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Species Responses to Environmental Fluctuations

- impacts of food web interactions and noise color

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*To my family and friends.
Thank you for being there for me always.*

CONTENTS

ABSTRACT	vii
POPULÄRVETENSKAPLIG SAMMANFATTNING	ix
LIST OF PAPERS	xi
Contributions to the papers	xi
ACKNOWLEDGEMENTS	xii
1. INTRODUCTION	1
1.1. Environmental fluctuations	1
1.2. Species environmental responses	3
1.2.1. <i>Single species models</i>	3
1.2.2. <i>Food web models</i>	4
1.2.3. <i>Additional complexities of nature</i>	4
2. AIMS	6
3. METHODS	7
3.1. Population dynamics	7
3.1.1. <i>Food web modules</i>	7
3.1.2. <i>Species isolated from species-species interactions</i>	9
3.1.3. <i>The dynamic rate of food webs</i>	10
3.1.4. <i>Periodic boundary conditions</i>	11
3.2. Dispersal between subpopulations	12
3.2.1. <i>Mass-action mixing</i>	12
3.3. Environmental fluctuations	12
3.3.1. <i>Noise on carrying capacities</i>	12
3.3.2. <i>Temporal autocorrelation</i>	12
3.4. Species responses to environmental fluctuations	13
3.4.1. <i>Mean, variance and stability</i>	13
3.4.2. <i>Tracking error</i>	13
3.4.3. <i>Extinction risk</i>	14
3.4.4. <i>Descriptive statistics</i>	14
4. SUMMARY OF PAPERS	15
4.1. Paper I	15
4.2. Paper II	15
4.3. Paper III	15
4.4. Paper IV	16
5. DISCUSSION	17
5.1. Food web effects depend on noise color	17
5.2. Benefits of biodiversity	18
5.3. Future research needs	18
5.4. Conclusions	22
6. REFERENCES	23

PAPERS

- I. Environmental variability uncovers disruptive effects of species' interactions on population dynamics
- II. The dynamic rate of food webs: a race towards stability?
- III. Stability patterns of metacommunities in colored environments
- IV. Periodic food webs enable an infinite number of interacting species

ABSTRACT

Species constantly experience changes in their environmental conditions owing to natural or human induced reasons. Understanding how species respond to these fluctuations are important for ecology, especially given the ongoing climate change. Empirical studies have shown that species respond differently to the same disturbance. However, our knowledge of what create these differences in the environmental response is limited and in most cases based on studies focusing on single species. In this thesis, I have taken a theoretical approach and used dynamical models to investigate how the population dynamics of species are affected by species-species interactions and environmental fluctuations.

In the first paper (Paper I) I investigated how a species respond to environmental fluctuations when isolated or embedded in a food web. The study showed that species-species interactions had an effect in temporally positively autocorrelated environments (red noise) but not in uncorrelated environments (white noise). This was owing to species following their equilibrium densities in red environments which in turn enabled species-species interactions to come into play. Red environmental variables are more prominent in nature than white. Thus, these results show the importance of using a food web approach when analyzing species response to environmental fluctuations.

The most commonly discussed effect of climate change is an elevated mean temperature. This shift is expected to affect the growth rate of many species. However, there is no robust theory of how we should expect species in food webs to respond to a rise in temperature. In the second paper (Paper II) I defined and studied the dynamic rate of food webs (DR) acting analogously to single species growth rate. I found that the higher DR the easier for species population densities to follow their equilibrium over time. Both DR and noise color changed the temporal relationship between the population and the environmental noise. Thus, it is of major importance to take the scale of time into consideration when investigating species response to environmental fluctuations.

Another important factor which affect population dynamics is species spatial distributions. Dispersal between subpopulations enable individuals to rescue or prolong the time to extinction for the population seen as a whole. In the third paper (Paper III), I investigated how species in food webs respond to environments that varies both in time and space and compared the results with the one from single species. I found that single species were stabilized by an increased dispersal rate independent

of the noise color. Species-species interactions had an effect for some of the species in these landscapes. At red asynchronous noise, one resource species in each food web had a local minimum in stability at low dispersal rate. Here, dispersal decoupled local population dynamics and prevented species from tracking their equilibriums. At high dispersal rates, all resource species and their single species counterparts were stabilized by dispersal as local patch dynamics lost its importance. Environmental noise together with the spatial dimension does seem to explain much of the stability properties of species on our planet.

However, natural ecosystems are much more complex and species rich than the food web models I have used so far. Theoreticians have previously had a hard time describing stable complex systems that survive environmental fluctuations. Thus, in my fourth and last project (Paper IV) I investigated how species population dynamics are affected by environmental fluctuations when embedded in larger food webs. These systems were built by connecting food web modules with periodic boundary conditions (PBC). The PBC method has previously helped physicists to understand the nature of waves and particles by removing the edges in systems. I found that food web size does not have to have a negative effect on food web stability. I showed that by removing the destabilizing effect of edges it is possible to describe large stable food webs, more similar to natural ecosystems.

Overall, the research presented here give new insights into species responses to environmental fluctuations. They especially highlight the importance of considering both species interactions and environmental noise color when studying population dynamics in a fluctuating environment. A food web approach is necessary when analyzing species population dynamics and planning for conservation actions, especially when studying the effects of climate change on biodiversity.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Arter upplever ständigt en variation i deras yttre miljö, exempelvis en temperatur eller mängd nederbörd som varierar över tid. Omvärldsförhållanden påverkar i sin tur förutsättningarna för om en arts population ska växa eller minska. Ekologer är mycket intresserade av vad som påverkar en arts populationsstorlek speciellt när det gäller arter som riskerar ett utdöende. Förstår vi vad som påverkar en population och hur den svarar på olika förändringar i omvärlden så har vi en bra chans att hjälpa till för att behålla arten i ekosystemet. Det är dock ganska komplicerat att förutsäga hur en specifik art ska svara på omvärldsvariation. Tidigare studier har visat att arter kan svara olika på samma omvärldsvariation men kunskapen om varför det är så är bristfällig och ofta baserad på enartsstudier.

Ekosystem består av många olika arter som gynnas eller missgynnas av omvärlden men även av varandras populationsstorlekar. Ett mycket förenklat exempel på ett ekosystem är en näringskedja där den lägsta nivån är en resurs (gräs) som betas av en konsument (får) och som i sin tur jagas av en predator (varg). Lite nederbörd och varm temperatur kan missgynna resursen vilket leder till att konsumenten får dåligt med bete och predatorn får mindre byten. I denna avhandling visar jag att svaret på omvärldsvariation kan vara mer komplicerat än så här men att det i mina modeller fortfarande går att reda ut varför det blir som det blir. För att försöka reda ut grunden till varför arter svarar som dom gör på omvärldsvariation så har jag valt en teoretisk approach med dynamiska modeller av näringsvävar.

I min avhandling undersöker jag hur populationsdynamik påverkas av mellanartsinteraktioner och omvärldsvariation. I det första arbetet (Paper I) jämförde jag hur arter svarade på omvärldsvariation beroende på om dom var isolerade eller innefattade i en näringsväv. Mellanartsinteraktioner visade sig ha en stor effekt då omvärldsvariationen varierar på ett sätt mer likt uppmätta tidserier av t.ex. temperatur (temperaturen idag påverkas av vad temperaturen var i går – positiv autocorrelation över tid). I mitt andra arbete undersökte jag vad en temperaturökning, driven av exempelvis klimatförändringen, kan få för konsekvenser för arters populationsdynamik. Jag definierade och undersökte effekten av näringsvävars dynamiska hastighet som agerar likt isolerade arters tillväxttakt. Det visade sig finnas likheter mellan effekten av positiv autokorrelation i omvärldsvariationen (Paper I) och näringsvävars dynamiska hastighet (Paper II). Båda dessa parametrar visade sig påverka näringsvävens och omvärldsvariationens relation till varandra.

Detta gjorde att en ändring av den ena parametern kunde leda till en liknande effekt som en ändring av den andra. Studien understryker betydelsen av tidsskalan vid studier av populationsdynamik under omvärldsvariation. I mitt tredje arbete (Paper III) undersökte jag hur populationsdynamik för arter i näringsvävars påverkas av den rumsliga fördelningen av arter i delpopulationer. Jag visade här att en okorrelerad omvärld gynnar populationers stabilitet över tid men också att effekten av låg spridning mellan delpopulationer kan vara beroende av arters mellanartsinteraktioner. I mitt fjärde och sista arbete (Paper IV) tittade jag på vad som händer med arters populationsdynamik när påverkade av omvärldsvariation och samtidigt placerade i mycket stora periodiskt uppbyggda näringsvävar. Studien visade till skillnad från många tidigare studier att storleken på en näringsväv inte nödvändigtvis behöver leda till ett mindre stabilt system när placerad i en varierande omvärld.

Sammantaget så ger avhandlingen nya insikter i hur arter i ekosystem svarar på omvärldsvariation. Den understryker vikten av att ta hänsyn till mellanartsinteraktioner och autokorrelation i omvärldsvariationen vid studier av populationsdynamik. Dessa faktorer kan ha en mycket stark effekt på populationers stabilitet över tid vilket i sin tur påverkar arters risk för att dö ut. Hur arter svarar på omvärldsvariation är särskilt aktuell just nu, speciellt med tanke på klimatförändringen och dess påverkan på vår planets biodiversitet.

LIST OF PAPERS

- I. Gudmundson, S., Eklöf, A., & Wennergren, U. (2015)
Environmental Variability Uncovers Disruptive Effects of
Species' Interactions on Population Dynamics
Proceedings of the Royal Society: Biological Sciences. 282.¹
- II. Gudmundson, S., & Wennergren, U. (2017)
The Dynamic Rate of Food Webs: A Race Towards Stability?
Under review by:
Proceedings of the Royal Society: Biological Sciences
- III. Gudmundson, S., Årevall, J.,
Lögberg, F. & Wennergren, U. (2017)
Stability Patterns of Metacommunities in Colored
Environments
Manuscript
- IV. Gudmundson, S., & Wennergren, U. (2017)
Periodic Food Webs Enable an Infinite Number of
Interacting Species
Manuscript

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Contributions to the papers

Paper I-IV: Sara Gudmundson made major contributions in shaping the ideas, choosing the methodological tools and formulating the questions. SG took a major part in the data analysis and is the main author.

Paper I, II, IV: SG developed the main code and further developed a preexisting code for generating noise color. SG carried out the data simulation work.

Paper I, IV: SG drafted the manuscript together with the coauthors.

Paper II, III: SG drafted the manuscripts.

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1. INTRODUCTION

Species constantly experience changes in their environmental conditions owing to natural or human induced reasons. These fluctuations can affect population dynamics and thereby species risk of going extinct (Stenseth et al., 2002). Thus, how species respond to environmental fluctuations is an important question for ecologists, especially given the ongoing changes in mean and variability of climate conditions (IPCC, 2013). Empirical studies have shown that species can respond differently to the same environmental disturbance (Morris et al., 2008). However, our knowledge of what create these differences in species environmental responses are limited and in most cases based on studies focusing on single species.

In this thesis, I have taken a theoretical approach and used dynamical models to investigate how the population dynamics of species are affected by species-species interactions and environmental fluctuations.

1.1. Environmental fluctuations

Temperature and precipitation are two examples of common environmental indicators known to fluctuate over time and affect species population densities. Environmental indicators are expected to have positively autocorrelated time series (Halley, 1996), where adjacent values in time are similar. These time series are often termed pink or red noise (Mustin et al., 2013; Halley, 1996; Vasseur & Yodzis, 2004; Weber & Talkner, 2001). Red noise gives a slower change over time than noise without temporal autocorrelation (white noise) and noise with negative autocorrelation (blue noise). An increased positive autocorrelation is commonly described as an increased redness. Despite the frequent prevalence of red environmental fluctuations in nature there is a lack of knowledge regarding how noise color affect species environmental responses, especially in studies where species-species interactions are taken into consideration.

Box 1 | Glossary

Autocorrelation	the degree to which temporally adjacent values in a time series are similar
Environmental noise	time series of a fluctuating environmental indicator
Environmental redness	degree of positive autocorrelation in the environmental noise
Food web	ecological network of interacting species
Food web module	small food web model
Periodic boundary conditions	approximates a large (infinite) system by two-dimensional tiling of a unit cell so that when an object passes through one side of the unit cell, it re-appears on the opposite side.
Population dynamics	how a population density fluctuates over time
Species environmental response	change in population dynamic caused by environmental fluctuations
Species-species interaction	interaction between two different species
The dynamic rate of food webs	the growth rate when all species in the food web are taken into account
Tracking error	the degree to which a time series follows another time series through time.

1.2. Species environmental responses

The change in population dynamics caused by disturbances such as environmental fluctuations are commonly measured by the change in population mean, variance, stability and extinction risk. In addition to these measures, I have also used tracking error (TE) which measure the degree to which a time series follows another time series through time (Roughgarden, 1979; May, 1981).

1.2.1. Single species models

The first theoretical studies on how environmental noise color affects population dynamics were done on single species models (May, 1981; Roughgarden, 1979). Generally, single species population stability (defined as $1/CV$, where CV is the coefficient of variation – population standard deviation divided by population mean) decrease with increased redness and the growth rate of the population determines when the population and the noise will have the same variance over time. This response is linked to how a population track its environment. In the single species case, TE decrease with increased environmental redness. Thus, population densities follow the fluctuations in red noise more closely than white since the change over time is slower in red environments. Consequently, single species population stability will decrease with increasing redness until population stability resembles that of the environmental noise.

More recent studies have shown that single species with time-lags in their density dependence (e.g. discrete models with overcompensating dynamics) may respond differently to increased environmental redness (Ripa & Lundberg, 1996; Petchey et al., 1997; Cuddington & Yodzis, 1999). Population stability will here initially increase, reach a maximum and then start to decrease with further increase in redness. The increase in stability between low to mediate redness depends on population densities that overshoot their equilibrium when the environment change fast in comparison with the population dynamics.

Generally, both environmental redness and growth rate improve the tracking of the noise. Thus, single species with high growth rate are expected to be able to track environmental noise even in environments fairly close to having white noise (Ruokolainen et al., 2009; Petchey et al., 1997; Lögberg & Wennergren, 2012; Roughgarden, 1979). An increased growth rate is thereby expected to decrease single species stability (Roughgarden, 1979) and cause an increased risk of extinction (Petchey et al., 1997).

1.2.2. Food web models

In nature, species form complex networks of interactions with other species (Ives & Cardinale, 2004; Gårdmark et al., 2013; Sabo, 2005; Sabo, 2008). Thus, single species studies can misinform us regarding species responses to environmental fluctuations. Figure 1 show four examples of different food webs used in this theses. The food webs consist of three trophic levels with resource species (R) on the bottom level, consumer species (C) on the middle level and predators (P) on the top level. The models include common interaction types such as direct competition, indirect competition and predation.

The responses of species in food web models to environmental redness have been proven to be highly dependent on a number of different factors such as environmental sensitivity of species equilibria (Vasseur, 2007), if species are generalist or specialists (Murdoch et al., 2002) and the synchrony of species environmental responses (Ruokolainen & Fowler, 2008; Lögberg & Wennergren, 2012).

Even though species responses to increased environmental redness is quite straightforward for single species models, there is no consensus of how we should extend that knowledge when species are embedded in food webs.

1.2.3. Additional complexities of nature

In this thesis, I will unravel some parts of the mystery regarding what cause species in food webs to respond differently to the same environmental disturbance. I was able to do this by taking small steps forward, starting out with a single species model and comparing this null model with different scenarios. Besides adding food web interactions, I have also studied the effects of adding a spatial structure and larger food web structures with periodic boundary conditions. Each one of these complexities takes us one step closer to the systems actually found, outside the office, in nature.

Figure 1 | Illustration of species interactions used in this thesis.

a) Interspecific competition between two resources (R), b) a food chain with a resource which is consumed by a consumer (C) which in turn are consumed by a top predator (P), c) a food web with intraguild predation by a predator of one resource and indirect competition between two consumers, and d) a diamond shaped food web where the predator consumes two consumer species consuming a single resource.

2. AIMS

My overall aim was to analyze how the population dynamics of species in food webs are affected by environmental fluctuations with different temporal autocorrelation (noise color). I define the change in population dynamics caused by environmental fluctuations as species environmental responses. In more detail, my aims were to:

- I.** investigate how a species respond to environmental fluctuations when isolated or embedded in a food web,
- II.** define and study the dynamic rate of food webs (DR) and investigate how DR affect species environmental responses.
- III.** extend the theory of species environmental responses to metapopulations and metacommunities in a landscape, and
- IV.** develop a method for modeling large food webs that can withstand a fluctuating environment.

3. METHODS

3.1. Population dynamics

3.1.1. Food web modules

Eight different food web modules were used in Paper I and II (figure 2, M1-8). Two modules were used in Paper III (M2-3) and one in Paper IV (M2). The food web modules have three trophic levels: resource, consumer and predator species. They include basic types of trophic interrelationships such as apparent competition, omnivory and intraguild predation. Together, they represent a gradual shift from simple three trophic level food chains towards more complex food webs. The complexity is indicated by the grey gradient filled arrows in figure 2. Food web dynamics were developed from the generalised Lotka-Volterra model:

$$\frac{dN_i}{dt} = \left(r_i + \sum_{j=1}^s \tilde{a}_{ij}(t) N_j \right) N_i \quad \text{for } i = 1, \dots, s \quad (1)$$

dN_i/dt describes species i 's density change with respect to time in a species food web, r_i is the intrinsic per capita growth (mortality) rate for resource (consumer and predator) species i , and $\tilde{a}_{ij}(t)$ is the per capita effect of species j on the growth rate of species i at time t . The populations of the resource species grow logistically, and consumers and predators have natural background mortality. Competition (at the first trophic level) and consumption (at the second and third trophic level) were described by:

$$\left\{ \begin{array}{l} \tilde{a}_{ij} = a_{ij}(t), j \in L(i), \\ \tilde{a}_{ij} = -\frac{J_{ij}\Omega_{ij}}{H_j + T\sum_{n \in R(j)} \Omega_{nj}N_n}, j \in C(i), \\ \tilde{a}_{ij} = e\frac{J_{ji}\Omega_{ji}}{H_i + T\sum_{n \in R(i)} \Omega_{ni}N_n}, j \in R(i), \end{array} \right. \quad (2)$$

Figure 2 | The eight different food web modules studied were: M1, a diamond shaped food web with the top predator feeding on two intermediate consumers (apparent competition), M2, a triangular shaped food web with a diamond shaped core, M3, a triangular shaped food web including omnivory and species-species competition between resources, M4, a food web with consumer one feeding on the resource and on the second consumer (intraguild predation), M5, a triangular shaped food web including intraguild predation, M6, a food web with multiple resources, species-species competition between resources and omnivory, M7, a food chain with two resources, M8, a simple food chain with omnivory. Designations: P, the top predator; C, the consumer; and R, the resource species. The gray gradient denote a gradual shift in food web complexity from simple food chains to more complex food webs with multiple consumers, intraguild predation and interspecific competition.

$L(i)$ are species of the same trophic level as species i , $C(i)$ are species that consumes species i , $R(i)$ are resources to species i , a_{ij} is the inter-specific competition (defined as $r_i \hat{a}_{ij} / K_i$ where K_i is the carrying capacity of species i), J_{ij} is species j 's ingestion rate of species i , Ω_{ij} is the preference coefficient of species j on species i , H_i is the half saturation constant for species i , T is the handling time of prey, and e is the conversion efficiency.

In order to increase the generality of the results, I generated 20-25 different parameter setups for each one of the eight food web modules in Paper I-II. Module parameters were drawn from predefined parameter distributions (see below) and the setup was saved if it resulted in a locally

stable replicate food web. Replicate food webs were considered locally stable if the real parts of all eigenvalues of the Jacobian matrix were negative. Consumer and predator mortality rate (r_i), inter-specific competition (a_{ij}) and preference coefficient of predator j on prey i (Ω_{ij}) were randomly drawn from uniform parameter distributions. The parameter distributions were based on body sizes and metabolic categories of different species (Yodzis & Innes, 1992; McCann et al., 1998). Parameter values and their distributions are found in table S1-4 in the appendix of Paper I.

3.1.2. Species isolated from species-species interactions

In Paper I and III, a single species model was used to simulate species isolated from interactions with other species. The model was defined as the continuous logistic equation with density independent mortality:

$$\frac{dSS_i}{dt} = SS_i \left(r_i \left(1 - \frac{SS_i}{K_i} \right) - D_i \right) \quad (3)$$

where dSS_i/dt is the rate of increase of single species i , SS_i is the number of individuals, r_i is the per capita maximum growth rate and K_i is the carrying capacity. D_i is the per capita density independent mortality rate (equation 4), the summed effect of interacting species on species i when interacting species are at their equilibrium densities. Equilibrium densities were calculated using the function *fsolve* in MATLAB (MathWorks, 2014). *fsolve* numerically finds the equilibrium point (or roots) of a system of nonlinear equations. D_i was defined as:

$$D_i = \sum_{j \neq i}^S \tilde{a}_{ij} \bar{N}_j \quad (4)$$

where S is the number of species in the original food web and $\tilde{a}_{ij}$ is the per capita effect of species j on the per capita growth rate of species i . $\tilde{a}_{ij}$ includes the same functional responses as in equation 2 but all species densities within $\tilde{a}_{ij}$ are set to their equilibrium densities. $\bar{N}_j$ is the equilibrium density of species j . Species-species interaction effects was added together in D_i to isolate a species. I used this method to keep all parameter values the same as when the species is in its food web. I thereby assume that any differences in species environmental responses would be the result of adding feedback from species-species interactions.

3.1.3. The dynamic rate of food webs

The dynamic rate of food webs, DR, was changed by multiplying the differential equation system (equation 1) with a scale factor, dr (Paper II). The focus was set on food webs with proportional changes in species per capita growth rate, $dN_i/N_i dt$. These systems had one common dr and were defined as tuned food webs. To exemplify that there exist more complicated alternatives with independent dr :s for different species I also included a mismatched food web case in Paper II. In this case, scale factors, dr_i , were drawn from a normal distribution.

Species embedded in tuned food webs respond in a similar way to changes in their environment. All species thus experience a proportional change in per capita growth rate with increased DR. dr was multiplied to each food web model such that the per capita growth rate of each species were rescaled:

$$\frac{dN_i}{dt} = dr \left(r_i + \sum_{j=1}^s \tilde{a}_{ij}(t) N_j \right) N_i \quad \text{for } i = 1, \dots, s \quad (5a)$$

$$\frac{dN_i}{dt} = \left(dr r_i + \sum_{j=1}^s dr \tilde{a}_{ij}(t) N_j \right) N_i \quad \text{for } i = 1, \dots, s \quad (5b)$$

$dr=1$ equals the original model (equation 1) while $dr>1$ increase and $dr<1$ decrease DR of tuned food webs. For food webs with oscillating population dynamics, increased DR result in a shorter period and a larger magnitude of change in response to the perturbation (Paper II, figure 3a). For food webs with constant equilibrium densities an increased DR result in a larger magnitude of change in response to the perturbation and a higher rate of return to equilibrium (Paper II, figure 3b-c). By using this method generation time decrease and growth rate increase as DR increase.

DR relates to food web equilibrium densities in the same way as the growth rate relates to carrying capacity in single species systems. A change in growth rate will not affect single species carrying capacity and thus a change in DR will not affect the equilibrium densities of the food web. The procedure is comparable with multiplying a scalar to an eigenvector.

Figure 3 | An illustration of how to construct food webs with periodic boundary conditions. One food web module (a) is interacting with its neighbouring modules (b) creating an edge free circle (c).

3.1.4. Periodic boundary conditions

In Paper IV, I develop a new method to assemble large and stable food webs. Food web modules were used as building block to create large food web with periodic boundary conditions (PBC). PBC has previously helped physicists to understand the nature of waves and particles by removing the edges of systems. It resemble popular video games where an object passes through one wall of the window and reappears on the opposite wall with the same velocity, e.g. SNAKE. In our food web setting, each module (figure 3a) interacts with its neighbouring modules (figure 3b) creating an edge free system shaped as a circle (figure 3c). The interaction strengths within modules were kept the same as in the isolated module but the interaction strengths between modules were set to half the original value to compensate for the additional interaction links. Three different food web modules (M1-3) were used to exemplify that this method enable an infinitive number of interacting species. It shows that by removing the destabilizing effect of edges in food webs it is possible to describe large species rich and stable systems, more similar to natural ecosystems.

3.2. Dispersal between subpopulations

The models describing metacommunities and metapopulations in Paper III are equivalent to a discretized version of equation 1-2 for food webs and equation 3-4 for single species, except for one index, q . This index represents the spatial dimension and hence the number of the patch which either hold a food web (one of M2-3) or a subpopulation of the single species counterpart of the resource species. The discretization of the model was done as in Nguyen-Van & Hori (2013).

3.2.1. Mass-action mixing

Dispersal between five patches was governed by a mass-action mixing process without distance dependence (also denoted as a global dispersal process). Dispersal was described as a proportion of the population moving from patch q and being equally distributed between all other patches. The dispersal was calculated at each discrete step after population dynamics and the dispersal rate varied from 0 to 1.

3.3. Environmental fluctuations

Environmental fluctuations are from here on referred to as environmental noise. It was set to influence resource species carrying capacity.

3.3.1. Noise on carrying capacities

The environmental noise influenced the carrying capacity, K , of resource species (as done in (Borrvall & Ebenman, 2008; Ripa & Lundberg, 1996; Petchey et al., 1997; Gudmundson et al., 2015) via an additive function (Borrvall & Ebenman, 2008; Gudmundson et al., 2015):

$$K_{i_env}(t) = K_i(1 + env_i(t)) \quad (6)$$

where $K_{i_env}(t)$ is the carrying capacity affected by environmental noise at time t (noted more generally as K_{env}), K_i is the mean carrying capacity and $env_i(t)$ is the environmental noise at time t of resource species i .

3.3.2. Temporal autocorrelation

Natural variation is considered to be best represented by $1/f$ noise where the relationship between amplitudes and frequencies does not change dependent on the time scale (Caswell & Cohen, 1995; Halley, 1996; Ripa & Lundberg, 1996; Cuddington & Yodzis, 1999). Thus, we have used a $1/f$

noise method to create time series with different degree of autocorrelation, γ_{env} (Lögberg & Wennergren, 2012). Here, the mean and variance were kept the same independent of noise replicates and γ_{env} (see appendix of Paper I for more details of the $1/f$ noise method).

I refer $\gamma_{env} = 0$ to white, $0 < \gamma_{env} \leq 1$ to light red, $1 < \gamma_{env} \leq 2$ to red and $\gamma_{env} > 2$ to dark red environments, in line with earlier studies (Halley et al., 2004; Lögberg & Wennergren, 2012; Gudmundson et al., 2015). The degree of positive autocorrelation is referred to as environmental redness or γ_{env} to simplify notation.

3.4. Species responses to environmental fluctuations

The simulations were done in MATLAB for Paper I, II (MathWorks, 2014) and IV (MathWorks, 2016) and in PYTHON (Python, 2015) for Paper III.

3.4.1. Mean, variance and stability

The mean, variance and stability of population density time series were calculated for each population. Stability was measured as $1/CV_i = \mu_i/\sigma_i$, where CV is the coefficient of variation, μ_i the mean, and σ_i the standard deviation of species i 's density time series.

3.4.2. Tracking error

Tracking error (TE) was measured between species density and equilibrium density (TEE, Paper I-III), between species density and carrying capacity (TEK, Paper I, III) and between species equilibrium density and carrying capacity (ETEK, Paper I). TE was calculated according to Roughgarden (1979):

$$TE = \frac{\overline{(Y_i(t) - Z_i(t))^2}}{\sigma_Y^2} \quad (7)$$

where $Z_i(t)$ is the density (or equilibrium density in case of ETEK) of species i for time step t , $Y_i(t)$ represents carrying capacity (TEK) or equilibrium density (TEE) of species i for time step t and σ_Y^2 represents the variance of $Y_i(t)$. Equilibrium densities of species affected by environmental variation were calculated for each time step by using the function *fsolve* in MATLAB (MathWorks, 2014) in Paper I-II and in the Python library SciPy (Jones et al., 2001) in Paper III. The numerical

solver produced a new equilibrium for each time step as carrying capacity changed with the environmental noise.

3.4.3. Extinction risk

A population was considered extinct when decreasing below an extinction boundary of 10^{-6} . Replicates with extinctions of at least one population were removed from the analysis.

3.4.4. Descriptive statistics

I carried out descriptive statistics in RStudio (RStudio, 2015) in Paper II in order to get a better overview of important factors influencing species response to changes in DR. I used the R (RCoreTeam, 2015) package *rpart* to conduct an ANOVA and a classification tree.

4. SUMMARY OF PAPERS

4.1. Paper I

In the first paper (Paper I) I investigated how a species respond to environmental variation when isolated or embedded in a food web. The study showed that species-species interactions had an effect in temporally positively autocorrelated environments (red noise) but not in uncorrelated environments (white noise). This was owing to species following their equilibrium densities in red environments which in turn enabled species-species interactions to come into play. Red environmental variables are more prominent in nature. Thus, these results show the importance of using a food web approach when analyzing species response to environmental variation.

4.2. Paper II

The most commonly discussed effect of climate change is an elevated mean temperature. This shift is expected to affect the growth rate of many species. However, there is no robust theory of how we should expect species in food webs to respond to a rise in temperature. In the second paper (Paper II) I defined and studied the dynamic rate of food webs (DR) acting analogously to single species growth rate. I found that the higher DR the easier for species population densities to follow their equilibrium over time. Both DR and noise color changed the temporal relationship between the population and the environmental variation. Thus, it is of major importance to consider the scale of time when investigating species response to environmental variation.

4.3. Paper III

Another important factor which affect population dynamics is species spatial distributions. Dispersal between subpopulations enable individuals to rescue or prolong the time to extinction for the population seen as a whole. In the third paper (Paper III), I investigated how species in food webs respond to environments that varies both in time and space and compared the results with the one from single species. I found that single species were stabilized by an increased dispersal rate independent of the noise color. Species-species interactions had an effect for some of the species in these metacommunities. At red asynchronous noise, one resource species in each food web had a local minimum in stability at low dispersal rate. Here, dispersal decoupled local population dynamics and

prevented species from tracking their equilibriums. At high dispersal rates, all resource species and their single species counterparts were stabilized by dispersal as local patch dynamics lost its importance. Environmental noise together with the spatial dimension does seem to explain much of the stability properties of species on our planet.

4.4. Paper IV

Natural ecosystems are much more complex and species rich than the food web models I have used so far. Theoreticians have previously had a hard time describing stable complex systems that survive environmental fluctuations. Thus, in my fourth and last project (Paper IV) I investigated how species population dynamics were affected by environmental fluctuations when embedded in larger food webs. These systems were built by connecting food web modules with periodic boundary conditions (PBC). The PBC method has previously helped physicists to understand the nature of waves and particles by removing the edges in systems. I found that food web size does not have to have a negative effect on food web stability. I showed that by removing the destabilizing effect of edges it is possible to describe large stable food webs, more similar to natural ecosystems.

5. DISCUSSION

The results and newly developed methods used in this thesis helps us understand how and why species respond as they do to environmental fluctuations with different noise color. This will help ecologist to understand population dynamics better and thereby make better decisions regarding for example how to act in order to protect threatened species. The studies consider flow of biomass between populations affected by environmental noise in four different ways; (1) between species on the same trophic level, (2) between species on different trophic levels, (3) between populations subdivided in a landscape and (4) between modules in a periodic boundary condition food web.

5.1. Food web effects depend on noise color

Independent on which type of flow we focused on, food web interaction effects were hidden in white environment but not in red. The analysis in Paper I showed that food web interactions have an effect when species are able to follow their equilibrium in slowly fluctuating red environments. At what specific redness this tracking will occur depends on the dynamic rate of the system (Paper II). This relates to how growth rate affect single species population dynamics yet the outcome can be different in the food web context. Thus, a change in either environmental redness or the dynamic rate of food webs can result in large population dynamics differences caused by top-down/bottom-up control or cascading extinctions.

For example, a resource species which fluctuates with its carrying capacity in white environments can stop fluctuating and become stable as the environmental redness increase (Paper I, figure 2). This response is related to the paradox of enrichment which show that a change in carrying capacity can have an effect on the consumer species instead of the resource species (Rosenzweig, 1971). However, an increased environmental redness does not always have a stabilizing influence on species in food webs. Some species in food webs will have a similar response as single species which results in a lower stability in red environments than white. This response can be seen as a sudden, but temporary, drop in population density as the population starts to track its environmental variable more closely. This drop may be misinterpreted as a regime shift or large extinction risk when in reality it can be a temporal decrease followed by a proportional increase in the same population density.

Dispersal between subpopulations is another factor which affect species ability to track their local population dynamics over time. Paper III showed that some species in food webs will lose their ability to track their equilibrium at intermediate dispersal rate and a red environment. In this case, dispersal played the same role as adding white noise or lowering the dynamic rate of the food web.

Stability at the food web level may depend on biodiversity. Paper IV showed this by repeating similar modules of food webs by using the PBC method. Yet the stability increased less with the number of modules, i.e. biodiversity, in red noise than in white. This is explained further in the next paragraph.

5.2. Benefits of biodiversity

The benefits of biodiversity is not as easy to explain as one could have hoped for. The PBC food webs in Pape IV showed us that without disturbance, a module is stabilized by 2-3 modules but at more modules there is no further effect at the module scale. However, when species are affected by an uncorrelated environmental noise the temporal stability of biomass on the food web scale had a close to linear positive relationship with the number of modules. This result depended on the averaging effect between modules, i.e. the rescue effect. When one module is suppressed by the noise another one is favored and these dynamics level out each other on the food web scale. The result is similar to the ones found when species are subdivided in patches. An uncorrelated environmental fluctuation will have an averaging effect between patches (Paper III) as between modules in PBC food webs (Paper IV). Yet, this positive effect of uncorrelated environmental fluctuations is reduced in red environments due to the increased variance of most populations in red noise (Paper I).

5.3. Future research needs

Red environments are prominent in nature. This thesis together with previous studies on this subject show that environmental redness can have a strong effect on the population dynamics of both single species and species embedded in food webs. Still, there is much to be done in this field. More studies are needed that measure the actual environmental redness that species in different ecosystems are subjected to. Table 1 summarize some of the studies in this filed. Another important question is how the dynamic rate of food webs and environmental redness are expected to change with climate change.

There will likely be a large difference in these factors between different ecosystems so if we are going to be able to predict the outcome for certain food webs it is important to also make local investigations of both the environment and the food web structure.

Paper II showed that the effect of environmental redness is highly dependent of the dynamic rate of the food web. In white environments, all resource species with just a few exceptions were destabilized by increased DR, similarly to how single species populations respond to an increased growth rate. In red environments an increased DR result in some species reaching a stable constant equilibrium while others started to fluctuate more and were thereby destabilized. Thus, it is important to consider the dynamic rate when studying species responses to environmental fluctuations. It is important that we are careful when rescaling food webs before studying their response to the environment. This normalization will likely cover potential differences between the dynamic rate of different food webs and should thus be avoided in comparative studies.

One mechanism that I did not study in this thesis is detrital links between resources and top predators. These links may have similar stabilizing effect as the PBC method since these remove the edges at the bottom and the top of food webs. It would be interesting to study how these links affect mechanisms such as the paradox of enrichment.

Another angle which would be interesting to study is the evolutionary aspects of my results. I believe, in line with theories such as the intermediate-disturbance theory (Levin & Paine, 1974; Kondoh, 2001), that complexities such as environmental fluctuations in time and space play a major role in explaining the biodiversity and thereby evolution of species and ecosystems. Without disturbances such as these we would likely have much less of the biodiversity we observe in nature today. My results show that food web interactions come into play in red environments. Thus, species in red environments are forced to adapt to interactions from other species more strongly than species in white environments.

Table 1 | The color of environmental fluctuations, part I

Authors	Measuring method	Time series	Color
Vattay & Harnos (1994)	$1/f$	Humidity	0.61
Hurrell & Van Loon (1997)	lag one autocorrelation	North Atlantic oscillation (1865-1994)	0 - 0.4
		Temperature anomalies	-0.1 - 0.3
Pelletier & Turcotte (1997)	$1/f$ (Bartlett window)	Temperature (worldwide)	0.43
		River discharge (US)	0.5
		Tree ring width (west US)	0.54
		Precipitation	0.52
Vasseur & Yodzis (2004)	$1/f$ (Parzen window)	Mean terrestrial temperature	<0.5
		Terrestrial costal temperature	0.5 - 2
		Marine temperature	1 - 2
		Surface water temperature	0.5 - 2
		Minimum and maximum temperature	0.5 - 1.5
		Precipitation	0 - 0.75

Table 1 | The color of environmental fluctuations, part II

Authors	Measuring method	Time series	Color
Newbery & Lingenfelder (2009)	$1/f$	El Niño–Southern Oscillation drought	2
		Daily rainfall	0.16
		Total rainfall 30 days	1.91
Garcia-Carreras & Reuman (2011)	unsmoothed periodogram (spec.pgram in R)	Mean temperature	-0.5 – 0.5
van de Pol et al. (2011)	periodogram (spec.pgram in R)	Temperature	-0.4 – 0.3

5.4. Conclusions

Overall, these results show that species responses to environmental fluctuations are highly dependent on both food web interactions and noise color. In order to make good predictions of how species respond to changes in environmental variability it is thus necessary to consider both of these. The most striking and somewhat surprising result is that strong food web interaction effects are hidden in white environments but come into play in red environments. This thesis shows the impact of this phenomenon on population dynamics with or without food web interactions (Paper I), with different dynamic rate (Paper II), when species are subdivided in patches with dispersal (Paper III) and when smaller food web modules are connected in large PBC food webs. Since red environments are prominent in nature, our results points out that a food web approach is necessary when analyzing ecosystems and planning for conservation actions, especially when studying the effects of climate change on biodiversity. This has become an urgent issue since climate change and direct anthropogenic effects are challenging the existence of these systems.

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Papers

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