Extinction:

The Role of Habitat Fragmentation and Environmental Variability

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Abstract

In this thesis I address the roles that habitat fragmentation and environmental variability play in bringing about extinction.

The microcosm philosophy makes no fundamental distinction between the ecological organisation of the faster spatial and temporal dynamics of small ecosystems and those of larger dynamically slower systems. The implication is that natural microcosms may be used as surrogates in the study of long-term events and processes such as extinction. Here I use a bryophyte-based field ecosystem to experimentally study the response of a multi-species community to habitat fragmentation. A more traditional microcosm, consisting of populations of protists and bacteria was used to study the interaction between population dynamics and patterns of environmental variability in the laboratory.

Habitat fragmentation of moss landscapes resulted in considerable local extinction and reduction in population size. Within a given community rare species with small populations were most at risk of extinction. I also provide the first experimental test that the establishment of habitat corridors between fragments can slow local extinction resulting in a higher local and regional diversity.

Small spatially isolated populations are most at risk of extinction in the face of variability in the environment. To predict the lifetime of such small populations, previous theoretical investigations have modelled environmental variability as 'white noise'. Analysis of real environmental variables reveals that this assumption is incorrect, and that such variability is well described as a 'red noise' process. That is, there is considerable temporal autocorrelation. A theoretical analysis indicates that populations are sensitive to the level of autocorrelation in the environment. The predicted lifetime of a single small population in a temporally autocorrelated environment is found to be contingent upon the nature of the density dependence exhibited by that population. Metapopulation persistence is considerably shortened by the inclusion of autocorrelated noise, irrespective of the type of density dependence.

An experiment and simulation model of *Paramecium tetraurelia* is conducted to examine the effects of temporal correlation in environmental variability on real populations. An apparatus designed and built to allow replicated populations to experience complex patterns of environmental variability is described. Results from this study demonstrate that fluctuations in the densities of real populations are sensitive to the colour of environmental noise.

Declaration

The work described in this thesis is entirely my own, except for the following:

Chapter 3 This chapter contains a multi-authored paper:

Gilbert, F. S., Gonzalez, A. & Evans-Freke, I. — submitted to *Proceedings of the Royal Society of London Series B.*

The original idea and the experimental design were mine. The data was collected by IE-F. The analysis was shared. FSG wrote most of the paper.

Chapter 4 This chapter contains work from a collaborative modelling project.

Petchey, O. L., Gonzalez, A. & Wilson, H. B. — accepted for publication in the *Proceedings of the Royal Society of London Series B.*

The paper was conceived jointly. OLP performed all the analyses on the single-patch model. The idea for the spatial model was mine and I performed all the analysis. The paper was written jointly with OLP.

Chapter 5 This chapter contains work resulting from a collaborative project.

Cohen, A. E., Gonzalez, A., Lawton, J. H., Petchey, O. L., Wildman, D. & Cohen, J. E. — accepted for publication in the *Proceedings of the Royal Society of London Series B.*

The idea for the study was mine. The computer software was written by AEC. The design and manufacture were highly collaborative. The paper was written jointly with OLP.

Chapter 6 The data from the empirical study were collected in collaboration with Owen Petchey. All other work is my own.

Signed.....Andrew Gonzalez

Confirmed.....Professor John Lawton

To my Family and Michelle,

for their perpetual love and support...

It forms a little world within itself-a microcosm within which all the elemental forces are at work and the play of life goes on in full, but on so small a scale as to bring it easily within the mental grasp.

Stephen Forbes (1887)

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It is nearly five years ago that my interest in the field of ecology was first stimulated. Before then I had shown very little real enthusiasm for biology and science in general. For that initial spark I so needed I must thank Francis Gilbert. It was his third year course in ecology at Nottingham and my final year project with him, during which I first studied the moss system as a microcosm, that made me think about ecology and want to understand.

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Contents

Page

Abstract.....2

Declaration.....3

Acknowledgements.....6

Table of Contents.....7

List of Figures.....10

List of Plates.....14

List of Tables.....15

Chapter 1. Introduction..... 17

1.1 Habitat Destruction.....18

1.1.1 Habitat fragmentation.....18

1.1.2 Community collapse.....19

1.2 Environmental Variability.....22

1.3 What is this thesis about?.....28

1.4 A microcosm approach.....28

1.4.1 Habitat fragmentation experiments.....28

1.4.2 Environmental variability experiments.....29

1.5 An epistemological consideration: the microcosm philosophy.....30

1.6 Thesis Outline.....33

Chapter 2. Habitat fragmentation: an experimental approach using the moss microcosm.....35

2.1 Introduction.....36

2.2 Methods.....37

2.3 Results.....40

2.3.1 Species richness response.....40

2.3.2 Abundance.....44

2.3.3 Predictors of extinction.....44

2.3.4 Community Response.....48

2.4 Discussion.....49

Page

Chapter 3. A multi-species experimental test of corridor efficacy.....53

3.1 Introduction.....54

3.2 Chapter Outline.....55

3.3 Study design.....56

3.4 Experiment One.....59

3.4.1 Introduction.....59

3.4.2 Methods.....60

3.4.3 Results.....63

3.4.4 Discussion.....66

3.5 Experiment Two.....69

3.5.1 Methods.....69

3.5.2 Results.....69

3.6 General Discussion.....74

Chapter 4. Effects on population persistence: The interaction between environmental noise colour, intra-specific competition and space.....77

4.1 Introduction.....78

4.2 Importance of competition.....79

4.3 Importance of space.....86

4.4 Discussion.....90

4.5 Acknowledegements.....92

Chapter 5. A novel experimental apparatus to study the impact of white noise and 1/f noise on animal populations.....93

5.1 Introduction.....94

5.2 The apparatus.....95

5.3 Synthesis of temperature series.....99

5.4 Preliminary results.....101

5.5 Concluding remarks.....101

5.6 Acknowledgements.....102

Page

Chapter 6. A model and experiment examining the population dynamic response of *Paramecium tetraurelia* to 1/*f* temperature fluctuations.....103

6.1 Introduction.....104

6.2 Experiment and modelling overview.....105

6.3 Study design.....106

6.3.1 Other experimental details.....107

6.3.2 Mathematical model.....111

6.4 Results.....113

6.4.1 Model results and predictions.....113

6.4.2 Experimental results.....119

6.5 Discussion.....128

Chapter 7 Discussion.....132

7.1 Caveats and future work.....134

7.2 The microcosm philosophy.....137

References.....139

List of Figures

Page

Chapter 1:

Figure 1.1 (a) Series (Fahrenheit) of mean daily temperatures at recorded at Silwood Park in 1952. (b) Shows the noise in the temperature series once the seasonal variability, the dominant cycle of one year, has been removed. This was removed by subtracting average temperature at each date (calculated from previous years data) from the corresponding actual temperature (Hastings and Sugihara 1991).....23

Figure 1.2 Temperature series and their respective correlograms. (a) Shows the 'noise' in the original time series once the seasonal variability, the dominant cycle of one year, has been removed. This annual cycle was removed by subtracting average temperature at each date (calculated from previous years' data) from the corresponding actual temperature. (b) shows the same de-trended series re-sequenced randomly to produce a 'white noise' series. (c) and (d) show the correlogram for the corresponding time series (Each correlogram includes a pair of solid horizontal lines representing the limits $\pm 2/\sqrt{n}$, which are used for informal assessment of departure from white noise.....24

Figure 1.3 Shows the 'noise' in the original time series once the seasonal variability, the dominant cycle of one year, has been removed. This annual cycle was removed by subtracting the average temperature at each date (calculated from previous years data) from the corresponding actual temperature. (3b) Shows this de-trended data rearranged randomly to create a 'white noise' series. (3c and 3d) show the power spectral density for above series. This analysis emphasises the difference in the relative influence of high and low frequency fluctuations in the series 25

Chapter 2:

Figure 2.1 The effect of fragmentation on total species richness in (a) small (20 cm^2) and (b) large (200 cm^2) moss islands. Control is shown by the solid black circles and the fragments by the open circles. All data show the mean and 1± S.E.....40

Figure 2.2 (a) The difference in the total number of species (species in controls-species in fragments) found on small control and small fragmented islands.(b) The percentage difference between the total number of species found on control and fragmented islands.....43

Figure 2.3 The effect of fragmentation on total abundance (a) small ($20cm^2$) and (b) large ($200cm^2$) moss islands. Control is shown by the solid black circles and the fragments by the open circles. All data show mean and 1±S.E.....45

Figure 2.4 The binary response (1=extinct 2=not extinct) of the mites found in the small patches after 12 months (a) extinction response against total control patch abundance (b) extinction response against percentage control of patches occupied (c) extinction response against body size (mm).....47

Page

Figure 2.5 Percent incidence (% patches occupied) of mite species across all 8 replicates against total abundance. Abundance and incidence were measured in control (unfragmented) patches Open circles represent those species that went extinct in the fragments. Data shown are for small islands after 12 months.....48

Figure 2.6 The relationship between abundance and body size of the micro-athropods extracted from the control moss islands after 12 months. Body size is in millimetres.....48

Figure 2.7 The ranked total abundance of micro-arthropods extracted from all eight replicates of the control and fragment islands after (a) 2 months and (b) 12 months (species ranked 1,2....n, in (a) are the same species in (b)). The black bars represent abundance of those species extracted from the controls whilst the shaded bars show the abundance of those species extracted from the fragmented islands. Note the community wide decline in abundance in the in the fragmented islands after 12 months.....49

Chapter 3:

Figure 3.1 Schematic representation (not to scale) of the treatment design used in experiment 1: (a) continent, (b) corridor, (c) broken-corridor, (d) insular.....57

Figure 3.2 Schematic representation (not to scale) of the treatment design used in experiment 2.....57

Figure 3.3 Species richness after six months. Treatment factor (1) mainland (2) corridor (3) broken corridor (4) island. The open circles correspond to mean species richness per island (±1S.E.), whilst the closed circles correspond to the mean cumulative richness of the four islands or γ-richness (±1S.E.).....63

Figure 3.4 The decline in the mean proportion of predators per island at six months. Treatment factor: (1) Mainland, (2) Corridor (3) Broken Corridor, (4) Island.....64

Figure 3.5 Mean total arthropod abundance (±1s.e.) in the moss islands after (a) three months (b) six months. Treatment factor: 1: Mainland 2: Corridor 3: Broken 4: Isolate.....70

Figure 3.6 Mean species richness (±1s.e.) in the moss islands after (a) three months (b) six months. Treatment factor: 1: Mainland 2: Corridor 3: Broken 4: Isolate.....72

Chapter 4:

Figure 4.1. Mortality as k-values ($\log(N_t/N_{t+1})$) against log population size for (a) equation (1) and (b) equation (2) showing the effect of altering (a) b and (b) γ on the type of intra-specific competition. A high value of b or γ results in overcompensatory dynamics (or scramble

Page

competition); a low value of b or γ results in undercompensatory dynamics (more similar to contest competition).....81

Figure 4.2 Mean persistence time (of 1000 simulations) as a function of temporal autocorrelation in the environment, α, and the dynamic behaviour of the model, controlled with b, for the non-spatial model ((a) Equation 4-3, and (b) Equation 4-2). The carrying capacity K_t is given by the stochastic process $K_{t+1}=K_0+\phi_{t+1}$; $\phi_t=\alpha\phi_t+\beta\varepsilon_t$, where ε_t is a normally distributed deviate with mean zero and unit variance. The amplitude of the noise, β, is given by $\beta=\sigma(1-\alpha^2)^{1/2}$, hence the variance($K_t$)=$70^2$ for all α. Other parameters are $r=\lambda=1.5$, K_0=100 and $t(max)$=200000.....83

Figure 4.3 Frequency distributions of (a) population size $N_{t(e-1)}$, and (b) $\log_{10}(N_{t(e-1)}/K_{t(e-1)})$ one time step prior to extinction, $t(e-1)$, for Equation 4-3. Four distributions are shown, for each combination of low (0.0) and high (0.95) α with undercompensatory (b=0.1) and overcompensatory (b=1.0) dynamics. All other model details are as in Figure 4-2.....85

Figure 4.4 Mean persistence time (of 100 simulations) as a function of temporal autocorrelation in the environment α and the degree of environmental heterogeneity, σ, among the 100 patches. K_t is the mean patch carrying capacity at time t and is given by the same stochastic process as in the non-spatial model. σ is the standard deviation of patch carrying capacities at any one time. $t(max)$=100000, individuals dispersal probability = 0.05.....88

Figure 4.5 Time series of metapopulation size and patch carrying capacity K_t for the spatial model with (a) no autocorrelation (α=0.0) in K_t, and (c) positive temporal autocorrelation (α=0.95) in K_t. Scatter plots of K_t against metapopulation size for (b) α=0.0 and (d) α=0.95 indicate how closely metapopulation size tracks K_t.....89

Chapter 5:

Figure 5.1 Schematic diagram of the temperature control system. Numbers in parentheses are referred to in the text.....96

Figure 5.2 Performance of the temperature control system. The square wave (thicker line) is the control temperature, the thinner fluctuating line is the actual temperature recorded by the temperature sensor in a representative culture vessel.....98

Figure 5.3 Control series synthesized as described in the text (a & c) and their power spectra (b & d). (a) shows a white series (γ=0), (b) its power spectra, showing γ at 0.00225 (half the gradient of the least squares linear regression). (c) shows a 1/f series (γ=1), (d) its power spectra showing γ=0.943.....100

Page

Figure 5.4 Results from a preliminary experiment in which population sizes of *P. tetraurelia* (solid lines with circles) were estimated every other day whilst temperature (solid lines with no circles) was (a) held constant or (b) varied with reddened (1/f) spectra or (c) white spectra. The data are for one representative culture from each treatment.....**102**

Chapter 6:

Figure 6.1 Examples of growth of *Paramecium tetraurelia* in 15°C and 20°C environments. Note the good approximations to logistic growth.....**107**

Figure 6.2 Logistic growth of *Paramecium tetraurelia* at 30°C plotted in linear form: Ln[K-N/N]=a-rt. The slope of the least squares regression provides the estimate of the growth rate (slope = growth rate = 2.03).....**108**

Figure 6.3 The relationship between r and temperature over a 4 - 30°C temperature range. Error bars are ±1 standard error from Table 6-1. The equation of the least squares regression is shown..**109**

Figure 6.4 The relationship between growth and temperature once the value for 40°C is included. The linear relationship know no longer holds over the entire span of the thermal niche of this organism. The equation for the third order polynomial least squares regression is shown..**110**

Figure 6.5 Population response of *P.tetraurelia* during a 3 week pilot experiment to (a) white noise (b) red noise temperature fluctuations between 5-25°C. Dynamics show very little difference to those exhibited by cultures grown in a constant environment.....**111**

Figure 6.6 Sample population dynamics predicted by the model for (a) red temperature fluctuations (b) white temperature fluctuations and (c) constant environment.....**114**

Figure 6.7 Examples of population size against two-day mean temperature. (a) Shows the relationship for constant temperature, (b) for the white noise environment and (c) for the red noise environment.....**117**

Figure 6.8 Example output of the Fourier transform analysis of the simulated population dynamics in the (a) white and (b) red environments. Note that white temperature fluctuations (open circles) produce population dynamics (closed circles) with equal power at all frequencies whilst red temperature fluctuations show high power at low frequencies.....**118**

Figure 6.9 Example dynamics from the analysis of persistence of small populations (k=100) in (a) white and (b) red environments using the parameterised model of *Paramecium* growth, imposing 90%mortality every two days).....**120**

Figure 6.10 Population densities (ml^{-1}) from the constant temperature treatment. Population densities are shown by the open circles joined by a thick line. Two-day average temperature is shown by small open circles joined by a grey line.....**122**

Page

Figure 6.11 Population densities (ml^{-1}) from the white noise treatment. Population densities are shown by the open circles joined by a thick line. Two-day average temperature fluctuations are shown by small open circles joined by a grey line.....**123**

Figure 6.12 Population densities (ml^{-1}) from the red noise treatment. Population densities are shown by the open circles joined by the thick black line. Two-day average temperature fluctuations are shown by the small open circles joined by the grey line.....**124**

Figure 6.13 Examples of population size against two-day mean temperature with a time lag of one. (a) Shows the relationship for constant temperature. (b) Shows the relationship for white noise environment and (c) for the red noise environment. Compare with Figure 6-7.....**126**

Chapter 7:

Figure 7.1 1/*f* landscapes that can be used to vary spatial heterogeneity when coupled to a metapopulation model (a) Reddened landscape with a high spatial correlation (b) White noise landscape with no spatial correlation.....**136**

List Of Plates

Chapter 2:

Plate 2.1 Photograph of one of the eight blocks used in this experiment taken immediately after fragmentation. Note there are 6 small and 6 large islands to the right of the large control block.....**38**

List of Tables

Page

Chapter 2:

Table 2.1 The effect of fragmentation on micro-arthropod species richness over time. The response of species richness to fragmentation through time was assessed using repeated ANOVAs. For each individual contrast an adjusted experiment wide error was used. To maintain an overall α of 0.05, a Bonferroni adjustment of $\alpha=0.05/5=0.01$.....**42**

Table 2.2 ANOVAs for linear, quadratic and cubic contrasts for the moss fragmentation experiment. Significant values ($P<0.05$) are in bold. Note that there is a significant cubic effect of time and that there is a significant overall treatment effect. Treatment here tests the hypothesis that the linear, quadratic and cubic trends for the two treatments are equal vs. the alternative that they are different i.e. whether there is an interaction between the treatment effect and the linear, quadratic or cubic effect of time. Here in no case is there any significant interaction, as expected by inspection of figure 2.1(a).....**43**

Table 2.3 The effect of fragmentation on micro-arthropod abundance over time. The response of abundance to fragmentation through time was assessed using repeated ANOVAs. For each individual contrast an adjusted experiment wide error was used. To maintain an overall α of 0.05, a Bonferroni adjustment of $\alpha=0.05/5=0.01$ was applied.....**46**

Chapter 3:

Table 3.1 The effect on mean species richness per island (the dependent variable) after six months of *fragmentation* (a treatment factor with four levels), replicated on different *rocks* (a block factor with six levels), was assessed using an analysis of variance with normally distributed errors and square-root transformed richness.....**65**

Table 3.2 The effect on the proportion of predators (the dependent variable) of *fragmentation* (a fixed treatment factor with four levels), replicated on *rocks* (`block factor with six levels), was assessed using an analysis of variance with normally distributed errors, implemented using GLIM4 (see Crawley 1993). Proportions were not arcsine transformed because without it the fit to the normal distribution was improved. The treatments were: mainland, corridor, broken corridor, and insular. We tested the *a priori* contrasts of connected treatments (mainland plus corridor) versus disconnected treatments (broken corridor plus insular) and mainland versus corridor and broken versus island.....**65**

Table 3.3 The effect of the fragmentation on micro-arthropod abundance after three months. The response of abundance to fragmentation was assessed using an analysis of variance with normal errors and square root transformed abundance.....**71**

Table 3.4 The effect of fragmentation on micro-arthropod abundance after six months. The response of abundance to fragmentation was assessed using an analysis of variance with normal errors and square root transformed abundance.....**71**

Table 3.5. The effect of fragmentation on micro-arthropod species richness after three months. The response of micro-arthropod species richness to fragmentation was assessed using an analysis of variance with normal errors and square root transformed richness.....**73**

Table 3.6 The effect of fragmentation on micro-arthropod species richness after six months. The analysis was conducted using ANOVA with normal errors and square root transformed richness.....**73**

Table 3.7 The effect of fragmentation on the proportion of predators using an analysis of variance with normally distributed errors. Proportions were not arcsine transformed because without it the fit to the normal distribution was improved.....**74**

Chapter 6:

Table 6.1 Estimates of K (ml^{-1}) and r (day^{-1}) for the logistic curve fitted to growth data of *Paramecium tetraurelia* at 6 different temperatures. Three replicate time series were used to provide a mean and (±1) standard error for each temperature.....**109**

Table 6.2 Summary statistics of the model simulations with mean and ±1 standard error. All densities are for 1 ml. Each line of data is for a single simulation (see text). Pairs of 'white' and 'red' simulation are I the same sequence in each block.....**115**

Table 6.3 Correlation analyses between the temperature and simulated population density. Values (a) represent analysis of population with actual temperatures whilst values (b) represent correlation with both temperature and density as 2 day averages.....**116**

Table 6.4 Summary of the exponents (see text) of the environment and population series estimated using linear regression of log (power) against log (frequency).....**118**

Table 6.5 Time to extinction, if recorded, of small populations exposed to white and red $1/f$ noise, subject to 90% harvesting every two days.....**120**

Table 6.6 Summary statistics of each population time series replicate with mean and ±1 standard error. All densities are for 1ml.....**125**

Table 6.7 Results from the correlation analysis between the temperature fluctuations and population dynamics.....**127**

Table 6.8 Summarises the effect of red of and white environmental fluctuations on the exponent of the fluctuations of the population dynamics as estimated using Fourier analysis.....**128**

1

An Introduction

Extinction is the ultimate population catastrophe. It represents the final deletion of the taxon, and as such its causes and consequences are of central importance to ecology. The absolute extinction of a species occurs when various ecological, genetic and environmental processes and events, operating on a multitude of time-scales (Roy *et al.* 1996; Solé *et al.* 1997), conspire to result in the elimination of all the local populations of that species across it entire geographical range.

Local population extinction occurs because population size is rarely constant. Indeed fluctuations in the number of individuals over time and space are typical for all animal and plant populations (Andrewartha and Birch 1954; den Boer 1981). Whilst the causes of such fluctuation are much debated (Davidson and Andrewartha 1948; May 1978) it inevitably results in periods in which the population exists at low numbers and low density and it is here that the population is most susceptible to so-called 'proximate causes', or stochastic causes of extinction (Simberloff 1986). Such proximate causes include unpredictability in environmental and demographic events. However, because local populations tend to fluctuate asynchronously across a species' range (Ranta *et al.* 1995; Sutcliffe *et al.* 1997) proximate causes are rarely entirely responsible for extinction.

Whether a species is susceptible to proximate causes, it seems, depends upon various 'ultimate' causes of extinction-those factors that determine whether a species is rare or not (Simberloff 1986; Jablonski 1995; Gaston and Blackburn 1997). For example, the range size-abundance relationship indicates that not all species are equally abundant or widespread (Gaston 1994). For some species there is the double jeopardy of being spatially restricted and low in population size (Lawton 1995). Whether such species are disproportionately susceptible to proximate extinction causes is matter of contention; however it is often these species that are now most at risk from anthropogenic ultimate

causes of extinction, such as hunting and habitat destruction. The range contraction that inevitably results from habitat loss can leave a rare species in marginal and or small isolated pockets of habitat (Thomas and Jones 1993; Lawton 1995). Such deterministic decline when coupled with the stochasticity of the environment has considerable power to drive populations to extinction.

In fact, habitat destruction is now so prevalent that it is perceived to be the dominant factor determining species ranges, population processes and community structure (Vitousek 1994; Wernnegren and Karieva 1996). It is also clear that because of such range and population size contraction, ever-increasing numbers of even formerly abundant species are becoming vulnerable to the proximate effects of environmental and demographic variability. Destruction and fragmentation of natural habitat is now thought to have increased the ubiquity and frequency of local extinction events to such an extent that it is now causing taxonomic extinction at a rate 100-1000 times the 'normal' or background rate (May *et al.* 1995).

1.1 Habitat Destruction

1.1.1 Fragmentation

Habitat fragmentation is the subdivision of continuous habitat into smaller pieces. This can of course be a natural process caused for example by fire or wind. However, the most important and large-scale cause of habitat fragmentation is the expansion and intensification of human land use. The process has three major components:

a) Loss of original habitat.

b) Reduction in habitat patch size.

c) Increasing isolation of habitat patches.

Theory and evidence suggest all three combine to cause a decline in local species richness (Wilcox and Murphy 1985, Andrén 1994).

Traditionally the effects of fragmentation have been explained in the context of Island Biogeography theory (MacArthur and Wilson 1967), or in the absence of clear source areas, by Metapopulation Theory (Levin 1968; Hanski and Gilpin 1991). In both approaches the processes of extinction and immigration create the observed patterns of species presence/absence across habitat patches. However, Conner and McCoy (1979) have proposed a simpler, more parsimonious, explanation for the decline in species

richness with decreasing patch size. That is, habitat islands can be considered as random samples from source areas; a single small area is more or less bound to have fewer species than a single large sample. The natural question to ask is whether we need more complex theory to understand the process of extinction in fragmented landscapes? And if we do, are there interacting effects between the three components of habitat fragmentation?

Simulation of habitat destruction by the simple exercise of randomly removing 'habitat' from a continuous block shows that up to a certain threshold (≈60%), the habitat remains connected and made up of a few relatively large patches. Continued removal of habitat, however, results in an exponential increase in the distance between the patches of original habitat (Andrén 1994). As increasing amounts of habitat are removed, fragmentation of the landscape is intensified, suggesting a shift in the processes causing the observed species patterns, from a simple random sampling phenomenon to a more complex, non-linear response, in which area and isolation interact to create progressively higher extinction rates. Thus the effects of habitat fragmentation will depend not only on the amount of habitat lost but also on the spatial pattern of the remaining habitat. Indeed, we know from the measurement of the 'species nestedness' of habitat islands that they are often made up of non-random subsets of the total available species pool (Patterson and Atmar 1986; Cutler 1990; Bolger *et al.* 1991). A community of organisms seems to respond to fragmentation by going through a temporal process of 'faunal relaxation' to a new level of lower diversity. Species appear to have differential responses to habitat loss.

Habitat fragmentation is thus a pattern and a process. As a process it is dynamic. At any given scale one observes a shift in the importance of those processes governing species presence and absence depending on the degree of habitat loss and fragmentation. But of course the process is highly scale dependent, and organisms will vary in their response to the pattern depending on their perception of the landscape (Doak *et al.* 1992; Lord 1990; Wiens 1995).

1.1.2 Community Collapse

To date, experimental investigations of habitat fragmentation have dealt predominantly with single species, or pairwise interactions (Karieva 1990), or with interactions of many species at only one trophic level (but see Robinson et al. 1992; Wright and Coleman 1993; Kruess and Tscharntke 1994). Extrapolating from such data and predicting what happens to community assemblages as a whole may be virtually impossible. However, as a starting

point for investigation, food web theory makes several predictions about the structural response of a community to a change in habitat area, productivity and predictability.

The Cascade Model.

The cascade model (Cohen and Newman 1985) accounts for various empirical observations about food webs. Of particular relevance, the model predicts how the average and maximal lengths of food chains should depend on the number of trophic species in a community (Cohen and Newman 1991). A combination of Schoener's power law (the number of trophic species is proportional to the 0.68 power of the number of investigator-defined species, Schoener 1989), a species area curve, and the cascade model yields a testable prediction of how food-chain lengths should vary on islands of different areas (Cohen and Newman 1991). If the process of fragmentation results in a decline in the number of biological species, via an area dependent extinction, at equilibrium the number of trophic species will be related to the number of investigator defined species by Schoener's power law. This would predict shorter average and maximal food chain lengths in habitat fragments; that is, habitat fragmentation should effectively result in shorter food chains. But by what mechanism, and from which trophic level(s) will the losses occur (solely from the upper levels or randomly from all levels)? Energetic and dynamic constraints offer two possible predictions (Lawton 1989).

Energetic constraints.

Energy transfer through a food chain is inefficient (Elton 1927). Thus because eventually there is too little energy to support another link in the chain it is predicted that islands of similar productivity but decreasing area, and vice versa, will result in shorter chains, as species are lost from the upper levels (Schoener 1989). To date only Schoener (1989) provides any evidence for his 'productive space' hypothesis, whilst evidence for a chain length productivity/energy relationship is equivocal at best. Jenkins et al. (1992) showed that both a ten and hundred fold reduction in productivity in an experimental manipulation of artificial tree holes resulted in a reduced chain length of a single link. However, Briand and Cohen (1987), in the most extensive test to date, could find no difference in the chain length of 22 published webs that were recorded from environments differing in productivity by an order of magnitude.

It appears for natural systems that energy restrictions will only be important in the limit in structuring the size and height of a food web (Lawton 1989). For a pre-fragmentation community, however, existing in a recently created habitat fragment such a limit may well be reached. Although there is no empirical evidence, the productive space hypothesis suggests that it is unlikely that such a pre-fragmentation community will be maintained for long in a smaller habitat unit, simply because of energetic considerations. In other words, the species will be lost differentially from higher trophic levels.

Dynamic constraints.

Other factors such as disturbance will also prove to be important in defining the structure and complexity of the post-fragmentation community. For example, dynamic effects such as decreases in environmental predictability, associated with small habitat fragments (Saunders et al. 1991), may combine with energetic effects to produce a strong disturbance to community structure.

Such dynamic effects result from the inter-linked consequences of resilience (the rate at which a population density returns to equilibrium after a disturbance away from equilibrium (Pimm 1991)) and population variability. It is thought that because species higher in the chain are dependent on the recovery of species below them, being embedded in a food chain results in reduced resilience (Pimm and Lawton 1977; but see Sterner *et al.* 1997 for a recent discussion). Intuitively therefore food chains will be shorter and less complex in more variable environments because the top predators spend much of the time recovering slowly from population crashes (see Pimm 1991 for a review of how trophic position influences population dynamics and persistence). Jenkins *et al.* (1992) provides some evidence to support this prediction and show that chains are shorter under less predictable conditions. Systems like Jenkins *et al.*'s aquatic microcosms, and others that are periodically disturbed may not be able to accommodate a predator whose generation time is longer than the frequency of the perturbation, even if there were enough prey to sustain it (Jenkins *et al.* 1992). Again the general insight to be gained from this body of theory and data is that species higher in the food chain will be most vulnerable to habitat fragmentation.

Top down Disassembly.

In a community food web one would expect those species that are the least resilient to suffer extinction. Likely candidates are large bodied species, trophic specialists and species higher up the food chain; interestingly these are all correlates of rarity (Lawton 1995). Thus, we might again predict that food webs would collapse from the top down in the event of fragmentation.

Despite compelling theoretical arguments for the 'top-down' disassembly of food-webs in fragmented landscapes, the empirical data available to test these predictions are extremely sparse, and the available evidence uncompelling. Thus whilst Patterson (1984) found that carnivorous boreal mammals became extinct faster following forest fragmentation, Mikkelson (1993) could detect no differences in the extinction susceptibilities of different trophic levels in a variety of data sets from 'natural experiments'. Mikkelson suggested that this was consistent with 'mounting evidence' for random/homogeneous rather than top down extinction of species during relaxation. The theoretical basis for this empirical observation is weak.

1.2 Environmental Variability

A major, arguably the major cause of population variability which may ultimately drive small isolated populations extinct is environmental variability. It follows that if we wish to understand extinction risk we need to understand environmental variability.

Perhaps the only constant thing in nature is its inconstancy. The clearest examples of this are the fluctuations we observe in our environment. If we look at a particular time series of an environmental variable, such as temperature, over a period of a year (Fig 1.1) we can see that there is a sinusoidal 'signal' rising and falling with the seasons. However, it is also clear that this signal is corrupted by noise. This noise is that part of the variable we are measuring that is unexplained by our model, conceptual or otherwise (Halley 1996). Typically in many of the environmental variables that we measure the magnitude of this noise is large; but what can we say of its nature? Two analyses of the structure of the noise in this example will allow us to reveal several characteristics that are ecologically important.

First the autocorrelation function of this series (Diggle 1990) (Figure 1.2) allows one to measure the serial dependence between successive time points. Here, in figure 1.2(a), it is clear that there is a strong correlation between one time point and the next. In

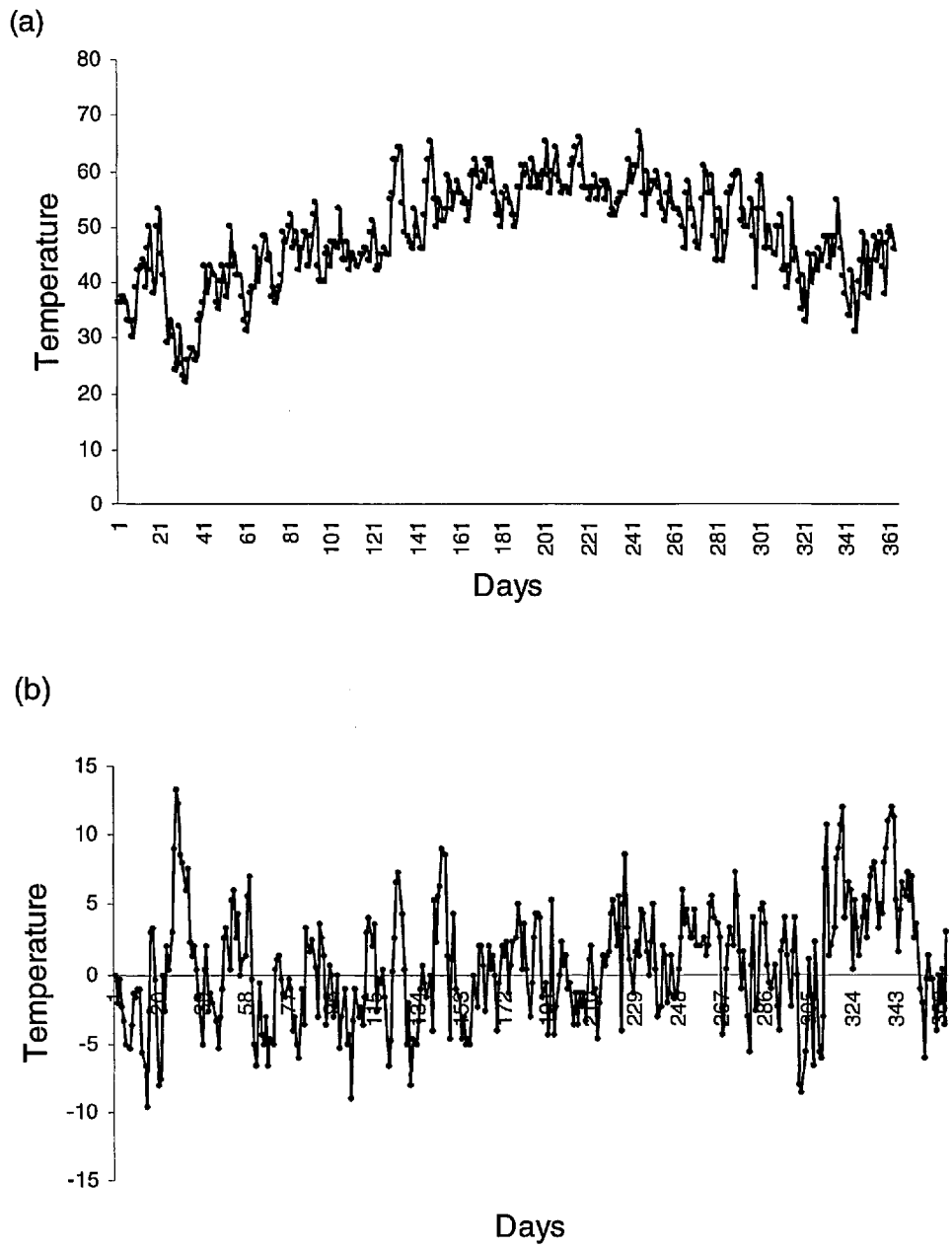


Figure 1-1. (a) Series (Fahrenheit) of mean daily temperatures at recorded at Silwood Park in 1952. (b) Shows the noise in the temperature series once the seasonal variability, the dominant cycle of one year, has been removed. This was removed by subtracting average temperature at each date (calculated from previous years data) from the corresponding actual temperature (Hastings and Sugihara 1991).

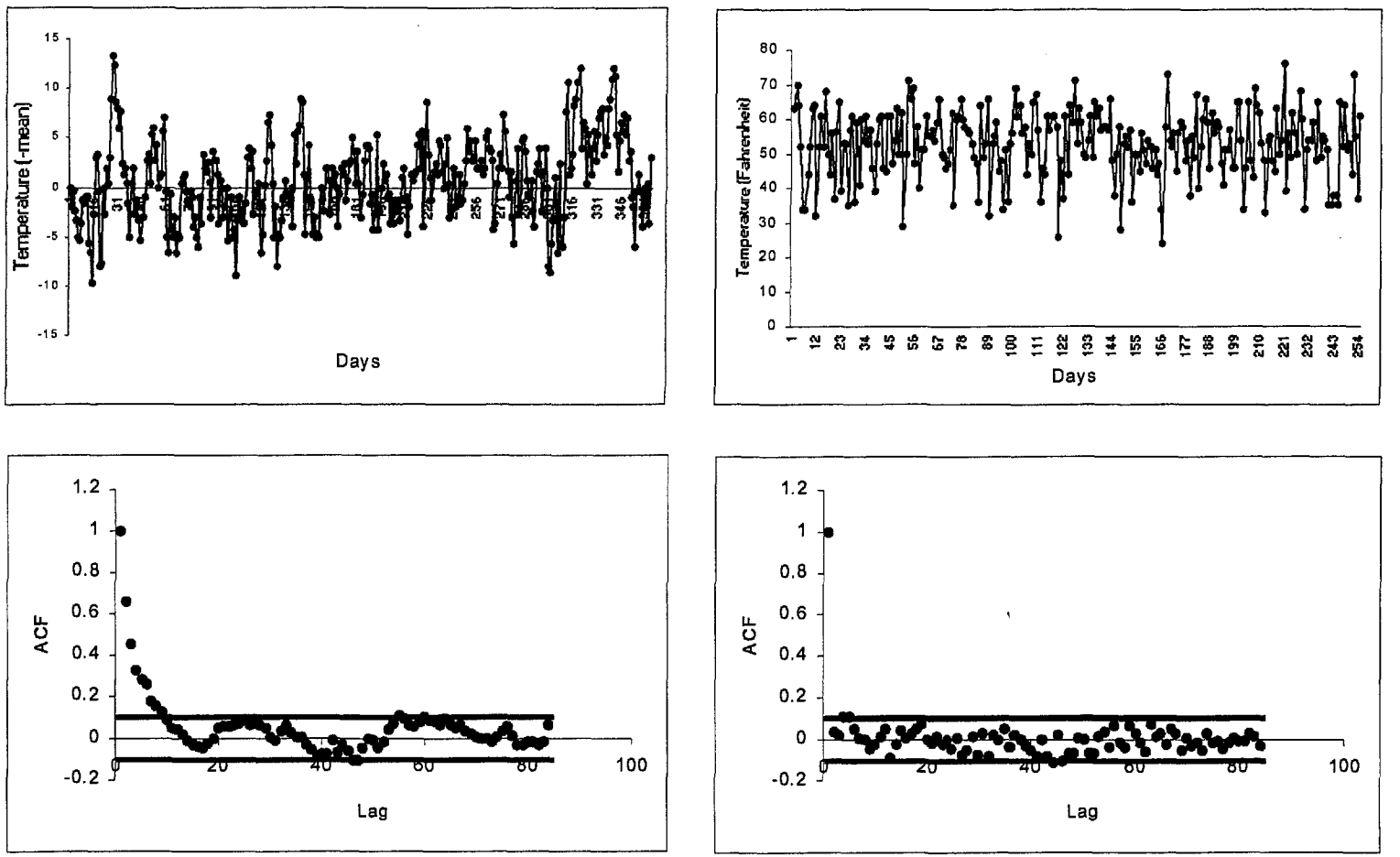


Figure 1-2. Temperature series and their respective correlograms. (a) Shows the 'noise' in the original time series once the seasonal variability, the dominant cycle of one year, has been removed. This annual cycle was removed by subtracting average temperature at each date (calculated from previous years' data) from the corresponding actual temperature. (b) shows the same de-trended series re-sequenced randomly to produce a 'white noise' series. (c) and (d) show the correlogram for the corresponding time series (Each correlogram includes a pair of solid horizontal lines representing the limits $\pm 2/\sqrt{n}$, which are used for informal assessment of departure from white noise.

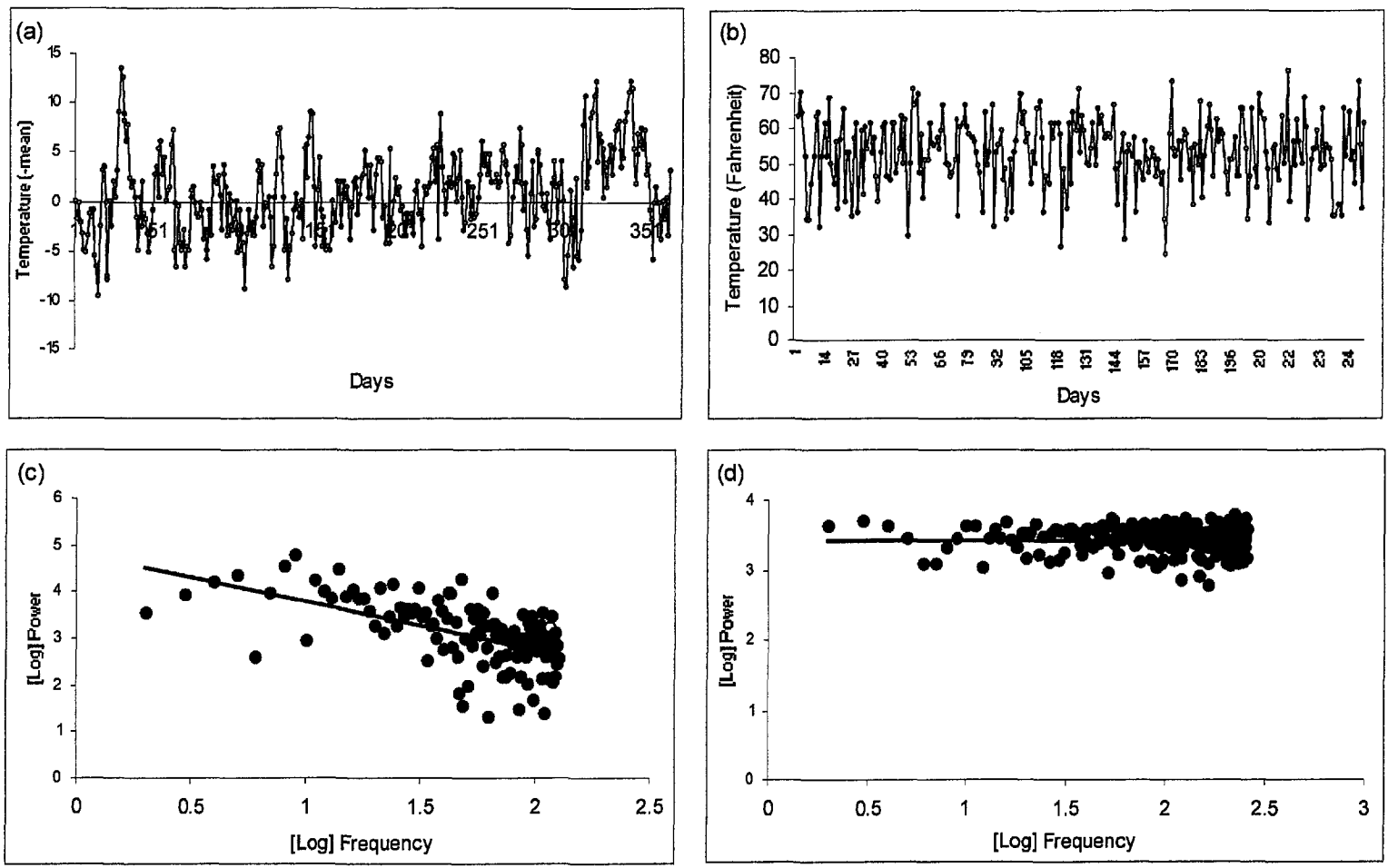


Figure 1.3. Shows the 'noise' in the original time series once the seasonal variability, the dominant cycle of one year, has been removed. This annual cycle was removed by subtracting the average temperature at each date (calculated from previous years data) from the corresponding actual temperature. (3b) Shows this de-trended data rearranged randomly to create a 'white noise' series. (3c and 3d) show the power spectral density for above series. This analysis emphasises the difference in the relative influence of high and low frequency fluctuations in the series.

fact the analysis shows that there is positive correlation over more than one time point. That is the temperature at any given day was very similar not just to yesterday but in this case also up to nine days before. Randomisation of this series to produce a random sequence of temperatures destroys this temporal correlation (Figure 1.2 d).

Another method that is much used in the analysis of time series data is the Fourier Transform (Platt and Denman 1975; Kreysig 1988; Diggle 1990). Figure 1.3(c) shows the output from a Fourier analysis of the series. This Fourier Transform interprets a time series of fluctuations of a variable in terms of a summed series of sine waves with different period and amplitude. By deconstruction of this series into its power spectrum, the Fourier Transform allows us to determine whether it is dominated by particular frequencies. Here (Fig 1.4c), because the slope is negative, it is possible to see that low frequencies have the greatest power (amplitude squared).

When interpreting a series in terms of its frequency spectrum, the results are often reported in terms of 'spectral colour'. This provides a simple and powerful means of describing the inherent pattern within a series of fluctuations. So here, and by analogy to light (in which light at the red end of the spectrum is dominated by low frequency, high amplitude wavelengths), because the noise series is dominated by low frequency (long-term) fluctuations the series is, said to be reddened. If we had found that all frequencies had equal amplitude, as in the randomised sequence, and that there was no overall frequency dominance (Figure 1.3 b, d) then by the same analogy such a series would be described as white noise. It is the relative importance of high and low frequency fluctuations that is the key.

These analyses have provided us with two important features of the above 'noise' time series of environmental noise. Firstly, at any given scale, because of the dominance of low frequencies, the implication is that the longer one observes a real environmental time series, the more likely it is to make excursions into increasingly extreme values. Secondly, because of its inherent correlation structure (at any given temporal scale correlation exists between time points by virtue of the sine wave describing their relation) it is likely to stay there for prolonged periods of time (Lawton 1988).

Over the last 30 years it has been firmly established that the fluctuations of a large number of environmental variables, over many temporal scales, are reddened (Mandelbrot and Wallis 1969; Monin *et al.* 1977; Steele 1985; Williamson 1988). In marked contrast, for reasons of mathematical tractability, the variability in the environment has often been treated in models as a white noise process (see Fig 1.3b) (May 1973; Allen *et al.* 1993).

Clearly, though, successive time points in a series of weather data are not independent variables. Sometimes, in an attempt to improve the realism of such descriptions of the environment, theoreticians have tried to capture the correlation structure within environmental noise as first or second order autoregressive processes (Roughgarden 1975; Leigh 1981; Mode and Jacobson 1987 a, b; Foley 1994). Whilst this somewhat improves the realism, the decline in correlation is exponential resulting in a process with a very short 'memory'. Furthermore, such a model can only ever be phenomenological. By merely mimicking the correlation, an autoregressive model of the environment fails to provide a mechanistic explanation of the processes creating this correlation structure.

In an attempt to consider the implications of a more realistic null model of environmental noise, a significant part of this thesis examines the implications of the assertion that 'pink' $1/f$ noise may be a better description of the fluctuations we see in the environment (Halley 1996) than white noise, or other forms of 'coloured' noise. $1/f$ noise is a random process defined in terms of its power spectral density $S(f)$ (the decomposition of a noise signal into its various component frequencies per unit frequency). In $1/f$ noise the power, the square of some variable associated with the random process, (for example fluctuation amplitude), is roughly proportional to the reciprocal frequency (Keshner 1982).

The low frequency dominance of $1/f$ noise results in strong temporal correlation and a reddened series. $1/f$ noise also possesses other desirable characteristics as a model of real environmental fluctuations. Where white noise has no memory of the past, $1/f$ is a random process with a very long memory. Autocorrelation functions of $1/f$ noise decay as a power of time, slower than any exponential model as seen, for instance, in autoregressive models (Keshner 1982).

Evidence to support the realism of such a $1/f$ model was provided by Mandelbrot and Wallis (1969) in a study of long term geophysical records. Many of the records studied indicated considerable long-range statistical dependence. Indeed the authors concluded that the span of such statistical interdependence was infinite, in the sense that the span was longer than the longest records so far studied. One can visualise, therefore, the processes responsible for variation in environmental temperature as a series of summed sine waves of increasing amplitude. Instead of settling down to a constant mean and variance, characteristic of other noise processes, the variance of $1/f$ noises increases with the length of the series (Halley 1996). 'Normal variation' does not exist; $1/f$ noise implies that such environmental systems fluctuate with wider and wider limits, over longer and longer periods (Lawton 1997).

The implications of such a description of environmental noise for population ecology are profound. Theoretical analyses of extinction predict that populations are sensitive to the colour of environmental variability (e.g. Leigh 1981; Goodman 1987, Foley 1994; Ripa and Lundberg 1997; Petchey, Gonzalez and Wilson 1997). However, the great majority of stochastic population models in ecology incorporate white, or more rarely, autoregressive noise processes. Given what we know about the structure of environmental stochasticity this suggests that such an assumption is unrealistic and maybe dangerously conservative when trying to estimate extinction risk and predict the expected lifetime of small populations.

1.3 What is this thesis about?

I focus in this thesis on one ultimate cause and proximate cause of extinction, the former being habitat fragmentation and the latter environmental variability. Given the ubiquity of habitat fragmentation, the concept of the small population paradigm (Caughly 1994) is becoming increasingly relevant. In this context, consideration of the threat of environmental stochasticity as a proximate cause of extinction becomes all the more necessary. By adopting various experimental and theoretical approaches I examine the effect of habitat fragmentation as a cause of local extinction in communities and the effect of different colours of environmental variability on population persistence and extinction.

1.4 A Microcosm Approach

1.4.1 Habitat Fragmentation Experiments

In order to study the role that habitat fragmentation plays in increasing extinction risk, data from replicated manipulations of habitat subdivision are needed. Since experiments of this nature are prohibitive on a large scale, both spatially and temporally (but see Bierregard *et al.* 1991), the need for a model system becomes all the more important. In an attempt to approach this problem I have chosen as a model system a temperate bryophyte-based invertebrate ecosystem. This system is essentially a decomposer community that includes taxa from the groups Acarina, Colembolla, Nematoda, Protista, Rotifera and Tardigrada, Algae, Bacteria and Fungi.

The same system has been studied extensively by Antarctic biologists where it represents one of the few terrestrial communities (Block 1994). The Antarctic invertebrate moss communities however comprise fewer species than their temperate equivalents. A great deal of work has been conducted that has exploited this simplicity especially in the area of community and ecosystem structure and dynamics. These include the influence of predation and competition and the overall affects of low temperature environments (Jennings 1979; Davis 1981; Maslen 1981; Block 1982; Usher and Booth 1986). Whilst a great deal of work on trophic ecology and community stability has been done using temperate soil decomposer communities (Moore 1988, 1993; Wright and Coleman 1993; de Ruiter 1995), by contrast the moss invertebrate communities of temperate regions, which share the same basic community structure, have been largely ignored by ecologists. In fact the only work to date has been descriptive, involving species collection and description (Seyd 1992).

With high species diversity on a small spatial scale and the discrete nature of the habitat (moss carpets or cushions) the moss system has great potential as a model for studying many of the spatial aspects of population and community ecology. Moss communities are microcosms of many, much larger, terrestrial ecosystems, and offer enormous potential to "reconcile the vast diversity of theory [on spatial processes] into a more unified form and to better address applications of theory to particular systems" (Karieva 1990).

1.4.2 Environmental Variability Experiments

In order to investigate experimentally the effects of different coloured environments on the population dynamics of organisms, it is important to use a model system in which population dynamics are being measured. Thus what is required is an organism with short generation times that is easy to culture and maintain for prolonged periods of time. To meet these requirements populations of the protozoan, *Paramecium tetraurelia* were used. There has been a long history of the use of these organisms as living models for the study of various aspects of population and community ecology in the laboratory (Woodruff 1928; Luckinbill 1974; Salt 1974; Dickerson and Robinson 1989; Lawler and Morin 1993). Their biology and behaviour are well understood and easily modelled, and as such they represent ideal organisms for such a study. At normal laboratory temperatures, for example, these

bacteriverous protozoa have a generation time of eight hours (Salt 1974). Thus during a six month experiment they can pass through over 500 generations.

1.5 An Epistemological Consideration: The Microcosm Philosophy

Conger (1922) in his monograph Theories of Macrocosms and Microcosms in the History of Philosophy, states that according to microcosm theory, "portions of the world which vary in size exhibit similarities in structures and processes, indicating that one portion imitates another or others on a different scale." He refers to such generalised schools of thought involving the concept of analogy as "microcosmic theories".

Science exists because we perceive regularities in the external world that allow a modelling approach (Rosen 1991). Microcosm philosophy holds that there are regularities that are repeated across spatial and temporal scales. Thus when applied to complex ecological systems a particular modelling and epistemological approach is suggested. It asserts that we can understand such systems by analogy. By studying dynamically smaller and faster systems, for example, we can arrive at the principles of how a larger, slower system is organised and how such organisation is maintained. What is critical here, and why it is that small systems are so useful, is that the completeness of the system used as a surrogate (the microcosm) is maintained.

In the current ecological literature, however, the microcosm concept has a rather limited definition and a rather different connotation (Fraser and Keddy 1997). It is generally understood that a microcosm is solely a container experiment often performed in a laboratory and containing only a subset of the organisms and processes present in the 'real' system. They are merely laboratory simplifications, reductionist alternatives, of the ecosystems being studied. The microcosm approach however, is not reductionist by definition, only by interpretation. Unfortunately this interpretation stems from the highly reductionist approach that pervades ecology and science in general. Here we unveil the crux of the misinterpretation.

It is generally asserted that in order to understand a particular complex system it is necessary to break it down into its constituent components. As an understanding of the mechanics of these constituent parts is arrived at, reconstruction of the system is undertaken in an attempt to understand the existence of the whole. Implementation of this methodology is conducted with the use of microcosms. Thus, as they are currently used, microcosms epitomise the reductionist approach. Unfortunately there is no evidence that

such an epistemology has brought any deep understanding to the science of ecology. In what Ulanowicz (1997) has described as "Oecologia ex machina", ecologists seek to portray an ecosystem as a grand machine whose working parts are its component populations and whose linkages are its trophic physical transfers. We then employing differential equations or algorithmic statements to represent these interactions and then by integrating these mathematical constructs we endeavour to predict how the system as a whole will behave. However, whilst such mechanical models of single processes or isolated populations often capture the behaviours of ecosystem components with reasonable fidelity (Platt, Mann and Ulanowicz 1981), a problem arises when the component models are spliced together. The ability of these mechanical constructs, or ecosystem models, to predict the behaviour of the ensemble ecosystems is notoriously poor.

As a modular decomposition of a given 'real' system then, the contemporary microcosm has major weaknesses (Rosen 1991; Carpenter 1996; Ulanowicz 1997). The following statement concerning assembly of ecological communities perhaps best expresses the essence of the argument:

Consider the establishment of ecological communities upon colonisation of islands or the growth of secondary forests. Both of these examples are regular phenomena in the sense that a more or less predictable ecological structure arises via a stereotypic pattern of intermediate steps, in which the relative abundance of various types of flora and fauna follow a well-defined sequence. The regularity of these phenomena is obviously not the consequence of an ecological program encoded in the genomes of the participating taxa. (Stent in Lewin 1984: 1328)

Stent is emphasising that there are higher levels of cause that are important in the organisation of a community. He is suggesting that complete answers to how ecological communities organise and persist will not be found by only studying lower levels of causation. Such analysis of cause is reminiscent of the Aristotelian discussion of causal categories (Magee 1987). Aristotle's image of causality was more complicated than the one adopted by most contemporary biologists (Rosen 1991; Ulanowicz 1990, 1997). He considered that cause could take any four essential forms: 1) material; 2) efficient, or mechanical; 3) formal; and 4) final. Any event in nature could have as its cause one or more of the four types.

Consider for example causation in the outcome of a military battle. The material causes of a battle are the weapons as used by the soldiers. Those soldiers, in turn, are the

efficient causes, as it is they that actually fire the guns. The formal level of cause is represented by the juxtaposition of the armies as determined by the officers. In the end the armies were set against each other for reasons that were economic or socio-political in nature; it is these that provide the final cause of the battle.

In ecology it is normally assumed that events at any particular level are contingent upon elements at lower levels. Hence when attempting to comprehend the structure and function of a community, or ecosystem, ecologists typically break it down into its constituent parts. However this necessarily obviates the existence of any level of cause that derives from the structure of the whole or that is autonomous of lower-level events and processes. Should such higher levels of cause be important in the structure and organisation of communities and ecosystems, any attempt to predict the future behaviour of such a system by reduction to its material and mechanical constituents are inevitably bound to fail. It is imperative therefore that we consider all levels of causation in ecological systems.

The microcosm philosophy asserts that because these principles of organisation pervade all ecological systems, it is appropriate to study small systems in order to gain answers to questions that would otherwise be difficult to tackle in systems with dynamics operating at larger temporal and spatial scales. However, in order to study the full spectrum of causation in ecological systems, such a premise only remains valid whilst the integrity of the system is maintained. Ironically such a methodology makes laboratory study of ecosystems via microcosm simplification rather difficult. If we accept the meaning of the microcosm approach as it was originally intended it becomes no longer justifiable to bring the parts of the whole into the laboratory. The microcosm now becomes the lake, the pond, the puddle, and the moss-covered rock.

The true microcosm approach and the one partly adopted in this thesis is revealed by the correct interpretation of the philosophy (Conger 1922). By returning to the microcosm philosophy as Aristotle originally stated it we not only arrive at the correct microcosm approach, but perhaps more importantly, we move towards an appropriate philosophy for ecology.

Not all of this thesis has taken this approach. Moss-covered rocks are 'real' microcosms. However I also resort to simplified laboratory experiments using simplified 'microcosms' of *Paramecium* and bacteria. This reductionist approach is valid for some types of ecological question, and widely used. But by eliminating many of the major linkages and feedbacks that exist in intact ecosystems, it may also be highly misleading. As

I will show later in the thesis, how populations respond to environmental noise depends strongly on numerous 'details' that are not captured in simplified laboratory microcosms. We need to use simplified laboratory systems to sharpen our thinking about ecological systems. But we need to recognise that our ultimate goal is to understand the behaviour of intact, complex ecosystems, with all that implies.

1.6 Thesis Outline

This chapter has introduced the phenomenon of extinction and described the processes in terms of proximate and ultimate causes. In particular I have highlighted and briefly reviewed the literature on habitat fragmentation and environmental variability and identified gaps in our understanding of how these two factors may bring about such extinction. I have also discussed the shortcomings of the microcosm approach as is it currently adopted in ecology and proposed an alternative interpretation which is more in keeping with the philosophy as it was originally stated. I have also provided a brief description of the two microcosms (one a real, complex field microcosm, the other a simplified laboratory system) I have used in this thesis to address the questions posed.

In Chapter 2 I describe an experimental approach using the moss systems as a natural microcosm to test the affects of habitat fragmentation on a multi-species assemblage. Replicated treatment allowed repeated measurement of the effects spatial subdivision on the community through time.

Use of the moss system is continued in Chapter 3 in which two experiments were designed to examine the role of habitat corridors as landscape features designed to alleviate the detrimental effects of fragmentation. Again replicated treatment allowed repeated measurement of the response of the community to fragmented landscapes with and without corridors. A large part of this chapter takes the form of a manuscript that has been submitted to Proceedings of the Royal Society, Series B.

When studying population dynamics in the laboratory ecologists typically do so in order to avoid the noise in the environment – the unpredictable vagaries of everything that isn't what the experiment is supposed to test. However it has been shown that it is very relevant to consider just what effects this noise (and it's different colours) may have on the dynamics of populations. In order to achieve this it is necessary to expose fast growing organisms, with short generation times, to environments that are identical in every way except for their spectral colour-the treatment effect. So in Chapter 4 I describe an

experimental methodology and apparatus designed to create and impose complicated patterns of thermal fluctuations on populations of protozoa. This chapter takes the form of a manuscript to be published shortly in the Proceedings of the Royal Society, Series B (Petchey, Gonzalez and Wilson 1997).

Chapter 5 reports on the results from an experiment that used this apparatus to expose populations of Paramecium tetraurelia to different thermal environments characterised in terms of their power spectral density. As such it represents the first experimental test of whether population dynamics may be sensitive to the colour of their environment. The data are analysed using standard time series techniques and the results are compared to the predictions obtained from a fully parameterised model of Paramecium growth exposed to red and white noise density-independent fluctuations.

Often it is suggested that in a fragmented landscape a species will persist as a number of small patchy populations-a metapopulation. Such patchy populations of individuals, are of course, highly susceptible to proximate causes of extinction. However theory suggests that such patchy populations may persist in the landscape via a high rate of colonisation. In order to synthesise the topics of this thesis I describe in Chapter 6 an investigation of single population and metapopulation persistence in stochastic environments of different spectral colour. This chapter takes the form of a manuscript that is also to appear in the Proceedings of the Royal Society, Series B (Cohen, Gonzalez, Lawton, Petchey, Wildman and Cohen 1997).

Chapter 7 is a general discussion. I briefly review the main results from the thesis and place them into context of current ecological theory. I then highlight some of the caveats of the study and work that still remains to be done.

2

Habitat fragmentation: an experimental approach using the moss microcosm.

Recent reports suggest that population extinction arising from habitat loss is currently at a level three orders of magnitude higher than 'natural' or 'background' species extinction rates. Habitat fragmentation is now perceived to be *the* dominant processes determining these extinction rates. Despite this very little is known about the effect of fragmentation of the landscape on extinction rates in remnant habitat patches.

Here I describe an experiment in which landscapes of large continuous tracts of moss were experimentally fragmented. The response to fragmentation of the community of micro-arthropods inhabiting this system was followed for a year. There was a significant effect of fragmentation in this system. Moss fragments were found to contain fewer species than equivalent sized areas of control patches of moss after 12 months. Abundance of the micro-arthropods was also found to be lower in fragments. Initial abundance and patch incidences were found to be significant predictors of extinction. Large bodied species were also found to have a significantly greater risk of extinction than smaller bodied species. Although fragmentation resulted in considerable extinction and a community wide reduction in abundance over time Canonical Variates Analysis revealed no effect of fragmentation on community composition.

2.1 Introduction

Destruction and fragmentation of natural habitats is now thought to have increased the ubiquity and frequency of local extinction events to such an extent that they are causing taxonomic extinction at a rate 100-1000 times the 'normal' or background rate (May *et al.* 1995) and population extinction maybe 10-100 times more (Hughes *et al.* 1997). These enhanced rates of extinction result initially and predominantly because of direct destruction of habitat. However habitat destruction is rarely complete and in many cases the end result is a new landscape consisting of a mosaic of habitat fragments in which extinction is still the dominant population process. The effects of habitat loss, it seems, depend not only on the amount of habitat lost but also on the spatial pattern of this remaining habitat (Andrén 1994). The challenge facing ecology is the urgent necessity for a deeper understanding of the processes resulting in extinction and community collapse following the initial phase of habitat destruction.

This initial destruction may be represented as ~~a high frequency~~, high amplitude press perturbation (Bender *et al.* 1984) in the temporal dynamics of the community or ecosystem. Although the community found within any given patch following fragmentation may be simply seen as an area-dependent random sample from the previous continuous habitat tract (Conner and McCoy 1979), the dynamics of such a community are likely to be complex because of the delayed direct and indirect effects resulting from the reduction in patch size and persistent patch isolation.

Traditionally the effects of such spatial patchiness have been explained in the context of equilibrium, ~~and~~ island biogeography theory (MacArthur and Wilson 1967) or more recently in terms of metapopulation theory (Levin 1968; Hanski and Gilpin 1991, 1997). Whilst these theories have provided an important conceptual foundation for understanding single species dynamics in patchy landscapes, our inability to predict the response of communities to fragmentation result from the fact that ecology lacks an appropriate, and empirically tested, theory.

The only example of explicit theory, attempting to predict the response of communities to fragmentation, suggests that the effects are likely to be delayed and result in a considerable extinction debt (Tilman *et al.* 1994). However this much cited model is underpinned by an unlikely competition-colonisation trade-off assumption (as yet little evidence exists that such an assumption is broadly relevant to animal and plant communities) which calls into question a key prediction of the model, namely the

likelihood that good competitors are most at risk from habitat fragmentation (McCarthy *et al.* 1997).

General food web theory predicts that in the limit, energetic and dynamic constraints will be imposed upon communities existing in post-fragmentation patches and that disassembly will be inevitable (Cohen and Newman 1991; Lawton 1989; Schoener 1989; Holt 1996). However it is the pattern and processes of this disassembly that is important. Whether species are lost from the community at random (Mikkelson 1993) or from the top down (Patterson 1984) may have important consequences for the functioning of the remnant ecosystems (Naeem *et al.* 1995).

Much of our empirical knowledge of the response of post-fragmentation communities is based upon snapshot data obtained from fragments sampled at indeterminate times following fragmentation. Time series data of the dynamic response of communities to fragmentation measured over adequate spatial and temporal scales are rare and much needed if any general theory is to be realised (but see Robinson *et al.* 1992; Bierregard *et al.* 1992; Wright and Coleman 1993). Much of the problem stems from the difficulty of studying extinction and community disassembly. Because rates of extinction are generally too slow in large-scale systems to be tractable experimentally (see Schmiegelow *et al.* 1997), I use a small-scale moss ecosystem as a microcosm (Davis 1981; Moore *et al.* 1996). Moss patches are ideal systems for experiments of this sort because they contain an easily sampled, diverse community of micro-fauna at high densities (Kinchin 1992). Furthermore they occur naturally in patches which are large relative to the size and dispersal powers of the populations that live in them; a feature that may make them ideal models for the macrofauna of larger landscapes. In this experiment I set up a series of replicated fragmented landscapes and followed the response of the faunal community to this perturbation over a period of several generations.

2.2 Methods

The response of the community to fragmentation was studied by tracking the change in species richness and species abundance at regular two-month intervals over the course of one year. In March 1995, a randomised block design was established in which eight replicate moss (*Hypnum cupressiforme* and *Tortella tortuosa*) covered dry stone boulders were selected at a site in the Derbyshire Peak District (OS map ref SK 264566). Each replicate comprised 12 experimentally created islands; six large (200cm^2) and six small islands

($20cm^2$) of moss and a large continuous area of moss acting as a control (at least 50cm x 50cm) (see Plate 2.1). Habitat fragments were created using a template that ensured constancy in island area, and the maintenance of a minimum distance between islands (15cm). Islands were formed by scraping and removing the moss from around the template leaving them in a 'sea' of bare rock, a habitat considered to be inhospitable for most taxa.

Every two months for the ensuing 12 months (a period equivalent to tens of generations for many of the lower trophic groups e.g. protista and nematoda and several

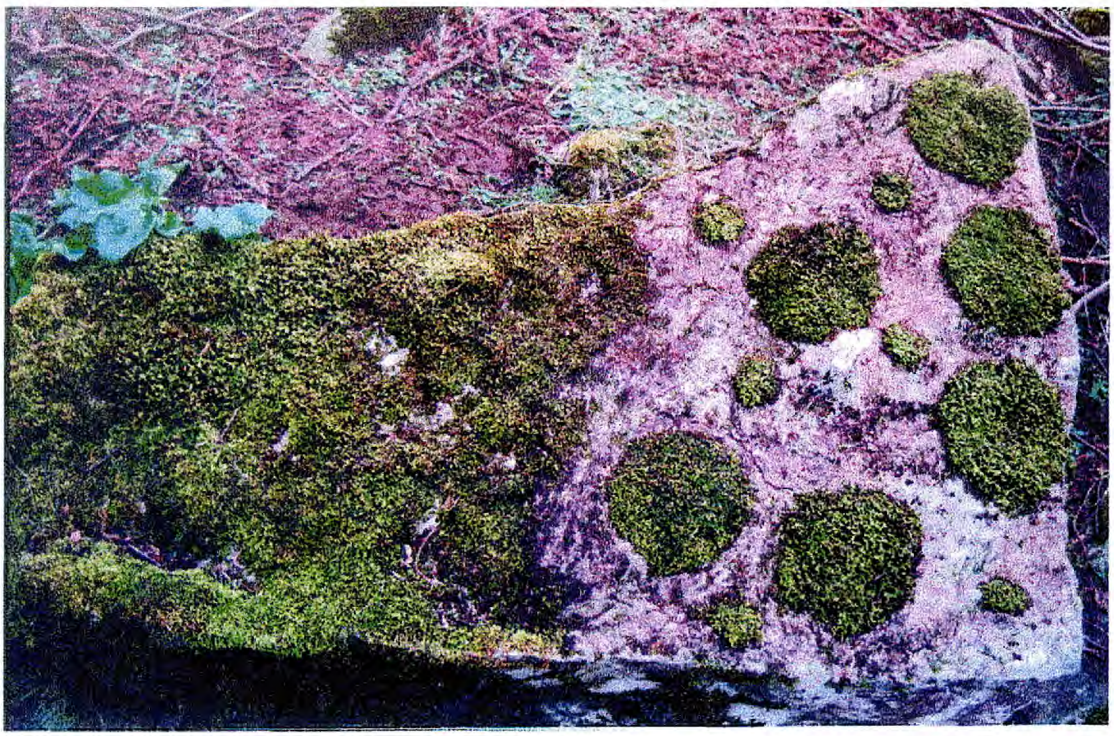


Plate 2.1. Photograph of one of the eight blocks used in this experiment taken immediately after fragmentation. Note there are 6 small and 6 large islands to the right of the large control block.

generations for some of the mites) one large and one small island were randomly chosen and removed from each of the replicates. At the same time and from each replicate two equivalent areas of moss were removed from the control continuous patch of moss. Such a control was established to account for any confounding effects of seasonal changes in abundance and diversity (Evans *et al.*1961, Schenker and Block 1989). Island samples were then returned to the laboratory whereupon micro-arthropods were extracted using a Tullgren funnel. All samples were left under the heat and light gradient for 72 hours. The emerging fauna were collected into an alcohol/glycerol/water (7:2:1) mix and identified and sorted into morphospecies (using Evans *et al.* 1961; Krantz 1978; Eisenbeis and Wichard 1987 as reference texts). In total 133 microarthropod types were extracted.

Because of time constraints, the great majority have not been identified to named species and thus this figure is probably a cautious overestimate. In all samples ≈98 000 individuals were counted and identified. Most belonged to the Acari (63%) and Collembola (24%). In addition, and to examine the susceptibility of different trophic groups, species were classified as predators (Mesostigmatid and Prostigmatid mites, pseudscorpions) or non-predators (cryptostigmatid mites and Collembola).

A species was considered locally extinct if it did not appear in the suite of organisms contained in the Tullgren funnel extraction. This is necessarily a working definition and although the extraction efficiency of this system is high, it is impossible to establish with certainty whether a species has disappeared from an island, or is so rare that surviving individuals were not extracted by the Tullgren funnels. Importantly for this working definition of 'extinction' control and moss fragments experienced identical extraction regimes.

Because identification of soil fauna is problematic, during counting the operational taxonomic units I used were morphotypes-mites and collembola with distinct sets of morphological characters. When a new morphotype was encountered it was kept and preserved for future reference. During this chapter and the next the term species is used loosely and to refers to distinct morphotypes.

Statistical analysis of repeated measures is very much a grey area, with several schools of thought adopting quite different positions (see Scheiner and Gurevitch 1996 for a review). In the following analysis I adopt two approaches. First I perform a series of pair-wise comparisons at each sampling date to examine the main effects of treatment on species richness and abundance in which I adopt a conservative level of significance. Data were square root transformed where necessary to improve 'normality'. Then examine whether the treatments differed in the pattern of responses over time I used a repeated measures analysis algorithm as detailed by Gurevitch and Chester (1986). This algorithm is designed for the analysis of repeated measures experiments using the appropriate test statistics for multivariate analysis, while allowing the straightforward testing of time trends or other contrasts of interest. The algorithm functions by reducing each set of measurements on a subject to a single weighted sum, and then performs a univariate analysis on the weighted sums as if they were original measurements. It thus allows an assessment of the overall treatment effect and determination of whether there is any significant interaction of treatment with time.

To determine whether predators were differentially suffering extinction following fragmentation a further factor, predator/non-predator, was added to an analysis of variance. Logistic regression was used to determine whether population and body size were significant predictors of extinction in habitat fragments.

To examine whether fragmented habitat or control habitat differed in overall community structure and composition, a Canonical Variates Analysis (CVA), using log-transformed data was applied. The analysis was performed using Genstat (Genstat 5 release 3.22).

2.3 Results

Over the course of the 12 months following fragmentation I observed significant changes in the abundance and diversity of the microarthropod community.

2.3.1 *Species Richness Response*

There were strong effects of fragmentation on species richness in both the small and large islands (Figure 2.1 a,b). To avoid unnecessary repetition, I only report on results from the large islands where they differ from those of the small islands.

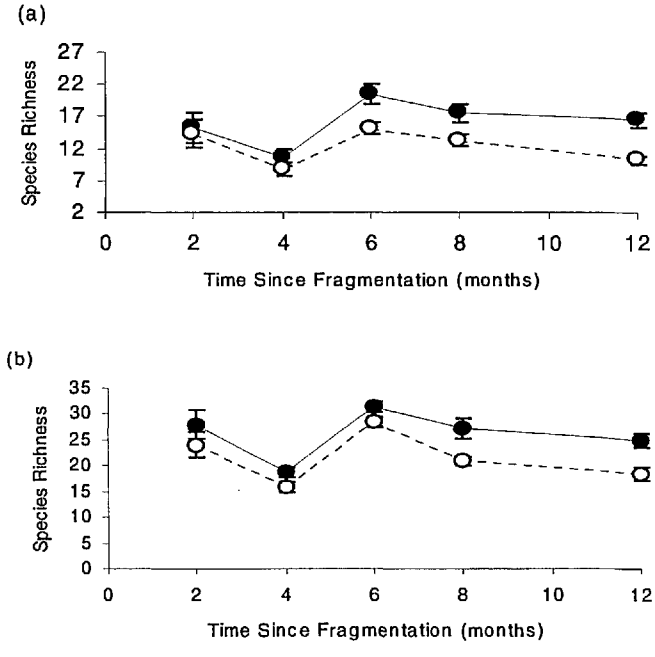


Figure 2.1. The effect of fragmentation on total species richness in (a) small (20 cm^2) and (b) large (200 cm^2) moss islands. Control is shown by the solid black circles and the fragments by the open circles. All data show the mean and 1± S.E.

Pair-wise comparison between the treatments at each sampling date indicates that there is a significant effect of fragmentation at six months in the small islands (Table 2.1). Because of the conservative error used there is not a significant effect at eight months, however by 12 months fragmentation has had a very strong effect on species richness. In the large islands a significant difference between control and fragmented species richness was not observed until 8 months had elapsed ($F_{1, 15} = 7.71$, $P \leq 0.05$) (not assuming a Bonferroni correction). Given that these islands are ten times larger than the small islands, this is a result one would predict.

The repeated measures algorithm (Gurevitch and Chester 1986) was used to analyse the response of the islands through time. This algorithm is made more complicated if the repeated measures are not equally spaced, so only the first eight months of data was used. The analysis demonstrated that for the small islands there was a significant overall effect of treatment on species richness (Table 2.2). Furthermore the temporal dynamics of species richness showed a significant cubic effect of time (Table 2.2). However rather than describing some complex community trajectory following fragmentation, the cubic function is significant because of the large reduction in species richness observed at four months, a response due entirely to the drought during the June of that year. More importantly, there was no significant interaction between the cubic effect of time and the treatment.

The key feature of Figure 2.1, especially for the small islands, is the increasing separation between the two community trajectories. A significant positive linear regression ($r^2=0.75$, $F_{1.4}$, $p=0.05$) (figure 2.2a) was found in the difference in the number of species between the treatments through time. The magnitude of this increasing difference in species richness is reflected in the significantly ($r^2 = 0.77, F_{1, 4}$, $P=0.04$) increasing linear proportion of species lost from the small habitat fragments when compared to the control (Figure 2.2b). By twelve months almost 40 percent of the species in the original small island community had suffered local extinction.

The decline in species richness observed in both the control and fragmented islands at four months and their subsequent differential recovery is a significant feature of both graphs. The decline coincides with the extremely hot and dry weather experienced in June 1995. The organisms of this community are well adapted to extreme changes in the moisture content of the moss; however, the normal response of these organisms is to enter some form of anhydrobiosis. Because they are not in an active state they therefore do not respond to the light and heat gradient of the Tullgren funnel and are therefore not

extracted. The observed, simultaneous, declines in species richness in month four therefore reflects changes in arthropod activity, and do not reflect a real loss of species.

Table 2.1 The effect of fragmentation on micro-arthropod species richness over time. The response of species richness to fragmentation through time was assessed using repeated ANOVAs. For each individual contrast an adjusted experiment wide error was used. To maintain an overall α of 0.05, a Bonferroni adjustment of $\alpha=0.05/5=0.01$.

Source	d.f.	SS	MS	F	P
Contrast:2months					
Treatment	1	3.10	3.10	0.34	n.s.
Block	7	534.9	76.4	8.4	0.01
Error	7	63.4	9.05		
Total	15	601.4			
Contrast: 4months					
Treatment	1	14.0	14.06	2.03	n.s.
Block	7	104.9	14.9	2.16	n.s.
Error	7	48.4	6.91		
Total	15	167.4			
Contrast: 6months					
Treatment	1	115.6	115.6	9.21	<0.01
Block	7	106.9	15.27	1.26	n.s.
Error	7	87.9	12.55		
Total	15	310.4			
Contrast: 8months					
Treatment	1	68.0	68.0	4.75	0.05
Block	7	65.4	9.3	0.65	
Error	7	100.4	14.3		
Total	15	233.9			
Contrast: 12months					
Treatment	1	114.1	114.1	27.9	<0.01
Block	5	38.4	7.68	1.87	n.s.
Error	5	20.4	4.08		
Total	11	172.9			

Table 2.2. ANOVAs for linear, quadratic and cubic contrasts for the moss fragmentation experiment. Significant values (P<0.05) are in bold. Note that there is a significant cubic effect of time and that there is a significant overall treatment effect. Treatment here tests the hypothesis that the linear, quadratic and cubic trends for the two treatments are equal vs. the alternative that they are different i.e. whether there is an interaction between the treatment effect and the linear, quadratic or cubic effect of time. Here in no case is there any significant interaction, as expected by inspection of figure 2.1(a).

		Linear		Quadratic		Cubic		Total	
Source	d.f.	SS	F	MS	F	MS	F	MS	F
Grand mean	1	6240.1	1.14	11.57	0.02	1527.5	**9.81**	.....	
Treatment	1	1264.0	3.25	8.64	0.21	248.6	2.23	714	**8.41**
Error	14	5433.4		550.5		1556.0		1187.7	
Total	15								

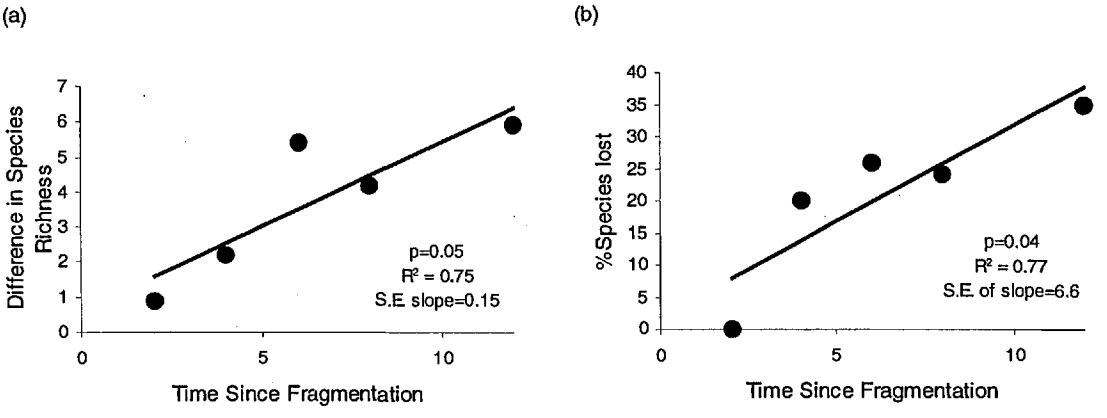


Figure 2.2. (a) The difference in the total number of species (species in controls-species in fragments) found on small control and small fragmented islands.(b) The percentage difference between the total number of species found on control and fragmented islands.

The interesting feature of figure 2.1 is that following the drought perturbation the fragmented community returned to significantly lower species richness than the control (see Table 2.1). The relative contributions of drought, patch isolation and reduced patch size in creating this response are not easily determined. The linearly increasing trend in the difference in species richness between control and fragmented communities suggests that the dominant effect is due to the temporally increasing impact of fragmentation. It is likely that drought enhanced the amount of local extinction at that time, although there is no statistical evidence for any interaction between the perturbation as defined by the drought and the resulting fragmented community response.

Species richness was broken down into predator and non-predator categories in order to examine whether higher trophic levels were disproportionately suffering extinction. The biggest effect should be on the smallest islands, but in this experiment there was no significant difference in the proportion of predatory species of mite found in the small islands when compared to the proportion obtained from the control patch after 12months ($F_{1, 10}$, = 0.10, P=0.75). Thus there is no evidence for the predicted top down disassembly within these mite communities in the face of fragmentation. (Note that larger patches, as expected, also showed no evidence for the differential loss of predators).

2.3.2 *Abundance*

The existence of considerable local extinction in this system suggests that other things being equal (an absence of density compensation, for example (Williamson 1981)) the population sizes of surviving biota within habitat fragments will be smaller than those extracted from the similar sized areas of the mainland. Figure 2.3 (a, b). shows the total abundance of micro-arthropods extracted from the small and large islands. The most striking feature of these graphs is the considerable variability in abundance extracted from islands within a given sampling date. The reason for this is likely to be because moss micro-arthropods are highly spatially aggregated (Usher and Booth 1986). Fragments are deliberately a random sample of the habitat and so the abundance extracted from these islands will reflect the rather patchy distribution of individuals in space. Some samples contain vast numbers of micro-arthropods (sometimes up to 800 in one 20 cm^2 island) whilst others are virtually empty. Although the mean abundance from the small fragments was consistently lower than the control in small islands, not surprisingly the repeated pair-wise ANOVA did not reveal any significant differences until after 8 months (Table 2.3). A similar pattern is observed in the large islands but at no point during the course of the experiment was the abundance of micro-arthropods extracted from large islands statistically significantly different from the control. This result is consistent with the prediction that larger islands should take longer to show any effect of fragmentation.

2.3.4 *Predictors of Extinction*

Logistic regression was conducted with the 12 month data set in order to estimate whether for individual species, control patch abundance, total proportion of control

patches occupied across all 8 replicates and body size were significant predictors of extinction (Figure 2.4 a, b, c).

Initially, the full model, with all the main effects and all possible 2 and 3 way interactions was fitted. Step-wise deletion of these effects from the model revealed that there were no significant interactions. Furthermore sequential removal and replacement of the main effects, abundance, incidence and body size, also showed no significant change in deviance. However in a separate analysis fitting the main effects independently revealed that the species that went extinct were significantly lower in abundance (χ^2 =20.12, df=1, P<0.001) and that these same species were found in significantly fewer patches (χ^2 =16.44, df=1, P<0.001). The implication is that these two variables, not surprisingly, are strongly inter-related. Thus not only are species that are low in abundance likely to suffer extinction but these same species are also low in incidence across the experimental landscapes. Plotting incidence against abundance of all mite species of the control patches and highlighting those species that were lost from the community confirms that it is the rare species that were predominantly lost (Figure 2.5).

The main effect of body size was also significant. Large bodied species of mites had a greater probability of extinction in this system (χ^2 =4.23, df=1, P<0.05). The simplest explanation for this last result is the fact that body size is negatively related with abundance in this system (Figure 2.8) and hence is a correlate of rarity.

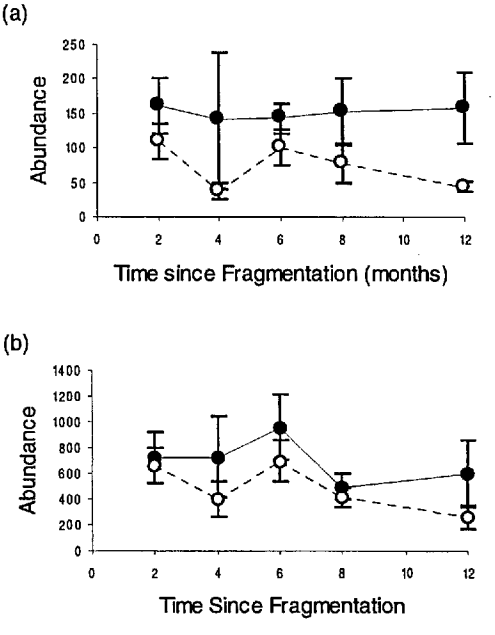


Figure 2.3. The effect of fragmentation on total abundance (a) small (20cm^2) and (b) large (200cm^2) moss islands. Control is shown by the solid black circles and the fragments by the open circles. All data show mean and 1±S.E.

Table 2.3. The effect of fragmentation on micro-arthropod abundance over time. The response of abundance to fragmentation through time was assessed using repeated ANOVAs. For each individual contrast an adjusted experiment wide error was used. To maintain an overall α of 0.05, a Bonferroni adjustment of $\alpha=0.05/5=0.01$ was applied.

Source	d.f.	SS	MS	F	P
Contrast: 2 months					
Treatment	1	11025	11025	1.00	n.s.
Block	7	52946	7563.7	0.68	n.s.
Error	7	76997	10999		
Total	15	140968			
Contrast: 4 months					
Treatment	1	40905	40905	1.2	n.s.
Block	1	260438	37205.4	1.09	n.s.
Error	1	238181	34025.8		
Total	15	539525			
Contrast: 6 months					
Treatment	1	7353	7353	1.46	n.s.
Block	7	26512	3787.4	0.75	n.s.
Error	7	35091	5013		
Total	15	68956			
Contrast: 8 months					
Treatment	1	23180	23180	8.71	<0.01
Block	7	165202	23600	8.86	<0.01
Error	7	18629	2661		
Total	15	207011			
Contrast: 12months					
Treatment	1	45264	45264	6.05	<0.05
Block	5	40345	8069	1.07	n.s.
Error	5	37383	7476.6		
Total	11	122993			

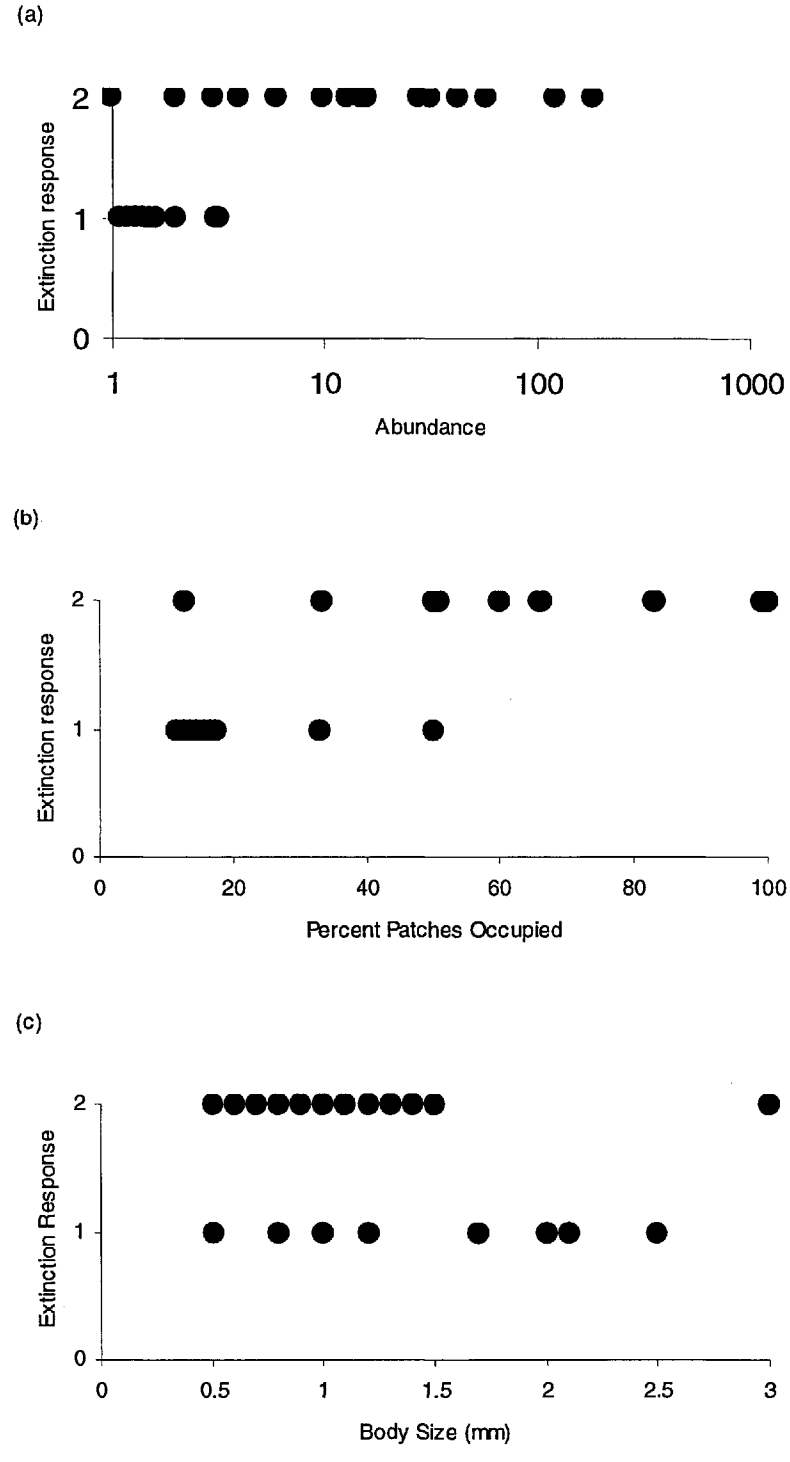


Figure 2.4. The binary response (1=extinct 2=not extinct) of the mites found in the small patches after 12 months (a) extinction response against total control patch abundance (b) extinction response against percentage control of patches occupied (c) extinction response against body size (mm).

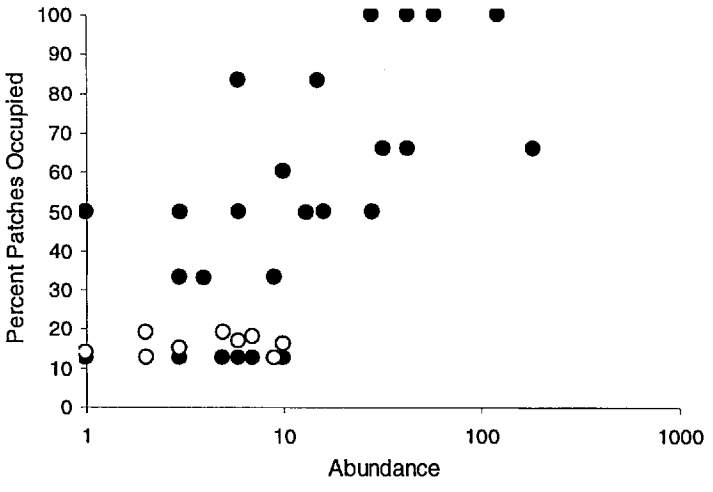


Figure 2.5. Percent incidence (% patches occupied) of mite species across all 8 replicates against total abundance (logged). Abundance and incidence were measured in control (unfragmented) patches. The open circles represent those species that went extinct in the fragments. Data shown are for small islands after 12 months.

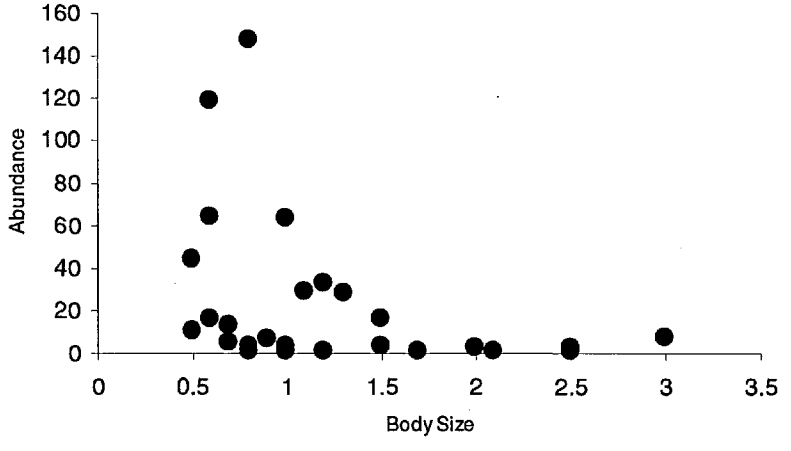


Figure 2.6. The relationship between abundance and body size of the micro-athropods extracted from the control moss islands after 12 months. Body size is in millimetres.

2.3.3 *Community Response*

To establish whether the fragmentation treatment created differences in micro-arthropod community structure, a canonical discriminant analysis was performed on the two-month and 8 month data set of the small islands. Abundance was log-transformed to increase normality. Results from this analysis revealed that there was no significant difference in the co-ordinate variation between control and fragmented communities (first axis χ^2 =72.64, df=69; second axis χ^2 =28.78, df=44). Although we have seen that fragmentation altered the communities in terms of individual species (that went extinct) and the abundance of

surviving species, rather surprisingly, reveals no significant change in overall 'community structure'. I interpret this to mean that there has been no major change in the dominance rankings. Figure 2.7 supports this conclusion, showing that after 12 months the same core set of species is still present within the community; however these species show a consistent, community wide, decline in abundance.

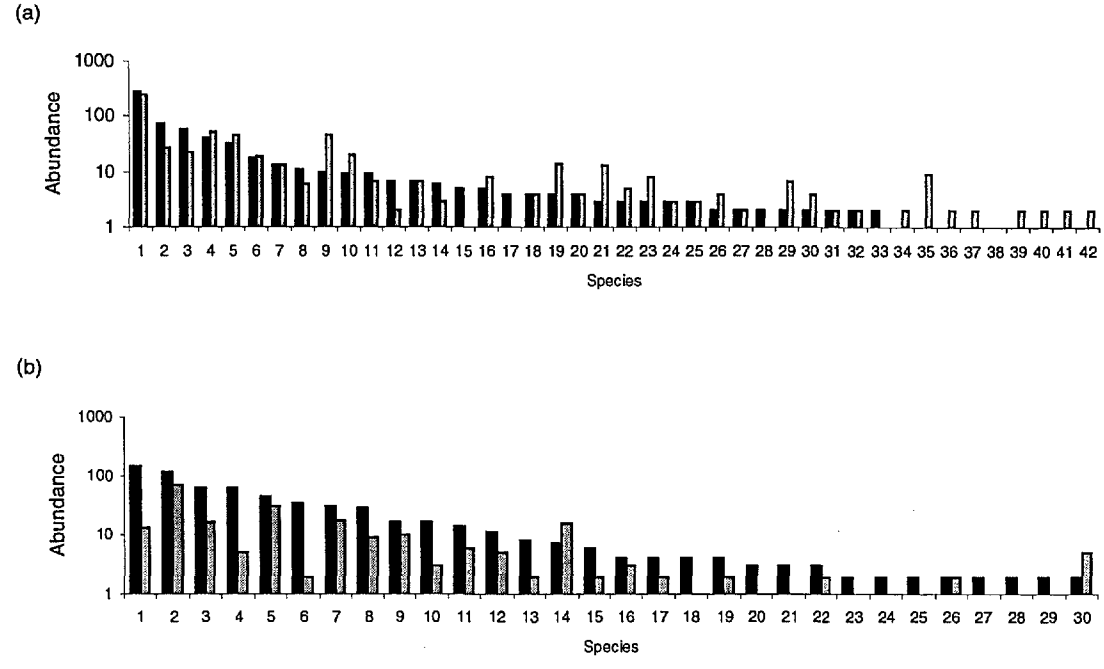


Figure 2.7. The ranked total abundance of micro-arthropods extracted from all eight replicates of the control and fragment islands after (a) 2 months and (b) 12 months (species ranked 1,2....n, in (a) are the same species in (b)). The black bars represent abundance of those species extracted from the controls whilst the shaded bars show the abundance of those species extracted from the fragmented islands. Note the community wide decline in abundance in the in the fragmented islands after 12 months.

2.4 Discussion

Destruction and fragmentation of large continuous moss landscapes resulted in reduced species richness and reduced total abundance in both small and large islands. This effect of fragmentation became increasingly pronounced through time and was most apparent in the small islands. In fact by the end of the experiment some 40% of the original community had suffered extinction. This extinction was found to be due to a linearly increasing effect of fragmentation through time (see figure 2.2). Furthermore there was no evidence that this extinction was slowing

Populations in this system it appears are highly dispersal limited. The constant increase in species loss suggests that there is very little inter-patch movement and re-

colonisation occurring in this system. Therefore either the inter-patch distances, or the bare rock surface, or both represent a considerable barrier to dispersal for the micro-arthropods in this system. In the absence of a rescue effect (Brown and Kodric-Brown 1977) the small populations found within these patches have very little chance of persistence. At the scale of fragmentation implemented in this experiment there thus appears to be very little evidence for the creation of a metapopulation or metacommunity through which persistence may be achieved. Scale is the all-important factor here, and it is probable that in many cases networks of small fragmented systems will not behave as metapopulations (Harrison 1994). What is often occurring in fragmented landscapes is almost certainly the initiation of a series transient dynamics, in which a previously more continuous population or community becomes divided into smaller units, with consequent local extinction, but no functional metapopulation being created, merely an assemblage of populations all slowly declining to extinction.

Predictors of Extinction Proneness

More detailed analysis discovered that species that suffered extinction were found to possess certain characteristics. Those species that were low in abundance, and low in incidence across the landscape, were found to be particularly susceptible. In this system there are many rare species and it is these that predominantly disappeared. Rarity is therefore the most important predictor of extinction during the first 12 months following fragmentation a conclusion that supports the assertion that the model of Tilman *et al.* (1994) may not be generally applicable in predicting the loss of species in the face of habitat destruction. In the present experiments, habitat destruction and fragmentation resulted in a substantial decline in the abundance of both rare and common species (Fig 2.7), a result supported by other studies (McCarthy 1997 and references therein).

Body size was also shown to be a significant, although weaker, predictor of extinction. Although there is reason to believe that large bodied species may be susceptible to extinction following a population crash because of their lower reproductive rate (Pimm 1991), it is much more likely, in this case, to be due to the fact that body size is a correlate of low population size, and hence rarity within this system (see Gaston 1994 and references therein for other examples).

Overall, though, none of the above predictors accounted for more than 45% of the variance in extinction risk. In short, these results suggest that approaches that use broad

species characteristics such as body size and abundance as correlates of extinction risk are likely to be of limited use (Pimm *et al.* 1988; Tracey and George 1992).

Community response

There was no evidence in this experiment of any differential extinction of predators. Much of web food theory predicts top-down community disassembly and one would expect that the lower population densities and greater range requirements of predators to be would important factors increasing their extinction risk (Patterson1984).

Whilst fragmentation resulted in a community wide reduction in species richness (caused predominantly by loss of rare species), and a reduction in abundance of surviving species within this system, there was no evidence of any significant change in overall community structure in terms of dominance. Direct and indirect effects resulting from the loss of some species and changes in abundance in almost all others might be expected to cause changes in community structure (Yodzis 1988). Although there is much evidence, in this experiment, at the population level for severely detrimental effects of fragmentation, the absence of any community level response may suggest that the experiment was run for an insufficient length of time for these effects to become important. An interesting follow up experiment would extend the length of the study to establish at what point community wide interactions become identifiable.

Mechanisms of Extinction

The main cause of extinction in these moss fragments is most likely to be increased environmental stochasticity. For various reasons following fragmentation, remnant patches are likely to represent considerably poorer habitat (Saunders *et al.* 1991). Because edge effects become especially important in smaller fragments, prolonged exposure to environmental conditions can result in a deterioration of patch quality. In the moss system, smaller fragments have a greater surface-area to volume ratio and such geometry almost certainly results in higher desiccation rates and a higher wet/dry frequency (personal observation). For the organisms occupying this habitat, moist conditions are imperative for feeding and locomotion. Although the majority of taxa, especially in lower trophic levels, are well adapted to periods of drought, persistently dry conditions will result in a lethal loss of water for many of the micro-athropods, especially larger species (Worland and Block 1986).

Implications

These results confirm the prediction that populations existing within small remnant patches are more prone to extinction than populations in large continuous patches. Proximate causes such as environmental stochasticity in the form of enhanced drought disturbance or chance demographic events resulting from small numbers, ensured in this system that extinction continued to occur long after the initial area loss. Should such results prove to be system independent (the answer to this will depend on the dispersal abilities of the organisms in question and the inter-patch distances within the landscape) then the reality is that there is a considerable extinction debt awaiting most post-fragmentation communities (Tilman *et al.* 1994). Although the details of extinction in this study are inconsistent with the predictions of the model of Tilman *et al.* (1994), the evidence for an extinction debt suggests that the recent estimates of population and species extinction based solely on area loss are likely to be extremely conservative (Budiansky 1994; Lawton and May 1995; Pimm *et al.* 1997; Hughes *et al.* 1997).

3

A Multi-Species Experimental Test of Corridor Efficacy

Theory predicts that corridors of habitat connecting isolated fragments can act as a means of slowing local extinction through improved dispersal between resource patches. To date there has been no experimental test of this theory involving a multi-species community over several generations.

Two experiments were conducted using the moss natural microcosm to test the efficacy of habitat corridors as a means of ameliorating the deleterious effects of habitat fragmentation. Both experiments were run over six months, a period equivalent to several generations for many of the moss fauna. Connected fragments of moss were found to have significantly higher population sizes and species richness than unconnected fragments of equivalent area. Evidence for the prediction of increased extinction susceptibility of predatory species compared to non-predatory species is given. The gamma diversity of connected landscapes was found to be greater than that of disconnected landscapes.

3.1 Introduction

In a modern landscape dominated by habitat fragmentation and increasing inter-patch distances, whether an organism will survive will depend critically on its ability to move quickly and easily between resource patches. Indeed the degree to which a landscape facilitates or impedes movement among resource patches is the most crucial determinant of population persistence in a fragmented landscape. Such landscape 'connectivity' (Taylor *et al.* 1993, Keitt *et al.* 1997, With 1997) is perhaps the most fundamental measure of landscape structure. But whilst ecologists are highly aware of the heterogeneity in the landscape, previous theoretical examinations of metapopulation persistence have dealt with problems of space indirectly by focusing on patterns of dispersal.

Metapopulation persistence in fragmented landscapes is typically discussed in terms of the dispersal ability of the organisms making up the population such that the primary determinants of patch-colonisation probability are movement rates and inter-patch distances (Hanski and Gilpin 1991 and refs. therein). Defining whether an organism has a high or low ability to disperse has allowed one to ignore explicit consideration of the structure of the landscape mosaic. However, such an approach omits consideration of many important aspects of the heterogeneity that may affect metapopulation persistence. Populations occur in habitat patches that are immersed in a complex mosaic of other habitat patches, corridors, and edges (Wiens 1997). The most obvious effects of these complex mosaics are on individual movement patterns among patches, and patch-recolonisation probabilities. The ability of an organism to move to, and utilise, a resource patch will depend upon the biophysical nature of the route taken, not just the distance to it. Clearly organisms have various habitat preferences; therefore consideration of the long-term persistence of a population in a fragmented landscape should consider details of landscape connectivity.

Based on these considerations the retention of corridors of habitat between remnant patches has been identified as a potentially effective means of achieving the necessary connectivity to ameliorate the deleterious effects of fragmentation (Wilson and Willis 1975; Harris and Scheck 1991; Harrison 1992; Hobbs 1992). Conceptually the idea of habitat corridors follows logically from island biogeography and metapopulation theory (MacArthur and Wilson 1967; Levin 1968). The suggestion is that corridors of habitat, by improving immigration and dispersal, will allow increased effective population sizes, patch re-colonisation following local extinction, and sustained local species richness. Despite

some obvious negative possibilities such as enhanced disease transmission (Simberloff *et al.* 1992; Hess 1994; Ims and Stenseth 1989) the consensus is that corridors are an effective conservation strategy. Perhaps because of the intuitive appeal of the theory, and the pressing need for quick conservation remedies, the need for a connected systems of reserves has been widely accepted by conservation biologists and in some situations adopted at considerable cost (Mann 1995; Mann and Plummer 1995) despite of the lack of any experimental data to support the theory (Simberloff *et al.* 1992).

This lack of empirical data is largely due the difficulties of conducting appropriately replicated and controlled long-term experiments on the efficacy of corridors (Nicholls and Margules 1992; Underwood and Inglis 1992). There are a growing number of studies demonstrating that some fauna will sometimes disperse along or inhabit habitat remnant strips (Beier 1993; Dunning *et al.* 1995; Haas 1995; Bentley and Catterall 1997). However, no studies have provided evidence that corridors can maintain local species richness by slowing the rate of local extinction through improved dispersal. These considerations are rarely discussed in the context of corridors but they must surely be the long-term aim of any such conservation strategy.

Multi-generation community level experiments are thus needed. The work in this chapter uses the moss micro-ecosystem to addresses the question: Do corridors maintain species richness by reducing the rate of local extinction in habitat remnants? I explicitly consider corridors in terms of facilitating dispersal rather than as areas of extra habitat. The role of dispersal in structuring and stabilising ecological communities is an important general theoretical consideration and experiments specifically addressing this are few are far between.

3.2 Chapter Outline

This chapter consists of two experiments designed to test the efficacy of habitat corridors. The basic design of the both of these experiments is outlined in section 3.3. The results from the first experiment are reported (see 3.4) in slightly modified form, from a manuscript that has been submitted to the Proceedings of the Royal Society of London. *Series B* (The figures and table numbers have been adjusted to conform to the requirements of the thesis, and all references cited are in the main thesis bibliography). The results of the second experiment are described in section 3.5. The chapter closes with a general discussion of the results from both experiments (see 3.6).

3.3 Study Design

This study used two different experimental designs to test whether corridors enhance the species richness of remnant patches relative to unconnected patches of equal area. A description of the study site can be found in chapter 2. Eight replicate large limestone boulders of continuous moss (*Hypnum cuppressiforme, Tortella tortuosa* and *Thuidium tamariscinium*) carpets or 'landscapes' were fragmented to provide a randomized block design consisting of four treatments. In both experiments the treatments were: **continental** (a large habitat block of moss, at least 50x100cm in area, from which isolates were sampled), **corridor** (connected islands), **broken**-corridor (same as the corridor treatment, but corridors were split in the center and separated by 5cm (Exp1) or 2 cm (Exp2) and **insular** (isolated fragments of moss).

Full details of each experiment are in sections 3.4 and 3.5. The basic design of Experiment One consisted of treatments clustered as a series of four habitat islands (each single island was $10cm^2$) (see Figure 3.1). These experimental units were created using a template that ensured constancy in size. The moss from around the template was cleared leaving the treatment units in a 'sea' of bare rock. This design was replicated twice on the rock to allow destructive sampling at 3 months and 6 months. The design of Experiment Two consisted of habitat isolates centred on a large continental block of moss (see Figure 3.2). Treatments differed in their connectivity with this large central patch.

Islands were sampled at three-month and six-month intervals. Following removal the micro-arthropod fauna were extracted from the islands using the Tullgren funnel technique described in chapter 2. The organisms were then sorted into morphospecies and preserved in a glycerol/alcohol mixture to be counted.

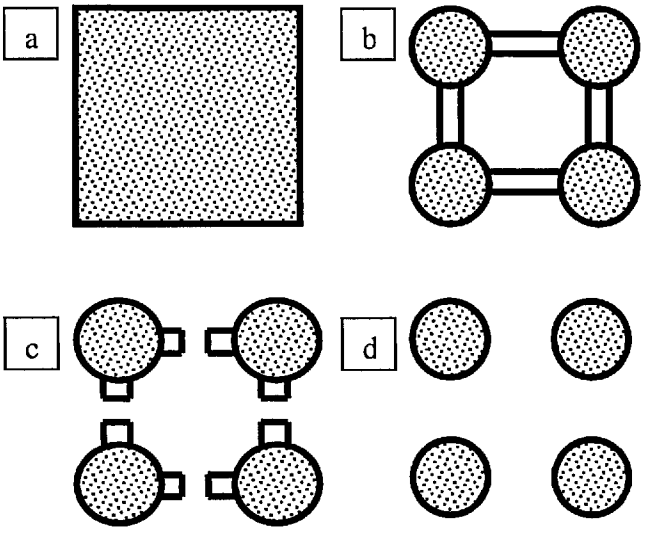


Figure 3.1. Schematic representation (not to scale) of the treatment design used in experiment 1: (a) continent, (b) corridor, (c) broken-corridor, (d) insular.

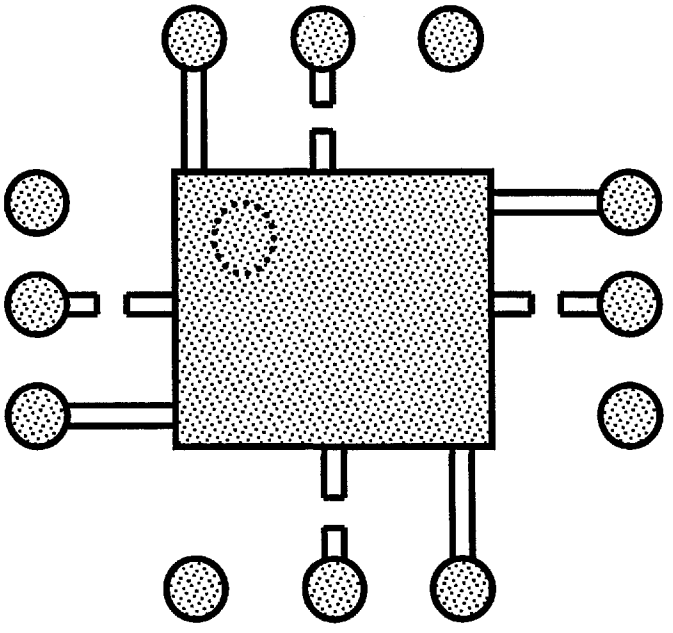


Figure 3.2. Schematic representation (not to scale) of the treatment design used in experiment 2.

3.4 Experiment 1

Corridors maintain species richness in the fragmented landscapes of a microecosystem

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Summary

Theory predicts that species richness or single-species populations can be maintained, or at least extinctions minimized, by boosting rates of immigration. One possible way of achieving this is by establishing corridors of suitable habitat between reserves. Using moss patches as model microecosystems, we provide here the first field experimental test of the idea that corridors can reduce the rate of loss of species, and therefore help to maintain species richness. Connecting patches of habitat with corridors did indeed slow the rate of extinction of species, preserving species richness for longer periods of time than in disconnected habitat patches. The pattern of γ-diversity, the cumulative species richness of entire connected systems, is similarly higher than that of fragmented systems, despite the homogenising effects of movement. Predators are predicted to be more susceptible to fragmentation because of their greater mobility and smaller population sizes. Our data are consistent with this prediction; the proportion of predators declines significantly in the disconnected, compared with the connected treatments.

3.4.1 Introduction

Conservation biologists frequently advise the establishment of corridors to connect isolated reserves (Saunders & Hobbs 1991; Harris & Scheck 1991; Meffe & Carroll 1994; Noss 1994; Harris 1996), based on various theoretical rationales (Wilson & Willis 1975; Harrison 1994; Lynch, Conery & Bürger 1995; Hanski, Moilanen & Gyllenberg 1996). The potential cost of creating a connected system of reserves can be huge (Mann 1995; Mann & Plummer 1995), but surprisingly there are virtually no field experimental data supporting the major theoretical prediction that species richness is maintained, or losses minimized (Nicholls & Margules 1991; Simberloff *et al.* 1992; Hobbs 1992; but see Schmiegelow *et al.* 1997). Almost the only field data suggesting that corridors actually work in promoting migration between patches, or slowing the rate of extinction of populations, consist of observations that some organisms do indeed sometimes use corridors (papers in Saunders & Hobbs 1991; Beier 1993; Haas 1995; Dunning *et al.* 1995; Downes *et al.* 1997a,b); experimental results are very few, and largely laboratory-based (Imms & Stenseth 1989; Holyoak & Lawlor 1996; Burkey 1997; but see Schmiegelow *et al.* 1997). In contrast, there has been a great deal of theory associated with the idea that corridors between habitat patches might offset some of the deleterious effects of habitat fragmentation, principally loss of species richness (Saunders & Hobbs 1991; Harrison 1992; Lindenmayer & Nix 1993; Hill 1995). The suggestion is that species richness or single-species populations can be maintained, or at least extinctions minimized, by boosting rates of immigration via the establishment of corridors of suitable habitat between reserves. Despite some obvious negative possibilities such as enhanced disease transmission (Simberloff *et al.* 1992; Hess 1994), the consensus is that corridors are beneficial.

Rather little theory exists on the relationship between food webs and habitat patchiness (Cohen & Newman 1991; Pahl-Wostl 1993; Holt 1996): what there is predicts that certain types of species are more susceptible than others in the fragmentation process, with predators, large species, and habitat specialists (all correlates of rarity) apparently being extinction-prone (Diamond 1984; Schoener 1989; Cohen & Newman 1991; Tracy & George 1992). There is some evidence for and against these predictions: the proportion of carnivores amongst boreal mammals of montane fragments in the USA declines with decreasing species richness (Patterson 1984); many parasitoids 'failed to colonise' small patches of experimentally established plants where their hosts had colonized, leading to relatively fewer predators on smaller patches (Kruess & Tscharntke 1994); and top

predators suffer extinction in isolated microcosms (Wright and Coleman 1993; Burkey 1997). In contrast, no such differences in extinction susceptibilities were detected in a variety of datasets from 'natural experiments' (Mikkelson 1993). Differential dispersal abilities, with predators generally better than non-predators, means that the presence of corridors may help predator populations more than those of non-predators in avoiding extinction after habitat insularisation. The only experimental tests of this idea used laboratory microcosms: Holyoak & Lawlor (1996) confirmed that moderate levels of dispersal maximised persistence and predator abundance. In contrast, Burkey (1997) found, surprisingly, that top predators died out more rapidly in connected as opposed to disconnected systems.

Alternative approaches suggest that differential rates of extinction across trophic levels may be difficult to demonstrate. Cohen & Newman (1991) suggested that because food chain length increases only slowly with the number of species in a web, and that the number of species in a habitat increases only logarithmically with habitat area, there should only, at most, be a weak link between area and food chain length. Holt (1996) predicts an increasing effect of area on the number of species in higher trophic ranks, but that the effect might be difficult to detect. A deeper understanding of what makes a species vulnerable to extinction is considered vital to efforts to solve the biodiversity crisis by applying ecological principles (Simberloff 1988; Ehrlich 1993).

We use here an experimental microecosystem, island-like patches of moss containing diverse communities of microarthropods, to test experimentally for the first time the idea that corridors can reduce the rate of loss of species, and therefore help to maintain species richness. We predicted that connecting patches of habitat with corridors would slow rates of extinction of these microarthropods, retaining species richness for longer than in isolated habitat patches. We further predicted that predators would suffer disproportionately in the extinction process, but corridors would help predators more than non-predators because of their better dispersal abilities.

3.4.2 Methods

Rates of extinction are too slow in large-scale systems to be tractable experimentally (see Schmiegelow *et al.* 1997), and therefore we used a small-scale moss ecosystem as a microcosm (de Ruiter *et al.* 1995; Moore *et al.* 1996). Moss patches are ideal systems for experiments of this sort because they are easy to manipulate, contain an easily sampled, well-known, diverse community of microarthropods at high to very high densities (Gerson

1969; Corbet & Lan 1974; Eisenbeis & Wichard 1987; Kinchin 1992), and occur naturally in patches which are large relative to the size and dispersal powers of the populations that live in them (which may make their microarthropods communities good models for the macrofauna of real nature reserves). Experimental tests of insular processes have often used such microcosms because of their tractability and the short times scales of change: for example, studies of colonisation have used ciliates (Henebry & Cairns 1980; Robinson & Dickerson 1987; Have 1987; Azovsky 1988), fungi (Wildman 1987), lichens (Armesto & Contreras 1981) and marine invertebrates (Schoener & Schoener 1981); studies of extinction have used protozoa (Dickerson & Robinson 1985, 1986; Warren, 1996; Burkey 1997); of relaxation, soil nematodes (Wright & Coleman 1993); and of turnover, protozoa (Cairns *et al.* 1969), and fungi (Kinkel *et al.* 1987).

We set up a field experiment in which we manipulated habitat connectivity, while allowing for the inevitable increase in area that connections bring with them. There has been some discussion in the literature about an appropriate design (Nicholls & Margules 1991; Inglis & Underwood 1992; Lindenmayer & Nix 1993); we deliberately chose to consider connections between already fragmented habitats, rather than connections between fragments and a large mainland. We chose six large flat limestone rocks, originally continuously covered in moss (mainly *Hypnum cupressiforme*, *Thuidium tamariscinum* and *Tortella tortuosa*), near Wirksworth in the Peak District (Derbyshire, UK; OS map ref SK 264566). In October-November 1995, five 10-cm-diameter circles were sampled from the continuous moss of each rock before clearance to give data on the initial species richness of the 'mainland' moss. Then we partially cleared the moss to the bare rock (assumed to be a relatively inhospitable environment for the majority of moss taxa) in order to set up four experimental fragmentation treatments, each consisting of four circular islands 10-cm in diameter. Island centres were placed at the corners of a square of side 17 cm (i.e. islands were 7 cm from each other); treatments were at least 10 cm apart on each rock, and at least 10 cm from the remaining 'mainland' moss. Fragmentation treatments (cf. Fig.3.1) were: **mainland** (four 10-cm circular sample areas in the surrounding matrix of continuous moss), **corridor** (four islands connected along the sides of the square by corridors 7 cm long by 1 cm wide), **broken**-corridor (as the corridor treatment, but corridors split in the middle and separated by a gap of 5 cm- this controls for the increased area of the corridor treatment), and **insular** (no corridors present). We therefore had four replicate islands per treatment, with two replicates of all four treatments on each of six rocks. As in real nature reserves, the 'inhospitable' habitat between islands is probably a partial rather than an absolute barrier to movement; there is very little information about the dispersal abilities of

microarthropods (see Schenker & Block 1986) across such open rock habitats, but they clearly provide a physically more inhospitable habitat than the moss cushions, as well as less protection from larger predators.

Treatments were removed from each rock after 6 months (in March) for analysis; this time period is equivalent to several generations of most of the fauna in the moss. We also had samples from 3 months to compare the time course of the relaxation process, but results from these are only briefly reported here. When sampled, each 10-cm island (a 'sample') was placed in a Tullgren funnel for 48 hours and all emerging animals collected into alcohol, identified to major group (using, amongst other reference works, Evans *et al.* 1961; Krantz 1978; Eisenbeis & Wichard 1987), and sorted to morphospecies. In all samples, 30 000 individuals were counted and identified; most belonged to the Acari (32% of species) and Collembola (23%). In addition, species were classified as predators (prostigmatid and mesostigmatid mites, spiders, pseudoscorpions) or non-predators (cryptostigmatid mites, collembolans, beetles, etc.). All mean values cited here in the text are given with standard errors.

In the first analysis, the species richness of the average of the group of 4 10-cm islands was the dependent variable. Using the appropriate orthogonal contrasts, we tested the *a priori* prediction that connected treatments (mainland + corridor) would retain more species than the disconnected treatments (broken + insular) and then tested within these pairings, whether mainland vs. corridor and broken-corridor vs. islands differed in species richness.

We then calculated the proportion of predators amongst the species present, and used this as the dependent variable in a second similar 2-way analysis of variance (fragmentation $\times$ rocks), but this time using normally distributed errors. Proportions were not arcsine transformed because the transformation worsened the fit to the normal distribution. Again using a contrast, we tested the *a priori* prediction that connected treatments (mainland + corridor) would retain a higher proportion of predators than the disconnected treatments (broken + insular).

The above analyses considered the average of each group of four islands as a replicate. We then repeated these analyses using γ-diversity as replicates, i.e. treating the cumulative species richness of all four 10-cm islands in any one treatment on each rock as a single replicate. Finally, we also ran similar analyses on the square-root transformation of the total number of individuals.

3.4.3 Results

There was an overall rise in background species richness per 10 cm^2 island between the initial (18.6 ± 1.4, n=30) and final (23.2 ± 1.2, n=24) mainland samples (means are given ±1 S.E.). This was probably a seasonal effect, an interpretation supported by intermediate values for 3-month background samples (20.7 ± 0.9, n=24). There were significant effects of 'treatment' and 'rock', but no significant interaction (Table 3.1): 93% of the effects of the treatment were contained in the contrast between connected and disconnected treatments (see Table 3.1). Between 3- and 6-months, the background moss gained in species richness (by a mean of 2.5 species - see above); the corridor treatment lost a mean of 3.5 species, but the broken-corridor samples lost a mean of 6.5 species, and the insular samples 4.8 species.

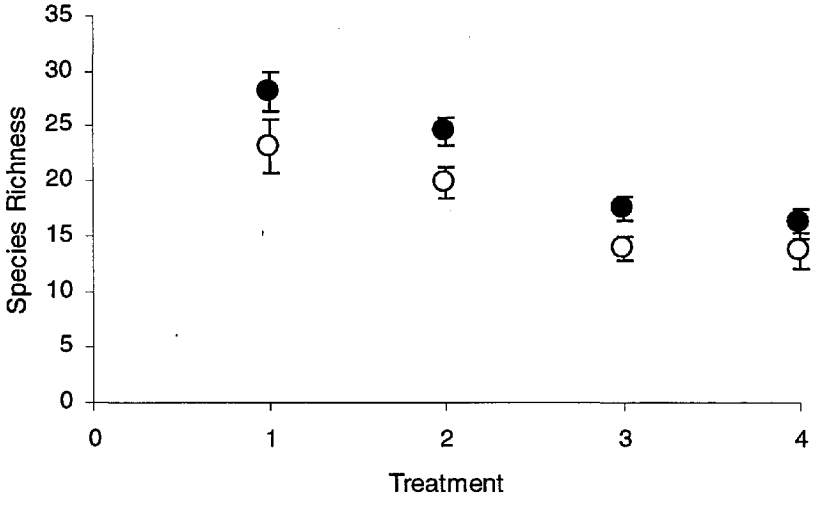


Figure 3.3 Species richness after six months. Treatment factor (1) mainland (2) corridor (3) broken corridor (4) island. The open circles correspond to mean species richness per island (±1S.E.), whilst the closed circles correspond to the mean cumulative richness of the four islands or γ-richness (±1S.E.).

The magnitude of the treatment effects on species richness were considerable (Fig. 3.3). In addition to the significant main connected vs. disconnected contrast there was also a significant difference in the mainland vs. corridor contrast (Table 3.1). Over 6 months the islands with corridors lost an average of 14.5% of their species, whilst the disconnected islands (broken + island treatments) lost almost 41%. Since no differences existed between broken-corridor and insular treatments (Table 3.1 broken vs. island contrast), islands with broken corridors therefore behaved like islands without corridors - there was no detectable

effect on species richness of the small amount of extra area entailed by this treatment. This implies that it is dispersal in the corridors that is creating the observed pattern.

The mean number of individuals per island likewise increased seasonally, from the initial mainland islands (132 ± 14, n=30), to mainland samples at 3-months (234 ± 12) and 6 months (297 ± 12). The mean number was strongly affected by fragmentation treatments ($F_{3,23} = 33.6$, $p<0.001$), and 77% of the sum of squares was accounted for by the connected vs. disconnected contrast ($F_{1,23} = 77.3$, $p<<0.001$). The mean numbers of individuals in mainland islands was >50% greater than in corridor islands (182 ± 16), and about three times greater than in broken-corridor (86 ± 7) or insular samples (113 ± 10).

The proportion of predators (assessed only at six months) declined significantly between connected and disconnected treatments (Figure 3.4), and the main connected vs. disconnected contrast was also strongly significant, accounting for 91% of the treatment sum of squares (see Table 3.2). Furthermore, the broken vs. island contrast was not significant confirming the important result that broken corridors are ineffective. In this system, therefore, there is strong evidence that predators were more sensitive to the impact of fragmentation and its amelioration by corridors than were non-predators.

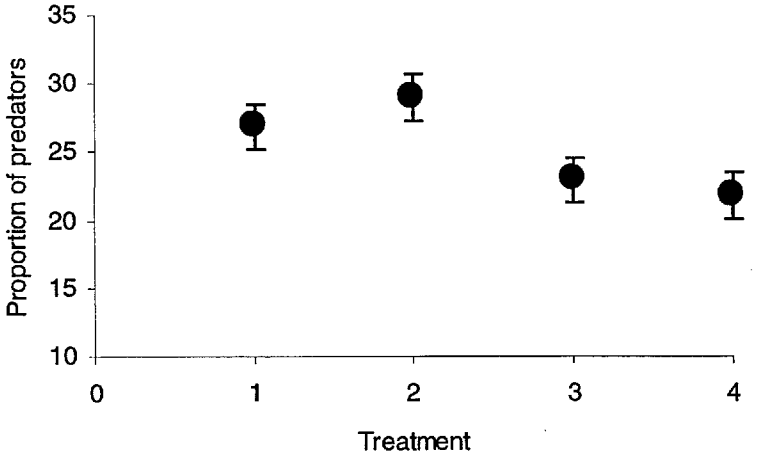


Figure 3-4 The decline in the mean proportion of predators per island at six months. Treatment factor: (1) Mainland, (2) Corridor (3) Broken Corridor, (4) Island.

Table 3.1. The effect on mean species richness per island (the dependent variable) after six months of *fragmentation* (a treatment factor with four levels), replicated on different *rocks* (a block factor with six levels), was assessed using an analysis of variance with normally distributed errors and square-root transformed richness.

Source	d.f.	SS	MS	F	P
Fragmentation	3	5.38	1.79	28.41	0.001
Connected vs. Disconnected	1	5.02	5.02	79.68	<0.001
Mainland vs. Corridor	1	0.36	0.36	5.71	<0.05
Broken vs. Island	1	0.002	0.02	0.31	n.s.
Rocks	5	4.01	0.802	12.7	0.01
Residual	15	0.94	0.063		
Total	23	10.34			

Table 3.2. The effect on the proportion of predators (the dependent variable) of *fragmentation* (a fixed treatment factor with four levels), replicated on *rocks* (`block factor with six levels), was assessed using an analysis of variance with normally distributed errors, implemented using GLIM4 (see Crawley 1993). Proportions were not arcsine transformed because without it the fit to the normal distribution was improved. The treatments were: mainland, corridor, broken corridor, and insular. We tested the *a priori* contrasts of connected treatments (mainland plus corridor) versus disconnected treatments (broken corridor plus insular) and mainland versus corridor and broken versus island.

Source	df	SS	MS	F	P
Fragmentation	3	203.35	67.8	11.56	0.0002
Connected vs. Disconnected	1	185.37	185.37	31.63	<0.0002
Mainland vs. Corridor	1	14.19	14.19	2.42	n.s.
Broken vs. Island	1	3.79	3.79	0.64	n.s.
Rock	5	43.19	8.63	1.47	n.s.
Residual	15	88	5.86		
Total	23	334.5			

In the analysis of γ-diversity (see Fig. 3.1), there was also a significant effect of fragmentation treatment on larger-scale species richness (accumulated species richness over four islands) ($F_{3,20} = 16.68$, $p<0.001$), 93% of which lay in the connected vs. disconnected contrast ($F_{3,20} = 26.46$, $p<<0.001$). All the fragmented treatments lost species relative to the background (see Fig. 3.1). However there was no significant difference in the mainland vs. corridor contrast ($F_{3,20} = 2.84$, n.s.) and similarly none in the broken vs. island contrast ($F_{3,20} = 0.61$, n.s.). Analysis of the number of individuals (square-root transformed) gave similar results.

3.4.4 Discussion

"The ecological value of ... corridors is disputed by some of the discipline's leading researchers. ... wildlife corridors have quietly become one of the most important battlegrounds for conservation, with major development projects and the future of valuable nature preserves at stake" (Mann & Plummer 1995). Some think that corridors "hold more promise for the management of the diversity of life than any other management factor except stabilization of the human population" (Keith Hay of the Conservation Fund, reported by Mann & Plummer 1995), whereas others such as Dan Simberloff (Simberloff *et al.* 1992) remain much more cautious or sceptical of the rationale behind the use of corridors. One of the main reasons for this dispute is the lack of experimental data supporting the role of corridors in maintaining biodiversity. Our results demonstrate experimentally that in the moss-island micro-ecosystem, intact corridors do indeed slow down the process of extinction following fragmentation. The obvious difference between intact and broken corridors means that the extra area in corridors is not important; this in turn implies that restriction of movement is the key to understanding the dynamics of the experiment.

We interpret these results as indicating that in this moss micro-ecosystem, inter-patch movement maintained by the existence of corridors may allow small extinction-prone populations to persist longer than those existing in the unconnected fragmented landscapes. Harrison (1994) reviewed evidence for metapopulation behaviour, and concluded that the conditions leading to the maintenance of an extinction - migration balance are probably rather unusual in nature: it is possible that the relative sizes of islands, corridors and taxa in our micro-ecosystems were conducive to obtaining a corridor effect. We think that dispersal to adjoining patches on the scale of the experiment probably

ameliorated localised population crashes via a 'rescue effect' (Brown and Kodric-Brown 1977), and that the absence of corridors precluded this process, resulting in permanent extinction. We therefore predict that the population impact of corridors will depend on the scale of the island-corridor system, relative to the size and dispersal powers of species (Harrison 1994; Hanski *et al.* 1996), thus affecting species differentially and possibly predictably. The extent to which these results can be scaled up to macro-scale ecosystems needs to be investigated - small mammals in patches of woodland might be a suitable macroscale analogue of our experiment. Further experiments using the micro-ecosystem could manipulate the relative sizes of islands and corridors to explore scale effects further. Despite the effectiveness of corridors, however, they only slowed the extinction process, rather than preventing it altogether. It is unclear from the present experiment what the long-term (>6months) outcome of fragmentation with corridors might have been, and hence whether the equilibrium number of species in the fragmented landscape with corridors would have been higher than in the totally fragmented landscapes. The observation of fewer species in the connected landscape when compared to the mainland suggests that long-term persistence may only be achieved by connection to an extinction-buffered mainland.

The larger scale γ-diversity (the species richness of the four islands treated as a single replicate) is interesting in the context of whether many small islands accommodate more species than the same area as a single large island (the SLOSS debate: Higgs 1981; Baz & Garcia-Boyero 1996; Boecklen 1997). Having corridors and hence allowing movement might affect this because movement might increase the homogeneity of species composition across connected islands. This idea predicts that the local per-island species richness may be greater than the equivalent disconnected system, but the cumulative species richness for the whole connected system might be lower. However, our data show that, like local species richness, the γ-diversity of connected systems is greater than that of disconnected ones, and there is no evidence for reduced diversity caused by homogenising movement.

The differential impact of fragmentation on predators is a result predicted to a greater or lesser extent by theory (e.g. Cohen & Newman 1991; Holt 1996). The simplest explanation is that the greater movement of predators means that corridors are more important to them. This result supports the body of theory proposing top-down community disassembly (Schoener 1989).

In conclusion, our results support current predictions about the likely effects of corridors; in our moss micro-ecosystem, corridors between isolated habitats slowed the rate of extinction of species relative to fragmented habitats without corridors. We found strong support for the idea that predators suffer more than non-predators, and benefit more from corridors. The data also suggest that the cumulative species richness of entire connected systems is higher than that of fragmented systems. We think more emphasis needs to be placed on the important effects of the larger scale at which processes can operate and the scale over which corridors are effective.

Acknowledgements

We thank Howard Mace for help with a pilot study (done with AG at Nottingham); Paul Murphy for help with mite identification; Jack Rieley for identifying the mosses; Robert Dean for logistical help; Tom Day, and John Lawton for comments on the ms. AG was supported by a NERC studentship. We thank three unknown referees who made important improvements to an earlier version, including the suggestion of analysing γ-diversity.

3.5 Experiment Two

3.5.1 Methods

An interesting and obvious follow up to experiment one would investigate whether islands connected to an extinction buffered mainland show improved persistence of species richness when compared to islands connected only to each other. Thus, here I describe an experiment in which habitat islands were centred on a large continental block of moss (see figure 3.2) and where the different treatments consisted of islands differing in their connectivity with this large central patch.

In November 1996, 7 rocks were partially cleared of moss to the bare rock. Subsequently, and on each rock, one experimental unit (as seen in figure 3.2) was created. Each unit consisted of twelve 10cm^2 habitat islands centred around a large block 30x30cm square. The four fragmentation treatments therefore consisted of a **mainland** (three 10cm^2-sample areas surrounded by the central block of continuous moss), **corridor** (three islands connected to the large central block by a 7cm long and 2cm wide corridor of moss), **broken**-corridor (as the corridor treatment, but the corridors were split by a 3cm gap-thereby controlling for the increased area of the corridor treatment), and **insular** (no corridors present). Islands were sampled from all seven blocks at three-month intervals. There was thus one island per treatment for each sampling date. The experiment was originally planned to run for 12 months, however, because some blocks were partially destroyed by foraging birds the experiment was terminated after six months.

Treatments were removed from each rock after three months and six months. Each island sample was then placed in Tullgren funnel for 48 hours and all the emerging animals collected into alcohol, and identified to major group, and as in the previous corridor experiment, sorted into morphospecies. Species were again sorted into predators and non-predators and preserved in an alcohol:glycerol:water mix.

3.5.2 Results

In the following analyses the dependent variables were the number of individuals and species richness within each 10cm^2 island. Treatment (4 levels) and rock (7 levels) were fitted as factors using GLIM (Crawley 1993). Using the appropriate orthogonal, *a priori,* contrast I tested the prediction that connected treatments (mainland and corridor) would sustain a greater numbers of individuals and species than the disconnected treatment (broken and insular). In addition the remaining orthogonal contrasts were made within

these pairings (mainland vs. corridor and broken corridor vs. island). ANOVA on abundance was conducted on square-root transformed variables and with normal errors. Analysis of variance with species numbers were also conducted with normal errors and square root transformed data. The proportion of predators within each island was added as a further factor to an analysis of variance. Arcsine transformation was not conducted, as there was no improvement in normality. The same orthogonal, *a priori*, contrasts were conducted to examine whether there were higher proportions of predators in connected treatments.

Population response

The micro-arthropod population response to the fragmentation treatment after three and six months is shown in Figure 3.5 a, b.

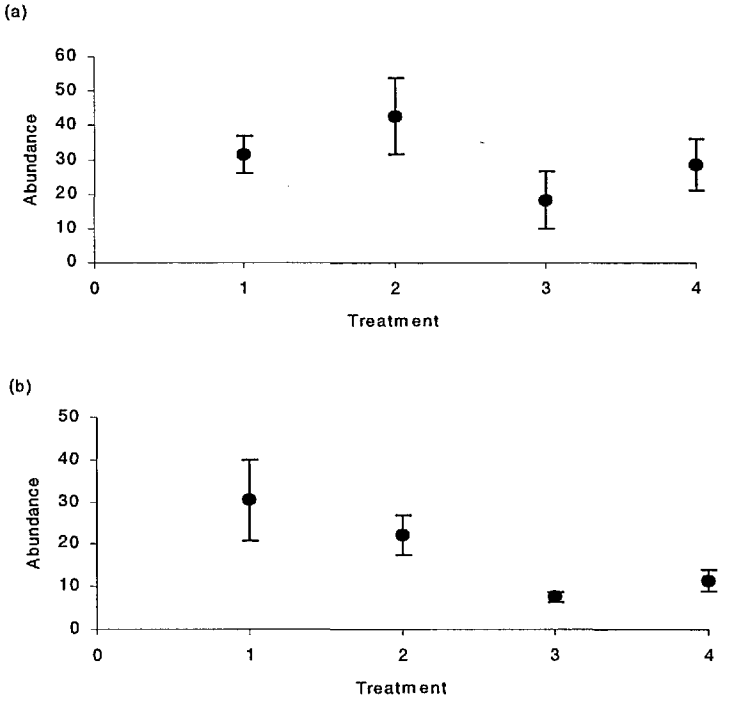


Figure 3.5 Mean total arthropod abundance (±1s.e.) in the moss islands after (a) three months (b) six months. Treatment factor: 1: Mainland 2: Corridor 3: Broken 4: Isolate.

After three months there was a significant overall effect of the fragmentation treatment and the main contrast was also significant (Table 3.3). The mean number of micro-arthropods in the broken-corridor (18±8) and isolated fragments (28±7) was 58% and 34% lower than that of the corridor treatment (42±5).

Table 3.3. The effect of the fragmentation on micro-arthropod abundance after three months. The response of abundance to fragmentation was assessed using an analysis of variance with normal errors and square root transformed abundance.

Source	d.f.	SS	MS	F	P
Fragmentation	3	24.09	8.03	3.56	0.05.
Connected vs. Disconnected	1	21.21	21.21	9.42	<0.01
Mainland vs. Corridor	1	1.03	1.03	0.45	n.s.
Broken corridor vs. Island	1	1.85	1.85	0.82	n.s.
Rock	6	112.9	18.8	8.35	0.01
Residual	24	40.52	2.25		
Total	27	177.51			

After six months there was also a significant effect of treatment (Table 3.4). The mean number of micro-arthropods in the mainland islands (30.4±9.5) was 30% higher than the corridor islands (22.3±4.74) and 60-80% greater than the broken corridor (7.5±1.32) and isolated islands (12±2.21). 92% of the effect of treatment was contained in the highly significant *a priori* contrast between connected and disconnected treatments (Table 3.4). Again there was no significant difference between the total abundance in the mainland vs. corridor contrast nor in the broken corridor vs. island contrast. There was no significant block effect and no significant interaction between blocks and treatment.

Table 3.4. The effect of fragmentation on micro-arthropod abundance after six months. The response of abundance to fragmentation was assessed using an analysis of variance with normal errors and square root transformed abundance.

Source	d.f.	SS	MS	F	P
Fragmentation	3	26.3	8.76	4.80	0.01
Connected vs. Disconnected	1	24.2	24.2	13.9	<0.01
Mainland vs. Corridor	1	0.34	0.34	0.19	n.s.
Broken vs. Island	1	1.76	1.76	1.01	n.s.
Rock	6	13.38	2.23	1.28	n.s.
Residual	18	31.19	1.73		
Total	27	70.8			

The absence of any difference between the broken corridor and isolated fragment treatments is an important result that corroborates the conclusion from Experiment 1 that broken corridors are essentially no better than isolated fragments as a means of maintaining population sizes. The implication is that these organisms are dispersal limited even over

short distances and that intact corridors are necessary to sustain local population size. Importantly the small extra area associated with the broken corridor treatment imposed no measurable effect on the abundance within the islands.

Species Response

The response of species richness to fragmentation after three months and six months is shown in Figure 3.6.

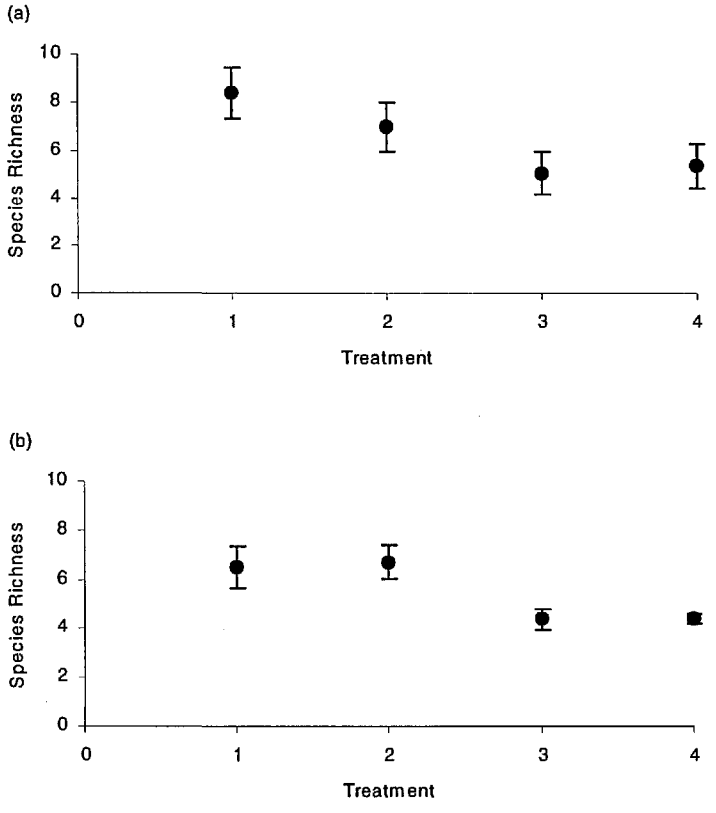


Figure 3.6. Mean species richness (±1s.e.) in the moss islands after (a) three months (b) six months. Treatment factor: 1: Mainland 2: Corridor 3: Broken 4: Isolate.

At three months (Table 3.5) there was as a significant overall effect of 'treatment': and a significant connected vs. disconnected treatment contrast, with 81% of the treatment effects contained in the main contrast. At this stage there were 29% percent fewer species in the fragmented (5.4±0.9) and broken corridor (5.1±0.9) treatments than were present in the corridor treatment (7±1), and 38% fewer than were present in the mainland treatment (8.4±1). Furthermore there was a significant mainland vs. corridor contrast.

Table 3.5. The effect of fragmentation on micro-arthropod species richness after three months. The response of micro-arthropod species richness to fragmentation was assessed using an analysis of variance with normal errors and square root transformed richness.

Source	d.f.	SS	MS	F	P
Fragmentation	3	3.66	1.22	12.07	<0.01
Connected vs. disconnected Contrast	1	2.97	2.97	29.7	<0.01
Mainland vs. Corridor	1	0.44	0.44	4.4	<0.05.
Broken corridor vs. island	1	0.25	0.25	2.5	n.s.
Rock	6	10.59	1.76	17.65	n.s.
Residual	18	2.4	0.10		<0.01
Total	27	16.65			

After six months there was still a significant effect of treatment (Table 3.6), with now 99% of the treatment effect contained within the connected vs. disconnected contrast. The disconnected treatments had ≈35% fewer species than the connected treatments. However there was no significant difference between the mainland and the corridor and similarly no significant difference between the broken corridor and fragmented treatments (Table 3.6). Again there was no significant block effect or any significant interaction between blocks and treatment.

The result in the previous section that intact corridors were necessary to maintain species abundance is therefore also reflected by species richness. Broken corridors, are again completely ineffective at maintaining species richness.

Table 3.6. The effect of fragmentation on micro-arthropod species richness after six months. The analysis was conducted using ANOVA with normal errors and square root transformed richness.

Source	d.f.	SS	MS	F	P
Fragmentation	3	1.335	0.44	4.4	0.01
Connected vs. Disconnected	1	1.331	1.331	13.31	<0.01
Mainland vs. Corridor	1	0.003	0.003	0.03	n.s.
Broken vs. Island	1	$0.4x10^{-3}$	$0.4x10^{-3}$	0.004	n.s.
Rock	6	0.36	0.06	0.66	n.s.
Residual	24	2.19	0.09		
Total	27	3.88			

Predators constituted 13.1%±4.6 of the mainland community, 5.14%±3.4 of the corridor community, 3.43%±3.5 of the broken corridor community and 0% of the island community. The overall effect of fragmentation on the proportion of micro-arthropod

predators in the community though, was marginally non-significant after six months (Table 3.7). However, the main connected vs. disconnected contrast was significant. There is therefore some evidence (and support for the results of Experiment one) that predators were disproportionately sensitive to fragmentation and it's amelioration by corridors. There was no difference in the proportion of predators in the mainland vs. corridor contrast nor in the broken vs. island contrast.

Table 3-7. The effect of fragmentation on the proportion of predators using an analysis of variance with normally distributed errors. Proportions were not arcsine transformed because without it the fit to the normal distribution was improved.

Source	d.f.	SS	MS	F	P
Fragmentation	3	647.7	215.84	2.82	0.07
Connected vs. Disconnected	1	378.89	372.55	4.86	**0.05**
Mainland vs. Corridor	1	224	224	2.92	n.s.
Broken vs. Island	1	44.64	44.64	0.58	n.s.
Rock	6	578	96.3	1.25	n.s.
Residual	18	1377.2	76.5		
Total	27	2602.9			

3.6 General Discussion

Connecting isolated patches in the fragmented landscapes of a moss micro-ecosystem resulted in increased effective population size and sustained local species richness compared with disconnected fragments. This is the first experimental evidence that corridors can enhance species richness over several generations. Furthermore the inclusion of a broken corridor treatment ruled out the simple effect of corridor area, and allowed the interpretation that dispersal was important in determining this result.

The declining species richness in Experiments one and two indicates that corridors in this landscape are acting to slow local extinction rather than prevent it entirely; however, because both experiments were terminated after six months it is unclear what the long term equilibrium number of species will be in the connected landscapes. The significant mainland vs. corridor contrast after six months in Experiment one suggests that sustained prevention of local extinction may well only be achievable through connection of islands to a large extinction buffered mainland (Table 3.1). This conclusion finds support in the

result of experiment two in which no significant difference was observed between the species richness of the mainland and corridor connected islands after six months (see Figure 3.6 and Table 3.6).

In the long-standing SLOSS debate over design principles for reserves it has been suggested that minimising extinction will be best achieved through the establishment of large spatially continuous reserves (Wilson ands Willis 1975) a result supported here. However the opponents of this view focused on maximising species richness (e.g. Simberloff and Abele 1976, 1982), through assertion that it is possible to pack more species into a set of smaller reserves. Here the support for this appears to be dependent on whether the system of small reserves is connected or not. In the moss landscapes of this study the four connected islands contained a similar gamma diversity to the mainland whilst the four disconnected patches exhibited a significantly lower gamma diversity than both of these treatments. The results of these studies and that of the previous chapter suggest that over intermediate spatial scales, if the conservation goal is maximisation of species richness, then fragmentation should be kept to a minimum. If fragmentation is unavoidable then movement should be encouraged and corridors established. Even if greater habitat diversity, and subsequently greater species richness, is attainable through the design of a system of spatially separated reserves, corridors should be established to minimise the greater likelihood of stochastic extinction of the smaller populations via the 'rescue effect' (Brown and Kodric-Brown 1977). The movement encouraged by corridors can apparently do a great deal to slow the onset of local extinction and improve the gamma diversity of a connected system of reserves.

The prediction that area sensitive species with low population densities, such as predators, should be differentially susceptible to the effects of fragmentation was supported by these studies. A greater proportion of predators was found on connected islands than disconnected islands.

Given that our understanding of how terrestrial vertebrates respond to corridors and habitat edges is in its infancy (Lidicker and Koenig 1996) it is interesting to consider what general conclusions can be made from this study by scaling up. Even in the absence of specific data for a particular organism or community of conservation concern, one can make several statements of considerable value.

First, extinction is clearly an important population process that can structure communities through effects on incidence no matter what the size and scale of the system (Wright and Coleman 1993; and see Chapter 2). For example the results of this study and those of the previous chapter are consistent with results from work on terrestrial and

aquatic communities (Brown 1977; Brown and Kodric-Brown 1977; Dickerson and Robinson 1985) suggesting that population input/loss processes (and factors that modify them) can be important in determining the local number of species.

Second is the unquestionable importance of connectivity in any landscape. Quite short distances (even for mites!) can represent a considerable barrier to immigration and recolonisation especially if the intervening habitat matrix discourages movement. Once patch size becomes too small to maintain self-sustaining populations, immigration becomes the key population process. Thus if fragmented landscapes are to maintain levels of species richness approximating that pre-fragmentation levels, it is imperative to maximise individual dispersal and movement rates through maximisation of patch density and minimise population loss through increased patch size.

Continued habitat fragmentation, though, at the expense of population size and landscape connectivity will result in irrepressible extinction. Ultimately, population size is the most important factor determining long-term persistence, and no amount of corridors can ensure the long-term viability of small and dwindling populations (Hughes *et al.* 1997).

4

Effects on population persistence: The interaction between environmental noise colour, intra-specific competition and space†

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It is accepted that accurate estimation of risk of population extinction, or persistence time, requires prediction of the effect of fluctuations in the environment on population dynamics. Generally, the greater the magnitude, or variance, of environmental stochasticity, the greater the risk of population extinction. Another characteristic of environmental stochasticity, its colour, has been found to affect population persistence. This is important because real environmental variables, such as temperature, are reddened or positively temporally autocorrelated. However, recent work has disagreed on the effect of reddening environmental stochasticity. Ripa & Lundberg (1996) found increasing temporal autocorrelation (reddening) decreased the risk of extinction, whereas a simple and powerful intuitive argument (Lawton 1988) predicts increased risk of extinction with reddening. This study resolves the apparent contradiction, in two ways. Firstly, by altering the dynamic behaviour of the population models. Overcompenastory dynamics result in persistence times increasing with increased temporal autocorrelation; undercompensatory dynamics result in persistence times decreasing with increased temporal autocorrelation. Secondly, in a spatially subdivided population, with a reasonable degree of spatial heterogeneity in patch quality, increasing temporal autocorrelation in the environment results in decreasing persistence time for both types of competition. Thus, the inclusion of coloured noise into ecological models can have subtle interactions with population dynamics.

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4.1 Introduction

Physical environments are rarely static and the variability in important environmental parameters, such as temperature and rainfall, have widely recognised impacts on natural populations of plants and animals. It is generally acknowledged that an important characteristic of environmental variability, or noise, is its temporal variance (Leigh 1981; Goodman 1987; Wissel & Stöcker 1991; Lande 1993). Recently the potential importance of another characteristic of environmental noise has been recognised: the variance spectra, or colour of the noise (Goodman 1987; Halley 1996). White noise (or noise with a white variance spectrum) contains no temporal autocorrelation and is essentially a series of independent random numbers. For example, if a series of daily temperatures were white, tomorrow's temperature would be independent of today's temperature. Red noise, however, contains positive temporal autocorrelation: tomorrow's temperature is likely to be similar to today's. The colour of environmental noise is potentially important because: (i) the variance spectra of real environmental variables are reddened (Mandlebrot & Wallis 1969; Monin *et al.* 1977; Steele 1985; Williamson 1987; Halley 1996); (ii) the variance spectra of natural population sizes through time are reddened (Pimm & Redfearn 1988; Ariño & Pimm 1995; Sugihara 1995); and (iii) recent theoretical investigations suggest that population dynamics are sensitive to noise colour (Roughgarden 1975; Foley 1994; Caswell & Cohen 1995). A seemingly strong intuitive argument for how noise colour might affect population dynamics is that reddened noise contains runs of bad conditions, and whereas a population may survive one setback, a series of poor conditions will lead to a higher risk of extinction (Lawton 1988; see also Halley 1996). Thus, deciding whether environmental fluctuations are correlated or not is essential when attempting to estimate a population's probability of extinction.

This paper investigates the problem of how environmental autocorrelation affects time to extinction and, specifically, why in some cases it increases estimated persistence time, whilst in others it decreases estimated persistence time (Ripa & Lundberg 1996; Foley 1994). In an interesting recent paper, Ripa & Lundberg (1996) (hereafter referred to as R&L) showed that increasing temporal autocorrelation in the noise process (reddening the noise) caused a *decrease* in extinction risk. This is in direct contradiction to Lawton's (1988) intuitive argument, which predicts reddened noise to *increase* (relative to white) the risk of population extinction. Both over-estimation of time to extinction, and under-estimation are potentially very dangerous; while species become extinct at unprecedented rates (Lawton &

May 1995), and more become endangered, accurate predictions about extinctions are paramount. The apparent contradiction in the effects of environmental autocorrelation on extinction probabilities raises serious doubts to the accuracy of predictions of population persistence: not even the expected direction of the effect of reddened spectra appears to be consistent, let alone the magnitude. R&L suggest that model choice may severely influence estimates of extinctions times. This paper extends that of R&L by including different forms of intra-specific competition, thereby changing the dynamic behaviour of the model and identifying the difference between R&L's study and the intuitive argument. The significance of spatial subdivision of populations on the risk of extinction under different types of noise is also investigated, further demonstrating that the inclusion of coloured noise into extinction models can have subtle interactions with population dynamics.

4.2 Importance of competition

Model formulation

R&L used the discrete-time Ricker growth model to investigate the effect of the colour of environmental noise on the probability of extinction of a single-species population.

Density dependence in the Ricker model results in overcompensatory dynamic behaviour. In order to investigate the effects of a range of dynamic behaviour, the model used by R&L was generalised to:

$$N_t + 1 = N_t \cdot \exp\left(r \cdot \left[\frac{N_t}{K_t} \right]^b \right) \qquad \textit{Equation 4-1}$$

Here, the parameter b controls the dynamic behaviour, from overcompensatory dynamics when $b = 1.0$ (the case of R&L) with a continuous change to undercompensatory dynamics when $b \approx 0.1$ (with perfect compensation lying somewhere in between)(Figure 4.1). The form of mortality for Equation 4.1 is unusual because mortalities are not equal at low densities for different values of b (Figure 4.1(a)). Whereas in the model of Hassell (1975), given by:

$$N_{t+1} = \frac{\lambda \cdot N_t}{1 + \left[\frac{N_t}{K_t} \right]^\gamma} \qquad \textit{Equation 4-2}$$

mortalities are equal at low densities (Figure 4.1(b)). In Equation 4-2, K_i is the reciprocal of the a usually used in the Hassell model. We concentrate on Equation 4-1 to allow comparison with R&L, but also present results using the Hassell model (in both cases the qualitative results are the same). Demographic stochasticity was included in both models by taking population size as an integer. The population size in the next generation was then a random number taken from a Poisson distribution with the deterministic expectation of the population size as its mean. Hence, Equation 4-1 becomes:

$$N_{t+1} = Z\left(N_t \cdot \exp\left(r \cdot \left[\frac{N_t}{K_t}\right]^b\right)\right) \qquad \textit{Equation 4-3}$$

where $Z \sim \text{Poisson}(N_t \exp(r\,(1-[N_t/K_t]^b)))$. The distribution of the sum of N_t independent Poisson distributions each with the same mean $(\exp(r\,(1-[N_t/K_t]^b)))$, is the same as a Poisson distribution with mean $(N_t \exp(r\,(1-[N_t/K_t]^b)))$. Therefore, Equation 4-3 can be interpreted as representing N_t individuals each having a random (Poisson distributed) number of offspring with mean $\exp(r\,(1-[N_t/K_t]^b))$, so that competition between individuals decreases per capita fecundity. By formulating the model in a stochastic framework, extinctions occur in a biologically plausible manner, rather than by setting a minimum population size.

Environmental noise entered the model in exactly the same manner as in the model studied by R&L. Noise had an additive effect on the mean carrying capacity K_0; $K_{t+1}=K_0+\phi_{t+1}$. Autocorrelation in the noise process, ϕ_t, was determined by a first order autoregressive process described by:

$$\phi_{t+1} = \alpha \cdot \phi_t + \beta \cdot \varepsilon_{t+1} \qquad \textit{Equation 4-4}$$

where the parameter α controls the degree of autocorrelation, ε_t is a normally distributed random deviate with zero mean and unit variance and β determines the magnitude of the environmental fluctuations. When $\beta = C\,(1-\alpha^2)^{1/2}$, the variance in K_t is constant for any value of α. C is therefore used to alter the magnitude of environmental fluctuations and is set here at 70. (R&L used C = 20, but this results in very long persistence times when the parameter b is low, hence C = 70 is used instead. The exact value of C used does not influence the qualitative results presented later.) As in R&L, our objective is simply to study the effects of the degree of autocorrelation in the noise process, not to study the full range

of possible noise signals. When α =0, the noise is white; for $0 < \alpha < 1$, the noise is positively autocorrelated; i.e. reddened. If $-1 < \alpha < 0$ the noise is negatively correlated (blue noise); however, blue noise is not generally considered to be a relevant model of environmental variation and is not included in this study.

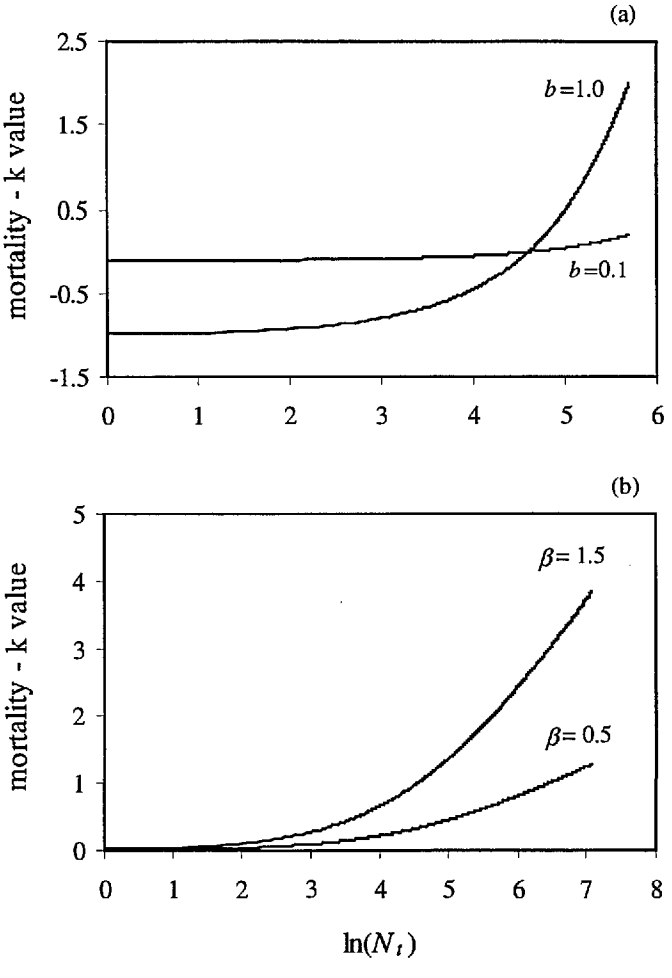


Figure 4.1. *Mortality as k-values ($log(N_t/N_{t+1})$) against log population size for (a) equation (1) and (b) equation (2) showing the effect of altering (a)* b *and (b)* γ *on the type of intra-specific competition. A high value of* b *or* γ *results in overcompensatory dynamics (or scramble competition); a low value of* b *or* γ *results in undercompensatory dynamics (more similar to contest competition).*

Although threshold effects (such as the probability of extinction within 1000 model generations) are a perfectly reasonable measure for comparing different effects, where exactly the threshold is drawn can be arbitrary. Instead, therefore, we used the mean persistence time, $t(e)$, over 1000 independent simulations. The maximum length of one

simulation $t(max)$ was set very large (200,000 generations); if extinction did not occur by $t(max)$, $t(e)$ was set to $t(max)$.

Results of model simulation

For Equation 4-3 when $b = 1$ (overcompensatory dynamics), our results concurred with the study of R&L: increasing autocorrelation in the noise process increased mean persistence time from about 8 generations at $\alpha = 0$ to about 100 generations at $\alpha = 0.95$ (in both cases all 1000 simulations went extinct by $t(max)$) (Figure(a)). However, when $b = 0.1$ (undercompensation) mean persistence time decreased from 150,000 generations (572 extinctions by $t(max)$) when $\alpha = 0.0$ to about 700 generations (1000 extinctions by $t(max)$) when $\alpha = 0.95$.

The effect of increasing autocorrelation in the noise process was, therefore, reversed by decreasing b, and the effect was continuous from $b = 1.0$ to $b = 0.1$. The Hassell model returns qualitatively similar results: overcompensatory dynamics result in an increase in persistence time with increased autocorrelation and a decrease in persistence time with undercompensatory dynamics (Figure(4.2b)). In the Hassell model only γ affects whether the model is overcompensatory ($\gamma > 1$), undercompensatory ($\gamma < 1$) or has perfect compensation ($\gamma = 1$). The value of λ has no effect on this (although it can change the stability of the equilibrium). Therefore, the change in the two types of pattern seen in figure 4-2(b) occurs at $\gamma = 1$. In equation (4-1), the change from over- to undercompensation is a complex function of both r and b; an increase in either leading to more overcompensatory dynamics. However, the change in the types of pattern seen in figure 4-2(a) occurs, as in the Hassell model, at the point where the dynamics change from over- to undercompensation. It should be stressed that we are interested in making comparisons of how persistence time changes with α; rather than comparing persistence times for different values of b (as, for example, changing γ in the Hassell model changes the equilibrium population size).

By examining the distribution of population sizes just before extinction ($N_{t(e-1)}$), R&L identified the mechanism causing extinction as overcompensatory crashes (all population sizes prior to extinction were greater than K). Figure 4-3(a) shows distributions of $N_{t(e-1)}$ for the four combinations of α and b representing the four extremes of the simulations. The distribution of $N_{t(e-1)}$ when $\alpha = 0$ and $b = 1$ was spread widely, but the high population

density prior to extinction suggests that demographic stochasticity was not the mechanism responsible for extinction. When α =0.95 and b = 0.1, all values of $N_{t(t-1)}$ were less than 10. This strongly suggests that demographic stochasticity was the mechanism responsible for extinction; an overcompensatory crash would be very unlikely from such a low density. Due to the fluctuating carrying capacity, however, distributions of $N_{t(t-1)}$ give limited information when attempting to determine the extinction mechanism.

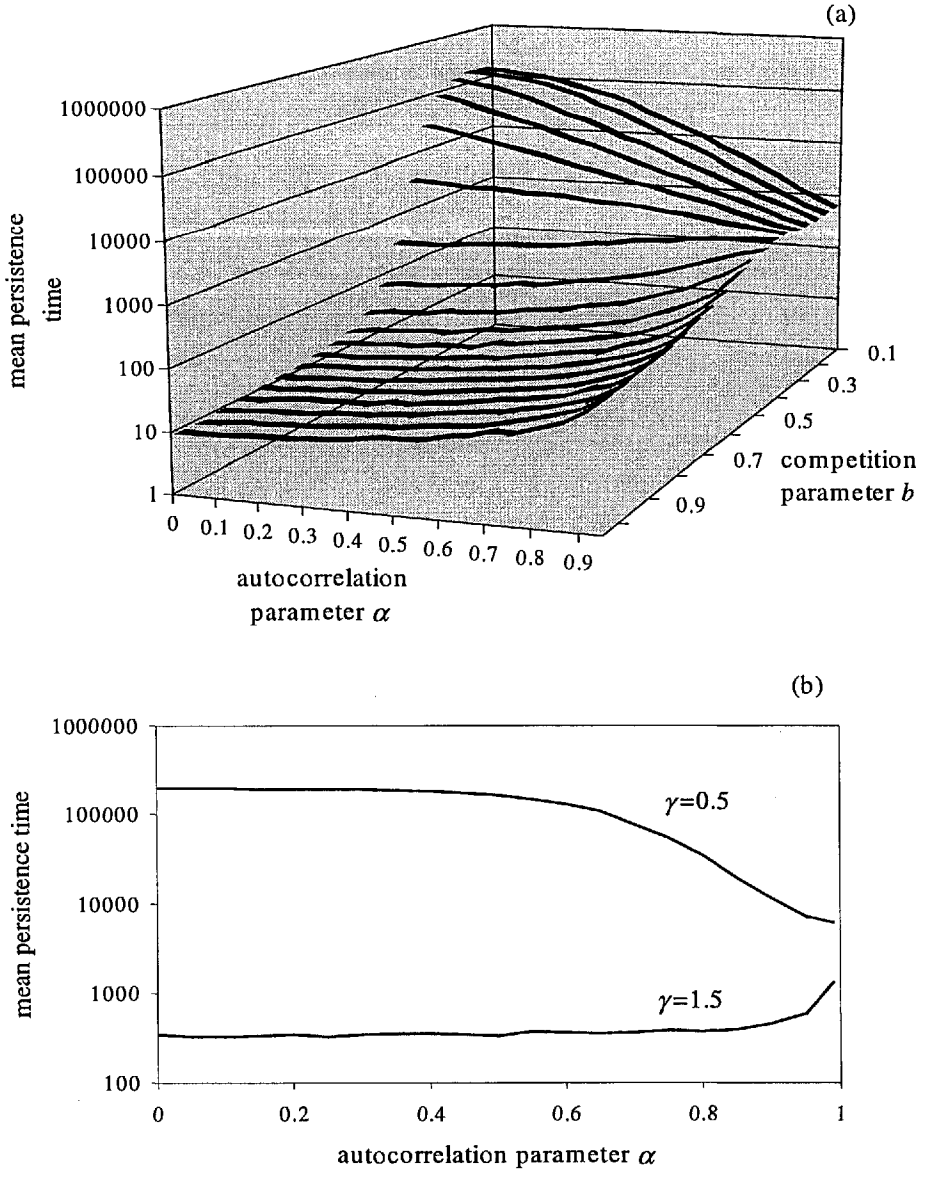


Figure 4.2 *Mean persistence time (of 1000 simulations) as a function of temporal autocorrelation in the environment,* α*, and the dynamic behaviour of the model, controlled with* b*, for the non-spatial model ((a) Equation 4-3, and (b) Equation 4-2). The carrying capacity* K_t *is given by the stochastic process* $K_{t+1}=K_0+\phi_{t+1}$; $\phi_{t+1}=\alpha\phi_t+\beta\varepsilon_{t+1}$, *where* ε_t *is a normally distributed deviate with mean zero and unit variance. The amplitude of the noise,* β, *is given by* $\beta=70(1-\alpha^2)^{1/2}$, *hence the variance*$(K_t)=70^2$ *for all* α. *Other parameters are* $r = \lambda = 1.5$, $K_0=100$ *and* t(max)=200000.

To elucidate the mechanisms causing extinctions, therefore, the distributions of $\log_{10}(N_{t(e-1)}/K_{t(e-1)})$ were plotted for each case (Figure 4-3(b)). $\text{Log}_{10}(N_{t(e-1)}/K_{t(e-1)})$ was used to determine whether population size should have increased or decreased from $t(e\text{-}1)$ to $t(e)$, and then to infer the mechanism responsible for extinction. If $\log_{10}(N_{t(e-1)}/K_{t(e-1)}) > 0$, population size should have decreased from $t(e\text{-}1)$ to $t(e)$ and if, in addition, population density was high, an overcompensatory crash alone is inferred to have caused extinction. Conversely, if $\log_{10}(N_{t(e-1)}/K_{t(e-1)}) < 0$, population size should have increased from $t(e\text{-}1)$ to $t(e)$ and if, in addition, population density was small, demographic stochasticity alone is inferred to have caused extinction. Simulations with b=1 resulted in distributions with $\log_{10}(N_{t(e-1)}/K_{t(e-1)})$ generally greater than zero (see Figure 4-3(b)) and population densities were generally high before extinction (see Figure 4-3(a)). Thus, overcompensatory crashes were inferred as the extinction mechanism. Distributions from simulations with b=0.1 were generally less than zero indicating that population growth was expected, when actually the population density decreased to zero (see Figure 4-3(b)). In addition, population sizes were generally small (see Figure 4-3(a)), so that demographic stochasticity was therefore the mechanism responsible for extinction.

The patterns in persistence times described above were, for both models, with parameters that resulted in single point equilibria. The models can display non-equilibrium dynamics when density dependence is highly overcompensatory. However, the stability of the local equilibrium has no effect on the general pattern of increasing or decreasing persistence time with changes in the autocorrelation parameter (although it may have an effect on the absolute value of the persistence time). This is because fluctuations in K_t results in fluctuations in the population size far from the local equilibrium point. The effects of the type of competition (under- or overcompensation) are then the determining factor, rather than the dynamics in one local area of the phase space (around the equilibrium). To confirm this, we investigated the effects of noise colour on persistence times for parameter combinations that resulted in non-equilibrium dynamics. We found that persistence time increased with autocorrelation. This is consistent with the dynamic behaviour of the models being overcompensatory, the dominant cause of extinction being overcompensatory crashes and white noise therefore resulting in lower persistence times.

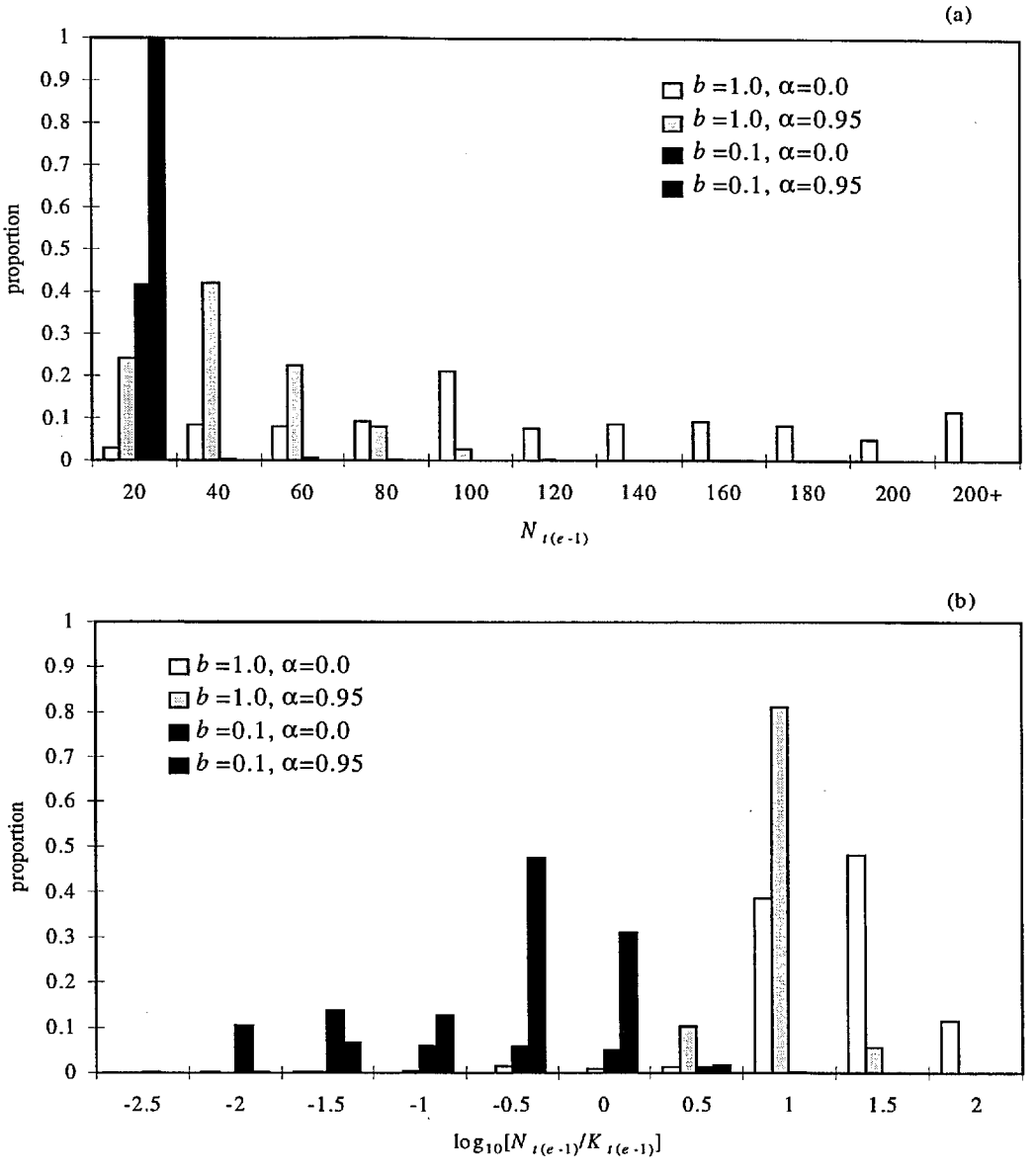


Figure 4-3 *Frequency distributions of (a) population size* $N_{t(e-1)}$, *and (b)* $log_{10}(N_{t(e-1)}/K_{t(e-1)})$ *one time step prior to extinction, t(e-1), for Equation 4-3. Four distributions are shown, for each combination of low (0.0) and high (0.95)* α *with undercompensatory (b=0.1) and overcompensatory (b=1.0) dynamics. All other model details are as in* ***Figure*** *4-2.*

The conclusions about the mechanisms responsible for extinction in different simulations were reinforced when the strength of demographic stochasticity was increased (by increasing the variability around the mean population size). For example, a negative binomial distribution, with the variance greater than the mean, could be used in Equation 4-3, instead of a Poisson distribution. Since demographic stochasticity does not cause extinction in the overcompensatory model, changing its strength should not change the mean persistence time. Accordingly, changing the strength of demographic stochasticity

was found to decrease mean persistence time in the model with undercompensation, but to have no effect in the model with overcompensation.

The opposite effects of noise colour seen with different types of competition, and therefore dynamic behaviour, represent the intuitive argument of the introduction in this paper and the theoretical study of R&L. The intuitive argument assumes demographic stochasticity as the extinction mechanism. R&L studied the effects of noise colour in a model with overcompensatory dynamics, and thereby revealed a fascinating counter-intuitive result caused when overcompensatory crashes are the mechanism responsible for extinction.

4.3 The importance of space

Model formulation

Consider a spatially subdivided population. Changing habitat quality across a landscape leads to spatial variation in the chances of individual survival and reproduction, resulting in heterogeneity in the local number of individuals. This spatial variability, when coupled to temporal environmental variability, leads to an ever-changing spatial pattern in the chances of survival and reproduction for an individual and consequently local variability in population size. Such circumstances, it has been suggested, result in a regional metapopulation structure in which persistence is attained via constant dispersal between transient local sub-populations (Gilpin & Hanski 1991).

The consequences of changing the temporal correlation in environmental noise for metapopulation persistence in a spatially heterogeneous environment were explored by employing a spatial extension of R&L's model.

The metapopulation structure was modelled as 100 patches linked by dispersal. Local, within patch, dynamics were modelled using equation 4-1 with $b = 1.0$ (overcompensatory dynamics for all simulations) and are therefore identical to those in R&L except for the addition of demographic stochasticity. After the local dynamics a dispersal phase follows, with the probability of any given individual dispersing being fixed and density independent. The dispersal process is global rather than local, so that the probability of a dispersing individual reaching any patch in the landscape is identical.

Metapopulation extinction occurs when $N_t = 0$ for all patches. Mean persistence time of the metapopulation over 100 simulations was used as the response variable. The maximum length of one simulation $t(max)$ was large (100,000 generations); if extinction did not occur by $t(max)$, $t(e)$ was set to $t(max)$.

Environmental variability is included in two ways. Temporal variability is due to fluctuations in the mean carrying capacity across the landscape, K_t, determined in the same way as in the previous section. The value of α therefore determines the level of autocorrelation in the variability in K_t. In addition, there is spatial heterogeneity in patch quality across the landscape, represented by different carrying capacities of the individual patches. At any time the carrying capacities of individual patches are normally distributed with mean K_t and standard deviation σ. The standard deviation, σ, is therefore a parameter that controls the heterogeneity in patch quality across the landscape.

Results of model simulation

When the model is run with a single patch, or when $\sigma = 0$, the results are qualitatively the same as those of the previous section and of those of R&L. However, when the population is subdivided between a number of patches (100 in this case), and σ is large enough, the results are reversed (Figure4-4). An interaction between the temporal autocorrelation in K_t and the level of spatial heterogeneity in patch carrying capacity (determined by σ) in determining mean metapopulation persistence time was found. With $\sigma < 20$, increasing α leads to increasing $t(e)$; but with $\sigma > 20$, increasing α leads to decreased $t(e)$.

The effect of σ reveals the underlying mechanism behind this result. Starting with α low (i.e. white noise), increasing σ increases the spatial heterogeneity in the carrying capacity of the environment. Above $\sigma = 20$, the carrying capacity of the patches at any given t now differ sufficiently such that when an unfavourable environmental event (for population growth) occurs, although some patches suffer local extinction through over compensatory crashes, others persist. Extinct patches are then rescued by dispersal from those that survived. It is the spatial heterogeneity of the landscape, which desynchronises population dynamics (Heino *et al.* 1997), and then the rescue effect that promotes persistence. Increasing the level of temporal autocorrelation causes this mechanism to break down. The

temporal smoothing of the environmental noise that results from an increase in autocorrelation now allows the populations to track their envir onment (Figure 4-5) and synchronise through space, increasing extinction risk. Thus during periods of poor environmental quality, because one bad event is more likely to be followed by another and more and more patches suffer sequential extinction, there is a decline in the number of rescuing patches. If the series of unfavourable events is long enough, the number of rescuing patches becomes too small to keep pace with the extinction of existing ones.

The results of the spatial model were found to be sensitive to the number of patches in the landscape, more patches increasing persistence times. Landscape size did not alter the interaction of spatial heterogeneity (σ) with temporal autocorrelation, only the level of heterogeneity needed to cause reversal in the effect of environmental autocorrelation. The larger the landscape, the greater the probability that the dynamics in some patches are not in synchrony with all the other patches, and the lower the level of spatial heterogeneity therefore needed.

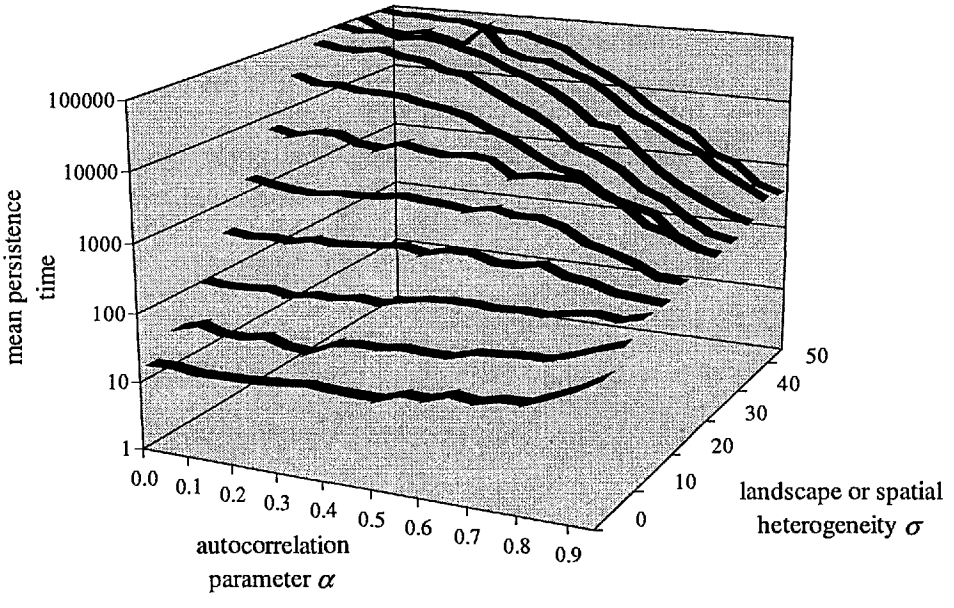


Figure4-4. *Mean persistence time (of 100 simulations) as a function of temporal autocorrelation in the environment* α *and the degree of environmental heterogeneity,* σ*, among the 100 patches.* K_t *is the mean patch carrying capacity at time* t *and is given by the same stochastic process as in the non-spatial model.* σ *is the standard deviation of patch carrying capacities at any one time.* t(max)*=100000, individuals dispersal probability = 0.05.*

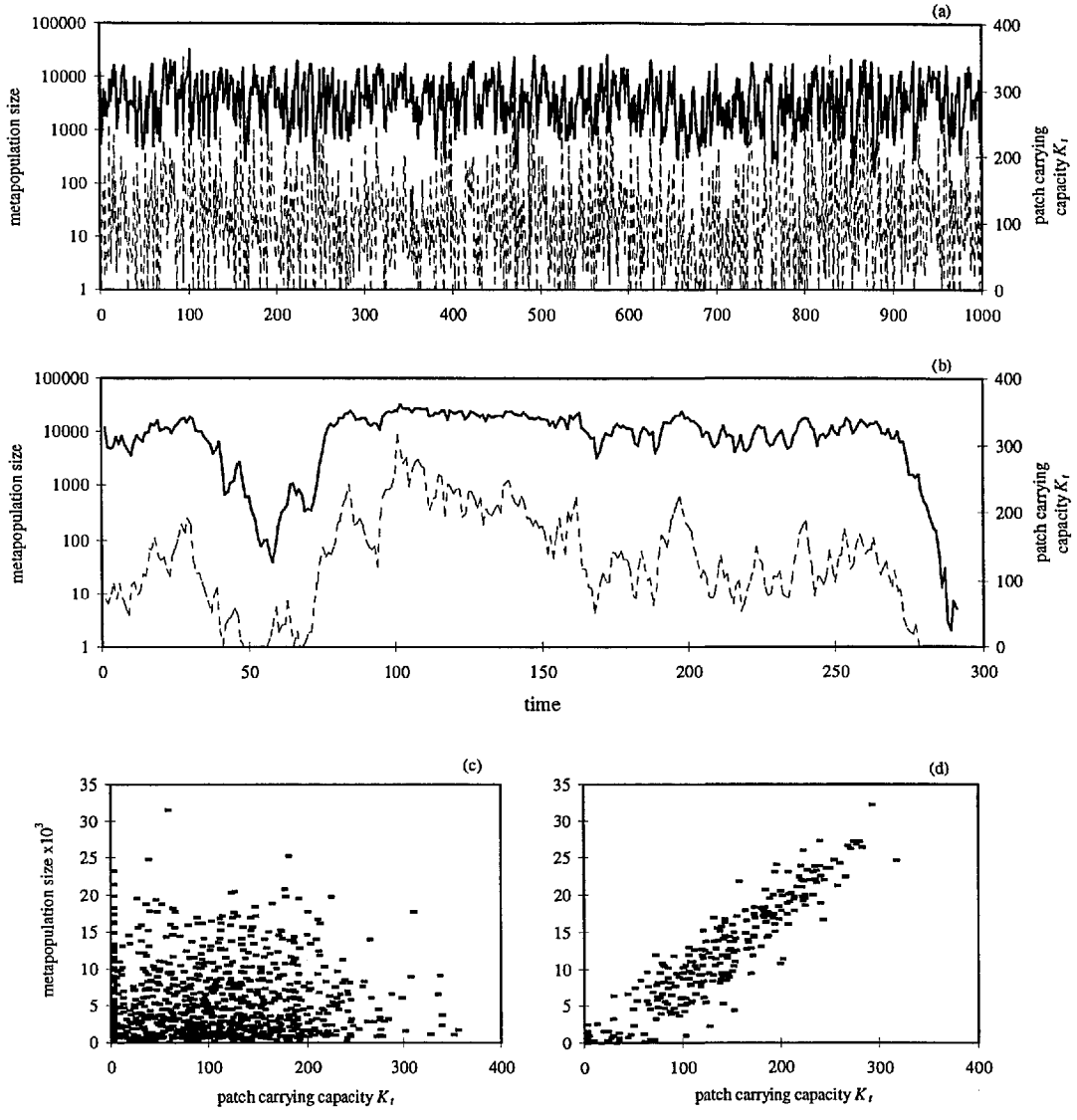


Figure 4-5. *Time series of metapopulation size and patch carrying capacity* K_t *for the spatial model with (a) no autocorrelation (*α*=0.0) in* K_t*, and (c) positive temporal autocorrelation (*α*=0.95) in* K_t*. Scatter plots of* K_t *against metapopulation size for (b)* α*=0.0 and (d)* α*=0.95 indicate how closely metapopulation size tracks* K_t*.*

When the assumption of global dispersal was relaxed to local dispersal (dispersal only to 8 nearest neighbours) persistence times were not affected significantly, and the reversal in the effect of autocorrelation still occurred when environmental heterogeneity was increased. In this case, assuming local dispersal has little effect since an individual's probability of dispersal is low (0.05), so that neither a decrease in the rescue effect, or a decrease in synchrony occurs as a result of assuming local dispersal (although at higher dispersal rates local dispersal can have an effect). The synchrony in population dynamics over the landscape, and therefore population extinction risk, is overwhelmingly determined by

landscape heterogeneity. However, when there are non-equilibrium population dynamics (e.g. chaos), changes in the persistence time effected by autocorrelation and environmental heterogeneity are complex. Asynchrony between patches (which promotes persistence) is now affected by the local dynamics, the landscape heterogeneity and the degree of dispersal between patches. In this case the outcome can be complex, for example with local dispersal and chaotic dynamics the relationship between autocorrelation and persistence can be humped with greatest persistence at intermediate autocorrelation. Lack of space here prevents exhaustive reporting of these results.

Summing up, in our simple, spatially heterogeneous model, R&L's result is now seen to be a non-general case, in which populations exhibit overcompensatory dynamic behaviour, and where patches are relatively uniform in quality across the landscape (σ <20). Where habitat quality varies from patch to patch (σ >20), even with overcompensatory dynamics, the assertion that white noise leads to an optimistic extinction probability (Lawton 1988; Halley 1996) remains valid.

4.4 Discussion

R&L showed that the probability of extinction in a single-species, single patch model decreased as noise colour was reddened. As R&L suggested, this result is contingent on overcompensatory population dynamics. When dynamic behaviour is undercompensatory, reddening environmental noise increases the probability of extinction. It is the dynamic behaviour of the models that determines the effect of environmental noise colour. The dynamic behaviour of the models was controlled by changing the type of competition (Figure 4.1) from scramble competition, where high population densities result in high mortality, through pure contest competition, where a constant number of individuals survive competition, to undercompensatory competition. A new result has been found - the colour of environmental noise and the dynamic behaviour of the population interact. Furthermore, whether a population is spatially subdivided also has important influences on population persistence. Here it is shown that, when coupled with overcompensatory intra-specific competition, white noise results in a highly persistent metapopulation. Persistence of the same metapopulation, however, is significantly reduced as the environment is increasingly reddened, a process shown to be due to the sensitivity of population dynamics to noise colour. Harrison and Quinn (1989) showed a similar effect of decreased metapopulation persistence by reddening the temporal sequence of extinction probabilities.

However, population dynamics were not explicitly modeled in this study, thereby precluding more detailed analysis of possible extinction causing mechanisms.

An immediate question raised by our results is what relationship between environmental autocorrelation and persistence time would we predict in real populations. We would argue that populations generally display undercompensatory dynamic behaviour and, therefore, that their persistence time will be overestimated (rather than underestimated as predicted by R&L) by the assumption of white noise. Although the evidence is limited for this assertion, Hassell, Lawton and May (1976), and Bellows (1981), estimated γ of the Hassell model for a limited number of (insect) taxa and found values that were typically less than 1 (i.e. the predicted dynamic behaviour of the populations is undercompensatory).

Moreover, most natural populations are spatially subdivided, increasingly so due to habitat destruction. The results of the previous section suggest that, once again, use of white noise will overestimate population persistence times. The spatial model investigated above could also be extended to explore effects of spatial autocorrelation in patch quality: patches close to each other would be more similar than distant patches. This is obviously a more realistic assumption than assuming no spatial correlation, as in this study. The likely outcome is that since spatial autocorrelation will lead to less environmental heterogeneity, its effect should be the same as decreasing σ it should lead to a greater risk of metapopulation extinction.

In summary, the demonstrated importance of intra-specific competition, through how it alters dynamic behaviour, and space strongly suggest that, for the majority of real populations, assuming white environmental noise in population models will bias estimates of risk of extinction and persistence time, and that the direction of this bias will be non-conservative.

These results need placing in context in the way in which environmental noise was simulated: an autoregressive process was used to produce reddened noise (as did R&L). Other processes can also produce reddened noise, such as $1/f$ processes (Halley 1996). An important difference between a first order autoregressive process and a $1/f$ process is that where a first order process converges with time to have a constant variance, the variance of a $1/f$ process increases continually with time without limit. The likely importance of these two different ways of generating reddened environmental noise on the persistence of populations requires further investigation. An experimental system designed to investigate the effects of $1/f$ noise on real populations has been designed (Cohen *et al.* 1997, see

chapter 5) and should provide insight into the sensitivity of real organisms to coloured noise.

With ~~growing~~ evidence that environmental variables really are reddened, the need to understand how this might affect population dynamics also grows. Theoretical studies have already shown environmental colour to influence populations (Roughgarden 1975; Foley 1994) and communities (Caswell & Cohen 1995). Here the form of competition (under- or overcompensation) has been shown to have a large effect on the influence of environmental colour, similarly so the effect of spatial subdivision of a population on the influence of noise colour. These interactions between noise colour and competition and noise colour and spatial subdivision, leads us to echo R&L's closing statements. If ecological theory is to give accurate, non-biased information on how best to direct conservation and restoration efforts it must realise the importance of an accurate model of environmental variability, accurate with respect to mean, variance *and* colour.

4.5 Acknowledgements

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5

A novel experimental apparatus to study the impact of white noise and 1/f noise on animal populations†

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This paper reports on the design and construction of a novel apparatus that allows a set of aquatic microcosms to experience complex temporal environmental fluctuations. Replicate microcosms were maintained in 18 water baths with independent environmental controls. We give results from a preliminary experiment designed to look at the effects of varying temperatures with different variance spectra (i.e. white noise or 1/*f* noise) on single species population dynamics. Matching time series (with identical elements, differently ordered) of environmental temperatures with different Fourier spectra were created for use as input to the apparatus using a novel spectral mimicry method. The apparatus functioned well during the course of the experiment making this an extremely useful research tool. This apparatus now provides ecologists with a means of studying how environmental variability, and directional trends in this variability, are filtered and translated by real populations and micro-ecosystems.

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5.1 Introduction

Population biologists have traditionally undertaken studies on the dynamics of species in the laboratory to escape the uncertain nature of a fluctuating environment. A controlled laboratory environment remains a valuable simplification of the real world (Lawton 1996; Lawler and Morin 1996). However, the predictive power of population dynamic theory will remain uncertain until the effects of stochastic environments are understood (Roughgarden 1975; Halley 1996).

The effects of different levels of variability (variance) in the environment on population dynamics are well researched (Leigh 1981; Goodman 1987; Pimm 1991; Lande 1993). Indeed, models used to predict minimum viable population size, maximum harvesting levels or reserve size (to give but three examples) incorporate various levels of environmental variance. Traditionally, 'white noise' has been chosen to model this variability (May 1973; Halley 1996); white noise assumes no correlation, and constant variance over time. Real marine and terrestrial physical variables show increasing variance through time and temporal autocorrelations on a multitude of scales. For example, the variance of temperature (and other variables) increases through time (Monin *et al.* 1977; Steele 1985; Williamson 1987; Pimm 1991). That is, environmental variation is better described as '$1/f$ noise' (Halley 1996). In the $1/f$ model, the power or amplitude of fluctuations is proportional to the reciprocal of their frequency. Daily, high-frequency events have low amplitude; yearly or decadal low-frequency events have higher amplitude; and very rare events (ice ages, for instance) have enormous amplitude. Unlike 'white noise', $1/f$ noise has a reddened spectrum in which long wavelengths predominate. This model has the important feature of increasing variance through time, closely approximating the temporal correlation observed in real environments (unpublished data).

The importance of the distinction between $1/f$ noise and white noise becomes apparent when one considers the effect of the uncertain nature of the environment on the persistence of plant and animal populations. To the extent that population densities are driven by environmental fluctuations (Pimm and Redfearn 1988; Ariño and Pimm 1995) the continued use of white noise in population models ignores the very real problem that populations will encounter unfavourable events with increasing probability the longer they persist (Lawton 1988). Incorporation of white noise instead of $1/f$ noise will hence tend to

underestimate the population size required for persistence in the long term, according to some theories of population dynamics.

Whether this distinction matters in reality depends, it seems, on a number of factors, most notably on the degree of density dependence within a population and the spatial concordance in fluctuations between populations (Hanski, Foley and Hassell 1996; Ripa and Lundberg 1996; Petchey *et al.* 1998). The response also depends on how fast the population can change density relative to how quickly the environment changes (Hubbell 1973; Roughgarden 1975; Nisbet & Gurney 1982). However, until we know how environmental variability is filtered and translated by real populations, development of more realistic population models will remain an uncertain process.

To test the sensitivity of real populations to the colour of the noise they experience, we ideally need replicates of long time series of data from populations that have been exposed to distinctly different patterns of environmental noise. Such data do not exist because field studies cannot provide the necessary environmental control combined with sufficiently long time series. Here we describe a microcosm approach to this problem, in which we expose populations of freshwater protozoa to temperature fluctuations with different variance spectra. The short generation times of freshwater protozoa allow long time series to be collected quickly and temperature is a relatively easy environmental variable to control. The novel apparatus which allows replicated temperature control is described, together with the method used to synthesise noise with different colours, as input into the apparatus.

5.2 The apparatus

The apparatus was designed to allow small replicated aquatic microcosms to experience accurate, complex temporal temperature fluctuations. The experimental design required 18 independent water baths. The apparatus is described in Figure 5-1 and the text that follows; superscript numbers in the text refer to the parenthetical numbers in Figure 5-1.

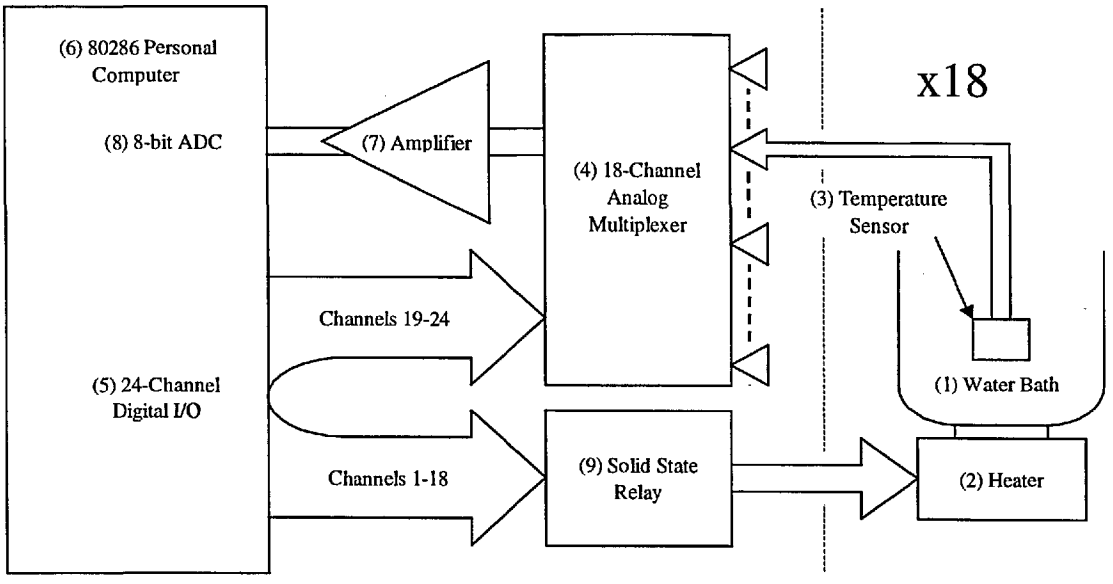


Figure 5-1. Schematic diagram of the temperature control system. Numbers in parentheses are referred to in the text.

Microcosms are contained in covered water baths[1] (5 litre aluminium pans with lids) which, in addition, contain a heating element[2] and a temperature sensor[3]. The heating element is two 100ohm aluminium clad resistors (RS Components stock code 157-588) in parallel, mounted on a small aluminium heat sink. All electrical connections are insulated with adhesive lined heat shrink tubing and covered with epoxy resin. When on, the heating element is driven by a 60volt supply, and delivers 72watts heating power. The water baths are housed in a 2°C refrigerator which has a cooling power of approximately 35watts per water bath. Therefore, when the heating element is on, the baths are heated. When the heating element is off the baths are cooled.

The temperature of each water bath is monitored by a LM35CZ temperature sensor[3] (RS Components stock code 317-960) which provides an output of 10 mV/°C. The initial accuracy of this item is ±0.4°C but sensor specific corrections are applied in software to improve this to ±0.2°C. A 'pulldown' resistor connects each sensor output to -12V to maintain accuracy at lower temperatures. The sensor electrical connections are protected with adhesive lined heat shrink tubing, which is extended over part of the sensor body to prevent water ingress. The whole sensor is varnished for further protection.

The temperature sensor outputs are presented to the multiplexer system[4] as analogue inputs. The multiplexer system comprises two Integrated Circuits (I.C.). Since the

experimental design required 18 channels and standard multiplexers come in 8 or 16 channels, a 16 channel device (I.C. 4067B; R.S. Components stock code 640-636) and an 8 channel device (I.C. 4051B; R.S. Components stock code 640-585) were combined to perform the function of an 18 channel multiplexer. Sensor outputs 1 to 15 are connected to the 4067B I.C. and sensors 16 to 18 are connected to the 4051B. The multiplexer "Address" lines (i.e. the digital signals which determine which input is to be selected) are controlled by a Programmable digital Input/Output card[5] (digital I/O, Maplin Professional Supplies stock code AM11M) which is fitted into a 80286 Personal Computer[6] (P.C.).

The address lines for the 4067B I.C. are driven by channels 19 to 22 of the digital I/O card, the 4051B has its address lines driven by channels 23 and 24. Thus the P.C. can monitor the temperature of each water bath in turn. Unused inputs of the multiplexer I.C.s are deliberately left unconnected to allow each multiplexer I.C.'s output to float while its partner is active: i.e. while the 4067B is active, the output of the 4051B is set to a floating input, and *vice versa.*

The multiplexer output (i.e. the bath temperature being monitored) is amplified[7] and applied to an Analogue to Digital convertor[8] (Pico Technologies Ltd. 8 bit converter ADC10, Farnell Components stock code 256-122), which plugs directly into the parallel port of the P.C.

Bath temperature is then compared with the setpoint temperature (as determined by the required temperature time series) and the digital I/O card channels 1 to 18 are used to turn the appropriate bath heater on or off as necessary. This is achieved by applying a digital signal to the control terminal of a Solid State Relay[9] (CTX240D3Q quad units, Farnell Components stock code 529-771) which controls power to the appropriate heater element. To protect the digital I/O, its outputs are buffered into the Solid State Relays using 74LS244 I.C.s (Maplin Professional Supplies stock code QQ56L).

The control software, written in QBasic, takes as inputs the required temperature time series for each bath and the actual temperature of each bath. The software sequentially reads the temperature in each bath (by connecting the temperature signal from each bath to the ADC via the multiplexer and amplifier). If the actual temperature in the bath is higher than the required temperature for that bath at that time, the corresponding heater is turned off. If the actual temperature is lower than the required temperature the heater is turned on. At user-selected intervals, the software moves to the next temperature value in

all of the required temperature time series. The software also records to a file, at user defined frequency, the actual temperature of each bath.

The apparatus performs as designed. Figure 5-2 shows actual bath temperature and required bath temperature and is typical of the results of other baths. The temperature control is not perfect: the actual temperature in the baths fluctuates around the desired temperature with an amplitude of 0.1-0.5°C and variable period (up to 30 minutes). It is unlikely in theory (and preliminary results suggest) that the population dynamics of the aquatic organisms the apparatus is designed for will respond to fluctuations of this amplitude and period.

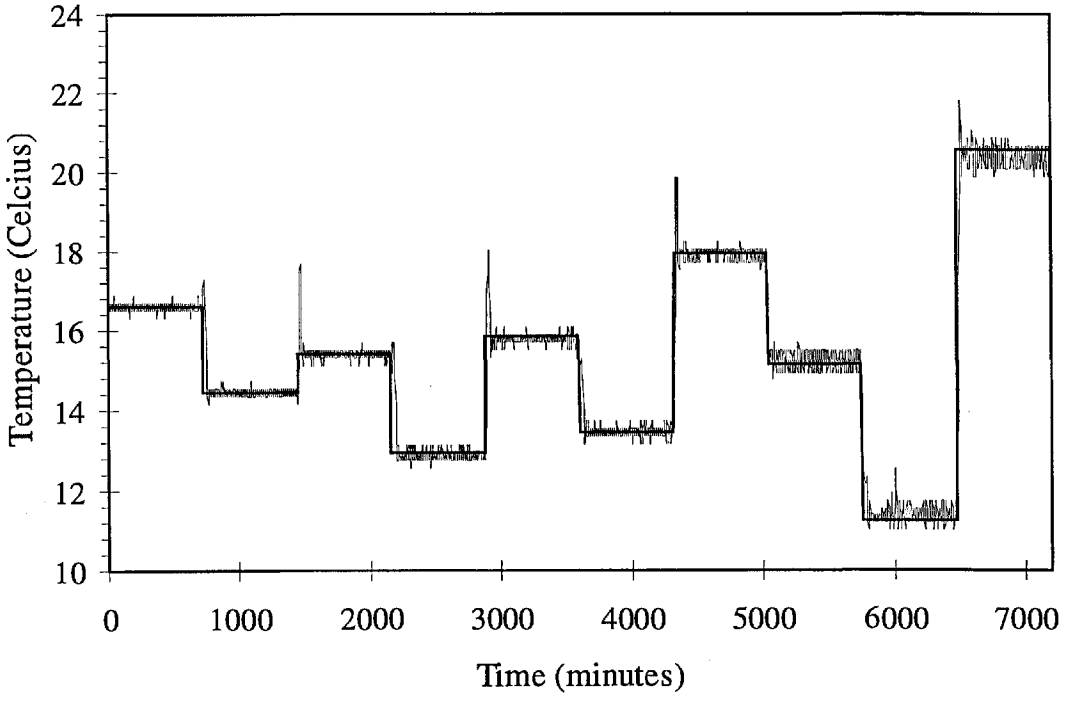


Figure 5-2. Performance of the temperature control system. The square wave (thicker line) is the control temperature, the thinner fluctuating line is the actual temperature recorded by the temperature sensor in a representative culture vessel.

The difference between the mean actual bath temperature over time (12 hours with temperature recorded every 5 minutes) and the required bath temperature is consistently less than 0.3°C. The sign and magnitude of the difference between actual temperature averaged over time and required temperature seems to be bath-specific. This means that the cumulative temperature of baths over time will differ even if they have identical

required temperatures. Correction of the bath specific biases is achieved by measuring the bias over a short time (for example two weeks) and then adjusting the required temperature time series. The adjustment consists of a permanent addition to, or subtraction from the required temperature time series to prevent further biases, and a similar short-term correction to eliminate cumulative temperature differences that have already occurred. Regular monitoring of cumulative temperature during an experiment and continuous adjustment of control temperature series allows bath specific biases to be minimized. Numerical investigation of such manipulations of the required temperature time series show little effect on the colour of the time series.

5.3 Synthesis of temperature series

Time series synthesis allowed control of the spectral properties of the time series with all other statistical properties of the series held constant. The basis of the synthesis was the summation of sine waves and is described next.

The required temperature time series, each of length n, where n is even, were synthesised by the addition of $n/2$ sine waves with phase randomly and uniformly distributed between 0 and 2π. The period of the longest sine wave was n (frequency 1 cycle per time series), the shortest period 2 (frequency $n/2$ cycles per time series), and the remainder $n/2$-2 sine waves with frequencies equally distributed between $n/2$ cycles per time series and one cycle per time series. The relationship between the frequency f and amplitude $S(f)$ of the component sine waves defines the variance spectra (colour) of the fluctuations (Halley, 1996):

$$S(f) = \frac{1}{f^{\gamma}} \qquad \textit{Equation 5-1}$$

To produce white noise, γ was set at 0: all frequencies had equal amplitude. To produce reddened ($1/f$) noise, γ was set at 1, i.e. amplitudes were the reciprocal of frequency.

Pairs of series thus produced, one red and one white, differed in variance and mean. To correct these differences one series was transformed to give the desired range and mean. The other untransformed time series was then mimicked (Cohen *et al.* submitted) to the transformed to ensure that both time series were composed of exactly the same numbers

but in different orders. The order of the numbers defined the variance spectra of the time series.

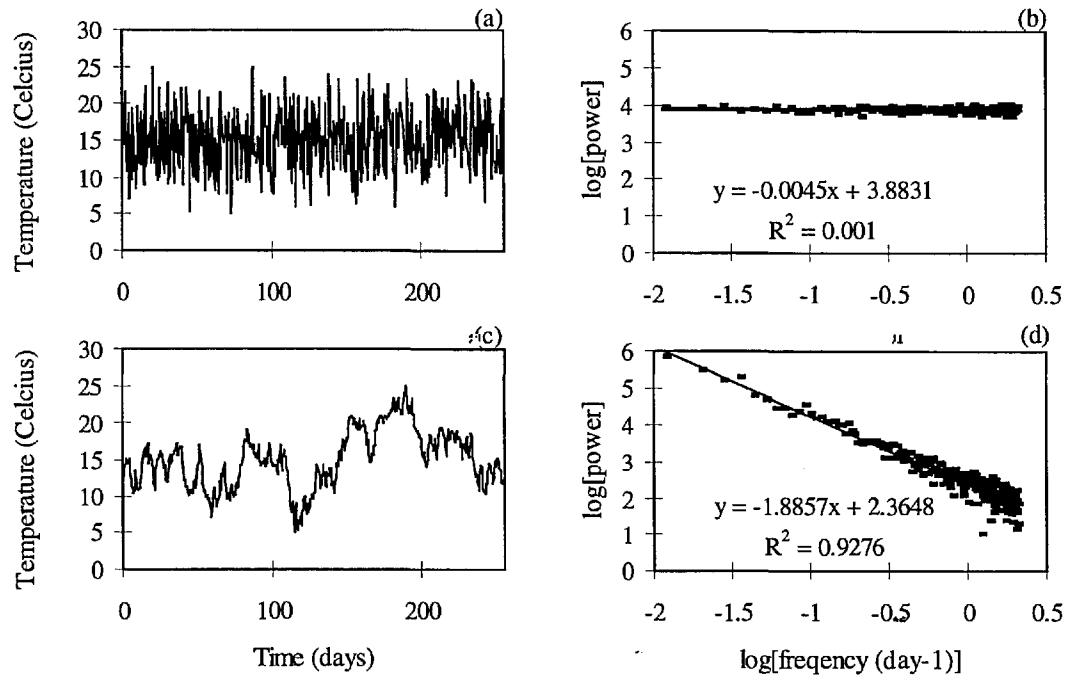


Figure 5-3. Control series synthesized as described in the text (a & c) and their power spectra (b & d). (a) shows a white series (γ=0), (b) its power spectra, showing γ at 0.00225 (half the gradient of the least squares linear regression). (c) shows a 1/f series (γ=1), (d) its power spectra showing γ=0.943.

Examples of time series produced using this method are given in Figure 5-3(a & c). This method of time series synthesis gives very good control over the variance spectra of the noise. To check this we calculated the Fourier transform of the series and retained only the first half of the output (due to the symmetry about its middle) and also discarded the first element. Each of the remaining elements of the transform was then multiplied by its complex conjugate to give the squared amplitude at the corresponding frequency (the power spectral density, psd). The relationship between the power and frequency of fluctuations in the time series is given by plotting log(psd) against log(frequency) (Figure 5-3(b & d)). The slope of the linear regression of this plot is -2γ .

The advantages of this method of time series synthesis over other methods that control the variance spectra are that the variance and mean are exactly controlled, even in a time series of finite length. Further, when γ is set at one, $1/f$ noise is produced (over a finite range of frequencies) and not a statistical analogue of $1/f$ noise such as is produced by an

autoregressive process. That is, our method of synthesizing a $1/f$ noise yields a signal with a psd in which amplitude is exactly proportional to the inverse of frequency, whereas autoregressive noise yields a signal with a psd in which there is statistical fluctuation in amplitude around the reciprocal of frequency. The advantage of $1/f$ noise as a model of environmental variability is that it is more mechanistic. Autoregressive noise models the correlations between numbers in the time series and is therefore a phenomenological model. $1/f$ noise models many different processes that each have characteristic frequency and amplitude, the final signal being the sum of all these processes.

5.4 Preliminary results

A pilot experiment was conducted to test whether cultures of protozoa behaved normally in the water baths and to check the reliability of the temperature control apparatus over several weeks. Six of the baths were set at a constant 15°C and the temperature of the remaining 12 fluctuated between 5°C and 25°C, 6 baths with white and 6 baths with reddened ($1/f$) spectra. Each bath contained a 175ml glass jar containing a 100ml culture of *Paramecium tetraurelia*. Population density of the cultures was estimated every two days by measuring the density of *P. tetraurelia* in approximately 0.5ml of culture media. At the same time 60% of the culture was removed and replenished with sterile media. Population densities of one culture from each of the temperature treatments are shown in Figure 5-4. The cultures grew and persisted in the apparatus. Any further interpretation of these results will have low statistical power since the time series are relatively short. Much longer experiments (approximately 9-12 months) are required to test the sensitivity of these populations to temperature variations with different variance spectra.

5.5 Concluding remarks

The new temperature control apparatus described above is a powerful experimental tool to study the effects of complex and varying patterns of temperature fluctuations on laboratory populations of protozoa and small aquatic invertebrates. Although it was designed with a specific study in mind, its generality and flexibility allow many potential uses. For example, the same principles could be applied to small terrestrial microcosms (when the baths contain no water, control of air temperature is good). It could also easily be adapted to control other environmental variables, such as light or precipitation.

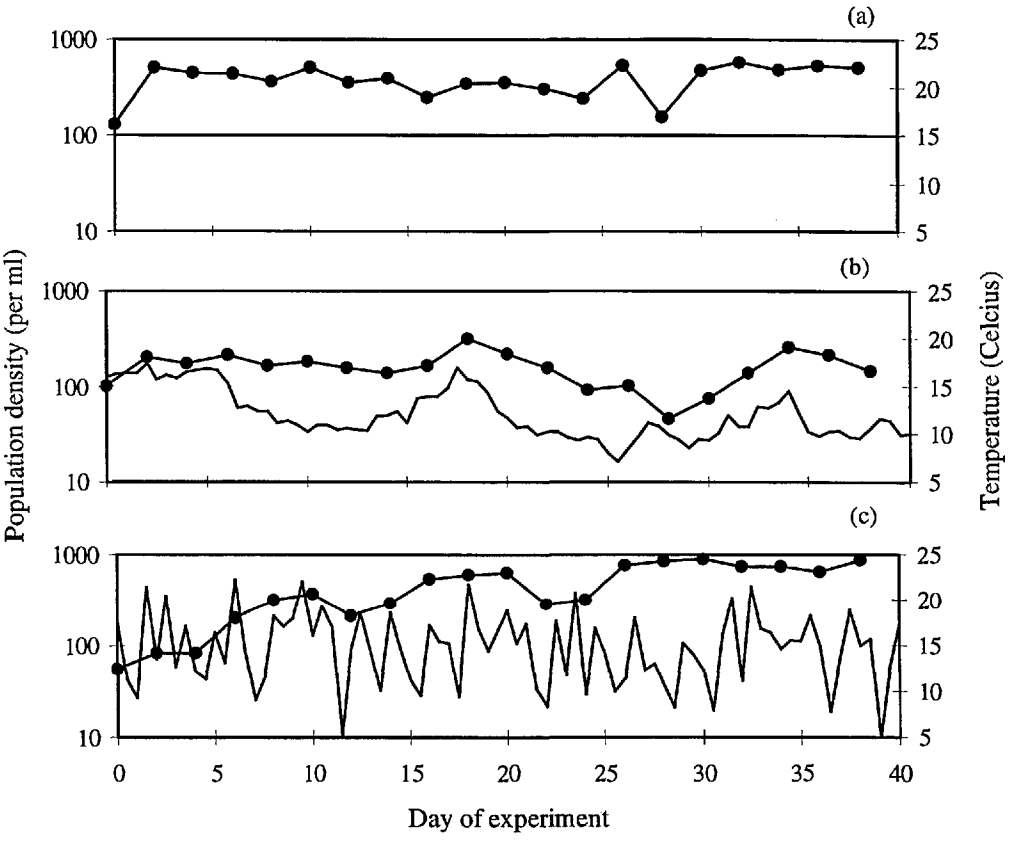


Figure 5-4. Results from a preliminary experiment in which population sizes of *P. tetraurelia* (solid lines with circles) were estimated every other day whilst temperature (solid lines with no circles) was (a) held constant or (b) varied with reddened (1/f) spectra or (c) white spectra. The data are for one representative culture from each treatment.

Laboratory microcosms have played an important role in the development of population ecology (Kareiva 1989; Lawton 1995), but have almost invariably been run under constant conditions. We now have the means to extend the use of microcosms to study the population dynamics of organisms under precisely controlled, but variable, environmental conditions, simulating different types of environmental noise.

5.6 Acknowledgements

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6

A Model and Experiment Examining the Population Dynamic Response of *Paramecium tetraurelia* to 1/*f* Temperature Fluctuations.

Replicate populations of the protozoan *Paramecium tetraurelia* were exposed to fluctuating thermal environments with white and red variance spectra.

Recent theoretical work has demonstrated that populations are sensitive to the colour of environmental noise. Furthermore a growing body of theory implicates the reddened nature of environmental fluctuations as causal in the reddening of population dynamics.

A parameterised simulation model predicted that red environmental fluctuations would redden the dynamics of *P.tetraurelia* whilst white fluctuations would not. Furthermore, reduction in the carrying capacity of the environment resulted in the model predicting extinction under red noise but not under white noise.

A novel experimental test of this theory was conducted. However support for these predictions was limited, due to the premature and unavoidable termination of the experiment, generating shorter than expected time series.

6.1 Introduction

The causal factors responsible for the irregular fluctuations observed in natural populations have been at the centre of a long debate in theoretical ecology. Initially such patterns were mostly attributed to stochastic environmental factors (Davidson and Andrewartha, 1948). However, in the mid-1970s (May, 1974), it was proposed that these fluctuations might be generated intrinsically by the underlying non-linearity of population processes. Such theory has acted as a strong counter-balance to the view that patterns of population fluctuations are predominantly caused by stochastic factors in the environment (Chesson 1981; DenBoer 1981). The relative importance of both processes is still much debated, but because of the practical difficulties involved in the experimental treatment of these problems (very long time series are required to detect the presence of chaos (Hastings *et al.* 1993)) clear examples of both chaotic dynamics and stochastic environmental factors acting in the same population are rare (but see Ostfeld *et al.* 1993; Leirs *et al.* 1997).

This lack of suitable data has meant that in recent years the argument has shifted emphasis and increasingly focused on the statistical properties of population fluctuations. Many of these studies show that ecological systems tend to be dominated by low frequency or long term dynamics (Pimm and Redfearn 1988; Arino and Pimm 1995; Sugihara 1996); that is population fluctuations are 'reddened' (see section 1.3). This relatively new insight has important implications for population persistence. The increasing variance characteristic of reddened fluctuations leads to the prediction that populations will inevitably, eventually make extreme excursions to low population densities (Lawton 1988), with enhanced risks of extinction.

We still do not know why population fluctuations are reddened (e.g. Cohen 1995; Halley 1996; Sugihara 1996; White et al 1996; Kaitala and Ranta 1996). However, the belief that environmental variables are the major driving force (Steele 1985; Pimm 1991; Sugihara 1996) is greatly strengthened by the observation that such environmental variability is itself 'reddened' (Mandelbrot and Wallis 1969; Monin 1977; Steele 1985; Williamson 1988). Yet despite this knowledge, for reasons of mathematical tractability, environmental variability has typically been incorporated into population models as white noise (May 1973). The consequences of this disparity are largely unknown.

However theoretical investigations suggest that populations are sensitive to the colour of environmental fluctuations (Kaitala *et al.* 1997; Petchey, Gonzalez and Wilson 1997; Ripa and Lundberg 1997). For example, whether the resulting colour of population fluctuations

mirrors that of the environment appears to be contingent on the nature of the density dependence exhibited by the population (Petchey, Gonzalez and Wilson 1997). However the exact nature of the relationship between colour of the fluctuations in the environment and the colour of the resulting population dynamics becomes less clear as the complexity of the dynamics increases (Cohen 1995; Kaitala *et al.* 1997).

An important first step towards resolving these problems may be made by comparing sufficiently long time-series (Royama 1992 *et al.*) of experimental populations grown under constant and fluctuating environments with different variance spectra. I report here on the results of one such experiment. It is a novel study, using protist microcosms, designed (see chapter 5) to examine whether thermal environments with different variance spectra (red or white) result in population dynamics of different colour. This experiment is coupled with a simulation model of protozoan growth. The population model incorporates white and red $1/f$ temperature fluctuations into an experimentally measured, temperature dependent, growth function. This is the first use of $1/f$ noise to examine the population dynamic consequences of different coloured environmental fluctuations.

Temperature was chosen because vital processes, such as energy transduction, reproduction, and growth are all affected by temperature change. Whilst every organism has the potential to exist over a range of temperature conditions, towards the extremes of this range vital processes start to operate sub-optimally (in the sense of Huey and Stevenson 1979), threatening population viability.

6.2 Experiment and Modelling Overview

This study set out to examine how the population dynamics of the protozoan, *Paramecium tetraurelia*, responded to environments with different patterns of variability between two non-lethal temperature extremes. Thus the objective was not to cause extinction in the experimental populations but rather to examine whether white noise or red noise environments generated different patterns of population variability.

In order to extend the empirical work and to provide some form of prediction, a model of the protozoan population was parameterised and calibrated, with additional experiments. Using this model it was possible to examine the potential response of the protozoan to environments with fluctuations of different colour. The model was also used to extend the study to allow analysis of extinction likelihood in these environments.

6.3 Study Design

Populations of the protozoan, *Paramecium tetraurelia*, were grown in the controlled environment facility described in chapter five. The equipment delivered environments that differed in their variance spectra. There were six replicates populations per treatment experiencing a constant environment, an environment in which the fluctuations in temperature had a white variance spectrum, and an environment in which temperature fluctuated with a red variance spectrum.

Time series of environmental temperatures were created using a $1/f$ process as described in Chapter five. To reiterate, the temperature series were created by summing series of sine waves in which the relationship between their power $S(f)$and frequency was determined using the following equation:

$$S(f) = \frac{1}{f^{\gamma}} \qquad \textit{Equation 6- 1}$$

Where $\gamma = 0$ all frequencies have equal power (white noise) and if $0<\gamma<2$ power decreases with increasing frequency. In this study red environments had a $\gamma=1$ thus we had true reddened $1/f$ noise. The required red and white series were constructed with identical mean and variance, by permuting the identical elements in a different order.

Populations were maintained in 100ml of nutrient medium, made from autoclaved and filtered pond water. To each litre of pond water a single (0.70g) Carolina Biological Supply protozoan pellet was added. Each stock was then inoculated with three species of bacteria (*Serratia marcescens*, *Bacillus subtilus* and *Bacillus cereus*). The 100ml of medium were contained in 175ml jars, covered with an aluminium foil lid and placed in the relevant temperature control apparatus (during calibration experimental jars were maintained in constant temperature incubators).

Populations were sampled, and their densities estimated every two days. On each occasion jars were gently swirled to produce an even suspension of the organisms throughout the water column. A small sample was removed using a Pasteur pipette and the contents were added to a counting slide. Each counting slide consisted of two (4cm long and 2mm wide) channels into which the sampled medium was added via capillary action. The numbers of protozoa per slide were counted under a dissecting microscope. From this sample an estimate of the density of the population per ml was made.

6.3.1 OTHER EXPERIMENTAL DETAILS

In this section I describe the results from a series of preliminary experiments conducted to establish the behaviour of the population in different thermal environments. From these experiments important parameters such as realised growth rate and carrying capacity were estimated.

Growth rate and Carrying Capacity Estimation

In order to establish the range of the thermal niche of *P.tetraurelia* replicate observations of growth over a range of temperatures (4°C, 10°C, 15°C, 20°C, 30°C, 40°C) were made. Populations of *Paramecium* were maintained in incubators at these temperatures for 10 days. This allowed sufficient time for the populations to come to equilibrium. During this period population density was estimated every two days by measuring the number of individuals in approximately 0.5 ml of medium. Typical population growth curves during are shown in Figure 6-1.

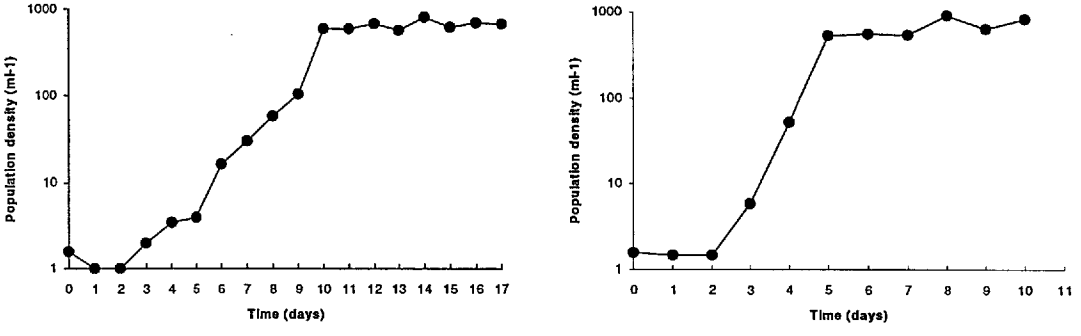


Figure 6-1. Examples of growth of *Paramecium tetraurelia* in 15°C and 20°C environments. Note the good approximations to logistic growth.

The growth displayed by these populations is assumed to be a good approximation to the logistic growth curve and as such these data can be used to estimate growth rate using the method of Pearl (1930).

By rearranging the integral form of the logistic equation we get:

$$\ln\frac{K-N}{N} = a - rt \qquad \textit{Equation 6-2.}$$

This is the equation for a straight line in which the y co-ordinate is ln [(K-N)/N], the x co-ordinate is time, and the slope of the line is r. With this equation an approximate estimate of the growth rate, r, can be made. The asymptotic density is estimated by taking the mean of these data points that appear to be at equilibrium density. Once K is estimated, one can estimate the (K-N)/N term of the equation. These data can then be plotted in the linear form and the slope of this line is an estimate of the rate of population growth (see Figure 6-2). This is repeated for each replicate so that means and standard errors for growth rate are acquired at each temperature (see Table 6-1).

Growth rate is then is plotted against temperature in order to establish the growth response function of the protozoan across different temperatures. Figure 6-3 shows that between the temperature of 5-25°C growth is always positive and is well approximated by a linear relationship. Below 5.15°C growth is predicted to become negative and the population is incapable of sustaining itself. Inclusion of the growth response at 40°C on this plot complicates this relationship so that a third order polynomial is more appropriate (see Figure 6-4).

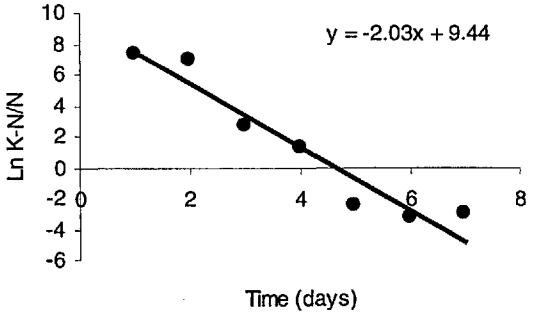


Figure 6-2 Logistic growth of *Paramecium tetraurelia* at 30°C plotted in linear form: Ln[K-N/N]=a-rt. The slope of the least squares regression provides the estimate of the growth rate (slope = growth rate = 2.03).

The effects of temperature on growth rate may therefore be described as a vertical perturbation *sensu* Royama (1992). In effect the population can only persist within a certain temperature range, outside which the effect of decreasing temperature is to cause the reproductive rate to decrease to zero or become negative so that the population has no chance of persisting. As the temperature is increased the reproductive rate reaches a maximum (where the chance of persistence is greatest). For *P.tetraurelia* in this experiment we find that this is achieved at approximately 30°C. Beyond this the reproductive rate declines again so that at 40°C the reproductive rate becomes zero.

Table 6-1 Estimates of K (ml^{-1}) and r (day^{-1}) for the logistic curve fitted to growth data of *Paramecium tetraurelia* at 6 different temperatures. Three replicate time series were used to provide a mean and (±1) standard error for each temperature. Estimate of $K(ml^{-1})$ pertains to the maximum attainable.

Temperature (°C)	$K(ml^{-1})$	$r(day^{-1})$
4	966.09±164.25	0.02±0.01
10	966.09±164.25	0.20±0.05
15	966.09±164.25	0.74±0.20
20	966.09±164.25	1.22±0.19
30	966.09±164.25	1.90±0.19
40	966.09±164.25	0

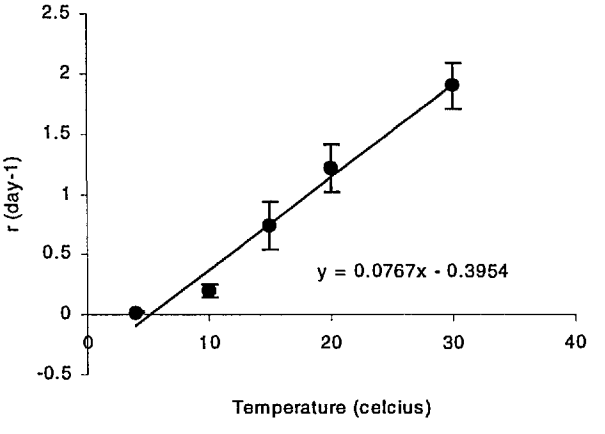


Figure 6-3. The relationship between r and temperature over a 4 - 30°C temperature range. Error bars are ±1 standard error from Table 6-1. The equation of the least squares regression is shown.

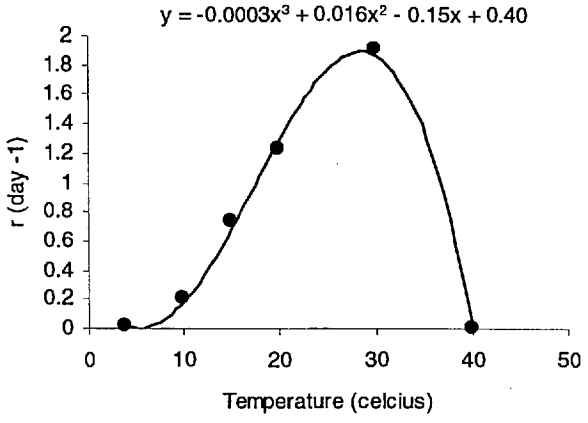


Figure 6-4. The relationship between growth and temperature once the value for 40°C is included. The linear relationship know no longer holds over the entire span of the thermal niche of this organism. The equation for the third order polynomial least squares regression is shown.

Experimental Aim

In order to study the relative effects of red and white environmental noise on the population dynamics of the protozoan the key requirement is for time series of sufficient length to provide adequate statistical power. In order to achieve this it is necessary to prevent extinction. Thus the range of temperature fluctuations experienced by the organisms was restricted to 5-25°C. Within this range population growth is always positive. Furthermore, and perhaps most importantly, because the total variance of the red and white noise treatments is only defined, and equal, for the entire, planned length of the experiment persistence throughout the duration of the experiment was essential.

Preliminary experiments (Figure 6-5) showed remarkably little difference in the dynamics of *P.tetraurelia* under red and white environmental noise. The main reason appears to be that in attempting to avoid temperatures that lie at *P.tetraurelia* physiological limits too few animals suffered sufficient mortality to perturb the populations away from equilibrium. Accordingly at each census (every 2 days) in the main experiment, 60% of the *P.tetraurelia* population were harvested, thereby repeatedly pushing the populations away from equilibrium.

The population harvest was conducted after the normal sampling procedure described in 6.3. After the jars had been swirled 60% of this even suspension was poured into a measuring cylinder and discarded. This was then replaced with sterile, fresh nutrient

medium (filtered and autoclaved pond-water containing a single Carolina supplies wheat pellet) to the pre-harvest level.

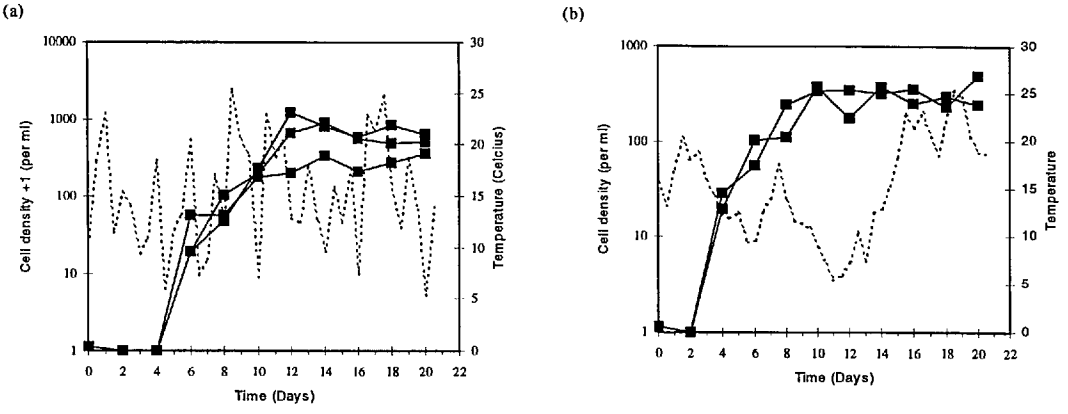


Figure 6-5. Population response of *P.tetraurelia* during a 3 week pilot experiment to (a) white noise (b) red noise temperature fluctuations between 5-25°C. Dynamics show very little difference to those exhibited by cultures grown in a constant environment.

6.3.2 MATHEMATICAL MODEL

A simulation model of *P.tetraurelia* population dynamics was parameterised using the above estimates for reproductive rate at different temperatures, and the carrying capacity. With this parameterisation it was possible to predict the population dynamic response of *P.tetraurelia* to the constant, red and white noise treatments. Furthermore it was possible to extend the analysis to examine the conditions necessary to cause extinction in small populations. This was done by reducing the carrying capacity of the model environment.

A recurrence-equation representing logistic growth in continuous time was used to model the growth of *P. tetraurelia* (Royama 1992). In the logistic process, density x is a continuous function of time. However because population growth was actually measured at regular, discrete time intervals (every 2 days) it was more realistic to express continuous growth in terms of those discrete measurements.

$$x_{t+1} = x_t e^{\gamma} / [1 + (e^{\gamma} - 1)x_t / K] \qquad \textit{Equation 6-3}$$

Representing continuous growth using this expression does not change the underlying ecological mechanism (Royama 1992). This model is purely deterministic. Such an approach is justifiable in systems such as these in which populations behave very predictably and when population sizes are so large (≈ 1000 per ml).

To simulate the experiment, each of the parameters in the model was replaced by measured estimates, i.e. γ was replaced with the linear function shown in Figure 6.3 and the carrying capacity, K was set to the maximum observed at the highest temperature used in the empirical work (25°C)(see Table 6-1). Populations were simulated to represent 100ml cultures, and simulations lasted 256 days with temperature changing every 12 hours, just as in the experiment. Population density was recorded every two days when 60% of the population was removed and replaced with sterile nutrient medium. Starting density was set to the carrying capacity at 15°C.

The simulation study deviated from the experimental study only in that for each run of the model a different realisation of environmental noise was used. Because the simulation was deterministic, replicate realisations of the noise were necessary. Six environmental replicates were used for each noise colour (These included those used in the actual experiment in order to provide direct comparisons). White and red noise realisations were produced in pairs, each pair being identical with respect to mean and variance (Cohen *et al.* submitted). This design resulted in six pairs of series of environmental fluctuations and a single constant temperature series.

STATISTICAL METHODS

The quantitative predictions of the model are initially presented using various summary statistics. These are then followed with two types of time series analysis. The series were analysed in the time domain using correlation analysis. Correlation coefficients were used as a measure of the covariance between the population and the temperature series (Willis *et al.* 1995). Analysis in the frequency domain was conducted using Fourier analysis (Platt and Denham 1975). This allowed identification of the frequency structure of the population time series, specifically whether particular frequencies in the temperature fluctuations are manifest within the population fluctuations. These analyses were then repeated on the time series produced by the experiment in order see whether the real populations conformed to model predictions.

6.4 Results

6.4.1 MODEL RESULTS AND PREDICTIONS

The simulations predict a series of differences in the population dynamics in response to the red and white noise treatments (see figure 6-6 for examples).

Summary statistics of the 13 simulations are shown in Table 6-2. Initial inspection indicates that there are some clear differences in terms of minimum density observed, and standard deviation of log density (S.D.L.D.). Although the variance in the temperature fluctuation treatments is identical, S.D.L.D. indicates that the populations growing in the red environment show greater variability in population density. The prediction of constant population dynamics in the constant temperature treatment means that populations are capable of replacing themselves quickly enough to return to equilibrium within the two-day sampling interval.

Correlation Analysis and Population Tracking

Some insight as to why this may be so is provided by a correlation analysis between the fluctuations of the population and noise series (see Table 6-3 and Figure 6-7). These results indicate that there is a strong degree of covariance exhibited by the simulated populations growing in both environments. However the magnitude of this correlation is dependent on whether the temperature fluctuations between sampling dates are averaged or not. Population fluctuations in the red environment are also positively correlated with a lag of minus one (Table 6.3).

The correlation coefficients in Table 6.3 provide one, relatively simple picture of the model's dynamics. More detailed information is provided by plotting population density against temperature (see Figure 6-7). The positive relationship in (c) shows that when the temperature drops in the red environment the population is liable to drop to a lower density than is observed by an equal drop in temperature in the white environment (b). The model thus predicts low variance fluctuation around the carrying capacity in the white environment. Although there is no difference between the maximum and minimum temperatures in the two variable temperature treatments, the implication is that the greater serial correlation in the red environment causes the populations to follow the extremes in

temperature more closely. The population fluctuations mimic the greater serial dependence inherent within the reddened environmental variability.

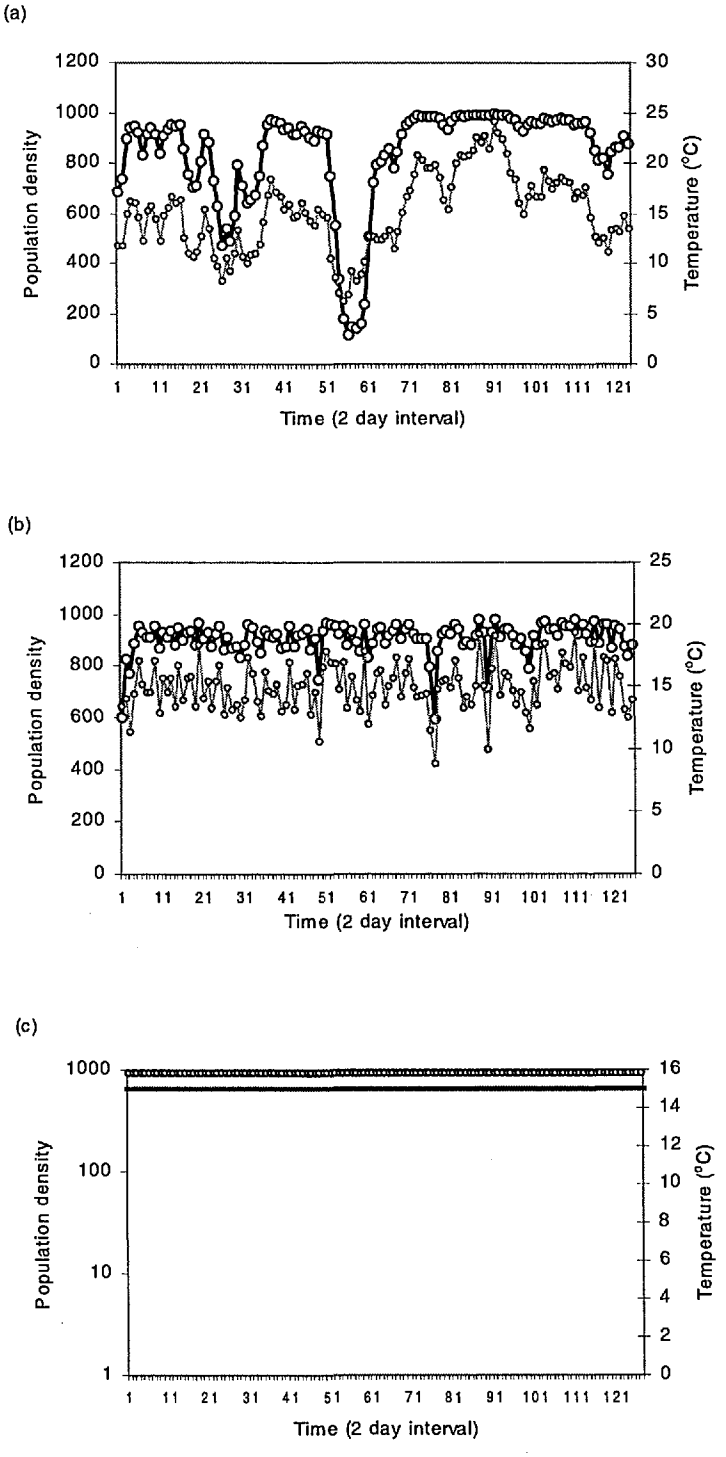


Figure 6-6. Sample population dynamics predicted by the model for (a) red temperature fluctuations (b) white temperature fluctuations and (c) constant environment.

Table 6-2. Summary statistics of the model simulations with mean and ±1 standard error. All densities are for 1 ml. Each line of data is for a single simulation (see text). Pairs of 'white' and 'red' simulation are I the same sequence in each block.

Temperature Treatment	Max	Min	Geomean	Population Variability S.D. Log ([n])
Constant	923.0	923.0	923.0	0
Variable, White	977.0	833.5	916.9	0.01
	981.8	800.5	917.5	0.01
	972.1	777.0	914.7	0.01
	969.0	762.5	913.9	0.01
	962.8	743.0	931.6	0.01
	979.5	591.8	909.3	0.01
Mean	**973.7**	**751.3**	**917.3**	**0.01**
Variable, Red	991.7	565.3	912.2	0.03
	993.3	760.6	932.8	0.02
	996.2	351.1	843.1	0.08
	976.2	319.8	841.8	0.09
	987.0	287.1	878.8	0.08
	995.2	116.2	795.2	0.18
Mean	**989.9**	**400.0**	**867.3**	**0.08**

Fourier Analysis

The FFT analysis of the population fluctuations provides an estimate of the relationship between the power and the frequency of the variability exhibited. Gamma in equation 6-2 can be found (see chapter 5) by calculating the FFT of the data and discarding the first element, and for reason of symmetry, the second half of the output. The resulting complex numbers are multiplied by their complex conjugate to give the power spectral density (PSD). The gradient of the linear regression of log PSD against log frequency is -2γ. As mentioned previously it is the slope of this regression that determines the colour of a series. A negative slope indicates low frequency dominance and hence a reddened spectrum. A summary of the exponents of the population fluctuations produced by the model can be seen in Table 6-4. Figure 6-8 gives examples of PSDs for populations from a red, white and constant series.

It is apparent from Table 6-4 that white noise fluctuations produce population dynamics with low values of gamma. That is population fluctuations with no overall frequency dominance (Figure 6-8a). Whilst red noise fluctuations result in considerably

higher values of gamma. The population fluctuations of these series are dominated by high power, low frequency fluctuations (Figure 6-8b. Thus in both cases the population fluctuations mirror the fluctuations in their environment.

Table 6-3. Correlation analyses between the temperature and simulated population density. Values (a) represent analysis of population with actual temperatures whilst values (b) represent correlation with both temperature and density as 2 day averages.

Treatment	Correlation Coefficent (no lag)	Significance (df=122)	Correlation Coefficient (for a Lag of 1)	Significance (df=121)
White	(a) 0.96	0.01	(a) 0.25	0.05
	(b) 0.17	ns	(b) –0.05	ns
	(a) 0.95	0.01	(a) 0.13	ns
	(b) –0.12	ns	(b) 0.18	ns
	(a) 0.95	0.01	(a) 0.15	ns
	(b) 0.10	ns	(b) –0.10	ns
	(a) 0.96	0.01	(a) 0.09	ns
	(b) –0.05	ns	(b) –0.008	ns
	(a) 0.95	0.01	(a) 0.24	0.05
	(b) 0.09	ns	(b) –0.07	ns
	(a) 0.91	0.01	(a) 0.19	ns
	(b) –0.01	ns	(b) 0.07	ns
Red	(a) 0.87	0.01	(a) 0.84	0.01
	(b) -0.49	0.01	(b) -0.51	0.01
	(a) 0.91	0.01	(a) 0.83	0.01
	(b) 0.15	ns	(b) 0.11	ns
	(a) 0.89	0.01	(a) 0.83	0.01
	(b)-0.20	0.05	(b) -0.17	ns
	(a) 0.88	0.01	(a) 0.87	0.01
	(b)-0.52	0.01	(b) -0.50	0.01
	(a) 0.82	0.01	(a) 0.81	0.01
	(b) 0.54	0.01	(b) 0.52	0.01
	(a) 0.80	0.01	(a) 0.79	0.01
	(b) –0.22	0.05	(b) -0.17	ns

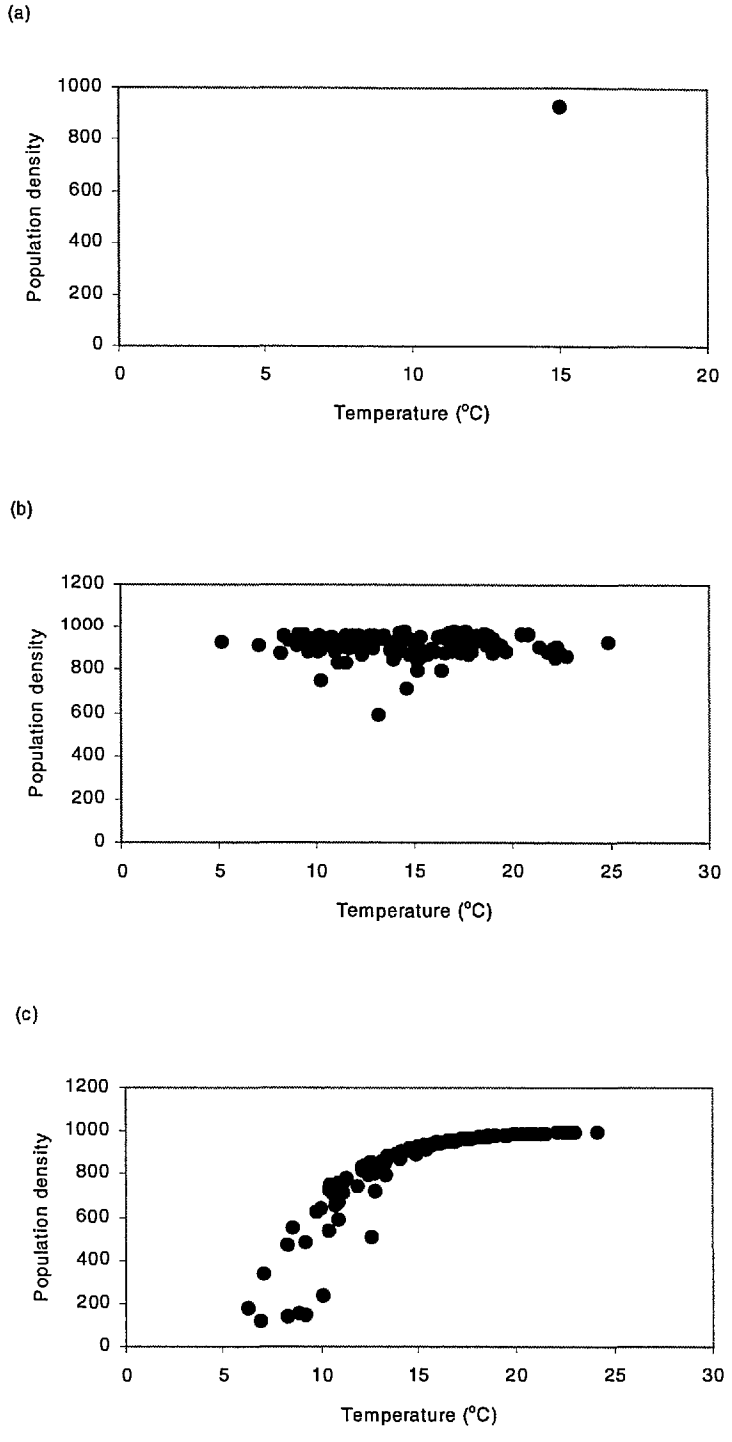


Figure 6-7. Examples of population size against two-day mean temperature. (a) Shows the relationship for constant temperature, (b) for the white noise environment and (c) for the red noise environment

Table 6-4. Summary of the exponents (see text) of the environment and population series estimated using linear regression of log (power) against log (frequency).

Treatment	Exponent of Temperature Series	Exponent of Model Dynamics
Constant	0	0
White Noise	-0.04	0.21
	0.06	0.07
	-0.03	0.05
	-0.01	0.04
	-0.04	-0.11
	0.002	-0.08
Red Noise	0.91	1.18
	0.94	1.10
	0.96	1.12
	0.82	0.95
	1.02	1.00
	0.96	1.58

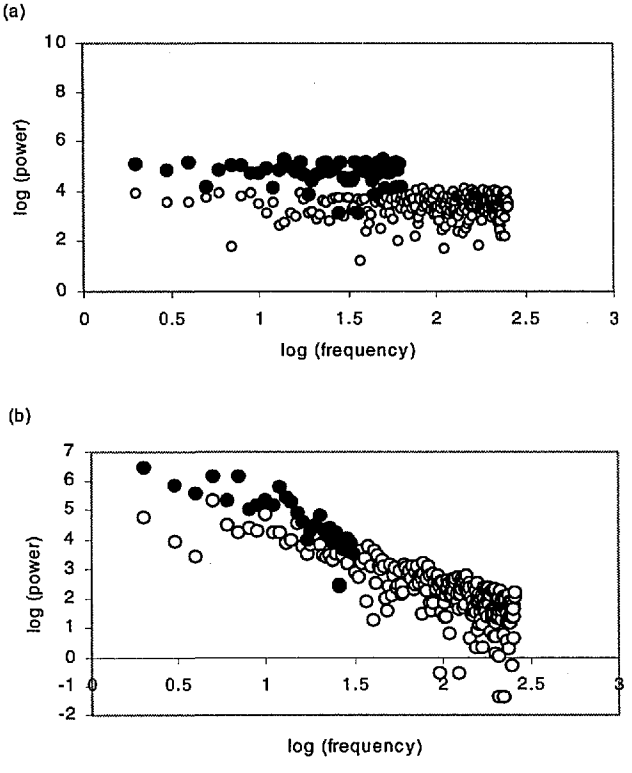


Figure 6-8. Example output of the Fourier transform analysis of the simulated population dynamics in the (a) white and (b) red environments. Note that white temperature fluctuations (open circles) produce population dynamics (closed circles) with equal power at all frequencies whilst red temperature fluctuations show high power at low frequencies.

Extinction Analysis

Populations in the above simulations and following experiments were deliberately maintained at a large size to reduce the likelihood of extinction. Nonetheless it is extremely relevant to consider the possible effect of these different patterns of environmental fluctuation on the persistence of small populations. Assessment of extinction risk under red and white $1/f$ environments using the above model was achieved by restricting the carrying capacity to a 100. Model simulations were identical to those carried out earlier, except that in order to ensure extinction populations growing under both environmental treatments suffered 90% mortality every 2 days (≈4 generations) (rather than the 60% used in the first set of simulations). A more thorough analysis of extinction probability in red and white stochastic environments that also includes demographic stochasticity, is examined in Chapter 4.

Figure 6-9 provides an example of the resulting population dynamics whilst Table 6-5 summarises the results from these simulations. From the previous results of this model we might predict that populations in red $1/f$ environments will be most at risk of extinction. Results indicate that this is indeed the case. Whilst the variance in environmental fluctuations was identical in the two environments only those populations experiencing the reddened environmental fluctuations suffered extinction.

6.4.2 EXPERIMENTAL RESULTS

Results from the empirical study of the fluctuations of *P.tetraurelia* to the red and white and constant environments are now given. Although the experiment was intended to last for 256 days, during which 18 series each 128 data points long were to be recorded, unforeseen technical problems precluded this. The control apparatus described in Chapter 5 lost reliability in temperature control on day 73 of the experiment. On this day several of the water baths overheated producing temperatures lethal to the cultures in excess of the maximum recordable by the sensors -50°C. The exact cause of the problem has not been accurately identified; however after some examination it was found to be unrelated to the external hardware board. The problem thus appears lie within the control computer. Further work is required to establish the exact nature of the problem.

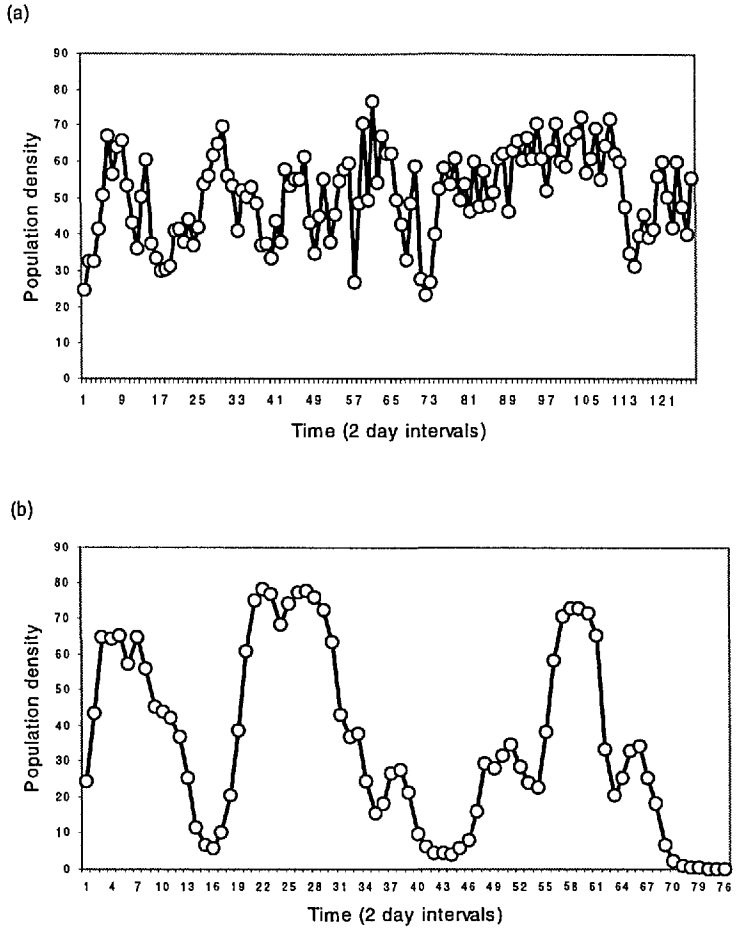


Figure 6-9. Example dynamics from the analysis of persistence of small populations (k=100) in (a) white and (b) red environments using the parameterised model of *Paramecium* growth, imposing 90%mortality every two days).

Table 6-5. Time to extinction, if recorded, of small populations exposed to white and red $1/f$ noise, subject to 90% harvesting every two days.

Treatment	Persistence Time (2 day intervals)
White	No extinction
	No extinction
	No extinction
	No extinction
	No extinction
	No extinction
Red	122
	No extinction
	71
	106
	122
	30

As a consequence of this failure the, experiment produced 18 time series, each 72 days in length and containing only 36 data points. More importantly, though, the early termination of the experiment meant that the populations in the red and white noise environments experienced different amounts of total variance in temperature fluctuations. The slower cumulative increase in the variance of the red noise treatment resulted in the populations in the red noise environments experiencing less variance (1.90 and 3.20 standard deviations) than the white noise environments (3.85 and 3.85 standard deviations).

Figures 6-10, 6.11 and 6-12 show the population time series. Visual inspection indicates that all the populations were variable through time, in all the treatments including, the constant temperature environment. Table 6-6 provides summary statistics of these series.

Summary statistics of the simulated population dynamics predicted lower minimum size, lower geometric mean size and greater variance in the fluctuations of the populations in the red environment. We can see that because of the early termination of the experiment the predictions of the model were only equivocally upheld in the experiment. The minimum density appears in the red treatment and despite the fact that the red noise populations received lower variance than the white noise populations they still show a slightly greater (though not significant) S.D. in log density. These results strongly suggest that if the experiment had continued, the reddened populations would have shown greater population variability. The insight from the model is that this greater variability maybe due to the populations showing greater tracking of the red noise fluctuations. Plotting population size against temperature best depicts the presence of population tracking.

Evidence for tracking would be provided by a positive relationship between temperature and population density. High temperatures should result in high population densities. Figure 6-13 shows the series of these plots for the three noise treatments, whilst Table 6-6 shows a summary of the correlation coefficients estimated between the 2 day mean of the temperature series and the population density.

The most important result to emerge from this analysis is strong evidence for a positive correlation between population size and temperature in the red environment. This becomes most apparent, and statistically significant in 5 out of 6 replicates, with the inclusion of a negative lag of one time point in the response of the populations to the temperature fluctuations (Figure 6-13c and Table 6-6).

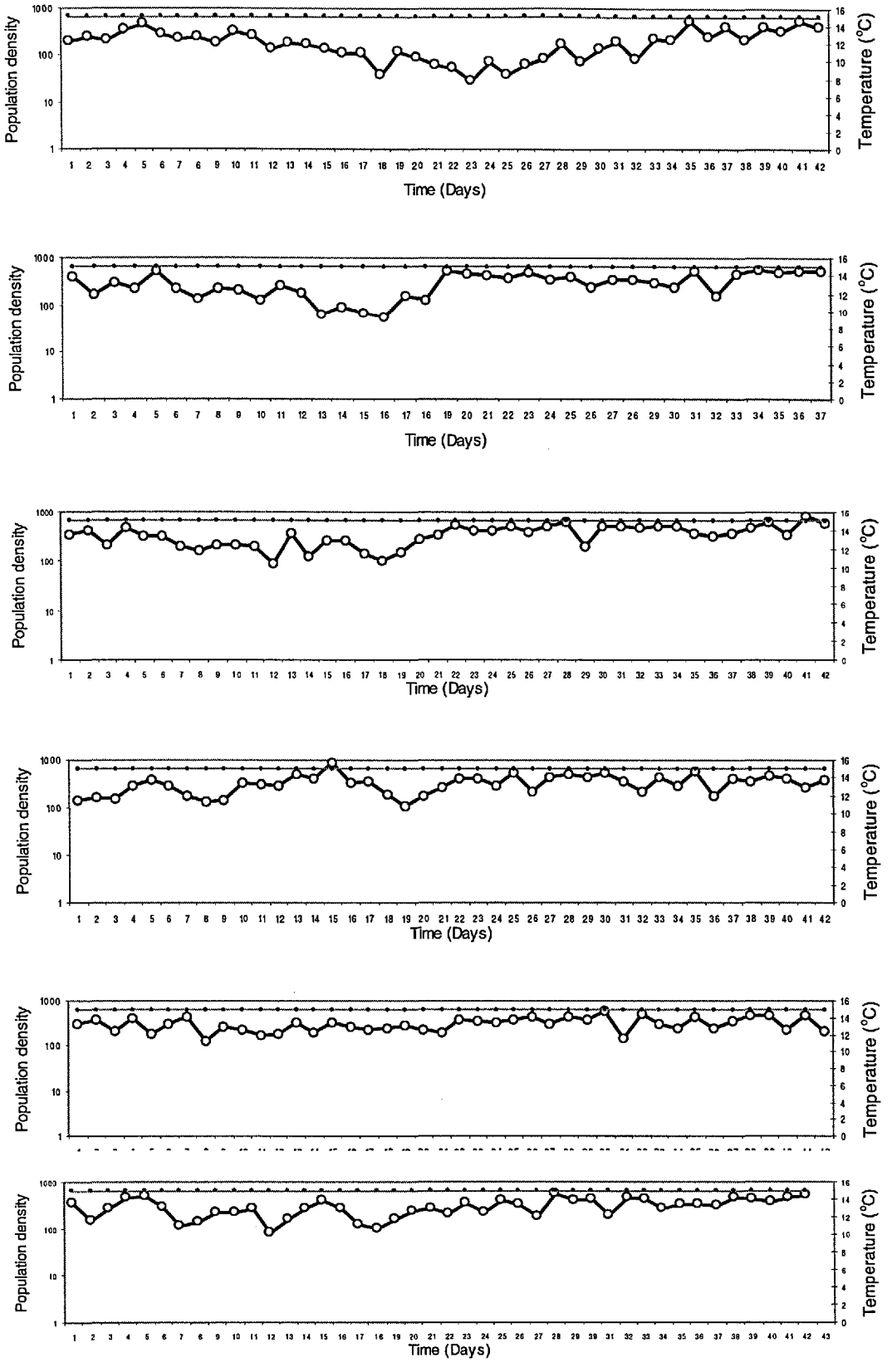


Figure 6-10. Population densities (ml^{-1}) from the constant temperature treatment. Population densities are shown by the open circles joined by a thick line. Two-day average temperature is shown by small open circles joined by a grey line.

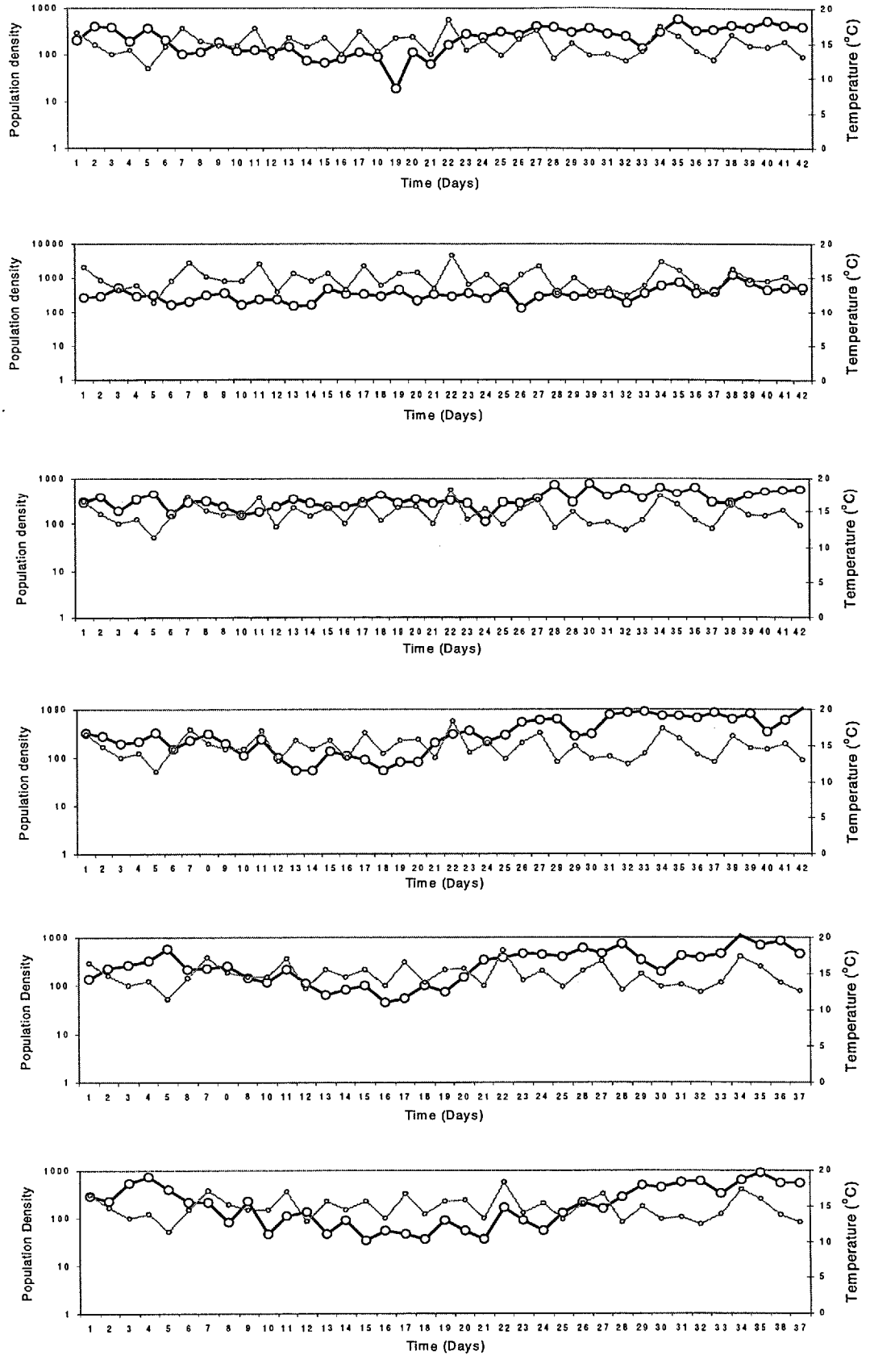


Figure 6-11. Population densities (ml^{-1}) from the white noise treatment. Population densities are shown by the open circles joined by a thick line. Two-day average temperature fluctuations are shown by small open circles joined by a grey line.

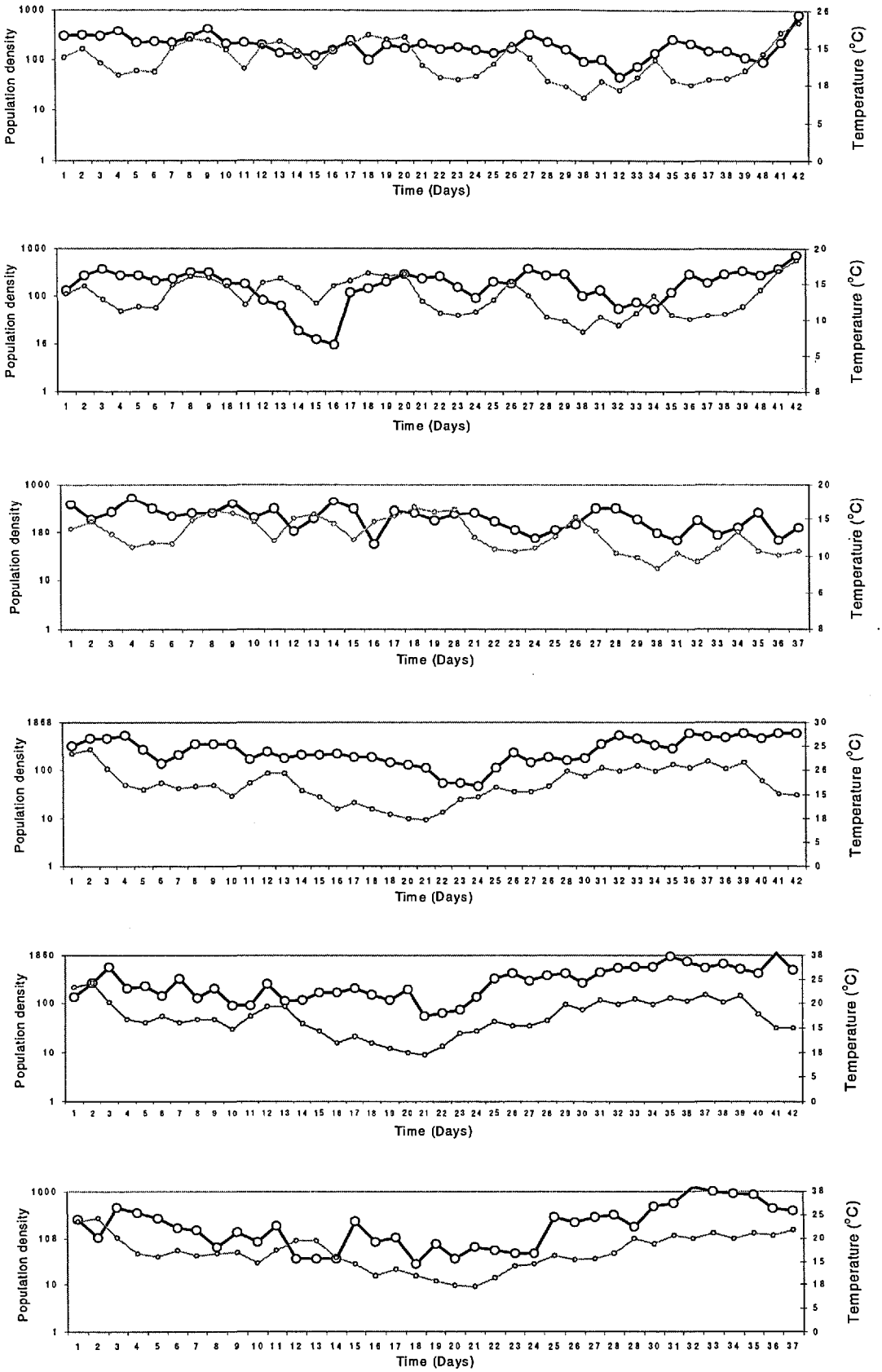


Figure 6-12. Population densities (ml^{-1}) from the red noise treatment. Population densities are shown by the open circles joined by the thick black line. Two-day average temperature fluctuations are shown by the small open circles joined by the grey line.

Table 6-6. Summary statistics of each population time series replicate with mean and ±1 standard error. All densities are for 1ml.

Treatment Regime	Max	Min	Geom mean	Population variability S.D. (log[n])
Constant	514.7	27.6	161.1	0.32
	579.0	55.1	259.7	0.28
	836.4	91.9	320.9	0.22
	866.6	110.3	299.1	0.20
	615.8	128.7	298.7	0.16
	551.4	82.7	267.6	0.20
mean	660.6	82.7	267.9	0.23
Variable, White	1056.9	55.1	279	0.37
	1084.5	45.9	249	0.35
	900.8	33.3	173	0.43
	1213.2	128.7	330.8	0.19
mean	753.7	110.3	325.2	0.18
	579	18.4	201.2	0.31
	931.3	65.2	259.6	0.31
Variable, Red	808.8	45.9	182.5	0.22
	716.9	9.2	40.1	0.39
	523.8	55.1	182.3	0.24
	597.4	45.9	246.2	0.28
	1121.3	55.1	254.0	0.32
	1240.8	27.6	163.5	0.46
mean	834.7	39.8	178.1	0.32

Analysis that omits a lag results in lower correlation coefficients for the red noise treatments. This is a result predicted by the model and is strong evidence that the population is tracking its environment.

Although the population fluctuates in the white noise environment, the lack of any positive relationship in Figure 6-13 (b) is good evidence that there is very little tracking in the white noise treatment. Note that the unexpected variability within the constant treatment is also clearly apparent in Figure 6-13(a).

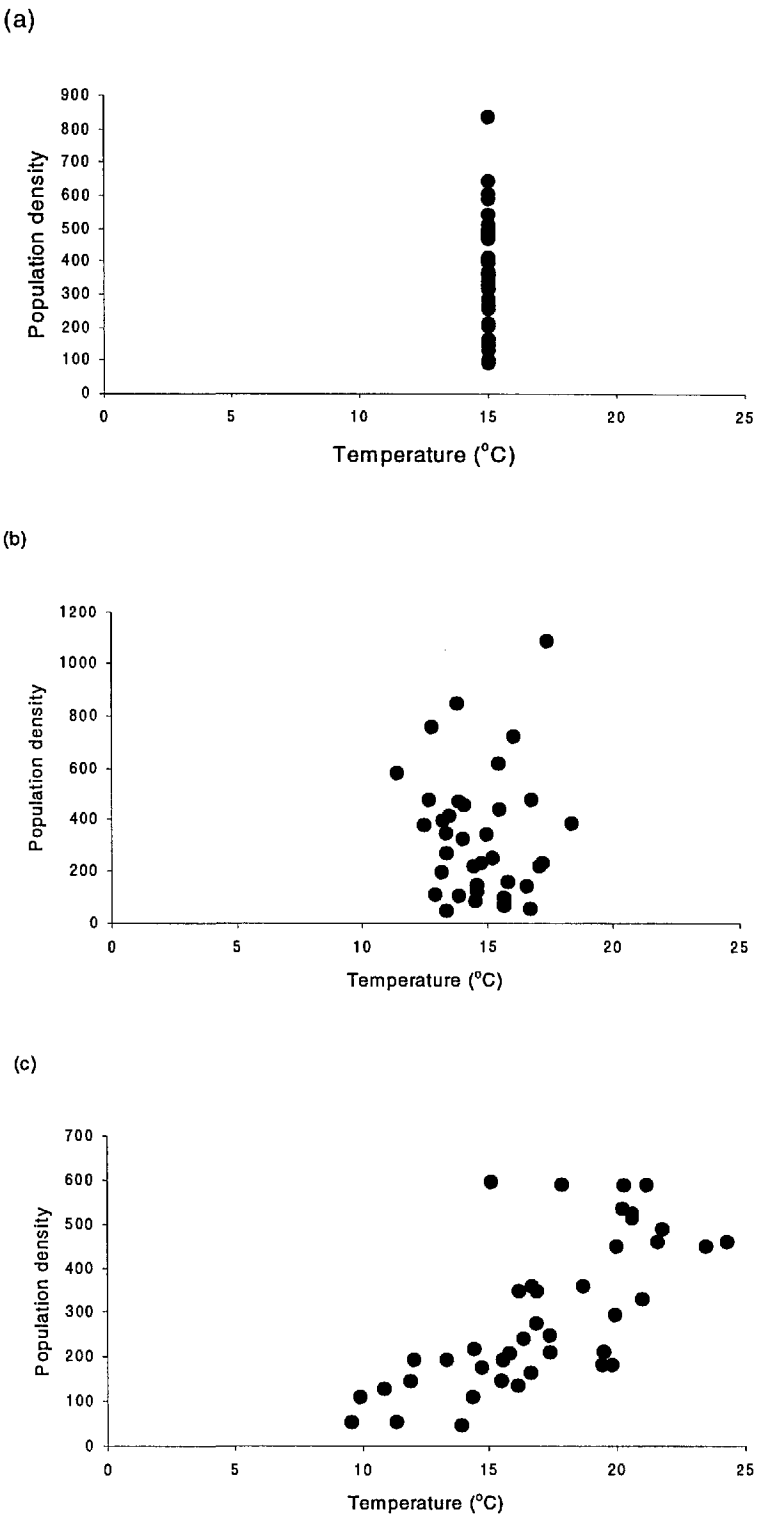


Figure 6-13. Examples of population size against two-day mean temperature with a time lag of one. (a) Shows the relationship for constant temperature. (b) Shows the relationship for white noise environment and (c) for the red noise environment. Compare with Figure 6-7.

Fourier Analysis

Model predictions suggest that the high power of the low frequency environmental fluctuations present in the red noise environment will create dominant, low frequency in the *P.tetraurelia* populations. Essentially the prediction is that red noise environments will create reddened population fluctuations, whilst populations from the white noise environments should show virtually no evidence of high power, low frequency fluctuations and hence have a white noise structure.

Table 6-7. Results from the correlation analysis between the temperature fluctuations and population dynamics.

Temperature Regime	Correlation Coefficient (no lag)	Significance	Correlation Coefficient for a lag of 1	Significance
Variable, White	0.08	Ns (df=39)	0.05	Ns (df=39)
	-0.24	Ns (df=39)	0.17	Ns (df=39)
	-0.15	Ns (df=39)	0.03	Ns (df=39)
	-0.16	Ns (df=40)	-0.05	Ns (df=40)
	-0.03	Ns (df=35)	0.04	Ns (df=35)
	-0.20	Ns (df=35)	-0.15	Ns (df=35)
Variable, Red	0.43	0.01(df=39)	0.50	0.01(df=41)
	0.27	Ns (df=39)	0.30	ns (df=41)
	0.22	Ns (df=34)	0.59	0.01(df=36)
	0.54	0.01(df=39)	0.71	0.01(df=41)
	0.46	0.01(df=39)	0.55	0.01(df=41)
	0.56	0.01(df=34)	0.55	0.01(df=36)

Table 6-8 summarises the exponents (the slope of the regression of power against frequency estimated from the populations) of the FFT. The results of this analysis are clearly equivocal. The estimated exponents are all greater than zero for the populations in the red noise environments; however there is considerable variability in these values. Furthermore, the exponents estimated from the populations in the white noise and constant environment are also positive and show similar values and variability. Thus a white noise environment has resulted in a reddening of the population dynamics in a manner very similar to the red noise fluctuations. There is thus no evidence here that there is any difference between the treatments with regards to the frequency structure of these population fluctuations. In fact, the low frequency variability in the constant environment suggests that reddened dynamics maybe generated intrinsically.

More clear treatment effects may well have shown had the experiment not been terminated early. It is reasonable to speculate that the populations in the red noise

environments had not received enough of the low frequency fluctuations for these to be reflected in the population dynamics. However, anything other than speculation requires a complete re-run of the experiment.

Table 6-8. Summarises the effect of red of and white environmental fluctuations on the exponent of the fluctuations of the population dynamics as estimated using Fourier analysis.

Temperature Regime	Exponent of temperature series	Exponent of resulting population dynamics
Constant	0	0.33 -0.09 0.52 0.30 0.58 0.92
Variable, White	-0.19 -0.19	0.20 0.28 0.76 0.67 0.65 1.08
Variable, Red	1.3 1.03	0.57 0.99 0.40 0.39 0.40 1.30

6.5 Discussion

Empirical support for the predictions from a simulation model of a differential response in the population dynamics of *Paramecium tetraurelia* to thermal environments with different variance spectra was equivocal. Previous theoretical investigations (Kaitala 2 1997; Petchey, Gonzalez, and Wilson 1997) have predicted that populations exhibiting compensatory dynamics should mirror the colour of their environmental fluctuations. This result is supported by a simulation model of the dynamics of *P.tetraurelia* but replicated microcosms of populations of this species, that displays perfect compensatory dynamics, failed to support the prediction. Fourier analyses of the population dynamics of this protozoan indicate highly variable estimates of the colour of the fluctuations observed in the white noise and red noise treatments. In fact reddened fluctuations were observed in both constant and white noise treatments as well as the red noise treatment.

There are several possible reasons for this; however, at the moment the most parsimonious explanation is that it is due to experimental error, because the experiment was terminated early. A second, major reason may lie in the unexplained variation observed in the dynamics of the real populations in the constant environment, when the simulation model predicted constant dynamics in the constant environment (compare figure 6.5 and fig 6.10).

The method of density estimation of populations of protozoa is standard and well known to give consistently accurate estimates (Lawlor and Morin 1993) and every effort was taken to apply this methodology accurately. However other experimental errors, at other stages in the experiment, may have been important. For example, a discrepancy in the temperature of replacement media during the 2-day harvest may have been a significant perturbation to growth. Error as this stage may explain why constant dynamics were not seen in the populations growing under constant temperature conditions. The model does not take into account any perturbation to growth caused by such a discrepancy in medium temperature and it is likely that inconsistencies in the environment like this may well result in a slower than predicted return time.

Sampling problems aside, the shorter than expected time series acquired during this experiment certainly limited the likelihood of the discovery of treatment differences. Because of the manner in which the noise series are created (summing a series of different frequency and power) the variances of the two treatments are not equal until very near the end of the series. In the red noise environment the fundamental sine wave, that which has a period equal to the duration of the experiment, also has the greatest power and hence ability to perturb the populations. The phase of that wave will determine when the population will experience this minimum value. Because phase is defined randomly this minimum value will differ in its occurrence between series. In the actual experiments, the populations in the red environment had not experienced the full range of temperature fluctuations. Thus in effect the populations, especially in the red treatment, had only partially 'sampled' the variance in their environment. Had the experiment continued for longer the power of the analyses to pick up treatment differences would have been greater.

Implications, and Reddened Population Dynamics

The calibrated simulation model of this study indicates that the inclusion of red environmental fluctuations can cause a reddening of the underlying variance spectra of

protist populations. This result supports the finding of Kaitala *et al.* (1997) who also showed, with the use a Moran-Ricker equation for growth, that for low values of *r*, when the population is inherently stable (population dynamics converge exponentially to an equilibrium level), the colour of the environmental noise is transmitted to the population dynamics. This now appears to be a robust theoretical expectation for single-species populations showing stable compensatory dynamics (see also Petchey, Gonzalez and Wilson 1997). Under these conditions the prediction is a positive correlation between the fluctuations in population density and fluctuations in the environment. As Royama (1992) points out, the environment can thus be said to govern the pattern of population fluctuations.

If this is common in natural populations, then the method of directly using the nature of the variability in the environment as a direct, surrogate measure for predicting future variability in a population is justifiable (Foley 1994). However, reality is likely to be more complex, if different forms of density dependence and higher values of *r* are considered. Indeed, there may then not be a simple relationship between the colour of population variance spectra and that of the environment (Kaitala *et al.* 1997).

The evidence of reddened dynamics in the constant environmental treatment of this study is an intriguing result. Although the source of the variability in this treatment cannot be separated from sampling error, the possibility of intrinsically created reddened population dynamics requires further experimental investigation. Interestingly, a simple model of population growth with a small amount of demographic stochasticity in which there is no environmental forcing will also produce a reddened power spectrum (O. Miramontes and P. Rohani 1997 unpublished). If this result is at all realistic, it suggests that fluctuations in all natural populations will be reddened to some extent, without any environmental forcing (Pimm and Redfearn 1988). The relative contribution of intrinsic and extrinsic factors in the reddening of population dynamics still remains unanswered, and considerably more work needs to be done on this subject. Clearly there is a need for the prematurely terminated experiment described in this chapter to be repeated. Unfortunately, this was not possible with the time and resources available.

Extinction Analysis

A second, important insight to emerge from the simulation model was the predicted increase in the likelihood of extinction of populations in the reddened environments. This

is the first example of the use of $1/f$ noise to model fluctuations in the environment, coupled with a realistic model in which the relationship between growth and temperature is properly calibrated. A predicted increase in risk of extinction under red noise supports previous theoretical work on the detrimental affects of temporal correlation in the variability of the environment on population persistence (Goodman 1987; Petchey, Gonzalez and Wilson 1997). The important insight from this model is that even in an environment where positive net population growth is guaranteed, random correlated noise can cause extinction where white noise will not.

Clearly small populations are most at risk. The inclusion of demographic stochasticity would have improved the realism of this study. However it is likely that inclusion of demographic stochasticity would not have changed the result qualitatively but merely increased the risk for larger populations. As it stands the model does provide further support for the assertion that continued use of white noise will lead to a bias in the estimation of extinction risk in populations displaying compensatory dynamics (Petchey, Gonzalez, and Wilson 1997).

7

Discussion

Wholesale destruction of the earth's natural habitats is resulting in what has been defined as the 'sixth' great extinction (Leakey and Lewin and others). Estimates of such massive extinction are based solely on area loss due directly to destruction as defined by the species-area relationship (Heywood *et al.* 1994; Budiansky 1994; Lawton and May 1995). Whilst this approach is conveying an important message to the general public of the catastrophic effects habitat destruction is having on the earth's ecosystems in actuality, such figures are likely to be underestimates. Because the various population and community processes underlying extinction are dynamic, theory suggests that there is likely to be a significant extinction debt associated with the fragmentation of the landscape caused by habitat destruction (Tilman *et al.* 1994).

These effects of habitat fragmentation *per se* are much less widely understood, however, as I highlighted in chapter one, small populations existing in a landscape of remnant patches are at a greater risk from proximate causes of extinction such as demographic and environmental stochasticity. Because of this, recolonisation and dispersal, become the dominant processes of population persistence.

In chapters two and three of this thesis I explicitly examined the effects of habitat fragmentation and landscape connectivity on the community dynamics of micro-arthropods in a moss micro-ecosystem. This system is treated as a natural microcosm and hence as a surrogate for larger, dynamically slower, systems. Over a period equivalent to several generations of many of the moss fauna I observed a considerable extinction debt associated with fragmentation of the moss habitat. Initially, following habitat destruction, very little difference in the species richness of the control and treatment fragments was observed, however, by the end of the experiment prolonged fragmentation had resulted in extirpation of 40% of the fragmented community. During this experiment fragmentation had caused a community wide reduction in population size and thus rare species were

found to be most at risk of extinction. This result contradicts the prediction of the model of Tilman *et al.* (1994), and supports the growing evidence that fragmentation does not differentially cause the extinction of competitively and hence numerically dominant species (McCarthy *et al.* 1997).

Chapter three examined the effects of improving landscape connectivity by joining fragments of moss with corridors. In agreement with theoretical expectations connected patches had significantly higher species richness and higher population sizes than unconnected patches. Corridors improved both local and regional diversity.

It is long been widely acknowledged that small populations face considerable risk of extinction in the face of fluctuating environments. However only recently have the effects of the colour of environmental fluctuations been considered relevant. In chapter four I described new theoretical results which identified the mechanisms by which single-species populations may suffer extinction when autocorrelated environmental fluctuations are imposed. I found that overcompensatory dynamics resulted in persistence times that increased with increasing autocorrelation in environmental fluctuations, whilst undercompensatory dynamics resulted in persistence times that decreased with temporal autocorrelation. In a spatially subdivided population, with a realistic degree of spatial heterogeneity in patch quality, increasing temporal autocorrelation in the environment resulted in decreased persistence times for populations displaying both types of intraspecific competition. This was found to be because temporally autocorrelated noise resulted in the synchronisation of population dynamics across the landscape so that during a long enough series of unfavourable environmental events the number of rescuing patches (those providing colonisers) became too small to keep pace with the extinction of existing ones.

To date no experimental evidence has been acquired that shows real populations to be sensitive to the colour of environmental fluctuations. An experimental approach designed to test the effect of red and white $1/f$ noise on the population dynamics of the protozoa *P.tetraurelia* was described in chapters five and six. Because of the early termination of this experiment the results of this study were inconclusive, however, a detailed simulation model predicted that the population dynamics of this protozoan would be sensitive to autocorrelated noise. Furthermore there is a greater risk of extinction for this organism in autocorrelated environmental fluctuations than in white noise environments.

7.1 Caveats and Future Work

Habitat Fragmentation

The results from the studies of chapter two and three very clearly illustrate the detrimental effects that habitat fragmentation can have on species richness. However the results of these studies remain restricted to the micro-arthropods of the moss microcosm. Future studies using this system would consider the effect of fragmentation on other important groups allowing for a better test of community disassembly theory. Furthermore longer term studies maybe used to specifically test the predictions from the specific habitat fragmentation model of Tilman *et al.* (1994).

The experiments in this thesis raise interesting questions about the effects of scale. For example, are the results from the experiments described in chapters two and three particularly dependent on the fragment sizes and inter-patch distances created? If so what are the general messages from this microcosm regarding population processes occurring at the macroscale?

An important feature of this system is that all relevant factors can be measured and a direct comparison with larger scales can be made by 'scaling up'. For example, it appears that the micro-arthropods are relatively dispersal-limited in the absence of moss habitat and hence the relatively short inter-patch distances of these experiments resulted in considerable local extinction. An obvious prediction therefore is that the impact of corridors on population persistence will depend on the scale of the island-corridor system, relative to the size and dispersal powers of the species, thereby affecting species differentially and possibly predictably.

The continued use of microcosms such as these requires very careful consideration of how population and community processes scale with space and time. This is an obvious criticism of the microcosm approach, however, by using natural microcosms the stronger criticism of loss of relevance associated with artificial microcosms no longer holds. The explicit consideration of scale enforced by the use of natural microcosms inevitably requires careful experimental design, but the small spatial scale and the fast dynamics of the system enables very focused questions to be asked of the same system over and over again.

Environmental Variability

Recent theoretical investigations have demonstrated that populations are sensitive to the colour of temporal environmental variability (Roughgarden 1975; Goodman 1987; Ripa and Lundberg 1997; Petchey, Gonzalez and Wilson 1997). This discovery has emphasised the necessity for a realistic model of environmental fluctuations if population theory is to have any predictive power (Halley 1996).

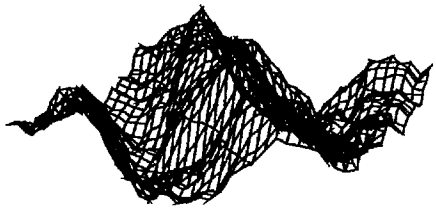
In this thesis I have investigated in detail whether populations were sensitive to reddened environmental fluctuations and in particular whether populations of *P. tetraurelia* were sensitive to red and white forms of $1/f$ noise. Results from these experiments were equivocal. The likely reasons for this were: (a) small inconsistencies in the application of the experimental protocol and (b) premature and unavoidable termination of the experiment. A repeat of this experiment is required in order to establish unequivocally whether experimental single-species populations are sensitive to the colour of environmental fluctuations. A successful experiment must necessarily run for the entire duration as defined by the length of the time series of environmental fluctuations. Only then will the populations undergoing the red and white noise treatments have experienced equal variance and, importantly, only then will the red noise populations have experienced the full power of the lowest frequency fluctuation.

The new temperature control apparatus described in this thesis offers a unique opportunity to study the effects of complex and varying patterns of environmental fluctuations on aquatic or terrestrial multi-species communities. A growing theoretical framework (McNaughton 1994; Chesson 1989) now exists within which experimental results can be tested. Questions of particular interest include the mechanisms of the maintenance of species coexistence (Caswell and Cohen 1995; Chesson and Huntly 1997) and the role of species redundancy in ecosystems as a buffer against severe environmental fluctuations (Schulze and Mooney 1994 and chapters therein).

The theoretical investigations in chapters four and six indicated the sensitivity of single populations and metapopulations to temporally correlated environmental fluctuations and to white noise spatial fluctuations. Future work in this direction will couple realistic models of spatial variability (spatially correlated) with individual-based as well as population level models. $1/f$ noise can easily be modelled in two dimensions to create red and white noise fractal landscapes (Hastings and Sugihara 1991)(see Figure 7.1). Such an approach offers great scope to synthesise the spatial and temporal topics

Such an approach offers great scope to synthesise the spatial and temporal topics considered in this thesis. By coupling such landscapes with metapopulation models one is provided with a means of exploring the effect of varying certain aspects of landscape structure (such as spatial correlation and relative habitat abundance and connectivity) on population persistence

(a)



(b)



Figure 7-1. $1/f$ landscapes that can be used to vary spatial heterogeneity when coupled to a metapopulation model (a) Reddened landscape with a high spatial correlation (b) White noise landscape with no spatial correlation.

(With 1997; Moloney and Levin 1996; With *et al.* 1997). The interaction of individuals and populations with complex landscapes such as these offers the opportunity to study 'species perceptions' of landscapes and hence begin to address the all-important issue of scale.

Ultimately, one may then incorporate temporal and spatial variability using the same $1/f$ model in order to create more sophisticated analyses of how complex patterns of spatial subdivision and temporal autocorrelation can lead to species extinction. We have seen that extinction is caused by the interaction between landscape structure,

fragmentation (critical thresholds in landscape structure and population subdivision) and the correlation structure of temporal fluctuations in those landscapes.

7.2 The Microcosm Philosophy

The results obtained using the moss micro-ecosystem suggest that the system may be successfully used to address various issues in community and ecosystem ecology. The high species diversity on a small spatial scale is of course its great benefit and its downfall. Further work on the taxonomy of the other important groups within the community, such as the nematodes and protozoa, will go a long way towards reducing the inherent difficulties of working with the organisms of this system. The small spatial scale allows one to study the response of the entire system to many ecological questions and to create the necessary replication needed for such studies. Furthermore the short generation times of all the organisms in this system allow one to truly study system dynamics. Much of the empirical work in ecology is weakened through its over simplification and inadequate because of the short time scales considered. Such problems can be reduced by the use of a natural microcosm such as the moss micro-ecosystem.

Most importantly though, because the moss system is a true microcosm (as defined in chapter one), it permits a more holistic and relational (Rosen 1991) epistemology. The benefits of adopting such a methodology can only be currently measured against the success/failure of contemporary reductionism in ecology to provide any deep understanding of the 'whys' and 'hows' of the earth's ecosystems. The following quotation taken from a paper by Lane (1986) rather pertinently expresses the sentiment behind the philosophical views held within this thesis.

When I was a child, kaleidoscopes were my favourite toys; I had a whole collection of them. I spent hours studying the patterns and alternately trying to find new and then repetitive ones. I was convinced that the complexity in the patterns must be related to the complexity of the machine. My curiosity so overcame me that I risked a parental reprimand and completely disassembled one of my precious possessions. I can remember being very disappointed at the collection of simple objects that fell onto the table as I took the instrument apart. How could a few bits of glass, some fragments of mirror, and a cardboard tube produce such a wondrous array of images? I was never able to fit the sorry pile of pieces together. Regardless of the observing mode employed, reductionism, which in the extreme is analogous to dismantling nature's kaleidoscope, precludes the delineation of symmetry, change, and perturbation at the community

level. Meaningful theory cannot be developed if ecologists are equipped only with some bits of glass, mirror fragments, and a broken cardboard tube.

Finally, this thesis is the direct result of some advice I received some four years ago. On asking my undergraduate supervisor what steps I should take to become a good conservation biologist his reply was that, first and foremost, I should seek to become a good ecologist/scientist. It is hoped that the blend of theoretical and empirical science I have learnt and applied to the problem of causes of extinction within this thesis have put me on that path towards becoming a better conservation biologist.

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