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PREDICTING THE IMPACTS OF BIOLOGICAL AND PHYSICAL DISTURBANCES: DOES THEORETICAL ECOLOGY HOLD ANY ANSWERS?

Summary: Biological and physical disturbance has had a severe impact on New Zealand's endemic flora and fauna. Along with the lessons of the past, predicting the sensitivity of communities to disturbance in the future may help direct more attention to those communities with a greater need for preservation (i.e., a lower ability to recover from any such disturbances). In theory it is possible to measure the resilience (or local stability) of a community by constructing a matrix to describe that community and then examining its eigenvalues. Local stability characteristics of invertebrate communities in 11 aquatic habitats were examined with respect to differing levels of habitat disturbance. It was predicted that communities in more unstable habitats would be more resilient in order to persist despite more frequent disturbances. All communities had eigenvalues outside the stability criteria, although those in the unstable habitats did have eigenvalues closer to these criteria. The open and/or patchy nature of stream communities may explain why local stability is not a prerequisite for these communities, however examining the local stability of community matrices still remains a potentially useful tool for predicting the effects of physical and biological disturbances.

Keywords: community resilience; conservation; disturbance; local stability; resource management; stream invertebrate communities.

Introduction

Biological disturbance from introduced predators, competitors and disease has had a severe impact on much of New Zealand's endemic biota, while physical disturbances such as habitat destruction and fragmentation have had similar, if not greater detrimental effect on the same organisms (Lockley and Cusa, 1980; this symposium). Although we have learnt much from past mistakes, our native flora and fauna continues to be exposed to a wide range of disturbances. New species are continually being considered for introduction to New Zealand under the guise of agricultural diversification and as biological control agents, and although strict guidelines regarding their importation are adhered to, there always remains the opportunity for accidents and miscalculations (Howarth, 1991). Furthermore, although much of New Zealand's pristine habitat is preserved in the conservation estate, many of these protected environments still experience varying levels of disturbance above natural levels, such as the spread of exotic plants and animals, and increasing levels of tourism.

Biological and physical disturbances are a natural feature of many environments (Power *et al.*, 1988) and have received considerable attention from ecologists interested in understanding how such forces structure natural communities (Pickett and White, 1985). Theoretical ecologists in particular have given this topic extensive coverage, both from the perspective of understanding current community patterns, and for predicting the effects of such things as species introductions and exploitation (e.g., May, 1981; Pimm, 1991).

Many of the mathematical studies of ecological systems (e.g., May, 1972, 1973; DeAngelis, 1975) have been based on the analysis of local stability, defined as the tendency of a system to return to its original state following a small disturbance. Local stability can be assessed by examining the eigenvalues of the matrix (in ecological applications the matrix is known as the community matrix). An eigenvalue is a property of all square matrices (i.e., the number of columns = the number of rows) such that $A\underline{x} = \lambda\underline{x}$, where A is an n x n matrix, λ is an eigenvalue and $\underline{x}$ is its corresponding eigenvector. Thus, if a matrix A can be factorised into two matrices (i.e., A = B x C) so that one contains all zeros except on the diagonal, the diagonal entries are the eigenvalues and the columns of the other matrix are their corresponding eigenvectors. If the eigenvalues fall within certain constraints (these depend on the underlying structure of the matrix), the matrix will be stable (i.e., return to its original state following a small disturbance), otherwise the system will be unstable and move to another point in mathematical hyperspace following any small disturbance. The situation may however, change if global (i.e., stability in the face of large disturbances) rather than local stability is considered.

Assessing the local stability of a matrix describing a community can be useful for evaluating

different permutations of model communities, however, it will also give a measure of the stability of real communities. That is, it will give a measure of whether or not a community should recover from a disturbance, and if so how quickly it should recover (the return time). Although assessing the susceptibility of different communities to disturbance would seem to be a logical priority for conservation planning, achieving this in practise poses major difficulties. To examine whether habitats differ with respect to their ability to cope with a disturbance, one could disturb the habitats and see which ones recovered more quickly. However, recovery from a disturbance may take centuries, (beyond the time frame of individual ecologists!) if at all, and in the process negate any need to preserve the habitat in the first place. Theoretically, it should be possible to evaluate the sensitivity of different communities to both physical and biotic disturbances (the model does not differentiate between types of disturbance) simply by describing community structure and examining this within the context of local stability.

In this paper I examine the local stability of community matrices calculated for invertebrate communities of 10 streams and a lake shore in the Southern Alps of New Zealand. The streams and lake shore have similar physicochemical characteristics but differ with respect to their thermal and hydrologic stability (Death and Winterbourn, 1994). Communities in unstable streams are predicted to have eigenvalues indicative of high

resilience (i.e., rapid ability to recover from disturbance) as they experience disturbances on a regular basis and should be structured in a way to cope with this effect. The communities at stable sites, in contrast, are expected to exhibit lower resilience; as they rarely experience disturbances and therefore are predicted to have communities that are not structured with respect to recovery from disturbance. As a result the largest eigenvalues for communities at the frequently disturbed sites are predicted to be more negative (if the system is modelled by differential equations) or smaller in absolute size (if the system is modelled by difference equations) than those at the stable sites.

Study sites

The study sites were all on small tributaries of the Waimakariri River, on the eastern side of the Southern Alps in the South Island of New Zealand. They occupy 3 valleys within 18 km of each other, experience similar climatic conditions and range in altitude from 580 m to 790 m a.s.l. (Death, 1991). Half the streams arose from either a spring or lake and were relatively stable (both in temperature and discharge), whereas streams with more diffuse origins had more variable flow and temperature regimes and were considered unstable. The stony, wave-washed southwestern end of Lake Grasmere was also included in the study because it was a stable environment that superficially resembled a

Table 1: *Physical and chemical characteristics of the study sites. Sites are listed in order from least stable to most stable as measured by their multivariate instability scores. Craigieburn Cutting Stream and Middle Bush Stream have forest canopies, all other streams are open. All streams had nitrate-nitrogen (NO_3-N) and reactive phosphorus (PO_4-P) concentrations below 0.05 mg l^{-1} and 0.004 mg l^{-1}, respectively.*

SITES	Order	Width (m)	Slope	Mean depth (cm)	Mean current velocity (cm s^{-1})	Mean temperature (°C)	Mean particle size (cm)	Mean pH	Mean Alkalinity (mg CaCO$_3$ l^{-1})
UNSTABLE									
Bruce Stream	3	6.3	0.03	34	94	8.8	7.4	7.4	26.1
Kowai River	2	5.3	0.03	29	103	13.0	7.4	7.7	17.8
Dry Stream	2	1.9	0.05	9	44	10.0	5.4	7.6	18.4
Whitewater Stream	3	5.8	0.03	16	75	10.4	7.8	7.5	17.6
Craigieburn Cutting Stream	1	1.1	0.07	8	40	8.9	8.1	7.3	17.7
STABLE									
Grasmere Stream	1	3.4	0.01	29	85	11.7	4.7	7.4	33.2
Middle Bush Stream	2	0.9	0.14	5	36	8.0	6.4	7.8	35.0
Porter River	2	4.9	0.03	21	90	9.0	6.6	7.5	20.3
Lake Grasmere	NA	NA	NA	29	NA	13.0	5.7	8.0	32.2
Cora Lynn Stream	1	1.3	0.07	11	37	8.6	7.2	7.6	41.6
Slip Spring	1	2.5	0.09	9	46	8.1	8.5	7.2	22.2

stream. Its fauna is similar to that of streams in the region (Stout, 1977). Craigieburn Cutting Stream and Middle Bush Stream had forest canopies; all other streams and the lake shore were open.

Mean values for physical and chemical measures made at the study sites between October 1987 and May 1989 are given in Table 1. The streams were small to moderate in size, with all study sites having similar substrate size distributions, moderately hard water (17.6-41.6 mg $CaCO_3$), circumneutral pH (7.2-8.0) and low nutrient concentrations (NO_3-N < 0.05 mg l^{-1}, reactive PO_4-P < 0.004 mg l^{-1}). Mean annual depth and current velocity, both measured at midstream, ranged from 5-34 cm and 36-103 cm s^{-1}, respectively. Overall, physical ($F_{8,1}$=23.44, P=0.16, MANOVA) and chemical characteristics ($F_{3,7}$=2.8, P=0.12, MANOVA) did not differ between the "stable" and "unstable" site groups, with both small and moderate sized streams included in each group.

Materials and methods

Measurement of habitat stability

As none of the study sites has a monitored discharge, and as no single measure can give an accurate assessment of overall environmental stability (Death and Winterbourn, 1994) six variables were monitored to evaluate habitat stability. These variables covered a range of hydrological and thermal characteristics which have been shown to affect the distribution and abundance of stream invertebrates (e.g., Vannote and Sweeney, 1980; Winterbourn and Collier, 1987). The measured variables included the Pfankuch (1975) stability index, an index of stream channel stability at the reach scale. Following Winterbourn and Collier (1987) and Death and Winterbourn (1994) I only used one component of the index which assesses stability of the substrate component of the complete index, and was considered most relevant to the scale of stream invertebrate dynamics.

Measurements of temperature range, and the movement of 5 marked stones in each of 3 size categories (corresponding to the size of stone collected for invertebrate samples) were also made monthly at each site. Temporal variation in depth and current speed were calculated by taking the absolute difference between the value recorded in one month and that for the preceding month. Finally, stream reach tractive force was calculated as detailed by Newbury (1984). This relates channel slope and depth to substrate size distribution and predicts the proportion of substrate particles likely to be moving

in uniform flow conditions within the entire stream reach. It was used to calculate the percentage of substrate predicted to be moving at any given time at the study sites. Methods for the assessment of habitat stability are detailed more fully in Death and Winterbourn (1994).

Substrate movement as predicted by tractive force was the only stability measure that did not differ significantly between the "stable" and "unstable" sites. To evaluate overall stability, based on all 6 variables, the measures were combined into a single, multivariate index of instability using principal components analysis (PCA) (Death and Winterbourn, 1994). Site scores on PCA axis 1 for this analysis accounted for 64% of the variation in the measures and had factor loadings which were approximately equal for all the stability variables except predicted substrate movement. The PCA scores for axis 1 were scaled to give an index where an increase in the multivariate instability score was indicative of decreasing stability. Mean values for each stability measure and the multivariate instability scores are given in Table 2 along with correlations between the instability scores and the other stability measures.

Biological sampling protocol

Collections of invertebrates were made from riffles at the study sites on two or three consecutive days in October 1987 (Spring 1), January 1988 (Summer), April 1988 (Autumn), July 1988 (Winter), and October 1988 (Spring 2). Fifteen stones were sampled at each site, five stones being selected at random from each of three size classes (maximum linear, planar dimension 91-180 mm, 60-90 mm, and < 60 mm). Stones were sampled as the collector moved progressively upstream. A 250 µm mesh net was held behind each stone, which was lifted rapidly into it. Adjacent stones were disturbed as little as possible but any fine sediment or detritus immediately below a stone was disturbed and therefore any associated invertebrates were collected. Samples were preserved in 10% formalin. Where possible, invertebrates were identified to species level using available keys. Although some taxa could not be named, they were still differentiated into apparent morphospecies. Details of the invertebrate communities found at these study sites can be found in Death and Winterbourn (1995) and Death (1995).

Community matrix construction

Community matrices are composed of elements that represent the effect of each species on each other

Table 2: *Mean stability values calculated from monthly measurements at each of the study sites between December 1987 and May 1989 and their correlations (r$_s$) with the multivariate instability score. Sites are listed in order from least stable to most stable as measured by their multivariate instability scores.*

	Depth variability (cm)	Current variability (cm s^{-1})	Temperature range (°C)	Bottom component Pfankuch index	Stone movement measure (%)	Predicted substrate movement of tractive force (%)	Multivariate instability score (PCA axis 1)
UNSTABLE SITES							
Bruce Stream	19	46	9.4	50	96.9	70	2.33
Kowai River	9	44	9.8	50	63.8	72	1.85
Dry Stream	6	35	9.8	42	12.0	50	1.24
Whitewater Stream	4	27	9.8	39	17.2	28	1.03
Craigieburn Cutting Stream	3	18	5.8	44	18.6	66	0.95
STABLE SITES							
Grasmere Stream	4	34	6.3	36	3.0	13	0.83
Middle Bush Stream	3	11	5.7	42	1.4	68	0.76
Porter River	3	29	2.2	31	0.7	68	0.59
Lake Grasmere	7	NA	8.4	30	0.0	NA	0.52
Cora Lynn Stream	4	13	2.5	31	6.3	76	0.51
Slip Spring	2	18	0.5	31	0.0	63	0.39
Correlations with multivariate instability score	0.85	0.73	0.87	0.89	0.89	0.01	

species (and the impact of their own population) in the community. Entries may be zero (no effect), negative (e.g., competitive) or positive (e.g., mutualistic). Often the matrices are constructed on the basis of competitive interactions and consequently their elements are frequently termed competition coefficients. Most studies of this type (e.g., Levins, 1968; MacArthur, 1968; Levins Pressick and Heatwole, 1973; Culver, 1974; Bruns and Minshall, 1983) have evaluated such competition coefficients by examining resource overlap. The link between resource overlap and competitive interaction is rather tenuous however, and although several techniques for relating the two have emerged (e.g., MacArthur and Levins, 1967; Schoener, 1974; Crowell and Pimm, 1976), there does not appear to be any "perfect" substitute for examining population interactions experimentally (Rosenzweig *et al*., 1985). While it may be possible to determine interaction terms experimentally for small communities, and has been accomplished successfully for both water-filled *Heliconia* bract-insect communities (Seifert and Seifert, 1976) and simple planktonic communities (Levitan, 1987), it rapidly becomes impractical as the community becomes larger. It also becomes increasingly difficult to evaluate secondary effects of other species on those interactions (e.g., species A keeps the population of species B so low that it does not

affect species C which it would otherwise do). Thus, although construction of community matrices using resource overlap data is by no means a perfect solution, it does at least serve as an approximation, albeit a rough one, for examining the question of community stability (Lawlor, 1980; Bruns and Minshall, 1983; Pimm, 1985).

I used the technique outlined by Bruns and Minshall (1983) for calculating the interaction terms for the community matrix. Thus, pairwise Spearman rank correlations for each species in the community were calculated for the fifteen stone samples collected at each of my sites. To avoid possible distortions inherent in this form of analysis, any species represented by only one individual was omitted (rare species are unlikely to have a significant effect on community stability anyway) and any double-zero matches were eliminated (Legendre and Legendre, 1983).

Non-significant correlations were given interaction terms of zero. Negative correlations (except those between predators and prey) were taken to represent competitive interactions. Schluter (1984, Table 4) listed the possible ecological basis of negative and positive associations of species on a resource state (in this case stones), and while it is possible that both negative and positive associations may be a result of competition there seems to be some evidence to suggest that the former is the case

in at least some stream communities (e.g., McAuliffe, 1984a, 1984b; Hart, 1985; Hawkins and Furnish, 1987; Hemphill, 1988; Dudley *et al.*, 1990). Therefore, I took positive associations (except those between predators and prey) to represent weak or nil interactions and ascribed a value of zero to them. Significant associations between predators and prey on the stones were attributed to the effects of one feeding on the other and not to an interaction for spatial resources. Thus, predators were given positive interaction terms and prey negative interaction terms. The sizes of the interaction terms were determined by the size of the correlation coefficients. Diagonal entries in the matrix (i.e., intraspecific interactions) were set to -1 following Pimm (1982).

Eigenvalues for each of the matrices were extracted using PC-Matlab (Moler, Little and Bangert, 1987).

Results

In all but two cases more correlations between species densities were recorded than would be expected by chance (Death, 1991) providing some support for the idea that resource overlap reflects biotic interactions. As most matrices were asymmetrical, some of the eigenvalues associated with them were conjugate eigenvalues (i.e., they had both real and imaginary parts). The imaginary parts of the eigenvalues indicate that the system oscillates (either away from or towards equilibrium) if disturbed (May, 1973; Pimm, 1982).

As mentioned in the introduction, the constraints on the eigenvalues for stability differ depending on the underlying structure of the matrix, that is, whether the population growth models for the constituent species in the community are modelled better by differential or difference equations. Many insect populations, particularly those with distinct generations, are modelled best by difference equations (Hassell, 1979; Pimm, 1982). However, for them to be the most appropriate choice the time lag between generations needs to be relatively long (e.g., a year), so that the density of species in one year will depend on its interaction with other species in the previous year and not more recently. It is unlikely that the time lag between successive generations of most New Zealand stream invertebrates is very long, as many exhibit poorly synchronised life histories and multiple generations (although the nature of life history patterns in New Zealand aquatic invertebrates is in general poorly understood) (Winterbourn, 1987). Most populations are probably modelled best by equations that lie

somewhere between difference and differential equations (Pimm, 1982), and the population dynamics of most New Zealand benthic invertebrates would seem to fall in line with this. Consequently, I considered stability criteria for both difference and differential equation based matrices, but as it turned out this made little difference to the interpretation.

For a differential based system the criterion for stability is that all eigenvalues have negative real parts, and for difference equation based systems the square of both the real and imaginary parts of all eigenvalues must be less than one (May, 1973). For simplicity I have ignored the imaginary parts of the eigenvalues in presenting the analysis, but this made no difference to the interpretation. The mean maximum and minimum eigenvalues (i.e., the real parts) are plotted in Fig. 1. All but two matrices (these only had intraspecific interaction terms) had eigenvalues outside the stability envelope of either type of equation. However, it is interesting to note that the more unstable sites had eigenvalues closer to the criterion for stability.

Given that only two of the matrices (and these have no interspecific interaction terms) are stable, it can be inferred that if disturbed, even slightly, all the
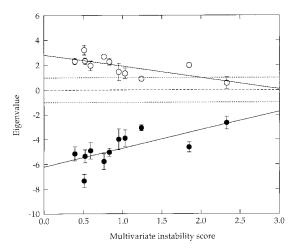

Figure 1: *Mean maximum (○) and minimum (●) eigenvalues (± 1 SE) for community matrices based on samples collected at each of my study sites between October 1987 and October 1988, as a function of overall (multivariate) environmental stability. The area within the dotted lines is the stability criterion for matrices based on difference equations and the area below the dashed line is the stability criterion for a differential equation based system. Low environmental stability is indicated by increasing multivariate instability scores.*

communities would move to a new configuration rather than returning to the status quo. Clearly, this does not happen, and Death and Winterbourn (1994) found the communities to be relatively constant in composition over time. How then does the resilience of the communities compare if eigenvalues outside the stability criterion are ignored? Assessment of this again depends on the type of equations involved. For differential equations the return time is given by -1/(the real part of the largest eigenvalue) (Pimm and
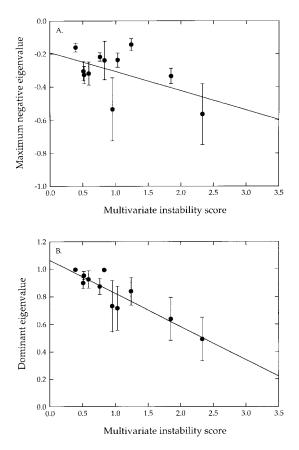
Lawton, 1977). Thus, the more negative the largest eigenvalue, the more rapidly will the matrix return to its predisturbance state. For difference equation systems the smaller the dominant eigenvalue (the largest eigenvalue ignoring the sign) the more resilient the matrix (most advanced algebra texts e.g., Edelstein-Keshet, 1988; Fraleigh and Beauregard, 1989).

The measures of resilience for both equation types are plotted in Fig. 2. For both equation systems the matrices in the more unstable streams had greater resilience. The maximum eigenvalue (ignoring all positive eigenvalues) decreased as the multivariate instability index increased ($F_{1,49} = 4.55$, $P = 0.04$, $r^2 = 0.11$), and the dominant eigenvalue (ignoring those greater than or equal to one) decreased as environmental stability increased ($F_{1,49} = 23.65$, $P < 0.001$, $r^2 = 0.43$).

Discussion

The fact that the majority of the community matrices were outside the limits for local stability is somewhat perplexing because it implies that the slightest disturbance should plummet all communities to a new state, perhaps extinction! It may be that constructing a community matrix by measuring interactions (the elements of the matrix) using spatial overlap measures is not the most appropriate approach to take. However, Seifert and Seifert (1976) constructed their matrices of *Heliconia* bract communities by manipulative examination of all possible species interactions (the most appropriate technique for constructing community matrices) and found they too were locally unstable.

There seem to be two likely possibilities as to why stream invertebrate communities persist in time despite an inherent instability in their structure. It may be that the very open nature of the communities (i.e., invertebrates are continually colonising and drifting in and out (Allan, 1995)) means that stability at any given point in time is not necessary. The continual turnover of animals may in itself place stability constraints on a system that if isolated would quickly become unstable and consequently go extinct. The assessment of community stability in open systems appears to be an area of theoretical ecology that needs further investigation, given that the generality of inherently stable (closed) communities is debatable (e.g., Seifert and Seifert, 1976). My analysis has also failed to consider the possibility of nonlinear or periodic (limit cycle) solutions and is an aspect of stream ecology which is also in need of more attention.

Figure 2: *Mean maximum eigenvalue (A) (ignoring all positive eigenvalues) and mean dominant eigenvalue (B) (ignoring all those equal to or greater than one) as a function of overall environmental stability. Plotted values are averages of the seasonal means ± 1 SE. Regression analysis was performed including seasonal comparisons to yield the equations: maximum eigenvalue = -0.17 - 0.12*(environmental instability score), r² = 0.11 and dominant eigenvalue = 0.97 - 0.24*(environmental instability score), r² = 0.43.*

Another possibility, that has received considerable attention in the theoretical ecological literature, is the idea that communities are composed of compartments. A number of modelling studies (e.g., May, 1972; Goh, 1979; but see Pimm, 1979) have shown that communities are more stable if they are organised into compartments, within which interactions are strong but between which interactions are weak. The idea that stream habitats are composed of patches is gaining increasing credence (Pringle *et al.*, 1988; Frid and Townsend, 1989; Townsend, 1989) and my own observations of stream habitats support this view (Death and Winterbourn, 1995). It may be that I have considered stability at the wrong scale, and that while individual patches may be unstable, the community as a whole gains stability from the arrangement of patches in space and the movement of individuals between patches.

Finally, assessing the stability of stream communities by considering only invertebrates, may be inappropriate. Several studies have shown significant interactions between invertebrates and higher or lower trophic levels within stream systems (e.g., Allan, 1983; Bott, 1983; Winterbourn, 1990). Perhaps the appropriate stability constraints are only evident when all these components are considered (Death, 1991).

Given that my stream communities are inherently unstable (by local stability criteria anyway), strictly speaking it would not seem valid to compare their resilience characteristics. However, it is interesting to note that the communities in the more unstable streams (those predicted to have the greatest resilience) had eigenvalues closer to the criterion for stability, and that there did in fact seem to be increasing community resilience as the stability of the habitat decreased. This was the predicted result; communities at the unstable sites should exhibit a greater ability to recover from disturbances, because they experience these on a regular basis.

An experimental test of whether communities at unstable sites did recover from a small disturbance more quickly did not suggest this was the case however, and communities at the stable sites appeared to be more resilient (Death, in press). The experiment consisted of disturbing baskets of cobbles (30 x 15 x 10 cm) for a set period of time at differing intervals in the study streams. Critics of small scale experiments to test disturbance effects (e.g., Fisher, 1987; Minshall, 1988; Lake, 1990) would be quick to point out, that patches in the stable sites may have been colonised more quickly simply because of the larger pool of colonists in the surrounding substrate (stable streams, because they are stable have greater abundances of animals)

(Death and Winterbourn, 1995). However, the concept of local stability relates to the ability to recover from small disturbances. Although it is sometimes difficult to relate mathematical definitions to the real world, my experimental disturbances would certainly appear to be small. Furthermore, while major floods may disturb entire streams, most increases in discharge below bankfull (i.e., spates) appear to disturb the substrate patchily, particularly with respect to substrate size (Doeg, Lake and Marchant, 1989 and personal observations). Therefore, given the scale at which most spates affect stream beds, it would seem that substrate patches (as used in the experiment) are appropriate units for studying the effects of spates and concepts of local stability. Finally, if the observed patterns were simply the result of random colonisation from the surrounding substrate, then similar assemblages to those represented in the baskets could be constructed by simulating random removal and colonisation, in a sequential manner that mimicked the field experiment, from the total pool of insects collected in the baskets. This was not the case and differences (relative Euclidean distance) between real assemblages in the experimental treatments were 5-65 times greater than those values obtained between randomly constructed assemblages (Death, 1991).

What are the implications from this study for conservation and resource management? There would seem to be obvious benefits to be gained from an ability to predict the impacts of disturbance on different communities, such that those more susceptible to disturbance can be given more protection. While in theory this seems possible, my study indicates that an appropriate technique for doing so is not quite so obvious. Local stability, as measured by the eigenvalues, did not appear to give an accurate indication of the current state of these stream communities which changed little over the duration of my study, despite numerous disturbances (Death and Winterbourn, 1994), in contrast to the predictions of the eigenvalues. Furthermore, although there was a suggestion that communities in the unstable habitats were better able to recover from disturbances, at the level of a patch this did not seem to be the case for some community characteristics (Death, in press). Although there would appear to be great benefits in using theoretical measures to assess the ability of communities to cope with physical or biological disturbances, the link between such measures and the real world, particularly with respect to scale, remains to be explored.

There needs to be a greater link between theoretical ecology and conservation biology (Ehrlich, 1989; Pimm and Gilpin, 1989).

Conservation biologists need to give more consideration to developing theoretical ideas in model systems, such as streams, which can in turn be applied to the solution or prevention of more pressing problems in the management of our native flora and fauna. Theoretical ecologists, particularly the more mathematical, in turn need to develop their concepts with some consideration of real world problems, such as the appropriate scales for testing local stability effects.

Acknowledgements

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