

Teppo Hiltunen

Environmental Fluctuations and
Predation Modulate Community
Dynamics and Diversity



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Esitetään Jyväskylän yliopiston matemaattis-luonnontieteellisen tiedekunnan suostumuksella
julkisesti tarkastettavaksi yliopiston Ambiotica-rakennuksen salissa YAA303
tammikuun 18. päivänä 2008 kello 12.

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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2008

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Jyväskylä Studies in Biological and Environmental Science

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Department of Biological and Environmental Science, University of Jyväskylä

URN: ISBN: 978-951-39-8592-9

ISBN 978-951-39-8592-9 (PDF)

ISSN 1456-9701

ISBN 978-951-39-3077-6

ISSN 1456-9701

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University Printing House, Jyväskylä 2008

ABSTRACT

Hiltunen, Teppo

Environmental fluctuations and predation modulate community dynamics and diversity

Jyväskylä: University of Jyväskylä, 2008, 33 p.

(Jyväskylä Studies in Biological and Environmental Science

ISSN 1456-9701; 186)

ISBN 978-951-39-3077-6

Yhteenveto: Ympäristön vaihtelut ja saalistus muokkaavat yhteisön dynamiikkaa ja diversiteettiä

Diss.

Predation, environmental fluctuations, and immigration are commonly expected to affect community dynamics and diversity. However, interactions between these factors are largely unknown. A further complication is that rapid evolution of species interactions potentially alters ecological community dynamics. The role of environmental fluctuations in ecological dynamics of competitive communities was explored in a simulation study. We explored how the patterns of species diversity are affected by the frequency spectrum of stochastic environmental variations and density independent immigration rates in a competition model. Next, three microcosm experiments were conducted where heterotrophic aquatic bacteria were exposed to different resource fluctuation regimes and / or a protozoan predator *Tetrahymena thermophila*. Both the simulation study and the experiments revealed that fluctuating environments can promote diversity. Furthermore, diversity patterns produced by fluctuations are altered by immigration and predation. These results suggest that the environmental fluctuations and predation jointly affect community dynamics and diversity. In experiments with predation, the bacteria evolved to resist predation better. These changes altered the ecological properties of the predator-prey interaction. For example, an increase in prey grazing resistance may explain the observed strong decrease in predator densities during experiments. Thus, the ecological consequences of predator-induced rapid evolution need more attention.

Keywords: Bacteria; evolution; microcosm; resources; *Tetrahymena thermophila*; stability; stochastic environment.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-IV. I have been involved in the planning and execution of all studies. I have conducted most of the data collection in studies II-III, and contributed significantly in data collection in study IV. Studies I-III are mainly written by me and I have also contributed in writing of study IV. I have also done most of the simulations in study I, analysed data in studies II-III and have given minor contribution in data analysis of the study IV.

- I Hiltunen, T. Laakso, J. & Kaitala, V. 2006. Interactions between environmental variability and immigration rate control patterns of species diversity. *Ecological Modelling*, 194: 125-131
- II Hiltunen, T. Laakso, J. Kaitala, V. Suomalainen, L-R. & Pekkonen, M. Temporal variability in detritus resource maintains diversity of bacterial communities. *Acta Oecologia*, in press.
- III Hiltunen, T. Friman V-P. Laakso, J. & Kaitala, V. Predation in a fluctuating environment promotes diversity in an evolving prey community. Manuscript.
- IV Friman V-P. Hiltunen, T. Laakso, J. & Kaitala, V. Availability of prey resources drives evolution of predator-prey interaction. Submitted manuscript.

1 INTRODUCTION

All populations are affected by various intrinsic and extrinsic forces, and by their interactions. Intrinsic forces are, for example, competition within species. Extrinsic forces influencing populations are usually divided into abiotic, such as climate and resource availability, and biotic factors, such as competitors and predators. Another categorization classifies whether populations are controlled by forces acting from above or below in the trophic structure, i.e. whether populations are bottom-up or top-down controlled. It has been debated for a long time whether the abundance of a species in a particular trophic level is primarily controlled by predation or by resource availability, i.e. bottom-up or top-down control of populations (for reviews see Hunter & Price 1992). Bottom-up regulation can result from scarcity of basal resources leading to stronger competition for resources. In contrast, top-down regulation emphasizes the role of predators in food webs. Many theoretical and empirical studies have traditionally focused on only one of these factors despite the fact that these factors often work simultaneously and interact in a complex way, particularly in fluctuating environments.

One of the most striking features of life is the overwhelming diversity. The question that continues to fascinate biologists is: why are there so many different species or genotypes even in seemingly simple environments? Thus, many theories have been developed to explain diversity patterns found in natural communities.

1.1 Forces that affect diversity

There are many mechanisms that affect diversity, such as fluctuations in resources and predator pressure. Mechanisms maintaining or generating diversity can be divided into fluctuation-independent and fluctuation-dependent mechanisms (Chesson 1995). Examples of fluctuation-independent mechanisms are resource partitioning, frequency dependent predation, and immigration (Abrams 1998, Grover 1997, Roughgarden 1995, Tilman 1982,

Gendron 1987, Huntly 1991). These mechanisms can also operate in the presence of environmental fluctuations, but do not necessarily require them. Fluctuation dependent mechanisms can be divided into two broad classes: relative nonlinearity and storage effect (Chesson 2000).

1.1.1 Fluctuation independent mechanisms

Prey resources (or environmental productivity) and intensity of predation are independently expected to have a unimodal relationship with prey diversity (Connell 1978, Tilman 1982, Buckling et al. 2000, Kassen et al. 2000). Reason for decreased diversity in high productivities may be increased total competition or faster population dynamics which leads to faster exclusion of competitive inferior species. Moreover, with complex resources species can use different parts of resource and avoid competitive exclusion. A mechanism by which a predator promotes diversity is e.g. when prey species or genotypes have a trade-off between competitive ability and predator defense such that competitively superior species are more vulnerable to predation (Leibold 1996, see also figure 1c). Predation can also reduce the prey population size which can decrease interspecific competition (Paine 1966, Meyer & Kassen 2007). However, if predation is too intense or predators selectively feed on competitively inferior species, it can also have a negative effect on species diversity (Sih 1985, Cadotte & Fukami 2005). The effect of predation is also found to depend on environmental productivity (Jiang & Krumins 2006). The relative importance of predation is expected to be higher in productive environments, whereas when resources are rare, the relative importance of competition is greater (Proulx & Mazumber 1998, Worm et al. 2002).

Coupling the local competition process to density-independent immigration has been suggested to have a very large positive effect on diversity in addition to reducing variability in the total number of individuals in the community (Loreau & Mouquet 1999, Ives & Hughes 2002). The species that are driven to a low density or extinct by the local competition process can be rescued by density-independent immigration. Moreover, under strictly exclusive local competition, the distribution of competing species is expected to change from a monoculture to unimodal distribution, and then more evenly distributed when the rate of immigration increases.

1.1.2 Fluctuation dependent mechanisms

The competitive exclusion principle predicts that competition in a homogenous environment will reduce species diversity (Hardin, 1960). However, several processes can slow down or prevent the decline of diversity. At a local scale, fluctuating environmental conditions, or disturbances, can decrease the population size of dominant competitors or reverse the competitive ranking. One of the earliest ideas about the mechanisms maintaining diversity was proposed by G. E. Hutchinson (1961). He noticed that the commonly used equilibrium competition theory is contradictory with the fact that 30 to 40

species of planktonic algae, with similar resource needs, could be found in the same lake. Since its discovery, this apparent failure of competition theory is known as the “paradox of plankton”. Hutchinson (1961) then proposed that a gradually changing physical environment could explain the diversity of plankton in natural populations. When the physical environment gradually changes over time, no single species remains competitively superior a sufficiently long time so that it could exclude other species. Later, J. H. Connell (1978) introduced his intermediate disturbance hypothesis (IDH) based on Hutchinson’s earlier work. In this seminal work, Connell proposed that both frequency and intensity of disturbances would affect patterns of diversity. He suggested that the highest diversity would be maintained by disturbances that occur with intermediate frequency and intensity. This is because with weak disturbance, competitive exclusion by the dominant species occurs, and with strong disturbance, only species tolerant of the stress can persist. More recently, the positive effects of various environmental fluctuations on diversity have been demonstrated in many experimental studies, especially with plankton (summarized in Grover 1997; Sommer 2002; Shea et al. 2004). In contrast to many studies done with plankton, to my knowledge there are no experimental studies with bacterial systems where a chemically complex detritus resource temporally fluctuates independently of the level of detritus input. Moreover, there are no studies which simultaneously investigate the effects of fluctuations and predation in this type of study system.

Variation in resources can have particularly profound effects on population growth rates, community composition, and productivity (Grover 1997, see also figure 1A). However, a fluctuating environment does not itself promote diversity, but creates conditions for coexistence-promoting mechanisms to work (Chesson & Huntly 1997; Chesson 2000; Roxburgh et al., 2004; Shea et al. 2004). In competition theory, the two mechanisms that promote coexistence are relative nonlinearity and the storage effect (Chesson 1994; 2000). Species are defined to be relatively nonlinear when they have differently shaped curves defining growth as function of some environmental factor. (see also figure 1B). For example some species may have better performance in high resource environments and other species have better performance in low resource environments. Furthermore, when resources fluctuate, bot species can coexist. Moreover, relative nonlinearity is potentially an important mechanism that promotes diversity in communities utilising multiple resources, such as a chemically complex detritus resource (Huisman et al. 1999). However, in the presence of multiple limiting factors, theoretical and empirical investigations on the effect of relative nonlinearity have so far been poorly investigated (Huisman et al. 1999). Generally, storage effect occur when there are overlapping generations and it is a refuge from bad environmental conditions. Moreover, populations build up “storage” of dormant forms during the favourable environmental conditions so that species are buffered against extinctions during unfavourable conditions (Chesson 1994). This type of buffer may result from a variety of life-history traits: seed banks in annual plants, resting eggs in freshwater zooplankton, and long-lived adults in perennial organisms (Chesson

2000, and references therein). In these systems germination or hatching can occur over the number of seasons from seeds or eggs produced in any single year. One example of a buffer mechanism included in the storage effect in bacteria could be the production of spores during favourable environmental conditions, which could help the species avoid becoming extinct during unfavourable periods.

1.2 Evolution as a community shaping force

Recently, rapid evolution in species interactions has been shown to alter the ecological dynamics of the interacting species in laboratory experiments. This potential overlap between ecological and evolutionary time scales potentially makes the testing of purely ecological models difficult. Predation is one of the strongest selection pressures in interactions between species. Rapid evolution in prey defenses can lead to increasingly resource-controlled population dynamics (Pace & Funke 1991, Balciunas & Lawler 1995, Morin & Lawler 1995), reduce the strength of trophic interactions between predators and prey (Yoshida et al. 2007), or change the phase of predator-prey cycles (Yoshida et al. 2003). Furthermore, an evolutionary increase in prey defense is predicted to stabilize population dynamics of prey and predators (Abrams & Matsuda 1997, Abrams 2000). In addition to prey evolution, predators may also evolve to be more efficient and thus, co-evolution is also possible in microbial systems. For example, tightly coupled coevolution has been shown to occur between the bacterial host and the parasitoid phage (e.g. Bohannan & Lenski 2000).

1.3 Aims of the study

My aim was to test how temporal variability in the environment and predation affect community dynamics and diversity. I used simulation modelling and experiments with aquatic microcosms to explore these questions (for an overview of the studies see table 1). In the first study, the aim was to explore the effect of temporal variability using a simulation modelling approach. In the microcosm experiments, the effects of temporal resource fluctuations (study II), predation (III, IV), and rapid evolution (III, IV) was explored on several properties of a prey community consisting of aquatic bacteria and their protozoan predators. Some of the studies presented in this thesis deal with evolutionary issues, but the main focus is still on ecological questions. My aim was to also test whether the rapid evolution of prey defense occurs, and if so, whether it can alter ecological community dynamics. If evolution occurs, the interpretation of purely ecological models without incorporating potential evolutionary change could lead to misinterpretation of results. For example, if prey defense increases over time, predator pressure should not be misinterpret

as a constant force affecting prey populations. Moreover, allocation to costly predator defense could change competitive properties of the interacting prey species. These changes could potentially modify how environmental fluctuations transfer to community dynamics and affect diversity. Obviously these broad issues cannot be comprehensively dealt with in a single thesis. Thus, the main research objectives in this thesis were limited to the following:

Within these general objectives, more specific hypotheses can be addressed based on ecological and evolutionary theory:

- What is the role of temporal environmental fluctuations and density-independent immigration in community dynamics and diversity? (Study I)
- Will environmental fluctuations and predation promote diversity in aquatic, bacterial communities? (Studies II and III)
- Can predation modulate effects of environmental fluctuations? (Study III)
- Can predation cause rapid evolutionary changes in prey species? (Studies III and IV)
- Can the predator evolve, i.e. does co-evolution occur? (Studies III and IV)
- If the species evolve, can this have ecological effects on the predator-prey interaction? (Studies III and IV)

2 MATERIALS AND METHODS

2.1 Methods in the simulation study

We constructed a discrete-time competition model with stochastic environmental effects on population renewal. All species competed with an equal contribution to the density-dependent feedback of population growth. Our model was constructed so that in a constant environment, all but one species was excluded from the community. We also introduced scenarios where each species received a constant amount of immigrants per time step. The species were assumed to differ in the location of optimal growth performance with respect to a continuous environmental variable. The performance of a species followed a Gaussian function with mean μ and variance δ (Fig. 1 a). The species i growth rate R_i is in the interval $0 < R_i < R_{\max}$. The population renewal is density dependent, following the equation:

$$N_{i,t+1} = \frac{N_{i,t} R_{\max} P_i(w_t)}{(1 + a \sum_{j=1, \dots, i} N_{j,t})^\gamma} + S_i$$

Eq. (1)

Where:

- N_i Population size of i :th species at time t
- R_{\max} Maximum intrinsic rate of population growth
- w Environmental stochasticity
- $P_{i,t}$ Proportion of R_{\max} that species i can achieve in the environment at time t as a function of environment w at time t
- γ Determines the strength of density dependent regulation, and is set to $\gamma = 1$ ("contest" type competition)

- a A scaling parameter that determines carrying capacity
 s_i The density-independent number of individuals that immigrate to the population

The simulations explored community dynamics with a different number of species (2 – 100) and fluctuations types. The fluctuations had similar statistical distributions (mean of 1 and range 0.5 – 1.5) but different autocorrelation structures, or spectra. These ranged from rapidly fluctuating (negatively autocorrelated), to slowly fluctuating (positive autocorrelation) types. As a special case, there was uncorrelated white noise. For details about generating the fluctuations, see Cohen et al. 1998, Heino 1998, and Cohen et al. 1999, as well as figures 2a and 2b for examples of fluctuations used. Maximum population growth rates of the species varied between 1.5 and 10, and data were analyzed using a mean of 100 replicate simulations. The number of simulation steps was 1000.

2.2 Methods in the experimental approach

2.2.1 Study species and culture mediums

Heterotrophic bacterial species obtained from the American Type Culture Collection (ATCC) and from the Belgian Co-ordinated Collections of Microorganisms (BCCM) were used in our experiments. For species names, see table I. Our criteria for selecting these species included positive growth on both the nutrient broth agar and hay extract medium used in our experiments. Most of our test species can also be found in freshwater habitats where they can encounter protozoan predators and experience resource fluctuations. As a predator species, an asexual strain of the ciliated protozoan *Tetrahymena thermophila* (ATCC 13880) was used. *T. thermophila* can also be found in freshwater habitats and has widely been used in microcosm experiments (Laakso et al. 2003, Jiang & Morin, 2004 Ketola et al. 2004, Mayer & Kassen 2007).

Three types of culture media were used. When cultivating the predator without living prey, a sterilized proteose peptone-yeast medium was used. When cultivating the prey bacteria, a medium containing hay extract and phosphate buffer was used. It is important to note that when predators were cultivated with bacteria, the predators were not able to use the hay extract as an energy source. For live cell counts, or when setting up experiments, bacteria were grown on peptone-yeast agar plates.

2.2.2 Microcosms and set up of the experiments

We utilized three types of microcosms in our experiments. For short term experiments and measurements, a plate reader was used. The reader measured biomass as an optical density from microplate wells which contained 300 or 400 μ l of culture medium. In studies III and IV, evolutionary changes in the predator were assessed in loosely capped 15ml conical centrifuge tubes with 9 or 10ml of culture medium. Microcosms in studies II, III, and IV were 250ml polycarbonate Erlenmeyer flasks capped with membrane filters and filled with 40ml of culture medium (for set-up of the experiments, see figures 3 and 4).

For experiments II and III we developed a resource flow apparatus where programmable peristaltic pumps fed the resource to the microcosms (see figure 4). With this apparatus, we were able to individually control the in- and outflow of 30 microcosms. For examples of resource fluctuations used, see figures 2c and 2d. Immediately after pumping in the resource, an equal amount of medium was pumped out of the microcosm to maintain a constant volume in the reactor. The fluid was mixed with a magnetic stirrer at 440 rpm for 1 minute every hour prior to the addition and removal of medium. To prevent contamination, the microcosms and tubing were autoclaved using standard aseptic techniques prior to assembling the communities. Thermostatically controlled heaters in the tubing set at 95°C were used to block microbial growth through the tubes that connected the microcosms to the sterile resource stock bottles. In addition, the outlet tube was submerged in 70% ethanol.

The populations and communities were assembled as follows: if using only individual species, for example, for growth rate measurements, a small inoculum (<1% of carrying capacity) was added to a fresh culture medium. When measuring grazing resistance or setting up long term experiments with predators, the prey was first grown to carrying capacity and then a small predator inoculum was added. In multi-species experiments, the species were grown to their respective carrying capacities separately and then mixed in even proportions prior to the experiment.

2.2.3 Main variables measured

In all studies, population densities and community composition were measured. For bacteria, a live cell count (serial dilution and colony count from agar plates) was used as a measure of population density, and optical density measurements were used as a measure of biomass. For determining predator population sizes, a well-mixed sample of the medium was fixed in Lugol's solution and digitized images of the sample were taken using a binocular microscope attached to a video camera. *T. thermophila* individuals were identified automatically from digitized images using an image recognition script (Jouni Laakso, unpubl.). Temporal stability of population sizes and biomasses were estimated from the time series data as a coefficient of variation (CV) of each microcosm (i.e. a higher CV indicated lower stability). As a measure of diversity, we used Shannon's diversity index (eq. 2). In studies I-III,

the Shannon index was used to measure species diversity, while in study IV the index was used to estimate genetic diversity via different colony types of *S. marcescens*. The advantage of the Shannon index is that it takes into account both the number of species and the evenness of the species. The index increases with species number and species evenness. Thus, the index is perhaps a more sensitive measure of diversity than just species number. In studies III and IV, we also measured the evolutionary change in prey species or the prey community. Competitive ability traits were measured as the maximum growth rate (r_{\max}), or carrying capacity (K). Changes in grazing resistance (defense against predation) traits were measured as a prey's minimum biomass in the presence of a predator. A potential evolutionary change in the predator's maximum growth rate and carrying capacity were assessed as well. Moreover, we used the predator's growth rate and maximum population size as measures of prey food value.

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad \text{Eq. (2).}$$

Where H' is the Shannon diversity index, S is species number, and p_i is the proportion of i :th species in the community.

2.2.4 Statistical analysis

The effect of treatments on the measured variables (population densities, biomasses, and Shannon diversity index) was analyzed with repeated measurements ANOVA (RMANOVA). When the sphericity assumption of RMANOVA was not met, Greenhouse-Geisser corrected F values were used. The coefficient of variation and evolutionary changes were analyzed with two-way ANOVA.

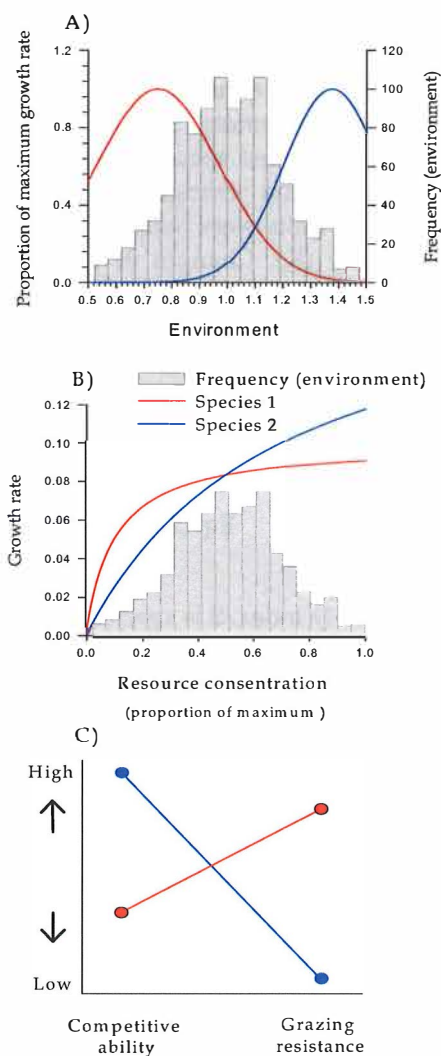


FIGURE 1 Examples of tradeoffs between two species that are required in the maintenance of diversity. A) Examples of optimum growth responses (curves) to environment (X-axis) and distribution of the environmental values (indicated by bars). B) Examples of Monod growth responses (curves) to resource concentration (X-axis), growth rate (Y-axis) and distribution of the environmental values (indicated by bars). C) Two species showing a hypothetical trade off between competitive ability and predator defence.

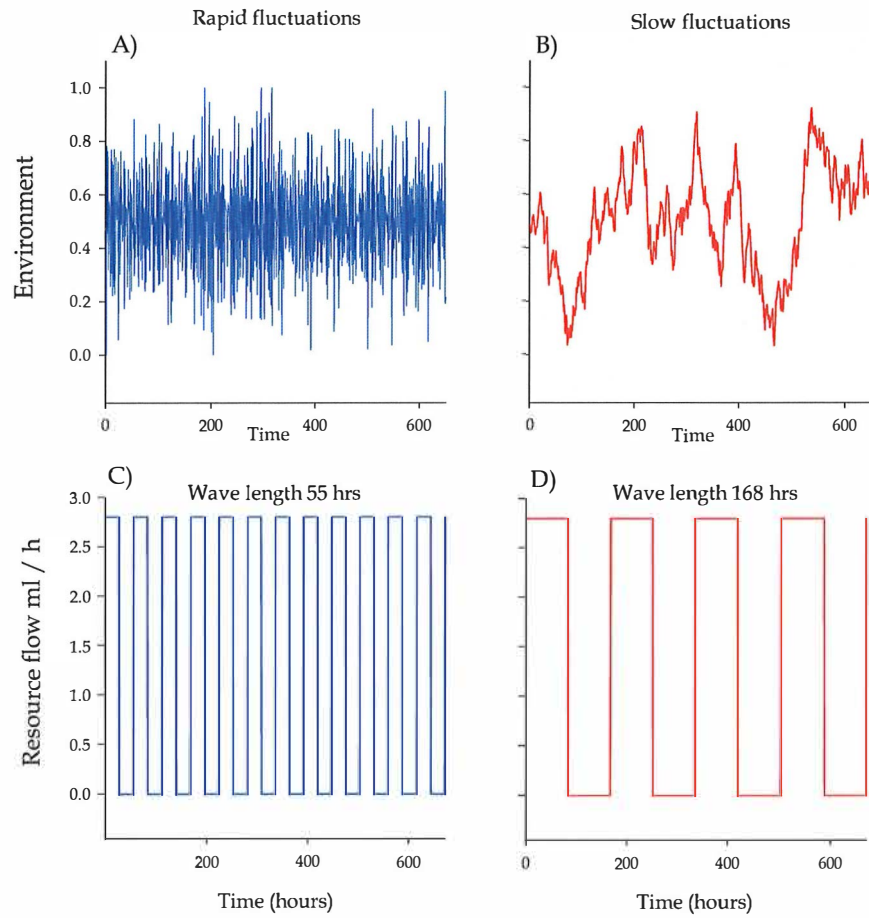


FIGURE 2 Examples of temporal fluctuations used. A) Rapid and B) slow fluctuations used in simulation study I. C) Rapid resource fluctuations used in the experimental studies II and IV. D) Slow fluctuations used in the same studies.

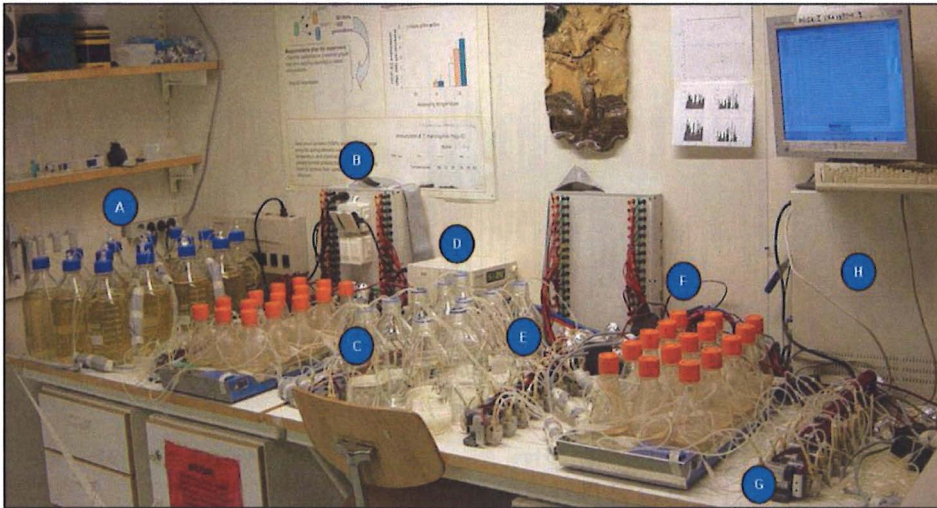


FIGURE 3 Experimental apparatus used in studies II and III. Different components in set-up: A) resource stock bottles; B) relay card connected to computer controlling peristaltic pumps, heaters and magnetic stirrer; C) resource outlet; D) power supply for pumps and heaters; E) peristaltic pumps for outflow; F) microcosm; G) peristaltic pumps inflow; H) computer controlling pumps.

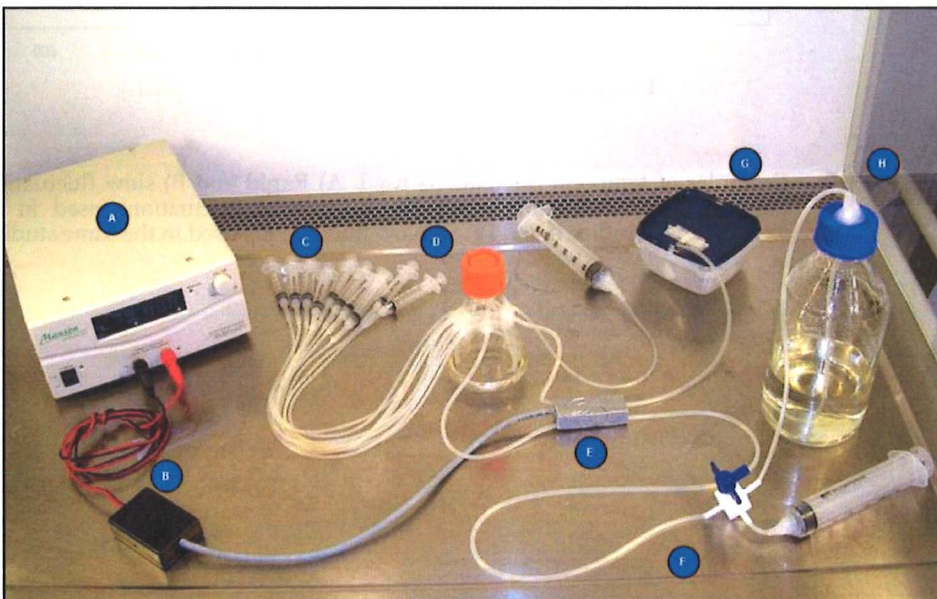


FIGURE 4 Experimental set-up used in study IV. Different components in set-up: A) power supply for heater; B) thermostat for heater; C) sampling syringes; D) microcosms; E) heating resistor; F) resource renewal syringe and valve; G) resource renewal outlet; H) resource stock bottle.

TABLE 1 General overview of studies presented in this thesis

Study	I	II	III	IV
Type of study	Simulation model	Microcosm experiment	Microcosm experiment	Microcosm experiment
Outline of the study	Competition model with immigration	Factorial experiment with two four species communities and three types of resource fluctuations	Factorial experiment with prey community consisting of three species with and without predators in three types of resource fluctuation regimes	Factorial experiment with one prey and one predator species in low and high prey resource environment
Type of environmental fluctuations	Autocorrelated noise	Resource pulses with 168, 55, and 1h wave length	Resource pulses with 155, 55, and 1h wave length	Weekly resource renewal
Species composition	2-101 species	Community 1 <i>Novosphingobium capsulatum</i> <i>Pseudomonas putida</i> <i>Bacillus megaterium</i> <i>Budwicia aquatica</i> Community 2 <i>Serratia marcescens</i> <i>Bacillus cereus</i> <i>Comamonas aquatica</i> <i>Cupriavidus necator</i>	Predator: <i>Tetrahymena thermophila</i> Prey: <i>Novosphingobium capsulatum</i> <i>Serratia marcescens</i> <i>Bacillus cereus</i>	Predator: <i>Tetrahymena thermophila</i> Prey: <i>Serratia marcescens</i>
Length	Simulation run for 1000 generations	28 days <690 generations	48 days <1180 prey generations	98 days <2400 prey generations

3 RESULTS AND DISCUSSION

3.1 Environmental fluctuations as driver of communities

Environmentally driven fluctuation-dependent mechanisms that maintain diversity require that environmental fluctuations change species growth rates, which then translate into fluctuations in population densities (Ives 1995, Chesson 2000). For these mechanisms to work, it is essential that the population growths of different species fluctuate in asynchrony so that no individual species can dominate long enough for extinctions to occur. These asynchronous fluctuations can emerge if species have trade-offs in performance, for example in high and low resource environments. We found that in study II that species have trade-offs between growth in low and high resource environments (see also figure 1B). In study III, we also found that species have similar trade-offs in their ability to grow in high and low resource environments. Moreover, the species showed trade-offs between competitive ability and predation resistance: *N. capsulatum* had the highest growth rates in low resource environments whereas *S. marcescens* excelled in high resource environments. *B. cereus* had the lowest growth rates in all resource concentrations, but notably the strongest predator defense (data on the tradeoffs found in study III is not included in this thesis). Thus, it tentatively appears that the trade-off requirement for diversity-promoting mechanisms to work was fulfilled in the experimental communities.

Studies II and III demonstrated that fluctuations either made total community biomass more unstable, or had no effect. In both of the communities in study II, total biomass was more stable in a constant environment than in a slowly fluctuating environment. In study III, fluctuation treatments had no effect on total prey community stability. However, in studies II and III we did not find that the fluctuation treatment affected the stability of populations of individual species. This does not necessarily mean that the populations did not fluctuate, because our sampling interval was quite sparse compared to the high bacterial growth rates. Thus, rapid changes in population abundances were probably not recorded due to low statistical power of the experimental data.

Results from studies I-III supported the general view that environmental fluctuations promote diversity. In addition we found at least indirect evidence that relative nonlinearity and other diversity-promoting mechanisms could have operated (Chesson 2000, Vasseur et al. 2007). In study I, the interaction between environmental fluctuations and immigration strongly modulated diversity patterns. Diversity was generally higher in rapidly fluctuating environments, but this pattern was also affected by density independent immigration. With more than two species in the community and intermediate immigration rates, maximum diversity was found during intermediate fluctuation frequencies. Moreover, a high immigration rate reduced the roles of environmental fluctuations and population growth rate in the patterns of species diversity. These results suggest that predicting community dynamics in natural systems based solely on fluctuations might be difficult unless immigration rates and biological details of the community are known. In experimental studies II and III, the slowly fluctuating environment produced a higher diversity than the constant environment. These results imply that the slow resource fluctuations allowed sufficiently long periods of low and high resource levels.

Many previous studies suggest that fluctuations in resources and disturbances maintain diversity (e.g. Grover 1997, Sommer 2002 for summary). Our results mainly support these findings. The classic experimental approach has been to test how temporal resource fluctuations affect species diversity. These experiments were often conducted with phytoplankton communities that were exposed to a pulsing supply of a single chemically defined nutrient, such as phosphorus or silicon (summarized in Sommer & Worm 2002). For example, Sommer (1984, 1985) found that only two species of phytoplankton coexisted when inorganic nutrients were supplied continuously, while seven phytoplankton species coexisted when nutrients were supplied in weekly pulses. Kirk (2002) reported that when planktonic rotifer species were fed on algae at 0, 4, or 8 day resource renewal rates, the slowest decline of diversity was found for the 8 day renewal rate. However, McIsaac & Gilbert (1991) found that the longest coexistence between two rotifer species occurred with rapid, 0.5 day interval fluctuations of resource addition. In our studies, the highest diversity was found for fluctuations with a long 155 or 168h wave length. It must be noted however, that our study species have faster growth rates than phytoplankton or rotifers. These results highlight a problem with the scale of variability that produces the highest diversity: it depends on the life history of the study species (Hubbell 1973, May 1976, Pimm 1991).

3.2 Effects of predation on diversity

We used the protozoan predator *Tetrahymena thermophila* to feed on bacteria in studies III and IV. Our results supported the general view that predation modulates community composition and promotes diversity due to differential

responses of the species to predation. In study III, the predator maintained a higher species diversity, and in study IV a higher genetic diversity (the latter measured using the Shannon diversity index of different colony colour variants of the prey *S. marcescens*). A positive effect of predation on diversity has been also found in other studies with bacteria. Mayer and Kassen (2007) showed that predation by *T. thermophila* can diversify *Pseudomonas fluorescens* colony morphology through negative frequency-dependent selection on the *P. fluorescens* wrinkly-spreader and smooth colony types. In their experiment, *T. thermophila* less effectively preyed upon the wrinkly-spreader prey type, forming biofilm on the water-air interface of the microcosm. Furthermore, the wrinkly spreader was also less competitive than the smooth form when abundant. We found similar tradeoffs between species in our study system which will be discussed below.

If predation by the protozoa could also maintain and generate bacterial diversity in natural systems, this could have important functional implications for an ecosystem. The increased diversity could, for example, increase the flow of energy from dissolved organic matter to higher trophic levels if more diverse community is able to utilize dissolved organic matter more efficiently (Sommer 1989). In aquatic ecosystems, the microbial loop is a trophic pathway where dissolved organic carbon is reintroduced to the food web through bacteria (Sommer 1989). Bacteria are consumed in the loop mostly by protists such as flagellates and ciliates (Sommer 1989). Our study system describes a similar detritus-bacteria-protozoan pathway. Thus, a basic understanding of predation by a protozoa on bacteria gained with microcosm experiments could also help in understanding the interactions of natural ecosystems where microbes are among the most important components, in terms of energy flow and diversity (Madigan et al. 2000).

3.2.1 Interaction between predation and environmental fluctuations

There was an interaction between predation and resource fluctuations in study III such that predation promoted diversity only in the fluctuating environments. Menge and Sutherland (1976, 1987) found that disturbance could modify the effect of predation in a case where the disturbance affects predators more than the prey. The stronger effect of disturbance on predators can be found, for example, under conditions where the prey can spatially escape disturbance, but the predator can not. Another mechanism could be that predators usually have longer generation times than prey, and therefore recovery from a disturbance may be slower. In previous study Gallet et al. (2007) did not find that parasitoid bacteria (*Bdelliovibrio bacteriovorus*) preying on bacteria (*Pseudomonas fluorescens*) was affected by environmental fluctuations. In our study system predator growth rates were however lower than with *B. bacteriovorus*. Therefore the ability of our predator species to recover from disturbances was probably lower. Moreover, we found evidence that the predator was more affected by disturbances caused by resource outflow mortality than prey. An indirect indicator for this was a higher CV in predator populations. In addition, prey

populations can be indirectly affected by fluctuations if fluctuations are transferred into predator populations and predators are at the same time major force modulating prey populations. Therefore, the interaction between predation and temporal fluctuations can have an additional diversity-promoting effect if the predator pressure is influenced by fluctuations.

3.3 Evidence for rapid evolution and the ecological consequences

We did not find evidence of evolutionary changes in predator growth rate or carrying capacity, which indicated that co-evolution did not occur in our study system. One explanation for this is that predators have less potential for evolution due to longer generation times than prey, and because prey population sizes are larger. Moreover, selection for prey defensive traits is thought to be stronger than the selection for predator efficiency, e.g. “life vs. dinner” dichotomy (Dawkins & Krebs 1979; Vermeij 1994). Unlike most of the previous studies conducted with bacterial host and viral or bacterial parasitoids (Bohannan & Lenski 1999, Buckling & Rainey 2002, Gallet et al. 2007), our study system is a classical predator-prey system where the predator has longer generation time than the prey and consumes multiple preys before reproducing.

In both of the studies where the predator-prey system was used, the prey evolved to have a stronger resistance against predation. This reduced prey food value for the predator. In study III, grazing resistance was measured as the whole community’s resistance, i.e. an aggregate measure of the different species. The evolutionary dynamics were studied in more detail in study IV with only one bacterial prey species, *S. marcescens*. Exposure to predators increased the grazing resistance of *S. marcescens* only in the high resource environment, while a decrease in prey competitive ability (biomass production in the absence of the predator) was observed mainly in the low resource environment. These results support the theoretical prediction that when anti-predatory adaptation is costly, evolution of predator-prey interaction is constrained by prey resource availability (Hochberg & van Baalen 1998; Abrams 2000; Yamauchi & Yamamura 2005).

The predator to prey ratio declined during the experiments in both studies. This indicates that evolution in prey grazing resistance also had a considerable effect on ecological dynamics of the predator-prey system. Resources may start to play a more important role in controlling prey communities when the effect of predation decreases. Further support for the evolving trade-off in competitive ability and predator defense is found in study IV. It is also possible that rapid evolution of grazing resistance interferes with diversity-promoting mechanisms. One mechanism through which this could occur is when population dynamics becomes more stable. The stabilization of prey population dynamics is expected to occur when predation increases prey diversity by selecting for more defensive individuals (Johnson & Agrawal

2003). In a fluctuating environment, stabilization can ultimately lead to decreased diversity if the diversity-promoting mechanisms are no longer able to operate. For example, if species diversity is maintained because good competitors are more vulnerable to predation, reduced vulnerability and competitive ability may lead to lower diversity because species become too similar and the tradeoff disappears. This situation is similar to fig. 1C, but with more similar trait properties between the species. Moreover, the ability to allocate to different traits depends on the resource environment. The potential effect of evolution on trophic dynamics and diversity highlights the need for a deeper understanding of how evolution could change predictions of ecological models.

4 CONCLUSIONS

Tradeoffs were found between species performance in low and high resource environments. This could have led to a situation where fluctuations destabilized predator populations and total prey community biomass. The existence of tradeoffs gives support to the hypothesis that fluctuations are transferred to populations, and consequently the frequency dependent mechanisms that maintain diversity could have operated. With slow fluctuations, the longest periods of low and high resources could have occurred. Consequently, these periods could have also been most efficient for diversity promoting mechanism to operate. Furthermore, our results support the general view that environmental fluctuations and predation are forces that can maintain species and genetic diversity. Evidence that these factors promote diversity was found in all of our studies (fluctuations: studies I-III, predation: studies III and IV). Interestingly, both predation and density independent immigration interacted with environmental fluctuations and produced diversity patterns which were different from those that fluctuations produced as an isolated factor.

All experiments reported in this thesis were conducted according to similar methodology used in many previous microcosm studies where a protozoan predator feeds on bacteria, which in turn feed on a nonliving detritus resource (e.g. Gause 1934, Petchey 2000, Morin 2004). However, studies presented in this thesis also take into account the composition of the bacterial community. We found that predation causes rapid evolution of prey and consequently impacts the ecological properties of the predator-prey interaction. Without knowledge of the evolutionary changes, ecological models may no longer produce meaningful explanations for the observed community dynamics.

Acknowledgements

I would like to thank all the people who have contributed to my thesis directly or indirectly, especially my supervisors Jouni Laakso and Veijo Kaitala. Jouni has been both a patient and encouraging supervisor and most of all, he has been a good friend. With Jouni's guidance, we built a new study system and conducted meaningful science with it. It has not always been easy but we have gotten to where we are now with help from each other. I would like to particularly acknowledge Jouni for teaching me the practical application of Ohm's law after a major meltdown of inappropriate electric wires in our lab. Without support from Veijo during the early stage of this project, this thesis would not have been possible. Many trainees helped me in the lab work, especially Sanna Piirainen and Mikko Niskanen who gave valuable help with laborious experiments. Lotta-Riina Suomalainen and Heidi Kunttu introduced me to the possibilities of DNA level microbiology during our collaboration. Elina Virtanen, Juha Ahonen and Hannu Kautto helped me with various technical issues.

During my visits to Helsinki I had interesting discussions with Esa Ranta, Mike Fowler and Minna Pekkonen. I would like to thank Sami Aikio for the same reason as well as for valuable comments on my thesis. A short visit to the University of Lund at the very beginning of my PhD studies was influential for my later work thanks to Niclas Jonzén. In Jyväskylä, Johanna Mappes supported and motivated me in the later stages of my thesis. Mika Mökkönen and Roger Jones improved the language in my thesis, while Roger also provided beneficial comments for a rather difficult second manuscript.

I have been privileged to work with my friends and have shared many memorable moments in science and leisure with my young colleagues: Tarmo Ketola gave valuable comments on my work during many occasions over these years. With Jari Syväranta, I have had interesting discussions about life (and about life in aquatic environments). I have enjoyed the good company of Carita Lindsted, Jarkko Routtu and Ville Selonen at many scientific and not-so-scientific gatherings. I would like to particularly thank my friend and coauthor Ville Friman. Ville's enthusiastic way of conducting science has inspired me during some difficult moments.

I also have a few friends outside of the scientific community. These people made life meaningful during my free time. Most of them were partners in crime during the Kirjailijatalo disaster, 7th of June 2007. I would like to thank Matti Häkkilä for his continuing friendship and for peeling tons of potatoes and carrots for our gourmet club. I also have some very nice memories of outdoor activities with my friends Henri and Teemu Hölttä: trips to Lake Puulavesi have been an enjoyable retreat from life in Jyväskylä.

Most of all, I would like to thank my family for their support during the years that I have been doing this thesis. My parents, Pirjo and Erkki Hiltunen, have always been very encouraging. Conversations with my mother about biology beyond university circles have been very fruitful. I would also like to

thank my sister Päivi Tasapuro, my brother-in-law Arto Tasapuro and my aunt, Mirja Messo, for being there for me.

This thesis would not have been possible without funding and so I would also like to thank the Academy of Finland, the Centre of Excellence in Evolutionary Research and the Ellen and Artturi Nyysönen Foundation for funding this project.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Ympäristön vaihtelut ja saalistus muokkaavat yhteisön dynamiikkaa ja diversiteettiä

Populaatioekologia tutkii populaatiokokojen vaihteluita ja niihin johtavia syitä. Vaihtelu populaatiokoossa voi olla seurausta populaation sisäisistä ja ulkoisista tekijöistä tai niiden vuorovaikutuksesta. Ulkoisia populaatiokokoihin vaikuttavia tekijöitä ovat mm. eloton ympäristö ja sen vaihtelut sekä vuorovaikutukset toisten lajien kanssa. Sisäisiä populaatiokokoihin vaikuttavia tekijöitä on esimerkiksi kilpailu saman lajin eri yksilöiden välillä. Paljon keskustelua on myös herättänyt kysymys sääteleekö populaatioita sen ylä- vai alapuoliset tekijät ravintoketjussa. Yläpuolisena säätelynä pidetään yleisesti saalistajia ja alapuolisena ravinnon saatavuutta.

Saalistus, ympäristön vaihtelut ja tulomuutto ovat populaatioiden kannanvaihteluihin ja yhteisöjen monimuotoisuuteen vaikuttavia tekijöitä. Aiemmissa tutkimuksissa on yleensä keskitytty vain yhden tekijän vaikutuksen tutkimiseen, kun taas tärkeät tekijöiden väliset vuorovaikutukset ovat saaneet vähemmän huomiota. Perinteisesti käytetyt ekologiset mallit olettavat lajien välisten vuorovaikutuksien olevan muuttumattomia. Viimeaikaisissa tutkimuksissa on kuitenkin havaittu, että nopea evoluutio voi muuttaa lajien välisiä vuorovaikutussuhteita. Nopean evoluution mahdolliset vaikutukset populaatioiden kannanvaihteluihin tulisikin tarkemmin huomioida ekologisessa tutkimuksessa tulevaisuudessa.

Syrjäyttävän kilpailun periaate ennustaa, että tasaisessa ympäristössä parhaiten kilpaileva laji syrjäyttää muut lajit. On kuitenkin olemassa mekanismeja, jotka hidastavat tai estävät lajien häviämistä, ja näin ollen ylläpitävät yhteisön lajistollista monimuotoisuutta. Mekanismit voidaan jakaa ympäristön vaihtelusta riippuviin ja riippumattomiin. Vaihtelusta riippumattomia mekanismeja ovat mm. saalistus ja tulomuutto. Saalistus voi esimerkiksi lisätä yhteisön monimuotoisuutta, jos lajeilla on allokaatiokustannuksia kilpailukyvyin ja petopuolustuksen välillä. Tulomuutto voi lisätä yhteisön monimuotoisuutta kasvattamalla häviämiskäytössä olevien lajien populaatiokokoja. Vaihtelusta riippuvat mekanismit voidaan jakaa myös kahteen pääluokkaan: mekanismeihin, joissa lajit reagoivat eri tavoin ympäristöön ja mekanismeihin, joissa lajit pystyvät varastoimaan huonoja oloja kestäviä lepoasteitaan siihen asti kunnes ympäristö on niille taas suotuisa. Esimerkkinä varastoinnista on mm. kasvien kestävä siemenet tai bakteerien lepoitiöt, jotka selviävät huonojen olosuhteiden yli ja taas hyvien olojen aikana elvyttävät populaation. Jos eri lajeilla on allokaatiokustannus kyvyssä kasvaa korkeassa tai matalassa ravintotasossa, voi ympäristön vaihtelu edistää lajistollista monimuotoisuutta. Kun ympäristö vaihtelee, ei mikään laji pääse vallitsevaan asemaan ja kilpailullista syrjäytymistä ei pääse tapahtumaan.

Ensimmäisessä osatyössäni tutkin vaihtelevan ympäristön ja tulomuuton vaikutusta yhteisön monimuotoisuuteen simulaatiomallin avulla. Väitöskirja-

työni kokeellisessa osuudessa tutkin miten ajalliset resurssin vaihtelut, saalistus ja evoluutio saalin puolustuskyvyssä vaikuttavat kannanvaihteluihin ja yhteisön lajistolliseen monimuotoisuuteen. Kolmessa viimeisessä osatyössäni käytin akvaattisia mikrokosmoksia. Käyttämäni kokeelliset yhteisöt koostuivat toisenvaraisista bakteerilajeista ja niitä saalistavasta *Tetrahymena thermophila* alkueliöpedosta. Osatöissäni I-III huomasin, että ympäristönvaihtelut lisäävät yhteisön monimuotoisuutta. Osatyössä I havaitsin myös tulomuuton muokkaavan ympäristönvaihtelun vaikutusta siten, että suurin yhteisön monimuotoisuus saavutetaan keskimääräisillä ympäristönvaihtelun taajuuksilla. Osatyössä III ympäristönvaihteluiden ja saalistuksen vuorovaikutus näkyi siten, että saalistus nosti bakteeriyhteisön monimuotoisuutta vain kun ympäristö vaihteli. Vakaassa ympäristössä saalistuksella ei ollut vaikutusta bakteeriyhteisön monimuotoisuuteen. Viimeisessä osatyössä havaitsin, että saalistus lisäsi *Serratia marcescens* saalisbakteerin geneettistä monimuotoisuutta, jota mittasin erilaisten pesäketyyppien avulla.

Osatöissä III ja IV, joissa käytin alkueliösaalistajaa, mittasin myös mahdollista evolutiivista muutosta peto-saalissuhteessa. Osatyössä III havaitsin saalis-yhteisön ja osatyössä IV yksittäisen lajin muuttavan evoluution myötä paremmin saalistusta kestäväksi. Saaliin evolutiivisella muutoksella oli myös ekologisia seurauksia peto-saalis yhteisölle. Esimerkiksi pedon populaatiokoko laski kokeiden edetessä mikä luultavasti johtui siitä, että saaliin ravintoarvo pedolle aleni evoluution myötä.

Tutkimukseni osoittaa, että ympäristön vaihtelut, saalistus ja tulomuutto kaikki lisäävät saalis-yhteisön monimuotoisuutta. Lisäksi näiden tekijöiden havaittiin vuorovaikuttavan keskenään. Nämä vuorovaikutussuhteet ovat jääneet aiemmin vähäiselle huomiolle, vaikka niiden tutkiminen ja selvittäminen on olennaista yhteisöekologian teoriaa kehitettäessä. Havaitsemani evolutiivinen muutos saaliin puolustuskyvyssä on myös syytä huomioida ekologisia malleja kehitettäessä ja mikrobikokeita tehtäessä. Perinteinen mikrobiekologinen lähestymistapa on pitänyt bakteeriresurssia muuttumattomana "mustana laatikkona" alkueliösaalistajille. Viimeaikaisten tutkimusten valossa tämä oletamus on kuitenkin väärä, sillä saalis-yhteisön evolutiiviset muutokset voivat heijastua yhteisön ekologisiin ominaisuuksiin. Näin ollen evolutiivisten voimien vaikutus yhteisöjen ekologisiin ominaisuuksiin on huomioitava tulevaisuudessa tarkemmin kokeiden tuloksia tulkittaessa.

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ORIGINAL PAPERS

I

**INTERACTIONS BETWEEN ENVIRONMENTAL VARIABILITY
AND IMMIGRATION RATE CONTROL PATTERNS OF
SPECIES DIVERSITY**

by

Hiltunen, T. Laakso, J. & Kaitala, V. 2006.
Ecological Modelling. 194: 125-131

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<https://doi.org/10.1016/j.ecolmodel.2005.10.010>

II

TEMPORAL VARIABILITY IN DETRITUS RESOURCE MAINTAINS DIVERSITY OF BACTERIAL COMMUNITIES

by

Hiltunen, T. Laakso, J. Kaitala, V. Suomalainen, L-R. & Pekkonen, M.

Acta oecologia, in press

<https://doi.org/10.1016/j.actao.2007.12.002>

III

**PREDATION IN A FLUCTUATING ENVIRONMENT
PROMOTES DIVERSITY IN AN EVOLVING PREY
COMMUNITY**

by

Hiltunen, T. Friman, V-P. Laakso, J. & Kaitala, V.

Manuscript

<https://doi.org/10.1016/j.actao.2011.09.010>

IV

**AVAILABILITY OF PREY RESOURCES DRIVES EVOLUTION
OF PREDATOR-PREY INTERACTION**

by

Friman, V-P. Hiltunen, T. Laakso, J. & Kaitala, V.

Submitted manuscript

<https://doi.org/10.1098/rspb.2008.0174>