

Final Thesis

Stabilizing factors in spatially structured food webs
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Sammanfattning

Abstract:

Ecological models have problems showing the positive relationship between diversity and stability found in nature. Theory states that complex food webs have high extinction risks and low stability. However, persistent food webs found in nature are large and complex containing many interconnections between species. There are many possible mechanisms enabling persistent food webs such as; complex interaction patterns, asynchronous fluctuations of species densities, environmental fluctuations and spatial distribution. These factors have not been used in classical models. In this study, coloured environmental 1/f noise and dispersal between subpopulations were incorporated into a diamond shaped food web based on a model by Vasseur and Fox 2007. Contradictions between theoretical and empirical results regarding food webs can be resolved by detailed analyses of models, withholding stabilizing mechanisms. Weak environmental 1/f noise generated an increased coefficient of stability but the stabilizing effect of noise can be questioned because of a decreased mean food web biomass and reduced stabilizing effect when reddened. However, detailed studies of the food web revealed that noise can redistribute density proportions between species, evading lowest species density and thereby increase food web resistance to demographic stochasticity and catastrophes. Noise induced density proportion shifts imply that large population sizes are no insurance towards future increase in environmental variance. Synchrony of species environmental responses and dispersal between subpopulations can both have major influences on stability and extinction risk of smaller food webs indicating that spatial structure could be one of the dominating factors stabilizing complex food webs found in nature.

Nyckelord

Keyword:

Dispersal, extinction risk, food web, metapopulation, noise, spatial distribution, stability, synchrony.

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1 Abstract

Ecological models have problems showing the positive relationship between diversity and stability found in nature. Theory states that complex food webs have high extinction risks and low stability. However, persistent food webs found in nature are large and complex containing many interconnections between species. There are many possible mechanisms enabling persistent food webs such as; complex interaction patterns, asynchronous fluctuations of species densities, environmental fluctuations and spatial distribution. These factors have not been used in classical models. In this study, coloured environmental $1/f$ noise and dispersal between subpopulations were incorporated into a diamond shaped food web based on a model by Vasseur and Fox 2007. Contradictions between theoretical and empirical results regarding food webs can be resolved by detailed analyses of models, withholding stabilizing mechanisms. Weak environmental $1/f$ noise generated an increased coefficient of stability but the stabilizing effect of noise can be questioned because of a decreased mean food web biomass and reduced stabilizing effect when reddened. However, detailed studies of the food web revealed that noise can redistribute density proportions between species, evading lowest species density and thereby increase food web resistance to demographic stochasticity and catastrophes. Noise induced density proportion shifts imply that large population sizes are no insurance towards future increase in environmental variance. Synchrony of species environmental responses and dispersal between subpopulations can both have major influences on stability and extinction risk of smaller food webs indicating that spatial structure could be one of the dominating factors stabilizing complex food webs found in nature.

Keywords: dispersal, extinction risk, food web, metapopulation, noise, spatial distribution, stability, synchrony.

2 Introduction

Classical ecological models have not been able to show the positive relationship between diversity and stability found in nature (May 1974). May 1974 argue that large food webs with high connectance contain more characteristic modes of oscillation than smaller food webs. Many modes of oscillation imply high risk of instability. Recent results from theoretical modelling show that species-rich food webs are more sensitive to environmental variation and have higher species-specific extinction risk than species-poor food webs (Borrvall & Ebenman 2008). Complicated model webs having a high extinction risk is being explained by complexity implying increased variation of species abundances and positive feedback loops, generating secondary extinctions (Tilman 1999, Green et al. 2005).

Food webs found in nature are known to be species rich and to contain many interconnections between species. Natural food webs can survive in an unstable environment for several generations despite their complexity (Vasseur & Fox 2007). Simplified model assumptions could be one of the reasons of contradictions between theoretical and empirical results. Many theoretical studies on food web stability use randomly assembled interaction strengths between species in a constant environment. Food webs found in nature on the other hand have evolved through historical processes controlled by species living in a dynamic environment (May 2006). This study has explored if contradictions between theoretical modelling and empirical results, regarding the stability of complex food webs, can be resolved through detailed analyses of a smaller model food web. The food web can be considered as a building block for larger more complex food webs, withholding stabilizing mechanisms.

There are many studies trying to determine the important factors enabling complex food webs. A large number of weak interaction links relative to the number of strong links

have been shown, both in empirical and theoretical studies, to be of great importance for maintaining large stable food webs (Polis 1991, McCann et al. 1998). High connectivity, withholding a mix of weak and strong links of interactions, has stabilizing effect on large food webs (Polis 1991). Asynchronous consumers coupled with environmental stochasticity can improve food web stability by dampening oscillations between resource and consumers (McCann et al. 1998, Vasseur & Fox 2007).

Environmental variation has a large effect on the stability and extinction risk of ecological systems, as has been shown both in theoretical models (Lande 1993, Halley & Dempster 1996, Ripa & Lundberg 1996, Kaitala et al. 1997) and in laboratory experiments (Fontaine & Gonzalez 2005). Results of climate data analysis predict a future increase in the temporal and regional environmental variance, measured in impact and frequency of extreme weather events (Easterling et al. 2000). Generally, an increased variance of environmental stochasticity implies a greater risk of population extinction (Engen et al. 2002, Lande 1993). Most theoretical studies that investigate the effect of environmental variation use white noise, which means randomly drawn values without temporal correlation. However, stochasticity found in nature is considered to be autocorrelated, which means that values in the time series are dependent on previous ones (Caswell & Cohen 1995, Halley 1996, Ripa & Lundberg 1996). For instance, measurements of air temperature are dependent on values measured time steps before. Temperatures seldom fluctuate from extremely low to extremely high values in just a few short time steps. Low temperature, one short time step before, gives a high possibility of low temperature also in the next time step.

1/f noise is used to represent autocorrelated environmental time series but it is also used in other fields regarding studies of economic time series, traffic flow and music. In 1/f noise, correlation between two values decrease with time according to a power law and not, such as in autoregressive time series, exponentially with separation in time. The type and degree of autocorrelation is described by noise colour. If values are similar to previous ones the series is dominated by low frequency variation and positively autocorrelated. Positively autocorrelated time series are described as red noise because red colour is dominated by low frequency light. 1/f noise has the autocorrelation properties that are considered to be closest to variation found in nature (Halley 1996, Cuddington & Yodzis 1999). Pink 1/f noise is a good representation of stochasticity when both common and rare events are important, such as in ecological systems. It describes correlations in many different scales and does not priorities between timescales of disturbances. (Halley 1996)

Many theoretical studies in ecology are focusing on the spatial dynamics of ecological systems and its importance for population stability and persistence (Halley 1996). Landscapes found in nature are known to have a diverse spectrum of level of suitability for different species. This variation gives rise to subdivided populations where individuals from the same species are found in suitable patches within the landscape. Populations with a spatial distribution where patches are connected through dispersal are called metapopulations. The patches can have different biotic and abiotic conditions and therefore own subpopulation specific growth rates. As the level of dispersal between patches increases, and there is no additional risks connected with dispersal, the metapopulation will start to behave more and more as one population.

When investigating metapopulations, the question of synchrony between patches will be of great interest. Synchrony is a way of describing how subpopulations or species fluctuate in relationship to each other, measured as spatial correlation. The Moran effect, dispersal and trophic interactions with other species that fluctuate synchronous, can all have an influence on the level of synchrony between subpopulations (Engen et al. 2002, Liebhold et al. 2004, Fontaine & Gonzalez 2005). The Moran effect describes the synchronising power of exogenous random factors, such as environmental variation, on subpopulations. The temporal

structure of environmental variation may affect the strength of the Moran effect (Fontaine & Gonzalez 2005). The level of subpopulation synchrony will have an effect on metapopulation extinction risk. High synchrony implies short time to extinction whereas low synchrony implies long time to extinction (Engen et al. 2002, Liebhold et al. 2004, Greenman & Benton 2005^a). Spatial distribution increases the chance of survival by enabling re-establishment in extinct patches. Low patch synchrony favours re-establishment. Individuals from good conditions can help patches with poor conditions by dispersing from large to small subpopulations. However, without spatial distribution, synchrony has been shown to imply a lower extinction risk than when there is an asynchronous response (Borrvall & Ebenman 2008). The effects of density regulation, environmental autocorrelation and dispersal on food webs situated in space and time are still in need of further investigations. These processes are known to have an important effect on local population dynamics and should be included in investigations regarding population dynamics and extinction risks (Engen et al. 2002).

The aim of this study was to explore how coloured environmental noise, dispersal and response synchrony affect food web stability and synchrony between species. I searched for explanations to contradictions between theoretical and empirical results regarding complex food webs through detailed analyses of a smaller model food web. The model can be considered as a building block for larger food webs, withholding stabilizing mechanisms. Coloured environmental noise and dispersal were incorporated into a food web based on a model by Vasseur and Fox 2007.

3 Materials and methods

3.1 The diamond shaped food web

The diamond shaped food web contains four species. Two consumer species share one resource and have one common predator.

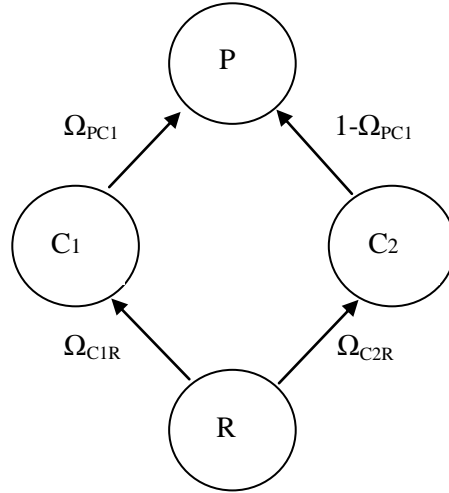


Figure 1. The diamond shaped food web, where P is the density of the top predator, $C1$ the first consumer species, $C2$ the second consumer species and R the resource species. Preference coefficient, $\Omega_{i,j}$, represent the strength of the trophic interaction between species i and j .

The dynamics of the food web are described by a differential equation system (1-4) in continuous-time, modelled by Vasseur & Fox 2007 after McCann et al. 1998. Resources grow logistically and the consumers and the predator have natural background mortality. Consumption is gradually saturated when resource density increases according to a type II functional response. (Yodzis & Innes 1992, McCann et al. 1998, Vasseur & Fox 2007) Model parameters are explained in Table 1.

$$\frac{dP}{dt} = -M_P P + \frac{J_P P [\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2]}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0} \quad (1)$$

$$\frac{dC_1}{dt} = -M_{C_1} C_1 + \frac{\Omega_{C_1R} J_{C_1} C_1 R}{R + R_{0_1}} - \frac{\Omega_{PC_1} J_P P C_1}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0} \quad (2)$$

$$\frac{dC_2}{dt} = -M_{C_2} C_2 + \frac{\Omega_{C_2R} J_{C_2} C_2 R}{R + R_{0_2}} - \frac{(1 - \Omega_{PC_1}) J_P P C_2}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0} \quad (3)$$

$$\frac{dR}{dt} = rR \left(1 - \frac{R}{K}\right) - \frac{\Omega_{C_1R} J_{C_1} C_1 R}{R + R_{0_1}} - \frac{\Omega_{C_2R} J_{C_2} C_2 R}{R + R_{0_2}} \quad (4)$$

3.1.1 Parameterization

The parameter values in the diamond shaped food web model have previously been used by Vasseur & Fox 2007 and McCann et al. 1998 to investigate effects of consumer asynchrony and environmental variation on food webs. The parameters were estimated with help from studies on different species' body mass versus metabolic and ingestion rate (Dickie et al. 1987, Yodzis & Innes 1992, McCann et al. 1998, Vasseur & Fox 2007), with the aim of achieving a biologically plausible parameterization. Parameter values for resource gain and predator preference are set higher for C_1 than for C_2 . The parameter values make C_1 the strongest resource competitor and the preferred prey of the top predator. The competition irregularity causes intrinsic asynchronous fluctuations of consumer densities. The second consumer's ability to persist is dependent on the predator's predation selection (Vasseur & Fox 2007). The densities of the four species fluctuate in a stable limit cycle when being situated in a constant environment with model parameter values as described in Table 1.

Table 1. Model parameter descriptions and their values. Parameters with white background were constant while parameters with shadowed background varied.

Parameter	Description	Value
r	Resource intrinsic rate of growth	1.0
K	Resource carrying capacity	1.0
J_{C_1}	Consumer (C_1) ingestion rate	0.8036
J_{C_2}	Consumer (C_2) ingestion rate	0.7
J_P	Predator ingestion rate	0.4
$M_{C_1}(0)$	Medial consumer (C_1) mortality rate	0.4
$M_{C_2}(0)$	Medial consumer (C_2) mortality rate	0.2
M_P	Predator mortality rate	0.08
R_{0_1}	Half saturation constant	0.16129
R_{0_2}	Half saturation constant	0.9
C_0	Half saturation constant	0.5
Ω_{PC_1}	Preference coefficient	0.92
Ω_{C_1R}	Preference coefficient	1.0
Ω_{C_2R}	Preference coefficient	0.98
σ_{env}	Standard deviation of environmental noise	0 - 0.6
ρ_{env} (synchrony)	Cross-correlation of consumers and their different subpopulations in their environmental noise response	-1,0,1
γ_{env}	Colour of environmental noise	0 - 0.6
Dispersal	Dispersal or no dispersal between subpopulations	1, 0

3.2 Environmental noise

The environmental fluctuations affected the mortality rates of the two consumer species through an exponential filter (Gillooly et al. 2001, Vasseur & Fox 2007):

$$M_{C_i}(t) = M_{C_i}(0)e^{env_i(t)} \quad (5)$$

where $M_{C_i}(t)$ is the mortality rate at time t , $M_{C_i}(0)$ is the medial mortality rate, $env_i(t)$ is the environmental noise at time t for consumer i . The standard deviation, σ_{env} , and cross-

correlation of consumer response, ρ_{env} , to environmental noise are independent parameters affecting the mortality rates of the consumers. The model was integrated with environmental noise of σ_{env} in a range from 0 to 0.6 in steps of 0.05. The synchrony of consumers' environmental response, ρ_{env} , had values -1, 0 and 1. $\rho_{env} = -1$ represented perfect negative correlation between species while all subpopulations within species responded the same. $\rho_{env} = 0$ represented independent response of all subpopulations regardless of species, $\rho_{env} = 1$ represented perfect positive correlation for all pairs of subpopulations regardless of species.

White environmental noise, without temporal autocorrelation, was generated from a random normal distribution with zero mean and σ_{env}^2 variance. Fourier transform was used to generate coloured 1/f noise, with temporal autocorrelation. The discrete Fourier transform of the coloured environmental noise, $P(f)$, was scaled according to:

$$P(f) = |X(f)|^2 f^{-\gamma} \quad (6)$$

where f is frequency, $X(f)$ is the discrete Fourier transform of the previously generated white environmental noise and the colour of $P(f)$ is determined by the value of the spectral exponent, γ . $\gamma=0$ gives white noise and $\gamma>0$ gives red noise. After colouring the noise, inverse Fourier transform was used on $P(f)$ to generate the resulting time series, $env(t)$, of coloured environmental noise.

3.3 Dispersal

I made the assumption that dispersal between all six subpopulations of all species was governed by a mass-action mixing process with no distance dependence. All subpopulations within species were interconnected through a dispersal matrix (Table 2) and had the same probability of dispersal between each patch (Caswell 2001 and Wennergren et al 1995).

Table 2. Dispersal matrix with six patches. d_{ij} represents the proportion of the subpopulation in patch i that migrates to patch j in one time step.

0	d_{21}	d_{31}	d_{41}	d_{51}	d_{61}
d_{12}	0	d_{32}	d_{42}	d_{52}	d_{62}
d_{13}	d_{23}	0	d_{43}	d_{53}	d_{63}
d_{14}	d_{24}	d_{34}	0	d_{54}	d_{64}
d_{15}	d_{25}	d_{35}	d_{45}	0	d_{65}
d_{16}	d_{26}	d_{36}	d_{46}	d_{56}	0

Nonzero elements in the dispersal matrix was generated from a random normal distribution with mean $(\text{number of patches})^{-1}$ and variance $0.2 * (\text{number of patches})^{-1}$. The distribution was truncated by 0 and $1.2 * (\text{number of patches})^{-1}$ in order to avoid negative and unreasonably large elements in the matrix.

3.4 Simulation and analysis

The model food web was simulated in MATLAB 7.5.0 (R2007b) with 100 replicates over a time period of 3000 time-steps. The initial densities for each of the six subpopulations of each species and simulation were chosen on the uniform interval; 0.1 to 1.0. In cases of no dispersal, subpopulation densities that decreased below a threshold of 10^{-6} were considered to be extinct. In cases with dispersal subpopulations within a species were considered to be extinct when the sum of all subpopulations within that species decreased below the threshold of 10^{-6} . Replicates that included extinctions in the food web were only analysed in respect to extinction risk.

The first quarter of the simulated time series was excluded from analysis in order to avoid initial transients. Mean, variance and stability of patch density, species density and food web biomass, cross-correlation of consumer species, colour of species time series and extinction risk were calculated for each of the combinations of varied parameters represented with grey background in Table 1. Food web biomass was the sum of all species' subpopulations. Stability of population density was measured as:

$$\frac{1}{CV} = \frac{\mu_i}{\sigma_i} \quad (7)$$

where CV is the coefficient of variation, σ_i the standard deviation and μ_i the mean of population i 's time series of density. Cross-correlation of consumer densities in simulated time series was calculated through:

$$\rho_c = \frac{1}{N\sigma_{C_1}\sigma_{C_2}} \sum_{t=1}^N (C_1(t) - \mu_{C_1})(C_2(t) - \mu_{C_2}) \quad (8)$$

where N is the length of the time series, σ_i is the standard deviation and μ_i is the mean of consumer species i 's time series. The cross-correlation between consumer time series and environmental noise was also calculated as equation (8), when $\rho_{env} = 1$, in order to evaluate the impact of environmental variation on the time series of each consumer species.

Extinction risk was calculated in two different ways, as the risk of subpopulations decreasing below an extinction boundary and in how many replicates that had all subpopulations surviving until the end of the time interval. The number of times each subpopulation decreased below the threshold of 10^{-6} and the number of replicates that survived during the time period of 3000 time-steps was registered.

The colour of species time series before and after being affected by autocorrelated environmental fluctuations was calculated with the same method that generated coloured environmental noise. The colour of species time series γ_{spec} is responsible for the slope of the line generated from the discrete Fourier transform of the time series, $P_{spec}(f)$, placed in the $\log(\text{amplitude}) \log(\text{frequency})$ plane, according to:

$$P_{spec}(f) = |X_{spec}(f)|^2 f^{-\gamma_{spec}} \quad (9)$$

4 Results

4.1 Population densities

4.1.1 Mean population densities

Mean food web biomass decreased with increasing standard deviation of the environmental noise, σ_{env} , regardless of the value of correlation of consumer responses to environmental noise, ρ_{env} (Figure 2a). As σ_{env} increased, mean density of the first consumer, C_1 , and the resource, R , increased whereas the second consumer, C_2 , and the predator, P , decreased (Figure 3a). Reddening of the environmental noise enhanced the effect of increasing σ_{env} on mean food web biomass (Figure 3b) and mean species densities. Mean food web biomass, density of C_2 and density of P decreased even further and C_1 , and R increased with a steeper curve with increasing σ_{env} . When the correlation of consumer response to environmental variation was zero, $\rho_{env} = 0$, dispersal reduced the effect of increasing σ_{env} on mean species densities (Figure 3a) and food web biomass (Figure 2b, 3b).

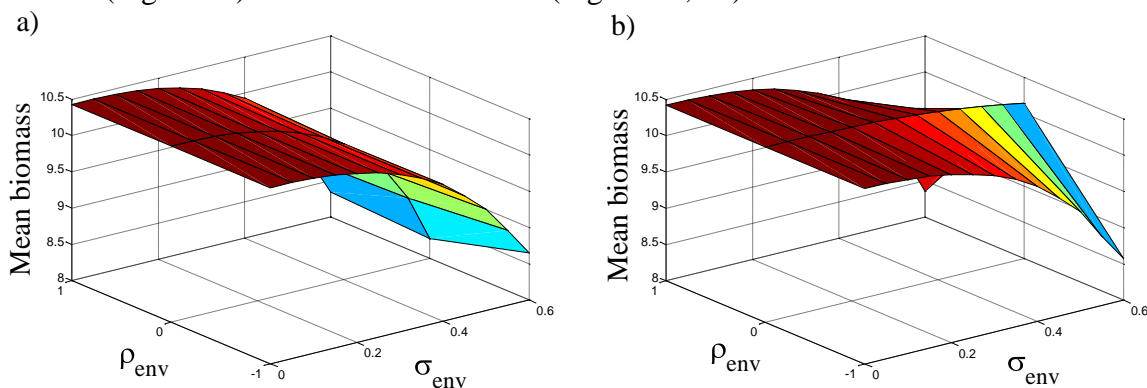


Figure 2. Mean food web biomass affected by white environmental fluctuations with standard deviation σ_{env} and correlation of consumer response to environmental variation ρ_{env} . a) is the food web without dispersal and b) is the food web with dispersal between subpopulations.

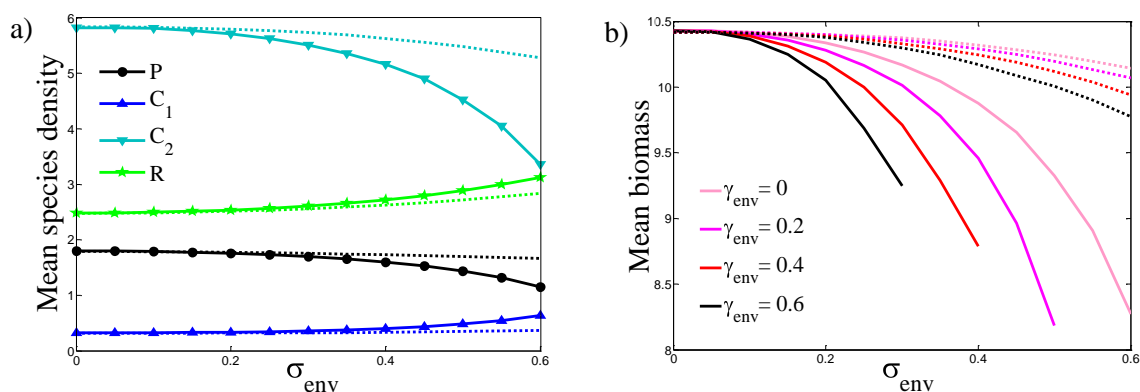


Figure 3. Mean densities without and with (crosshatch lines) dispersal affected by environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise $\rho_{env}=0$. a) Mean species densities where P is predator, C_1 first consumer, C_2 second consumer and R resource. b) Mean food web biomass with reddened environmental noise of $\gamma_{env}=0-0.6$.

4.1.2 Variance of population densities

Food web biomass variance increased with increasing environmental fluctuation strength, σ_{env} , regardless of correlation of consumer response to the environment, ρ_{env} (Figure 4a). However, the value of σ_{env} that gave the minimum variance of density was not zero. There was a slight decrease in the variance of population densities when the food web was affected by weak environmental noise when compared to the influence of a constant environment. As σ_{env} increased, variance of the density of the second consumer, C_2 , and the resource, R , increased rapidly, whereas the variance of the first consumer, C_1 , and the predator, P , increased more gradually (Figure 5a). Reddening of the environmental noise enhanced the effect of increasing σ_{env} on the variance of food web biomass (Figure 5b) and the variance of species densities. When the correlation of consumer response to environmental noise was zero, $\rho_{env} = 0$, dispersal reduced the effect of increasing σ_{env} on the variance of species densities (Figure 5a) and food web biomass (Figure 4b, 5b).

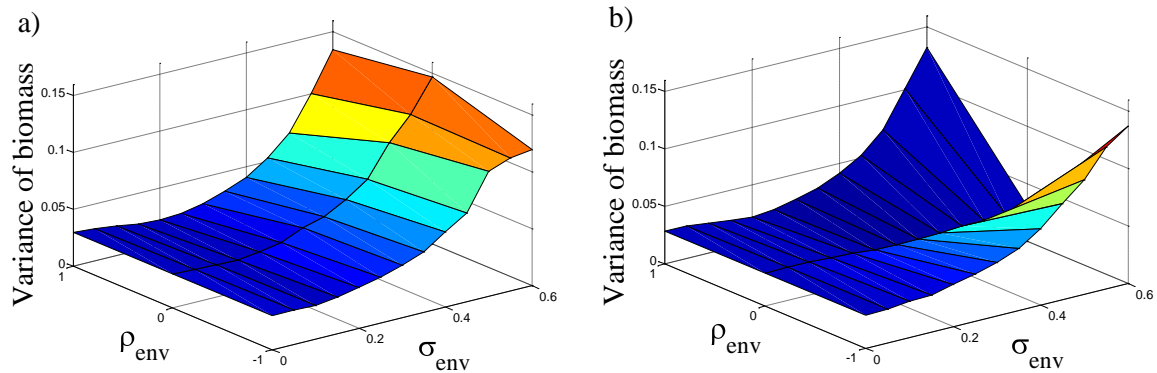


Figure 4. Variance of food web biomass affected by white environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise ρ_{env} . a) is the food web without dispersal and b) is the food web with dispersal between subpopulations.

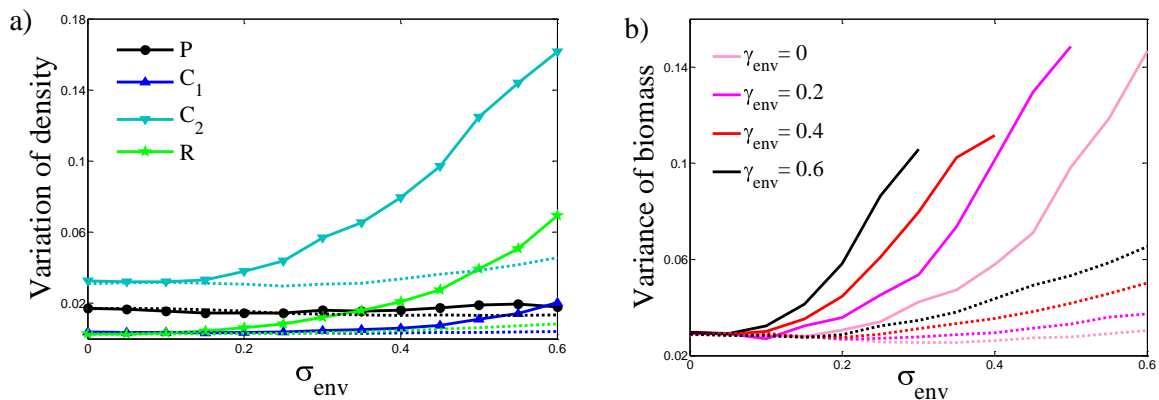


Figure 5. Variance of densities without and with (crosshatch lines) dispersal affected by environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise $\rho_{env}=0$. a) Variance of species densities where P is predator, C_1 first consumer, C_2 second consumer and R resource. b) Variance of food web biomass with reddened environmental noise of $\gamma_{env}=0-0.6$.

4.1.3 Stability

The stability (mean/standard deviation) of the diamond shaped food web biomass increased with increasing standard deviation of the environmental noise, σ_{env} , it reached a maximum under the influence of weak environmental noise of $\sigma_{env} \approx 0.1-0.2$, the value of σ_{env} depended on the correlation of consumer response, ρ_{env} . However, the stability of food web biomass affected by stronger environmental fluctuations decreased with increasing σ_{env} (Figure 6a). A similar pattern of change in stability with increasing σ_{env} was found for each of the species in the food web. However, each species had its own preferred σ_{env} value, under each case of ρ_{env} , which gave the highest stability. The first consumer and the predator preferred stronger environmental noise than the second consumer and the resource (Figure 8). Reddening of the environmental noise enhanced the effect of high σ_{env} values on the stability of food web biomass (Figure 7b) and the stability of species densities. When the correlation of consumer response to environmental variation was zero, $\rho_{env} = 0$, dispersal reduced the effect of increasing σ_{env} on the stability of species densities (Figure 7a) and food web biomass (Figure 6b, 7b).

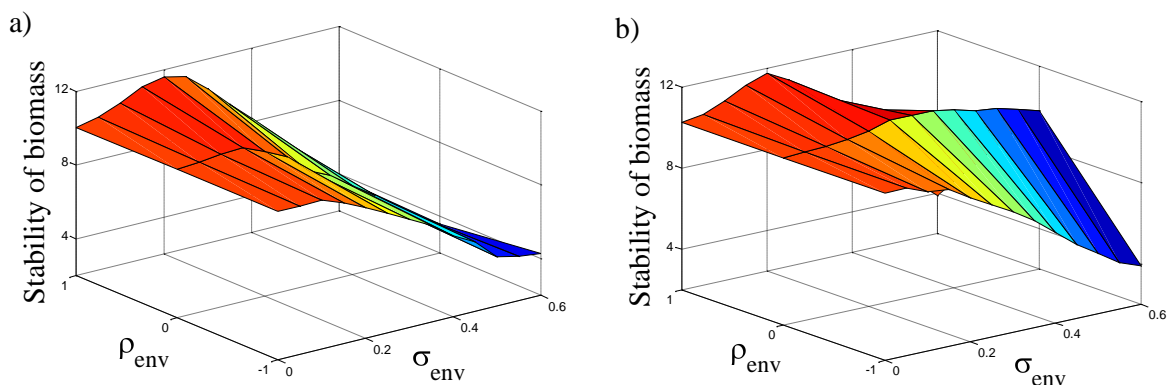


Figure 6. Stability of food web biomass affected by white environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise ρ_{env} . a) is the food web without dispersal and b) is the food web with dispersal between subpopulations.

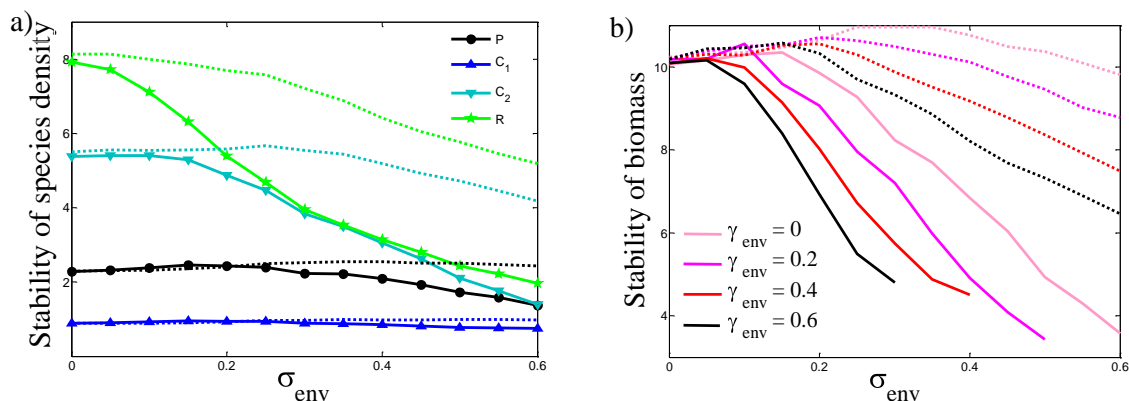


Figure 7. Stability of densities without and with (crosshatch lines) dispersal affected by environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental variation $\rho_{env}=0$. a) Stability of species densities where P is predator, C_1 first consumer, C_2 second consumer and R resource. b) Stability of food web biomass with reddened environmental noise of $\gamma_{env}=0-0.6$.

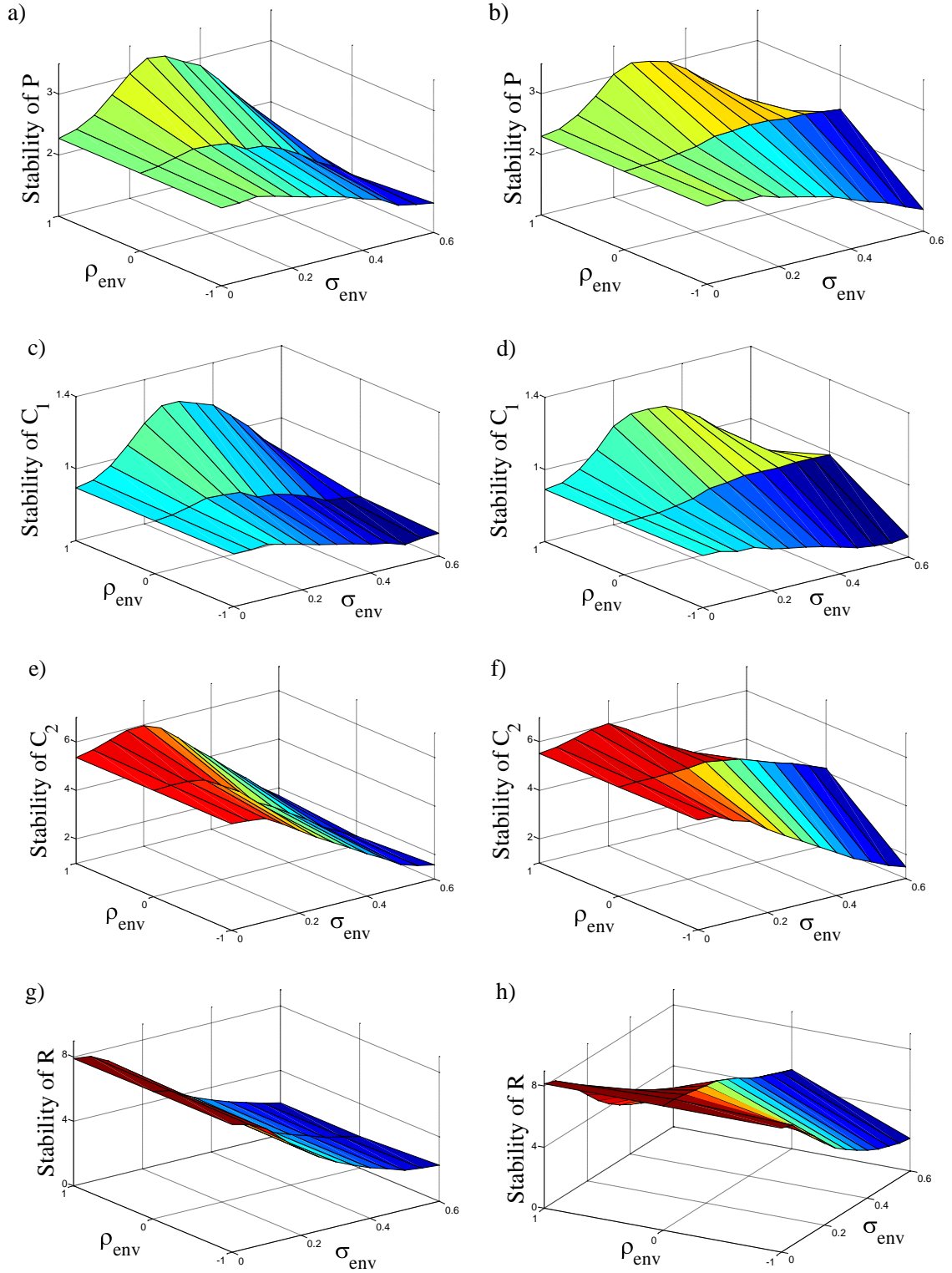


Figure 8. Stability of species biomass affected by white environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise ρ_{env} . a), c), e) and g) are the species without dispersal and b), d), f), and h) are the species with dispersal between subpopulations. P is predator, C_1 first consumer, C_2 second consumer and R resource.

4.2 Extinction risk

Mean subpopulation extinction risk, measured as the number of times subpopulation decrease below the extinction threshold during the time interval, increased with increasing standard deviation of the environmental noise, σ_{env} , regardless of the value of correlation of consumer response to environmental variation, ρ_{env} (Figure 9a). $\rho_{env} = -1$ gave highest, then $\rho_{env} = 0$ and $\rho_{env} = 1$ gave the lowest subpopulation extinction risk at large environmental fluctuations. A similar pattern of increased extinction risk with increasing σ_{env} was found for each of the species. However, the second consumer, C_2 , showed the highest sensitivity to increasing σ_{env} (Figure 10a). Reddening of the environmental noise enhanced the effect of increasing σ_{env} on the mean extinction risk of subpopulations in the food web (Figure 10b) and the mean extinction risk of each species subpopulations. Dispersal reduced the extinction risk of increasing σ_{env} . Especially when the correlation of consumer response to environmental variation was zero, $\rho_{env} = 0$, (Figure 9b, 10b).

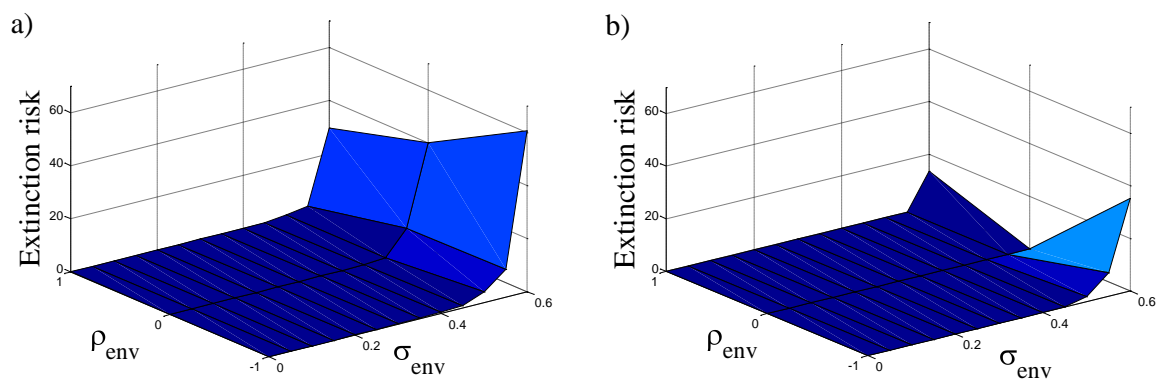


Figure 9. Mean extinction risk of subpopulations in the food web affected by white environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise ρ_{env} . a) is the food web without dispersal and b) is the food web with dispersal between subpopulations.

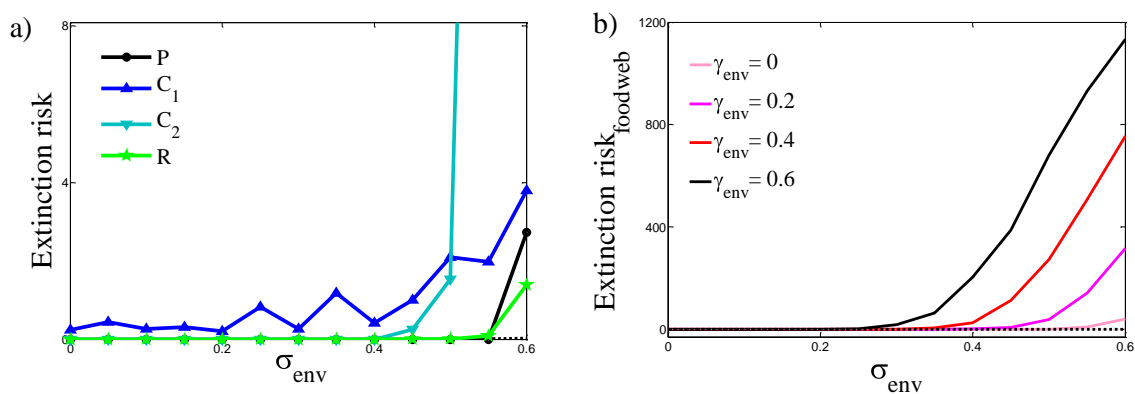


Figure 10. Extinction risk without and with (crosshatch lines) dispersal affected by environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental variation $\rho_{env}=0$. a) Extinction risk of species densities where P is predator, C_1 first consumer, C_2 second consumer and R resource. b) Extinction risk of food web biomass with reddened environmental noise of $\gamma_{env}=0-0.6$.

4.3 Cross-correlation

4.3.1 Consumer correlation

Both negative and positive values of the correlation of consumer responses to environmental noise, ρ_{env} , gave rise to an increase in correlation between the two consumer species, ρ_C , with increasing standard deviation of the environmental noise, σ_{env} (Figure 11a). Reddening of the environmental noise enhanced consumer synchronization. When the correlation of consumer responses to environmental noise was zero, $\rho_{env} = 0$, dispersal reduced consumer synchronization with increasing σ_{env} (Figure 11b).

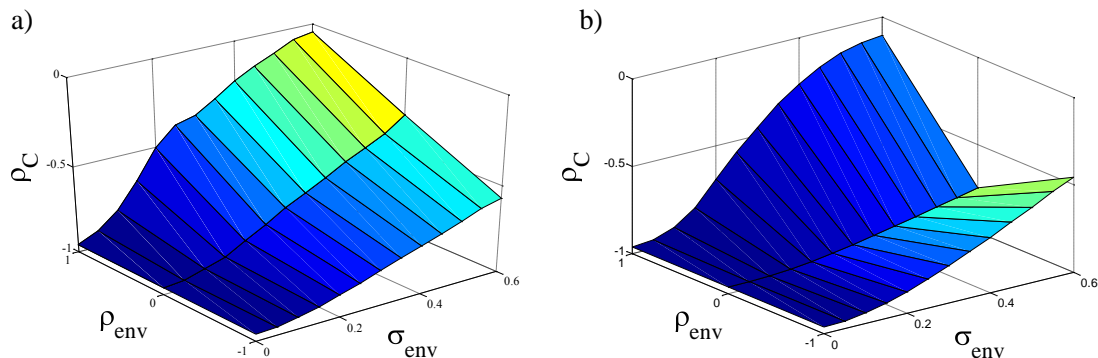


Figure 11. Consumer correlation in the food web affected by white environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise ρ_{env} . a) is the food web without dispersal and b) is the food web with dispersal between subpopulations

4.3.2 Cross-correlation between consumers and environmental noise

The correlation between each of the consumer species and the environmental noise decreased from zero towards -0.2 with increasing standard variation of the weak environmental noise, $\sigma_{env} \approx 0 - 0.3$ (Figure 12). However, correlation of each consumer with its environmental noise differed between consumer species when affected by large environmental fluctuations. The correlation of C_1 and environmental noise continued to decrease (Figure 12a) while the correlation of C_2 and environmental noise began to increase, from its lowest level around $\sigma_{env} \approx 0.3$, with increasing σ_{env} (Figure 12b). Dispersal increased the difference between the two consumers correlation with environmental noise at strong fluctuations (Figure 12c).

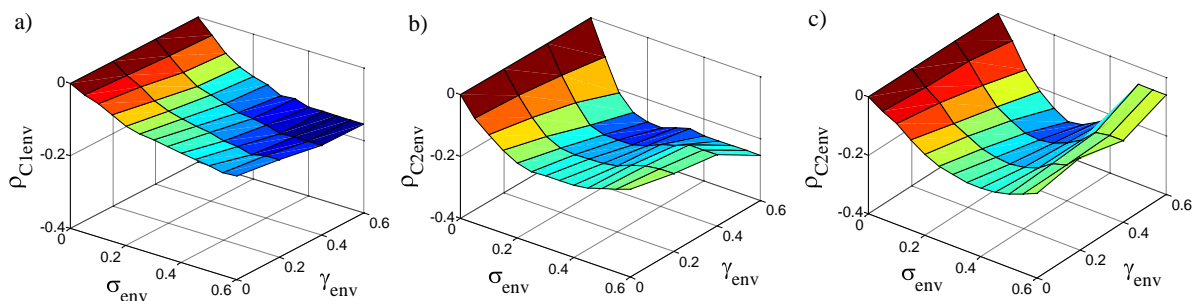


Figure 12. Cross-correlation between each consumer and the environmental noise with standard deviation σ_{env} and colour γ_{env} . a) Cross-correlation between the first consumer, C_1 , and environmental noise, without dispersal b) Cross-correlation between the second consumer, C_2 , and environmental noise, without dispersal c) Cross-correlation between the second consumer, C_2 , and environmental noise, with dispersal between subpopulations.

4.4 Colour of species time series

The colour of density, γ_{spec} , represented the type of temporal correlation in species density time series. Species was reddened with increasing standard deviation of weak environmental noise, σ_{env} , regardless of the value of correlation of consumer responses to environmental noise, ρ_{env} . All species except the predator reached an equilibrium colour level at $\sigma_{\text{env}} \approx 0.15$ (Figure 14a). There was however a decreasing redness tendency for all species except the predator, for large values of σ_{env} when $\rho_{\text{env}} = 0$. The resource experienced the largest colour shift during weak environmental noise (Figure 13b) but the reddening of the predator continued and did not reach a stable level within the interval of σ_{env} (Figure 13a). Even though the colour of C_1 , C_2 and R reached a maximum redness, the variance of all species except the predator was continuing to increase with increasing σ_{env} (Figure 14b). Reddening of the environmental variation, γ_{env} , increased the reddening of all species time series. When the correlation of consumer response to environmental variation was zero, $\rho_{\text{env}} = 0$, dispersal reduced the reddening effect of increasing σ_{env} drastically. The consumers with dispersal affected by low γ_{env} values, below 0.2, was even experiencing a decreased redness with increasing σ_{env} (Figure 14a).

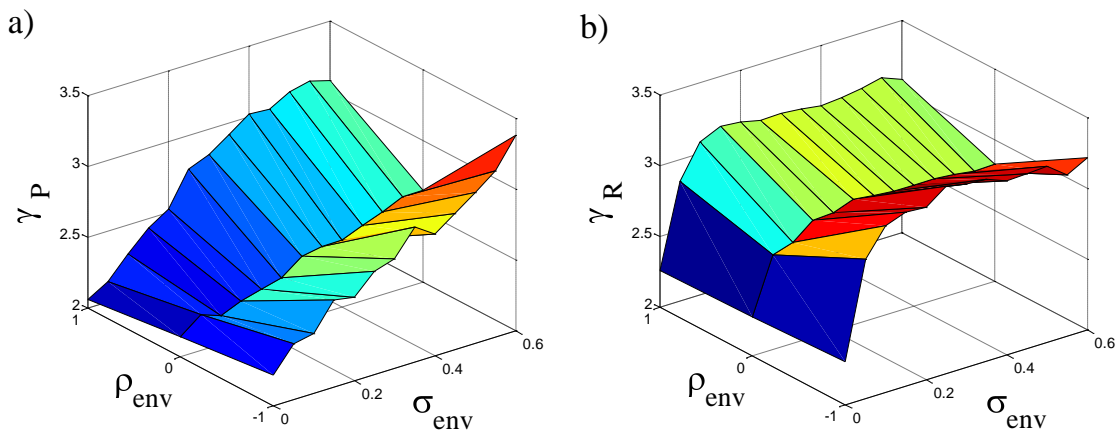


Figure 13. Colour of species density time series with dispersal affected by white environmental noise with standard deviation σ_{env} and correlation of consumer responses to environmental noise ρ_{env} . a) colour of the predator, P and b) colour of the resource, R .

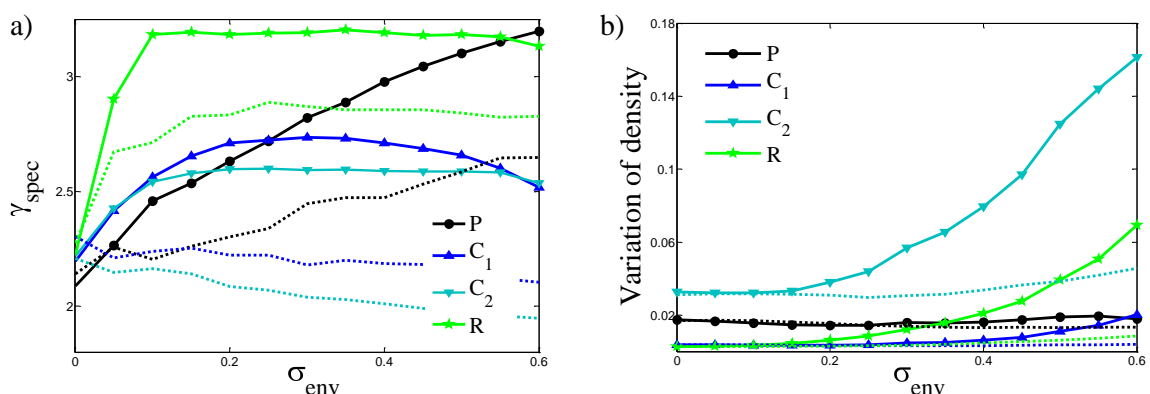


Figure 14. Colour of species density time series without and with (crosshatch lines) dispersal affected by environmental noise with standard deviation σ_{env} and correlation of consumer response to environmental noise $\rho_{\text{env}}=0$. a) Colour of species density time series b) Variance of species densities where P is predator, C_1 first consumer, C_2 second consumer and R resource.

5 Discussion

The study has investigated stabilizing factors in a spatially structured food web which consisted of four species with environmental noise affecting the consumers. I explored the effects of coloured environmental $1/f$ noise, dispersal and synchrony in environmental response on food web stability, extinction risk, synchrony between species and colour of population time series.

Mass action mixing has no distance dependence, which infers similar probabilities of dispersal between all patches. The assumption can be far from dispersal found in nature. However, results from Petchey et al. 1997 showed minor differences in population persistence when comparing landscapes with global and local dispersal. Adding dispersal between patches had no great effect during correlated environmental response between consumers (Figure 6). However, during an uncorrelated response, dispersal had a strong effect on the diamond shaped food web. Dispersal contributed to an equalizing effect between patches only visible when patches had varying environmental conditions.

5.1 Stability

When studying food webs, it is hard to state general conclusions of stabilizing mechanisms. Each food web's stability level is reached as a result of complex interactions between species in different trophic levels and between each species and the abiotic environment. In the diamond shaped food web, noise interrupts initial asynchrony and changes consumers' densities, which affects their resource. The change in resource density leads to another quick consumer response. The predator has a slow response to these dynamics because of time lags between consumers and predator. The noise dampens predator fluctuations which results in a reduced food web variance (Vasseur & Fox 2007). Weak environmental noise stabilized and lowered the variance in the diamond shaped food web, whereas stronger noise had a destabilising effect (Figure 6a). Without dispersal, the highest level of stabilization and lowest variance occurred during positive correlation in species responses to noise. These results are in line with another study which claims that positive correlation in species responses to noise lowers species specific density variance (Borrvall & Ebenman 2008).

Cross-correlation between each consumer and environmental noise decreased with weak environmental fluctuations strengths (Figure 12). Environmental noise was placed on mortality rates, which means that low noise values represent positive population density effects. Cross-correlation decrease represented increased synchrony between consumers and noise. Environmental noise generated a shift in species density proportions (Figure 3a). The second consumer, C_2 , had the largest density in the food web when situated in a constant environment. Increasing σ_{env} increased the stability of C_2 , but only for rather weak environmental fluctuations (Figure 8e). The decreased stability with large σ_{env} resulted from rapid variance increase and mean density decrease of C_2 . The cross-correlation between C_2 and environmental noise (Figure 12b) indicated an instability threshold for C_2 which could help explain C_2 's rapid increase of variance at high σ_{env} . The first consumer, C_1 , had the smallest density of the four species when situated in a constant environment. Increasing σ_{env} increased the stability of C_1 . The stabilizing effect was retained for rather large environmental fluctuations (Figure 8c) in contrast to C_2 and the whole food web (Figure 6a). Cross-correlation between C_1 and environmental noise indicated an increase in synchrony between C_1 and noise. C_1 mean density increased and variance was held close to constant with increasing σ_{env} . C_2 seems to have problems following the resource at strong fluctuations strength (Figure 12 b, c). This may explain the decreased density of the originally dominating C_2 during high environmental variance. C_1 is a better tracker of the resource during high environmental variance and takes advantage of the liberated resources. The low rate of increase of C_1 , despite liberated resources, could depend on high predation pressure. Even

though the predator, P, prefer C_1 it will still be negatively affected by the drastic density decrease of the originally large C_2 population.

Natural environmental variation is considered to be autocorrelated, mostly of pink colour (Halley 1996). Results from this study showed that reddening reduced the stabilizing power of environmental noise and moved the peak of maximum stability to lower fluctuation strengths. The decreased stability depends on an increased variation (Figure 5b) and decreased mean of food web biomass (Figure 3b) which speaks against the importance of noise as a stabilizing property of complex food webs. However, white and reddened noise in particular affected density proportion between species, indicating that pink noise can have a major effect on food webs. The standard deviation, which created the maximum stability peak, was lowered with increasing redness of the noise (Figure 7b). The result can be traced back to change in minimum variance (Figure 5b). The difference between colours could be explained by resonance frequencies in the dynamics of the diamond shaped food web according with the environmental noise of a certain colour and standard deviation. Weak noise can excite internal dynamical modes in the food web and the position of the peaks of resonance depends on the characteristics of the noise (Greenman & Benton 2005^a).

When comparing the sum of all subpopulations of each species with and without dispersal, with correlated environmental response, the stability of the metapopulation without dispersal was larger than the one with dispersal. These results come from the synchronizing effect of dispersal. Without dispersal, all subpopulations will fluctuate in their own phase, under the influence of weak noise, depending on their initial density. This asynchrony minimises the variance of the sum of all subpopulations which leads to larger landscape stability. With dispersal, patches that originally fluctuate in their own phase will be more synchronized, preserving variance from each patch to the summed variance. Time lagged dispersal would decrease this synchronizing effect. Food web variance and stability were measured at patch level in this study, when comparing food webs with and without dispersal. It is important to consider the differences between patch and landscape level when measuring populations empirically. It may have large effects on species estimated extinction risks.

Dispersal had a strong stabilizing effect on the food web and its species during uncorrelated environmental response. The food web with dispersal affected by dark pink environmental noise was more stable than the food web without dispersal and white noise (Figure 7b). Mean biomass increased and variation of biomass decreased in the landscape with dispersal when compared with no dispersal. Dispersal between patches had an equating effect, which reduced negative impacts in patches with poor environmental conditions through immigrating individuals from patches with better conditions (Engen et al. 2002, Liebhold et al. 2004). The results indicated that spatial distribution can be essential for stabilization of complex food webs, overshadowing stabilizing effect of weak environmental variation.

5.2 Extinction risk

As expected from earlier studies (Lande 1993, Engen et al. 2002), extinction risk for each species in the food web increased with increasing environmental variation. Increased variance and lowered mean densities increased the risk of reaching extinction boundaries. C_2 had the highest risk of extinction at strong environmental variance despite being the largest population in a constant environment. C_2 's high extinction risk was caused by high density variance. The predator had the next highest extinction risk caused by low density. Another reason for predator instability, despite low variance, could be the redness of predator time series increasing with environmental variance.

Extinction risk was affected by the correlation in consumer responses to environmental noise, ρ_{env} . An uncorrelated and negatively correlated consumer response gave higher mean

subpopulation extinction risks than positively correlated consumer response. These results are confirmed by an earlier study that applies environmental variation on growth rates of all species (Borrvall & Ebenman 2008).

Redness in the environmental noise increased variation and lowered mean population densities even further, increasing the extinction risk in comparison to white noise. Pink noise is known to make coexistence of different species more difficult (Halley 1996). Reddened environmental noise has a synchronising effect on populations, increasing the risk of subpopulations having low densities in the same time (Greenman and Benton 2005^a). Cuddington and Yodzis 1999 show that reddening of noise decreases mean persistence time in overcompensating single population models. However, in the case of low growth rates, reddened noise can have a positive effect increasing the degree of environmental fluctuation tracking (Ripa & Lundberg 1996).

Dispersal lowered species extinction risk during uncorrelated environmental response. Extinction risk was close to zero, during the interval of fluctuation strength, even for red noise. For larger values of environmental variance, similar effects of redness as in the case of no dispersal were distinguishable. Kaitala et al. 1997 supports these results by showing that the effect of redness decreases as you add system complexity. Engen et al. 2002 showed, in a single species system, that increasing dispersal between patches results in longer time to extinction. Dispersal seems to be the dominating stabilizing factor in comparison to environmental noise. However, dispersal had no negative effect in this study, such as additional death rates affecting migrating individuals between patches (Engen et al. 2002).

5.3 Consumer correlation

Correlation between consumers increased, from asynchronous towards zero, with environmental variance, regardless of correlation of responses (Figure 11a). These results are in line with the study by Vasseur & Fox 2007. The increase in consumer correlation should be called a decrease in consumer asynchrony. The consumers in the diamond shaped food web are perfectly negatively correlated in a constant environment. When affected by noise, the consumer asynchrony will be disturbed and each consumer will be less dependent of internal dynamics of the food web and more dependent of the noise. Irrespective of ρ_{env} , disturbances will push consumer correlation toward zero.

The results of cross-correlation between each consumer and the environmental noise supported this theory by showing an increased dependence between consumer and noise as σ_{env} increased. The differences between the cross-correlations could depend on resource tracking ability. C_1 seems to be a better tracker of the resource than C_2 .

The increase in correlation between consumer species is more rapid with reddened noise than with white noise. Similar effects has been observed in a study made on different food webs affected by weak red noise (Greenman and Benton 2005^a). Reddened noise had stronger effects on time series than white noise, causing larger colour shifts and increased variance. These effects caused the negative consumer correlation to increase more rapidly towards zero when affected by coloured noise. Dispersal decreased the rate of increase in consumer correlation when increasing σ_{env} , by lowering the destabilizing effects.

5.4 Colour of species time series

The primary impact of environmental noise is placed on the consumer species. Thereafter, the noise will travel along the interaction paths between all species of the diamond shaped food web. The resource and the predator species will define a subsystem, a filtering device, responsible for redistributing the noise. The redistribution will be dependent on the similarity of the spectral frequencies of the noise and the resonance frequency of the subsystem. Some frequencies will be suppressed whereas other frequencies will be enhanced. The filtering of

white noise often result in a power shift in one direction, toward high (blue filter) or low (red filter) frequencies. Coloured noise, with uneven distribution of amplitudes to frequencies, will result in a much more complicated excitation process of dynamical modes. These processes contribute to populations in the same food web having different responses to coloured environmental noise. (Greenman & Benton 2005^a)

The colour of time series represents temporal correlation types. All species in the diamond shaped food web fluctuated in stable limit cycles in a constant environment, which infers positive temporal correlations. Species redness increased with weak environmental noise (Figure 14a) and all species except the predator reached an equilibrium level at low levels of environmental fluctuation strengths. However, the variances of all species except the predator were continuing to increase with increasing σ_{env} . Differences between species can occur because of different efficiencies between bottom-up versus bottom-down transfer. Power distribution from consumer to predator has been shown to be lower than from predator to consumer (Greenman and Benton 2005^a). Additionally, changes in consumer densities affect the resource quicker than the predator because of the time lag in logistic models. Redness of population time series increases with redness of the noise, increasing the risks connected with positive autocorrelation, such as enhanced resonance and increased power redistribution (Greenman and Benton 2005^b). The shapes of species colour shifts are similar from white to pink noise. These results speak against Greenman & Benton 2005^a assumption of coloured noise having a much more complicated excitation process of dynamical modes. Time series, affected by coloured noise, doesn't have to show a more complicated response than during white noise.

5.5 Concluding remarks

Stability, as defined in this study (μ/σ), is a coefficient including both mean and standard deviation of densities. An increase in the coefficient of stability can either denote an increase in mean density in relation to standard deviation or a decrease in standard deviation in relation to mean density. When studying food webs, it is important to analyse other factors than the coefficient of stability, such as mean and variance one by one. Otherwise, a food web consisting of only a few individuals can be considered as more stable than one with large populations of each species.

Vasseur & Fox 2007 state that weak white environmental noise can increase the stability coefficient (μ/σ) of the diamond shaped food, as did this study (Figure 6). However, the positive effect of environmental noise can be questioned because of the resulting decrease of mean food web biomass. A decreased mean has negative effects on population persistence, such as increased effects of demographic stochasticity and catastrophes (Lande 1993). Also, the stabilizing effect of environmental noise decreased when reddened and thereby more likely to be encountered in nature.

However, detailed studies of the food web showed that noise changed density proportions between species. C_2 goes extinct first of the four species in the food web with strong environmental fluctuations despite its highest mean density in a constant environment. The first consumer species, C_1 that originally had the lowest mean density of all species in the food web, increased in mean density. Its variance was only slightly affected with increasing environmental fluctuation strength. The change of proportions occurred for weaker fluctuation strengths during reddened environmental noise. The result of change in density proportions could be valued more highly than change in stability, measured as mean divided with standard deviation. Density proportion shifts, that results in evasions of low species densities, decreases the extinction risk of species in the food web. By increasing the density of the smallest population, the food web as a whole will be less sensitive to demographic stochasticity and catastrophes, more outlasting despite lowered mean food web biomass.

It is important to have in mind that food web structure and choice of model parameter will affect the degree of sensitivity to different kinds of environmental noise (Greenman and Benton 2005^a). Investigations of spectral peaks and distribution of powers between populations will provide a more detailed view of the diamond shaped food webs response to coloured environmental fluctuations.

Contradictions between classical theoretical studies and empirical results regarding food webs can be resolved by increasing the complexity of ecological models. Food web stability and extinction risk is affected by density regulation, environmental autocorrelation and spatial distribution. Including asynchronous fluctuations of consumer densities, coloured environmental variation and spatial distribution in theoretical models can help resolve contradictions in food web research. Results from this study showed that coloured environmental noise can have a stabilizing effect on food webs by increasing the coefficient of stability and changing density proportions between species. However, noise induced changes in density proportions implies that present large population sizes are no insurance towards future increase in temporal and regional environmental variance. Synchrony of species responses to noise and dispersal between subpopulations can both have major influences on stability and extinction risk of smaller food webs indicating that spatial structure could be one of the dominating factors stabilizing complex food webs found in nature.

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