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Food Webs, Models and Species Extinctions in a Stochastic Environment

Patrik Karlsson

Dissertation

Lund 2007



LUND
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Department of Ecology
Theoretical Ecology

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Abstract <p>In light of the current global mass extinction of species, ecologists are facing great challenges. In order to reverse the path towards additional extinctions early warning systems to guide management actions need to be developed. However, considering the countless species to monitor and the complexity of interactions affecting species abundances in ecological communities, this is not an easy task. Before this goal can be reached our understanding of how community structure and species interactions interact and affect the risk of extinction of single species needs to be increased. Thus the primary aim of the present thesis is to study this interaction and contribute to a theoretical basis for the identification of extinction prone species.</p> <p>In paper II it is concluded that spectral analysis of population time series may function as a tool to predict extinctions at an early stage. More specifically, I show that extinction risk of producer species in food webs under influence of uncorrelated environmental stochasticity increases with intensified red-shift of population time series. However, this relationship is strictly context-dependent, which means that a producer with red dynamics might survive in one type of food web, but the same producer species with a similar magnitude of spectral redness can go extinct in another food web where the interactions with other species are arranged in a different manner.</p> <p>Then I turn to look at which species might be more prone to become endangered or to go extinct in food webs experiencing various types of uncorrelated environmental stochasticity. In paper I I show that producer species are more likely to reach endangered population levels (according to The World Conservation Union, IUCN, criterion), whereas paper III demonstrates that consumer species more frequently go extinct. This seemingly contradiction may be explained by characteristics inherent to many producer species (e.g. high growth rate, short generation time) that enable them to recover from low population levels and thus escape extinction. Furthermore, in both the second and the third paper I show that the structure of food webs as well as the presence, position and direction of a strong interaction between two species in a food web play significant roles in the likelihood of a species reaching endangered population levels or going extinct.</p> <p>In paper IV I show that small and condensed food webs are likely to express fundamentally different dynamics compared to large and well-resolved versions of the same natural food webs. Starting from a well-resolved version of a real food web, local dynamics of the ecological system change in a non-linear manner, during gradual lumping of the functionally most similar species into aggregated species (or trophospecies). Here it is also suggested that functional redundancy exists in natural food webs. This may imply support for the 'insurance hypothesis' since sequential extinction of one of the species in the functionally most similar pair of species initially did not generate any significant changes in local dynamics of the system.</p> <p>To sum up, in this thesis I present a prototype of a predictive tool to discover species at risk of going extinct. I also present directions to which type of species to look for and what type of structures and interactions to pay attention to when searching for presumptive victims of extinction in ecological systems. However, the features of the ecological models I have used for my research are in many cases incomplete. For example, my food webs contain relatively few species without competitive interactions subjected to only uncorrelated environmental variability. Further research will have to test the generality of the results and the robustness of the conclusions drawn from them.</p>		
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Food Webs, Models and Species Extinctions in a Stochastic Environment

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Dissertation

Lund 2007



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Department of Ecology
Theoretical Ecology

A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarizes the accompanying papers. These have either already been published or are manuscripts at various stages (in press, submitted or in ms).

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To my beloved Lisa

LIST OF PAPERS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals. The papers are appended at the end of the thesis.

- I Karlsson, P., Jonsson, T. & Jonsson, A. Food web structure and interaction strength pave the way for vulnerability to extinction. (Submitted)
- II Karlsson, P., Jonsson, T. & Jonsson, A. Food web structure and population dynamics: the colour of extinction. (Submitted)
- III Jonsson, T., Karlsson, P. & Jonsson, A. (2006) Food web structure affects the extinction risk of species in ecological communities. *Ecological Modelling* 199 (1): 93-106
- IV Karlsson, P. & Jonsson, T. Aggregation of species and species redundancy in models of natural food webs. (Manuscript)

Paper III is reprinted with permission from the publisher.

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SUMMARY (in Swedish)

Näringsvävar, modeller samt utdöenden av arter i en slumpmässig miljö

Vi upplever i detta nu att arter dör ut med en hastighet jämförbar med vart och ett av de fem stora globala utdöendena av arter i geologisk tid (inkl. dinosauriernas försvinnande). Vad som gör det pågående massutdöendet unikt är att det *inte* kan härledas till abiotiska (icke-levande) faktorer, såsom meteoritnedslag eller rörelser i kontinentalplattorna. Mycket tyder istället på att människans handlingar på relativt kort tid, direkt och indirekt, gett upphov till starka störningar av de ekologiska samhällena. Människan är en naturlig del av ekosystem och kommer därför alltid att utnyttja jordens resurser och interagera med andra arter. Vi har emellertid mycket att tjäna på att begränsa vårt ekologiska fotavtryck. Med nuvarande exploateringstakt kommer vi att förlora förutsägbarheten hos många av de livsviktiga ekologiska varor och tjänster (ex. fisk och rent vatten) som vi erhåller av naturen, och som vi lärt oss att ta för givet.

Av ovanstående anledning är det av hög prioritet att försöka begränsa och i möjligaste mån reparera människans störningar innan de hunnit bli oåterkalleliga. Med dagens kunskap kan det emellertid vara svårt att veta exakt när vi stör ett ekologiskt samspel i alltför stor utsträckning. Det är därför en stor utmaning för dagens ekologer:

- Att hitta indikatorer som kan ge tidig varningssignal om att arter riskerar att dö ut.
- Att ta reda på var varningssystemen gör bäst nytta. I en komplex värld med en myriad av arter som samspelar har ekologer ingen möjlighet att övervaka allt, utan behöver troligtvis koncentrera resurserna till den typ av arter som löper störst risk att dö ut.
- Att förstå störningsprocessens förlopp. Läggs en serie störningar till varandra i ett linjärt förlopp, eller existerar det trösklar som gör att ytterligare en liten störning kan få exceptionella effekter på stabiliteten i ett ekosystem?

I min avhandling ger jag viktiga pusselbitar till var och en av dessa frågeställningar.

I andra delen av avhandlingen (*Paper II*) visar jag att spektralanalys av en arts tidsserie (d v s data om artens förekomst över tid) kan fungera som ett tidigt varningssystem inför förestående utdöende. Spektralanalys är en metod som beräknar likheten mellan två efterföljande observationer. Till exempel, en väderserie skulle betecknas som röd ifall alla i en rad efterföljande vintrar var kalla, medan väderserien skulle betecknas blå ifall varannan kall vinter följdes av en mild. Mer i detalj visar jag att ökad rödnyans av en producentarts populationsdynamik ökar risken för dess utdöende. Det är emellertid inte så enkelt att om rödheten för en arts tidsserie passerar en gräns så kommer arten per automatik att dö ut. Utdöenderisken för en art är istället i hög grad beroende av vilka arter den interagerar med. Således kan en art med röd

populationsdynamik i ett ekosystem löpa stor risk att dö ut, medan samma art med ännu rödare populationsdynamik, fast i ett annat ekosystem, ha liten utdöenderisk.

I avhandlingens första och tredje delar (*Paper I* och *III*) studerar jag vilka typer av arter i ekosystem påverkade av slumpmässiga miljöväxlingar som löper störst risk att nå så låga förekomster att de anses som hotade (enl. IUCN, den internationella miljöförbundet), respektive vilka typer av arter som tenderar att verkligen dö ut mest frekvent. I studierna används olika sorters slumpmässiga miljöväxlingar och i *Paper I* konstateras att arter som är producenter oftare erhåller hotstatus, medan jag i *Paper III* visar att konsumenter är de arter som i större utsträckning verkligen dör ut. En förklaring till att det förhåller sig så kan vara att producentarter ofta har egenskaper som gör att de relativt snabbt kan återhämta sig från låga förekomster (ex. snabb reproduktion, tidig könsmognad). Vidare visar jag i båda studierna att strukturen i ett ekosystem (ex. antal interaktioner mellan arter, förekomst av allätare) samt förekomsten, positionen och riktningen av en stark interaktion mellan två arter har betydelse för en arts risk att nå kritiskt låga nivåer eller att dö ut.

Existerar det överflödiga arter? Med andra ord, finns det arter som till sin funktion (ex. vad de äter och vem som äter dem) är så lika andra arter att om de försvann så skulle inte deras frånvaro märkas. Istället skulle deras funktioner övertas av deras "tvillingar", varpå ekosystemet skulle kunna fortsätta att fungera nästan som vanligt. I avhandlingens fjärde del (*Paper IV*) konstateras att ett visst mått av redundans (överflödighet) förekommer i naturliga ekosystem. Successivt utdöende av arter som funktionellt sett liknar andra arter mest leder inledningsvis inte till stora förändringar av hur ett ekosystem reagerar på en störning. Alltså skulle man kunna påstå att "överflödighet" försäkrar ett ekosystem mot starka stabilitetsförändringar, givet att det är de överflödiga arterna som dör ut först. Emellertid, under varaktiga perioder av utdöenden, såsom idag, är sannolikheten stor att "tvillingarna" tar slut, d v s att ett ekosystem förlorar en hel grupp av arter med en specifik funktion. Risken är då uppenbar att ekosystemet står inför ett skifte med stora konsekvenser för dess stabilitet.

En modell är en förenkling av verkligheten med avsikt att skala bort de ovidkommande aspekterna kring det man önskar studera, men som förhoppningsvis ändå lyckas fånga de väsentliga delarna av verkligheten. Av olika anledningar har teoretiska ekologer endast studerat modeller av ekosystem med ett mycket begränsat antal arter. Hur pass representativa är resultaten från dessa jämfört med verklighetens detaljerade vävar av arter? I *Paper IV* visas att när ett från början detaljrikt ekosystem successivt förenklas (genom sammanslagning av arter som har liknande diet och predatorer), så ökar sannolikheten att ekosystemets reaktion på en störning skiljer sig från reaktionen i det ursprungliga, icke-komprimerade ekosystemet. Detta förhållande behöver inte nödvändigtvis vara linjärt, utan en mindre förenkling kan mycket väl generera liknande resultat som det ursprungliga ekosystemet, men generellt kommer sannolikheten att en modell lyckas fånga egenskaper hos ett verkligt ekosystem att minska med graden av förenkling.

Slutligen, de modeller jag använt för att studera vad som pågår i ekosystem är inte heltäckande. Jag har t ex använt mig av ett relativt litet antal arter som påverkas av ett fåtal typer av miljövariationer. Om mina resultat äger allmängiltighet kommer kompletterande forskning att kunna ge svar på.

SUMMARY

The extraordinary biodiversity of the Earth is a source of great admiration and amazement. However, one of the most striking features of contemporary global change is the rapid loss of species richness in various ecological communities. This decline occurs at a rate similar in magnitude to the five or more mass extinction events in the history of life on earth. Biodiversity loss may not only be associated with decreased levels of species richness, but can also result in losses of genetic and functional diversity (i.e. the building material of species and their roles in a community, respectively). Loss of functional diversity may initiate unpredictable ecosystem change that in the long run could affect the survival of other species and the sustainability of the entire ecosystem. Thus, one of the central issues of community ecology is to understand the mechanisms of biodiversity loss, with the primary goals of finding features that make species more vulnerable to extinction and detecting indications of imminent species loss (The secondary goals being the prevention of undesirable anthropogenic species loss and predicting the outcome of species loss that have taken place or are about to occur.).

The main topic of this thesis is natural species extinctions, and key objectives were to study: (a) which species in a multi-species community go extinct as a result of environmental stochasticity, (b) why different species are more or less extinction prone, and (c) whether we can predict imminent extinctions. Or, more specifically:

- (a) Are there certain types of species that become endangered or die out more often than other species?
- (b) What characteristics of ecological communities, species and species interactions might contribute to increased risks of extinction?
- (c) Are there any tools with which we can detect species that are likely to go extinct in the future, but not yet have reached endangered population levels?

Another important question for theoretical ecology is to what degree food web models can be simplified without losing relevance to the more complex reality. What happens to population dynamics if we in a model aggregate species that we perceive have similar functions (i.e. two species that consume similar prey and are consumed by similar predators)? Simplifications are needed in multi-species modeling for many reasons, e.g. easier comprehension of more complex phenomena or the limitations set by the computational tools. In theoretical community ecology, food web models have often been reduced to simple settings, sometimes comprising only a single food chain (or even a pair of species). However, natural communities are not undersized food chains. They contain numerous species that are members of a complex web of trophic and non-trophic interactions. If, or to what extent conclusions drawn from such

simplifications are scale-dependent is largely unknown, and we try to bring light to some of the differences between smaller and more reticulate models.

In the search for answers to the questions above we simulated and analyzed multi-species food web models, described by Lotka-Volterra differential equations coupled by trophic interactions (in some cases competitive interactions too), and influenced by different types of uncorrelated stochasticity.

In *Paper I* we show that producer species are more likely to reach endangered population levels (according to The World Conservation Union, IUCN, criterion) by a rapid decrease in abundance. We demonstrate that food web structure and the position and direction of strong interactions play dominant roles in generating such dynamics in environments with uncorrelated noise that influence recruitment favorably and adversely with the same likelihood (i.e. in a neutral manner). However, whether species at the base of food webs are more prone to extinctions than consumers is beyond the scope of this study. In this study, producers are considered to be of small size, have high growth rate and short generation time. These traits often generate population dynamics that are dominated by rapid fluctuations. Thus, although producers ‘pay a visit’ to population levels vulnerable to extinction, they might also have a capacity of swiftly bouncing back to safer grounds.

Spectral analysis is a method to measure the self-similarity or contribution of different wavelengths in a time series. Often a prevalence of long wavelengths is referred to as ‘red noise’ by analogy with the visible light spectrum. In simpler words, in a red noise environment there is a greater likelihood of a cold winter subsequent to a cold winter the year before, i.e. the self-similarity is high. In *Paper II* we show that in an environment with white (i.e. no self-similarity) and neutral noise, the resulting time series of consumer species nonetheless turn out red, and that redness increases with trophic height. Both food web structure and the position and direction of a strong interaction were shown to influence the colour of species dynamics. Furthermore, for producer species the increased red-shift of the dynamics was significantly positively related to risk of extinction. However, the relationship was strongly context-dependent, that is, a producer with very red dynamics might survive in one food web, but the same producer species with a similar magnitude of spectral redness could go extinct in another food web, where the interactions with other species were arranged in a different fashion.

In *Paper III* we show that consumer species are going extinct more frequently than producer species in food webs with a majority of weak interactions. Furthermore, extinctions of primary consumers (intermediate species) occurred more commonly than the secondary consumer (top species). Food webs experienced uncorrelated environmental noise that was detrimental to recruitment of all species in an attempt to resemble contemporary negative anthropogenic stress on natural communities. Again,

the structure of a food web affected the risk of extinction of species. For example, number of links or number of omnivorous links in a web tended to be of significance for all consumers. Strong interactions also had significant effects on extinction risk. This feature was largely context-dependent, and which species went extinct depended strongly on the position and direction of a strong interaction in the web.

Simplification is a necessary element of food web modeling. To attain a simpler food web that still encapsulates the essential behavior of some characteristic may be important for several reasons (e.g. easier comprehension). In food web modeling the number of species (and abiotic nutrient sources) has routinely been aggregated into assemblages based on trophic similarity (also known as *trophospecies*). However, any simplification must not generate characteristics and dynamical behavior completely different from the original system. In *Paper IV* we study large natural food webs and show that sequential aggregation of functionally similar species into trophospecies generates smaller, more condensed food webs with fundamentally different local dynamics compared to the original food webs.

Dynamics such as environmental variability and predator-mediated coexistence can set aside competitive exclusion and maintain consumer overlap in resource use. Functional similarity among species, expressed as interspecific competition for resources, brings up the question if some species can be perceived as functionally 'redundant'. That is, whether the probability is less that ecosystem function will be altered by the extinction of one species in a group of functionally similar species. The mechanism would be that the remaining species are able utilize the surplus, and hence, to maintain ecosystem function. However, when gradual biodiversity loss is persistent, the likelihood of dramatic alteration of ecosystem functioning eventually increases due to the loss of an entire functional group. The issue of functional similarity, loss of biodiversity and ecosystem dynamics is dealt with in *Paper IV*. We show that the reliability of local food web dynamics (measured as the change of stability between extinctions) decreases with continuous reduction of biodiversity.

The main messages of the work in this thesis are:

- Not just the intrinsic traits of a species determine the extinction risk of species, but also the structure of the community it inhabits and the interactions with other species. More specifically, the strength of a trophic interaction, its position in the food web and its direction between two species may give guidance to which species in the community is at most risk of reaching endangered levels or even going extinct. To uncover the trophic interactions in a community is arduous fieldwork, but to acquire the *strengths* of interactions using an empirical approach is even more difficult, if possible. Estimates using allometric relations of for example body sizes may therefore be a shortcut to obtain relevant data.
- We need tools that bring early warnings on species that run a high risk of going extinct in the future, so that we can take actions before the prospects of recovery are too bleak. Spectral analysis seems to provide such information. However, we need more specific knowledge of the population dynamics generated in different communities under different stochasticity regimes, in order to use spectral analysis as a diagnostic tool for conservation purposes.
- Size matters! The degree of resolution too. Local stability (and most probably population dynamics) differs between smaller food webs with a high degree of aggregated species and larger food webs with high species resolution. The relationship between metrics of local stability and species resolution is likely to be non-linear. Therefore, in matters relating to local dynamics, conclusions drawn from small systems may find less relevance when scaled up to natural, less aggregated systems.

If the facts don't fit the theory, change the facts.

Albert Einstein (1879-1955)

INTRODUCTION

Food Webs and Models

What is a food web?

There is some confusion regarding the concepts food web, community and ecosystem. Some people may use them interchangeably. Although definitions vary, you may distinguish them by scale. An ecosystem is a complex set of relationships among the habitats (e.g. forest, lake) and the organisms living there. Thus, both biotic and abiotic components of space and time are taken into account. A community is often described as a well-defined assemblage of organisms within an ecosystem (e.g. plant or bird community). A food web is also a simpler representation of an ecosystem, but restricted to describe the functional properties of the members within it. Basically, it reduces the interactions between species to their trophic links, i.e. who is eating whom. Thus, you may look upon a food web as a smaller ecosystem stripped from the characteristics and interactions that are not dealing with feeding relations. A food web can be portrayed graphically as a network (Fig. 1a) or described mathematically by a binary predation matrix (Fig. 1b). Today, food web theoreticians are becoming increasingly aware of the importance of non-trophic interactions and now include interspecific interactions such as direct competition or mutualism more often (e.g. *Paper IV*).

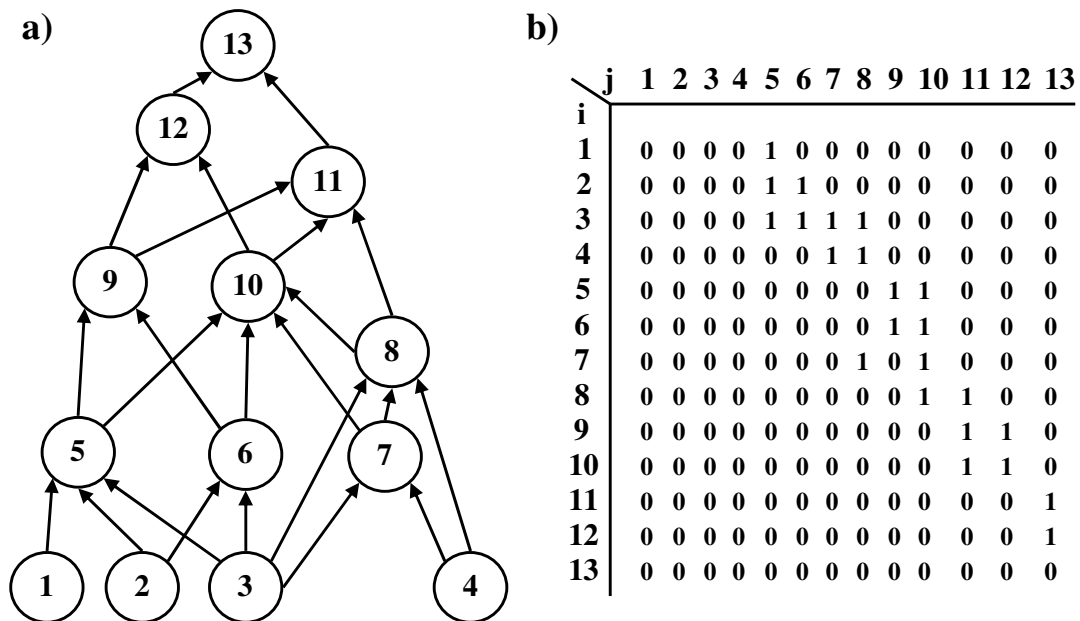


Figure 1. a) Food web with thirteen species. Arrows indicate trophic interactions between two species, representing the flow of biomass from a resource species to a consumer species. b) Predation matrix. Binary representation of trophic interactions between species such that a '1' indicates that species j consumes species i (a '0' indicates that no feeding relationship exists between species i and species j).

On the origin of species by means of natural selection by Charles Darwin (1859) was an important book in recognizing the complexity of the living earth. For a long time, however, community-level studies were largely overlooked, in favour of a mounting research on singular species. The foremost reason was the difficulty with which to get a clear picture of cause and effect, even with few interconnected species in a controlled setting. Another explanation was a lack of analytical tools. Today, with better statistical tests and an ever increasing capacity of computers, the prospects of understanding dynamics and mechanisms in multi-species settings have improved.

A classical and often used approach to represent the dynamics of ecological systems is by means of non-linear continuous-time Lotka-Volterra equations. Originally, the model described a simple two-species predator-prey system (Lotka 1925; Volterra 1926), however, it can be expanded to involve many more species. In the Lotka-Volterra model the growth rate of each species i is represented by coupled differential equations (shown in its generalized form below):

$$\frac{dN_i}{dt} = N_i \left(b_i + \sum_{j=1}^n a_{ij} N_j \right) \quad (\text{eq. 1})$$

where N_i is the abundance of species i . b_i is the per capita rate of growth or death of species i . a_{ij} is the per capita effect of species j on the per capita growth rate of species i . In this form, there is no migration of individuals in and out of the system.

The Lotka-Volterra model – and why use models at all?

A model is a simplification of the real world. Just as a map is a simplification of a real landscape that omits some details and enables you to use a more manageable model of reality instead of a 1:1 representation of the real thing, a food web is a simplification of all the intricate features within a natural ecosystem. The objective is to find the right level of simplification that captures enough complexity to describe the phenomena under study but leaves out superfluous and distracting details. Thus, the use of food web models is justified by the unfeasibility or impracticality to describe the entire scope of an ecological system, whilst the model should try to capture the essentials of what an investigator intends to study. Consequently, a model always can be criticized for its simplifying assumptions, the Lotka-Volterra model being no exception.

A fundamental supposition often used in community ecology is the concept of stability and equilibrium point. The intuitive rationale is that ecological communities should possess a dynamical capacity to recover from disturbances (i.e. to return to an equilibrium point). In stable systems this tendency may be illustrated by a trajectory moving towards the equilibrium level, either monotonically or by damped oscillations (Fig. 2).

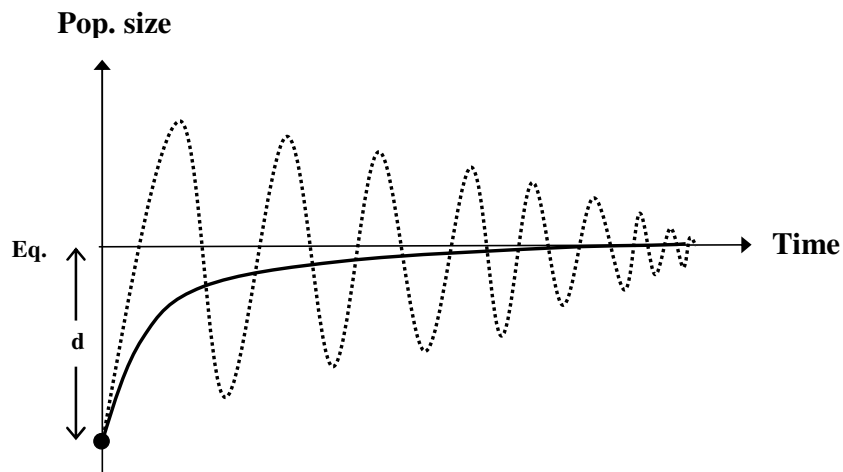


Figure 2. The dynamics of a population over time in a locally stable system. The horizontal line indicates the equilibrium abundance of the population. d denotes the magnitude of a disturbance. Dotted line: return to the equilibrium population level through damped oscillations. Line: monotonic return to the equilibrium population level.

A limitation of the Lotka-Volterra model, using the *local* stability criterion, is that it may be an adequate description of the dynamics of an ecological system only in the vicinity of the equilibrium point (Haydon 1994). For example, much critique of the original Lotka-Volterra model stems from the omission of potentially important behavioural aspects such as predator saturation and prey refuge, the use of constant interaction coefficients and absence of stochasticity. Thus, the model may say little about the dynamics farther away from the equilibrium point, subsequent to a large perturbation. Additional critique includes the lack of spatial and temporal components (e.g. stage structure, heterogeneous distributions of populations in space and time) (Holling 1959; DeAngelis *et al.* 1975; Abrams & Walters 1996). Although later modifications have included one or a few of the elements above, models will always be subject to criticism of oversimplification.

Even though more realism might be beneficial to models there is disagreement on how to incorporate it mathematically. The debates on functional response and mode of noise (stochastic perturbation) are two vivid examples (see also section *Stochasticity* below). Holling (1959) introduced two non-linear functions of predator functional response (commonly referred to as type II and III), which deny predators unlimited consumption with increasing prey abundance. In simple words, with prey abundant a predator cannot consume faster than up to a certain level due to constraints of time to find, hunt, kill and digest prey. Although Holling's equations have found widespread use, they too are subject to criticism. The main objection stems from their exclusive focus on absolute prey abundance (prey-dependent functional responses). Would it not be plausible to consider that the predator functional response is influenced by predator abundance as well? This assertion was justified by observations of predator-dependence in the field through, for example, interference competition (Beddington

1975), and in laboratory environments (Arditi & Ginzburg 1989). To deal with this, a ratio-dependent functional response has been proposed. Here, the response depends on the ratio of prey-to-predator population sizes, not on the absolute number of either species. Appealing features of ratio-dependent predator-prey models are that they solve the problems of paradoxes of enrichment and biological control (Arditi & Ginzburg 1989; Arditi & Berryman 1991; Berryman 1992). The first theoretical models based on a ratio-dependent functional response of the predator was presented long ago (Leslie 1948), but it is not until recently it has gained some recognition and have been implemented (Arditi & Akcakaya 1990; Berryman *et al.* 1995). However, criticism has also emerged that the application of a ratio-dependent model might be unreasonable in many circumstances, suggesting a predator-interference model as a better solution in for example pelagic food webs, (McCann *et al.* 1998b). The debate is still very much alive and the differences between prey- and ratio-dependent are discussed by proponents from both sides (Abrams & Ginzburg 2000, for a review).

Despite its shortcomings, the Lotka-Volterra model brings various advantages to theoretical ecologists (which are not necessarily provided by other model approaches): First, vital rates of species and interactions between species are relatively easy to grasp intuitively and could in theory be straightforward to parameterize (see below). Secondly, there are clear-cut analytical solutions to stability properties of food webs that are relatively easy to obtain. To obtain corresponding features from time series would require cumbersome and time-consuming simulations, and the results would be less clear-cut. Thirdly, results obtained from the Lotka-Volterra model has proven to be an extensive source for developing new hypotheses. Finally, theoretical research based on the Lotka-Volterra model is extensive. Therefore many aspects of population dynamics in a wide array of special cases are well-known (e.g. linear vs. non-linear intraspecific density-dependence, functional or numerical responses).

Facets of food webs

To represent an ecological community by a model may serve both descriptive and explanatory purposes. A model may assist with depicting the complex organization of immense number of species in a natural ecological community in a more structured and comprehensible way. What's more, models of systems of species have rendered insight into a variety of features of natural communities, e.g. (a) distribution of interaction strengths, (b) body sizes, (c) food web structure, (d) indirect interactions, (e) compartments and (f) networks. Finally, when new features of community structure and function have gained wider acceptance, they may serve as fundament for new hypotheses, i.e. models may function as a predictive tool.

(a) Interaction strengths and their distribution

Links are what connect two species in an ecological community. A link may consist of a feeding relationship (e.g. herbivory, predation, omnivory, parasitism,

cannibalism) or be of a non-feeding nature (e.g. competitive, mutualistic, commensalistic). In food webs *one* trophic link means the two-way (bilateral) relationship between two species. For example, the negative per capita impact of moose (*Alces alces*) on the per capita growth rate of young pine (*Pinus sylvestris*), and the positive per capita effect of pine on the per capita growth rate of moose constitute the two opposing interactions of a single trophic link. A pair of interactions within a link is often not of the same magnitude. Pimm and Lawton (1977) asserted that the effect of a predator on its prey is a great deal stronger than vice versa. This is because a consumer is unable to consume and convert all energy stored in the resource for reproduction, and if the predator is larger than the prey this implies that the per capita effect of the predator on the prey species is larger in magnitude than the per capita effect of the prey on the predator (Peters 1983; Neutel 2001).

There is an agreement on the meaning of interspecific interactions, however, the quantification of interaction *strengths* has developed into a wide array of measures (Laska & Wootton 1998; Berlow *et al.* 1999, for reviews on theoretical and empirical measures respectively), which complicates a comparison of studies (Berlow *et al.* 2004). Field ecologists have predominantly quantified the strength of consumer impacts on resources by measuring the difference in resource abundance before and after removal of one species. For example, to quantify interaction strengths, Paine (1992a) used the effect on the abundance of a set of resource species after *complete* removal of one consumer species. From a predator point of view this clearly is a press-perturbation. Whether this is the case from a prey point of view as well depends on if the prey have reached a stable state (equilibrium or limit cycles) or not. Thus, to equate consumer per capita Lotka-Volterra interaction strengths with the per-capita effect of a consumer on the change in abundance of its resources it must be assumed that there exists an equilibrium and that the resources have reached it at the end of the experiment or that the change in abundance of the resources change linearly with time. Other approaches to quantify interaction strengths are, for example to perform *incomplete* predator removals where the objective is to examine community change in response to a small, temporary perturbation of one species (i.e. ‘pulse’ perturbations, Bender *et al.* 1984; Yodzis 1988; De Ruiter *et al.* 1995b). Again, community equilibrium and linearity in response with respect to time is assumed as the perturbation occurs. This measure equates to the elements of the community (Jacobian) matrix, which represent the direct per-capita effect of one species on the total population of another species at or near equilibrium. Another alternative is to perform manipulations where the abundance of one species is kept at a constant level (lower or higher) away from the equilibrium (‘press’ perturbation experiments). This generates the total direct and indirect per-capita effects of one species on a per-capita equilibrium abundance of another species (Bender *et al.* 1984; Yodzis 1988), and equates to the elements of the inverted interaction matrix (Berlow *et al.* 2004). In all papers of this thesis (*Paper I-IV*), however, we use the elements of the interaction matrix to denote direct interaction strengths between species (which are equal to the

per-capita change in growth rate of one species as a consequence of a small per-capita change in abundance of another species). Interactions may also be intraspecific, i.e. the effect of one individual on an individual of the same species. Typically, intraspecific interactions are depicted as negative effects, denoting density-dependence (but could also indicate cannibalism between individuals of different life stages). A less used case of positive opposing intra- or interspecific interactions would result from mutualism between individuals.

When more links in a food web were put forward as a destabilising factor (May 1972; Hastings 1982), it started a discussion about the meanings of stability and the mechanisms maintaining stability in systems since links (and species) obviously are abundant in natural communities (but according to May should decrease the probability of stability with increasing species richness unless average interaction strength decreases). In many studies it has been shown that weak interactions probably predominate (Paine 1992a; Fagan & Hurd 1994; De Ruiter *et al.* 1995b; Power *et al.* 1996; Raffaelli & Hall 1996; Wootton 1997b; Woodward *et al.* 2005, but see Sala & Graham 2002). Explanations to such a distribution might be metabolic scaling of species (West *et al.* 1999), species-area relationships (Harte *et al.* 1999) or predator-prey body size ratios (Cohen *et al.* 1993; Warren 1996; Cohen *et al.* 2003). Strong interactions may generate increased temporal variation of populations (May 1973, Polis & Strong 1996, Benedetti-Cecchi 2000). A skewed distribution pattern of interaction strengths, expressed as a lower average strength of interactions with increasing number of links, has been shown to compensate for the instability invoked by many links, since weak interactions tend to dampen amplified fluctuations (May 1972; McCann *et al.* 1998a; Berlow 1999b; Kokkoris *et al.* 1999; Neutel 2002; Neutel *et al.* 2002b; Jansen & Kokkoris 2003). Several mechanisms by which weaker interactions may act to suppress potential wild fluctuations have been introduced: (i) exploitative competition between consumers over a common resource may prevent the stronger oscillatory dynamics of a single consumer-resource relation, and (ii) apparent competition between resources of a common generalist consumer may initiate oscillatory dynamics in the system, which can be dampened by the consumer switching preference between resources, and thus changing its interaction strengths (Post *et al.* 2000). The distribution of interaction strengths in our studies were skewed towards weak interactions (*Papers I-IV*). In *Paper IV* the interaction strengths were derived from body size ratios based on empirical measurements. In *Papers I-III* we formulated ecologically feasible weak interaction strengths. Any strong interaction was derived from a corresponding weak interaction. We showed that the exact position and direction of a strong interaction were related to the risk of endangerment of species (*Paper I*), the spectral colour of a population's time series (*Paper II*), and the risk of extinction of species (*Paper III*).

(b) Body sizes and their distribution

The distribution of body sizes in a community seems to be comparable to the distribution pattern of interaction strengths, i.e. a distinct skew towards the smaller (Jonsson *et al.* 2005). Furthermore, interaction strength and predator-prey body size ratios are hypothesized to be linked (Jonsson & Ebenman 1998, Emmerson & Raffaelli 2004). It has been shown that interaction strengths derived from body size ratios increase the stability of food webs compared to food webs with interaction strengths uniformly distributed between zero and unity (Emmerson & Raffaelli 2004b). Currently anthropogenic perturbations repeatedly disrupt the distribution of body sizes in many ecological communities via species extinctions (Duffy 2003) initiated for example by harvesting or introductions of novel species. Such alterations may thus (through a change in average interaction strength, Borrvall *et al.* 2000a; Chase *et al.* 2002) have consequences for community stability (Emmerson & Raffaelli 2004b) and perhaps even ecosystem functioning (Solan *et al.* 2004). However, in the study of Emmerson & Raffaelli (2004b) all interaction strengths representing the impact of a resource species on its consumer species (a_{ji}) were set as a fixed fraction of the opposing effect of consumer species on the resource species ($a_{ji} = 0.1 \times |a_{ij}|$), and is in this way a derivation, not an independently obtained entity. This ratio ($|a_{ji}|/|a_{ij}|=0.1$) represented the conversion efficiency by which consumers are turning resource biomass (energy) into new consumer biomass. This generalization may serve as an approximation (for the case when consumer species are bigger than resource species, Peters 1983; Neutel 2001) until research has elucidated the actual relationship between resource-consumer body size ratios and interaction strengths describing the effect of resource species on their consumers (if such a relationship exists).

That the body size of species is closely correlated to many species characteristics with potential consequences for food web properties and our understanding of community functioning is beginning to emerge (Woodward *et al.* 2005). For example, there is a positive correlation between body size and trophic height of species (Warren & Lawton 1987; Cohen *et al.* 1993; Jonsson *et al.* 2005) and a negative relationship between body size and numerical abundance (however, not necessarily between body size and species biomass) (Jonsson *et al.* 2005). Additionally, body size is a determinant of intrinsic characteristics of species with demographic traits like generation time, reproductive rate and longevity being closely linked to body size (Calder 1984; Peters 1986). Thus, quantifying body sizes could be an approach to reduce an array of co-varying elements of communities and species to a single variable (Woodward *et al.* 2005). This is promising considering the difficulties in actually measuring many features of ecological communities (e.g. interaction strengths) and species life history traits in a laboratory experiment or field setting. The condensation of variables is truly valuable to empirical studies of ecological communities, and imperative to food web theoreticians, who frequently face the dilemma of reducing the number of parameters without a significant loss of information. For example, by a simple rule of ranking of species, Cohen and Newman

(1985) with their cascade model constructed predation matrices (i.e. food webs) randomly that successfully reproduced several properties of natural food webs (as described in the ECOWeB). Warren and Lawton (1987) later suggested that body size as a single parameter could serve as a guideline for the ranking of species.

(c) Approaches to model the structures of natural food webs

The *cascade model* was among the first which sought to unify food web patterns (Cohen & Newman 1985). In contrast to the Lotka-Volterra model presented above, the cascade model focuses on the static properties of a food web (i.e. ignores the population dynamics). In the cascade model, predation matrices/food webs are generated randomly by distributing trophic links between species stochastically by rule of a one-dimensional feeding hierarchy such that a species can only feed on other species lower in the hierarchy. The probability of a feeding link is determined by the link density (L/S) in the food web. Any rule may be used to construct the feeding hierarchy, however, body size difference (i.e. larger species consume smaller species) was proposed as a promising candidate (Warren & Lawton 1987). In a series of publications Cohen and colleagues found that the cascade model successfully reproduced the values of food web topologies of described food webs (Cohen *et al.* 1985; Cohen *et al.* 1986). Soon enough criticism of the cascade model appeared. One conclusion was that the cascade model did not manage to capture the patterns of compiled webs as well as stated (Schoener 1989b), and that data from generated model webs were over-dispersed in relation to model predictions (Solow 1996). The main objections, however, originated from the representation of the described food webs used in the studies of Cohen and colleagues, implying that the cascade model made correct predictions of incorrect webs (Paine 1988; Polis 1991; Hall & Raffaelli 1993; Winemiller & Polis 1996; Hall & Raffaelli 1997). The compiled webs had very low biodiversity compared to real ecosystems. Furthermore, the resolution of species was questionable as many categories of organisms were aggregated or missing. An obvious reason was that the compiled webs had been put together by numerous researchers using a variety of methods and different sampling efforts for purposes other than studying network topology. Later studies found that several of the food web properties that were used to corroborate the predictive capability of the cascade model (e.g. chain-length and trophic-level statistics as well as proportions of links between trophic levels) were very sensitive to aggregation (Sugihara *et al.* 1989; Martinez 1991; Schoenly *et al.* 1991). The risk of using food webs with low resolution was further emphasized by a gut content analysis of fish showing that the failure to include weaker trophic links in aquatic food webs (defined as low gut content of certain prey), which could be an indication of a smaller sampling effort, had effect on food web properties (Winemiller 1990).

The *niche model* was put forward as an alternative stochastic approach to explain observed food web characteristics (Williams & Martinez 2000). The niche model, like the cascade model, ranks species along one single niche axis. The order of species

along the axis is generated through assignment of random niche values, corresponding to specific positions on the axis. Then each species is randomly assigned a feeding range, which midpoint is randomly located below the niche value of each species on the axis. This condition makes certain that at least half of the interval is located below the niche value of a species. The trophic links of a species are then distributed by studying which species' niche values fall within its feeding range. Unlike the cascade model the distribution of trophic links in the niche model may possess some features found in real food webs: (i) cannibalism, (ii) feeding of species with higher niche values, and (iii) larger predator overlap, since two species with similar niche values are more likely to share consumers. Assessment of the correspondence of a large number of food web properties from improved datasets of empirical communities with food webs generated by different model approaches showed that the niche model generally performed better than the cascade model (terrestrial, Williams & Martinez 2000; and aquatic communities, Dunne *et al.* 2004), and that both models performed much better than the random model (Williams & Martinez 2000). However, with further improved datasets even the niche model seems to fail to adequately describe recent food webs (Cattin *et al.* 2004).

The *nested-hierarchy model*, proposed by Cattin *et al.* (2004), shares many features of the cascade and niche models (e.g. ranking of species along a single axis, stochastic distribution of trophic links). A central theme of the method is that the assignment of a species' new feeding links is governed by the diet of consumers sharing at least one resource species. This procedure ensures greater trophic overlap than the niche model (Solow & Beet 1998). On comparison with twelve food web structure properties analyzed by Williams and Martinez (2000) and a few additional properties dealing with intervality*, Cattin *et al.* (2004) asserted that the nested-hierarchy model performed as well as the niche model regarding the twelve properties describing food web structure, but that the nested-hierarchy model better reconstructed a lesser degree of intervality known to reside in larger natural food webs (Cohen & Palka 1990). However, the increased fit in favour of the nested-hierarchy model over the niche model to larger well-resolved natural food webs has later been disputed (Martinez & Cushing 2006).

(d) Indirect interactions

Indirect interactions, or indirect effects, are two concepts that are used more or less interchangeably to describe when two species interact not directly but through one or more intermediate species (e.g. direct effect of species A on species B which directly influences a species C causing an indirect effect between species A and C). Although the concept of indirect *interactions* addresses a pathway of influence while the concept of indirect *effects* deals with the actual impact, they both recognize that a third party (species C) has to experience some kind of change as a result of the mutual interaction between species A and B. Species C may be linked directly to species B (Fig. 3a-c), or species C may be situated further away within the same ecological community) (Fig. 3d).

* Interspecificity: Species can be ordered on a line in such a way that the diet of each consumer is a contiguous set (Cohen 1978).

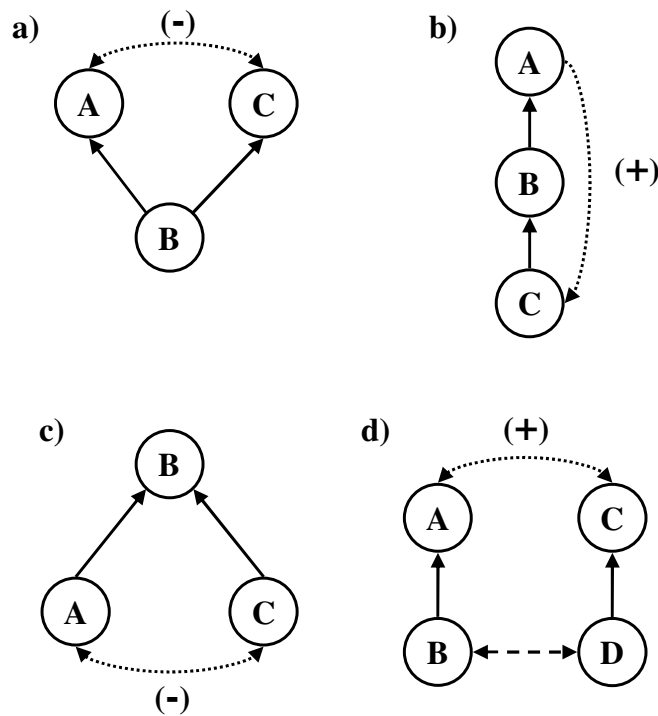


Figure 3. Examples of indirect interactions. One-way arrows indicate trophic interactions, i.e. the flow of biomass/energy from a resource (B) to a consumer (A). Two-way, dashed arrows indicate competitive interactions, and two-way, dotted arrows denote the indirect interaction between species. + or – indicates a positive or negative effect of the indirect interaction. a) Exploitative competition. b) Trophic cascades. c) Apparent competition. d) Indirect mutualism.

At least four different types of indirect interactions are commonly distinguished (Abrams 1992; Abrams *et al.* 1996; Webster & Almany 2002, even more types are described by Menge 1995): (i) Exploitative competition between two consumer species (Schoener 1993a), (ii) Trophic cascades (Hairston *et al.* 1960; Paine 1980), (iii) Apparent competition between two resource species (Holt 1977), and (iv) Indirect mutualism (Vandermeer 1980) (Fig. 3a-d). A special case of indirect interaction is when a single species A modifies the direct trophic *interaction* between species B and Species C (i.e. interaction modifications, Wootton 1994). A real world example would be African honey guides (*Indicator spp.*) directing honey badgers (*Mellivora capensis*) onto bee colonies.

It has been argued that direct interactions should be stronger than indirect interactions, and that strong direct effects are a prerequisite of indirect effects, since many indirect effects appear only as a result of strong direct effects (Schoener 1993a). From this argument follows that the strength of indirect effect should diminish with distance from the strong direct effect. This does not rule out the fact that species may have a strong effect on other species via indirect pathways, which has been demonstrated in empirical studies (Paine 1966; Vandermeer 1980; Wootton 1994). However, direct

interactions may in some cases also be weaker than indirect interactions (Power 1990; Abrams 1992; Wootton 1992) and indirect interactions far from the direct interactions may be strong (Brown *et al.* 2001a). When indirect effects are stronger than direct ones, there is a high likelihood that perturbation experiments may generate responses opposite to the expected (Yodzis 1988; Schmitz 1997).

Although existing in theory, strong indirect interactions are often difficult to detect in nature. Possible reasons are that they may be cancelled out by counteracting direct interactions (Bender *et al.* 1984) or by environmental stochasticity. Another obscuring factor is that indirect interactions may take time to develop, sometimes longer than the duration of many field experiments (Menge 1997). To overcome this problem theoretical ecologists have introduced the negative inverse of the Jacobian matrix (see stability section), which measure the sum of direct and indirect effects on a species to a constant rate of removal (or addition) of another species (Laska & Wootton 1998). This is equivalent to a press perturbation and it is assumed that the perturbed species does not go extinct (compare this situation with the methods used by empiricists to measure direct interaction strengths by studying the effect of a species prior and after the complete removal of a species). Another important difference is that using the empirical method developed by Paine (1992a) to measure direct interactions generates the *per capita* interaction strengths, whereas the elements of the negative inverted Jacobian matrix are not per capita-related (Laska & Wootton 1998).

(e) Compartments

Delimiting the boundaries of an ecological community is generally a tricky task (Polis *et al.* 1997). Even when there is a physical border between abiotic properties of the landscape, e.g. a shoreline that separates water from land, it does not mean that the beach is a distinct property unconnected to the sea. Some species will cross the shoreline and interact with species in both communities. Then what is an ecological community? Basically it is a matter of scale. You need to answer two questions: Which interactions (species and abiotic resources) do you consider to be vital to your study? And, what is the geographical range of these species? The home range of a species is connected to the distribution of resources and the physical structure of a habitat (Ritchie & Olff 1999). Furthermore, home range/habitat size is positively correlated with body size, and body size is positively correlated with trophic level (Woodward *et al.* 2005). Thus, ultimately, body size seems to be the factor that determines the scale of landscape that a species perceives. Therefore, a presumably straightforward approach to delimit an ecosystem of interest is to identify the top predators and their home ranges.

A compartment is a subset of an ecological community. It consists of a unit of species that are distinguished from other species by numerous (and sometimes strong) links within the unit and few (and often weak) links to species outside the unit (Pimm 1991a). This, however, does not mean that separate compartments are effectively decoupled from each other. Local, within-compartment interactions may carry

profound indirect effects across compartment boundaries (Knight *et al.* 2005). Another aspect of interactions between compartments is allochthonous inputs of feeding supplies (i.e. biotic or abiotic resources entering from another habitat). Allochthonous inputs can propagate through trophic links and indirectly change the abundance of populations other than the recipient species (Polis *et al.* 1997), and may exert either stabilizing or destabilizing effects on modelled food chains depending on, for example, the magnitude of input and the trophic level of the recipient species (Polis *et al.* 1996; Huxel & McCann 1998; Huxel *et al.* 2002).

The fractal dimension of the environment may account for the compartmentalization of an ecological community (Ritchie & Olff 1999). Resources and physical properties of the environment change at different scales. Thus, like ecological communities may be separated by abiotic properties (e.g. a shoreline that separates land from sea), compartments may be separated from other compartments (within the same ecological community) by abiotic properties, but at a finer scale. For a sample of closely linked species along a coral reef the reef comprises a natural boundary of their physical environment and their resources – the habitat. If only a few interactions stretch outside the reef, it could be considered a compartment, from the perspective of those species.

Models of ecological systems with the same biodiversity and connectance implied that the probability of local asymptotic stability is greater if links are arranged into compartments than if links are homogeneously distributed (May 1972, 1973a). Solow *et al.* (1999) disputed this and showed that modelled food webs with compartments were not locally stable to a greater extent compared to food webs with a random arrangement of links. The conclusions from the link distribution-stability debate initiated by May and later Pimm (1979; 1982) have developed into a new interesting field – network theory.

(f) Networks

Network anatomy, i.e. the configuration of nodes and links in complex systems, is attracting an increasing amount of attention across the scientific community. Input to network theory originates from studies of ecosystems (Williams & Martinez 2000), metabolism (Jeong *et al.* 2000), the World Wide Web (Broder *et al.* 2000), social, scientific and economic communities (Newman 2001) and various other fields (see review by Strogatz 2001). Why is the understanding of network structure valuable? For example, the structure of electrical power grids is critical to the extent of household power cuts in the aftermath of a severe hurricane. The spread of computer viruses across the Internet is another present-day illustration of an area where an understanding of network structure may be important for effectively reducing the risk of large-scale attacks. Obviously, the structure of a network affects its function. Since ecosystem function on a local as well as global scale has become something of a buzzword in ecological research today, the study of how food web structure affects the flow of energy/biomass has received growing attention. In this thesis we studied

the influence of food web structure on population dynamics in multi-species food webs, by creating a large number of unique food webs using a fixed number of species, but varying the position and number of trophic interactions. Furthermore, various food web metrics were used to study how variability in the number of links per species and its distribution may influence population dynamics of species in food webs, and ultimately spectral colour of species time series (*Paper II*), risk of reaching endangered levels (*Paper I*), or extinction risk (*Paper III*). We found that the generality of a primary consumer species increased the risk of reaching endangered population levels for both producer species and the primary consumer itself (*Paper I*), and that the number of links and/or the number of omnivorous links in a food web affected the extinction risk of intermediate and top species (*Paper III*). Furthermore, both the number of links and the number of omnivorous links in a food web significantly influenced the colour of population dynamics of species at all trophic levels (*Paper II*). Generally, the food web metric irregularity (describing the distribution of number of links per species in a food web) expressed weaker relationships to the spectral colour of primary consumer dynamics (*Paper II*), and the extinction risk of top species (*Paper III*). To be able to discriminate any significance of irregularity to population dynamics (and eventually extinction) of species, studies of larger food webs (more species) with a greater variation in number of links per species are required.

A few distinct non-exclusive types of networks have been described, readily identified by the method of construction: (a) Random, (b) Small world and (c) Scale-free networks (Fig. 4a-c).

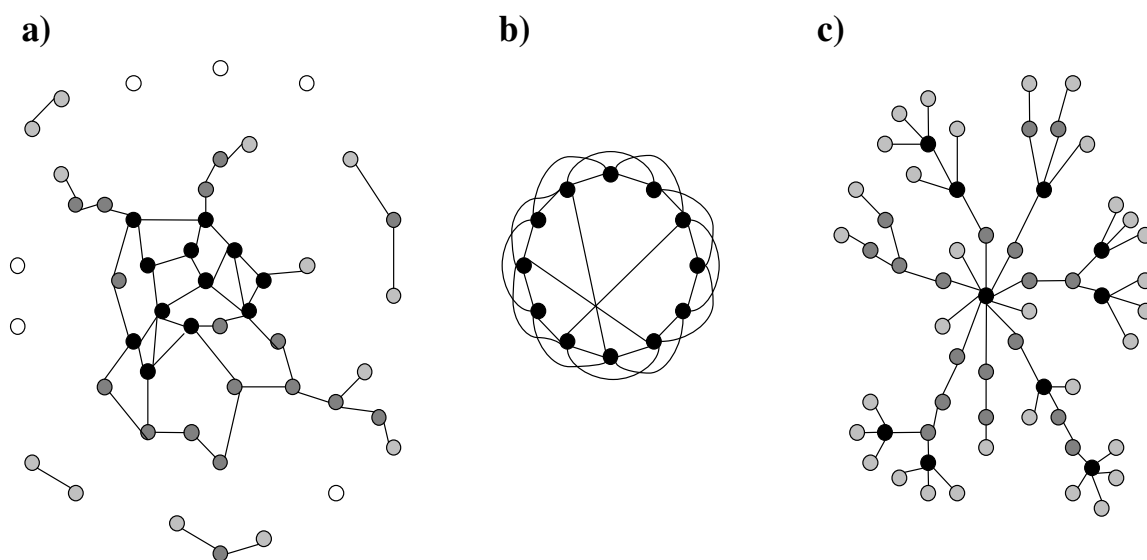


Figure 4. Examples of types of network structures. a) Random, b) Small world (after Strogatz 2001), and c) Scale-free networks. Lines indicate links between nodes (circles) in a network. The greater number of links to/from a node, the darker the node.

(i) *Random network*

A random network can be described as a set of balls (nodes) spread over the floor. Then two balls at a time are chosen randomly and connected by a string (link). Any node may be picked several times or not at all. As the number of strings increases, certain features start to develop (Fig. 4a):

- A tangle of criss-crossed links.
- A large, main body of interconnected balls and subsets of balls that are interlinked with only a few other balls or no balls at all.
- Absence of any dominant hubs.

Montoya and Solé (2002) demonstrated that the distribution of links per species in natural food webs deviated from that of random networks.

(ii) *Small world network*

Again, starting with a randomly distributed set of balls on a surface, a string is attached from each ball to the ball closest by some sort of distance. This procedure is repeated for the next nearest neighbour and so on. Soon enough a pattern is distinguished, the emergence of well interconnected clusters of balls that are closely situated to each other (Fig. 4b). Between the clusters there are only a few links. The structure would resemble that of a compartmentalized ecosystem described above (Montoya & Solé 2002). Watts and Strogatz (1998) found that dynamical systems coupled in this way would display enhanced signal propagation speed (through the short within-cluster links) and synchronization of distant nodes (through the few but longer between-cluster links). In food web terms this means that within a compartment the population dynamics will tend to be coupled tighter since species will react faster to a sudden shift in the abundance of another species within the same compartment. Furthermore, the positive correlation of population dynamics of species remotely situated in the food web may increase as a result of a few but longer links between species in separate compartments.

(iii) *Scale-free network*

Scale-free networks are constructed by linking new nodes to previously existing nodes in such a manner that the probability of a new link is positively related to the number of links of the existing node. As a consequence, nodes with abundant links tend to get increasingly connected. The result is a network with a few key hubs (Fig. 4c) and a skewed distribution of links per node (Barabasi & Albert 1999). This kind of network finds its resemblance in for example the WorldWideWeb (Broder *et al.* 2000), where new nodes (web pages) are added continuously and are connected preferentially to existing nodes. It has been suggested that scale-free networks are more resistant to

random failure of nodes. If any node stops functioning there is a quite good chance that it causes limited damage to the network functioning, since most nodes are dispensable. On the other hand, directed (non-random) “attacks” on hubs may inflict serious damage to network functioning (Albert *et al.* 2000; Solé & Montoya 2001; Montoya & Solé 2003).

Recent studies suggest that natural food webs possess features that resemble scale-free (Solé & Montoya 2001) or small world networks (Montoya & Solé 2002). In the second study small world patterns seemed to agree better with natural food webs with increasing resolution of observed food webs. For example, comparing well-resolved webs (e.g. Silwood, Ythan Estuary) with less-detailed webs (e.g. the ones compiled in the ECOWeB database) revealed that a coarse-grained resolution may conceal a higher degree of clustering, representative of compartmentalized food webs (Montoya & Solé 2002). Small world webs seem to respond quickly to perturbations (Watts & Strogatz 1998), which may enhance the homeostatic capacity of natural food webs (measured as the resistance to secondary extinctions or disintegration of the food web into smaller, disconnected subsets) subsequent to random removals of species (Solé & Montoya 2001). The homeostatic features observed during random removals of species were not observed following selective removals of the most-connected species (Solé & Montoya 2001). Others, however, point out that real-world food webs often lack the small-world and scale-free structure in food webs above a certain level of connectance (e.g. low clustering) (Dunne *et al.* 2002). Thus, it may turn out that large, well-resolved real food webs neither are small-world nor scale-free networks.

Stability

What is stability?

Intuitively, the idea of stability in nature may seem easy to grasp: Populations of a community that has been disturbed will attempt to return to the pre-perturbation state, or to another stable equilibrium. The notion is that most of what we observe in nature is what is left in a selection process – unstable systems are transient and thus will be extinct. Then, whether a system of species ever reaches back to its equilibrium point in a world that is subjected to continuous perturbations is of less importance, the significant thing is the inclination to return, either monotonically or through damped oscillations (Fig. 2).

Mathematically the concept of asymptotic stability is split into two – local asymptotic and global stability. The distinction lies in the ability of a biological system to return to an equilibrium state depending on the strength of the perturbation. Global stability prevails when all populations in the system return to an equilibrium point following a displacement of any size (May 1973b). And, a dynamical system is recognized as locally stable if it returns to equilibrium after only a small temporary (pulse) perturbation in a deterministic environment (Lewontin 1969; May 1973b; Yodzis 1989). The weaknesses of the local stability concept are (i) that it only explores the

dynamics in the vicinity of the equilibrium point and (ii) the vagueness in how large a small perturbation is. Considering these drawbacks, one may ask why studies using the global stability concept are relatively sparse. One disadvantage of the global stability criterion is that species may reach extremely low population densities without ‘hitting rock bottom’. At such low levels real populations are very sensitive to stochastic events and might go extinct even though the system tends back to the equilibrium. Another answer to the widespread use of the local stability criterion lies in the manageability of the mathematics. In local stability analysis there is no need for an explicit solution to the continuous-time Lotka-Volterra equation. Instead, the analysis involves an examination of the dynamics around the equilibrium points, which entails a rather straightforward procedure to calculate the eigenvalues (λ_i) of the Jacobian matrix of a system. The community is termed locally stable if the greatest real part of the eigenvalues is negative, i.e. $(\text{Re}(\lambda_i))_{\max} < 0$. In other words, when this condition is fulfilled, all eigenvalues are negative, which mean that all species will counteract any disturbance and return to the stable state before the perturbation took place. If the real part of at least one eigenvalue is positive, the system is unstable and the deviation inflicted by a perturbation will grow leading either to extinction or reaching some other internal attractor. Resilience (Λ) is a measure of the rate by which the system returns to the equilibrium following a small disturbance (Pimm 1991a; Tilman & Downing 1994; Ives 1995; Mittelbach *et al.* 1995; Neubert & Caswell 1997). The speed of recovery differs between systems and is obtained as the absolute value of the greatest real part of the eigenvalues. This means that the resilience of a community is governed by the species with the greatest λ , i.e. the slowest rate of recovery. Return time (T_R) is the inverse of resilience ($T_R = 1/\Lambda = -1/\max(\text{Re}(\lambda_i))$) and measures the time taken until $1/e$ (~37%) of a temporary disturbance is cancelled out.

Critique of the local stability criterion

Generally speaking, criticism of the local stability criterion stems from beliefs that coexistence of species may prevail without the system residing at a specific equilibrium point. For example, species may coexist on cyclic or chaotic orbits inside the phase space (Huisman & Weissing 1999). The permanence criterion is an approach, which adopts the idea of a system where asymptotic stability is not a necessary component (Hofbauer & Sigmund 1988; Anderson *et al.* 1992). Instead of dynamics governed by attractors, the dynamics of a permanent system are guided by repellors. That is, the trajectories of all populations, which start with non-zero positive population densities greater than a certain extinction threshold, will be forced away from the extinction boundary and thus stay within the positive phase space for infinite time, unless subjected to intrinsic or extrinsic stochasticity. Just as the local stability criterion has been criticized for not being able to define the size of a small perturbation, the permanence criterion fails to delimit the size of the extinction threshold. That is, in some permanent systems some species may reach extremely small population sizes.

Stability and extinctions

Species are going extinct at an unprecedented rate. From a theoretical point of view species extinctions are a result of a system being either unstable and/or affected by perturbations that may be intentional or stochastic. In general, stochasticity (see below) is mostly considered to increase the risk of extinction of species, but see Chesson and Huntly (1997), who proposed that stochasticity might facilitate species coexistence, e.g. by preventing a dominating species from outcompeting a subordinate species (Huston 1979). Species are continuously going extinct due to natural causes in communities constantly disturbed by small or large perturbations. In *Paper I-III* locally stable systems of species were subjected to various types of uncorrelated continuous perturbations in order to “provoke” populations to decline to abundance levels where they were classified as endangered (*Paper I*) or labeled as extinct (*Paper II* and *III*). In nature extinction is an absolute measure indicating zero abundance of a species. In dynamic models, however, zero abundance may constitute a problematic threshold since the abundance may reach a fraction of one individual for a considerable length of time. Thus, other extinction thresholds indicating the imminent risk of extinction might be more appropriate. At what level the threshold of imminent extinction risk rests is up for discussion, and depends most likely on type of organism among others (although a general guideline for conservation based on genetics has been proposed, see Franklin 1980). In *Paper I* we used a criterion (developed by the IUCN) to define species endangered by extinctions based on a sudden shift downwards in population abundance relative to their equilibrium abundance. We found that the abundance of producer species most frequently dropped to endangered population levels first among the species types in our food webs. In both *Paper II* and *III* the extinction threshold was set to 5% of the equilibrium abundance of a species (the equilibrium abundance being the abundance at the start of the simulations). Applying various types of stochasticity extinctions of producer species were more frequent in *Paper II*, whereas consumer species almost exclusively went extinct in *Paper III*, indicating that the category of species most vulnerable to extinction depends on the type of environmental variability the system is exposed to.

In order to describe community stability under circumstances when communities are disturbed by a single large perturbation, Pimm (1979) introduced the concept species deletion stability. Species deletion stability deals with species loss (which is a major perturbation) and measures the resistance of a community to further (secondary) extinctions subsequent to the initial species loss. Species deletion stability allows us to view communities as variable entities, which enable studies of: (i) what types of communities are more resistant, (ii) the identity of species initiating or undergoing secondary extinctions, (iii) time to secondary extinctions, and (iv) if the sequence of species extinctions are random or ordered. Borrvall et al. (2000a) showed that resistance of a system to secondary extinctions increases with number of species per functional group in model webs. Also, the quasi-collapse risk (defined as the probability that the number of species in a community falls below some defined value

within a fixed period of time following the loss of a species) decreased with increasing biodiversity (measured as species richness within a trophic level) (Ebenman *et al.* 2004). In *Paper IV* we studied the effects on two measures of local stability from sequential non-random species deletion in natural food webs. Generally the deletion of one species of the most functionally similar pair of species resulted in greater changes in stability metrics later in the aggregation process. There was also a clear trend in reduced similarity between the most functionally similar species as biodiversity in the food webs decreased. These results indicate a prevalence of “functional redundancy” in more species-rich food webs, which may insure a system from sudden stability shifts when a few species associated with a functional group (or guild) have gone extinct. Loss of resource species and autotrophs has been shown to trigger more secondary extinctions than the loss of consumers and top predators (Paine 1966; Estes & Palmisiano 1974; Crooks & Soule 1999; Borrvall *et al.* 2000a; Christianou & Ebenman 2005; and Ebenman & Jonsson 2005 for a review). Furthermore, there is less time to secondary extinctions following the initial extinction of top predators compared to initial extinctions of species from other trophic levels (Borrvall & Ebenman 2006). In the preliminary results of *Paper IV* there were no signs that the extinction of a particular category of species (e.g. basal, intermediate or top species) would initiate a greater shift in local stability metrics. Instead larger shifts seemed to be determined solely by the level of functional similarity between the most functionally similar species in a food web. The order of species extinctions are not likely to be random, but appear in sequence of vulnerability to disturbances (Vitousek *et al.* 1997). It has been shown that the species identity of the first extinction is likely to affect which species go extinct next (Christianou & Ebenman 2005). Thus, extinctions seem to occur in a non-random manner in theoretical models. Ives and Cardinale (2004) showed that when species less resistant to a stress went extinct first, the remaining system maintained its resistance to the stress by retaining the compensatory potential (i.e. the capacity of some species to increase when their competitors and/or predators decrease in density due to the stress). By contrast, the compensatory potential decreased subsequent to random extinctions. In *Paper IV* we used an algorithm by which one species of the most functionally similar pair of species was deleted at each stage of the extinction process in a food web. Thus, the sequence of species deletions was non-random, and arranged in order of redundancy (i.e. the more redundant species being deleted earlier). The order of species extinctions caused by humans today is non-random, but it is unlikely that we are making any considerations of the functional redundancy of the species we “remove”. On these grounds we might expect severe stability shifts earlier in the extinction sequence of an ecological community than reported here.

Stability as an application for conservation

If most perturbations in nature are temporary and of small size local stability may be an appropriate concept for analysis of communities under these circumstances. Species loss in a biological community, however, is a permanent disturbance of

greater size, with a potential of triggering a cascade of secondary extinctions (Pimm 1980; Solé & Montoya 2001; Dunne *et al.* 2002). Species deletion stability is an assessment of the resistance of a community to further losses of species following the extinction of a species (Pimm 1979). The degree of resistance to further extinctions in a community may depend on the characteristics of the species that was lost (empirical studies: Paine 1966; Terborgh *et al.* 2001; theoretical studies: Borrvall *et al.* 2000; Ebenman *et al.* 2004; Borrvall & Ebenman 2006), as well as on the species of the remaining community (Ebenman *et al.* 2004; Borrvall & Ebenman 2006) and the community structure (Pimm 1979, 1980). For conservation biologists it is important to be able to identify characteristics of species and communities that make them more or less prone to secondary extinctions. Ultimately it is in their interest to recognize whether a community that lost a species is resistant to restoration measures (or natural re-invasions), that is if reintroduction of the extinct species is possible. Models by Lundberg *et al.* (2000a-b) showed that reintroduction of all native species often is impossible subsequent to a species removal and succeeding cascading extinctions. The reason is that lost species does not simply leave an empty space to be refilled, but that the remaining community in the meantime has changed its structure, which makes the adaptation of potential re-invaders to the new conditions more difficult.

Before extinction occurs, on the level of an individual species, sensitivity analysis and its close relative, elasticity analysis, are two methods that have proven their value as tools for the management of endangered populations. Both methods make use of matrix model calculations and eigenvalues (λ) of the projection matrix ($\mathbf{A}(t)$) of a biological single-species system. The population of a particular endangered species is divided into specific subpopulations (N_i), where each subpopulation commonly corresponds to a specific age class or life stage in the life cycle of the species. From one time step to another, an individual may, with some probability (a), 'travel' from one life stage (j) to another stage (i), or stay within the same life stage (arrows in Fig. 5a). The probabilities of transfer (a_{ij}) from life stage j to i are represented by a transition matrix ($\mathbf{A}(t)$) (Caswell 1989a, 1989b) (Fig. 5b). The usefulness of the methods for conservation biologists primarily relies in the precision in accurate predictions of future changes in population growth rate under various management practices (i.e. by targeting which of the elements in the transition matrix (a_{ij}) that would lead to the largest relative positive change in λ after a small perturbation/management action). Elasticity analysis has entered the mainstream of conservation biology, but should be interpreted with some caution, partially because they only provide a snapshot of a population (Mills *et al.* 1999; Ehrlén *et al.* 2001; Mills *et al.* 2001). For example, the qualitative ranking of the elasticity values calculated from a transition matrix that may guide towards multiple management measures, may not be valid as soon as one of the management actions have been implemented.

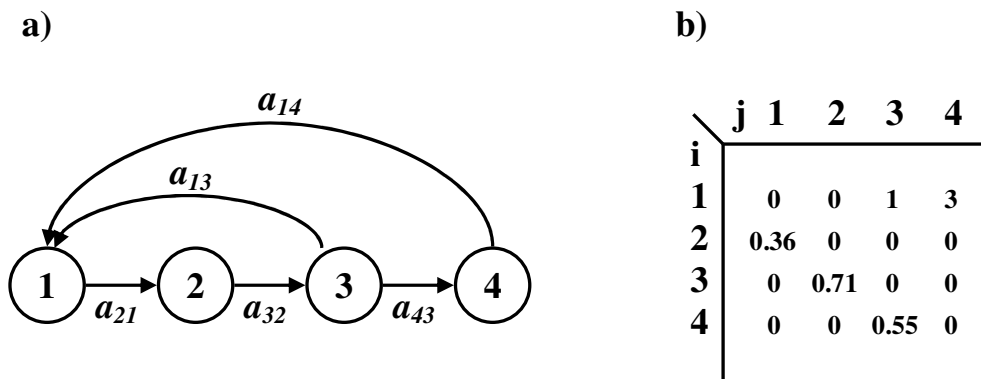


Figure 5. a) Schematic life cycle of a species with four life stages. The transition of an individual from one life stage to another (arrows) is illustrated by survival probabilities from life stage i to j (e.g. a_{21} , a_{32} and a_{43}), or fecundity probabilities from life stage j to i (e.g. a_{13} and a_{14}). b) Transition matrix. Actual transition values typically arranged such that the survival probabilities are located on the subdiagonal, and the fecundity probabilities are located on the top row.

Stochasticity

Stochasticity as a vital component of population dynamics

Deterministic food web models treat the vital rates of species (reproductive and mortality rates) and the interactions between species as constants. But are these parameters invariable entities? The answer is ‘no’. In nature, environmental and demographic conditions fluctuate in a random fashion causing temporal variation in vital rates (May 1973b) and in interaction strengths (Post *et al.* 1999a). Nonetheless, a proponent of deterministic models may state that use of average vital rates and average interaction strengths are appropriate estimations even for an entire life cycle of a species in a stochastic environment. May (1973b) asserted that the persistence of species in deterministic models are only adequately approximated as long as the stabilizing force of deterministic dynamics is greater than the variance of stochastic fluctuations. In other words, random fluctuations can cause extinctions even though average growth rate of a species is positive (Wissel & Stöcker 1991). Therefore, knowledge of the characteristics of random fluctuations in nature is essential for building the correct models, since leaving out stochasticity from a model could potentially seriously conceal important aspects of population dynamics. Stochasticity affecting population dynamics is usually divided into three components: demographic, genetic and environmental stochasticity. Demographic stochasticity is concerned with probabilities of births and deaths of individuals in a population in any given year, which for example may result in a skewed sex ratio. Genetic stochasticity is usually used to account for the impacts of founder effect, genetic drift, or inbreeding. Characteristically, the impact of demographic and genetic stochasticity is significant in small populations only. In contrast, environmental stochasticity involves the more-or-less unpredictable interactions with the abiotic and biotic surroundings, and may have great influence on larger populations as well. In this thesis, *Papers I-III* deal with environmental stochasticity only. In *Paper II* one purpose of studying the

spectral colour of species' time series was to establish whether the dynamics of population exposed to environmental stochasticity were affected by the trophic position of species and the food web structure. The choice to apply white noise (i.e. uncorrelated environmental stochasticity) was that it would provide a convenient null-model since it would not "add any colour" to the time series, thus enabling comparisons of spectral colour between species at various trophic positions or in various food webs. The application of a suggestively more natural red-shifted noise would have hampered such analyses. White noise was used in *Papers I and III* for similar reasons. The main objectives were to study any effects of food web structure on the risk of species becoming endangered/going extinct. Vital rates of species at various trophic levels differ, and certain vital rates in combination with a red-shifted environmental noise may enhance the risk of species becoming endangered/going extinct. Therefore, the choice of applying white environmental noise would not bias the risk of endangerment extinction of species, and thus not confound any analysis of effects of food web structure.

Spectral analysis and modeling stochasticity

Stochasticity and noise are two concepts that sometimes are used interchangeably. Here, I use noise in two ways: (i) to signify a certain type of perturbation signal that is applied on the deterministic dynamics of a model population (i.e. the in-signal), or (ii) to describe the type of response signal that results from spectral analysis of a population's dynamics (i.e. the out-signal). Stochasticity, on the other hand, is used in a more general way to indicate a component of randomness in a model.

Spectral analysis is a mathematical method whereby a time series can be decomposed into its frequency components (Cohen 1995; Lundberg *et al.* 2000b). Graphically the result is often presented with frequency (f) along the x-axis and the relative contribution (or power) of different frequencies along the y-axis. In the resulting power spectral density graph the regression coefficient can be calculated. The slope of the regression coefficient has traditionally been categorized by analogy with the frequencies of the visible light spectrum. Consequently, oscillations dominated by long wavelengths (low frequency fluctuations) that result in a negative slope of the regression coefficient are labeled as red noise, reddened variability or red-shifted population dynamics. This is to a large extent the same as saying that successive population sizes are more similar than expected by chance (i.e. positive autocorrelation). Conversely, a positive regression coefficient signifies blue variability (i.e. negative autocorrelation), whereas a regression coefficient of zero is typical of white variability (i.e. zero autocorrelation) (Lawton 1988; Cohen 1995). Bluntly, white variability may be characterized as noise without a memory (Jonsson 2000), but in essence, white noise, like white light, consists of an even mixture of all frequencies (Halley 1996; Lundberg *et al.* 2000b).

Basically, two different types of stochasticity models have been applied to incorporate noise into ecological models – autoregressive (AR) or $1/f^\gamma$ noise. Both methods may generate a wide spectrum of noise colours, from blue-shifted via white to red-shifted dynamics. Then how is noise modeled?

First order autoregressive noise (of any colour) of a time series (ϕ) can be generated by the following formula (Petchey *et al.* 1997):

$$\phi_{t+1} = \alpha\phi_t + \beta\varepsilon_{t+1} \quad (\text{eq. 2})$$

where the parameter α determines the degree of autocorrelation ($-1 < \alpha < 0$ leads to blue noise, $\alpha=0$ to white noise and $0 < \alpha < 1$ to red noise). The parameter ε_t is a random variable drawn from a specified distribution, which is in effect the same as white noise, whereas, β governs the magnitude of fluctuations.

$1/f^\gamma$ noise is often referred to as a ‘family’ of noises of different colours, distinguished by the size of the spectral exponent (γ). Spectral density (or power of different frequencies) is proportional to $1/f^\gamma$, with the exponent (γ) being zero in white noise, $\gamma = 2$ in brown noise and, in between, $\gamma = 1$ in pink noise (Halley 1996; Halley & Kunin 1999). Speaking in terms of only blue, white and red noise (i.e. no colour shades like pink or brown), red noise would be equivalent to $\gamma > 0$, $\gamma = 0$ would signify white noise and $\gamma < 0$ blue noise. White noise is simplest to simulate. It can be generated by drawing random variables from a specified distribution, which produces a flat power spectral graph (indicating that no frequency is dominating and the autocorrelation is zero). Brown noise has borrowed its name from the Brownian motion of particles in physics, which can be considered as an extreme red noise. The noise process can be described as adding a random variable (with zero mean) to the previous value from one time step ago. You may illustrate the dynamics as a random walk, where new values may wander up or down with respect to the latest footprint. Thus, in contrast to a white noise process, which has no memory, brown dynamics are intimately linked to prior time steps. This connection to recent history enables low/high values in succession (positive autocorrelation), as well as the emergence of extremely high values.

Regardless of subjected to an autoregressive or an $1/f^\gamma$ model of noise, time series expressing white dynamics are always stationary, meaning that variability around a mean value is constant over time. One significant difference between the autoregressive and the $1/f^\gamma$ noise models rests within the properties of variability in the red region of the spectrum. Initially, autoregressive reddening produces a similar pattern as a red-shifted $1/f^\gamma$ noise model, i.e. variance increases with length of time series (Fig. 6). However, while variance of red-shifted $1/f^\gamma$ noise models will increase indefinitely (non-stationarity), the variance of an autoregressive process with red noise will eventually come to a halt (stationarity) (Halley & Kunin 1999).

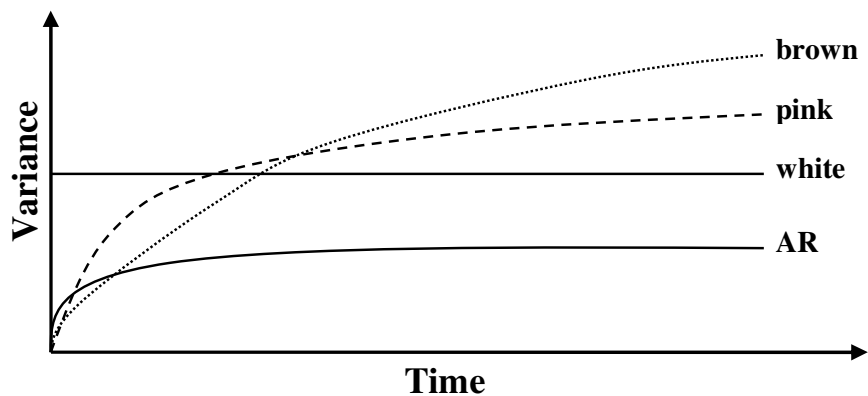


Figure 6. Schematic representation of stationary/non-stationary noise models. White noise and autoregressive red noise (AR) are stationary, meaning that variance of population fluctuations is constant with time (white noise) or become constant with time (AR). Red-shifted $1/f^\gamma$ noise models (e.g. pink or brown noise) are non-stationary, which means that variance of population fluctuations grows indefinitely with time.

Natural population time series have been shown to often exhibit red-shifted power spectra (Steele 1985; Pimm & Redfearn 1988a; Ariño & Pimm 1995a; Sugihara 1995a; Halley 1996), and in some cases white power spectra (Pimm 1991a; Sugihara 1995a; Halley 1996). Are these patterns congruent with power spectral density graphs of modeled time series? A comparison was performed by Cohen (1995), who concluded that eight deterministic, non-linear population models displaying chaotic dynamics had blue-shifted power spectra. Although the chaotic behavior of population fluctuations in the deterministic models was generated by internal dynamics (rather than by extrinsic factors) and even though later modifications of the parameters used by Cohen changed the power spectra towards more red dynamics (Blarer & Doebeli 1996; White *et al.* 1996), significant points were made – to what extent is variability of population dynamics internally or externally generated, what generates the red-shifted variability observed in natural time-series, and how do we model stochasticity best? A noise signal that propagates through an ecological community will be filtered by the population dynamics of the species. Thus, the spectral colour of a population's time series is likely to be affected not only by the internal dynamics of the species but also by how species are interlinked in the community (i.e. the community structure) (Ripa *et al.* 1998; Xu & Li 2002). This issue is dealt with in *Paper II* and we conclude that various food web metrics and the strength of trophic interactions influence the colour of population dynamics. Most commonly the autoregressive model has been used to generate external reddened noise (Foley 1994; Caswell & Cohen 1995; Ripa & Lundberg 1996; Petchey *et al.* 1997). Studies of natural ecological time series, however, suggest that dynamics are non-stationary (Steele 1985; Pimm & Redfearn 1988a). Therefore, using autoregressive models of noise may only be suitable for short-term simulations. On longer time-scales, such as in most viability projections of endangered species, non-stationary models of noise (i.e. $1/f^\gamma$ noise models) may be called for (Halley & Kunin 1999). More recently, several authors have reported

natural time series with a variability that tends to decelerate (Murdoch 1994; Ariño & Pimm 1995a; Cyr 1997; Inchausti & Halley 2002), which may draw attention to the $1/f^\alpha$ model of pink noise advocated by Halley (1996).

Stochasticity and extinctions

Random demographic and environmental variability is mostly regarded as harmful to population persistence (May 1973b; Chesson & Huntly 1997) and community resilience (Ives 1995), although stochasticity may impede competitive exclusion of a subdominant species (Huston 1979) and counteract species extinction in a metapopulation setting (with each subpopulation under influence of uncorrelated stochasticity) (Levin 1974; Morrison & Barbosa 1987). What's more, the nature of environmental stochasticity may have an impact on extinction risk (Halley 1996). Intuitively, a population should experience a greater extinction risk the more red-shifted an environment gets due to an increased probability of a succession of 'bad years' (Mode & Jacobson 1987; Lawton 1988). This general applicability of such an assertion may be questioned though, since populations under influence of reddened dynamics may also go through successive 'good years', hence wander toward relatively invulnerable population sizes (Halley & Kunin 1999). In *Paper II* we show that the spectral colour of producer species' time series is significantly correlated to their extinction risk, and that the spectral colour and extinction risk are related to the position and direction of the strong interaction in a food web. Recent studies have also revealed that an array of features, such as intraspecific competition (Petchey *et al.* 1997), spatial structure of populations (Allen *et al.* 1993) and the environment (Johst & Wissel 1997), metapopulation dynamics (Engen *et al.* 2002), size of vital rates (Luckinbill & Fenton 1978; Ripa & Lundberg 2000) may interact with environmental variability to generate a context-specific extinction risk.

Future Directions

Is interaction strength linear and body size constant?

A significant shortcoming of food web models today is that species are treated as static taxonomic entities. During a life time individuals experience different phases which involve changes in body size relative to other species and conspecifics at other stages of development (Woodward & Hildrew 2002; Scheffer & Carpenter 2003; Woodward *et al.* 2005). Alterations in body size ratio may change the fundament of feeding and competitive relations between individuals, and thus, interaction strengths. For example, during a life span an individual may make stopovers at detritivorous, herbivorous, predacious and cannibalistic stages, which not only changes strengths and presence of interactions with other species or the same species, but ultimately alters its position in the food web. New molecular ecology techniques, using for example stable isotopes and DNA markers, may assist in the often laborious effort to unravel the trophic relationships between species. A second limitation of food web models represented by coupled difference or differential equations is the use of linear interactions. True interaction strength values most probably vary in a non-linear

manner over space and time due to, for example, predator interference, prey refuge, prey switching and environmental conditions (Menge 1994; Spiller & Schoener 1994; Menge *et al.* 1997; Sanford 1999; Navarrete & Castilla 2003). The exact non-linear relationship is difficult to obtain empirically though, which results in use of linear estimations instead. An argument in favour of using linear interactions in differential equations is the mathematical tractability, as they can provide analytical solutions when executing, for example, local stability or sensitivity/elasticity analyses. Since these methods are analyzing the dynamics in the close vicinity of an equilibrium point, the use of linear interactions may hold as approximations within a narrow interval of the true (non-linear) relationships. However, for analyses further away from the equilibrium point (e.g. subsequent to one major catastrophe or recurring minor perturbations with limited relaxation periods), the assumption of linear interaction strengths may be inappropriate. To incorporate stage-determined characteristics and non-linear interaction strengths into multi-species communities represent a major challenge to ecological modelling (Jonsson *et al.* 2005).

Sensitivity/elasticity analysis of ecosystems

Sensitivity/elasticity analysis has found wide application in conservation biology in a setting of a single threatened population. As yet, no one has used sensitivity/elasticity analysis in a multi-species setting, although the analogy with the single-species model is rather straightforward. Instead of transition from one life stage to another in the single-species case, the elements of the transition matrix (a_{ij}) then would denote the intra- and interspecific interactions between species in a food web. Furthermore, a sensitivity/elasticity analysis of a single species will recognize the effect on the overall rate of increase (λ) of that particular species during a change of one of the matrix elements (a_{ij}). In a single-species setting, rate of increase is usually translated into change in number of individuals/females, the quantity of interest to most conservation biologists. In a multi-species setting, however, population growth rate would not be an applicable property of rate of change due to body size-related differences between species (e.g. generation time, reproductive rate). A more relevant alternative would instead be a measurement on the level of a biological community, for example sensitivity of community resilience to small changes in interaction strengths (a_{ij}) or growth/mortality rates (b_i) (Christianou & Ebenman 2006, submitted). Research in community ecology has extended our knowledge of ecosystem functioning, by comparing species-rich communities with species-poor (Naeem *et al.* 1994; Tilman *et al.* 1996), or by studying the role of functional diversity (Tilman & Knops 1997) or functional composition (i.e. the identity of functional groups) (Hooper & Vitousek 1997) in mainly terrestrial plant communities. Sensitivity/elasticity analysis of multi-species systems may contribute to our understanding of ecosystem functioning from a standpoint of a smaller, non-permanent perturbation (e.g. harvest) of a particular species within the community.

Extended network analysis

At an outset, when a new scientific field surfaces, simplifications are needed in order to make out the most basic elements of a more complex setting. Theoretical studies of ecological communities, for example, started out with simple few-species models. Network analysis is no exception; some complicating factors are ignored while others are high-lighted. Strogatz (2001) mentioned six complicating factors that make networks difficult to understand:

- i)* Structural complexity: The tangle of links between species (nodes).
- ii)* Network evolution: Networks change with time. Species and links evolve and go extinct continuously.
- iii)* Connection diversity: Links/interactions between species may have different strengths, directions and signs.
- iv)* Dynamical complexity: Species can be non-linear dynamical systems.
- v)* Node diversity: There are different types of species (e.g. predators, detritivores) and similar species are sometimes lumped together into functional groups.
- vi)* Meta-complication: Various complicating factors (see *i-v*, above) can influence each other.

To model one of factors *i-v* is an intricate task, nevertheless, for a deeper understanding, more realistic and elaborate networks may need to be studied.

Networks are all around us and come in many forms. Recently, structure and function of complex networks have attracted attention from a wide range of fields, e.g. community ecology, molecular biology, sociology and physics (Strogatz 2001). With so many disciplines involved the risk of translation errors prevail. Will scientists of different backgrounds speak the same language? For example, will a stable network mean the same to a theoretical ecologist as to an analyst of telecommunication sensitivity? Clearly there is a need of a concordance around issues as how to measure network structure and network (mal-)functioning.

Conclusions

Species extinction is a natural process and 99% of the species have disappeared during the history of the Earth. This means that the large majority of species today probably will become extinct in the future. From fossil data we have estimates of the rate of natural extinctions (or 'background extinction'). However, lately, the rate of extinctions has accelerated markedly relative to the background extinctions. It is believed that this process is induced by man through climate change, habitat modifications and destruction, increased rates of deliberate or accidental introduction of non-native species or over-harvesting.

The extinction of a species is not an isolated incident, secluded from the rest of the ecosystem. A singular species loss may set in motion undesirable dynamics that we are not able to anticipate. The consequences can be unwanted changes of ecosystem services (e.g. erosion control, greenhouse gas regulation, plant growth), reduced reliability in production of ecosystem goods that we depend upon (e.g. food, medicine, industrial products, genetic resources), or the initiation of additional species loss, including ourselves (*Homo sapiens*). The seriousness of these and related issues were manifested by the emergence of a new scientific field – conservation biology. Since the dawn of this 'crisis science', during the early 80's, significant leaps forward in understanding the mechanisms of extinction has been made through empirical studies and theoretical research.

To find out which species are at imminent risk of extinction we need to know which species are more prone to extinction due to intrinsic factors (e.g. vital rates), the community structure and the presence and strength of interactions with other species in a stochastic environment. This topic is dealt with in *Papers I-III*, and in *Paper III* we show that consumer species go extinct more frequently than producer species, whereas producer species are more prone to reach endangered levels (*Paper I*). We also show that food web structures and involvement in a strong interaction make species more vulnerable to extinctions (*Papers I and III*). More specifically, the exact position and direction of strong interactions affect the vulnerability to extinction. Knowledge of these matters may give significant aid in directing management actions towards where they may serve best. However, for guidelines to be of any use correct and detailed descriptions of food webs are imperative, which probably requires extensive empirical monitoring.

Species loss is an irreversible event that we can not undo (yet). Thus, to discover a species at risk of extinction well ahead of severe loss of abundance and, preferably, prior to embarkation on the treacherous path known as the 'extinction vortex', we need to develop warning systems. In *Paper II* we present that spectral analysis of a species' time series, generated in an ecosystem setting under the influence of uncorrelated environmental stochasticity, may give guidance as to which species will reach critically low abundances, and so, be at risk of extinction.

A model is a simplification of a more elaborate reality that hopefully manages to capture the true features of the trait under study. As to what extent food web models with few species accomplish this task has rarely been studied due to lack of descriptions of large well-resolved natural food webs. In *Paper IV* we found that measures of local dynamics differed significantly between well-resolved and condensed versions of the same natural food webs. This implies that conclusions drawn from smaller food web models with species representing aggregations of species (i.e. trophospecies) may hold limited applicability. Instead the results may be representative of only a smaller and secluded fraction of the entire food web.

It is of great importance to reveal the nature of change of ecosystem function when biodiversity decreases. Does the function change little with each species extinction, or are there biodiversity thresholds beneath additional extinctions may cause extensive shifts in ecosystem function? Using non-random species deletions in natural food webs we found that initial extinctions generally caused little or no changes in ecosystem function (measured by two metrics of local dynamics), but as deletions continued the likelihood of larger shifts increased. Since only the most functionally similar species was deleted at each stage of the extinction process, it raises questions whether greater biodiversity may “insure” an ecosystem from large changes in ecosystem function. However, species that go extinct as a result of human activities are likely to do so irrespective of functional similarity, which suggests that severe shifts in ecosystem function of a food web may enter earlier in a sequence of extinctions than presented in *Paper IV*.

The use of detailed descriptions of well-resolved natural communities to model food webs (such as in *Paper IV*) have been shown to enhance the likelihood that they are feasible and locally stable. The insight that feasible model systems simply *not* are a haphazard network of randomly assembled populations (obtained from an arbitrary ‘species pool’), which interact in an unsystematic manner, is encouraging and has improved our comprehension about the changes experienced by natural ecosystems today. Ecosystems are constantly being stressed by perturbations imposed by man and the environment, and knowledge of the exact nature of the structure and dynamics of stable vs. unfeasible large, complex networks may give valuable clues to conservation actions. With increasing computational power the prospect of studying increasingly realistic communities now seem to be within our grasp through incorporation of non-linear intra- and interspecific interactions, spatial components (e.g. migration and scale), together with elements of stochasticity into ecosystem models.

*As far as the laws of mathematics refer to reality, they are not certain;
and as far as they are certain, they do not refer to reality.*

Albert Einstein (1879-1955)

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*Whenever you are asked if you can do a job, tell 'em, 'Certainly I can!'.
Then get busy and find out how to do it.*

Theodore Roosevelt (1858-1919)

