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Evaluation of Environmental Factors to Determine the Distribution of Functional Feeding Groups of Benthic Macroinvertebrates Using an Artificial Neural Network

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ABSTRACT: Functional feeding groups (FFGs) of benthic macroinvertebrates are guilds of invertebrate taxa that obtain food in similar ways, regardless of their taxonomic affinities. They can represent a heterogeneous assemblage of benthic fauna and may indicate disturbances of their habitats. The proportion of different groups can change in response to disturbances that affect the food base of the system, thereby offering a means of assessing disruption of ecosystem functioning. In this study, we used benthic macroinvertebrate communities collected at 650 sites of 23 different water types in the province of Overijssel, The Netherlands. Physical and chemical environmental factors were measured at each sampling site. Each taxon was assigned to its corresponding FFG based on its food resources. A multilayer perceptron (MLP) using a backpropagation algorithm, a supervised artificial neural network, was applied to evaluate the influence of environmental variables to the FFGs of benthic macroinvertebrates through a sensitivity analysis. In the evaluation of input variables, the sensitivity analysis with partial derivatives demonstrates the relative importance of influential environmental variables on the FFG, showing that different variables influence the FFG in various ways. Collector-filterers and shredders were mainly influenced by Ca^{2+} and width of the streams, and scrapers were influenced mostly with Ca^{2+} and depth, and predators were by depth and pH. Ca^{2+} and depth displayed relatively high influence on all four FFGs, while some variables such as pH, %gravel, %silt, and %bank affected specific groups. This approach can help to characterize community structure and to ecologically assess target ecosystems.

Key words: Artificial neural network, Benthic macroinvertebrates, Contribution evaluation, Functional feeding groups, Prediction, Sensitivity analysis

INTRODUCTION

The distribution and abundance of species are governed by environmental conditions, including the diversity and stability of stream habitats (Cummins 1979, Ward and Stanford 1979) that comprise components of ecological niches (Malmqvist and Otto 1987). Therefore, understanding the environmental features associated with stream communities is of fundamental importance for ecosystem management. Benthic macroinvertebrates, which are taxonomically diverse, sedentary in behavior, and have long life cycles, respond to environmental disturbances in an integrated and continuous manner, and have therefore been widely used for assessing water quality in aquatic ecosystems. There have been numerous accounts of the use of benthic macroinvertebrates as indicators of short- and long-term environmental changes in running waters (Hellawell 1978, Lenat 1988, Smith et al. 1999, Hawkins et al. 2000). Species richness (i.e., the number of species occurring in a given area) is commonly used as an integrative descriptor of the community (Lenat 1988), as it is influenced by a large number of environmental factors, such as environmental stability (Cummins 1979, Ward and Stanford 1979), and heterogeneity (Malmqvist and Otto 1987), and biological factors (MacArthur 1965, Feminella and Resh 1990). The species richness of aquatic invertebrates is also strongly influenced by natural and anthropogenic disturbances (Rosenberg and Resh 1993), which may lead to spatial discontinuities in predictable gradients (Ward and Stanford 1979, 1983) and losses of taxa (Brittain and Saltveit 1989).

Spatial heterogeneity plays a governing role in determining biological communities and subsequently causes complex environment-

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community relationships (Turner and Gardner 1991, Levin 1992). Guilds of organisms can be used as expressions of spatial heterogeneity. Functional feeding groups (FFGs), which are guilds of macroinvertebrates that obtain food in similar ways regardless of taxonomic affinities, represent taxonomically heterogeneous assemblages of benthic fauna. Moreover, they reflect the food resources available in a given area, therefore their distributions respond mostly to disturbances that alter the food base of the system (e.g., Hershey et al. 1988, Hart and Robinson 1990). FFGs thus can be used to obtain information on a variety of disturbances. The proportion of different groups may change in response to a disturbance that affects the food base of the system, thereby offering a means of assessing disruption of ecosystem functioning. The percentages of FFGs have been commonly used as indicators for rapid bioassessment (Resh and Jackson 1993, Barbour et al. 1999).

Understanding the effects (or contribution) of environmental variables on the distribution of species is important for the evaluation and management of target ecosystems. One of the methods used to evaluate these effects, sensitivity analysis, is carried out using mathematical models of ecological processes. The purpose of sensitivity analysis is to determine the response(s) of the model dynamics to variation in the values of some parameters (Park et al. 2007). One or more outcomes of the model are selected (usually state variables or some statistical indicators) and their behaviour is evaluated across a plausible range of parameter values (McCallum 2000).

Artificial neural networks (ANNs) have been used as tools in ecological modelling (Lek and Guégan 1999, Lek et al. 2005, Park and Chon 2007). A multilayer perceptron (MLP) with a backpropagation learning algorithm (BP), which is a supervised ANN, has been used for various purposes (Lek and Guégan 2000): patterning complex relationships (Lek et al. 1996), predicting population and community development (Recknagel et al. 1997, Chon et al. 2000), and modelling habitat suitability (Paruelo and Tomasel 1997). The explanatory power of the MLP has been criticized due to its black-box model approach, but now sensitivity analysis methods have been developed to identify the most influential variables in MLP models (Lek et al. 1996). Although the apparent complexity of ANNs was originally believed to limit our ability to gain explanatory insight into the prediction process, recent advancements (Olden and Jackson 2002, Gevrey et al. 2003) have illustrated that this indeed not the case and researchers now have the ability to identify individual and interacting contributions of the predictor variables in ANNs (Olden et al. 2004).

In this study, we evaluated the contribution of environmental factors in determining the proportional distribution of FFGs using MLP and sensitivity analysis.

MATERIALS AND METHODS

Field Data

Benthic macroinvertebrate communities were collected at 664 sites in the province of Overijssel, The Netherlands (Verdonschot and Nijboer 2000) (Fig. 1). The sampling dates were spread across seasons as well as over several years (from 1981 to 1985). Six hundred and fifty sites were used for our study, as fourteen sites were discarded due to missing values or other inconsistencies. The sampling objective was to capture the majority of the species in sufficient numbers to determine their relative abundances at a given site. At each site, major habitats were selected over a 10- to 30-m stretch of the water body and were sampled with the same sampling effort. Macroinvertebrate samples were taken to the laboratory, sorted by eye, counted, and identified to species level.

We recorded a total of 854 species, and Chironomidae, Coleoptera, and Oligochaeta were the most abundant taxa. All species were categorized into 7 functional feeding groups (FFGs) (collector-filterer, collector-gatherer, predator, scraper, piercer, shredder, and scraper-miner) according to their functional feeding types. The proportions of the dominant four FFGs (collector-filterer, predator, scraper, and shredder) were calculated at each study site following Resh and Jackson (1993) and Barbour et al. (1999). The dominant four groups have previously been used for the rapid bioassessment of aquatic

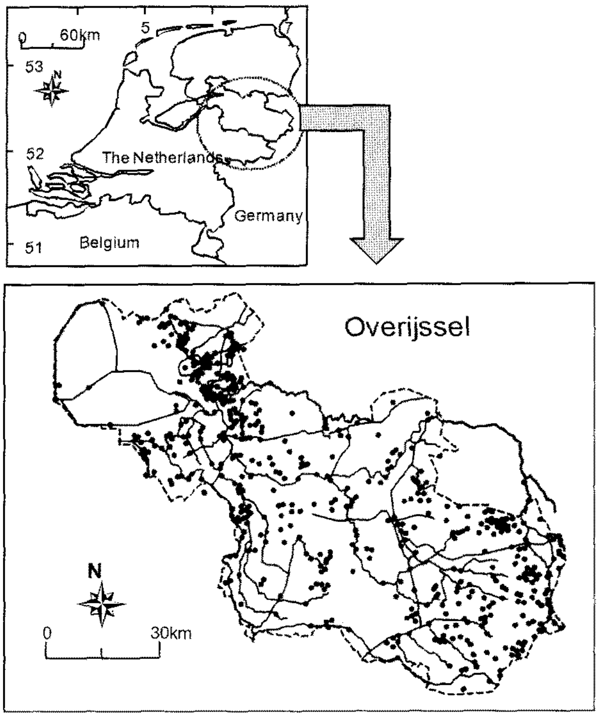

Fig. 1. Sampling sites in the province of Overijssel, The Netherlands. Each sampling site is marked with a dark circle.

ecosystems (Barbour et al. 1999). Additionally, among 90 environmental variables measured at each study site, we selected 17 environmental variables that made high contributions to the explanation of species richness on the basis of a sensitivity analysis performed on a preliminary multilayer perceptron model using a backpropagation learning algorithm, (Table 1). Correlation coefficients for the correlations among these 17 variables were low (less than 0.4) for most of the variables (Gevrey et al. 2005).

In the modelling process, all variables were proportionally rescaled between 0 and 1 in the range of the minimum and maximum values to give the same weight (or importance) to all variables. Before rescaling, the environmental variables were transformed by natural logarithm to reduce skewed distributions (Legendre and Legendre 1998, Lek and Guégan 1999).

Modelling Process

To evaluate the effects of environmental factors on the distribution of FFGs, we first predicted the proportion of the four selected FFGs based on the differences in the environmental conditions. MLP with BP was used as a nonlinear predictor (Haykin 1994) (Fig. 2). Next, the contributions of the environmental factors were estimated through a sensitivity analysis of the MLP model. BP is a supervised learning algorithm designed to minimize the mean square error between the computed output of the network and the desired output. The MLP normally consists of three layers: input, hidden, and output layers. It requires input vectors (17 environmental factors in this study) in the input layer, as well as target (or desired) values (proportions of each of the 4 FFGs in this study) in the output layer corresponding to each input vector. The modelling was carried out in three phases: learning, test, and sensitivity analysis. Of the 650 samples, 75% of the samples (433) were used as a training dataset and remaining 25% of the samples were for the testing dataset. Therefore, the dataset for training consisted of 433 samples with 17 input variables and 4 output variables. Through many trials with different numbers of neurons in a single hidden layer, a model with 5 hidden neurons was chosen as optimum size for this study. The training process was stopped at 500 iterationss to avoid the overfitting problem. A description of the learning rules can be found in Rumelhart et al. (1986), Kung (1993), and Lek and Guégan (2000). Correlation coefficients were calculated to verify the predictability of the network in both learning and testing phases.

Table 1. Environmental variables used in the model

Variable	Description	Unit	Mean	SD*
%Bank	Percentage sampled habitat: bank	%	18.3	23.6
%Emveg	Percentage sampled habitat: emergent vegetation	%	16.3	22.3
%Gravel	Percentage sampled habitat: gravel	%	1.3	5.3
%Silt	Percentage sampled habitat: silt	%	15.6	18.6
%Suveg	Percentage sampled habitat: submerged vegetation	%	12.0	19.5
%Vegta	Percentage sampled habitat: floating vegetation	%	13.0	20.6
Ca^{2+}	Calcium	mg/L	51.0	25.9
Conduc	Electric conductivity	μS/cm	428.4	237.3
Depth	Depth	m	1.1	1.6
NH_4^-	Ammonium	mgN/L	1.3	2.5
NO_3^-	Nitrate	mgN/L	3.8	8.0
pH	Acidity		7.1	1.0
Season	Season: (0: summer, 1: winter)		–	–
Slope	Slope	m/km	5.7	20.4
Temp	Water temperature	℃	13.3	6.2
Velocity	Flow velocity	m/s	0.1	0.2
Width	Width of stream	m	65.4	472.8

* Standard deviation.

Sensitivity Analysis of MLP Model

After the learning process for the MLP models, a sensitivity analysis was carried out to evaluate the contribution of each input variable (parameters of the population dynamic models) to the output values of MLP. There are several ways to perform the sensitivity analysis with MLP (Dimopoulos et al. 1999). Following Gevrey et al. (2003), we used the 'partial derivatives' (PaD) method (Dimopoulos et al. 1995, 1999) to identify the degree of contribution of the input variables.

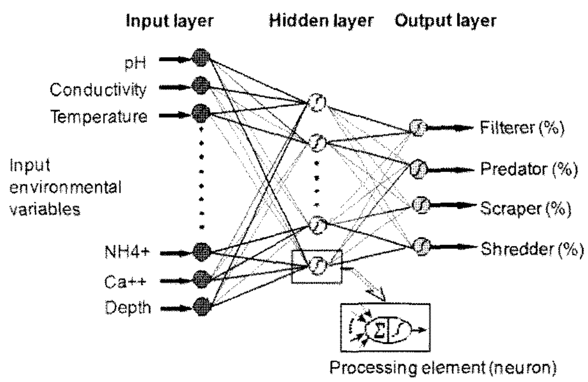

Fig. 2. Schematic diagram of a multilayer perceptron (MLP).

The PaD method presents the output of the MLP models with respect to the input to obtain the profile of variations in the output associated with small changes in one input variable (Dimopoulos et al. 1995, 1999, Gevrey et al. 2003). The formula used to obtain the partial derivatives (d_{ji}) is:

$$d_{ji} = S_j \sum_{h=1}^{nh} w_{ho} I_{hj} (1 - I_{hj}) w_{ih} \qquad (1)$$

where S_j is the derivative of the output neuron with respect to its input, I_{hj} is the response of the h^{th} hidden neuron, w_{ho} and w_{ih} are weights between the output neuron and h^{th} hidden neuron, and between the i^{th} input neuron and the h^{th} hidden neuron, respectively.

If the partial derivative is negative, then for each parameter being analyzed, the output variable will tend to decrease as the input parameter increases. Conversely, if the partial derivative is positive, the output variable will tend to increase as the input parameter increases. The relative contribution of input variables to the MLP output can be estimated as the percentage of the sum of the squared partial derivatives (SSD) obtained for each input variable using equation (2).

$$(\%)SSD_j = \frac{SSD_j}{\sum_{j=1}^{N} SSD_j} \times 100 \quad , \quad SSD_j = \sum_{i=1}^{N} d_{ji} \qquad (2)$$

where N is the number of input variables. The SSD values allow the classification of the variables according to their contribution to the output variable in the model: the input variable with the highest SSD value being the variable that most influences the output variable. The details of the MLP sensitivity analysis as applied to ecological modelling were fully described by Gevrey et al. (2003).

RESULTS

Among the seven FFGs in the dataset, the collector-filterer and collector-gatherer groups showed the highest number of species and number of individuals at each study site (Fig. 3). The number of species and their abundance were strongly correlated ($r = 0.91$, $p < 0.01$). Among the seven FFGs, the proportions of the dominant four FFGs (collector-filterer, predator, scraper, and shredder) were selected following Resh and Jackson (1993) and Barbour et al. (1999). These four groups have been proposed as appropriate for use in the the rapid bioassessment of aquatic ecosystems (Barbour et al. 1999).

The proportion of the 4 selected FFGs at each site were predicted by the MLP based on the 17 environmental variables with mean correlation coefficients of 0.78 ($p < 0.05$) and 0.68 ($p < 0.05$) between the observed and estimated values for the training and testing phases, respectively. The frequency histogram for the error values showed that most error values lie around zero, and mean error values ranged from 0.000 to 0.004 (SD 0.000~0.002) for all cases.

To evaluate the influence of environmental variables on FFGs, the PaD sensitivity analysis was conducted for each FFG. Fig. 4 shows the relative contribution of each variable to the prediction for different FFGs. Dotted lines on the figure show values mean valuesfor the 17 variables. Different variables influenced the FFGs in

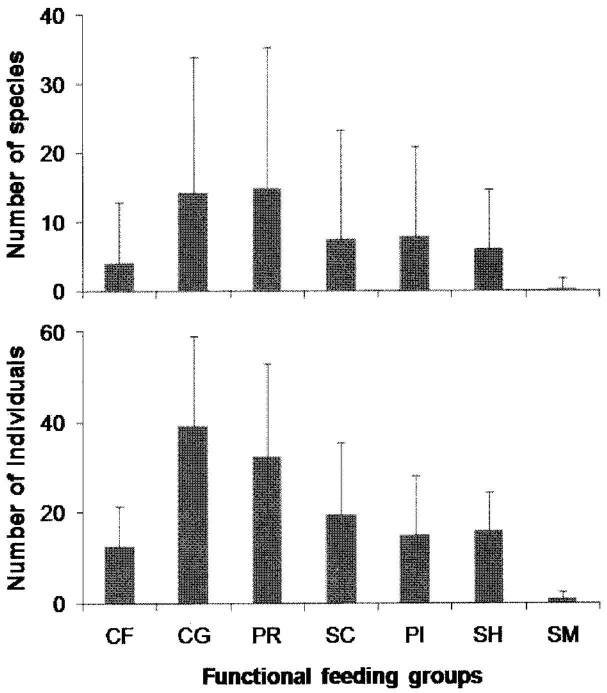

Fig. 3. Differences in the mean number of species and abundance in each functional feeding group. Error bars indicate the standard deviation. CF: collector-filterer, CG: collector-gatherer, PR: predator, SC: scraper, PI: piercer, SH: shredder, and SM: scraper-miner.

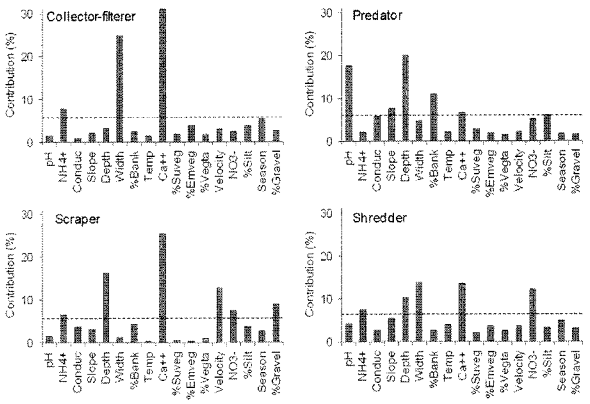

Fig. 4. Relative contribution of 17 environmental variables to the four functional feeding groups. Dotted lines indicate average values for the contribution of each environmental variable.

different ways. Collector-filterers were mainly influenced by Ca^{2+} which made a contribution of about 31% to the predicted outcome, followed by the width of the stream (25%) and NH_4^+ (8%). Shredders were also strongly influenced by Ca^{2-} (14%) and width (14%), as well as NO_3^- (12%), depth (10%), and NH_4^+ (7%). Scrapers were influenced by 6 variables: the most influential of which were Ca^{2+} (28%) and depth (18%), followed by NH_4^+, velocity, % gravel, and NO_3^-. Finally, predators were influenced by depth (20%) and pH (18%), while %bank, %silt, slope, and Ca^{2-} also made relatively small contributions to the representation of predators. Overall, Ca^{2+} and depth had a relatively high influence for all four FFGs, while pH, % gravel, and %silt, and %bank, affected only specific groups.

For selected variables showing higher-than-mean contribution values, partial derivatives of each variable were evaluated by plotting them against the corresponding input values. For shredders, the selected variables generally showed positive influences (Fig. 5). In particular, low values of NH_4^+ and width showed very strong positive influences, whereas high values of NO_3^- showed strong negative influences. This indicates the relative importance of shredders in natural springs and headwater streams. For scrapers, NH_4^+ and Ca^{2+} displayed negative influences, whereas depth, velocity, NO_3^-, and %gravel showed positive influences (Fig. 6). These are all variables indicating more natural running water environment. In particular, the proportion of scrapers increased with increasing depth, indicating their more important role in deeper running waters. For collector-filterers, the selected variables generally had a negatively influence. Width and NH_4^+, in particular, negatively influenced collector-filterers at low values, whereas Ca^{2+} had a strongly negative influence on the collector-filterers at high values (Fig. 7). However, low values of Ca^{2-} showed positive influences. Collector-filterers play a more important role in large, more or less enriched water bodies. For predators, the selected variables generally showed negative effects (Fig. 8). However, low values of Ca^{2+} showed a positive influence, which indicates their important role in acidic waters. Overall, predators were more dominant in 'extreme' environments, like intermittent or heavily polluted water bodies.

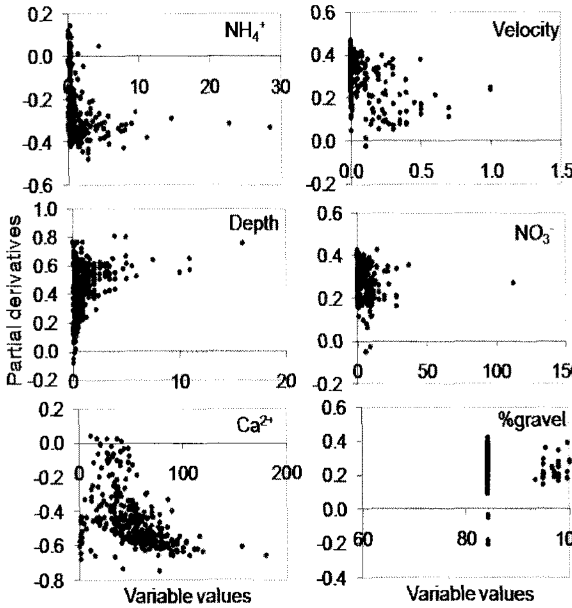

Fig. 6. Partial derivatives as a function of the selected environmental variables showing higher than average contribution to the output for scrapers in the MLP model.

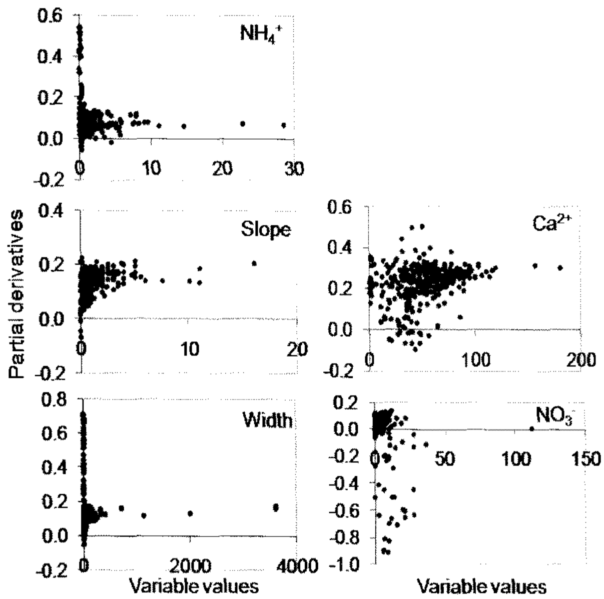

Fig. 5. Partial derivatives as a function of the selected environmental variables showing higher than average contribution to the output for shredders in the MLP model.

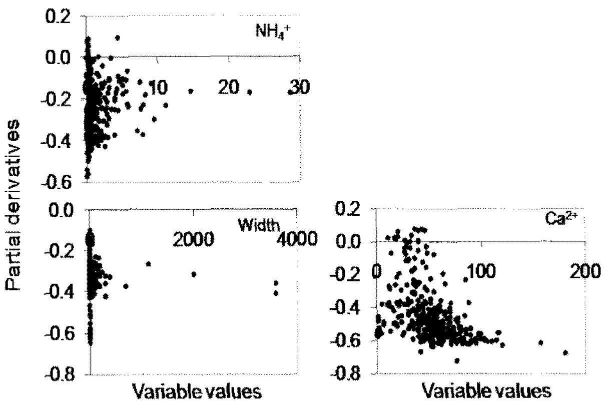

Fig. 7. Partial derivatives as a function of the selected environmental variables showing higher than average contribution to the output for collector-filterers in the MLP model.

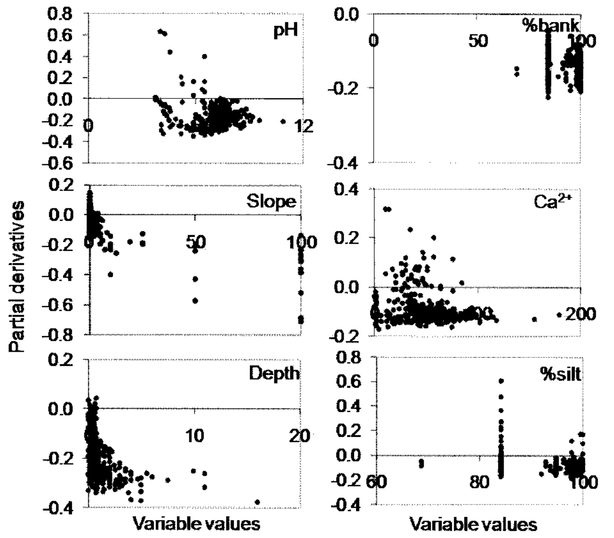

Fig. 8. Partial derivatives as a function of the selected environmental variables showing higher than average contribution to the output for predators in the MLP model.

DISCUSSION AND CONCLUSION

In this study we evaluated the contribution of environmental factors to the distribution of FFGs through sensitivity analysis of the MLP model. FFGs are based on associations among a limited variety of feeding adaptations found among the benthic macroinvertebrates and the basic categories of food resources available in the habitat (Callisto et al. 2001). Feeding measures or trophic dynamics encompass FFGs and provide information about the balance of feeding strategies and morphology in the benthic assemblage (Barbour et al. 1999). Trophic dynamics include the relative abundance of herbivores, carnivores, omnivores, and detritivores. The trophic dynamics in our study system were explained using the maximum exergy principle through dynamic structure models with the database used in this study (Jørgensen et al. 2002); the structure giving the highest exergy under the prevailing conditions represents the expected response to the prevailing conditions.

MLP has the capability to handle nonlinear, complex ecological data and to incorporate causality (Lek and Guégan 2000, Park et al. 2007). Although MLP models are able to make good predictions and are recognized as powerful tools (Skelton et al. 1995, Liong et al. 2000), at the beginning of their development they were considered as black-box approaches because of a lack of explanatory methods for relationships between input and output variables. Presently many different algorithms have been developed to avoid the "black-box" flaw of ANNs, and now they can be used as sensitivity analysis tools to determine the contributions of the independent variables and the way they act on the dependent variable (Garson 1991, Goh 1995, Lek et al. 1996, Balls et al. 1996, Maier and Dandy 1996, Scardi and Harding 1999, Dimopoulos et al. 1995, 1999, Olden 2003).

Through the sensitivity analysis of the MLP model, we evaluated the relative contributions of selected environmental variables on the composition of FFGs (Figs. 4~8) Different variables influenced the FFGs in different ways. Shredders and collector-filterers were strongly influenced by Ca^{2+} and stream width. Scrapers were influenced mostly by Ca^{2+} and stream depth. Finally, predators were influenced by depth and pH. Although Ca^{2+} and depth had strong effects on different FFGs, they affected each FFG differently. Increasing levels of Ca^{2+} had negative effects on shredders, and positive effects on scrapers and collector-filterers, whereas increasing depth had positive effects on scrapers, and negative effects on predators. These results reflected the relationship between actual habitat conditions and the distribution of FFGs. These results suggest that this sensitivity analysis approach has high potential for use as a tool for the evaluation of the importance of environmental factors for ecosystem management and in support of ecosystem restoration projects.

Patterns of FFG distribution reflect resource distribution and use, and facilitate the understanding of organic matter processing in streams (Vannote et al. 1980). Animal distribution patterns also, in part, reflect their tolerances to environmental variables and accordingly, community structure has been used in water quality monitoring (Furse et al. 1984). An imbalance in FFGs reflects unstable dynamics in their food resources, and may reflect stressed conditions in their environment (Barbour et al. 1999). Changes in food availability obviously play a potentially large role in determining the seasonal and spatial abundance of the various FFGs. Longitudinal changes in resource abundance were the basis of the river continuum concept (Vannote et al. 1980). Proportionately more genera of shredders are found in headwater streams compared to downstream (Wiggins and Mackay 1978). Specialist FFGs such as scrapers and shredders are more sensitive organisms and are thought to be well represented in healthy streams. Shredders utilize course particulate organic matter (CPOM) and associated bacterial and fungal colonizers as a food source, and are dominant in upper stream areas such as headwater streams in forests. Meanwhile, generalists such as collector-filterers have a broader range of acceptable food materials than specialists (Cummins and Klug 1979), and thus are more tolerant to pollution that might alter the availability of certain food sources. However, collector-filters are also thought to be sensitive in low-gradient streams, and dominant in downstream areas (Wallace et al. 1977). Collector-filterers and collector-gatherers utilize fine particulate organic matter (FPOM) as the primary food resource. Variability in the proportion of predators is less correlated to resource base changes resulting from natural changes in habitat and more attuned to changes in factors that cause significant changes in the availability of prey items, such as toxicity or nutrient supply. A relatively low to moderate proportion of predators reflects a balanced trophic structure, while extremely high or low proportions reflect an imbalance, possibly due to physicochemical perturbation (TNRCC 1999). Based on these characteristics, the proportions of these FFGs are sometimes used as indicators of habitat quality in rapid biological assessments of water quality.

FFGs constitute a good tool in biomonitoring programs, and are particularly useful for the evaluation of available trophic resources and their use in lotic ecosystems (Cummins and Klug 1979, Mihuc 1997, Callisto and Esteves 1998), allowing evaluation of the functional organization of communities. However, although FFGs are useful for evaluation of environmental conditions, their utility is not without limitations. For example, there can be difficulties in making the proper assignment of some taxa to functional feeding groups, as food sources can change between the developmental stages of a species. For example, predaceous stoneflies ingest more periphyton and detritus when small, and more animal prey when large (Allan 1982), and young nymphs of *Baetis* and *Cinygmul* feed as collectors in summer, but subsequently increase their consumption of diatoms (Allan and Castillo 2007).

In conclusion, the representation of functional feeding groups in stream ecosystems was effectively predicted from environmental variables using MLP with BP. In an evaluation of the input variables, sensitivity analysis using partial derivatives demonstrated the relative importance of environmental variables for the FFGs, and showed that different variables influence the FFGs in different ways. Our results demonstrated that MLP models can predict the proportional representation of functional groups based on ecological variables, demonstrating that FFG's may be a useful tool for the characterization of community structure and the ecological assessment of target ecosystems.

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LITERATURE CITED

Allan JD, Castillo MM. 2007. Stream Ecology: Structure and Function of Running Waters. Springer, Dordrecht, the Netherlands.

Allan JD. 1982. Feeding habits and prey consumption of three setipalpian stoneflies (Plecoptera) in a mountain stream. Ecology 63: 26-34.

Balls G-R, Palmer Brown D, Sanders G-E. 1996. Investigating microclimatic influences on ozone injury in clover (*Trifolium subterraneum*) using artificial neural networks. New Phytologist 132: 271-280.

Barbour MT, Gerritsen J, Snyder BD, Stribling JB. 1999. Rapid Bioassessment Protocols for Use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates and Fish, Second Edition. EPA 841-B-99-002. U.S. Environmental Protection Agency; Office of Water; Washington, D.C.

Brittain JE, Saltveit SJ. 1989. A review of the effect of river regulation on mayflies (Ephemeroptera). Reg Riv Res Manage 3: 191-204

Callisto M, Esteves FA. 1998. Categorização funcional dos macroinvertebrados bentônicos em quarto ecossistemas lóticos sob influência das atividades de umamineração de bauxita na amazônia central (Brasil). Oecologia Brasiliensis 5: 223-234.

Callisto M, Moreno P, Barbosa FAR. 2001. Habitat diversity and benthic functional trophic groups at Serra Do Cipo, Southeast Brazil. Rev Brasil Biol 61(2): 259-266.

Chon T-S, Park Y-S, Kim J-M, Lee B-Y, Chung Y-J, Kim Y. 2000. Use of an artificial neural network to predict population dynamics of the forest-pest pine needle gall midge (Diptera: Cecidomyiida). Environ Entomol 29: 1208-1215.

Cummins KW, Klug MJ. 1979. Feeding ecology of stream invertebrates. Ann Rev Ecol Syst 10: 147-172.

Cummins KW. 1979. The natural stream ecosystem. In: The Ecology of Regulated Streams (Ward JV, Stanford JA, eds). Plenum Press, New York. pp 7-24.

Dimopoulos I, Chronopoulos J, Chronopoulos-Sereli A, Lek S. 1999. Neural network models to study relationships between lead concentration in grasses and permanent urban descriptors in Athens city (Greece). Ecol Model 120: 157-165.

Dimopoulos Y, Bourret P, Lek S. 1995. Use of some sensitivity criteria for choosing networks with good generalisation ability. Neural Process Lett 2: 1-4.

Feminella JW, Resh VH. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. Ecology 71: 2083-2094.

Furse MT, Moss D, Wright JF, Armitage P. 1984. The influence of seasonal and taxonomic factors on the ordination and classification of running water sites in Great Britain, and on the prediction of their macroinvertebrate communities. Freshwat Biol 14: 257-280.

Garson GD. 1991. Interpreting neural network connection weights. Artificial Intel Expert 6: 47-51.

Gevrey M, Dimopoulos I, Lek S. 2003. Review and comparison of methods to study the contribution of variables in artificial neural network models. Ecol Model 160: 249-264.

Gevrey M, Park Y-S, Verdonschot P, Lek S. 2005. Predicting Dutch macroinvertebrate species richness and functional feeding groups using five modelling techniques. In: Modelling Community Structure in Freshwater Ecosystems (Lek S, Scardi M, Verdonschot P, Descy J, Park Y-S, eds). Springer, Berlin, pp 158-166.

Goh ATC. 1995. Back-propagation neural networks for modelling complex systems. Artificial Intel Eng 9: 143-151.

Hart DD, Robinson CT. 1990. Resource limitation in a stream community: Phosphorous enrichment effects on periphyton and grazers.

Ecology 71: 1494-1502.

Hawkins CP, Norris RH, Gerritsen J, Hughes RM, Jackson SK, Johnson RK, Stevenson RJ. 2000. Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. J N Am Benthol Soc 19: 541-556.

Haykin S. 1994. Neural Networks. MacMillian College Publishing Company, New York.

Hellawell JM. 1978. Biological Surveillance of Rivers. Water Research Center. Stevenage Laboratory, England.

Hershey AE, Hitner AL, Hullar MAJ, Miller MC, Vestal JR, Lock MA, Rundle S, Peterson BJ. 1988. Nutrient influence on a stream grazer: orthocladius microcommunities respond to nutrient input. Ecology 69: 1383-1392.

Jørgensen SE, Verdonschot P, Lek S. 2002. Explanation of the observed structure of functional feeding groups of aquatic macro-invertebrates by an ecological and the maximum exergy principle. Ecol Model 158: 223-231.

Kung SY. 1993. Digital Neural Networks. Prentice Hall, Englewood Cliffs, New Jersey.

Legendre P, Legendre L. 1998. Numerical Ecology. Elsevier, Amsterdam.

Lek S, Delacoste M, Baran P, Dimopoulos I, Lauga J, Aulagnier S. 1996. Application of neural networks to modelling nonlinear relationships in ecology. Ecol Model 90: 39-52.

Lek S, Guégan JF (eds). 2000. Artificial Neuronal Networks: Application to Ecology and Evolution. Springer-Verlag, Berlin.

Lek S, Guégan JF. 1999. Artificial neural networks as a tool in ecological modelling an introduction. Ecol Model 120: 65-73.

Lek S, Scardi M, Verdonschot P, Descy J, Park Y-S (eds). 2005. Modelling Community Structure in Freshwater Ecosystems. Springer, Berlin.

Lek S, Delacoste M, Baran P, Dimopoulos I, Lauga J, Aulagnier S. 1996. Application of neural networks to modelling nonlinear relationships in ecology. Ecol Model 90: 39-52.

Lenat DR. 1988. Water quality assessment of streams using a qualitative collection method for benthic macroinvertebrates. J N Am Benthol Soc 7: 222-233.

Levin SA. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943-1967.

Liong SY, Lim WH, Paudyal GN. 2000. River stage forecasting in Bangladesh: neural network approach. J. Comput. Civil Eng 14: 1-8.

MacArthur RH. 1965. Patterns of species diversity. Biol Rev 40: 510-533.

Maier HR, Dandy GC. 1996. The use of artificial neural networks for the prediction of water quality parameters. Water Resour Res 32: 1013-1022.

Malmqvist B, Otto C. 1987. The influence of substrate stability on the composition of stream benthos: an experimental study. Oikos 48: 33-38.

McCallum H. 2000. Population Parameters. Estimation for Ecological Models. Blackwell Science, Oxford.

Mihuc TB. 1997. The functional trophic role of lotic primary consumers: generalist versus specialist strategier. Freshwater Biol 37: 455-462.

Olden JD, Jackson DA. 2002. Illuminating the "black box": understanding variable contributions in artificial neural networks. Ecol Model 154: 135-150.

Olden JD, Joy MK, Death RG. 2004. An accurate comparison of methods for quantifying variable importance in artificial neural networks using simulated data. Ecol Model 178: 389-397.

Olden JD. 2003. A species-specific approach to modelling biological communities and its potential for conservation. Conserv Biol 17: 854-863.

Park Y-S, Chon T-S. 2007. Biologically-inspired machine learning implemented to ecological informatics. Ecol Model 203: 1-7.

Park Y-S, Rabinovich J, Lek S. 2007. Sensitivity analysis and stability patterns of two-species pest models using artificial neural networks. Ecol Model 204: 427-438.

Paruelo JM, Tomasel F. 1997. Prediction of functional characteristics of ecosystems: a comparison of artificial neural networks and regression models. Ecol Model 98: 173-186.

Recknagel F, French M, Harkonen P, Yabunaka K-L. 1997. Artificial neural network approach for modelling and prediction of algal blooms. Ecol Model 96: 11-28.

Resh VH, Jackson JK. 1993. Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In: Freshwater Biomonitoring and Benthic Macroinvertebrates (Rosenberg DM, Resh VH, eds). Chapman & Hall, New York. pp 195-233.

Rosenberg DM, Resh VH (eds). 1993. Freshwater Biomonitoring and Benthic Invertebrates. Chapman and Hall, New York.

Rumelhart DE, Hinton GE, Williams RJ. 1986. Learning internal representations by error propagation. In: Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Vol. I. Foundations (Rumelhart DE, McCelland JL, eds). MIT Press, Cambridge pp 318-362.

Scardi M, Harding LW. 1999. Developing an empirical model of phytoplankton primary production: a neural network case study. Ecol Model 120: 213-223.

Skelton PH, Cambray JA, Lombard A, Benn GA. 1995. Patterns of distribution and conservation status of freshwater fishes in South Africa. South Africa J Zool 30: 71-81.

Smith MJ, Kay WR, Edward DHD, Papas PJ, Richardson KSJ, Simpson JS. 1999. AusRivAs: using macroinvertevrates to assess ecological conditions of rivers in Western Australia. Fresh Biol 41: 269-282.

TNRCC 1999. Receiving Water Assessment Procedures Manual. Texas Natural Resource Conservation Commission, Austin TX.

Turner MG, Gardner RH. 1991. Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE. 1980. The river continuum concept. Can J Fish Aqua Sci 37: 130-137.

Verdonschot PFM, Nijboer RC. 2000. Typology of macrofaunal assemblages applied to water and nature management: a Dutch approach. In: Assessing the Biological Quality of Fresh Waters (Wright JF, Sutcliffe DW, Furse MT, eds). RIVPACS and other techniques. Freshwater Biological Association, Ambleside, Cumbria, UK. pp 241-262.

Wallace JB, Webster JR, Woodall WR. 1977. The role of filter feeders in flowing waters.

Ward JV, Stanford JA. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In: The Ecology of Regulated Streams (Ward JV, Stanford JA, eds). Plenum Press, New York, pp 35-55.

Ward JV, Stanford JA. 1983. The serial discontinuity concept of lotic ecosystems. In: Dynamics of Lotic Ecosystems (Fontaine TD, Bartell SM, eds). Ann Arbor Sci, Michigan, pp 29-42.

Wiggins GB, Mackay RJ. 1978. Some relationships between systematic and trophic ecology in Nearctic aquatic insects, with special reference to Trichoptera. Ecology 59: 1211-1220.

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