Critical threshold effects of benthiscape structure on stream herbivore movement

Julian D. Olden*

Centre for Limnology, University of Wisconsin–Madison, Madison, WI 53706, USA

In landscape ecology, substantial theoretical progress has been made in understanding how critical threshold levels of habitat loss may result in sudden changes in landscape connectivity to animal movement. Empirical evidence for such thresholds in real systems, however, remains scarce. Streambed landscapes provide a strong testing ground for studying critical thresholds because organisms are faced with substantial environmental heterogeneity while attempting to overcome the physical force of water. In this study, I report on the results from a series of experiments investigating the influence of habitat abundance and current velocity on the movement dynamics of two stream herbivores (caddisfly larva *Agapetus boulderensis* and snail *Physa* sp.) that differ substantially in how they perceive landscape structure. Specifically, I ask whether critical thresholds to herbivore movement exist in streambed landscapes. By exploiting the pattern recognition capabilities of artificial neural networks, I found that the rate, sinuosity and directionality of movement by *Agapetus* and *Physa* varied nonlinearly according to the abundance of habitat patches, current velocity and habitat–current interaction. Both the study organisms exhibited threshold responses to habitat abundance, yet the location and slope of these thresholds differed between species and with respect to different current velocities. These results suggest that a critical threshold in functional connectivity (i.e. the connection of habitat patches by dispersal) is not an inherent property of the landscape, but in fact emerges from the interplay of species' interactions with landscape structure. Moreover, current velocity interacted with habitat abundance to elicit strong upstream-oriented movement for both the species. This suggests that dispersing individuals may be polarized in the upstream direction and therefore functional connectivity is not equal in all directions. Such results highlight the need for future research addressing the sources of variability of critical threshold effects in ecological phenomena.

Keywords: artificial neural networks; movement behaviour; perceptual range; stream invertebrates; stream landscapes; landscape anisotropy

1. INTRODUCTION

Ecological thresholds have long intrigued scientists, dating from the study of threshold effects for age-specific human mortality (Gompertz 1825) to present-day investigations for biodiversity conservation and environmental management (Roe & van Eeten 2001; Huggett 2005; Groffman *et al.* 2006). Defined as a sudden change from one ecological condition to another, ecological thresholds are considered synonymous with discontinuities in any property of a system that occurs in nonlinear response to smooth and continuous change in an independent variable. Understanding ecological thresholds and incorporating them into environmental monitoring and management is seen as a major advance in our ability to forecast and thus properly cope with ecological surprises (Carpenter 2002). Consequently, ecologists and economists continue to be extremely attracted to the idea that ecological thresholds may exist and can be used in a management context (Muradian 2001).

Empirical studies of ecological thresholds are diverse and have grown in number in recent years (Resilience Alliance and Santa Fe Institute 2004). In landscape

ecology, a working hypothesis is the existence of critical threshold levels of habitat loss and fragmentation that result in sudden reductions in species' occupancy (Gardner *et al.* 1987; Andrn 1994; With & Crist 1995). As the landscape becomes dissected into smaller and smaller parcels, landscape connectivity—referring to the spatial contagion of habitat—may suddenly become disrupted (With & Crist 1995). In this case, habitat fragmentation leads to decreased landscape connectivity, thereby limiting organism dispersal that is essential for maintaining population viability (Kareiva & Wennergren 1995; Fahrig 2001). Critical thresholds, therefore, may also comprise so-called extinction thresholds (*sensu* Lande 1987), which represent a transition point in the functionality of a landscape when a population is abruptly and unpredictably lost. Evidence for such critical thresholds to animal movement has been advanced by advocates of neutral landscape models (Gardner *et al.* 1987; With & King 1997), in particular, the application of percolation theory used to describe how landscape structure affects the abundance, distribution and behaviour of organisms (McIntyre & Wiens 1999).

Simulation experiments have been used extensively to predict whether critical thresholds to landscape connectivity exist and how this affects the movement of animals (With *et al.* 1997). Empirical evidence for such

*olden@wisc.edu

One contribution of 15 to a Theme Issue 'The use of artificial neural networks to study perception in animals'.

thresholds, however, remains scarce and is limited almost exclusively to terrestrial insects (Wiens *et al.* 1997; McIntyre & Wiens 1999; Schooley & Wiens 2003). Moreover, while it is clear that critical thresholds to animal movement are likely to depend on a number of factors, including dispersal ability (Keitt *et al.* 1997), the movement 'rules' of an organism (Pearson *et al.* 1996) and the specifics of the environment (Loxdale & Lushai 1999), it is still unclear whether such hypotheses are supported by empirical data. Given differences in how species perceive and response to landscape heterogeneity (With 1994; Olden *et al.* 2004a), we might predict that critical thresholds to organism movement will differ not only between species, but also within species occupying different environments.

Stream ecosystems provide a strong testing ground for exploring the issues of environmental heterogeneity and the influence of habitat patchiness on animal movement behaviour (Downes *et al.* 1993; Palmer *et al.* 2000; Malmqvist 2002). Streams contain predominantly mobile rather than sessile invertebrates, and their dispersal is determined by many factors, including intrinsic characteristics of the species (e.g. mobility, resource specificity and perceptual range) and/or features of the environment (Mackay 1992). In streambed landscapes, or benthiscapes, the pervasive action of flowing water is a dominant physical force that generates habitat patches located in highly variable, near-bed current dynamics (Pringle *et al.* 1988; Statzner *et al.* 1988; Hart *et al.* 1996; Hart & Finelli 1999). As a result, benthic insects experience considerable physical heterogeneity during their normal activities (Palmer *et al.* 1996). From an insect's perspective, this heterogeneous benthic landscape represents a three-dimensional mosaic of both habitat patchiness and flow conditions, which can influence the connectivity or permeability of the landscape (*sensu* Taylor *et al.* 1993) to movement, foraging activities and likelihood of colonization (e.g. Hart & Resh 1980; Poff & Ward 1992; Lancaster 1999; Palmer *et al.* 2000; Wellnitz *et al.* 2001). Variation in dispersal ability means that patchiness of resources and habitat availability is likely perceived by different stream insects (Olden *et al.* 2004b). Consequently, benthiscapes are an ideal setting for addressing the influence of landscape processes on species' distributions, and thus searching for critical thresholds to animal movement in response to landscape connectivity.

The physical complexity of stream benthiscapes necessitates equally complex models that aim to unravel the threshold relationships between landscape structure and animal movement. These statistical approaches need to be able to model nonlinear relationships among variables, account for variable interactions and provide high predictive power without sacrificing explanatory power. One such technique that has gained greater attention in recent years is the application of artificial neural networks. An artificial neural network is an information-processing paradigm inspired by the way biological nervous systems, such as the mammalian brain, process complex information (McCulloch & Pitts 1943). The key element of this paradigm is the novel structure of the information-processing system, which is composed of a large

Figure 1. (a) The cased-caddisfly *Agapetus boulderensis* and (b) freshwater snail *Physa* sp. in their natural stream benthiscape. Photographs courtesy of Jeremy B. Monroe, Freshwaters Illustrated.

number of highly interconnected elements called neurons, working in unity to solve specific problems. Neural networks are being used in greater frequency by ecologists owing to their perceived predictive ability, although their explanatory utility is equally powerful but continues to be underappreciated (Olden & Jackson 2002; Olden *et al.* 2004c). Here, we used neural networks primarily as an explanatory tool to understand the direct and interactive roles of habitat abundance and current velocity for shaping threshold responses of animal movement in complex benthiscapes.

In this study, I report on the results from a series of streamside experiments investigating the influence of habitat abundance and current velocity on the movement dynamics of two ubiquitous herbivores. The study organisms are a caddisfly larva (*Agapetus boulderensis* Milne, 1936) and a freshwater snail (*Physa* sp.), benthic grazers that differ substantially in their body morphology and mobility and are therefore likely to perceive and respond differently to landscape structure (figure 1). Given these intrinsic differences in mobility and the manner in which they perceive and interact with extrinsic elements on the landscape (Kawata & Agawa 1999; Olden *et al.* 2004b), this study addresses the following questions: How do habitat abundance and current velocity interactively shape animal movement, including the rate of movement, pathway sinuosity and directionality in relation

to the direction of flow? Do critical thresholds to movement exist? If so, does the location and slope of this threshold differ between study organisms and/or differ within species for individuals exposed to different current velocities? Furthermore, does the critical threshold vary consistently across current velocities or vary similarly for the study organisms? This study uses an artificial neural network approach with recent methodological advances for exploring their explanatory capabilities to unravel the direct and interactive roles of habitat and current velocity for shaping herbivore movement, and to facilitate the detection of critical thresholds in complex benthoscapes.

2. MATERIAL AND METHODS

(a) Study organisms

Agapetus boulderensis (Trichoptera: Glossosomatidae) is a slow-moving herbivorous caddisfly that inhabits streams of western North America. *Agapetus* larvae (hereafter called *Agapetus*), or more generally members of the family Glossosomatidae, hatch in late spring, grow through five instars over the next three months, enter the pupal stage and emerge relatively synchronously over a period of approximately one month. Larvae construct and occupy hemispherical cases composed of sand grains cemented together with silk. A case contains two ventral openings located along the major axis, through which the larvae extend their thoracic legs and anal claws to grasp the substrate while moving and grazing algae (Wiggins 1996). Although the mineral case provides effective protection against many predators, its cost is the substantial energetic expense of carrying it around while being opposed by the drag force exerted by the flowing water, as well as the frictional force of the case against the substrate (Waringer 1993; Otto & Johansson 1995). Consequently, *Agapetus* mobility is greatly limited and is restricted to smooth surfaces of substrates (Poff & Ward 1992). The freshwater snail *Physa* sp. (Pulmonata: Physidae; hereafter called *Physa*), in contrast, is a highly mobile herbivore that is most often found on stones along stream margins in slow current velocity habitats. Individuals use a large muscular foot to slide over the rock surface and secrete mucus from specialized glands to lubricate their path (Dillon 2000). Like *Agapetus*, hydrodynamic drag on the shell of freshwater snails influences the mobility and directionality in running waters (Huryn & Denny 1997).

High-profile structural elements on the streambed that influence *Agapetus* and *Physa* movement include the silken retreats of the midge larva, *Pagastia partica* Roback, 1957 (Diptera: Chironomidae) that are colonized by filamentous algae (Monroe *et al.* 2005). The retreats of *Pagastia* are effective barriers to *Agapetus* movement, whereas the spaces between the retreats are typically dominated by low-profile matrix of algae and diatoms upon which *Agapetus* larvae can readily move and forage. In contrast, *Physa* individuals are better able to negotiate stands of thick *Pagastia* retreats and filamentous algae, albeit with more difficulty compared with the smooth, diatom matrix (J. D. Olden 2001, personal observation).

(b) Experimental design

Movement experiments were conducted during the summer of 2001 on artificial arenas placed in a streamside channel (185 × 60 × 10 cm) adjacent to the Upper Colorado River, Colorado, USA (40°11' N, 105°52' W; figure 2). The arena consisted of a 40.6 × 40.6 cm frame upon which 196 unglazed porcelain tiles

Figure 2. Streamside channel and experimental arenas used in this study to examine the movement behaviour of *Agapetus boulderensis* and *Physa* sp. Smooth tiles (i.e. habitat patches represented by white cells) and *P. partica* tiles (i.e. non-habitat patches represented by black cells) are used to create arenas with varying proportions of available habitat, e.g. $p_{\text{habitat}} = 0.8$ (second arena from the top), 0.2 (third arena from the top) and 1.0 (fourth arena from the top).

(each 2.54 × 2.54 cm) were arranged into a square matrix consisting of 14 rows and 14 columns. The streamside channel received water directly from the Upper Colorado River, and current velocity was controlled using six evenly spaced hoses that discharged water at equal rates to ensure consistent velocities. Water temperature was measured every 15 min in the experimental channel over the entire study period.

To mimic the mix of diatom patches and *Pagastia* retreats found in natural benthoscapes, porcelain tiles were used to create two patch types that imitate the form, size and complexity of these habitats. Some porcelain tiles were cultured in flow-through channels in the stream at a current velocity of 70 cm s⁻¹ to produce uniform, low-profile algal mats. These tiles were considered to represent 'habitat patches' because they provided a good medium for both movement and potential foraging (Poff & Ward 1992; Kawata & Agawa 1999). The remaining tiles were placed in the experimental streamside channel under slow velocities and subjected to the addition of hundreds of retreat-building *Pagastia* larvae that were collected from the adjacent stream. Silken retreats woven by the larvae were subsequently colonized by thick filamentous algae and were similar in both appearance and size to those in the stream (Olden *et al.* 2004b). Tiles containing *Pagastia* retreats were considered 'non-habitat' patches because they impeded movement of both *Agapetus* and *Physa*, although to a varying degree.

(c) Movement experiments

A two-by-two factorial design experiment was conducted to examine the effects of habitat abundance and current velocity on the movement dynamics of *Agapetus* and *Physa*. Two random arrangements of the experimental arenas were examined for each of five treatment levels of habitat: $p_{\text{habitat}} = 0.2, 0.4, 0.6, 0.8$

and 1.0, where p_{habitat} is the proportion of smooth habitat patches or tiles, and two treatment levels of current velocity: low velocity = 5–15 cm s⁻¹ and high velocity = 20–30 cm s⁻¹. These treatments were based on streambed surveys of *Pagastia* retreat densities (Monroe *et al.* 2005) and the range of velocities commonly experienced by insects on the streambed (Wellnitz *et al.* 2001). Current velocity was measured across the entire experimental arena using a Schiltknecht current probe (Schiltknecht Messtechnik AG, Zurich, Switzerland) to provide an integrated measure of velocity between 0 and 10 mm from the channel bottom.

Experimental animals were collected from the streambed minutes prior to performing a movement trial and placed at the centre of the experimental arena using a soft-bristled paintbrush. The movement pathway of 10 individuals of each species for each treatment combination of five p_{habitat} levels, two current velocities and two replicates of the experimental arena (i.e. two different random tile arrangements for a given p_{habitat}) was recorded every 3 min for 1 h for *Agapetus* and every 1 min for 20 min for *Physa* on a recording map. Spatial coordinates were taken for the entire observation period (20 time-steps) or until the individual left the arena via crawling or accidental dislodgment. The temporal scale of measurement intervals was based on a series of preliminary experiments and was chosen to reflect the time-scale of *Agapetus* and *Physa* movement.

The influence of food resources on *Agapetus* and *Physa* movement was examined by comparing algal ash-free dry mass and algal species composition from scraped habitat (diatom) and non-habitat (*Pagastia*) patches prior to the commencement of the experiments. Ash-free dry mass of non-habitat patches was an order of magnitude greater ($\bar{X} = 2.68 \text{ mg cm}^{-2}$, $n = 4$) than habitat patches ($\bar{X} = 0.22 \text{ mg cm}^{-2}$, $n = 4$), whereas both patch types contained high concentrations of diatoms (see Olden *et al.* 2004b for more details). These results support the structural differences and food similarities of the two patch types, and emphasize that the patch types differed only in that the *Pagastia* or non-habitat patches contained extensive filamentous algae that impede insect movement.

(d) Movement metrics

The x - y coordinates for each movement pathway were spatially referenced by digitizing the recording map in ArcView geographic information system (Environmental Systems Research Institute 2000). I calculated second-order statistics (i.e. individuals as replicates and not time-steps within an individual pathway) of four movement metrics using the appropriate mathematical protocols for angular data following Batschelet (1981): (i) net displacement; (ii) movement rate—calculated as the sum of the distances travelled for each time-step divided by the total time of the pathway; (iii) mean vector length (r) as a measure of sinuosity—calculated as $\sqrt{(\sin \bar{\theta})^2 + (\cos \bar{\theta})^2}$, where $\bar{\theta}$ is the turning angle between successive time-intervals ($r = 0.0$ represents random dispersion of turning angles between successive steps and $r = 1.0$ represents a perfectly straight line); and (iv) homeward component as a measure of upstream orientation—calculated as $r \cos(\bar{\phi} - \theta_0)$, where $\bar{\phi}$ is the mean angle and θ_0 is the direction of flowing water (0°). The homeward component measures how close the mean direction is to the ‘homeward’ (upstream) direction, and it ranges from 1.0 (precisely upstream) to -1.0 (precisely downstream). Together, this suite of movement metrics was chosen to represent the rate, direction and tortuosity of an individual’s movement pathway in response to landscape structure (Turchin 1991).

(e) Multi-response artificial neural network

A multi-response artificial neural network (MANN) was used to test for the effects for habitat abundance (five p_{habitat} levels) and current velocity (two levels) on *Agapetus* and *Physa* movement behaviour as depicted by the four movement metrics. The architecture of these networks (known as a multilayer perception) consisted of a single input, hidden and output layer. The input layer contained two neurons representing p_{habitat} and current velocity. The number of hidden neurons in the neural network was chosen to minimize the trade-off between network bias and variance by comparing the performances of different networks (see below). The output layer contained four neurons representing each of the movement metrics.

Each neuron in a multilayer perception is connected to all neurons from adjacent layers by axons that are assigned a connection weight that dictates the intensity of the signal they transmit. The ‘activity level’ of each input neuron is defined by the incoming signal (i.e. values) of the independent variables, whereas the state of the other neurons is evaluated locally by calculating the weighted sum of the incoming signals from the neurons of the previous layer. The mathematics of the neural network can be expressed as:

$$y_k = \phi_o \left\{ \beta_k + \sum_j w_{jk} \phi_h \left(\beta_j + \sum_i w_{ij} x_i \right) \right\}, \quad (1)$$

where x_i are the input signals, y_k are the output signals, w_{ij} are the weights between input neuron i to hidden neuron j , w_{jk} are the weights between hidden neuron j and output neuron k , β_j and β_k are the biases associated with the hidden and output layers, and ϕ_h and ϕ_o are activation functions (in this case logistic functions) for the hidden and output layers.

I used a two-phase training approach to account for the fact that different parameter optimization algorithms will perform best on different problems. In the first phase, I used the backpropagation algorithm (Rumelhart *et al.* 1986) and in the second phase, I used the conjugate gradient descent algorithm (Hestenes & Stiefel 1952); both of which train the neural network by iteratively adjusting the connection weights with the goal of finding a set of weights that minimizes the error of the network (in this case, the sums of squared error function). During network training using the backpropagation algorithm, observations are sequentially presented to the network and weights are adjusted in a backwards fashion, layer by layer, in the direction of steepest descent in minimizing the error function. Learning rate (which controls the step size when weights are iteratively adjusted) and momentum parameters (which adds inertia to the learning motion through weight space) were included during network training to ensure a high probability of global network convergence.

In the second phase, I used conjugate gradient descent, which is a batch update algorithm that calculates the average gradient of the error surface across all cases before updating the weights once at the end of each epoch (Bishop 1995). This algorithm can be regarded as a form of gradient descent with momentum that constructs a series of line searches across the error surface. However, instead of taking a step proportional to the learning rate as performed by the backpropagation algorithm, this algorithm projects a straight line in that direction and then locates a minimum along this line in error space (Bishop 1995). For both algorithms, I used a maximum of 500 epochs to determine the optimal axon weights. Prior to training the network, the independent variables were converted to z -scores to standardize the measurement scales of the inputs into the network.

I conducted an iterative search for the optimal neural network. One hundred networks based on different random initial connection weights were conducted for each network configuration with 1–10 hidden neurons (increasing by increments of unity) and random shuffling of presentation order was evoked during the backpropagation training. From this list of candidates, the top 20 networks that produced the greatest predictive performance were retained and compared with the ensemble network that combined the predictions from all the models. A single network that was deemed representative of the ensemble network based on model predictions and variable contributions was then selected as the final network. In a previous study, Olden *et al.* (2004b) showed no effect of replicate arena on movement rates, and therefore the two landscape replicates were pooled for all subsequent analyses. All neural network analyses were conducted using the DATA MINER toolbox of STATISTICA (v. 7.1, StatSoft Inc., Tulsa, Oklahoma, USA) and computer macros written in the MATLAB programming language (v. 7.0, The MathWorks, Natick, Massachusetts, USA).

Given the importance of connection weights in assessing the relative contributions of the independent variables, during the optimization process it is necessary that the network converges to the global minimum of the fitting criterion (e.g. prediction error) rather than one of the many local minima. Connection weights in networks that have converged to a local minimum will differ from networks which have globally converged, thus resulting in drastically different variable contributions. The iterative search for the optimal and most representative neural network employed in this study (see above) ensured the greatest probability of network convergence to the global minimum. Here, I used three complementary approaches to explore variable contributions: neural interpretation diagrams to visualize direct and interactive variable effects, a connection weight method to quantify the relative contributions of the variables to network predictions and a sensitivity analysis to explore the influence of the predictor variables across their entire range and test for the existence of critical thresholds.

(f) *Quantifying variable importance in neural networks*

Given the repeatedly demonstrated predictive power of artificial neural networks, recent efforts have focused on the development of methods for understanding the explanatory contributions of the predictor variables in the network (Olden & Jackson 2002). This was, in part, prompted by the fact that neural networks were coined a 'black box' approach to modelling ecological data. Recent studies in the biological sciences have provided a variety of methods for quantifying and interpreting the contributions of the independent variables in neural networks (see reviews by Gervey *et al.* 2003; Olden *et al.* 2004c). All of these approaches rely on the fact that the connection weights between neurons are the linkages between the inputs and the output of the network, and therefore are the link between the problem and the solution. Consequently, the relative contribution of each independent variable to the predictive output of the neural network depends primarily on the magnitude and direction of these connection weights. Input variables with larger connection weights represent greater intensities of signal transfer, and therefore are more important in predicting the output compared with variables with smaller weights. Negative connection weights represent inhibitory effects on neurons (reducing the intensity or contribution of the incoming signal and negatively affecting the output), whereas positive connection weights represent

excitatory effects on neurons (increasing the intensity of the incoming signal and positively affecting the output).

(i) *Neural interpretation diagram*

The neural interpretation diagram provides a visual interpretation of the connection weights among neurons and was first presented by Özesmi & Özesmi (1999). Tracking the magnitude and direction of weights between neurons enables researchers to identify individual and interacting effects of the input variables on the output. Variable relationships are determined in a two-step manner. Positive effects of input variables are depicted by positive input-hidden and positive hidden-output connection weights, or negative input-hidden and negative hidden-output connection weights. Negative effects of input variables are depicted by positive input-hidden and negative hidden-output connection weights, or by negative input-hidden and positive hidden-output connection weights. Therefore, the multiplication of the two connection weight directions (positive or negative) indicates how each input variable influences each output variable. Interactions among predictor variables can be identified as input variables with opposing (antagonist) or similar (synergist) connection weights entering the same hidden neuron.

With even small networks, however, the number of connections to examine and interpret in a network can be extremely large. For example, a network containing ten input neurons, seven hidden neurons and three output neurons would have a total of 91 connection weights to examine. Bishop (1995) suggested removing small weights from the network to ease interpretation; however, deciding the threshold value below which weights should be eliminated from the network is unclear. Recently, Olden & Jackson (2002) developed a randomization test to address this question. This approach randomizes the response variable, then constructs a neural network using the randomized data and records all input-hidden-output connection weights (product of the input-hidden and hidden-output weights). This process is repeated 1999 times to generate a null distribution for each input-hidden-output connection weight, which is then compared with the observed values to calculate the significance level. The randomization test provides an objective pruning technique for eliminating connection weights that have minimal influence on the network output.

(ii) *Connection weight approach*

A formal quantification of variable importance (as visually depicted in the neural interpretation diagram) was presented by Olden & Jackson (2002). In this approach, variable contributions are quantified by calculating the product of the input-hidden and hidden-output connection weights between each input neuron and output neuron, which are then summed across all hidden neurons. Positive values represent positive associations between input and output neurons, whereas negative values represent negative associations. The relative contributions of the variables are calculated by dividing the absolute value of each variable contribution by the grand sum of all absolute contributions. The connection weight approach is deemed to be one of the most appropriate methods as it has been shown to exhibit substantially higher sensitivity for identifying variable importance compared with other approaches (Olden *et al.* 2004c).

(iii) *Sensitivity analysis*

Sensitivity analysis is a commonly used approach for exploring variable contributions in statistical models. Quite simply, it involves varying each input variable across its entire

range (from its minimum to maximum value) while holding all other input variables constant, allowing the individual contributions of each variable to be assessed. This approach has been used for neural networks in the past (e.g. Lek *et al.* 1996) and here I constructed response curves for habitat abundance by varying p_{habitat} across its range while holding flow velocity at each of its two treatment levels.

3. RESULTS

The MANN exhibited high accuracy (R^2) and precision (RMSE) for predicting *Agapetus* and *Physa* movement as a function of p_{habitat} and current velocity (Table 1). Net displacement and movement rate were predicted with the greatest success for *Agapetus*, whereas movement rate and upstream homing were the most predictable for *Physa*. Next, network connection weights were examined to quantify the direct and interactive importance of p_{habitat} and current velocity for predicting each of the movement metrics. In the neural interpretation diagram, the set of input-hidden connection weights reflect the universal importance of p_{habitat} and current velocity for influencing overall movement dynamics, whereas the hidden-output connection weights modify the first set of weights by reducing, enhancing or even reversing the signals to maximize the model fit for each movement metric. Prior to interpretation, non-influential connection weights that were non-significant based on the randomization test ($p > 0.05$) were pruned from the diagram.

The neural interpretation diagram shows the positive influence of p_{habitat} on the net displacement, movement rate, mean vector length (i.e. increasingly straight pathways) and upstream homing of *Agapetus* through neurons D and I (figure 3a). These connections exceed the relatively small negative influence of p_{habitat} on net displacement through neurons A and B. In contrast, high current velocity was associated with decreased net displacement and slower movement rates via neuron I and less convoluted pathways via neuron J. Synergistic and antagonistic interactions between p_{habitat} and current velocity were evident through a number of hidden neurons. Most notably, increasing p_{habitat} and current velocity acted together to cause greater declines in net displacement (neuron E) and greater upstream homing (neuron J); but they acted in opposition for movement rates where increasing current velocity suppressed the positive influence of habitat transmitted through neuron I.

Movement dynamics of *Physa* were influenced predominantly by the direct effects of p_{habitat} and current velocity. Movement rates were positively associated with p_{habitat} and current velocity through neurons B–D and A, respectively (figure 3b), although these factors interacted negatively through hidden neuron B where high current velocities decreased the positive influence of habitat on movement rate. Similarly, increasing p_{habitat} was related to greater upstream homing (neuron E) and current velocity was positively correlated with mean vector length (i.e. lower pathway sinuosity) via neuron A. Synergistic interactions between habitat and current velocity were not evident.

According to all axon connections in the network, the total contribution of p_{habitat} and current velocity for

Table 1. Predictive performance of the MANN for predicting the movement metrics as a function of habitat abundance and current velocity (reported values represent model accuracy (Pearson correlation coefficient, R) and precision (root mean square error, RMSE)).

organism	accuracy		precision
movement metric	R	p	RMSE
<i>Agapetus</i>			
net displacement	0.67	<0.001	4.07
movement rate	0.60	<0.001	0.17
pathway sinuosity	0.50	<0.001	0.22
upstream homing	0.41	<0.001	0.35
<i>Physa</i>			
net displacement	0.46	<0.001	4.96
movement rate	0.77	<0.001	2.25
pathway sinuosity	0.50	<0.001	0.20
upstream homing	0.53	<0.001	0.48

predicting the movement metrics of *Agapetus* and *Physa* is presented in figure 4. For both species, p_{habitat} was the most important predictor of net displacement, sinuosity and upstream homing, whereas current velocity was the top predictor for movement rate. Although the best predictors were the same for both species, the contributions of p_{habitat} and current velocity were much more balanced for *Physa*, particularly for movement rate and pathway sinuosity. For *Agapetus*, p_{habitat} was positively related and current velocity negatively related to all movement metrics, with the exception of upstream homing where current velocity exhibited a weak positive influence. In contrast, both p_{habitat} and current velocity were positively associated with all movement metrics for *Physa*.

Given the direct and interactive effects of p_{habitat} and current velocity for movement behaviour, the results from the sensitivity analysis provide valuable insight into the shape and possible threshold response of the study organisms. Critical thresholds are represented in the response curves as sharp changes in a movement metric in relation to a small change in p_{habitat} . In low current velocities, the net displacement of *Agapetus* responded to increasing p_{habitat} in a two-stage manner; a punctuated increase in displacement at intermediate levels followed by a gradual increase (figure 5a). Movement rate similarly increased with p_{habitat} under low current velocity, but the response was not initiated until intermediate p_{habitat} , after which movement rates increased exponentially (figure 5b). In contrast, net displacement and movement rate showed a minimal response to p_{habitat} in the high current velocity treatment. Mean vector length increased immediately in response to increasing p_{habitat} under low current velocity (i.e. straighter movement pathways), showing a critical threshold at $p_{\text{habitat}} = 0.2$, whereas the threshold response was delayed until $p_{\text{habitat}} = 0.6$ in high current velocity (figure 5c). Upstream homing exhibited a threshold response to p_{habitat} in both current velocity treatments, where peak homing was observed at slightly lower p_{habitat} in high current velocities (figure 5d). In both the cases, upstream homing then gradually decreased at intermediate p_{habitat} and showed a similar levelling off response.

Figure 3. Neural interpretation diagram illustrating the contributions of habitat abundance (p_{habitat}) and current velocity for predicting the movement metrics of (a) *Agapetus* and (b) *Physa*. In this diagram, the relative magnitude of each connection weight is represented by line thickness (i.e. thicker lines representing greater weights) and line pattern represents the direction of the weight (i.e. solid lines represent positive, excitatory signals and dashed lines represent negative, inhibitor signals).

Net displacement of *Physa* showed a logarithmic response to increasing p_{habitat} in both low and high current velocities, gradually increasing at low to immediate levels of p_{habitat} and then stabilizing at higher levels (figure 6a). Movement rates exhibited comparable response curves in both velocity treatments at $p_{\text{habitat}} < 0.8$, after which the curves diverged sharply with elevated movement rates in high current velocities (figure 6b). Mean vector length showed a positive linear relationship with p_{habitat} in low current velocities (i.e. decreased sinuosity), whereas in high current velocities a gradual increase and levelling out of sinuosity at intermediate p_{habitat} was followed by a sharp threshold response at $p_{\text{habitat}} > 0.8$ (figure 6c). Mean vector length converged to similar values once $p_{\text{habitat}} = 1.0$. Upstream homing exhibited a strong logarithm response to p_{habitat} in low current velocities and a bimodal response in high current velocities (figure 6d).

Comparison of movement behaviours shows that net displacement and movement rate of *Agapetus* were distinctly higher in low current velocity; the magnitude of this difference generally increased with p_{habitat} .

This differed from the movement behaviour of *Physa* where net displacement was very similar between the velocity treatments, and movement rates in high current velocity were greater in high p_{habitat} landscapes. Response curves for *Agapetus* showed lower pathway sinuosity (i.e. greater mean vector length) and upstream homing in low current velocity until $p_{\text{habitat}} > 0.6$, at which the curves intersected and after which values were greater in high current velocity. For *Physa*, however, mean vector length and homing were almost always greater in low current velocity. Interestingly, the shape of the *Agapetus* response curves for net displacement, sinuosity and upstream homing in low current velocity corresponded closely to the same response curves for *Physa* but in high current velocity.

4. DISCUSSION

Of the many challenges that face landscape ecologists in the coming decades, understanding critical thresholds and how they influence animal movement is an important topic of research (Turner 2005). However, because habitat fragmentation can have

Figure 4. Relative variable importance of habitat abundance (P_{habitat}) and current velocity for predicting the movement metrics of *Agapetus* and *Physa*. '+' and '-' indicate an overall positive or negative influence of the variable, respectively.

nonlinear effects, it may be difficult to predict the consequences for animal movement until a threshold is exceeded. For this reason, critical threshold phenomena have been identified as a 'major unsolved problem facing conservationists' (Pulliam & Dunn 1997). We might expect that threshold behaviour will be affected by several interacting factors rather than one particular causal agent, and that these interactions might produce complex patterns of species' responses which are seemingly unpredictable. In an effort to make such investigations somewhat more tractable, at least in a statistical sense, this study couples the strong pattern recognition ability of artificial neural networks with recent methodological advances for exploring their explanatory capabilities.

The present paper illustrated that the movement behaviour of two benthic herbivores, *A. boulderensis* and *Physa* sp., varied nonlinearly according to the abundance of habitat patches, current velocity and the interaction of the two. *Agapetus boulderensis*, an insect with limited mobility and flow-constrained perceptual range (Olden *et al.* 2004b), showed increasing net displacement and movement rates with habitat

abundance in low current velocity. In high current velocity, however, *Agapetus* movement was unaffected by changes in habitat abundance. These results are corroborated by instream observational studies showing that *Agapetus* larvae exhibit lower rates of movement on smooth substrate surfaces under high current velocities (Poff & Ward 1992; Becker 2001). This observation supports the hypothesis that the magnitude of current velocity and associated shearing force that a larva experiences as it moves across the streambed (Waringer 1993) is a critical factor shaping movement behaviour (Olden *et al.* 2004b). Patterns of near-bed shear stress on natural streambeds can be highly variable, in response to an irregular bed topography that interrupts flow moving through the stream channel and creates areas of decelerating and accelerating local velocity (Davis & Barmuta 1989). Fine-scale structural elements, such as *Pagastia* retreats or physical irregularities in stone surfaces can interrupt the local flow field and create patches of slow near-bed current velocity, thereby shielding organisms from the highly erosive force of high current velocities (Lancaster 1999). As a result, while increasing proportions of diatom habitat may promote greater movement in low current velocities, it is likely associated with reduced flow refugia in high current velocities, effectively decreasing the amount of habitat that is considered 'suitable' (i.e. lower risk to erosion and downstream drift) for *Agapetus* movement. Functional connectivity, therefore, is observed to decrease with increasing habitat; a result that is seemingly counterintuitive. The question of 'how much habitat is enough?' (Fahrig 2001), in the case of *Agapetus* (and likely other benthic insects; Lancaster 1999) in high velocities, is perhaps better posed as 'how much habitat is too much?'

The movement rate of the freshwater snail *Physa* sp., a more mobile herbivore with a broader perceptual range (Kawata & Agawa 1999), also responded positively to habitat abundance, but unlike *Agapetus* was generally insensitive to changes in current velocity. This finding is supported by the observation of Poff & Nelson-Baker (1997) that snail movement is relatively independent of current velocity (but see Hutchinson 1947). Interestingly, *Physa* exhibited greater movement rates in high velocity when the landscape was completely composed of diatom habitat, suggesting that high current velocities may elicit an escape response.

Animal orientation is constrained by strong external physical gradients (Fraenkel & Gunn 1940). Directional stimuli associated with particular physical gradients, such as flow, wind or sunlight, play an important, but commonly overlooked, role in shaping an animal's perceptual range and influencing their movement behaviour (Olden *et al.* 2004a). Schooley & Wiens (2003) found that cactus bugs (*Chelinidea vittiger*) were more likely to orient and move towards cactus patches located upwind compared with those located crosswind or downwind. This study showed that physical habitat and current velocity interact to influence the movement directionality of *Agapetus* and *Physa* with respect to the direction of flow, a rheotaxis phenomenon supported by Poff & Ward (1992) and Poff & Nelson-Baker (1997). Increasing current velocity and abundance of low-profile diatom habitat

Figure 5. *Agapetus* response curves according to the sensitivity analysis for (a) net displacement, (b) movement rate, (c) mean vector length (0.0 represents random dispersion of turning angles between successive steps and 1.0 represents a perfectly straight line), and (d) upstream homing (1.0 represents precisely upstream direction of movement and -1.0 represents precisely downstream direction of movement).

lead to a punctuated and nonlinear increase in upstream homing, a finding supported by a biomechanical response to the fluid dynamics of water. For example, Waringer (1993) examined the resistance of six cylindrical-case caddis larvae to different current velocities and found that for dead larvae in their cases the critical entrainment velocity (i.e. flow to be dislodged) ranged from 3.0 to 70.5 cm s^{-1} in the frontal position and only 2.2 to 20.8 cm s^{-1} in the lateral position. This suggests that *Agapetus* can reduce their erosion probability by orientating themselves with the direction of flow. Similarly, Huryn & Denny (1997) showed that upstream movements by snails are a function of torque on the snail's foot generated by hydrodynamic drag on the shell. By positioning their shell in the upstream direction, snails were able to reduce torque and stabilize their orientation to the force of water.

The manner in which high-profile structural elements of the benthiscape (in this case, *Pagastia* retreats) interacted with current velocity to influence the 'suitability' of habitat patches to animal movement support the general notion that the interpatch matrix (i.e. the landscape located between patches) should not be viewed as 'ecological neutral' (Wiens *et al.* 1993).

In other words, the characteristics of the landscape matrix do appear to influence grazer movement by changing the suitability of habitat patches by interacting with larger, overarching stimuli such as the physical current of water. The strong interplay between the highly patchy nature of benthiscapes (Downes *et al.* 1993) and irregular near-bed current velocities (Hart & Finelli 1999; Lancaster 1999) illustrate the complex nature of both structural connectivity (i.e. the actual connection of habitat patches by corridors) and functional connectivity (i.e. the connection of habitat patches by dispersal) of stream benthiscapes. More generally, given that dispersing individuals may be polarized in certain directions within a landscape (Olden *et al.* 2004a), functional connectivity will not be equal in all the directions of movement. Such landscape anisotropy with respect to movement is an exciting research front in landscape ecology (Bélisle 2005). I argue that stream benthiscapes may represent an ideal model system for exploring this question and others regarding the temporal, spatial and biological sources of variability in the structural and functional connectivity of natural landscapes.

Do *Agapetus* and *Physa* show critical threshold responses to habitat abundance? This study suggests

Figure 6. *Physa* response curves according to the sensitivity analysis for (a) net displacement, (b) movement rate, (c) mean vector length (0.0 represents random dispersion of turning angles between successive steps and 1.0 represents a perfectly straight line), and (d) upstream homing (1.0 represents precisely upstream direction of movement and -1.0 represents precisely downstream direction of movement).

that critical thresholds do occur with respect to the rate, sinuosity and directionality of movement, and differed between species. Furthermore, a striking pattern was that the location and slope of these thresholds varied in response to current velocity. Critical thresholds to the net displacement and movement rate of *Agapetus* were observed in low current velocities, but were non-existent in high current velocity. In light of the above discussion, this result highlights the role that near-bed current velocity plays in shaping functional connectivity to *Agapetus* movement. Punctuated inclines in movement rates occurred at a lower habitat abundance for *Physa* compared with *Agapetus*, a result explained by the greater mobility of *Physa* and that the dichotomy of suitable habitat versus the inhospitable matrix is likely better applied to *Agapetus* than to *Physa*. In contrast, *Agapetus* and *Physa* were observed to exhibit similar threshold responses in their degree of upstream homing in response to habitat abundance. For both species, sudden increases in upstream homing in high current velocity occurred at lower levels of habitat abundance compared with slow current velocity. Taken together, these results illustrate that critical thresholds to animal movement are likely to depend on both intrinsic attributes of the species and extrinsic characteristics of the environment.

Results from this study support the general notion that species which vary in mobility and dispersal ability will vary in their response to fragmentation and will have different perceptions as to whether the landscape is fragmented (Doak *et al.* 1992; With & Crist 1995; Pearson *et al.* 1996). Therefore, a critical threshold of functional connectivity is not an inherent property of the landscape, but in fact emerges from the interplay of species' interactions with landscape structure (With & Crist 1995). As a result, a single critical threshold is not sufficient to describe the response of all species in a community to changes in landscape structure. This has important implications for the usefulness of the critical threshold concept in biological conservation (Huggett 2005) and more generally, resource management (Groffman *et al.* 2006). While this seems to necessitate a species-specific definition of critical thresholds to habitat fragmentation (With 1994), future studies should consider the possibility of grouping species with similar perceptual ranges and vagilities of movement to facilitate a community-level quantification of landscape connectivity.

5. CONCLUSION

Detecting the occurrence of critical threshold effects in ecological phenomena is a challenge because ecological

dynamics commonly occur over time- and spatial-scales that well exceed the extent of observation (Fukami & Wardle 2005). The study of critical thresholds to animal movement necessitates the application of quantitative approaches that can model the nonlinear complexities inherent to ecological series, while at the same time shedding insight into the interacting factors responsible for such thresholds. Statistical tools for identifying thresholds, however, are still generally lacking in this regard (Friedel 1991; Toms & Lesperance 2003), although artificial neural networks may provide a powerful approach. Future progress in this area will depend on the development of new research programmes and analytical methodologies aimed at detecting ecological thresholds in nature.

This research would not have been possible without the intellectual contributions of Jeremy Monroe, Aaron Hoffman and LeRoy Poff. I am especially indebted to Jeremy Monroe for first introducing me to life on the streambed through the eyes of an insect. I thank Pieter Johnson and two anonymous reviewers for providing valuable comments on the manuscript, and Tiffany for her invaluable help in the field. I express my sincere thanks to The Nature Conservancy and the Cedar Tree Foundation for support through a David H. Smith Conservation Postdoctoral Fellowship.

REFERENCES

- Andrén, H. 1994 Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–366.
- Batschelet, E. 1981 *Circular statistics in ecology*. New York, NY: Academic Press.
- Becker, G. 2001 Larval size, case construction and crawling velocity at different substratum roughness in three scraping caddis larvae. *Arch. Hydrobiol.* **151**, 317–334.
- Bélisle, M. 2005 Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* **86**, 1988–1995.
- Bishop, C. M. 1995 *Neural networks for pattern recognition*. Oxford, UK: Clarendon Press.
- Carpenter, S. R. 2002 Ecological futures: building an ecology for the long now. *Ecology* **83**, 2069–2083.
- Davis, J. A. & Barmuta, L. A. 1989 An ecologically useful classification of mean and near-bed flows in streams and rivers. *Freshw. Biol.* **21**, 271–282. (doi:10.1111/j.1365-2427.1989.tb01365.x)
- Dillon Jr, R. T. 2000 *The ecology of freshwater molluscs*. Cambridge, UK: Cambridge University Press.
- Doak, D. F., Marino, P. C. & Kareiva, P. M. 1992 Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theor. Popul. Biol.* **41**, 315–336. (doi:10.1016/0040-5809(92)90032-O)
- Downes, B. J., Lake, P. S. & Schreiber, E. S. G. 1993 Spatial variation in the distribution of stream invertebrates: implications of patchiness for models of community organization. *Freshw. Biol.* **30**, 119–132. (doi:10.1111/j.1365-2427.1993.tb00793.x)
- Environmental Systems Research Institute 2000 *ArcView v. 3.2a*. Redlands, CA: ESRI.
- Fahrig, L. 2001 How much habitat is enough? *Biol. Conserv.* **100**, 65–74. (doi:10.1016/S0006-3207(00)00208-1)
- Fraenkel, G. S. & Gunn, D. L. 1940 *The orientation of animals: kineses, taxes and compass reactions*. London, UK: Oxford University Press.
- Friedel, M. H. 1991 Range condition assessment and the concept of thresholds: a viewpoint. *J. Range Manage.* **44**, 422–426.
- Fukami, T. & Wardle, D. A. 2005 Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Phil. Trans. R. Soc. B* **272**, 2105–2115.
- Gardner, R. H., Milne, B. T., Turner, M. G. & O'Neill, R. V. 1987 Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecol.* **10**, 19–28. (doi:10.1007/BF02275262)
- Gevrey, M., Dimopoulos, I. & Lek, S. 2003 Review and comparison of methods to study the contribution of variables in artificial neural network model. *Ecol. Model.* **160**, 249–264. (doi:10.1016/S0304-3800(02)00257-0)
- Gompertz, B. 1825 On the nature of the function expressive of the law of human mortality and on a new mode of determining life contingencies. *Phil. Trans. R. Soc. B* **1825**, 513–585.
- Groffman, P. M. *et al.* 2006 Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems* **9**, 1–13.
- Hart, D. D. & Resh, V. H. 1980 Movement patterns and foraging ecology of a stream caddisfly larva. *Can. J. Zool.* **58**, 1174–1185.
- Hart, D. D. & Finelli, C. M. 1999 Physical-biological coupling in streams: the pervasive effect of flow on benthic organisms. *Annu. Rev. Ecol. Syst.* **30**, 363–395. (doi:10.1146/annurev.ecolsys.30.1.363)
- Hart, D. D., Clark, B. D. & Jasentuliyana, A. 1996 Fine-scale field measurement of benthic flow environments inhabited by stream invertebrates. *Limnol. Oceanogr.* **41**, 297–308.
- Hestenes, M. R. & Stiefel, E. 1952 Methods of conjugate gradients for solving linear systems. *J. Res. Natl Bur. Stand.* **48**, 409–436.
- Huggett, A. J. 2005 The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biol. Conserv.* **124**, 301–310. (doi:10.1016/j.biocon.2005.01.037)
- Huryn, A. D. & Denny, M. W. 1997 A biomechanical hypothesis explaining upstream movements in the freshwater snail *Elimia*. *Funct. Ecol.* **11**, 472–483. (doi:10.1046/j.1365-2435.1997.00116.x)
- Hutchinson, L. 1947 Analysis of the activity of the freshwater snail *Viviparus malleatus* (Reeve). *Ecology* **28**, 335–345. (doi:10.2307/1931226)
- Kareiva, P. & Wennergren, U. 1995 Connecting landscape patterns to ecosystems and population processes. *Nature* **373**, 299–302. (doi:10.1038/373299a0)
- Kawata, M. & Agawa, H. 1999 Perceptual scales of spatial heterogeneity of periphyton for freshwater snails. *Ecol. Lett.* **2**, 210–214. (doi:10.1046/j.1461-0248.1999.00071.x)
- Keitt, T. H., Urban, D. L., & Milne, B. T. 1997 Detecting critical scales in fragmented landscapes. *Conserv. Ecol.* **1**, 4. See <http://www.consecol.org/vol1/iss1/art4>.
- Lancaster, J. 1999 Small-scale movements of lotic macroinvertebrates with variations in flow. *Freshw. Biol.* **41**, 605–619. (doi:10.1046/j.1365-2427.1999.00410.x)
- Lande, R. 1987 Extinction thresholds in demographic models of territorial populations. *Am. Nat.* **130**, 624–635. (doi:10.1086/284734)
- Lek, S., Delacoste, M., Baran, P., Dimopoulos, I., Lauga, J. & Aulagnier, S. 1996 Application of neural networks to modelling nonlinear relationships in ecology. *Ecol. Model.* **90**, 39–52. (doi:10.1016/0304-3800(95)00142-5)
- Loxdale, H. D. & Lushai, G. 1999 Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Phil. Trans. R. Soc. B* **354**, 1479–1495. (doi:10.1098/rstb.1999.0492)
- Mackay, R. J. 1992 Colonization by lotic macroinvertebrates: a review of processes and patterns. *Can. J. Fish. Aquat. Sci.* **49**, 617–628.

- Malmqvist, B. 2002 Aquatic invertebrates in riverine landscapes. *Freshw. Biol.* **47**, 679–694. (doi:10.1046/j.1365-2427.2002.00895.x)
- McCulloch, W. S. & Pitts, W. 1943 A logical calculus of the ideas imminent in nervous activity. *Bull. Math. Biophys.* **5**, 15–133. (doi:10.1007/BF02478259)
- McIntyre, N. E. & Wiens, J. A. 1999 Interactions between habitat abundance and configuration: experimental validation of some predictions from percolation theory. *Oikos* **86**, 129–137.
- Monroe, J. B., Poff, N. L., & Thorpe, R. A. 2005 Natural history of a retreat-building midge, *Pagastia partica*, in a regulated reach of the Upper Colorado River. *West. N. Am. Nat.* **65**, 451–461.
- Muradian, R. 2001 Ecological thresholds: a survey. *Ecol. Econ.* **38**, 7–24. (doi:10.1016/S0921-8009(01)00146-X)
- 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. (doi:10.1016/S0304-3800(02)00064-9)
- Olden, J. D., Schooley, R. L., Monroe, J. B. & Poff, N. L. 2004a Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *J. Anim. Ecol.* **73**, 1190–1194. (doi:10.1111/j.0021-8790.2004.00889.x)
- Olden, J. D., Hoffman, A. L., Monroe, J. B. & Poff, N. L. 2004b Movement behaviour and dynamics of an aquatic insect in a stream benthic landscape. *Can. J. Zool.* **82**, 35–1146. (doi:10.1139/z04-094)
- Olden, J. D., Joy, M. K. & Death, R. G. 2004c An accurate comparison of methods for quantifying variable importance in artificial neural networks using simulated data. *Ecol. Model.* **78**, 389–397. (doi:10.1016/j.ecolmodel.2004.03.013)
- Otto, C. & Johansson, A. 1995 Why do some caddis larvae in running waters construct heavy, bulky cases? *Anim. Behav.* **49**, 473–478. (doi:10.1006/anbe.1995.0061)
- Özesmi, S. L. & Özesmi, U. 1999 An artificial neural network approach to spatial habitat modelling with interspecific interaction. *Ecol. Model.* **166**, 15–31. (doi:10.1016/S0304-3800(98)00149-5)
- Palmer, M. A., Allan, J. D. & Butman, C. A. 1996 Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends Ecol. Evol.* **11**, 322–326. (doi:10.1016/0169-5347(96)10038-0)
- Palmer, M. A., Swan, C. M., Nelson, K., Silver, P. & Alvestad, R. 2000 Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landscape Ecol.* **15**, 563–576. (doi:10.1023/A:1008194130695)
- Pearson, S. M., Turner, M. G., Gardner, R. H. & O'Neill, R. V. 1996 An organism-based perspective of habitat fragmentation. In *Biodiversity in managed landscapes: theory and practice* (ed. R. C. Szaro), pp. 77–95. New York, NY: Oxford University Press.
- Poff, N. L. & Ward, J. V. 1992 Heterogeneous currents and algal resources mediate *in situ* foraging activity of a mobile stream grazer. *Oikos* **65**, 465–478. (doi:10.2307/3545564)
- Poff, N. L. & Nelson-Baker, K. 1997 Habitat heterogeneity and algal-grazer interactions in streams: explorations with a spatially explicit model. *J. N. Am. Benthol. Soc.* **16**, 263–276. (doi:10.2307/1468256)
- Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., Welcomme, R. L. & Winterbourn, M. J. 1988 Patch dynamics in lotic systems: the stream as a mosaic. *J. N. Am. Benthol. Soc.* **7**, 503–524. (doi:10.2307/1467303)
- Pulliam, H. R. & Dunning, J. B. 1997 Demographic processes: population dynamics on heterogeneous landscape. In *Principles of conservation biology* (eds G. K. Meffe & C. R. Carroll), pp. 203–232. Sunderland, MA: Sinauer Associates.
- Resilience Alliance and Santa Fe Institute 2004 Thresholds and alternate states in ecological and social-ecological systems. Resilience Alliance. See <http://www.resalliance.org/index.php?id=183>.
- Roe, E. & van Eeten, M. 2001 Threshold-based resource management: a framework for comprehensive ecosystem management. *Environ. Manage.* **27**, 195–214. (doi:10.1007/s002670010143)
- Rumelhart, D. E., Hinton, G. E. & Williams, R. J. 1986 Learning representations by back-propagation errors. *Nature* **323**, 533–536. (doi:10.1038/323533a0)
- Schooley, R. L. & Wiens, J. A. 2003 Finding habitat patches and directional connectivity. *Oikos* **102**, 559–570. (doi:10.1034/j.1600-0706.2003.12490.x)
- Statzner, B., Gore, J. A. & Resh, V. H. 1988 Hydraulic stream ecology: observed patterns and potential applications. *J. N. Am. Benthol. Soc.* **7**, 307–360. (doi:10.2307/1467296)
- Taylor, P. D., Fahrig, L. & Merriam, G. 1993 Connectivity is a vital element of landscape structure. *Oikos* **68**, 571–573. (doi:10.2307/3544927)
- Toms, J. D. & Lesperance, M. L. 2003 Piecewise regression: a tool for identifying ecological thresholds. *Ecology* **84**, 2034–2041.
- Turchin, P., Odendaal, F. J. & Rausher, M. D. 1991 Quantifying insect movement in the field. *Environ. Entomol.* **20**, 955–963.
- Turner, M. G. 2005 Landscape ecology in North America: past, present and future. *Ecology* **86**, 1967–1974.
- Waringer, J. A. 1993 The drag coefficient of cased caddis larvae from running waters—experimental determination and ecological applications. *Freshw. Biol.* **29**, 419–427. (doi:10.1111/j.1365-2427.1993.tb00776.x)
- Wellnitz, T. A., Poff, N. L., Cosyleon, G. & Steury, B. 2001 Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. *Landscape Ecol.* **16**, 111–120. (doi:10.1023/A:1011114414898)
- Wiens, J. A., Schooley, R. L. & Weeks Jr, R. D. 1997 Patchy landscapes and animal movements: do beetles percolate? *Oikos* **78**, 257–264. (doi:10.2307/3546292)
- Wiens, J. A., Stenseth, N. C., Van Horne, B. & Ims, R. A. 1993 Ecological mechanisms and landscape ecology. *Oikos* **66**, 369–380. (doi:10.2307/3544931)
- Wiggins, G. B. 1996 *Larvae of the North American caddisfly genera (Trichoptera)*. Toronto, Canada: University of Toronto Press.
- With, K. A. 1994 Using fractal analysis to identify how species perceive landscape structure. *Landscape Ecol.* **9**, 25–36. (doi:10.1007/BF00135076)
- With, K. A. & Crist, T. O. 1995 Critical thresholds in species' responses to landscape structure. *Ecology* **76**, 2446–2459. (doi:10.2307/2265819)
- With, K. A., Gardner, R. H. & Turner, M. G. 1997 Landscape connectivity and population distributions in heterogeneous environments. *Oikos* **78**, 151–169. (doi:10.2307/3545811)
- With, K. A. & King, A. W. 1997 The use and misuse of neutral landscape models in ecology. *Oikos* **79**, 219–239. (doi:10.2307/3546007)