Incorporating ecological knowledge into ecoinformatics: An example of modeling hierarchically structured aquatic communities with neural networks

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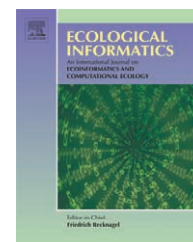**232** PUBLICATIONS   **36,099** CITATIONS

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Incorporating ecological knowledge into ecoinformatics: An example of modeling hierarchically structured aquatic communities with neural networks

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ABSTRACT

The field of ecoinformatics is concerned with gaining a greater understanding of complex ecological systems. Many ecoinformatic tools, including artificial neural networks (ANNs), can shed important insights into the complexities of ecological data through pattern recognition and prediction; however, we argue that ecological knowledge has been used in a very limited fashion to shape the manner in which these approaches are applied. The present study provides a simple example of using ecological theory to better direct the use of neural networks to address a fundamental question in aquatic ecology—how are local stream macroinvertebrate communities structured by a hierarchy of environmental factors operating at multiple spatial scales? Using data for 195 sites in the western United States, we developed single-scale, multi-scale and hierarchical multi-scale neural networks relating EPT (Orders: Ephermeroptera, Plecoptera, Trichoptera) richness to environmental variables quantified at 3 spatial scales: entire watershed, valley bottom (100s–1000s m), and local stream reach (10s–100s m). Results showed that models based on multiple spatial scales greatly outperformed single-scale analyses ($R=0.74$ vs. $\bar{R}=0.51$) and that a hierarchical ANN, which accounts for the fact that valley- and watershed-scale drivers influence local characteristics of the stream reach, provided greater insight into how environmental factors interact across nested spatial scales than did the non-hierarchical multi-scale model. Our analysis suggests that watershed drivers play a greater role in structuring local macroinvertebrate assemblages via their direct effects on local-scale habitats, whereas they play a much smaller indirect role through their influence on valley-scale characteristics. For the hierarchical model, the strongest predictors of EPT richness included descriptors of climate, land-use and hydrology at the watershed scale, land-use at the valley scale, and substrate characteristics and riparian cover at the reach scale. In summary, our results highlight the importance of incorporating environmental hierarchies to better understand and predict local patterns of macroinvertebrate assemblage structure in stream ecosystems. More generally, our case study serves to emphasize how incorporating prior ecological knowledge into ANN model structure can strengthen the relevance of ecoinformatic techniques for the broader scientific community.

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1.   Introduction

Predictive ability is viewed by many as the ultimate confirmation of theory and understanding in ecology (Pielke and Conant, 2003), and it is seen to play an increasing role in the evolving science of ecological forecasting (Clark et al., 2001). However, ecosystems are complex, adaptive systems characterized by historical legacies, time lags, non-linearities and feedback loops that vary in space and through time (see Levin, 1998), thus making it very challenging for scientists to explain variation in ecological attributes, let alone model or predict these attributes with any accuracy or precision (Peters, 1991). With the advent of complexity theory and a growing recognition of the multi-scaled and hierarchical nature of ecological systems (Allen and Starr, 1982), ecologists are now faced with the challenge of constructing more powerful and flexible models to help address issues of conservation and resource management.

The emergence of the field of Ecological Informatics or *Ecoinformatics* was largely inspired by the need to model complex ecological systems. A number of innovative analytical techniques have been promoted as powerful alternatives to traditional approaches for modeling ecological data (see Recknagel, 2003). For example, artificial neural networks (ANNs) have been embraced by many ecological modelers, as they are perceived to overcome many of the difficulties associated with ecological data, namely non-linearity (Lek and Guégan, 2000). Although ANNs technically do not differ from a number of standard statistical models (e.g., a neural network with no hidden layer is the same as simple regression and one with a small number of hidden neurons is analogous to polynomial regression—see Sarle, 1994), ANNs do provide a much more flexible approach to modeling ecological data. Model complexity can be varied by altering the transfer function or the inner architecture of the network by increasing the number of hidden neurons to enhance data fitting, or by increasing the number of output neurons to model multiple ecological response variables, such as multiple species (e.g. Özesmi and Özesmi, 1999) or entire communities (e.g. Olden, 2003). It is this flexibility that has likely led to the increased popularity of neural networks in ecology.

Like many models in ecology, statistical models should be crafted after an expert's mental map of how the focal system operates. Too often, however, this does not occur. In fact, one could argue that the sophistication of ANNs (and ecoinformatic tools in general) has discouraged the practice of using sound ecological principles during the modeling process. Indeed, a brief and selective perusal of the voluminous and rapidly growing literature using ANNs (for example in the journal *Ecological Modelling*) reveals that ecological knowledge is seldom considered in the model building process. Flood and Kartam (1994) emphasized this point when they stated, "there is a tendency among users to throw a problem blindly at a neural network in the hope that it will formulate an acceptable solution". As a result, the modeling process boils down to more of a fishing expedition than an educated exploration of the data. This is somewhat surprising given that domain knowledge continues to play an important role in other areas of ecoinformatics, such as the application of genetic and evolutionary computation approaches. Without doubt, ANNs can shed important insights into the complexities of ecological data through pattern recognition; however, their potential to incorporate prior ecological knowledge and address specific ecological theory has, in general, failed to be exploited. Incorporating prior ecological knowledge into model structure would, we believe, make the relevance of these techniques more obvious and attractive for the broader scientific community.

In this paper, we argue that ecoinformatic practitioners must begin to more rigorously incorporate existing knowledge into more ecologically informed statistical models. An obvious question then arises: *How can ecological knowledge advance our use of neural networks in ecological modeling?* Here, we present a case study that provides one example of how to address this question. Specifically, using the principles of spatial hierarchy we explore how a series of nested, hierarchical neural networks can be used to model stream macroinvertebrate assemblages as a function of environmental variables describing three nested spatial scales. Our intent is to illustrate that ecological principles have a vital role to play in improving the performance and interpretability of ANNs, and subsequently in advancing their use for addressing ecological theory and testing specific, conservation-relevant hypotheses.

2.   Case study—modeling stream macroinvertebrate assemblages using a hierarchical neural network

Understanding and predicting the distribution and abundance of species across the landscape is a fundamental research goal, and one certainly having important applications in riverine ecosystems. In the United States, and other developed countries, compliance with water quality standards is often judged with biological data, i.e., indicator species sensitive to water quality degradation. Explaining variation in the distribution of sensitive taxa in relation to environmental conditions at sampling sites is a key focus of many biomonitoring programs (e.g. Wright et al., 2000), and our ability to develop predictive models to explain biological condition in terms of landscape variables will directly inform stream conservation and resource management activities. Often aquatic insects, the immature stages of which live in close association with the stream bed (i.e. benthic), are used as indicators of water quality, and we focus on this group in the example below.

Our scientific understanding of how flowing water ecosystems are structured and how they function draws on several important advances over the last 20 years from general ecological theory that have been transferred or translated to the riverine environment (cf. Harris, 1998). Since the publication of Frissell et al. (1986), stream ecologists recognize that stream systems have a physical habitat hierarchy, i.e., local habitat conditions are influenced by landscape processes operating at broader spatial and temporal scales. For example, the stream-bed substrate characteristics at a point in the stream are dictated by the erosional forces operating at the reach scale and the sediment supply and type contributed by the entire

upstream catchment (as a function of geology, land cover, and precipitation regime). Thus, to characterize 'habitat' requires measurements at multiple scales and the incorporation of the hierarchical constraints imposed by the characteristics operating at broader scales (Townsend, 1996; Allan and Johnson, 1997).

A second major principle in stream ecology is that the spatial structure and temporal dynamics of 'habitat' strongly influence the distribution and abundance of aquatic species, including benthic insects. This so-called 'habitat template' provides a powerful framework for understanding among-site variation in benthic community composition in terms of environmental characteristics (Poff and Ward, 1990; Townsend and Hildrew, 1994). Because habitat is multi-scaled and hierarchical, it follows that biological responses to habitat can themselves be influenced by processes operating at multiple scales. Accordingly, local benthic community composition is dictated by spatial variation in habitat 'filters' operating at multiple landscape scales (see Poff, 1997). By characterizing how these filters change across the landscape, we can expect to explain substantial variation in benthic composition and move toward building more precise predictive models of use in conservation ecology and aquatic resource management (Petts, 2000).

In the case study that follows we apply ANN to a large biological dataset for streams in the western United States to explain variation in the composition of sensitive benthic taxa across these sites. We had three overarching goals: (1) build an ANN that captures our ecological understanding of the hierarchical structure of aquatic habitats by developing environmental descriptors that could serve as 'filters' at multiple spatial and temporal scales, from the local site to the entire catchment; (2) determine what new insights are gained from taking an integrative approach across multiple scales with a hierarchical vs. unstructured ANN (i.e. multi-scale but not hierarchical); (3) explore some implications of the case study results for broader conservation ecology and resource management of streams. Specifically, we constructed an ANN to investigate the influence of watershed-, valley-, and reach-scale environmental factors on local richness (number of species) of stream benthic insects. We focused on the well-known taxa groups EPT (Orders: Ephemeroptera, Plecoptera, Trichoptera), because abundance of these species is indicative of unimpaired water quality (Rosenberg and Resh, 1993).

3.   Methods

Our analysis examined 195 sites located in the Pacific Northwest and Southern Rocky Mountain regions of the western United States (Fig. 1). Macroinvertebrate communities were sampled between the years 1994 to 2001 as part of the U.S. Environmental Protection Regional Environmental Monitoring and Assessment Program (REMAP), which aims to assess the overall ecological condition of streams throughout the country (Kaufmann et al., 1999). The study sites (generally 1st through 4th order wadeable streams) were randomly selected
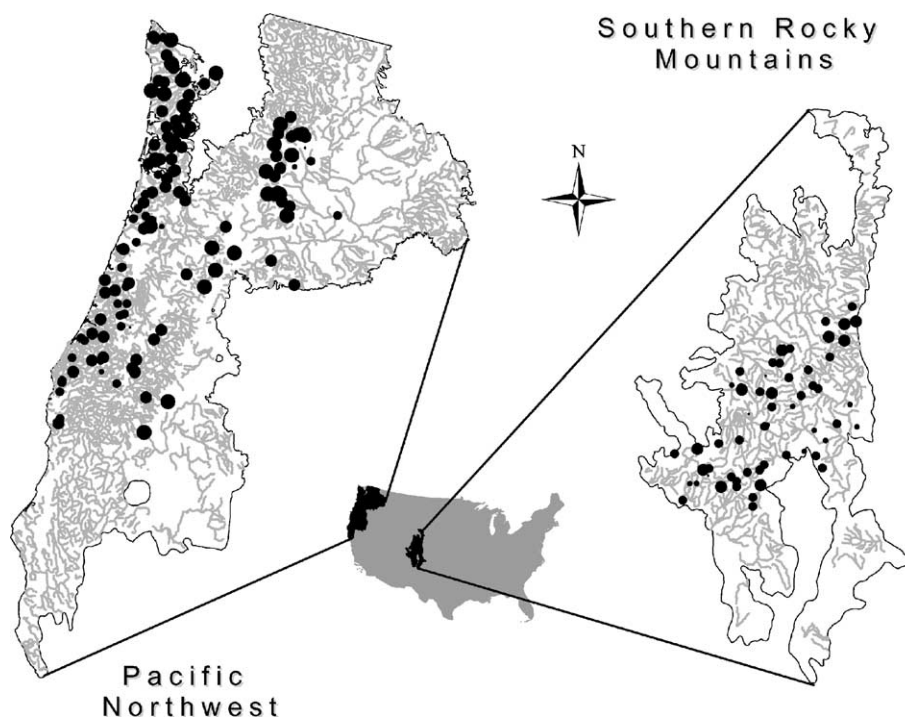

Fig. 1 – Map of the study area and sample sites (*n* = 195) in the Pacific Northwest and Southern Rocky Mountain regions of the United States. These sites are spatially distributed across 9 level-III ecoregions, including Southern Rockies (*n* = 53), Colorado Plateau (*n* = 5), Columbia Plateau (*n* = 9), Williamette Valley (*n* = 4), Coast Range (*n* = 86), Klamath Mountains (*n* = 4), Cascades (*n* = 16), Eastern Cascades Slopes and Foothills (*n* = 10) and North Cascades (*n* = 8). Symbol sizes are proportional to EPT taxa richness, i.e., larger symbols represent larger EPT richness.

according to a spatially balanced design, and were sampled using standardized protocols. Composite samples from stream reaches were used to characterize the macroinvertebrate assemblage at each site (see Kaufmann et al., 1999 for collection details), and the proportion of EPT taxa was calculated by dividing EPT taxa richness by total taxa richness (hereafter referred to as EPT richness). A total of 140 taxa were identified (mostly to genus level, except Chironomidae which were identified to tribe) and richness (total number of taxa recorded) per site ranged between 3 and 53 ($\bar{X}=34$, SD=11.3).

We quantified 33 environmental variables describing habitat conditions at the watershed ($n=15$), valley ($n=7$) and reach scales ($n=11$) (Table 1). Data from the U.S. Environmental Protection Agency's (EPA) Western Environmental Monitoring and Assessment Program (EMAP) and REMAP were used to describe reach-scale characteristics. The R/EMAP metrics are based on field measurements and observations of channel geometry, riparian characteristics, bed material, and woody debris at a length scale of tens of meters. Valley- and watershed-scale metrics were computed from remotely sensed data using a Geographic Information System. Spatial data were taken from several sources, including the U.S. Geological Survey, U.S. EPA, U.S. Department of Agriculture Natural Resources Conservation Service (NRCS), and PRISM developed by the Oregon Climate Service. Valley-scale metrics were developed to characterize landscape conditions upstream from the sampling site to the first major tributary to the main stream. Thus, they have a length scale on the order of 100s to 1000s of meters. Watershed-scale metrics apply to the entire drainage area or channel network above the sampling site and thus typically have a length scale >1000s of meters. The data used include 10-m digital elevation models (DEMs), soils, geology, land cover, and climate, which were characterized using models developed in Arc Macro Language and C++. Computed geomorphic metrics included slope and specific stream power ($SA^{0.4}$; where $S=$reach slope, $A=$watershed area, and 0.4 is a power function coefficient) using hydrologic distance-weighting schemes based on flow distance from the watershed outlet (study site), and valley confinement and hillslope connectedness to assess floodplain connectivity and the potential for colluvial inputs. Additional

Table 1 – Description of the 33 environmental variables used to model EPT richness

Scale	Category	Code	Description
Watershed	Hydrology	WH_Base	7-day minimum flow/mean annual flow
		WH_DLoP	Average duration of low pulses (day)
		WH_MA	Specific mean annual runoff (m^3/km^2)
		WH_NoFl	Mean number of discrete flood events ($year^{-1}$)
	Climate	WC_Aspt	Aspect (degrees)
		WC_AugT	August temperature (°C)
		WC_WinT	Five-month (Nov–Mar) winter temperature (°C)
	Geology	WGy_Sedi	Sedimentary geologic type (%)
		WGy_Volv	Volcanic geologic type (%)
		WGy_Buff	Calcareous rock (%)
	Geomorphic	WG_MSSP	Mean specific stream power (km)
		WG_Slop	Watershed slope (m/m)
	Land use	WL_Barr	Barren (%)
		WL_Fore	Forested (%)
		WL_Agri	Agricultural (%)
Valley	Geomorphic	VG_DWSP	Distance weighted stream power (km^2)
		VG_Powe	Last link specific stream power ($S*A^{0.4}$; $km^{0.8}$)
		VG_Entr	Valley entrenchment (m)
		VG_Conn	Average hillslope connectivity (m)
	Land use	VL_Barr	Barren (%)
		VL_Fore	Forested (%)
		VL_Agri	Agricultural (%)
		WL_Agri	Agricultural (%)
Reach	Geomorphic	RG_Slop	Channel slope (%)
		RG_Sinu	Channel sinuosity (m/m)
		RG_WiDp	Mean bankfull width/depth ratio (m/m)
		RG_RelR	Relative roughness—D_{84}/R
	Riparian	RR_Cano	Riparian canopy present (proportion of reach)
		RR_Dist	Proportion of riparian zone disturbed by human land uses
		RR_CDen	Riparian canopy density (%)
	Substrate	RS_D84	Substrate (mm)
		RS_SnFi	Sand and fines particles (%)
		RS_LWDV	Volume of large woody debris in bankfull channel (m^3/m^2)
		RS_BedS	Substrate mobility ($=Slope*(A/D_{84})^{0.4}$) ($km^{0.4}$)
		WL_Agri	Agricultural (%)

First two letters of the variable code refer to spatial-scale (W=watershed, V=valley, R=reach) and variable-category (H=hydrology, C=climate, Gy=geology, G=geomorphic, L=land-use, R=riparian, S=substrate), respectively.

metrics included physiographic, climatic, riparian disturbance, geological and hydrologic regime characteristics (Table 1).

We used a feed-forward neural network trained by the back-propagation training algorithm (Rumelhart et al., 1986) to model EPT richness as a function of the 33 environmental variables. The neural network architecture included an input layer containing a neuron for each environmental variable, a single hidden layer and one output neuron representing the predicted number of EPT taxa at a site. The optimal number of neurons in the hidden layer (optimal referring to minimizing the trade-off between network bias and variance) was determined empirically by comparing the performances of different cross-validated networks, with 1–30 hidden neurons, and choosing the number that produced the greatest predictive performance. Learning rate (η) and momentum (α) parameters (both varying as a function of network error) were included during network training to ensure a high probability of global network convergence and a maximum of 1000 iterations for the back-propagation algorithm to determine the optimal axon weights. Prior to training the network, the environmental variables were converted to z-scores to standardize the measurement scales of the inputs into the network. We refer the reader to Bishop (1995) and Olden and Jackson (2001) for more details regarding the ANN methodology.

The contribution of each independent variable to the predictive output of the neural network depends primarily on the magnitude and direction of the inter-neuron connection weights. We calculated the relative importance of the environmental variables in the neural network by quantifying the product of the input-hidden and hidden-output connection weights between each input neuron and output neuron and then summed the products across all hidden neurons. Relative importance (expressed as a percentage) was calculated by dividing the absolute value of each variable contribution by the grand mean (sum of all absolute variable contributions). The relative contributions of each variable were subsequently assessed for their statistical significance with a randomization test, which randomizes the response variable and then constructs a neural network based on the randomized data

and records the relative explanatory importance of each environmental variable. This process is repeated 9999 times to generate a null distribution for the relative importance of each variable, which is then compared with the observed values to calculate the significance level (see Olden and Jackson, 2002). The connection weight approach described above has been shown to be an unbiased estimator of variable contributions in neural networks (Olden et al., 2004). All neural network analyses were conducted using computer macros written in the MatLab® programming language (The MathWorks, Natick, Massachusetts, USA).

A series of neural networks were constructed to examine the relationship between EPT richness and single- and multi-scale descriptors of the environment. First, we developed single-scale models with the following numbers of input, hidden (optimized as discussed above) and output neurons that are reported in parentheses: watershed-scale (15-8-1), valley-scale (7-4-1) and reach-scale (11-5-1). Second, we developed a multi-scale model using environmental variables from all three scales (33-12-1). Third, we developed a hierarchical model using the following steps: (a) reach-scale variables were modeled as a function of valley- and watershed-scale variables using a multi-response ANN (22-9-11); (b) valley-scale variables were modeled as a function of watershed-scale variables using a multi-response ANN (15-8-7); (c) EPT richness was modeled as a function of the residuals from the models described in (a) and (b) plus the watershed-scale variables (33-12-1) (see Fig. 2). By using the residuals we account for the fact that valley- and watershed-scale drivers influence local characteristics of the stream reach, and we remove this influence in quantifying the unique effect of local-scale variables on macroinvertebrate assemblages. Therefore, variables at the watershed and valley scale can potentially have both a direct and indirect relationship with EPT richness. We used the same number of hidden neurons and same initial random connection weights when constructing the multi-scale and hierarchical ANNs so that the results would be directly comparable (i.e. model differences not related to differences in initial model weights). Models were validated using n-fold cross validation, and predictive performance was assessed using Pearson's product–moment correlation coefficient
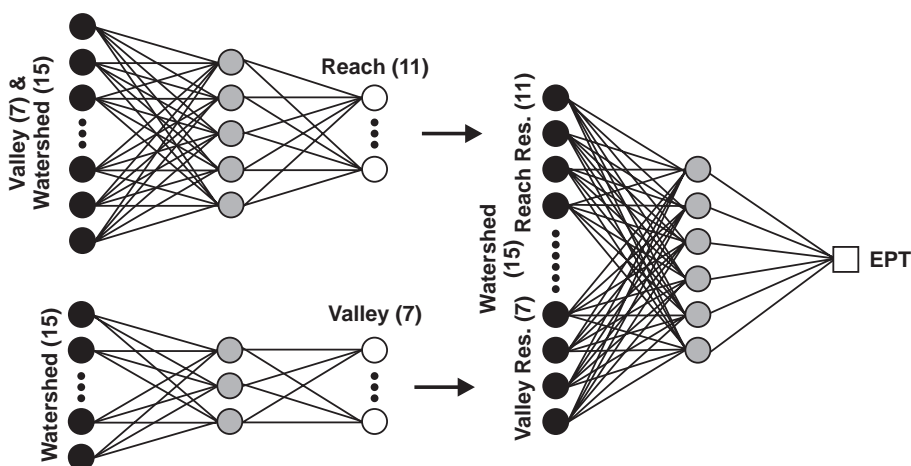

Fig. 2 – Schematic of the neural networks used to model EPT taxa richness in a spatially hierarchical manner.

between predicted and actual EPT values (expressed as the coefficient of determination), and the root-mean-square-of-error (RMSE) of the predicted values. The Pearson's correlation provides a measure of model accuracy, with better models being represented by correlation coefficients approaching 1; RMSE measures model precision, with smaller values representing higher precision.

4. Results

EPT richness at a site was variable across the study region, ranging between 0 and 100% ($\overline{X}$=62%), with some evidence for differences among 3rd-order Ecoregions (Fig. 1). Sites with lowest EPT richness were in the Colorado Plateau ($\overline{X}$=36%) and Williamette Valley ($\overline{X}$=39%), whereas highest observed richness was in the Eastern Cascades ($\overline{X}$=82%), North Cascades ($\overline{X}$=78%) and Cascades ($\overline{X}$=76%).

Single- and multi-scale ANNs illustrated differing abilities for predicting EPT richness (Fig. 3). Although all models were statistically significant based on *n*-fold cross validation (P<0.01), comparisons of single-scale models showed that watershed descriptors were the most predictive of EPT richness (R^2=0.64, RMSE=0.13), followed by reach descriptors (R^2=0.58, RMSE=0.14) and valley descriptors (R^2=0.32, RMSE=0.17). At the watershed scale, environmental variables statistically associated with greater EPT richness were warmer winter and cooler summer air temperatures, greater proportion of forested watersheds, higher stream baseflows, and shorter durations of low flow events (Table 2). At the valley scale, greater proportion of forested valleys and higher hillslope connectivity were strongly related to elevated EPT richness. At the reach scale, correlates of EPT richness were greater riparian density, greater width-to-depth ratio, high volume of large-woody debris, low substrate mobility, and low proportions of sand/fine substrates.

When combining environmental variables from all three spatial scales, ANNs were found to better predict EPT richness
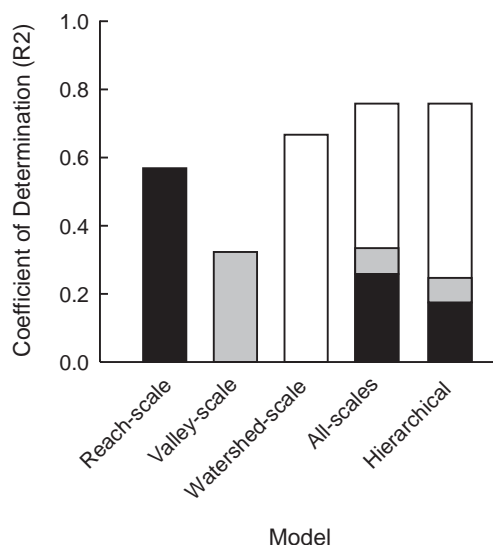
Table 2 – Relative importance (%) of environmental variables in neural networks based on single scales of watershed, valley, and reach; at all scales; and hierarchical organization of all scales

Variable	Watershed scale	Valley scale	Reach scale	All scales	Hierarchical
WH_Base	**6.3 (+)**			**6.8 (+)**	**4.2 (+)**
WH_DLoP	**6.0 (−)**			2.9 (−)	**4.0 (−)**
WH_MA	0.7 (−)			1.7 (−)	0.5 (−)
WH_NoFl	4.0 (+)			1.9 (+)	2.7 (+)
WC_Aspt	2.1 (−)			0.5 (−)	1.4 (−)
WC_AugT	**18.7 (−)**			6.4 (−)	**12.6 (−)**
WC_WinT	**25.7 (+)**			**12.4 (+)**	**17.2 (+)**
WGy_Sedi	1.7 (−)			0.8 (+)	1.2 (−)
WGy_Volv	5.1 (+)			**5.0 (+)**	3.4 (+)
WGy_Buff	1.4 (−)			0.7 (−)	0.9 (−)
WG_MSSP	0.3 (+)			0.2 (+)	0.2 (+)
WG_Slop	3.9 (−)			4.7 (−)	2.6 (−)
WL_Barr	3.5 (+)			0.5 (+)	2.4 (+)
WL_Fore	**12.9 (+)**			**4.9 (+)**	**8.7 (+)**
WL_Agri	7.6 (−)			6.3 (−)	**5.1 (−)**
VG_DWSP		0.5 (+)		0.2 (+)	0.4 (+)
VG_Powe		8.9 (+)		2.0 (+)	**2.7 (+)**
VG_Entr		10.9 (+)		1.9 (−)	1.4 (−)
VG_Conn		**29.1 (−)**		0.2 (+)	0.8 (+)
VL_Barr		14.0 (+)		0.4 (+)	0.5 (−)
VL_Fore		**30.4 (+)**		3.3 (+)	**3.2 (+)**
VL_Agri		6.2 (−)		2.2 (+)	0.8 (+)
RG_Slop			2.0 (+)	0.7 (−)	0.6 (−)
RG_Sinu			1.6 (−)	0.1 (+)	0.1 (+)
RG_WiDp			**12.2 (+)**	2.1 (+)	1.6 (+)
RG_RelR			0.2 (−)	1.4 (+)	1.1 (+)
RR_Cano			9.3 (+)	4.7 (+)	3.0 (+)
RR_Dist			9.3 (+)	3.1 (+)	2.6 (+)
RR_CDen			**19.9 (+)**	2.6 (+)	1.8 (+)
RS_D84			4.9 (−)	4.6 (−)	2.8 (−)
RS_SnFi			**15.4 (−)**	**7.1 (−)**	**4.3 (−)**
RS_LWDV			**11.7 (+)**	**5.5 (+)**	**4.1 (+)**
RS_BedS			**13.4 (−)**	2.3 (−)	1.2 (−)

Positive and negative contributions are represented by (+) and (−), respectively, and bold, underlined values are statistically significant based on α<0.05. Variable codes are described in Table 1.

Fig. 3 – Comparison of ANN performances based on different spatially scaled environmental variables.

(R^2=0.74, RMSE=0.12) compared to single-scale models (Fig. 3). Importantly, comparisons of adjusted *R*-values indicate that these differences are not attributed to greater predictive performance associated with greater number of independent variables included in the analysis (results not shown). We point out that the predictive performances of both the non-hierarchical multi-scale ANN and the hierarchical ANN are equivalent, because both approaches explain the same total explained variation in EPT richness. However, they partition this variation among the spatial scales in a different manner by removing redundancy among variables in a structured, nested manner.

Both multi-scale models identified the primary importance of environmental characteristics described at the watershed scale for predicting EPT richness, followed by the contributions of reach-scale and then valley-scale environmental variables. Comparison of the two models shows that a substantial proportion of variation in EPT richness
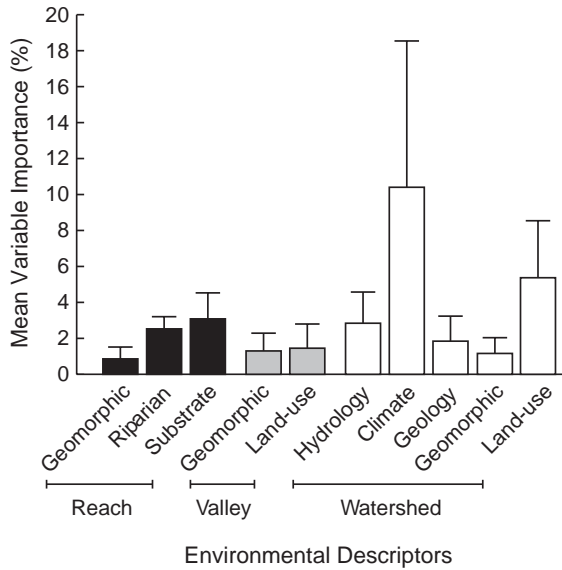
Fig. 4 – Mean relative importance (%) of the environmental variables in the hierarchical ANN according to spatial-scale and variable type. Whiskers represent 1 standard error.

model illustrated the positive influence of winter air temperatures, proportion of watershed and valley that is forested, stream baseflows, stream power and volume of large-woody debris, and the negative influence of summer air temperatures, proportion of watershed that is agricultural land, duration of low flow events and proportions of sand/fine substrates, on predicted levels of EPT richness (Table 2). In general, the strongest predictors of EPT richness included watershed descriptors of climate, land-use and hydrology, and reach descriptors of substrate size and riparian cover (Fig. 4). Our results also illustrate that although some environmental variables may be significant predictors of EPT richness when only single scales are considered, they are not necessarily important when multiple scales are considered, reflecting the inter-correlation of variables across scales.

We found significant differences in the mean model residuals among the ecoregions (ANOVA: $F_{8,186} = 2.81$, $P = 0.006$; Fig. 5). Model residuals from the hierarchical ANN were significantly greater than zero for sites in the Cascades ($t_{15} = 3.60$, $P = 0.003$) and North Cascades ($t_7 = 2.89$, $P = 0.023$) and moderately greater for the Eastern Cascades ($t_9 = 1.81$, $P = 0.104$), indicating that EPT richness was under-estimated in these regions compared to expectations based on environmental conditions across all regions. In contrast, EPT richness tended to be over-estimated for sites in the Colorado and Columbia Plateaus, although these were not statistically significant.

explained by reach-scale environmental drivers can be attributed to the indirect influence of valley- and watershed-scale variables. Specifically, because the hierarchical model respects the fact that valley- and watershed-scale drivers influence local characteristics of the stream reach, only the unique variation (i.e., non-redundant) at the local scale is available to explain residual variation in the hierarchical model, thereby leading to a reduced contribution of local variables and an increased contribution by the watershed variables. Because the relative contributions of valley-scale variables remained unchanged between the two models, it can be inferred that valley drivers are acting more independently in their predictions of EPT richness. The hierarchical

5. Discussion

Aquatic invertebrates exhibit great variation in distribution and abundance across riverine landscapes (Malmqvist, 2002). Although local stream processes were traditionally argued to be the ultimate drivers of local macroinvertebrate diversity (Vinson and Hawkins, 1998), numerous studies have established the utility of considering multi-scale processes in
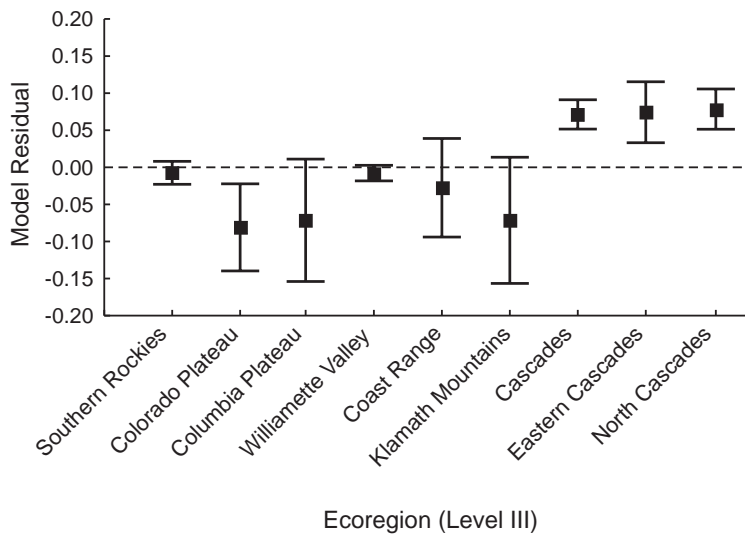

Fig. 5 – Residuals from the hierarchical ANN indicating that prediction errors were not randomly distributed in space. Positive values indicate cases where EPT richness was under-predicted (i.e., greater than observed values) and negative values indicate cases where EPT richness was over-predicted. Symbol represents mean and whiskers represent 1 standard error.

determining local assemblage structure (e.g., Wohl et al., 1995; Carter et al., 1996; Hawkins et al., 2000; Brosse et al., 2003; Lamouroux et al., 2004; Sandin and Johnson, 2004). Our results strongly support the use of multiple scales and further demonstrate that by structuring these scales hierarchically according to stream landscape principles (Frissell et al., 1986; Townsend, 1996), we can begin to distinguish the unique contributions of processes or variable contributions at different scales in the landscape hierarchy.

Ecological interpretation of our hierarchical ANN provides important insight into the factors shaping local macroinvertebrate diversity. At the watershed scale, climate was the most important variable overall. Greater EPT richness was associated with reduced extreme seasonal temperatures, e.g., warmer winter temperatures and cooler summer temperatures. This finding agrees with the fact that our study area encompasses a broad geographic and climatic gradient, ranging from high elevation, harsh conditions to lowland or plateau streams that may warm up significantly in summer (especially where riparian shading is lacking). Another important driver of EPT richness was the relative amount of forest vs. agricultural lands, where greater diversity was associated with more forested watersheds. Conversion of forest to agriculture at the watershed scale has frequently been shown to reduce sensitive insect species, including EPT (see Allan, 2004). Interestingly, a pair of hydrologic variables was important in explaining variation in EPT across the study sites. We found EPT richness to increase with higher baseflows and to decline with increased duration of low flow spells. Hydrologic regime is recognized as an important driver of ecological organization in streams (Poff et al., 1997) yet it is rarely included in broad-scale analyses of landscape controls on local community structure. A few papers have directly included flow (e.g. Poff and Allan, 1995 for fish), but typically some surrogate of flow is used (e.g., Richards et al., 1996; Townsend et al., 1997). Our study thus is among the first to demonstrate the direct importance of hydrologic conditions at the watershed scale across a broad geographic extent.

At the valley scale, EPT richness increased with stream power across the sites, suggesting that sites with greater flow energy may have coarser substrates, better riffle development and greater water aeration, and/or reduced fine sediments, which promote the existence of sensitive taxa (Zweig and Rabeni, 2001). We also found that EPT richness increased with percentage forest cover at the valley scale. This is not surprising; however, it is important to note that this is a unique contribution to the model, one not captured by the watershed-scale forest cover. Further, inclusion of valley-scale riparian cover as a variable (in conjunction with watershed forest cover) appears to remove the need to include a local-scale measure of riparian cover (see Table 2), suggesting a fair amount of redundancy in the predictive ability among riparian variables measured at small to intermediate scales. Several studies have shown that more intermediate-scale measures of riparian cover are good explanatory variables for reach-scale biotic condition in streams (e.g., Karr and Chu, 1999; Thompson and Townsend, 2004).

At the reach scale, we found substrate and large woody debris to have unique contributions to predicting EPT richness across our study sites. Our finding that increased fine sedi-

ments reduce richness is not surprising, as fine sediment deposition is widely recognized as a key indicator of habitat degradation (Waters, 1995; Allan, 2004). Interestingly, the importance of this local geomorphic variable was much reduced in the hierarchical model relative to the model that only included local variables (see Table 2). This observation indicates that there is local-scale control on fine sediment deposition that cannot be explained or predicted by larger-scale descriptors, which has important implications for conservation and biomonitoring (see below). We also found that large woody debris enhances EPT richness at sites. The presence of LWD promotes habitat stability in the stream and is often indicative of a more intact riparian zone and the associated positive benefits (Montgomery, 1997; Karr and Chu, 1999).

Our paper is one of a surprisingly small (but growing) number of studies using a hierarchical approach to distinguish among unique contributions of environmental drivers operating at multiple scales. Our paper both complements this body of literature and extends it in terms of model structure and geographic extent. For example, Brosse et al. (2003) studied 97 sites within the 5704 km^2 Taieri River catchment in New Zealand, and found variation in benthic invertebrate diversity to be best explained by variables quantified at the local scale (bedform), then reach scale, and finally catchment scale. By contrast, we found watershed-scale (i.e., catchment) variables to be more important than local-scale variables, which in turn were more important than valley-scale variables. Other recent studies conducted at broad spatial scales support the finding that large-scale variables are more important than local variables in explaining macroinvertebrate composition (e.g., Townsend et al., 2003; Bonada et al., 2005; but see Sandin and Johnson, 2004). The lack of consensus regarding the relative importance of local- vs. regional-scale variables in controlling stream benthic communities likely reflect a number of differences in study design, including spatial scale and modeling approach.

Our study encompassed a very broad geographic extent (Fig. 1), across which there is tremendous variation in climatic, geologic and land cover conditions. As a result, our study had a much greater gradient of possible watershed-scale characteristics compared to the single catchment modeled by Brosse et al. (2003). As geographic extent shrinks we would also expect reductions in the variation explained by large scale geographic differences in landscape setting, resulting in the likelihood that local-scale variables should naturally explain more variation at the reduced geographic scales. For example, in a series of studies of the effects of land use on water quality in Michigan, USA, Roth et al. (1996) observed that watershed-scale variables (forest cover) were more important than local scale variables (riparian cover) across a diversity of watershed types across a forested-agricultural gradient, whereas Lammert and Allan (1999) demonstrated that when only agricultural watersheds were examined, local riparian cover was a key explanatory variable. These examples illustrate both the importance of geographic extent and the associated length of the environmental gradient being sampled (Weigel et al., 2003), as well as suggesting the need to account for environmental hierarchies during modeling. This is supported by Sandin and Johnson (2004) who found that interactions among local, landscape and regional factors were

important in structuring benthic macroinvertebrate assemblages in Swedish streams.

Our study has interesting implications for aquatic resource conservation and stream biomonitoring in the western United States and other regions. First, one particular strength of our hierarchical model is that we can better identify the *unique* contributions of variables measured at different spatial scales for explaining and predicting variation in local macroinvertebrate assemblages. With the increased development of Geographic Information Systems for landscape analyses, there is a strong desire to 'map' aquatic habitat using only remotely sensed data in the hope of foregoing (or at least minimizing) the expense of collecting local site data. Our analysis indicates this may be feasible to an extent, but local information cannot be ignored. Specifically, our reach-scale variables of fine sediment and large woody debris remained as significant predictors in our model (although their importance decreased), even after accounting for the variation explained by watershed and valley-scale descriptors. This suggests that important habitat descriptors at the local scale cannot yet be entirely captured by larger-scale GIS-derived variables describing forest and riparian cover, lithology and potential erosibility of watershed bedrock, and sediment transport capacity and storage in stream channels as a function of channel slope from digital elevation models. In this sense, our model identifies critical research directions that GIS modeling might take in gaining more robust estimates of local scale variables that currently can only be measured in the field. It also confirms that variables operating at all hierarchical levels are, in fact, important (Allan et al., 1997).

In a conservation context, our findings suggest that a hierarchical approach may facilitate the identification of landscape conservation units and help advance the science of biomonitoring. Multi-scale modeling approaches that respect the hierarchy in which environmental drivers operate can help identify the critical habitat variables needed to be characterized at local scale and thus guide the more efficient collection of field data in the future. Moreover, our results suggest that valley-scale descriptors of the environment are important, in that they explained variation in macroinvertebate diversity independent of that explained by the watershed scale. This intermediate scale of characterization is almost always missing in biomonitoring (e.g., Hawkins et al., 2000), and may help explain the typically poor generality of RIVPACS-type models. We argue that future research in the field of bioassessment should respect the spatial hierarchy of aquatic ecosystems by exploring the manner in local assemblages are formed from the differential "filtering" of species from the regional pool. Species traits may provide a powerful currency for such analyses (Poff, 1997); as was illustrated recently by Chessman and Royal (2004).

6. Conclusion

The field of ecoinformatics aims to make sense of complex ecological data, yet we argue it has not fully realized its potential to better guide the application of its modeling tools, including the use of artificial neural networks. As Maier and Dandy (2000) accurately observed, "at present, there is a ten-dency among researchers to apply ANNs to problems for which other methods have been unsuccessful," and as a result the ecological literature has witnessed the repeated application of ANNs to an ever-increasing number of case studies. Advancing the field of ecoinformatics requires practitioners to challenge themselves to better incorporate their current ecological knowledge during the model building process, so that model results can be used to generate new questions that are recognized as ecologically insightful. Our study provides a simple example of using ecological theory to better direct the use of neural networks to address a fundamental question in aquatic ecology—how are local stream macroinvertebrate communities structured by a spatial hierarchy of environmental factors? Developing more ecologically relevant ANNs, in our view, is a necessary first step in better utilizing the statistical tools that ecoinformatics provide to ecology.

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REFERENCES

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Evol. Syst. 35, 257–284.

Allan, J.D., Johnson, L.B., 1997. Catchment-scale analysis of aquatic ecosystems. Freshw. Biol. 37, 107–111.

Allan, J.D., Erickson, D.L., Fay, J., 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshw. Biol. 37, 149–161.

Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspective for Ecological Complexity. University of Chicago Press, Chicago, IL, USA. 310 pp.

Bishop, C.M., 1995. Neural Networks for Pattern Recognition. Clarendon Press, Oxford, UK. 504 pp.

Bonada, N., Zamora-Muñoz, C., Rieradevall, M., Prat, N., 2005. Ecological and historical filters constraining spatial caddis fly distribution in Mediterranean rivers. Freshw. Biol. 50, 781–797.

Brosse, S., Arbuckle, C.J., Townsend, C.R., 2003. Habitat scale and biodiversity: influence of catchment, stream reach and bedform scales on local invertebrate diversity. Biodivers. Conserv. 12, 2057–2075.

Carter, J.L., Fend, S.V., Kennelly, S.S., 1996. The relationships among three habitat scales and stream benthic invertebrates community structure. Freshw. Biol. 35, 109–124.

Chessman, B.C., Royal, M.J., 2004. Bioassessment without reference sites: use of environmental filters to predict assemblages of river macroinvertebrates. J. North Am. Benthol. Soc. 23, 599–615.

Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O., Schlesinger, W.H., Wall, D.H., Wear, D., 2001. Ecological forecasts: an emerging imperative. Science 293, 657–660.

Flood, I., Kartam, N., 1994. Neural networks in civil engineering: I. Principles and understanding. J. Comput. Civ. Eng. 8, 131–148.

Frissell, C.A., Liss, W.J., Warren, C.E., Hurley, M.D., 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. 10, 199–214.

Harris, G.P., 1998. Predictive models in spatially and temporally variable freshwater systems. Aust. J. Ecol. 23, 80–94.

Hawkins, C.P., Norris, R.H., Gerritsen, J., Hughes, R.M., Jackson, S.K., Johnson, R.K., Stevenson, R.J., 2000. Evaluation of the use of landscape classifications for the prediction of freshwater biota: synthesis and recommendations. J. North Am. Benthol. Soc. 19, 541–556.

Karr, J.R., Chu, E.W., 1999. Restoring Life in Running Waters: Better Biological Monitoring. Island Press, Covelo, CA. 196 pp.

Kaufmann, P.R., Levine, P., Robison, E.G., Seeliger, C, Peck, D.V., 1999. Quantifying Physical Habitat in Wadeable Streams. EPA/620/R-99/003, Western Ecology Division, US Environmental Protection Agency, Office of Research and Development, Washington DC. 102 pp.

Lammert, M., Allan, J.D., 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environ. Manage. 23, 257–270.

Lamouroux, N., Dolédec, S., Gayraud, S., 2004. Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. J. North Am. Benthol. Soc. 23, 449–466.

Lek, S., Guégan, J.F. (Eds.), 2000. Artificial Neuronal Networks: Applications to Ecology and Evolution. Springer-Verlag, New York, USA. 262 pp.

Levin, S., 1998. Ecosystems and the biosphere as complex adaptive systems. Ecosystems 1, 431–436.

Maier, H.R., Dandy, G.C., 2000. Neural networks for the prediction and forecasting of water resources variables: a review of modelling issues and applications. Environ. Model. Softw. 15, 101–124.

Malmqvist, B., 2002. Aquatic invertebrates in riverine landscapes. Freshw. Biol. 47, 679–694.

Montgomery, D.R., 1997. What's best on the banks? Nature 388, 328–329.

Olden, J.D., 2003. A species-specific approach to modeling biological communities and its potential for conservation. Con. Biol. 17, 854–863.

Olden, J.D., Jackson, D.A., 2001. Fish–habitat relationships in lakes: gaining predictive and explanatory insight by using artificial neural networks. Trans. Am. Fish. Soc. 130, 878–897.

Olden, J.D., Jackson, D.A., 2002. Illuminating the "black box": a randomization approach for understanding variable contributions in artificial neural networks. Ecol. Model. 154, 135–150.

Olden, J.D., Joy, M.K., Death, R.G., 2004. An accurate comparison of methods for quantifying variable importance in artificial neural networks using simulated data. Ecol. Model. 178, 389–397.

Özesmi, S.L., Özesmi, U., 1999. An artificial neural network approach to spatial habitat modelling with interspecific interaction. Ecol. Model. 166, 15–31.

Peters, R.H., 1991. A Critique for Ecology. Cambridge University Press, Cambridge, UK. 384 pp.

Petts, G.E., 2000. A perspective on the abiotic processes sustaining the ecological integrity of running waters. Hydrobiologia 422/423, 15–27.

Pielke, R.A., Conant, R.T., 2003. Best practices in prediction for decision-making: lessons from the atmospheric and earth sciences. Ecology 84, 1351–1358.

Poff, N.L., 1997. Landscape filters and species traits: toward mechanistic understanding and prediction in stream ecology. J. North Am. Benthol. Soc. 16, 391–409.

Poff, N.L., Allan, J.D., 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76, 606–627.

Poff, N.L., Ward, J.V., 1990. The physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. Environ. Manage. 14, 629–646.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. Bioscience 47, 769–784.

Recknagel, F. (Ed.), 2003. Ecological Informatics: Understanding Ecology by Biologically-Inspired Computation. Springer, New York, USA. 398 pp.

Richards, C., Johnson, L.B., Host, G.E., 1996. Landscape-scale influences on streams habitats and biota. Can. J. Fish. Aquat. Sci. 53 (Suppl. 1), 295–311.

Rosenberg, R.H., Resh, V.H. (Eds.), 1993. Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman and Hall, New York, USA. 488 pp.

Roth, N.E., Allan, J.D., Erichson, D.L., 1996. Landscape influence on stream biotic integrity assessed at multiple spatial scales. Landsc. Ecol. 11, 141–156.

Rumelhart, D.E., Hinton, G.E., Williams, R.J., 1986. Learning representations by back-propagation errors. Nature 323, 533–536.

Sandin, L., Johnson, R.K., 2004. Local, landscape and regional factors structuring benthic macroinvertebrate assemblages in Swedish streams. Landsc. Ecol. 19, 501–514.

Sarle, W.S., 1994. Neural networks and statistical models. Proceedings of the Nineteenth Annual SAS Users Group International Conference, SAS Institute, pp. 1538–1550.

Thompson, R.M., Townsend, C.R., 2004. Land-use influences on New Zealand stream communities: effects on species composition, functional organisation, and food-web structure. N.Z. J. Mar. Freshw. Res. 38, 595–608.

Townsend, C.R., 1996. Concepts in river ecology: pattern and process in the catchment hierarchy. Arch. Hydrobiol., Suppl. 113, 3–21.

Townsend, C.R., Hildrew, A.G., 1994. Species traits in relation to a habitat templet for river systems. Freshw. Biol. 31, 265–275.

Townsend, C.R., Scarsbrook, M.R., Dolédec, S., 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnol. Oceanogr. 42, 938–949.

Townsend, C.R., Dolédec, S., Norris, R., Peacock, K., Arbuckle, C., 2003. The influence of scale and geography on relationships between stream community and landscape variables: description and prediction. Freshw. Biol. 48, 768–785.

Vinson, M.R., Hawkins, C.P., 1998. Biodiversity of stream insects: variations at local, basin and regional scales. Annu. Rev. Entomol. 43, 271–293.

Waters, T.F., 1995. Sediment in streams: sources, biological effects and control. Monograph, vol. 7. American Fisheries Society, Bethesda, MD, USA. 251 pp.

Weigel, B.M., Wang, L., Rasmussen, P.W., Butcher, J.T., Stewart, P.M., Simon, T.P., Wiley, M.J., 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the North Lakes and Forest ecoregion, USA. Freshw. Biol. 48, 1440–1461.

Wohl, D.L., Wallace, J.B., Meyer, J.L., 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (USA). Freshw. Biol. 34, 447–464.

Wright, J.F., Sutcliffe, D.W., Furse, M.T., 2000. Assessing the biological quality of fresh waters: RIVPACS and other techniques. Freshwater Biological Association, Ambelside, Cumbria, UK. 400 pp.

Zweig, L.D., Rabeni, C.F., 2001. Biomonitoring for deposited sediment using benthic invertebrates: a test on 4 Missouri streams. J. North Am. Benthol. Soc. 20, 643–657.