes the score to decrease (Connell 1978, Ward and Stanford 1983). The streams in our study were pristine to seminatural. Thus, the H-index would be expected to decrease along a gradient from seminatural to the most pristine conditions studied.

The rarity index (r-index; Nijboer and Verdonschot 2004) represents the extent of rare taxa in a sample. The r-index is expressed in 6 classes. Class 1 refers to a community composed mainly of very common taxa, whereas class 6 refers to a community composed mainly of very rare taxa. Natural streams have more rare taxa and higher r-index scores.

We classified all taxa as far as possible in each index. Scores for all indices except the H-index were calculated as:

$$\text{Index score} = \frac{\sum t_i n_i}{\sum n_n}$$

where $t_i$ is the indicative weight or class assignment of taxon $i$ in the sample and $n_i$ = total number of individuals of taxon *i* in the sample. We regressed macroinvertebrate index scores against discharge dynamic index (DDI) scores (see *DDI* in Results for details) and used *t*-tests to assess whether the slopes differed from 0 ($\alpha = 0.05$).

### Scenarios

*Climate scenarios.*—The Dutch National Research Programme commissioned the Hadley Centre for Climate Prediction and Research to provide a climate scenario for European weather in the period 2070–2100 using Hadley's General Circulation Model (GCM) (Viner and Hulme 1998, Verweij and Viner 2001). The predicted data for 2070–2100 were used as input to the hydrological model. The center of the grid cell of the GCM chosen (lat 51.25° to 53.75°N, long 5.625 to 9.375°E) lies in the eastern part of The Netherlands. The Hadley weather variables were daily precipitation (mm/d), temperature (°C), relative humidity (%), and total downward surface shortwave flux (W $m^{-2}$ $d^{-1}$).

Our 1st climate scenario represented current climate conditions based on national averaged actual precipitation data over the last 15 y. Our 2nd scenario was the Hadley Centre scenario for 2070–2100. This scenario predicted a 2.8°C increase in mean temperature. In the 3rd scenario, we corrected daily precipitation of the Hadley scenario (2nd scenario) by a 17% increase of all values in winter and a 3% increase in summer to account for the predicted effect of the 2.8°C increase in temperature on precipitation (Können et al. 1997, van Walsum et al. 2001). Thus, our 3rd scenario was the precipitation-corrected Hadley climate scenario for 2070–2100.

*Land- and water-use scenarios.*—Land and water use are expected to change between the present and 2100. Our 1st landuse scenario represented the expected situation after implementation of the Dutch Ecological Network, which will cause land use in some selected stream valleys to change to 'wet riverine grassland'. In this scenario, all ditches in Ecological Network stream valleys will be filled. Our 2nd landuse scenario represented the situation assuming creation of a 1-km-wide buffer zone on both sides of all main streams. With such buffer zones in place, the groundwater table will rise, surface-water extraction for sprinkling irrigation will be stopped, drainage facilities will be removed, ditches will be filled to a maximum depth of 0.9 m, a minimum distance of 100 m between ditches will be retained, and all land use will be changed to grassland. In our 3rd landuse scenario, the main streams will become shallower and will meander freely within the buffer zone.

*Hydrological model.*—We selected a regional comprehensive hydrologic model to predict the effects of climate and landuse changes on stream discharge. Comprehensive models have the advantage that they describe all aspects of the regional catchment stream system in great detail. 'Climate' is defined for a period of 30 y (2070–2100), so long periods of discharge must be simulated. A period of 30 y typically is used to reflect the long-term average of more or less dynamic weather-dependent discharge events. Such a data series allows estimation of statistics describing events with a recurrence interval of 5 y. We used the model SIMGRO (Veldhuizen et al. 1998) because it covers all relevant aspects of the regional hydrologic system in a way that allows simulation of long time periods for regional catchments. SIMGRO also has options suitable for describing special aspects of lowland stream hydrology. SIMGRO virtually sections streams into discrete units as a longitudinal sequence of stream components called 'gutters' or 'nodes' (Veldhuizen et al. 1998).

We selected the Beerze-Reusel catchment (~8800 ha) in the south of The Netherlands (lat 51°44′N, long 5°20′E) for model and scenario application. This catchment is representative of many northwestern European lowland catchments and includes 2 of our study streams. The catchment was described by 1663 nodes that represented individual streams and stream sections. After calibration, we input the precipitation and temperature scenarios into SIMGRO and computed average daily discharge statistics for each scenario for the 2070–2100 period. We summarized the results by calculating the mean and standard deviation of differences in DDI index scores (see *DDI* below) between scenarios over all 1663 stream nodes. The differences in DDI index scores for all nodes between pairs of scenarios were tested with paired 2-tailed *t*-tests assuming equal variance.

## Results

### Multivariate analyses

The 1st DCA axis was 2.87 SD long, indicating modest unimodality. Therefore, CCA was used for further analyses. The eigenvalue for the 1st axis was 0.45, and axis 1 explained 18.9% of the variance in macroinvertebrate species patterns. The eigenvalue for the 2nd axis was 0.28, and axis 2 explained an additional 12.3% of the variance. The total variance in the species data was 2.39.

For each discharge variable group (see Table 2 for variable group codes and individual variables), the eigenvalue of the 1st axis over all time periods was highest and the strength of the relationship between macroinvertebrate community composition and the discharge variables along axis 1 was higher when discharge variables were summarized over a period of 365 d than over any other antecedent time period (Table 3). The cumulative % variance in species composition was often much higher when discharge variables were summarized over a period of 365 d. The cumulative % variance in the species–environment relationship, expressing the fitted values of a multiple regression for each taxon against the discharge variables, was lowest when discharge variables were summarized over a period of 365 d (Table 3). Thus, an antecedent period of $\geq$365 d before sampling is best when describing the discharge conditions shaping macroinvertebrate community composition.

SCE/SE was highest when variables were summarized over 365 d. SCE/SE was highest for the variable group Eexceed, and 8 variables contributed significantly to the model (Table 4). The variable group Eclass had the 2nd highest SCE/SE, and 7 variables contributed significantly to the model (Table 4). Thus, over and under exceedance variables better described macroinvertebrate–discharge regime relationships than did quantitative discharge variables or discharge percentiles.

SCE/SE was 0.68 for all D*x*classes (Table 5). No effects of the linear or exponential indicative weights were detected. The marginal and conditional effect of each discharge dynamics variable were evaluated for each CCA, and the 2 variables with the highest LambaA in each discharge dynamics group are presented in Table 6. The discharge dynamics variables that best explained patterns in macroinvertebrate communities were Cr33 in D5combi and Uc34 in D1class, D5class, D16class (see Table 2 for codes). The 2nd best explanatory variable for all 3 D*x*classes was Oc23.

## *DDI*

One of the important objectives of our study was to define summary variables that are both simple to estimate and that most effectively explain the discharge regime related to macroinvertebrate community patterns. Our analyses showed that weighting of exceedance classes was unnecessary, groups of over and under exceedance classes were more explanatory than other variable groups, and individual over and under exceedance classes were most explanatory of macroinvertebrate community patterns. Thus, exceedance classes appear to be the most reliable and readily interpreted variables.

We developed a new DDI for use as a summarizing variable. The DDI captures discharge dynamics from continuously measured daily discharge data. The dynamics data are transformed into over and under exceedance indices (each based on 5 classes) or into 1 combined index. The DDI is calculated as:

$$\mathrm{DDI} = \frac{\sum R_i s_i}{\sum R_i}$$

where $s_i$ is the indicative weight for each discharge dynamic class ($i = 1\ldots5$) and $R_i$ is the total number of scores in the respective discharge dynamics class $R$. The indicative weight increases with increasing discharge extremity class. We explored 2 weighting schemes: 1 to 5 (D5C1) and 1, 2, 4, 8, and 16 (D16C1). We calculated the DDI separately for each over exceedance (D5O1–D16O1) and under exceedance (D5U1–D16U1) class and tested its ability to explain variability in macroinvertebrate index scores.

## *Macroinvertebrate metrics*

We regressed the 5 macroinvertebrate indices calculated for the combined spring and autumn samples against D5C1 and D16C1 (Fig. 1A, B, Table 7). The v-index and s-index were significantly negatively related to both combined DDIs (Fig. 1A, B). Thus, the higher the DDI score, the lower the share of macroinvertebrates in the community with a preference for faster current velocity or more meso- to oligosaprobic conditions. Adjusted $R^2$ values generally were lower for regressions with separated over and under exceedance DDIs than for combined DDIs, but the v-index and the s-index were significantly related to all 4 separated DDIs (except v-index vs D5O1 and s-index vs D16U1; Table 7). None of the regressions for r-index, H-index, and LIFE index vs DDIs were significant (except H-index vs D5U1; Table 7). All 6 DDIs were biologically relevant in terms of macroinvertebrate preferences for current velocity and organic matter content and were used to evaluate scenarios.

## *Scenarios*

All 6 DDI scores were calculated for each of the 6 climate and landuse change scenarios (Table 8). The current condition was taken as the reference scenario, and each of the other scenarios was compared to the reference scenario by calculating the difference in the logarithm of the DDI score for each node in the catchment between reference and test scenarios. DDI scores increased significantly in all test scenarios

TABLE 3. The eigenvalue, species-environment correlation, and cumulative percentage variance (cum % var) of species data and of species–environment relationship from canonical correspondence analyses (CCA) for each discharge variable group. Discharge data were collected for 1 y before the last macroinvertebrate sample was collected (antecedent period). Period refers to the length of the antecedent period summarized for the CCA. See Table 2 for explanation of discharge variable groups and abbreviations.

| Discharge variable group | Result | Period (day) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 3 | 6 | 11 | 23 | 46 | 92 | 182 | 365 |
| Qvalue | Eigenvalue | 0.39 | 0.39 | 0.39 | 0.39 | 0.41 | 0.41 | 0.41 | 0.40 | 0.44 |
| | Species–environment correlation | 0.98 | 0.97 | 0.97 | 0.98 | 0.98 | 0.98 | 0.98 | 0.97 | 0.99 |
| | Cum % var of species data | 16.4 | 16.3 | 16.3 | 16.5 | 17.2 | 17.1 | 16.9 | 16.5 | 18.3 |
| | Cum % var of species–environment relation | 66.5 | 64.8 | 64.8 | 64.5 | 49.6 | 48.7 | 51.2 | 47.3 | 33.2 |
| Qvalue/med | Eigenvalue | 0.17 | 0.30 | 0.30 | 0.38 | 0.39 | 0.39 | 0.35 | 0.37 | 0.44 |
| | Species–environment correlation | 0.79 | 0.89 | 0.89 | 0.95 | 0.96 | 0.96 | 0.94 | 0.95 | 0.99 |
| | Cum % var of species data | 7.1 | 12.6 | 12.6 | 15.9 | 16.4 | 16.2 | 14.7 | 15.3 | 18.4 |
| | Cum % var of species–environment relation | 100.0 | 100.0 | 100.0 | 40.3 | 100.0 | 100.0 | 100.0 | 63.2 | 27.5 |
| Pclass | Eigenvalue | 0.24 | 0.21 | 0.21 | 0.32 | 0.30 | 0.11 | 0.12 | 0.08 | 0.45 |
| | Species–environment correlation | 0.84 | 0.79 | 0.79 | 0.89 | 0.87 | 0.73 | 0.83 | 0.88 | 0.99 |
| | Cum % var of species data | 9.9 | 8.9 | 8.9 | 13.2 | 12.6 | 4.8 | 4.8 | 3.1 | 18.6 |
| | Cum % var of species–environment relation | 100.0 | 100.0 | 100.0 | 60.6 | 100.0 | 100.0 | 100.0 | 60.1 | 28 |
| Pexceed | Eigenvalue | 0.24 | 0.29 | 0.29 | 0.30 | 0.34 | 0.23 | 0.33 | 0.07 | 0.44 |
| | Species–environment correlation | 0.84 | 0.83 | 0.83 | 0.87 | 0.91 | 0.78 | 0.93 | 0.81 | 0.99 |
| | Cum % var of species data | 10.0 | 11.9 | 11.9 | 12.5 | 14 | 9.6 | 13.9 | 2.9 | 18.5 |
| | Cum % var of species–environment relation | 100.0 | 67.6 | 67.6 | 100.0 | 100.0 | 100.0 | 26.8 | 100.0 | 29.8 |
| Ecombi | Eigenvalue | 0.17 | 0.25 | 0.23 | 0.37 | 0.38 | 0.39 | 0.38 | 0.39 | 0.44 |
| | Species–environment correlation | 0.88 | 0.99 | 0.92 | 0.95 | 0.96 | 0.96 | 0.95 | 0.96 | 0.99 |
| | Cum % var of species data | 7.3 | 10.4 | 9.6 | 15.6 | 15.9 | 16.1 | 15.8 | 16.4 | 18.5 |
| | Cum % var of species–environment relation | 52.8 | 52.0 | 100.0 | 67.3 | 100.0 | 50.9 | 74.0 | 51.7 | 30.4 |
| Eclass | Eigenvalue | 0.17 | 0.22 | 0.22 | 0.36 | 0.38 | 0.36 | 0.35 | 0.39 | 0.44 |
| | Species–environment correlation | 0.88 | 0.94 | 0.94 | 0.95 | 0.95 | 0.94 | 0.93 | 0.95 | 0.99 |
| | Cum % var of species data | 7.3 | 9.3 | 9.3 | 15.2 | 15.7 | 15.0 | 14.8 | 16.2 | 18.5 |
| | Cum % var of species–environment relation | 52.8 | 62.6 | 62.6 | 66.9 | 64.8 | 100.0 | 63 | 48.6 | 27.3 |
| Eexceed | Eigenvalue | 0.17 | 0.22 | 0.22 | 0.37 | 0.38 | 0.37 | 0.37 | 0.39 | 0.45 |
| | Species–environment correlation | 0.88 | 0.94 | 0.94 | 0.95 | 0.96 | 0.96 | 0.94 | 0.95 | 0.99 |
| | Cum % var of species data | 7.3 | 9.3 | 9.3 | 15.6 | 15.9 | 15.6 | 15.3 | 16.1 | 18.6 |
| | Cum % var of species–environment relation | 52.8 | 62.6 | 62.6 | 67.3 | 100.0 | 100.0 | 61.5 | 49.3 | 26 |

TABLE 4. Sum of canonical eigenvalues (SCE) divided by sum of eigenvalues (SE) (SCE/SE) and the number of statistically significantly ($p < 0.05$) contributing variables ($n$) for each discharge variable group from the canonical correspondence analysis (CCA) for each discharge variable group. Discharge data were collected for 1 y before the last macroinvertebrate sample was collected (antecedent period). Period refers to the length of the antecedent period summarized for the CCA. See Table 2 for explanation of discharge variable groups and abbreviations. ns = not significant.

| Discharge variable group | Result | Period (day) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 3 | 6 | 11 | 23 | 46 | 92 | 182 | 365 |
| Qvalue | SCE/SE | 0.25 | 0.25 | 0.25 | 0.26 | 0.35 | 0.35 | 0.33 | 0.35 | 0.55 |
| | $n$ | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 | 5 |
| Qvalue/med | SCE/SE | ns | 0.13 | 0.13 | 0.39 | 0.16 | 0.16 | 0.15 | 0.24 | 0.67 |
| | $n$ | 1 | 1 | 1 | 4 | 1 | 1 | 1 | 2 | 7 |
| Qclass | SCE/SE | 0.10 | 0.09 | 0.09 | 0.22 | 0.13 | ns | ns | ns | 0.67 |
| | $n$ | 1 | 1 | 1 | 2 | 1 | 0 | 0 | 0 | 7 |
| Qexceed | SCE/SE | 0.10 | 0.18 | 0.18 | 0.12 | 0.14 | 0.10 | ns | ns | 0.62 |
| | $n$ | 1 | 2 | 2 | 1 | 1 | 1 | 0 | 0 | 6 |
| Ecombi | SCE/SE | ns | ns | 0.10 | 0.23 | 0.16 | 0.32 | 0.21 | 0.32 | 0.61 |
| | $n$ | 0 | 0 | 1 | 2 | 1 | 3 | 2 | 3 | 6 |
| Eclass | SCE/SE | ns | ns | ns | 0.23 | 0.24 | 0.15 | 0.23 | 0.33 | 0.68 |
| | $n$ | 0 | 0 | 0 | 2 | 2 | 1 | 2 | 3 | 7 |
| Eexceed | SCE/SE | ns | ns | ns | 0.23 | 0.16 | 0.16 | 0.25 | 0.33 | 0.72 |
| | $n$ | 0 | 0 | 0 | 2 | 1 | 1 | 2 | 3 | 8 |

(Table 8, Fig. 2A, B). Decreases in the share of macroinvertebrates in the community that prefers higher current velocity or more meso- to oligosaprobic conditions were associated with the increases in DDI scores. The largest change in DDI score occurred in the Hadley scenario. The precipitation correction in the Hadley scenario reduced DDI scores, but overall discharge dynamics still increased relative to current conditions. On the other hand, implementation of the Ecological Network landuse scenario increased DDI scores. Both of the other land- (and water) use scenarios decreased DDI scores relative to the Ecological Network landuse scenario and would lead to smaller changes in the macroinvertebrate community.

In the Hadley scenario, under exceedances were more important than over exceedances (Fig. 2B). The Hadley scenario was the driest scenario because precipitation was not adjusted for the temperature change and, therefore, was underestimated. This result indicates that under exceedances caused by drier periods would strongly affect the macroinvertebrate community. Drier periods are associated with lower current velocities and more siltation (higher saprobity). In the adjusted Hadley scenario, over and under exceedances played comparable and important roles. This result implies that the increase in discharge dynamics would be caused by both floods and droughts.

In the Ecological Network scenario, over exceedance DDI scores did not increase, but the combined and under exceedance DDI scores increased significantly relative to the adjusted Hadley scenario. Under exceedance (emphasized with the D16U1 index) was

TABLE 5. Sum of canonical eigenvalues (SCE) divided by sum of eigenvalues (SE) (SCE/SE) and the number of statistically significantly ($p < 0.05$) contributing variables ($n$) for each discharge dynamics (D) group from the canonical correspondence analysis (CCA) for each discharge dynamics group. Discharge data were collected for 1 y before the last macroinvertebrate sample was collected (antecedent period) and summarized over 365 d. The indicative weight of each exceedance class was multiplied by a factor of 1 (D group indicated by D1), by a linearly increasing weight class of 1 to 5 (1, 2, 3, 4, and 5 at both the high and low ends of the D group; D5), and by an exponentially increasing weight class of 1 to 16 (1, 2, 4, 8, and 16 at both the high and low ends of the D group; D16). As for E-based variables (see Table 2 last 3 columns) all 3 D groups were classified in combined over and under exceedance classes (D*x*combi = Ecombi), in separate over and under exceedance classes (D*x*class), and in separate ranges of over and under exceedance classes (D*x*exceed). There were 9 variables in each discharge dynamics group.

| Result | D1combi | D1class | D1exceed | D5combi | D5class | D5exceed | D16combi | D16class | D16exceed |
|---|---|---|---|---|---|---|---|---|---|
| SCE/SE | 0.61 | 0.68 | 0.60 | 0.61 | 0.68 | 0.60 | 0.59 | 0.68 | 0.61 |
| $n$ | 6 | 7 | 6 | 6 | 7 | 6 | 6 | 7 | 6 |

TABLE 6. The 2 highest marginal and conditional contributing discharge dynamics variables in the canonical correspondence analysis for each discharge dynamics group.

| Discharge dynamics group | Marginal | | Conditional | | | |
|---|---|---|---|---|---|---|
| | Contributing variable | LambdaA | Contributing variable | LambdaA | *F* | *p* |
| D1combi | C2 | 0.38 | C2 | 0.38 | 3.06 | 0.002 |
| | Cr11 | 0.38 | C5 | 0.24 | 2.00 | 0.002 |
| D5combi | Cr33 | 0.41 | Cr33 | 0.41 | 3.26 | 0.002 |
| | Cr44 | 0.40 | C2 | 0.21 | 1.86 | 0.002 |
| D16combi | Cr44 | 0.40 | Cr44 | 0.40 | 3.25 | 0.002 |
| | Cr22 | 0.39 | Cr11 | 0.22 | 1.85 | 0.002 |
| D1class | Uc34 | 0.41 | Uc34 | 0.41 | 3.29 | 0.002 |
| | Oc45 | 0.39 | Oc23 | 0.23 | 1.96 | 0.002 |
| D5class | Uc34 | 0.41 | Uc34 | 0.41 | 3.29 | 0.002 |
| | Uc23 | 0.40 | Oc23 | 0.23 | 1.98 | 0.002 |
| D16class | Uc34 | 0.41 | Uc34 | 0.41 | 3.29 | 0.002 |
| | Uc23 | 0.40 | Oc23 | 0.23 | 1.98 | 0.002 |
| D1exceed | O4 | 0.38 | O4 | 0.38 | 3.06 | 0.002 |
| | U2 | 0.38 | O2 | 0.24 | 2.04 | 0.004 |
| D5exceed | O4 | 0.38 | O4 | 0.38 | 3.00 | 0.002 |
| | O1+U1 | 0.36 | O2 | 0.24 | 2.01 | 0.002 |
| D16exceed | O1+U1 | 0.38 | O1+U1 | 0.38 | 3.00 | 0.002 |
| | O2 | 0.36 | OU5 | 0.24 | 2.01 | 0.002 |

especially important (Table 8). Thus, implementation of the Ecological Network would negatively affect the macroinvertebrate community. However, implementation of buffer zones and stream meandering would temper discharge dynamics and compensate for the consequences of climate change. Over exceedance DDI scores did not differ between these 2 scenarios and the adjusted Hadley scenario, but the combined and under exceedance DDI scores did (Table 8). Buffer zones and meandering caused the under exceedances to become significantly less dynamic (Table 8), but meandering did not add to the effect already caused by the buffer zones (Table 8). In conclusion, implementing Ecological Network with buffer zones and stream meandering would best compensate for increases in discharge dynamics, would lead to the smallest changes in the macroinvertebrate community, and therefore, would best mitigate climate change in lowland streams in northwestern Europe.

## Discussion

### *Flow parameter selection*

Hydrologic regime is a major determinant of the biotic composition, structure, and functioning of stream ecosystems (Richter et al. 1996, Poff et al. 1997). Flow characteristics probably are the most important drivers of stream ecosystem structure and processes (Stanford et al. 1996, Bunn and Arthington 2002), but relatively few studies have been done to determine biologically relevant hydrologic variables (Puckridge et al. 1998, Arthington et al. 2006). At fine habitat scales, lotic ecologists have assumed that the shapes and morphology of macroinvertebrates living in the boundary layer at the substratum surface are the consequence of natural selection to minimize the forces of flow that act upon them (Hynes 1970). However, streamlined or dorsoventrally flattened animals experience rather complicated flows and consequently endure the forces of flow (Statzner 1988). At a slightly larger spatial scale, flow stirs the substratum, delivers nutrients and food particles, and removes wastes, allelochemicals, and organisms (Allan 1995), and most effects on a stream community are assumed to be a consequence of low- (Lake 2003) or high- (Lytle 2002) flow events.

The intensity, frequency, and severity of extreme flow events determine the stability and composition of the stream bed and, thus, the characteristics of macroinvertebrate habitat (Resh et al. 1988, Biggs et al. 2005). Thus, a relationship must exist between the spatial and temporal scale of the hydrological influence and the scale at which macroinvertebrates experience its effects, e.g., the drag and lift forces caused by near-bed hydraulics. Macroinvertebrates are not bound to a single habitat (substratum type). Instead, they tend to be distributed across a range of available habitats (Wright et al. 2003). This broad distribution might ensure that the macroinvertebrate community is buffered against temporal variation in the availability of different habitats, and ultimately,

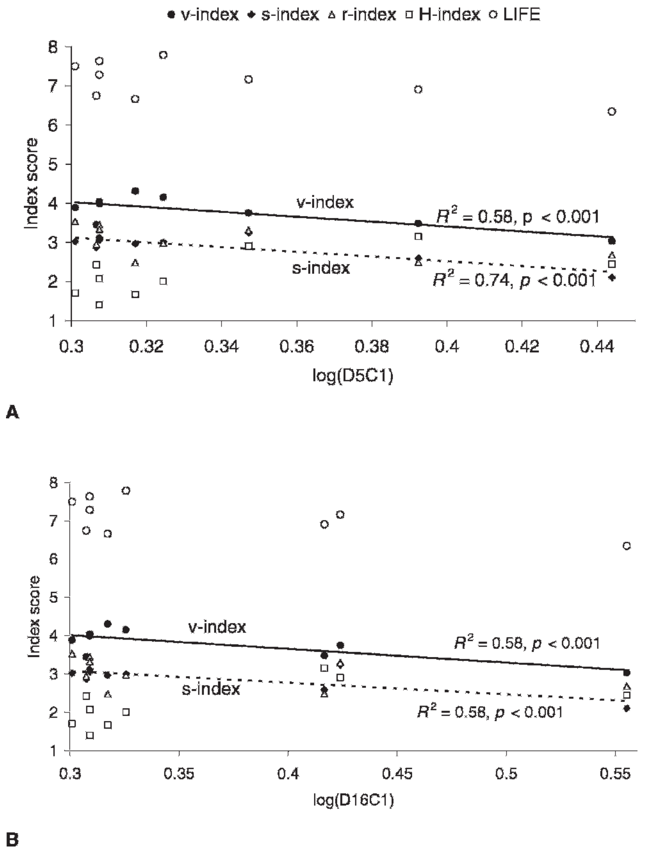

FIG. 1. Five biological metrics, calculated for the combined spring and autumn sample, plotted against the D5C1 (indicative weights 1–5) (A) and D16C1 (indicative weights 1, 2, 4, 8, 16) (B) discharge dynamics index over one hydrological year. Only the trend lines for significant relations are shown. v-index = current velocity index, s-index = saprobity index, r-index = rarity index, H-index = Shannon diversity, LIFE = Lotic-invertebrate Index for Flow Evaluation.

variability in the flow regime that creates and maintains habitat diversity (Bunn and Arthington 2002).

We compared the effects of quantitative discharge variables, percentiles, and metrics based on number of exceedance occurrences in the upper courses of 9 nearly natural lowland streams that differed in their hydrographs. Most explanatory power in several analyses of the relationships between discharge metrics and macroinvertebrate community structure was found in the number of over and under exceedance occurrences. This result is consistent with the idea that extreme flow events shape macroinvertebrate communities (Lytle 2002, Lake 2003, Lytle and Poff 2004). However, this result does not mean that local, short-term conditions are unimportant. These conditions can change macroinvertebrate abundances or local occurrences (Meffe 1984, Lytle 2002), but such changes do not persist for very long. Rapid recovery of stream communities after disturbances, i.e., high resilience (Webster and Patten 1979), is dependent on refugia, habitat and species availability, and species performance (Grimm and Fisher 1989, Lancaster et al. 2006).

### *A prior time period*

Translating a hydrological regime into ecologically meaningful characteristics requires consideration of the temporal features/complexity (including the predictability of extreme events) and the spatial complexity (effects on current velocity, depth, and substratum interactions) of the hydrograph. These features give rise to numerous flow characteristics. Richter et al. (1996) listed 64 indicators of hydrological alteration that could be used to assess anthropogenic hydrologic changes to flow regimes and to support ecosystem management and restoration. Magnitude, frequency, timing, duration, and rate of change of hydrological characteristics over time periods of days to years were proposed by Richter et al. (1997) and Poff et al. (1997). In contrast, proponents of the Instream Flow Incremental Methodology and the Physical Habitat Simulation procedures (Stalnaker et al. 1995, Bovee et al. 1998) regard near-substratum flow conditions and hydraulic parameters as crucial, ecologically relevant discharge characteristics (Gore et al. 2001).

We showed that flow exceedance occurrences explained most of the variability in the structure of macroinvertebrate communities in lowland streams. Macroinvertebrate responses to high and low extreme flow events and their ability to recover from such events probably are related to patterns in discharge regime or discharge dynamics over a certain time period (e.g., Webster and Patten 1979). Our analyses indicate that an antecedent time period ≥1 y is needed to describe the effects of flow variables on stream macroinvertebrate community structure. This time period encompasses the life cycles of most species (e.g., Lamouroux et al. 2004). However, in lowland streams, many indicator species have life cycles of 2 to 4 y, and it might be appropriate to analyze flow-regime characteristics over antecedent time periods as long as 4 to 5 y. Such long-term continuous measurements of discharge are often available for larger rivers in northwestern Europe, but these rivers are almost always disturbed by other stressors that prevent detection of a specific hydrological signal. In Europe, natural or near-natural conditions are found only in the upper or middle

TABLE 7. Adjusted $R^2$, *t*-statistic, and significance (*p*) for the regressions of 5 macroinvertebrate composition metrics vs the 4 discharge dynamics indices (v-index = current velocity index, s-index = saprobity index, r-index = rarity index, H-index = Shannon diversity, LIFE = Lotic-invertebrate Index for Flow Evaluation).

| Index | Statistic | D5C1 | D16C1 | D5O1 | D16O1 | D5U1 | D16U1 |
|---|---|---|---|---|---|---|---|
| LIFE index | Adjusted $R^2$ | 0.29 | 0.27 | 0.11 | 0.14 | 0.36 | 0.28 |
| | *t* | −2.05 | −1.99 | −1.41 | −1.53 | −2.37 | −2.01 |
| | *p* | 0.080 | 0.087 | 0.201 | 0.173 | 0.050 | 0.084 |
| v-index | Adjusted $R^2$ | 0.52 | 0.53 | 0.34 | 0.39 | 0.55 | 0.49 |
| | *t* | −3.09 | −3.09 | −2.27 | −2.45 | −3.28 | −2.95 |
| | *p* | 0.018 | 0.018 | 0.057 | 0.044 | 0.014 | 0.021 |
| s-index | Adjusted $R^2$ | 0.70 | 0.53 | 0.81 | 0.83 | 0.53 | 0.36 |
| | *t* | −4.46 | −3.14 | −5.91 | −6.35 | −3.15 | −2.35 |
| | *p* | 0.003 | 0.016 | 0.001 | 0.000 | 0.016 | 0.051 |
| r-index | Adjusted $R^2$ | 0.22 | 0.06 | 0.25 | 0.24 | 0.15 | −0.02 |
| | *t* | −1.82 | −1.23 | −1.93 | −1.88 | −1.54 | −0.94 |
| | *p* | 0.112 | 0.259 | 0.095 | 0.101 | 0.167 | 0.380 |
| H-index | Adjusted $R^2$ | 0.27 | 0.26 | 0.04 | 0.06 | 0.38 | 0.27 |
| | *t* | 2.00 | 1.97 | 1.17 | 1.21 | 2.42 | 1.98 |
| | *p* | 0.086 | 0.090 | 0.280 | 0.264 | 0.046 | 0.088 |

courses of rivers (e.g., Furse et al. 2006), and such streams almost always lack long-term discharge series. Thus, we had to take our own measurements of daily stream flows in the months prior to macroinvertebrate sampling.

### *Macroinvertebrate community parameters*

Only the v-index and the s-index were significantly related to DDI scores. The v-index assumes a linear relationship between current strength and species occurrence patterns. Its decreasing tendency along a gradient of increase in discharge dynamics suggests that less hydrologically dynamic streams are inhabited by a higher number of rheophilic species. Thus, species that are better adapted to higher velocity would be less well adapted to changes in velocity. A possible explanation for this apparent paradox is the observation that although more peak flows occur in more dynamic streams, $Q_{50}$ declines and more low-flow events also occur (Leopold et al. 1964). During low-flow events, the substratum can become silted and $O_2$ concentrations decrease. Most rheophilic species are sensitive to $O_2$ content. The same explanation should apply for saprobity. Low-flow conditions often result in more saprobic conditions (Verdonschot 1990), which would increase the s-index. However, in the streams we studied, another process appears to prevail. Streams with more dynamic flow regimes experience more scour, which washes out organic material. Thus, species that are less reliant on organic material will survive in more dynamic streams, and the s-index will decline. This process would contradict our rheophily trend, and indicates that rheophilic species might be sensitive to extreme discharge events and, thus, require stable hydrological conditions.

Neither rarity nor diversity appeared to be related to discharge dynamics within the ranges of flow variability we studied. Low and high-flow events do not necessarily drive macroinvertebrate species diversity directly, although drought and extended periods of low flow maintain diversity in lowland wet grassland, winterbournes, the inundation zones of ponds and rivers, and in rivers (Everard 1996). The intermediate disturbance hypothesis predicts that diversity will be highest in communities subjected to moderate levels of disturbance (Ward and Stanford 1983). Wright et al. (1998) and Boon (2000) showed, each from a different perspective, that natural stream conditions do not translate directly to high diversity but that diversity is likely to be related to the type and constancy of natural factors that influence species occurrences. Their results support our finding that rarity was not a useful index of the response of macroinvertebrate communities to discharge variability in lowland streams. Nijboer and Goedhart (2006) showed that, on a larger geographical scale, the number of rare taxa in lowland streams is positively correlated with naturalness and negatively correlated with disturbances like channelization and organic pollution. However, rare species often occur in low numbers and might be present by chance (Marchant 2002). The small number of samples in our study and the small number of rare species in our samples could explain our inability to detect an effect of discharge variability on rarity.

Variables used to summarize discharge dynamics should be biologically relevant and easy to calculate and interpret. However, useful information can be lost when different characteristics are summarized in one or few data points or index values. This

TABLE 8. *t*-statistics, significance (*p*), and effect size (*r*) for pairwise comparisons of discharge dynamics index (DDI) scores among climate change and land- and water-use scenarios. Cn = current climate, Hc = uncorrected Hadley Center prediction, Hp = corrected Hadley Center prediction, HpEn = corrected Hadley Center prediction with Ecological Network landuse change, HpEnBu = corrected Hadley Center prediction with Ecological Network landuse change and riparian buffers, HpEnBuMe = corrected Hadley Center prediction with Ecological Network landuse change, riparian buffers, and stream meandering.

| | | Cn vs | | | | | Hp vs | | | HpEn vs | | HpEnBu vs |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DDI | Statistic | Hc | Hp | HpEn | HpEnBu | HpEnBuMe | HpEn | HpEnBu | HpEnBuMe | HpEnBu | HpEnBuMe | HpEnBuMe |
| D5C1 | *t* | −8.860 | −4.732 | −6.663 | −3.260 | −2.920 | −2.082 | 1.554 | 1.952 | 3.620 | 4.029 | 0.385 |
| | *p* | 0.000 | 0.000 | 0.000 | 0.001 | 0.004 | 0.037 | 0.120 | 0.051 | 0.000 | 0.000 | 0.700 |
| | *r* | 0.60 | 0.44 | 0.32 | 0.28 | 0.21 | 0.11 | 0.18 | 0.17 | 0.19 | 0.20 | 0.05 |
| D16C1 | *t* | −8.353 | −4.439 | −6.390 | −2.738 | −2.430 | −2.075 | 1.773 | 2.133 | 3.830 | 4.202 | 0.344 |
| | *p* | 0.000 | 0.000 | 0.000 | 0.006 | 0.015 | 0.038 | 0.076 | 0.033 | 0.000 | 0.000 | 0.731 |
| | *r* | 0.61 | 0.45 | 0.33 | 0.26 | 0.19 | 0.12 | 0.22 | 0.19 | 0.22 | 0.22 | 0.04 |
| D5O1 | *t* | −6.187 | −7.704 | −8.032 | −7.118 | −6.972 | −0.344 | 0.632 | 0.769 | 0.977 | 1.114 | 0.139 |
| | *p* | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.731 | 0.527 | 0.442 | 0.329 | 0.266 | 0.890 |
| | *r* | 0.39 | 0.60 | 0.40 | 0.55 | 0.46 | 0.02 | 0.09 | 0.07 | 0.06 | 0.06 | 0.02 |
| D16O1 | *t* | −5.056 | −7.577 | −7.798 | −7.083 | −6.943 | −0.302 | 0.521 | 0.640 | 0.819 | 0.936 | 0.120 |
| | *p* | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.762 | 0.602 | 0.522 | 0.413 | 0.349 | 0.904 |
| | *r* | 0.29 | 0.54 | 0.36 | 0.50 | 0.42 | 0.02 | 0.07 | 0.06 | 0.05 | 0.05 | 0.01 |
| D5U1 | *t* | −8.430 | −3.308 | −5.361 | −1.692 | −1.321 | −2.211 | 1.705 | 2.129 | 3.888 | 4.325 | 0.407 |
| | *p* | 0.000 | 0.001 | 0.000 | 0.091 | 0.186 | 0.027 | 0.088 | 0.033 | 0.000 | 0.000 | 0.684 |
| | *r* | 0.52 | 0.27 | 0.24 | 0.13 | 0.08 | 0.10 | 0.17 | 0.16 | 0.19 | 0.20 | 0.04 |
| D16U1 | *t* | −7.910 | −3.819 | −5.805 | −1.959 | −1.665 | −2.093 | 1.923 | 2.264 | 3.994 | 4.350 | 0.322 |
| | *p* | 0.000 | 0.000 | 0.000 | 0.050 | 0.096 | 0.036 | 0.055 | 0.024 | 0.000 | 0.000 | 0.747 |
| | *r* | 0.58 | 0.38 | 0.31 | 0.19 | 0.13 | 0.12 | 0.24 | 0.21 | 0.23 | 0.24 | 0.04 |

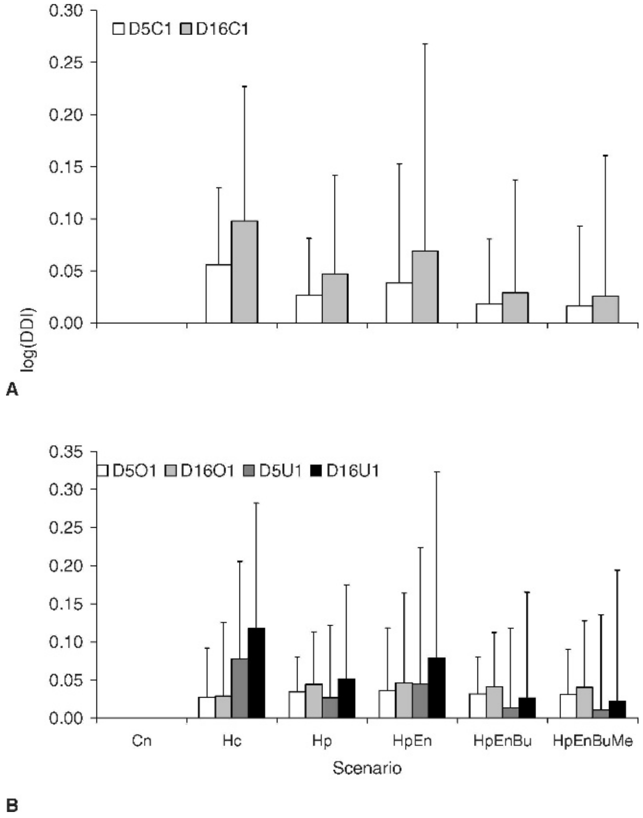

FIG. 2. Mean (+1 SD) difference in the discharge dynamics indices (DDIs) D5C1 and D16C1 for combined discharge exceedances (A) and DDIs D5O1, D16O1, D5U1, and D16U1 for separated over and under exceedances (B) between the current climate situation (scenario Cn) and all other climate or land- and water-use scenarios. Hc = uncorrected Hadley Center prediction, Hp = corrected Hadley Center prediction, HpEn = corrected Hadley Center prediction with Ecological Network landuse change, HpEnBu = corrected Hadley Center prediction with Ecological Network landuse change and riparian buffers, HpEnBuMe = corrected Hadley Center prediction with Ecological Network landuse change, riparian buffers, and stream meandering.

information loss was apparent when we combined 10 over and under exceedance variables into 2 summary variables (1 for over and 1 for under exceedance), and then into 1 combined variable. Nevertheless, such summary variables should still describe the relevant complexity of the flow regime. We found that the v-index and s-index were significantly related to the DDIs, and these results indicate the potential of the approach presented here.

### *Prediction*

Both duration of particular flow events and the predictability of the hydrologic regime affect ecological phenomena (Resh et al. 1988, Richter et al. 1996, Poff et al. 1997). The more predictable a flow regime, the more effectively the biotic community will be adapted to it (Horwitz 1978). Unpredictable flow regimes are likely to support less-adapted communities or communities composed of fewer taxa, fewer rare taxa, or more tolerant taxa.

The 9 study streams experienced predictable annual changes in $Q_{50}$ (high in winter, lower in summer), but specific timing of high or low discharges caused by thunderstorms, freezing, or drought were unpredictable. Macroinvertebrates living in natural lowland streams must be adapted to these unpredictable discharge events. Therefore, the dynamics of a natural hydrological regime should not alter the macroinvertebrate community. This type of response expresses the resistance of the community to the disturbances generated by both low- and high-flow conditions. Life-history attributes, such as opportunism, flexibility, and trophic generalism, are adaptations to unpredictable flow regimes (Puckridge et al. 1998) and can increase community resistance to flow variability.

Until now, few model simulations have linked climate change, changes in daily precipitation, and land- and water-use changes. We used DDIs to predict changes in climate and land and water use. Such models require a regional approach and a well-studied catchment. Predicted climate changes will result in an increase in precipitation in northwestern Europe (Mooij et al. 2005), which will lead to a more dynamic discharge pattern in lowland streams in all our scenarios. An increase of 17% precipitation would result in an increase in extreme high flows of ~50% (van Walsum et al. 2001). Changes in extreme flows will have a greater impact on discharge patterns than on annual means (Gleick 1990). In contrast to the results of Karl et al. (1995), our predictions showed a clear increase in extreme hydrologic events. When we applied changes in DDIs to the v- and s-indices, it became clear that stream macroinvertebrate communities will be negatively impacted by the predicted climate change. However, careful changes in land and water use could mitigate the effects of climate change, as shown by the results for the scenario in which buffer zones and meandering are implemented. Our results suggest that current restoration practices and planned restoration activities could interact positively to reduce effects of climate change on lowland stream ecosystems. However, restoration should be implemented at the catchment scale rather than limited to small areas or to single-stream stretches (e.g., Verdonschot and Nijboer 2002). We think it is not necessary (or practical) to renaturalize a 1-km-wide buffer zone along all streams, but restoration effort should be directed toward creating more constant hydrological regimes in several streams so that their riparian buffer zones can serve as a retention area. Restoration of stream ecosystem functioning through stream channel–valley coupling has been done successfully (Toth 1995, Hill and Platts 1998).

Detailed species responses to shifting discharge regimes cannot be simulated accurately. However, measures of over and under exceedance occurrences are useful tools for assessing the extent of climate-induced hydrological change. The type of analysis presented here could be used to do a sensitivity analysis to reveal which streams are most threatened by climate change. It offers the possibility to identify thresholds of ecological change induced by hydrological dynamics under scenarios of climate change at a regional scale that might include different types of hydrologic regimes (e.g., Arthington et al. 2006). We focused on macroinvertebrate community structure as one aspect of stream ecosystem structure. Many other groups (e.g., riparian and aquatic vegetation, fish) could and should be studied. Longer hydrological and ecological time series and robust ecological response models are needed to incorporate ecosystem structure and functioning into climate-change risk assessment (Meyer et al. 1999). Effects on presence/absence of species, seasonality (Power 1992), foodweb interactions (Power et al. 1995), productivity, and nutrient dynamics (Mulholland et al. 1997) should be addressed in these assessments.

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