

Habitat scale and biodiversity: influence of catchment, stream reach and bedform scales on local invertebrate diversity

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Abstract. Although many studies have investigated the influence of environmental patterns on local stream invertebrate diversity, there has been little consistency in reported relationships between diversity and particular environmental variables. Here we test the hypothesis that local stream invertebrate diversity is determined by a combination of factors occurring at multiple spatial scales. We developed predictive models relating invertebrate diversity (species richness and equitability) to environmental variables collected at various spatial scales (bedform, reach and catchment, respectively) using data from 97 sampling sites dispersed throughout the Taieri River drainage in New Zealand. Models based on an individual scale of perception (bedform, reach or catchment) were not able to match predictions to observations (r < 0.26, P > 0.01, between observed and predicted equitability and species richness). In contrast, models incorporating all three scales simultaneously were highly significant (P < 0.01; r = 0.55and 0.64, between observed and predicted equitability and species richness, respectively). The most influential variables for both richness and equitability were median particle size at the bedform scale, adjacent land use at the reach scale, and relief ratio at the catchment scale. Our findings suggest that patterns observed in local assemblages are not determined solely by local mechanisms acting within assemblages, but also result from processes operating at larger spatial scales. The integration of different spatial scales may be the key to increasing model predictability and our understanding of the factors that determine local biodiversity.

Introduction

Identification of the forces that determine patterns of biodiversity constitutes a central issue in ecology. While much is known about vertebrate diversity at global, regional and local scales, our understanding of the influence of environmental factors derived from different spatial scales on stream invertebrate diversity is less well developed. Diversity patterns have been investigated at the scale of individual basins, stream reaches, and habitat units (Minshall 1988), but the results have been inconsistent and a variety of trends in species richness have been described in relation to habitat variables (see Vinson and Hawkins (1998) for a review). In general, however, the trends indicate that (i) diversity increases with an increasing

range of conditions in the locality, (ii) species richness and equitability are reduced when conditions deviate from 'normal', and (iii) environmental stability is usually associated with higher richness and equitability. These three trends conform with predictions made half a century ago (Thienemann 1954), and provide some support for more recent theoretical constructs including habitat templet theory (Southwood 1977; Townsend and Hildrew 1994), the intermediate disturbance hypothesis (Connell 1978; Townsend et al. 1997a) and the river continuum concept (Vannote et al. 1980). While it is understood that stream components and processes can be viewed as part of a larger interconnected system (Vannote et al. 1980; Corkum 1989), most studies of stream biodiversity have assumed, at least implicitly, that local patterns are primarily determined by local processes (Palmer et al. 1996). On the other hand, several river health assessment procedures based on the prediction of macroinvertebrate taxonomic assemblages, such as RIVPACS (Moss et al. 1987; Wright et al. 2000) and AusRivAS (Smith et al. 1999), have used environmental descriptors measured at various spatial scales and provide interesting insights into the prediction of taxonomic composition of the studied communities. However, little attention has so far been paid to the relative influence of environmental variables measured at different spatial scales on the ability to predict local diversity of aquatic invertebrates (Vinson and Hawkins 1998). The processes that govern diversity and habitat selection may vary across scales of analyses and, according to Wiens et al. (1987) and Thomas and Taylor (1990), by ignoring scale we risk drawing incorrect ecological conclusions.

Until now, the most frequently used statistical and modelling methods to identify species- or diversity-environment relationships have been based on linear principles (see James and McCulloch (1990) for a review). However, these approaches cannot overcome some significant biases due both to the complexity and presumed non-linearity of invertebrate-habitat relationships and inherent correlations among variables (Winterbourn et al. 1981; Carter et al. 1996). To deal with such difficulties, transformation of non-linear variables by logarithmic, power or exponential functions can appreciably improve the results in certain situations, but this is far from always the case (Lek et al. 1996; Brosse et al. 1999a, 1999b). Artificial neural networks (ANN), on the other hand, are efficient in dealing with systems ruled by complex non-linear relationships and provide an alternative to traditional statistical methods (Lek et al. 1996; Lek and Guégan 2000). They have been successfully applied to the prediction of macroinvertebrates taxa number (Walley and Fontama 1998) and to the identification of habitat factors that account for species richness at different spatial scales (Guégan et al. 1998; Brosse et al. 2001). In addition to the predictive value of the models, the influence of each variable introduced in the modelling procedure can be quantified using specific algorithms (Garson 1991; Goh 1995; Lek et al. 1996).

In this paper, we used ANN to investigate the influence of bedform, stream reach and catchment environmental features on local insect diversity (species richness and equitability) in tributaries of the Taieri River in New Zealand. We used ANN models to describe local diversity in terms of environmental variables measured at a particular spatial scale (bedform, reach or catchment) and then in terms of a combination of variables from the three spatial scales simultaneously. Our objective was to test the hypothesis that local insect diversity is determined by a combination of factors occurring at multiple spatial scales and then to determine the relative importance of the main factors acting at each scale.

Methods

Study sites and sampling

The analysis of macroinvertebrate diversity was performed on 97 samples taken during summer 1990 from sites dispersed throughout the Taieri River basin, which lies between latitudes $44^{\circ}55'$ S and $46^{\circ}05'$ S in the southeastern quarter of the South Island of New Zealand. The Taieri River is the fourth longest in New Zealand and its catchment area of approximately 5704 km² is the fifth largest. The river flows for 318 km from the headwaters in the Lammerlaw and Lammermoor ranges at 1150 m above sea level before reaching the Pacific Ocean 30 km south of Dunedin (Figure 1).

For each of the 97 sampling sites, consisting of 30 m sections of stream, 30 environmental variables were recorded at each of the three scales (i.e. 10 bedform, 10 reach and 10 catchment variables). Catchment variables were estimated for the



Figure 1. Map of New Zealand showing the location of the Taieri River basin and a representation of the 97 sampling sites throughout tributaries of the Taieri River.

2060

Table 1. Catchment, reach and bedform variables, codes and units.

Scale/variable	Variable code	Units	
Catchment			
Alluvial parent and surficial material	Call	%	
(2) Schist and semi-schist	Csch	%	
Drainage area	Cdra	km ²	
(1, 2) Maximum elevation	Cmax	m	
(1, 2) Relief ratio ^a	Crel	_	
(1) Drainage density ^b	Cdrd	m^2/m	
Pasture area	Cpas	%	
Forest area	Cfor	%	
Native tussock area	Ctus	%	
(2) Barren area (e.g. roads, urban areas)	Cbar	%	
Reach			
Area of pools in reach	Rslo	%	
Stream order ^c	Rsto	_	
Average bankfull stream width	Rwid	m	
(2) Average bankfull stream depth	Rdep	m	
(1) Bedrock area outside stream	Rbed	%	
(2) Roughness ^d	Rrou	_	
(1, 2) Riparian pasture area	Rpas	%	
Riparian forest area	Rfor	%	
Riparian tussock area	Rtus	%	
Riparian barren area (e.g. roads, urban areas)	Rbar	%	
Bedform			
Stream power ^e	Bstp	_	
(1, 2) Median particle size ^f	Bmed	mm	
(2) Average bankfull stream width	Bwid	m	
(1) Average bankfull stream depth	Bdep	m	
Bedrock outside stream	Bbed	%	
Roughness ^d	Brou	_	
Riparian pasture area	Bpas	%	
Riparian forest area	Bfor	%	
(2) Riparian native tussock area	Btus	%	
(1) Riparian barren area (e.g. roads, urban areas)	Bbar	%	

Where terrestrial variables have the same names, equivalent measurements were derived but from the whole drainage basin feeding the site (catchment), or from a 200 m by 100 m riparian strip upstream of the site (reach), or within a riparian strip 5 m to each side and immediately adjacent to the site (bedform). Where instream variables have the same names, equivalent measurements were derived but from a 200 m section of stream upstream of the site (reach), or from the 30 m stream site itself (bedform). Variables used to predict species richness (1) and equitability (2) in the models combining the three-scale are indicated. ^a Relief, calculated as ((maximal elevation–minimal elevation)/horizontal distance along the longest basin dimension parallel to the main drainage line); ^b total stream length per unit area; ^c Strahler stream order; ^d average bankfull depth/average median particle size; ^e drainage area (as surrogate for discharge) times slope; ^f Wolman (1954) pebble count.

complete drainage area supplying each site, using satellite image data and other information included in a geographical information system (GIS) (Arbuckle et al. 1999). Reaches were defined as areas encompassing the stream plus surrounding land for 100 m on either side of the stream centre line and for a 200 m distance upstream of the study site; reach variables were estimated using site survey

techniques and from the GIS. Bedform-scale data were obtained using site surveys to define physical variables in the 30 m stream sections and land-cover in the 5 m riparian strip immediately adjacent. The variables chosen conform with those used in previous studies (Moss et al. 1987; Carter et al. 1996; Vinson and Hawkins 1998; Walley and Fontama 1998; Wright et al. 2000) and accounted for geological, morphological, altitudinal, land-cover and anthropogenic disturbance effects (Table 1). Within each scale, the 10 variables were not significantly correlated (Pearson test, P < 0.01).

Benthic macroinvertebrates were collected as part of a large-scale, long-term study of invertebrates within the Taieri River system (see Townsend et al. (1997a, 1997b) for more details). Two replicate Surber samples were taken from random locations in each site (mesh size 250 μ m, surface area sampled 0.06 or 0.11 m²). The samples were fixed in 5% formaldehyde and in the laboratory macroinvertebrates were sorted and identified to species level or to the lowest taxonomic level possible on the basis of keys in Winterbourn and Greston (1989). Although two differently sized Surber samplers were used in the study, estimates of insect density and species richness were not influenced by the size of the Surber sampler used at a site, as confirmed by Townsend et al. (1997b) on the same data matrix. Conceivably, however, the larger sampler could have recovered more rare species. We checked this possibility by comparing the mean species richness of macroinvertebrates from small and large samples and found no significant difference ($F_{1.59} = 2.39$, one-way ANOVA, P = 0.17). This shows that (i) the size of the Surber sampler did not affect abundance and richness measurements, and (ii) taxon richness was accurately estimated even using the smaller Surber sampler.

All macroinvertebrates were sorted and counted, and data from the two replicate Surber samples were pooled and abundance expressed as number of individuals per square meter. A total of 85 taxa were identified and richness (total number of taxa recorded) per site ranged between 7 and 33 (mean = 19, sd = 5.71). The three most abundant taxa were *Deleatidium* spp. (Ephemeroptera, Leptophlebiidae), *Potamopyrgus antipodarum* (Gastropoda, Hydrobiidae) and *Hydora* spp. (Coleoptera, Elmidae).

Equitability (E) was then calculated for each site as:

$$E = [1/(\sum P_i^2)](1/S)$$

where P_i is the proportion of individuals in the community belonging to the *i*th taxon and S is species richness. Equitability ranged from 0.07 to 0.44 (mean = 0.23, sd = 0.08).

Modelling procedure

The ANN architecture is a layered feed-forward network in which the non-linear processing elements (neurons) are arranged in successive layers, with a one-way flow of information from input layer to output layer, through a hidden layer (Figure 2). In ANN, the computational or processing elements are called neurons. Like a



Figure 2. Typical three-layered feed-forward ANN with one input layer corresponding to the input variables (i.e. environmental variables), one hidden layer with four intermediate neurons (the number of hidden neurons was set to obtain optimal results), and one output layer with a single neuron to estimate the output variable (i.e. species richness (SR) or equitability (E) according to the models). Solid lines show connections between neurons: each is associated with synaptic weights that are adjusted during the training procedure. The bias neurons (input value 1) are also shown.

natural neuron, they have many inputs but only a single output, which can stimulate other neurons in the network.

Neurons from one layer are connected to all neurons in the adjacent layer(s), but no lateral connections within a layer, nor feedback connections, are possible. Connections are given a weight that modulates the intensity of the signal they transmit. The weights play an important role in the propagation of the signal through the network. They establish a link between the input variables and their associated output variable and 'contain' the knowledge of the ANN about the problemsolution relation. The number of input and output units depends on the representations of the input and the output objects, respectively. In the present study, we used an ANN architecture with 10 input neurons to code the 10 different input variables (except for the three-scale species richness model, where only eight input variables were used and the network comprised eight input neurons). Four neurons in the hidden layer yielded the best compromise between computing time and lowest error in both training and testing. The output neuron computed the value of the output variable (species richness or equitability). As a complement, a 'bias' neuron was added to each computational layer (i.e. hidden and output layer); these two neurons (Figure 2) had a constant input value of one and were used to lower biases in the modelling procedure (Rumelhart et al. 1986). Training the network consists of using a training data set to adjust the connection weights to minimize the error between observed and predicted values. This training was performed according to an iterative process called the back-propagation algorithm (Rumelhart et al. 1986). The computational program was written in a Matlab® environment and computed with an Intel Pentium® processor. Model performance was determined using the correlation coefficient (r) between observed and estimated values of the output variable. However, because the *r*-value is likely to be biased by high values of the output variable, we used mean squared errors (MSE) between observed and estimated values as a second estimator of model quality (Brosse et al. 1999b). The number of iterations needed to set up an optimal model was determined using a bootstrap cross-validation method where three quarters (73 observations) of the data matrix was used as a training set and the remaining quarter (24 observations) as a testing set. In the training and testing procedure, as recommended by Lek et al. (1996), we used the MSE between observed and predicted values (in relation to the number of iterations) to determine the optimal training zone. This zone corresponds to the best compromise between bias and variance (i.e. the number of iterations yielding the lowest MSE in both training and testing; Geman et al. 1992; Lek et al. 1996). MSE in both training and testing is expected to decrease with an increasing number of iterations. However, a phenomenon called 'overtraining' may occur when too many iterations are used. When the model is overtrained, the MSE of the testing set increases due to a reduced generalization ability of the model. Training should therefore be stopped when the number of iterations corresponds to the optimal training zone, before overtraining occurs. This procedure is illustrated in Figure 3 for the model predicting richness using bedform variables. Optimal training of all the ANN models used in this study was achieved after a training procedure of 1000 iterations, which was therefore considered to provide the optimal model configuration

Once model architecture and number of iterations needed to obtain an optimal training had been determined, the modelling was carried out in two steps. First, model training was performed using the whole data matrix. This step was used to



Figure 3. Identification of the optimal training zone of an ANN model predicting macroinvertebrate richness using 10 environmental variables measured at the bedform scale. MSE between observed and predicted richness values during training (black circles) and testing (open circles) are represented in relation to number of iterations. This procedure was repeated four times using a bootstrap procedure. The optimal training zone (grey zone) is defined as the number of iterations producing the lowest MSE in both training and testing procedures.

estimate the performance of the ANN in learning data. Second, we used the 'leave-one-out' bootstrap cross-validation test (Efron 1983), where each sample is left out of the model formulation in turn and predicted once, to validate the models. This procedure is appropriate to our data, as it should be used when the amount of data is limited and/or when each sample is likely to have 'unique information' (Efron 1983; Kohavi 1995); moreover, it has previously been found to be efficient for ANN modelling of small data sets (Guégan et al. 1998; Brosse et al. 1999b). This second step allows the prediction capabilities of the network to be assessed.

In addition to the prediction, the impact of the explanatory variables in an ANN analysis was determined using specific algorithms: the relative contribution of each variable in the models was obtained by a weights partitioning method (Garson 1991; Goh 1995); and the sensitivity of the variables, i.e. the influence of the range of variation of each predictor on invertebrate diversity, was assessed by a simulation method established by Lek et al. (1996). These two explanatory procedures had previously been proved efficient in various applications of ANN in ecology (Lek et al. 1996; Guégan et al. 1998; Brosse et al. 1999a, 1999b, 2001).

We applied this procedure to obtain predictive models of invertebrate species richness and equitability for each spatial scale (i.e. bedform, reach and catchment), giving rise to six models (three for species richness and three for equitability). The contribution of a variable was assumed to be important if it was greater than the mean value of a theoretical homogeneous distribution of all the variables (see Kim et al. (2000) and Brosse et al. (2001) for more details). These significant variables were used to set up a new data matrix for analysis of the three scales simultaneously. We checked for collinearity and when a significant correlation (P < 0.01) was found between two variables, the one accounting for less variation in the single-scale models was removed. Then, we produced new ANN models for richness and equitability, each model accounting for the three environmental scales simultaneously. To check the relative effectiveness of ANN to predict invertebrate species richness and equitability, we compared the ANN model results with those obtained from the same data matrix using (i) a simple multiple linear regression (MLR) analysis (James and McCulloch 1990) without transformation of the variables, and (ii) a non-linear regression analysis, based on a generalized additive model (GAM) (Hastie and Tibshirani 1990). The latter model is a non-parametric regression method that models the output variable as an additive sum of unspecified functions of covariates. Aiming to optimize the prediction efficiency of the GAM models, the input variables were non-linearly transformed using the 'lowess' method (Trexler and Travis 1993). MLR and GAM models were set up using S-plus[®] software (see Brosse et al. (1999a) for more details).

Results

When each spatial scale was considered individually, all ANN model results for both species richness and equitability were highly significant after the training procedure (P < 0.01). However, *r* increased and MSE decreased from the largest to

Table 2. Correlation coefficient (*r*) and MSE between observed and estimated values of species richness and equitability in ANN training and testing for the bedform, reach and catchment single-scale models and the combined three-scale models.

Scale	Species richness				Equitability			
	Training		Testing		Training		Testing	
	r	MSE	r	MSE	r	MSE	r	MSE
Bedform	0.889**	6.786	0.253*	39.706	0.846**	0.0019	0.19 (ns)	0.0089
Reach	0.597**	20.797	0.103 (ns)	40.857	0.743**	0.0032	0.106 (ns)	0.0097
Catchment	0.555**	22.386	0.068 (ns)	45.887	0.613**	0.0044	0.026 (ns)	0.0094
Three scales	0.903**	6.010	0.642**	19.560	0.861**	0.0019	0.553**	0.0049

(ns) not significant, P > 0.05; * marginally significant, 0.05 > P > 0.01; ** highly significant, P < 0.01.

the smallest spatial scale (Table 2). In the testing procedure, only one model was marginally significant (species richness predicted using bedform-scale variables; r = 0.253, P = 0.012). Consequently, MSE was high (six times higher in testing than in training) and residuals were not independent of the estimated values (r = -0.486, P < 0.01), indicating poor predictive ability. The five remaining models were not significant (r < 0.20, P > 0.05) and had high MSE values. In other words, these single-scale models were able to recognize the ecological features in the training data matrix, but failed to generalize this information to new data during testing. Therefore, the information extracted from the training procedure of each model using Garson's algorithm was only applied to the training procedure. In each of the six models (Table 3), no variable accounted for more than 25% of the contribution, indicating that both species richness and equitability were governed by a combination of several variables. For each model, three or four variables each contributed more than 10% (i.e. the significance threshold previously defined), together representing more than 45% of the total information explaining species richness or equitability.

Taking the three single-scale models together, 12 and 11 variables were important in accounting for equitability and species richness, respectively (accounting for more than 10%; Table 3), and these were considered for the three-scale analyses. Highly correlated variables (i.e. P < 0.01) were removed from the three-scale data matrix to avoid statistical biases. (i) For species richness, the percentage of pasture measured at the catchment scale (Cpas), average bankfull depth (Rdep) and percentage of tussock measured at the reach scale (Rtus) were respectively correlated with percentage of pasture measured at the reach scale (Rpas) (r (Rpas, Cpas) = 0.778, P < 0.01), depth measured at the bedform scale (Bdep) (r (Bdep, Rdep) = 0.490, P < 0.01), and maximal elevation (Cmax) and drainage density at the catchment scale (Cdrd) (r (Cmax, Rtus) = 0.477, P < 0.01 and r (Cdrd, Rtus) = 0.430, P < 0.01). Rdep, Rtus and Cpas contributed less than Bdep, Cdrd and Rpas in the single-scale models and were removed from the three-scale data matrix. The remaining matrix contained three catchment-scale, two reach-scale and three bedform-scale variables: Cmax, Crel, Cdrd, Rbed, Rpas, Bmed, Bdep, and Bbar (see Table 1). (ii) For equitability, in addition to the correlation between Bdep and Rdep

Table 3. Percentage contribution, obtained by Garson's algorithm, of each of the 10 input variables accounting for the catchment, reach and bedform spatial scales, respectively, to the prediction of insect diversity in single-scale models: species richness and equitability.

Input variables	Contribution (%)			
	Richness	Equitability		
Catchment				
Alluvial parent and surficial material	6.64	7.21		
Schist and semi-schist	7.39	11.59		
Drainage area	9.79	8.09		
Maximum elevation	12.48	13.70		
Relief ratio	12.44	11.91		
Drainage density	14.49	9.09		
Pasture area	11.77	7.42		
Forest area	7.3	6.87		
Native tussock area	8.27	7.73		
Barren area	9.44	16.39		
Reach				
Area of pools in reach	8.00	7.85		
Stream order	9.57	6.48		
Average bankfull stream width	6.81	12.04		
Average bankfull stream depth	12.17	19.28		
Bedrock area outside stream	13.39	7.54		
Roughness	7.54	10.20		
Riparian pasture area	12.81	11.84		
Riparian forest area	9.29	7.51		
Riparian tussock area	11.98	8.81		
Riparian barren area	8.45	8.46		
Bedform				
Stream power	7.85	9.20		
Median particle size	23.56	13.39		
Average bankfull stream width	9.52	13.50		
Average bankfull stream depth	12.80	10.86		
Bedrock outside stream	8.75	7.82		
Roughness	6.40	7.12		
Riparian pasture area	6.33	9.59		
Riparian forest area	5.72	9.20		
Riparian native tussock area	8.34	11.45		
Riparian barren area	10.73	7.87		

Significant contributions are in bold (see text for details).

(*r* (Bdep, Rdep) = 0.490, P < 0.01), a highly significant correlation was found between average bankfull channel width measured at the bedform and reach scales (Bwid and Rwid), (*r* (Bwid, Rwid) = 0.864, P < 0.01). Bdep and Rwid contributed less than Rdep and Bwid and were removed. The remaining matrix contained four catchment-scale, three reach-scale and three bedform-scale variables: Cmax, Crel, Csch, Cbar, Rdep, Rrou, Rpas, Bmed, Bwid, and Btus (see Table 1).

Inclusion of these variables in three-scale analyses increased the reliability of both training and testing procedures (Table 2). In the training procedure, predictions of species richness and equitability were associated with correlation coefficients

2066

Table 4. Correlation coefficient (*r*) and MSE between observed and estimated values of species richness and equitability in training and testing procedures using MLR and GAM for three-scale models.

	Species richness			Equitability				
	Training		Testing		Training		Testing	
	r	MSE	r	MSE	r	MSE	r	MSE
MLR GAM	0.403** 0.807**	27.074 11.318	0.196 (ns) 0.422**	37.725 33.790	0.427** 0.778**	0.0055 0.0027	0.201* 0.313**	0.0081 0.0072

(ns) not significant, P > 0.05; * marginally significant, 0.05 > P > 0.01; ** highly significant, P < 0.01.

greater than 0.85 (P < 0.01), with low MSEs, and the residuals were independent of estimated values (r = 0.03, P = 0.74 for equitability and r = -0.05, P = 0.60 for species richness). All results were superior to those obtained for single-scale analyses. Even using only eight variables (i.e. less information given to the model), the result of the three-scale species richness model was better than any single-scale model with 10 variables. Results were poorer for the testing procedure, but remained highly significant (P < 0.01) with correlation coefficients greater than 0.5 for both diversity descriptors. In each case, MSE remained acceptably low, with error values about half of those obtained in single-scale models (Table 2), and the assumption of independence of residuals was verified (r = -0.16, P = 0.12 for species richness and r = -0.17, P = 0.11 for equitability).

To check the effectiveness of ANN in modelling diversity patterns, we compared the results with more classical modelling methods (Table 4). MLR produced significant results in the training procedure and residuals were independent of estimated values (r = 0.006, P = 0.95 for equitability and r = -0.001, P = 0.99 for species richness), but *r*-values were less than 0.5 and MSEs were high. GAM results were much better than those of MLR, with *r*-values about 0.8 and residuals independent of estimated values (r = 0.103, P = 0.315 for equitability and r = 0.078, P = 0.449 for species richness). However, the ANN models performed consistently better, with the highest *r*-values and MSE values about half those derived from GAM.

In the testing procedure, the performance of MLR models remained poor, with a non-significant species richness model (r = 0.196 between observed and estimated species richness, P = 0.055), high MSE and a significant correlation between residuals and estimated values (r = -0.283, P < 0.01). Results were a little better for equitability, with a marginally significant model (r = 0.201 between observed and estimated values (r = -0.313, P < 0.01). GAM provided better test results, with significant models for both species richness and equitability (P < 0.01). However, correlations between observed and estimated values (r = -0.313, P < 0.01). GAM provided better test results, with significant models for both species richness and equitability (P < 0.01). However, correlations between observed and estimated values for GAM models were less than, and MSEs greater than, those for ANN models. Moreover, the GAM models were invalid due to significant correlations between residuals and estimated values (r = -0.494, P < 0.01 for equitability and r = -0.536, P < 0.01 for species richness). Within the three methods, ANN models provided the best results and this was the only modelling procedure able to validate the models on new observations,

Table 5. Percentage contribution in the three-scale models (obtained using Garson's algorithm) of each input variable to the prediction of insect diversity: species richness (8 input variables) and equitability (10 input variables).

Input variables	Scale	Contribution (%)	
Richness			
Maximum elevation	Catchment	8.73	
Relief ratio	Catchment	14.07	
Drainage density	Catchment	9.20	
Bedrock area outside stream	Reach	9.46	
Riparian pasture area	Reach	16.53	
Median particle size	Bedform	24.12	
Average bankfull stream depth	Bedform	9.72	
Riparian barren area	Bedform	8.17	
Equitability			
Maximum elevation	Catchment	7.35	
Relief ratio	Catchment	13.53	
Schist and semi-schist	Catchment	9.71	
Barren area	Catchment	8.09	
Average bankfull stream depth	Reach	10.52	
Roughness	Reach	7.50	
Riparian pasture area	Reach	12.79	
Median particle size	Bedform	12.65	
Average bankfull stream width	Bedform	7.27	
Riparian native tussock area	Bedform	10.59	

Significant contributions are in **bold** (see text for details).

whereas MLR and GAM provided non-significant or biased predictions (non-independence of residuals and estimated values).

Considering the relative contributions of each variable in the ANN, the model for species richness had strong contributions by variables from each of the three spatial scales. Median particle size at the bedform scale (Bmed), percentage of pasture at the reach scale (Rpas) and relief ratio at the catchment scale (Crel) made contributions of about 24, 16 and 14% (Table 5), accounting together for over 50% of the model response. The five remaining variables contributed less than 10% each. The contribution profile was more complex for equitability (Table 5), but the same three variables (Bmed, Rpas and Crel) each accounted for about 13%. Three further variables each accounted for about 10%, namely the percentage of schist/semischist in the catchment (Csch), average bankfull depth along the reach (Rdep) and the percentage of tussock adjacent to the bedform (Btus).

Applying Lek's algorithm, the influence of the three environmental variables that accounted for most variation in species richness and equitability in the ANN models is illustrated by three curves for each diversity descriptor (Figure 4). Only one variable shows a linear response (Crel for the species richness model) and three other patterns can be identified: (i) right skewed: Crel for equitability and Bmed for species richness; (ii) U shaped: Rpas for species richness and Bmed for equitability; and (iii) sigmoid decrease: Rpas for equitability.

2068



Figure 4. Contribution profiles (sensitivity analyses) for each of the three most strongly contributing input variables (i.e. relief ratio of the catchment; percentage of riparian pasture area measured at the reach scale; and medium particle size at the bedform scale), in the three-scale ANN models, for the prediction of stream insect species richness and equitability. The values cover the whole range of variation of each of the input variables tested.

Discussion

It appears that the processes that determine ecological patterns can be approximated by linear functions only to a limited extent, even after attempting to transform

2070

variables to linearize their distributions (James and McCulloch 1990; Lek et al. 1996; Scardi 1996; Brosse et al. 1999a, 1999b). The enhancement of model quality between linear (i.e. MLR) and non-linear (i.e. GAM) regression analyses testifies to the non-linearity of relationships between the input and output variables in our data matrix. Although complex transformation of the variables using a non-parametric modelling method (i.e. GAM) clearly improved the model, predictive ability was less than that of models developed using the ANN approach. The improvement in quality of model predictions between MLR, GAM and ANN serves to emphasize the complex non-linear nature of relationships between environmental variables and invertebrate diversity in tributaries of the Taieri River. Moreover, these results provide justification for the use of ANN, which is known to be able to deal with such non-linear relationships and can successfully model non-linear ecological systems without complex transformations of the data (Lek et al. 1996; Scardi 1996; Lek and Guégan 2000).

Single-scale models

Many studies of stream benthic invertebrates have assumed, at least implicitly, that local patterns are determined primarily by local processes (Palmer et al. 1996; Vinson and Hawkins 1998). While river quality assessment procedures usually incorporate different spatial scales, they do not identify the relative influence of the different scales (Moss et al. 1987; Smith et al. 1999; Wright et al. 2000). Results from our single-scale analyses seem, at first sight, to be consistent with the assumption of a predominant effect of local variables, since bedform-scale variables produced models with the highest reliability during the model training phase.

However, results from the more important testing procedure do not support the assumption of local control of diversity. Thus, while models produced using bedform-scale variables were still marginally better than those using reach- or catchment-scale variables in terms of higher *r*-values and lower MSEs, all the single-scale models showed very poor predictive ability of new sites and yielded strong correlations between residuals and estimated values in the testing procedure. Put another way, the single-scale models were able to extract relationships between input and output variables for each sample (training procedure), but this information was never sufficient to generalize the predictions to new samples (testing procedure). We can therefore hypothesize, in accordance with Corkum (1989) and Carter et al. (1996), that multiple-scale processes act in the determination of stream insect diversity, and that each variable may act predominantly at a single scale of measurement.

The results of our ANN analyses help to explain the apparent discrepancies in studies that have identified a wide variety of local factors as explaining local diversity (Quinn and Hickey 1990; Wohl et al. 1995). In their review, Vinson and Hawkins (1998) noted that variables measured at a single habitat scale may have been sufficient to explain local diversity, but were not readily generalizable to other streams or even to sampling sites in the same stream. This could signify, on the one hand, that diversity in different streams is governed by different variables, support-

ing the hypothesis of unstructured or stochastic stream assemblages (Winterbourn et al. 1981). On the other hand, these results may simply reflect a lack of information (unmeasured variables). In other words, the information available from any single spatial scale may be insufficient to entirely explain local diversity patterns, as suggested by Corkum (1989) and Carter et al. (1996). A comparison of our single-scale and three-scale models, discussed next, is relevant in this context.

Three-scale models

When the three spatial scales were considered simultaneously (after removal of correlated variables) model reliability increased, with significant (i.e. r > 0.5, P < 0.5(0.01) and valid (residuals independent of estimated values, P < 0.01) models for training and, more importantly, testing procedures. The models were able to identify diversity features on the basis of the input variables in the training procedure, but also to reliably predict diversity for new samples. Thus, local stream benthic diversity was only successfully predicted when variables from several scales were modelled together. This result corroborates the use of a large range of variables measured at various spatial scales in most river health assessment procedures based on invertebrates assemblages, such as RIVPACS or AUSRIVAS (Moss et al. 1987; Smith et al. 1999; Wright et al. 2000). However, as shown by the decrease of model predictive efficiency between training and testing, the predictive ability of ANN models is limited by the information contained in the training data set (Lek et al. 1996). In our case, the limited number of samples did not allow the ANN to deal effectively with the full range of factors influencing diversity and some impaired prediction can also be due to unmeasured environmental variables of importance. For example, the high instability of some streambeds is known to influence macroinvertebrate diversity (Death and Winterbourn 1995; Townsend et al. 1997a; Matthaei et al. 1999), but this variable could not be taken into account here because information on streambed stability was only available for a limited number of the Taieri sites.

Sensitivity analyses

Results of the Garson analysis emphasize the influence of three variables in the determination of insect species richness and equitability. These variables are derived from bedform (median particle size), reach (% pasture) and catchment scales (relief ratio), respectively, testifying to the simultaneous influence of variables at different scales on stream insect diversity. The differential patterns of species richness and equitability in relation to these influential environmental variables can be used as a basis for hypotheses about the generation of diversity.

Relief ratio (maximum elevation – minimum elevation/basin length) is high for catchments with large slopes overall, but these usually have an assortment of water falls and other high gradient stretches together with lower gradient sections. Catchments with low relief ratios tend to be more uniform, with low gradient stretches predominating. Thus, relief ratio can be considered to be an index of

stream heterogeneity at the catchment scale, and therefore, according to general niche theory, drainages with higher relief ratios are expected to possess higher insect richness in the catchment as a whole because of a greater range of conditions and resources and therefore of potential niches. Our results suggest that local richness also increases with relief ratio in the catchment (Figure 4), because a larger number of species are available to colonize stretches throughout the catchment, particularly by drifting (Waters 1972; Townsend and Hildrew 1976). On the other hand, many of the species recorded in a site may have drifted there but be poorly fitted to local environmental conditions and therefore be present at low densities. This justifies higher species richness but lower equitability at higher relief ratios (Figure 4).

The influence of land use on diversity acts through two main processes: changes to light intensity and inputs of particulate or dissolved organic matter (Sweeny 1993; Scarsbrook and Halliday 1999; Townsend and Riley 1999). The percentage of pasture in riparian zones along the stream reach is an index of the principal anthropogenic influence in the Taieri River. Highest species richness and equitability occurred in sites with least pastoral development (Figure 4). Evidently, pastoral development is influential, but it is the prevalence of pasture in the riparian zone at the reach scale (or in the whole catchment, as Rpas and Cpas were highly correlated, r = 0.778, P < 0.01), rather than immediately adjacent to the site (i.e. Bpas), that matters most. Therefore, the influence of land use cannot be related to light intensity, which depends on shading by vegetation located immediately on the banks; the effect of land use is therefore related to the amount of particulate and dissolved matter introduced from the reach or catchment as a whole. Thus, reaches associated with a higher percentage of pasture can be considered disturbed by human activities and their lower richness and equitability, compared to more pristine sites, result from a lack of dependable sources of organic matter for shredders such as Austroperla cyrene (Newman) and filterers such as Austrosimulim australense (Schiner), species that are characteristic of native tussock grassland and native forest reaches (Winterbourn and Greston 1989). The increase in richness at the highest levels of pasture development may be related to high algal productivity where nutrient inputs (particularly phosphorus) are high (Krug 1993; Townsend and Riley 1999), providing rich resources for grazers and collector-gatherers (Vannote et al. 1980). Nevertheless, in these pastoral areas, equitability remains low due to the high abundance of tolerant and generalist species, such as the mayfly Deleatidium spp., known for its opportunistic habitat use (Winterbourn and Greston 1989).

Finally, sites with bedforms made up of very small or very large particles are associated with low species richness but high equitability. These sites have low bed heterogeneity and, according to general niche theory, are likely to sustain low species richness. Individuals are more evenly distributed among taxa (high equitability) in the finest and coarsest substrates (Figure 4). Intermediate median particle sizes are associated with a high degree of heterogeneity of substrate types and streambed habitats (C.R. Townsend, unpublished data), factors that can be expected to be associated with higher faunal diversity (Williams 1980; Townsend et al. 1997a; Vinson and Hawkins 1998). In the case of equitability, it may be that some rare habitat types are added where more substrate heterogeneity is available, leading to lower equitability.

The three most important variables in the prediction of both species richness and equitability were derived from different spatial scales, and were highly non-linearly related to the two diversity descriptors. The influence on diversity of a particular variable, but measured at different scales, may depend on quite distinct processes (e.g. pasture in this study). Thus, a given variable affects richness or equitability at one scale but not another. This could help explain the difficulty of many previous studies in identifying the environmental factors that determine benthic invertebrate diversity. Patterns observed in local assemblages are not only determined by local processes acting within assemblages, but also result from processes operating at larger spatial scales. Integration of different spatial scales, identification for each environmental feature of the scale that is relevant for the studied organism or process, and recognition that relationships are not likely to be linear, may be the key components for increasing model predictability and understanding of factors that determine local diversity.

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