

SEARCHING FOR BALANCE

Stability and equilibria of food webs

Cassandra van Altena

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Thesis

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Chapter 1

Searching for balance

General introduction

1.1 A world of wonders

“We live in a world of wonders”. This is how Brian Cox, professor in physics and TV celebrity, starts each episode of one of my favourite TV series, *Wonders of the Universe*. I always had to think about this line while writing the introductions of the chapters in this thesis. And I had to think about it again when I started to write this general introduction.

Why does this line keep popping up in my head when I write about my research? Because when I start to think about species communities and why we are interested in their stability, I have to think about the immense biodiversity that exists on our planet. We indeed live in a world of wonders when it comes to species diversity: think about what is living in the oceans, in the rain forests, on remote islands. Or even in the soil in our back garden. All the species in these ecosystems are living together, connected by a complex web of interactions that can hardly be comprehended.

1.2 Stability of species communities

Despite this complex entanglement of interactions, there seems to be a sort of balance in these communities: even when disturbances occur, such as heavy rain falls, fires, or temperature differences, most of the time the community does not break down. For example, ecosystems in the temperate region undergo quite large differences in temperature and rainfall during the seasonal cycle, yet the species community remains relatively constant (e.g. Gaedke et al. 2002). This is our intuitive feeling for a stable species community: it is in balance and resilient to disturbances.

On the other hand, the same disturbances can lead to severe fluctuations in species dynamics or even to species extinctions. In extreme cases, the total appearance of an ecosystem can change. For example, shallow lakes can turn quite suddenly from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state when there has only been a minor change in environmental conditions (Scheffer et al. 1993). In these cases, the communities are not resilient enough to cope with the disturbance, the stability of the previous state is lost and the system finds a new equilibrium.

In light of climate change, biodiversity crises, pollutions or other human interferences in ecosystems, we are much interested in what causes some communities to be resilient to perturbations, and what causes some communities to shift to a new equilibrium. That is: what makes species communities stable? This question can be approached via several ways. Long term monitoring studies can reveal how species communities change over time in the long run, while at the same time showing either a balance or unbalance in the short run (e.g. Bäuerle and Gaedke 1998, de Vries et al. 2003). Experiments in either the field or the lab can reveal what kind of disturbance the ‘mini-ecosystem’ under investigation can still endure, or what disturbance causes the system to change in whatever way (e.g. Urabe et al.

1997, McCauley et al. 1999, Aerts et al. 2004). And finally, models can be used to describe communities and their interactions so that their stability can be investigated mathematically (e.g. Hunt et al. 1987, Gaedke et al. 2002, Williams et al. 2007). In this thesis, I use mathematical models to explore stability of species communities.

1.2 Modelling species communities

How do we as ecologists put ‘the wonders of the world’ into mathematical models? Are species communities not far too diverse and far too complex to be captured in a model? Of course they are. However the aim of ecological modelling is not to make a full copy of the real world. Instead, modelling is like painting: those properties that represent the essence of the real world are captured in a model (Figure 1.1). What exactly this essence is depends on the aim of the modeller, and as a result some models are more abstract than others.

Modelling species communities allows us to understand which species, which interactions, and which functions are important for ecosystem stability. In food web ecology, the dominant view is that the essence of biological communities is captured by a network of species that are connected through their feeding interactions. Often, the nodes in the network (i.e. the food web) do not actually represent taxonomic species, but groups of species that feed on the same resources, and that are consumed by the same consumers. I refer here to such trophic species (or functional groups) as ‘the species’, ‘the consumer’, or ‘the resource’. The connections between the nodes represent the feeding relations between the species, referred to as trophic interactions.

The trophic interaction between a consumer and its resource lies at the basis of many biological studies at different levels of organization. At the individual level, food is needed for survival and metabolism. If food conditions are favourable, the organism can invest in growth and eventually reproduction, leading to increases in population abundances; we



Figure 1.1 Paintings by Piet Mondriaan. During his life, Mondriaan was searching for the essence of reality, which can be seen in this series of trees. The left panel shows a tree that can instantly be recognized as a tree. This holds for the middle panel as well, although it is much more abstract. In the right panel, Mondriaan has gone a step further in the level of abstraction: only hints of the trunk, branches and leafs can be seen. Left: *Avond; De rode boom* (1908-1910). Middle: *De grijze boom* (1911). Right: *Bloeierende appelboom* (1912).

enter the field of population dynamics. Furthermore, consumer-resource interactions, as well as the related interspecific interactions of competition and mutualism, shape ecological communities (Morin 1999). Finally, processing food leads to release of nutrients in the environment, so that trophic interactions are essential to understand nutrient cycling at the ecosystem level (Gaedke et al. 2002). In this thesis, I focus on food webs within a community and ecosystem context.

A food web is a conceptual model of the structure of a species community. It can be used to answer questions such as: why are some species (i.e. trophic groups) present or absent, are there general patterns in the number of links a single species can have, or in the ratio of the number of links and species in food webs (Martinez 1992, Dunne et al. 2002)? To answer questions on the response of a community to disturbances, or the stability of the community, we need to focus on the dynamics of the species community, or the food web.

In this thesis, the essence of the dynamics within a food web is captured by differential equations. These equations describe the change in a variable of interest over time. Hereafter, I refer to these variables as states. Often, it is easier to set up equations that describe how a state changes over time and derive from that the exact values of the state at certain times, than directly formulate a function that describes how a state depends on other states in the system. Thus, when the state represents a species, as is the case for food webs, its differential equation describes how biomass or numbers of individuals change over time. These changes are caused by growth through feeding and reproduction, and decline through predation and other causes of mortality. The dynamics of one species are influenced by other species: the more there is from resource A, the more food there is for consumer B and the more consumer B can grow. In turn, the growth in consumer B causes an increased consumption of resource A, thus decreasing resource A further. This example immediately raises the question: can resource A and consumer B coexist?

In this example with two interacting species, we have a good understanding of the patterns that arise from these dynamics (Lotka 1925, Volterra 1931, Rosenzweig 1971). For three species, however, it can already become quite complicated to follow the dynamics. Indeed, in some cases it can even become impossible to predict what will happen in a three species system, because the system dynamics become (mathematically) chaotic (Hastings and Powell 1991). The dynamics of food web models with more than three species become practically intractable. Therefore, I aim for finding general patterns that arise from food web structures and their dynamics that are related to food web stability, without going into the full details of the dynamics. For that, I use some well-known mathematical tools.

We have now specified our initial problem of how to investigate community stability into this: community stability is equivalent to food web stability, which is equivalent to stability of the dynamic model. The next step is to define stability of the model. The crucial question for community stability is: what happens to the community when it is disturbed?

Thus, the stability definition should encompass these disturbances or perturbations to the food web. In this thesis, I use two types of stability analyses that each use a different type of perturbation. First, I use the local stability approach to see how small perturbations affect the stability of the system. Second, I perform a bifurcation analysis with an external factor of the system (here, nutrient loading) as the bifurcation parameter to see how this changes the community in itself (i.e. the species abundances) and how that in turn affects stability. These two types of analyses and how they have been applied to explore food web stability are described below.

1.3 Local stability analysis

In local stability analysis, we first need to determine the equilibrium point(s) of the system. The mathematical model that we use to this end is the set of differential equations that describe the species dynamics. What does it mean to be in equilibrium? It means that there is no change, that the system is in balance. For example, reproduction causes an increase in the number of individuals, and mortality a decrease. If reproduction and mortality are equal, then there is no growth and no loss in the population: the population is in balance, in equilibrium. If the system is in equilibrium, then all species populations in the system are in this sort of equilibrium. The equilibrium point(s) are found by setting the differential equations equal to zero. The stability of an equilibrium is evaluated by moving the system a small distance away from the equilibrium, and then check whether it can return to the equilibrium point or whether it moves away from it. If this small perturbation makes the system move away from the equilibrium, it is unstable; if it returns back to the equilibrium, it is stable.

Whether the equilibrium is stable or not is determined via linearization of the system of differential equations. The interested reader can refer to mathematical textbooks on dynamics for the exact mathematics behind this process (e.g. Blanchard et al. 2002). It comes down to determining the eigenvalues of the Jacobian matrix, consisting of the partial derivatives of the dynamic system, evaluated at the equilibrium point. The maximum real part of all eigenvalues of this matrix determines the stability of the equilibrium: if this value is smaller than zero the equilibrium is stable, if it is bigger than zero the equilibrium is unstable. As is true for many cases in mathematics, if it is equal to zero, more investigation is needed.

In food web ecology, the Jacobian matrix plays a central role. Not only because the stability of the food web can be determined from it, but also because the elements of the matrix, the partial derivatives evaluated in equilibrium, are interesting in itself. These elements represent the per capita effects of one species on another species. Therefore, they are referred to as interaction strengths (Laska and Wootton 1998, Berlow et al. 2004,

McCann 2012), and I refer to the Jacobian matrix as the interaction strength matrix (Emmerson and Raffaelli 2004, McCann 2012) throughout this thesis.

Ever since May (1972) used interaction strengths and the interaction strength matrix to study food web stability, many studies in food web theory have focussed on this matrix and its elements (e.g. DeAngelis 1975, Yodzis 1981, de Ruiter et al. 1995, Berlow et al. 2004, Berg et al. 2011, Allesina and Tang 2012, Neutel and Thorne 2014, James et al. 2015). The results of the study of May (1972) were quite controversial. He defined a food web by constructing randomly assembled interaction strength matrices, inspired by the work of Gardner and Ashby (1970), and found that stability of the food web decreased when either number of species, level of connectance (the ratio of realized links to all possible links), or average interaction strength increased. These three food web properties express the ‘complexity’ of the food web. Complexity of food webs can be defined in different ways, but a food web can be considered to be complex when it has a large number of species, has many links, and when the species are interacting strongly. Thus, the result of May translates to: the more complex a food web, the less stable it is. However, because ‘we live in a world of wonders’ with all its complexity, one would expect that these complex food webs should be stable as well. This was also the consensus up till that time, formulated amongst others by MacArthur (1955).

Not only did May’s (1972) paper lead to the interesting complexity-stability debate that continued for decades (Pimm 1979, Chen and Cohen 2001, Neutel and Thorne 2014), it also inspired many ecologists to use the interaction strength matrix approach for numerous questions in food web ecology related to stability. For example, it has been used in studying the (de)stabilizing role of omnivory in food webs (Pimm and Lawton 1978, Gellner and McCann 2012), the maximum stable length of food chains (Pimm and Lawton 1977), the occurrence of loops of trophic interactions in webs (Neutel et al. 2002, Neutel et al. 2007), and the effects of press perturbations (Yodzis 1988, Montoya et al. 2009).

Over the years, the way interaction strength matrices were constructed became more realistic compared to how May (1972) constructed them. May assigned random numbers (both positive and negative values were possible for each element) to random matrix elements, not taking into account that predators generally negatively affect their resources, or interactions occur in complementary species pairs (e.g. resource i has a positive effect on consumer j , while consumer j has a negative effect on resource i). In further studies, interaction strengths were assigned in pairs, where effects of consumers were drawn from negative intervals and effects of resources from positive intervals, and these intervals were asymmetric so that the effect of consumers on resources was larger than the effect of resources on consumers (e.g. Pimm and Lawton 1977, Yodzis 1981, Allesina and Pascual 2008, James et al. 2015). Furthermore, food web topologies derived from real food webs were used to construct the interaction strength matrix (Yodzis 1980, Schmitz 1997).

May (1972) constructed the interaction strength matrix by directly assigning random values to the matrix elements. Because the interaction strength matrix is derived from a dynamical model, a logical step would be to first define the model equations and derive the matrix from this model. This has the advantage that the equilibrium at which the matrix is evaluated indeed exists and is feasible, that is, all species abundances are positive (Haydon 1994). More importantly, these differential equations can be parameterized using empirical data, increasing the level of realism of food web matrices (Yodzis 1981, de Ruiter et al. 1995, Schmitz 1997, Montoya et al. 2009, Neutel and Thorne 2014). Using ‘empirical matrices’, it was found that interaction strengths were distributed in the food web in non-random patterns. A common property in all these patterns was that the distribution of interaction strengths was skewed in the sense that there were many weak interactions and only a few strong ones (Emmerson and Yearsley 2004, James et al. 2015), a pattern that is related to food web stability (McCann et al. 1998, McCann 2012) and networks in general (Csermely 2006). Underlying causes for stabilizing interaction strength patterns have been proposed to be the pyramidal structure of biomasses in food webs (de Ruiter et al. 1995, Neutel et al. 2007) or predator-prey biomass ratios (Emmerson and Raffaelli 2004, Brose et al. 2006).

1.4 Bifurcation analysis

In local stability analysis, the stability of an equilibrium is examined through a small perturbation near the equilibrium. For this analysis to work, the perturbation should be extremely small. In bifurcation analysis, the system is also perturbed, but the perturbation that is used here is larger. We again start with a system of differential equations that describe the species dynamics of the food web. Such a dynamic system necessarily has several parameters that represent species specific parameters (e.g. growth rate, consumption efficiency) or environmental conditions. An interesting question to ask is: what happens to the food web’s equilibrium and its stability if we increase or decrease one of the parameters? Will the system gradually change when a parameter is changed, or will it suddenly shift to a completely different equilibrium? These are questions that can be answered by performing a bifurcation analysis, in which a parameter of interest (the bifurcation parameter) is varied and the equilibria and their stability are determined along the bifurcation axis. The term ‘bifurcation’ refers to a (sudden) change in stability.

I will illustrate the use of bifurcation analysis with two well-known examples. The first example is the so-called ‘paradox of enrichment’, introduced by Rosenzweig (Rosenzweig 1971) involving the Rosenzweig-MacArthur consumer-resource model (Rosenzweig and MacArthur 1963). The resource density in this model is bounded by a certain carrying capacity. If the carrying capacity is low, the consumer density is also low because there is only a small amount of food available. When the model is run for low

values of the carrying capacity, the consumer and resource coexist in stable equilibrium. When the resource's carrying capacity is increased, both consumer and resource density increase, but still they can coexist in a stable equilibrium. As the carrying capacity is increased further, at some point the consumer and resource densities will not move to a stable equilibrium, but start to oscillate: what once was a stable equilibrium, is now an unstable equilibrium around which the consumer and resource oscillate. This type of bifurcation, where oscillations arise, is called a Hopf bifurcation. The oscillations lead to an increased probability of extinction (of one) of the species. Thus, the paradox here is that while the availability of food increases, this is not beneficial for the species.

In the previous example, we saw that the resource and consumer densities gradually increase and then suddenly start oscillating. In this second example on shallow lakes, another sudden change occurs. Shallow lakes can be roughly categorized in two states: a clear macrophyte-dominated state and a turbid phytoplankton-dominated state. The transition of one state to the other can occur very rapidly (Scheffer et al. 1993). The transition can be facilitated by a change in a 'parameter', namely the nutrient load of the lake. When the lake is in the clear-water phase and the nutrient load increases, it can remain in the clear state due to the positive feedback mechanisms mainly caused by macrophytes (Carpenter and Lodge 1986). As the nutrient load increases further, at a certain nutrient load, referred to as the critical nutrient load, the clear-water state loses its stability and the lake becomes turbid rapidly. When the nutrient load is decreased again, the lake does not easily switch back to the clear-water state, not even at the critical nutrient load at which during eutrophication the lake switched from clear to turbid. The nutrient load has to be decreased well past this point, to a much lower critical nutrient load at which again there is a sudden 'jump' back to the clear-water state. This phenomenon, where the reverse shift is not easily attained when varying a parameter, is called hysteresis (and, to the interested reader, the bifurcation is called a subcritical pitchfork bifurcation). This type of bifurcation has been reported in several scientific fields, e.g. economics, physics, and social sciences (Scheffer 2009). In ecology, the theory behind regime shifts is referred to as alternative stable states theory (May 1977, Scheffer et al. 2001, Beisner et al. 2003), because two stable states can exist for a single parameter value due to positive feedback mechanisms. In the lake example, there is a range of nutrient loads at which both the clear-water and the turbid-water state can occur; which state the lake will be in for a certain nutrient load in that range depends on the lake's history (Jeppesen et al. 1990b).

In ecological models, alternative stable states and hysteresis events can be modelled by defining a dynamical system with two to three differential equations (e.g. May 1977, Scheffer 1990). An example of a more complex model is the ecosystem model PCLake (Janse 1997, 2005). This model includes not only species biomasses and trophic interactions between them, but also abiotic variables such as nutrient load, light attenuation,

turbidity, etc. This model is too complex to directly derive the equilibria and their stability, as was done in the local stability analysis described above. Therefore, stable equilibria are found by running the model for the time needed for the species densities to remain stable or to show repetitions in yearly fluctuations, because the seasonal forcing that is incorporated in the model causes fluctuations throughout the year.

1.5 Food web model and ecosystem model

In the previous two sections, we saw two types of models that describe species communities, each with its own stability analysis. The first model I refer to as the ‘food web model’, in which trophic species and trophic interactions are considered to be the essence of species communities. I use this model for the local stability analysis, or the interaction strength matrix approach. The second model I refer to as the ‘ecosystem model’, in which non-trophic interactions and abiotic processes are explicitly modelled in addition to the trophic interactions. I use this model for bifurcation analysis, where the bifurcation parameter is represented by an environmental variable and the equilibrium and its stability are determined along the bifurcation axis.

1.6 Outline of the thesis

In this thesis, I use both the food web model and local stability analysis, as well as the ecosystem model and bifurcation analysis to study how disturbances affect food web stability. I use them separately in the first three chapters (the food web model in chapter 2 and 3, the ecosystem model in chapter 4), and combine them in the fifth chapter.

In chapter 2, I investigate whether the choice of diagonal elements of the interaction strength matrix affects the results of local stability analyses. I do this for two types of analyses: one that compares stability between food webs, and one that determines the importance of a single interaction strength on stability. To parameterize the interaction strength matrices, I use data from soil food webs.

In chapter 3, I use the food web model to revisit the relation between food web complexity and stability as postulated by May (1972). However, where May used random matrices and binary (or unweighted) connectance as a surrogate for complexity, I again use empirical data of soil food webs to parameterize both the interaction strength matrices, as well as weighted connectance (i.e. empirically derived flux weights are taken into account in determining connectance).

In chapter 4, I use the ecosystem model PCLake to investigate the impact herbivorous birds have on macrophytes in shallow lakes, and ask the question whether they can facilitate a regime shift during eutrophication from a clear-water state to a turbid water

state. Thus, a bifurcation analysis is performed with nutrient load as the bifurcation parameter.

Finally, in chapter 5, I combine the food web model and the ecosystem model to investigate regime shifts in shallow lakes. I parameterize the food web model with data from the ecosystem model PCLake that is used here as a virtual reality. I then determine food web stability along the nutrient loading axis and investigate patterns in interaction strengths and loop weights.

Chapter 2

Patterns in intraspecific interaction strengths and the stability of food webs

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Abstract

A common approach to analyse stability of biological communities is to calculate the interaction strength matrix. Problematic in this approach is defining intraspecific interaction strengths, represented by diagonal elements in the matrix, due to a lack of empirical data for these strengths. Theoretical studies have shown that an overall increase in these strengths enhances stability. However, the way in which the pattern in intraspecific interaction strengths, i.e. the variation in these strengths between species, influences stability has received little attention. We constructed interaction strength matrices for 11 real soil food webs in which four patterns for intraspecific interaction strengths were chosen, based on the ecological literature. These patterns included strengths that were (1) similar for all species, (2) trophic level dependent, (3) biomass dependent, or (4) death rate dependent. These four patterns were analysed for their influence on 1) ranking food webs by their stability, and 2) the response in stability to variation of single interspecific interaction strengths. The first analysis showed that ranking the 11 food webs by their stability was not strongly influenced by the choice of diagonal pattern. In contrast, the second analysis showed that the response of food web stability to variation in single interspecific interaction strengths was sensitive to the choice of diagonal pattern. Notably, stability could increase using one pattern, and decrease using another. This result asks for deliberate approaches to choose diagonal element values in order to make predictions on how particular species, interactions, or other food web parameters affect food web stability.

Introduction

The stability of ecological communities expresses how resistant or resilient a community is to disturbances. Examples of disturbances are changes in the environment (e.g. in nutrient availability, soil acidity), changes in climatic conditions (e.g. in rainfall, temperature), or disturbances caused by humans (e.g. pollution, fire). Resistance can be expressed in terms of how strongly a community responds to a disturbance, for example in terms of population variation, or in terms of the loss of species. Resilience can be expressed in terms of the ability and rate with which a community can return to its original state from before the disturbance. In studies of community stability, much attention has been given to food web stability, in which the community is defined in terms of trophic interactions, i.e. interactions between consumers and resources, leaving out other types of ecological interactions, like competition, mutualism and facilitation.

A common approach to measure food web stability is to calculate the Jacobian matrix, in this context called the interaction strength matrix, which is derived from population dynamical models of the species in the community (May 1972, 1973, Yodzis 1988). Stability of the interaction strength matrix is measured with the maximum of the real parts of all eigenvalues, the inverse being a measure for the rate with which a food web recovers from a disturbance (Pimm and Lawton 1977, 1978). The interaction strength matrix is stable if this maximum real part of the eigenvalues is negative, and unstable if it is positive. The interaction strength matrix approach has been used in forming theories on a wide range of topics in community ecology, such as the occurrence of omnivory (Pimm and Lawton 1978), the maximum length of food chains (Pimm and Lawton 1977, Hairston and Hairston 1993, Moore et al. 1993), and the effects of nutrient enrichment (Rosenzweig 1971). It has also been used to investigate how patterns in the strengths of the interspecific interactions, which are represented by the off-diagonal elements of the interaction strength matrix, might be related to stability (Yodzis 1981, de Ruiter et al. 1995, Neutel et al. 2002, Berlow et al. 2004, Emmerson and Raffaelli 2004), and which species and/or interactions are important to stability (Yodzis 1988, Neutel et al. 2002, Montoya et al. 2009, Allesina and Tang 2012).

Methods and approaches to construct the interaction strength matrix for food webs have developed over the past decades, but these have primarily focussed on the values for *interspecific* interaction strengths. Initially, these values were obtained by randomly drawing them all from the same intervals (May 1972, 1973). This random assignment became more realistic when more plausible, asymmetric intervals were chosen to draw random values from (Pimm and Lawton 1978), so that negative effects were two orders of magnitude stronger than the positive effects. Later, inspired by empirical studies on food webs (Paine 1980, Wootton 1994), interaction strength matrices were derived from observations on real food webs (de Ruiter et al. 1995, Schmitz 1997, McCann et al. 1998, Emmerson and Raffaelli 2004, Banašek-Richter et al. 2009).

Much less attention though has been paid to how to define and represent the *intraspecific* interaction strengths in the interaction strength matrices. Intraspecific interaction strengths are the diagonal elements of the interaction strength matrix and represent per capita effects of species on itself, e.g. via density-dependent effects, also referred to as self-regulation, self-limitation, or intraspecific interference. Two problems arise when one wants to define the intraspecific interaction strengths. First, it is unclear which species are self-regulated and which are not; thus, which diagonal elements of the interaction strength matrix should be assigned negative values and which not. Second, how to determine the actual value of the strength of the self-limitation (compared with interspecific interaction strength)?

Given the scarcity of data on intraspecific interaction strengths, diagonal element values have been mostly obtained by randomly drawing negative values from plausible intervals, with some exceptions (Schmitz 1997). May (1972) simply chose a constant negative value for intraspecific interaction strengths ‘to set a time scale’. Yodzis (1988) assumed that the negative intraspecific interaction strengths should be much stronger (i.e. four orders of magnitude) for basal species than for higher trophic level species. Furthermore, intervals have been proposed that relate intraspecific interaction strength to both trophic level and population size (Berg et al. 2011) or to specific death rates (de Ruiter et al. 1995, Neutel et al. 2002).

The choice of diagonal strength is important for the outcome of stability analyses. It is well known that the stronger the negative strengths on the diagonal, the more likely the matrix will be stable (May 1972, Yodzis 1981, Haydon 1994). However, besides the importance of the numerical values of intraspecific interaction strengths, the way in which these values vary between species, that is, the *pattern* of the values of intraspecific interaction strengths as distributed over the food web species, might also be important to food web stability. For example, Yodzis (1981) varied the strength of intraspecific interference and the frequency with which it occurred in the consumer species populations, and showed that both influence food web stability. Furthermore, the relation between particular inter- and intraspecific interaction strengths is important for stability as well, as can be seen from the mathematical criterion quasi-diagonal dominance (QDD) for matrix stability. This criterion states that stability depends on how the diagonal value relates to its associated off-diagonal values within each row (Hofbauer and Sigmund 1988) and was used in Neutel et al. (2002).

Whether a food web is stable or unstable in itself is not always the main interest; it is also interesting to quantify whether a food web is ‘more stable’ than another food web, in which ‘more stable’ means a larger absolute value (more negative) for the maximum (negative) real part of the eigenvalues, correlating, for example, with a faster return time after a disturbance. One could compare stability of food webs that are derived from

different systems, e.g. from different sites or ecosystems (Moore et al. 2004, Rip and McCann 2011), or derived from the same system, but with different parameters for the interaction strengths, for example representing the effects of environmental change (Neutel et al. 2007), or perturbations of particular species or species interactions (Yodzis 1988, Montoya et al. 2009, Rip and McCann 2011). Stability comparisons between food webs have also been made to investigate what kind of patterns in interaction strengths are important for real food webs (DeAngelis 1975, Yodzis 1981, de Ruiter et al. 1995, Neutel et al. 2002, Emmerson and Raffaelli 2004). Studies on responses of food web stability to applied disturbances, or ‘press perturbations’, have mostly focused on the role of particular species or interactions on food web stability (Yodzis 1988, de Ruiter et al. 1995, Rip and McCann 2011). In all such studies, the focus is on ‘relative’ differences in stability: the exact stability values are of minor importance. It is therefore important to know how the pattern in intraspecific interaction strengths influences these ‘relative’ differences in food web stability.

The objective of the present study was to determine the influence of the pattern in intraspecific interaction strengths on food web stability, when stability comparisons are made between interaction strength matrices. The study was carried out using 11 soil food webs for which the interspecific interaction strengths could be derived from observations (Hendrix et al. 1986, Hunt et al. 1987, Andrén et al. 1990, de Ruiter et al. 1993, Neutel et al. 2007). For the values of the intraspecific interaction strengths, four patterns were selected from the ecological literature. These patterns included diagonal element values that were (1) the same for all species (May 1972, 1973), (2) trophic level dependent (Yodzis 1988), (3) biomass dependent (Berg et al. 2011), or (4) death rate dependent (de Ruiter et al. 1995, Neutel et al. 2002). These four patterns were analysed for their influence on 1) ranking food webs by their stability, and 2) the response in stability to variation of single interspecific interaction strengths. The question in the present study was whether the choice of a particular pattern may affect the outcome of such stability analyses in principle ways. For example, regarding the first stability analysis, if one choice of pattern in intraspecific interaction strengths, applied to two food webs, indicates that food web X is ‘more stable’ than food web Y, will this ranking in stability be the same if another choice of pattern is applied to these two food webs? Regarding the second stability analysis, if one choice of pattern in intraspecific interaction strengths, applied to one food web, indicates that increasing a specific interspecific interaction strength increases food web stability, will this also hold true for another choice of pattern on the diagonal?

Table 2.1 The four diagonal definitions, i.e. the four patterns in intraspecific interaction strength elements α_{ii} , selected from the literature. Values of g_i were either set to a fixed value (column Fixed) or drawn from uniform distributions (column Drawn). For diagonal definitions A, B, and C, the detritus diagonal element could either be as prescribed by the definition, or empirically derived (cf. Moore et al. 1993). For definition D, only the empirically derived detritus diagonal element was used.

Diagonal definition	Description	α_{ii} value	Value of g_i	
			Fixed	Drawn
A	Similar ¹	$\alpha_{ii} = -g_i$	$g_i = 1$	$g_i \in (0, 2)$
B	Trophic level dependent ²	$\alpha_{ii} = -g_i$	$g_i = 5.5$ for basal species and $g_i = 0.00055$ for consumers	$g_i \in (1, 10)$ for basal species and $g_i \in (0.0001, 0.001)$ for consumers
C	Biomass dependent ³	$\alpha_{ii} = -g_i B_i$	$g_i = 1$ for basal species and $g_i = 0.1$ for consumers	$g_i \in (0, 2)$ for basal species and $g_i \in (0, 0.2)$ for consumers
D	Death rate dependent ⁴	$\alpha_{ii} = -g_i d_i$	$g_i = 0.1$	$g_i \in (0, 0.2)$

1 May (1972). 2 Yodzis (1988). 3 Berg et al. (2011). 4 De Ruiter et al. (1995).

Methods

Food web data and construction of the interaction strength matrix

The analyses were carried out using data from 11 real soil food webs. Data available for these 11 food webs included biomasses, death rates and biomass conversion (from resource to consumer) efficiencies. To construct food webs, species were aggregated in (trophic) functional groups, based on species life-history characteristics and diet (Hunt et al. 1987, Moore and Hunt 1988). The number of functional groups in the 11 food webs ranged from 12 to 19. See the Appendix (Tables A2.1, A2.2) for more detailed information on the data used.

Interspecific interaction strengths, α_{ij} ($i \neq j$), were derived from measured biomasses, death rates and biomass conversion efficiencies, cf. de Ruiter et al. (1995). For intraspecific interaction strengths, α_{ii} , we selected from the literature four patterns to define these (Table 2.1), from here on referred to as *diagonal definitions*. Definition A is based on May (1972), representing a diagonal with diagonal values that are equally distributed. Definition B is based on Yodzis (1988), which represents a more asymmetric diagonal: the values for basal species (in our case detritus and roots, see Appendix) have much larger negative values than the consumer species. Definition C is based on Berg et al. (2011) and assumes that intraspecific interaction strength is proportional to the biomass of the species, where Definition D assumes that it is proportional to the death rate of the species (de Ruiter et al. 1995).

Table 2.2 Values of Spearman’s rank correlation coefficient ρ . All 11 food webs were ranked from ‘most stable’ (smallest $\text{Re}(\lambda)$) to ‘least stable’ (largest $\text{Re}(\lambda)$) for all four diagonal definitions A, B, C and D (Table 2.1). Values are the outcome of the pairwise comparison between two food web rankings of one diagonal definition for which values of g_i were fixed or drawn (see Table 2.1; for both detritus diagonal element prescribed by the definition and detritus diagonal element empirically derived cf. Moore et al. 1993), and between two food web rankings of one diagonal definition for which detritus diagonal element was prescribed by the definition or empirically derived cf. Moore et al. (1993) (for both g_i fixed and g_i drawn, see Table 2.1).

	Correlation between fixed and drawn values		Correlation between prescribed and empirically derived detritus	
	Prescribed detritus	Empirically derived detritus	Fixed g_i values	Drawn g_i values
Diagonal definition				
A	0.75	0.95	0.68	0.67
B	1.00	0.99	1.00	0.99
C	1.00	1.00	1.00	1.00
D	-	0.99	-	-

A: Similar: $\alpha_{ii} = -g_i$ with $g_i = 1$ or g_i drawn from the interval $(0,1)$ for all species (May 1972); **B:** Trophic level dependent: $\alpha_{ii} = -g_i$ with $g_i = 5.5$ or g_i drawn from $(1,10)$ for basal species and $g_i = 0.0005$ or g_i drawn from $(0.0001,0.001)$ for higher trophic level species (Yodzis 1988); **C:** Biomass dependent: $\alpha_{ii} = -g_i B_i$ with $g_i=1$ or g_i drawn from $(0,2)$ for basal-species and $g_i = 0.1$ or g_i drawn from $(0,0.2)$ for higher trophic levels species, where B_i is the equilibrium population size (biomass) of the species (Berg et al. 2011); **D:** Death rate dependent: $\alpha_{ii} = -g_i d_i$ with $g_i=0.1$ or g_i is drawn from $(0,0.2)$ in which d_i is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002).

The stability metric calculated in all analyses was the maximum real part of the eigenvalues of the interaction strength matrix, denoted here with $\text{Re}(\lambda)$. When comparing stability of food webs, a food web is called ‘more stable’ than another food web if its $\text{Re}(\lambda)$ is more negative. Here, we use the term ‘more stable’ to indicate that $\text{Re}(\lambda)$ of one food web is smaller than $\text{Re}(\lambda)$ of another food web. For example, if two food webs are both unstable (both $\text{Re}(\lambda)>0$), we still call the food web with the smallest $\text{Re}(\lambda)$ ‘more stable’, in the sense that this food web is ‘closer’ to being stable.

Comparing stability between different food webs

Stability of the interaction strength matrices of the 11 food webs was assessed for all four diagonal definitions (Table 2.1). This stability analysis also included two types of variations within these diagonal definitions. First, the value of g_i (see Table 2.1) that determines the value of α_{ii} was either fixed as the middle value of the proposed interval (Table 2.1), or drawn from the proposed interval. This first type of variation was applied to all four diagonal definitions. Second, the soil food web data enabled to estimate a diagonal value for the detrital component in the food web; therefore the analyses were carried out either

with this empirically derived value for the diagonal element for detritus (Table A2.3), or by choosing a value prescribed by the selected diagonal definition (Table 2.1). This second variation was only applied to diagonal definitions A, B, and C (Table 2.1). For diagonal definition D, the empirically derived diagonal element for detritus was used, because this definition is based on species death rates, which detritus does not have. These two variations led to a total of 14 types of diagonal patterns that were used in this analysis (3 (definitions A, B, and C) \times 2 (g_i fixed or drawn) \times 2 (detritus derived or prescribed) + 1 (definition D) \times 2 (g_i fixed or drawn) = 14).

For each food web, 1000 interaction strength matrices were generated, for which the interspecific interaction strengths α_{ij} were sampled from the uniform distribution $(0, 2\alpha_{ij})$ where α_{ij} is the empirically derived value; this allowed for variations in these elements, so that a more robust stability value was obtained (cf. Neutel et al. 2007). These 1000 matrices were used to calculate an average stability value for $\text{Re}(\lambda)$ for each of the 14 diagonal patterns. The 11 food webs were ranked from ‘most stable’ to ‘least stable’, that is, from the smallest value for $\text{Re}(\lambda)$ to the largest value of $\text{Re}(\lambda)$. Subsequently, similarity of stability rankings was tested in a pair-wise manner with Spearman’s rank correlation coefficient ρ for each of the diagonal definitions between 1) diagonal elements with fixed g_i and diagonal elements with drawn g_i (with the detrital diagonal element either prescribed or empirically derived, see Table 2.1), and between 2) detritus diagonal element prescribed by the definition (Table 2.1) and empirically derived (with g_i either fixed or drawn, see Table 2.1). Furthermore, for the four diagonal definitions for which values of g_i were fixed and for which in definitions A, B, and C the detritus diagonal elements were prescribed by the selected diagonal definitions (Table 2.1), we determined Kendall’s coefficient of concordance W , with $W = 1$ if rankings are completely similar, and $W = 0$ if rankings are completely dissimilar. With this test, the overall agreement of stability rankings for these four specific diagonal patterns was tested.

Response in food web stability to variation in single interspecific interaction strengths

For each food web, single (nonzero) interspecific interaction strengths α_{ij} were varied from 0 to $2\alpha_{ij}$ in 100 runs, holding all other elements the same (i.e. fixed to their originally calculated values). For each run, the matrix stability metric $\text{Re}(\lambda)$ was calculated. This was done for the four diagonal definitions with fixed values for g_i and with the detritus diagonal elements prescribed by the selected diagonal definitions for definitions A, B, and C (Table 2.1); for definition D, the empirically derived diagonal element for detritus was used. To see the similarities and dissimilarities in the responses in stability for these four diagonal definitions, we carried out a two-step analysis. First, the response in stability to the variation in α_{ij} was categorized according to its ‘strength’ by using four thresholds. These

four thresholds were defined in terms of $>5\%$, $>10\%$, $>25\%$, and $>50\%$ change in $\text{Re}(\lambda)$, relative to the original value of $\text{Re}(\lambda)$ (i.e. the $\text{Re}(\lambda)$ associated with the original value of α_{ij}). When the response was below a 5% change in $\text{Re}(\lambda)$ relative to the original value of $\text{Re}(\lambda)$, the response was denoted as ‘no response’. If varying an α_{ij} caused a response in $\text{Re}(\lambda)$ larger than the threshold for one of the four diagonal definitions, the α_{ij} was selected for further analysis. Second, for each selected α_{ij} and for each threshold, we tested similarities in responses of $\text{Re}(\lambda)$ between the diagonal definitions in a pair-wise manner with Spearman’s rank correlation coefficient ρ . For this, we defined three categories of similarities and dissimilarities in responses in $\text{Re}(\lambda)$: 1) *consistent* ($\rho \geq 0.9$): $\text{Re}(\lambda)$ shows no or similar responses for both diagonal definitions when varying α_{ij} , 2) *inconsistent* ($\rho < 0.9$): the responses in $\text{Re}(\lambda)$ are principally different for the two diagonal definitions, including cases that $\text{Re}(\lambda)$ shows a response for one diagonal definition and no response for the other diagonal definition, or that $\text{Re}(\lambda)$ shows a monotonous change (increase or decrease) for one diagonal definition while $\text{Re}(\lambda)$ shows a discontinuous response (with an increasing and a decreasing part – see for example Figure 2.2) for the other diagonal definition, 3) *opposing* ($\rho < 0$): the responses in $\text{Re}(\lambda)$ are completely contrasting, i.e. $\text{Re}(\lambda)$ increases for one diagonal definition, while $\text{Re}(\lambda)$ decreases for the other diagonal definition. Thus, the opposing responses are a subset of the inconsistent responses.

Results

Comparing stability between different food webs

The Spearman’s rank correlation coefficients ρ between two stability rankings of $\text{Re}(\lambda)$, based on the four diagonal definitions and their two variations, are given in Table 2.2. Stability rankings for which values of g_i were either fixed or drawn (see Table 2.1) were similar for the four diagonal definitions, for both detritus diagonal element prescribed by the definitions (all $P < 0.05$; no ρ for definition D for prescribed detritus diagonal element, because only empirically derived values were used), and for detritus diagonal element empirically derived (all $P < 0.05$). Stability rankings for which the detritus diagonal element was either prescribed or empirically derived were similar for the three diagonal definitions A, B, and C, for both fixed values of g_i , and for randomly drawn values of g_i (all $P < 0.05$; no ρ for definition D, because only empirically derived values were used).

As an example, rankings of $\text{Re}(\lambda)$ of the 11 food webs for the four definitions with fixed g_i and for definitions A, B, and C with the detritus diagonal element prescribed by the definition (Table 2.1), are given in Table 2.3. According to the Kendall’s coefficient of concordance, the stability rankings for these four specific diagonal patterns were similar ($W = 0.91, P < 0.001$). There were inconsistencies though, the largest inconsistency being

Table 2.3 Ranking and values of $\text{Re}(\lambda)$ for the 11 food webs and for each of the four diagonal definitions for which g_i was fixed (see Table 2.1) and detritus diagonal element was prescribed by the definition (except for diagonal definition D, for which detritus diagonal element was empirically derived). Values are based on mean stability values ($n = 1000$). All 11 food webs were ranked from ‘most stable’ (smallest $\text{Re}(\lambda)$), ranked 1) to ‘least stable’ (largest $\text{Re}(\lambda)$), ranked 11) for all four diagonal definitions A, B, C and D (Table 2.1)

Diagonal definition	Ranking				$\text{Re}(\lambda)$			
	A	B	C	D	A	B	C	D
Central Plains ¹	6	6	5	4	-0.813	0.169	0.059	-0.014
Horseshoe bend CT ²	1	1	2	1	-0.941	0.002	-0.008	-0.111
Horseshoe bend NT ²	3	3	1	3	-0.924	0.029	-0.010	-0.074
Kjettslinge B0 ³	4	5	6	5	-0.831	0.155	0.083	0.015
Kjettslinge B120 ³	7	7	7	7	-0.807	0.171	0.110	0.040
Lovinkhoeve Int ⁴	8	9	9	8	-0.717	0.286	0.259	0.070
Lovinkhoeve Con ⁴	10	10	10	10	-0.521	0.478	0.463	0.262
Schiermonnikoog 1 ⁵	2	2	3	2	-0.930	0.007	0.007	-0.097
Schiermonnikoog 2 ⁵	9	4	4	9	-0.621	0.045	0.019	0.125
Schiermonnikoog 3 ⁵	5	8	8	6	-0.815	0.177	0.168	0.024
Schiermonnikoog 4 ⁵	11	11	11	11	-0.185	0.816	0.812	0.602

A: Similar: $\alpha_{ii} = -g_i$ with $g_i = 1$ or g_i drawn from the interval (0,1) for all species (May 1972); B: Trophic level dependent: $\alpha_{ii} = -g_i$ with $g_i = 5.5$ or g_i drawn from (1,10) for basal species and $g_i = 0.0005$ or g_i drawn from (0.0001,0.001) for higher trophic level species (Yodzis 1988); C: Biomass dependent: $\alpha_{ii} = -g_i B_i$ with $g_i=1$ or g_i drawn from (0,2) for basal-species and $g_i = 0.1$ or g_i drawn from (0,0.2) for higher trophic levels species, where B_i is the equilibrium population size (biomass) of the species (Berg et al. 2011); D: Death rate dependent: $\alpha_{ii} = -g_i d_i$ with $g_i=0.1$ or g_i is drawn from (0,0.2) in which d_i is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002).

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (Neutel et al. 2007).

from the food web from the 2nd succession stage at Schiermonnikoog, which is ranked 9 for diagonal definitions A and D, but ranked 4 for diagonal definitions B and C. Other inconsistencies were smaller. For example, the food web of Horseshoe bend CT was ranked as ‘most stable’ (ranked 1) by the three diagonal definitions A, B, and D, and ranked as second ‘most stable’ (ranked 2) by diagonal definition C.

Table 2.4 The total number of interspecific interaction strengths α_{ij} per food web (Total), the number of selected α_{ij} for which at least one of the four diagonal definitions showed respectively a more than 5%, 10%, 25%, or 50% change in stability (S), the number of α_{ij} that caused *inconsistent* responses in $\text{Re}(\lambda)$ between diagonal definitions (I), and the number of α_{ij} that caused *opposing* responses in $\text{Re}(\lambda)$ between diagonal definitions (O).

		5%			10%			25%			50%		
	Total	S	I	O	S	I	O	S	I	O	S	I	O
Central Plains¹	94	42	37	5	38	33	5	21	16	2	14	9	2
Horseshoe Bend CT²	47	11	11	0	6	6	0	2	2	0	0	0	0
Horseshoe Bend NT²	47	19	19	0	15	15	0	6	6	0	0	0	0
Kjettslinge B0³	93	64	64	18	57	57	18	47	47	18	38	38	18
Kjettslinge B120³	93	70	69	18	62	61	16	49	48	15	33	32	10
Lovinkhoeve Int⁴	94	40	28	2	32	20	2	22	10	1	17	6	0
Lovinkhoeve Con⁴	92	35	18	0	29	12	0	19	2	0	14	0	0
Schiermonnikoog 1⁵	41	18	18	1	12	12	0	7	7	0	7	7	0
Schiermonnikoog 2⁵	59	42	38	7	37	31	7	28	23	7	23	19	7
Schiermonnikoog 3⁵	70	49	48	7	33	32	7	26	25	7	17	16	4
Schiermonnikoog 4⁵	86	29	1	0	26	0	0	17	0	0	12	0	0

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (Neutel et al. 2007).

Response in food web stability when varying single interspecific interaction strengths

The response in food web stability to the variation of (nonzero) single interspecific interaction strengths α_{ij} over the interval $(0, 2\alpha_{ij})$ is given in Table 2.4. The table summarizes the frequencies of the selected α_{ij} for the four thresholds (5%, 10%, 25%, 50%) and the frequencies of α_{ij} with *inconsistent* or *opposing* responses between the diagonal definitions. The frequency of interactions that produced $>5\%$ change in $\text{Re}(\lambda)$ relative to the original $\text{Re}(\lambda)$ value in one of the four diagonal definitions varied between 23% (Horseshoe Bend CT) and 75% (Kjettslinge B120); that is, for some food webs, more than half of the total number of interactions showed a response for any of the four diagonal definitions. Some food webs had a relatively high number of α_{ij} that were selected for the 50% threshold, such as the two food webs from the two sites of the Kjettslinge Experimental Farm. From the selected α_{ij} , a large proportion also produced inconsistent

responses. On average, the percentage *inconsistent* α_{ij} (within the selected α_{ij}) was 81%, 79%, 73%, and 64% for thresholds of 5%, 10%, 25%, and 50% respectively. Moreover, the percentage *opposing* α_{ij} (within the selected α_{ij}) was 10%, 11%, 12% and 16% for thresholds of 5%, 10%, 25% and 50% respectively. In summary, of the total of 816 (nonzero) α_{ij} analysed, 419 showed a response in $\text{Re}(\lambda)$ of more than 5%, of which 349 showed an inconsistent response and 57 an opposing response in $\text{Re}(\lambda)$ between diagonal definitions. Also, there were 184 α_{ij} with a response in $\text{Re}(\lambda)$ of more than 50%, of which 127 showed an inconsistent response and 41 an opposing response in $\text{Re}(\lambda)$ between diagonal definitions. Two examples of inconsistencies in the response of $\text{Re}(\lambda)$ for the four diagonal definitions to varying a single interspecific interaction strength are given in Figures 2.1 and 2.2. In Figure 2.1, this is for the relatively large negative effect $\alpha_{10,2}$ (caused by predatory nematodes feeding on phytophagous nematodes) in the food web of the 2nd succession stage at Schiermonnikoog (Neutel et al. 2007), and in Figure 2.2 for the relatively small positive effect $\alpha_{2,10}$ (caused by microbivorous macroarthropods being the resource for predatory arthropods) in the food web of the fertilized barley site (B120) at the Kjettslinge Experimental Farm (Andrén et al. 1990). Note that a decrease in y-value ($\text{Re}(\lambda)$) indicates an increase in stability for all four diagonal definitions. Figure 2.1 shows that increasing $\alpha_{10,2}$ in the Schiermonnikoog food web from twice its original negative value to 0 led to an increase in stability (decrease in $\text{Re}(\lambda)$) using diagonal definitions A and D, and a decrease in stability (increase in $\text{Re}(\lambda)$) using definitions B and C. Figure 2.2 shows that increasing $\alpha_{2,10}$ in the Kjettslinge food web caused ‘no’ response of stability using definition A, a small decrease in stability (increase in $\text{Re}(\lambda)$) using definition C, an increase in stability (decrease in $\text{Re}(\lambda)$) over a low range of $\alpha_{2,10}$ values and a decrease in stability at the higher $\alpha_{2,10}$ values using definition B, which was also seen when using definition D, but then in a weaker manner. Furthermore, definition B showed for most part of the $\alpha_{2,10}$ range a decrease in stability, whereas definition D showed for most part of the $\alpha_{2,10}$ range an increase in stability.

Discussion

The objective of the present study was to determine the influence of the pattern in intraspecific interaction strengths on food web stability, when stability comparisons are made between interaction strength matrices. By using four different patterns, or diagonal definitions, we analysed the influence on 1) ranking food webs by their stability, and 2) the response in stability to variation of single interspecific interaction strengths.

In the first analysis, we looked at potential differences in rankings of food webs by their stability, both within diagonal definitions, as well as between diagonal definitions. For the two variations that we investigated within diagonal definitions, that is, between fixed

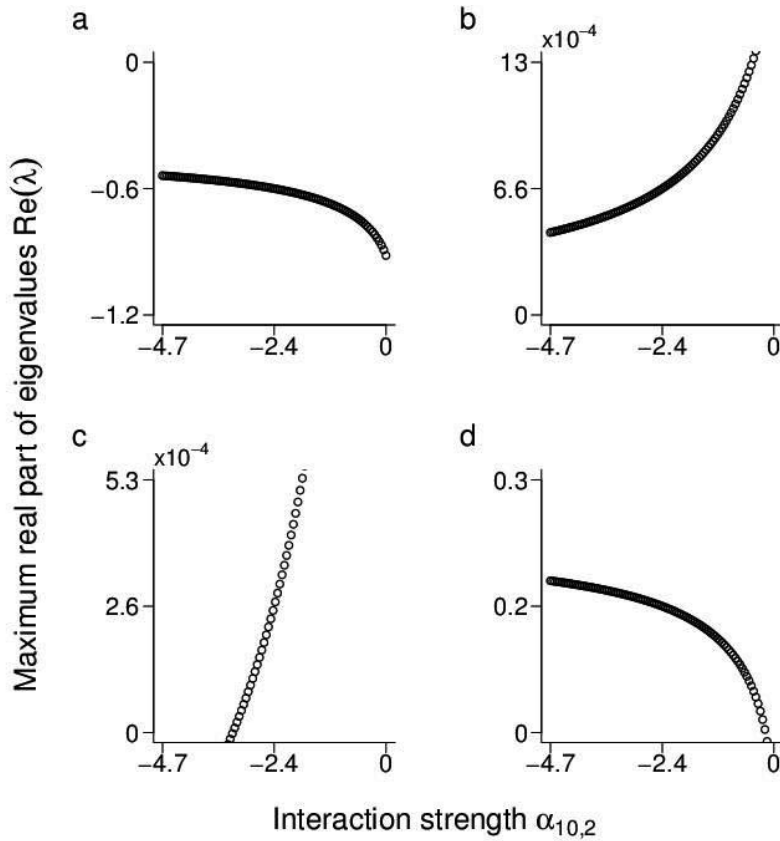


Figure 2.1 Inconsistencies in the response of food web stability to varying the negative interaction strength $\alpha_{10,2}$ for the four diagonal definitions A, B, C, and D (**a-d**; see Table 2.1). Interaction strength $\alpha_{10,2}$ is generated by the feeding of predatory nematodes on phytophageous nematodes in the food web of the 2nd succession stage at the island of Schiermonnikoog (Neutel et al. 2007). X-axes are scaled from $2\alpha_{10,2}$ to 0, with $\alpha_{10,2} = -2.37$ as its original interaction strength value. Y-axes are scaled for each stability method from 0 to $2\text{Re}(\lambda)$. Decreasing y-values indicate increases in stability for all diagonal definitions. Note that for each diagonal definition, the stability value associated with the original interaction strength value is somewhat different from the stability value used in the ranking analysis (Table 2.3). This is due to the sampling process that was used to generate average stability values for the ranking analysis. A: Similar: $\alpha_{ii} = -g_i$ with $g_i = 1$ or g_i drawn from the interval (0,1) for all species (May 1972); B: Trophic level dependent: $\alpha_{ii} = -g_i$ with $g_i = 5.5$ or g_i drawn from (1,10) for basal species and $g_i = 0.0005$ or g_i drawn from (0.0001,0.001) for higher trophic level species (Yodzis 1988); C: Biomass dependent: $\alpha_{ii} = -g_i B_i$ with $g_i=1$ or g_i drawn from (0,2) for basal-species and $g_i = 0.1$ or g_i drawn from (0,0.2) for higher trophic levels species, where B_i is the equilibrium population size (biomass) of the species (Berg et al. 2011); D: Death rate dependent: $\alpha_{ii} = -g_i d_i$ with $g_i=0.1$ or g_i is drawn from (0,0.2) in which d_i is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002).

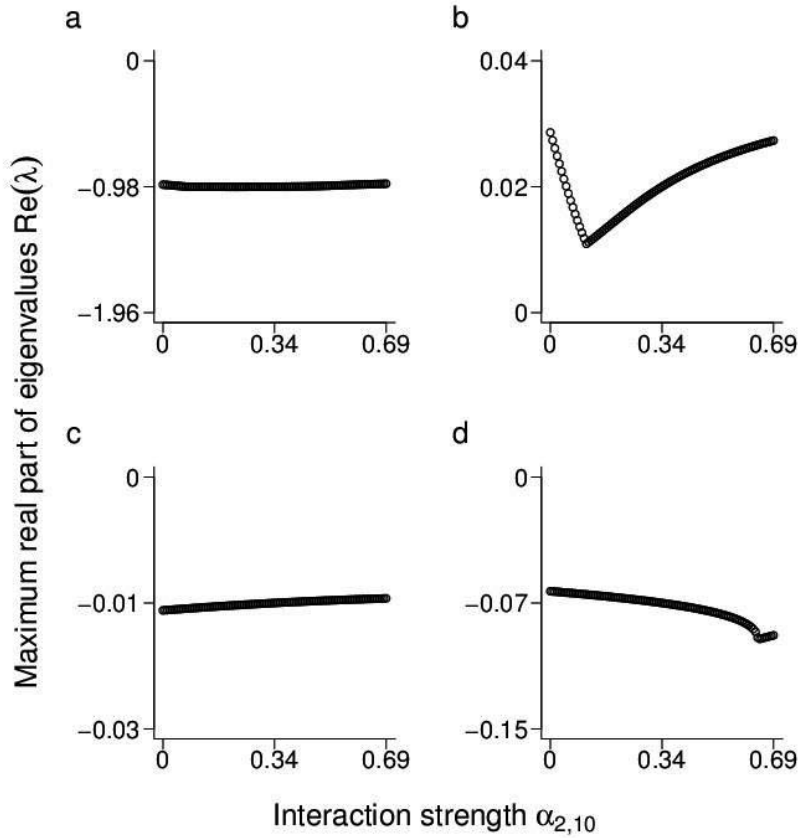


Figure 2.2 Inconsistencies in the response of food web stability to varying the positive interaction strength $\alpha_{2,10}$ for the four diagonal definitions A, B, C, and D (**a-d**, see Table 2.1). Interaction strength $\alpha_{2,10}$ is generated by microbivorous macroarthropods being the resource for predatory arthropods in the food web from the barley field at the Kjettslinge Experimental Farm with the use of fertilizer (Andrén et al. 1990). X-axes are scaled from 0 to $2\alpha_{2,10}$, with $\alpha_{2,10} = 0.34$ as its original interaction strength value, Y-axes are the same as in Figure 2.1. A: Similar: $\alpha_{ii} = -g_i$ with $g_i = 1$ or g_i drawn from the interval (0, 1) for all species (May 1972); B: Trophic level dependent: $\alpha_{ii} = -g_i$ with $g_i = 5.5$ or g_i drawn from (1, 10) for basal species and $g_i = 0.0005$ or g_i drawn from (0.0001, 0.001) for higher trophic level species (Yodzis 1988); C: Biomass dependent: $\alpha_{ii} = -g_i B_i$ with $g_i = 1$ or g_i drawn from (0, 2) for basal-species and $g_i = 0.1$ or g_i drawn from (0, 0.2) for higher trophic levels species, where B_i is the equilibrium population size (biomass) of the species (Berg et al. 2011); D: Death rate dependent: $\alpha_{ii} = -g_i d_i$ with $g_i = 0.1$ or g_i is drawn from (0, 0.2) in which d_i is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002).

and drawn values for g_i (see Table 2.1) and between detritus diagonal element prescribed by the definition and empirically derived, we saw no significant differences in rankings. Also, there were no large differences in stability rankings of food webs between the four diagonal definitions. This means that the choice of diagonal elements does not strongly influence the stability rankings of food webs. Note that this only holds for the stability *rankings* of food webs; the *values* of $\text{Re}(\lambda)$ were different for different diagonal definitions (Table 2.3).

It is not clear why the diagonal pattern does not influence stability rankings of food webs more strongly. It might be that stability rankings of food webs are mainly driven by food web architecture, i.e. in terms of number of trophic groups and frequency of interactions, and/or the differences in the values of the *interspecific* interaction strengths, rather than differences in the values of the *intraspecific* interaction strengths. This hypothesis could be tested for example by generating random matrices that differ in their interspecific interaction strength values, but that share the same network topology; if the stability rankings of these random matrices are the same for different diagonal patterns, this would confirm that network topology is more important for stability rankings than diagonal patterns. However, one should note that randomized food webs are very different from food webs that are based on empirical data in terms of their stability (de Ruiter et al. 1995). Preferably, analyses with randomized food webs should be complemented with analyses based on food webs derived from empirical data. For example, stability of food webs that have the same number of species could be compared for different diagonal patterns, to rule out, or confirm, that this number influences the effect of diagonal patterns on stability rankings.

The result of our first analysis implies in practice that if one wants to compare stability between different food webs, and only qualitative differences are of main interest (e.g. is food web X more stable than food web Y?), then it is likely that any (reasonable) choice of diagonal elements will reveal the most important differences in stability. One can consider though to repeat the analysis using different approaches to define the diagonal elements, for example to investigate more precisely how the relation between inter- and intraspecific interaction strengths influences stability. For example, the most notable difference in stability rankings in Table 2.3 could be found for the food web of the 2nd succession stage of Schiermonnikoog: definitions A and D ranked this food web as less stable than definitions B and C. Definitions B and C have in common that they assign more negative values to basal species. Thus, the differences in rankings might reflect the contribution to stability of interactions in which basal species are involved.

In the second analysis, the results can be summarized as that it is not uncommon to see large or fundamental differences in responses in $\text{Re}(\lambda)$ to variation of single interspecific interaction strengths between different diagonal definitions. More than half of

the 816 (nonzero) α_{ij} caused a response of >5% change in $\text{Re}(\lambda)$, 349 α_{ij} caused *inconsistent* responses in $\text{Re}(\lambda)$ between diagonal definitions, of which 57 were *opposing*. Inconsistent and opposing responses were found in all 11 food webs for this threshold of 5%. For the other thresholds (10%, 25%, and 50%), we found inconsistent and opposing responses as well. Thus, inconsistent responses can be found for both interactions that have a weak influence on stability and interactions that have a strong influence on stability.

These results imply that in this second type of comparative analysis, where the response of a single interaction strength on food web stability is analysed, the outcome of the analysis is highly sensitive to the choice of pattern in diagonal elements. The goal of studies that use this type of analysis is to find general relations between particular species, or particular interactions between species, and food web stability. These studies have been carried out for a wide array of ecosystems, using different kinds of empirical and theoretical approaches (de Ruiter et al. 1995, Montoya et al. 2009, Rip and McCann 2011). Our results show that the outcome of such analysis is influenced by the choice of pattern in diagonal elements, to the extent that an interaction strength can be found to be stabilizing for one diagonal pattern, while destabilizing for another diagonal pattern. This means that when the intraspecific interaction strengths are unknown, or when there is no data available for these strengths, and these strengths are defined in a more or less random manner, it is problematic to make general predictions on the effect of certain interactions, or related parameters, on food web stability. The least one can do in such analysis, is to repeat the analysis using different patterns for the intraspecific interaction strengths to increase confidence on the results. In such studies, special attention could be paid to how the value of a particular species interaction α_{ij} is related to its associated diagonal element α_{ii} , considering the quasi diagonal dominance criterion (Hofbauer and Sigmund 1988).

To summarize, our first result shows that data constraints on diagonal strength patterning do not hamper the assessment of overall food web stability. Our second result, however, shows that a better knowledge about the patterns in intraspecific interactions is necessary for the interpretation of how particular species, interactions, or other food web parameters affect food web stability. Our conclusions are based on analyses in which we used empirical data of soil food webs. The generality of the results could be tested by repeating the analyses with food webs from other ecosystems for which empirical data is available that can be used to construct interaction strength matrices. In addition, we conducted our analyses with four diagonal definitions that we encountered in the ecological literature. Besides that the diagonal could be defined in a different way, the four chosen diagonal definitions can be somewhat different for other food webs, which might affect the results as well. For example, the asymmetry in diagonal values in diagonal definition B (trophic level dependent, Yodzis 1981) changes with the number of basal species: the more basal species, the less asymmetric these values are. Similarly, aquatic systems have a

reverse biomass pyramid compared to soil systems; if diagonal definition C (biomass dependent, Berg et al. 2011) is used, top predators will thus have larger negative diagonal values than diagonal values of lower trophic groups, which is the other way around in soil food webs. Thus, how general our results are for other diagonal patterns, is an open question.

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Table A2.1 Averaged yearly biomasses (kg C ha⁻¹ yr⁻¹) for the functional groups of the 11 food webs.

	Central Plains ¹	Horse- shoe bend CT ²	Horse- shoe bend NT ²	Kjettslinge B0 ³	Kjettslinge B120 ³	Lovink- hoeve Int ⁴	Lovink- hoeve Con ⁴	Schier- monnikoog 1 ⁵	Schier- monnikoog 2 ⁵	Schier- monnikoog 3 ⁵	Schier- monnikoog 4 ⁵
Microorganisms											
Bacteria	304	690	440	740	900	245.75	227.5	1.14	4.72	18.75	17.82
Saprophytic fungi	63	150	160	1500	2300	3.28	2.13	0.03	0.13	0.21	0.29
Mycorrhizae	7	-	-	-	-	-	-	-	-	-	-
Protozoa											
Amoebae	3.78	50	40	110	34	18.90	11.53	0.01	0.03	0.20	0.35
Flagellates	0.16	-	-	-	-	0.63	0.53	0.0003	0.004	0.04	0.11
Nematodes											
Herbivores	2.9	0.5	0.4	0.18	0.29	0.36	0.19	0.000004	0.003	0.0009	0.0003
Bacteriovores	5.8	1.4	0.46	0.45	0.5	0.36	0.30	0.00006	0.01	0.04	0.07
Fungivores	0.41	0.08	0.12	0.2	0.12	0.13	0.08	0.000168	0.004	0.02	0.006
Omnivores	0.65	-	-	-	-	-	-	-	-	-	-
Predators	1.08	-	-	0.44	0.44	0.06	0.06	0.00003	0.03	0.009	0.005
Arthropods											
Herbivorous herbage arthropods	-	-	-	0.1	0.14	-	-	-	-	-	-
Predatory herbage arthropods	-	-	-	0.15	0.19	-	-	-	-	-	-
Microbivorous macroarthropods	-	-	-	0.25	0.25	-	-	-	-	-	-

(Continued)

Table A2.1 (Continued)

	Central Plains ¹	Horse- shoe bend CT ²	Horse- shoe bend NT ²	Kjettslinge B0 ³	Kjettslinge B120 ³	Lovink- hoeve Int ⁴	Lovink- hoeve Con ⁴	Schier- monnikoog 1 ⁵	Schier- monnikoog 2 ⁵	Schier- monnikoog 3 ⁵	Schier- monnikoog 4 ⁵
Predatory macroarthropods	-	-	-	0.49	0.49	-	-	-	-	-	-
Predatory mites	0.16	0.04	0.2	0.18	0.28	0.08	0.06	-	0.0009	0.02	0.08
Nematophagous mites	0.16	-	-	-	-	0.007	0.004	-	-	0.00008	0.01
Cryptostigmatic mites	1.68	0.22	0.8	-	-	0.003	0.007	0.00005	0.01	0.02	0.13
Noncryptostigmatic mites	1.36	0.39	0.9	-	-	0.04	0.02	0.0002	0.06	0.07	0.08
Bacteriovorous mites	-	-	-	-	-	0.0003	0.001	-	-	-	0.0005
Collembolans	0.46	0.09	0.3	0.17	0.17	0.38	0.47	-	0.002	0.06	0.07
Predatory collembolans	-	-	-	-	-	0.008	0.03	-	-	-	0.001
Annelids											
Enchytraeids	-	0.3	0.1	4.2	3.4	0.21	0.43	-	-	-	-
Earthworms	-	20	100	13	13	63.53	-	-	-	-	-
Basal groups											
Detritus	3000	8400	6000	22400	32000	2500	2500	4	25	250	2500
Roots	300	200	250	500	700	350	300	225	900	900	675

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (Neutel et al. 2007).

Table A2.2 Death rates (yr^{-1}) of the trophic groups, based on literature data (Hunt et al. 1987, De Ruiter et al. 1993)

	Death rates
Microorganisms	
Bacteria	1.20 ¹
Saprophytic fungi	1.20 ¹
Mycorrhizae	2.00
Protozoa	
Amoebae	6.00 ²
Flagellates	6.00
Nematodes	
Herbivores	1.08
Bacteriovores	2.68
Fungivores	1.92
Omnivores	4.36
Predators	3.00 ³
Arthropods	
Herbivorous herbage arthropods	1.84
Predatory herbage arthropods	1.84
Herbivorous macroarthropods	1.84
Microbivorous macroarthropods	1.84
Predatory macroarthropods	1.84
Predatory mites	1.84
Nematophagous mites	1.84
Cryptostigmatic mites	1.20
Noncryptostigmatic mites	1.84
Bacteriovorous mites	1.84
Collembolans	1.84
Predatory collembola	1.84
Annelids	
Enchytraeids	5.00
Earthworms	2.40
Basal groups	
Roots	1.00

1 In food webs of the Kjettslinge Experimental Farm Barley fields: 0.10

2 In food webs of the Kjettslinge Experimental Farm Barley fields: 1.00

3 In food web Central Plains Experimental Range (Hunt et al. 1987): 1.60

Table A2.3 Empirically derived detritus diagonal values (cf. Moore et al. 1993) for the 11 food webs.

	Empirically derived detritus
Central Plains¹	-0.733
Horseshoe bend CT²	-0.741
Horseshoe bend NT²	-0.871
Kjettslinge B0³	-0.108
Kjettslinge B120³	-0.062
Lovinkhoeve Int⁴	-0.994
Lovinkhoeve Con⁴	-0.660
Schiermonnikoog 1⁵	-1.325
Schiermonnikoog 2⁵	-1.180
Schiermonnikoog 3⁵	-0.404
Schiermonnikoog 4⁵	-0.050

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (Neutel et al. 2007).

Chapter 3

Food web stability and weighted connectance: the stability-complexity debate revisited

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Abstract

How complexity of food webs relates to stability has been a subject of many studies. Often, unweighted connectance is used to express complexity. Unweighted connectance is measured as the proportion of realized links in the network. Weighted connectance, on the other hand, takes link weights (fluxes or feeding rates) into account and captures the shape of the flux distribution. Here, we used weighted connectance to revisit the relation between complexity and stability. We used 15 real soil food webs and determined the feeding rates and the interaction strength matrices. We calculated both versions of connectance, and related these structural properties to food web stability. We also determined the skewness of both flux and interaction strength distributions with the Gini coefficient. We found no relation between unweighted connectance and food web stability, but weighted connectance was positively correlated with stability. This finding challenges the notion that complexity may constrain stability, and supports the ‘complexity begets stability’ notion. The positive correlation between weighted connectance and stability implies that the more evenly flux rates were distributed over links, the more stable the webs were. This was confirmed by the Gini coefficients of both fluxes and interaction strengths. However, the most even distributions of this dataset still were strongly skewed towards small fluxes or weak interaction strengths. Thus, incorporating these distribution with many weak links via weighted instead of unweighted food web measures can shed new light on classical theories.

Introduction

Food webs are networks of species linked via trophic interactions that in a simple way describe the biodiversity and feeding relations in ecosystems. To find universal laws that aid in understanding what maintains this biodiversity, several descriptors of food webs have emerged over the past decades, such as link density (the number of links per species; Levins 1977), trophic chain length (e.g. Pimm and Lawton 1977) and lengths and weights of trophic interaction loops (chains of trophic links that start and end with the same species; Levins 1977; Neutel et al. 2002).

The most studied food web descriptor is probably (unweighted) connectance (Gardner and Ashby 1970), which is the proportion of realized links in a food web. It was this food web descriptor that May (1972, 1973) used in his analysis to show that an increase in food web complexity, described in terms of connectance, number of species, and average interaction strength, does not necessarily lead to an increase in stability. Up till then it was considered true that ‘complexity begets stability’, an idea formulated among others by MacArthur (1955). The result of May led to a wealth of research that investigated the complexity-stability relation, often using connectance as a derivative of food web complexity (DeAngelis 1975, Pimm 1979, Martinez 1992, Chen and Cohen 2001, Dunne et al. 2002). Depending on definitions of stability, methods to construct theoretical food webs, or usage of empirical food web data or structures, some studies confirmed the negative relation between food web complexity and stability (Gardner and Ashby 1970, May 1972, Pimm 1979, Chen and Cohen 2001), but others found that highly connected food webs could still be stable (DeAngelis 1975, Haydon 2000, Dunne et al. 2002).

Connectance is a food web property that can be determined from the number of species and number of feeding links. Unweighted food web measures, such as connectance, treat all links as if they are equally important to the food web. However, it is very common in food webs, or even in networks in general (Csermely 2006), that material fluxes associated with the links (i.e. feeding rates) vary considerably in magnitude. To account for these differences in link ‘weights’, weighted food web descriptors have been introduced (Ulanowicz and Wolff 1991, Ulanowicz 1997, Bersier et al. 2002). These descriptors are based on principles from information theory (Shannon 1948) and often use Shannon’s diversity index. They assign more importance to strong links than to weak links and in that way take into account the unequal distribution of link weights in the food web.

Studies that use weighted food web measures focussed mainly on the weighted link density, which is the number of links per species, taking link weights into account (Ulanowicz 1997, Bersier et al. 2002, Banašek-Richter et al. 2009). Using this measure, Ulanowicz (1997, 2002) proposed a weighted equivalent to the complexity-stability criterion of May (1972). Ulanowicz (1997, 2002) showed that the weighted link densities of

real food webs complied with the weighted complexity-stability criterion, while those of randomly constructed networks did not.

Instead of using the weighted link density as in the analysis of Ulanowicz (1997, 2002), the relation between food web complexity and stability can also be re-examined by looking at weighted connectance (Bersier et al. 2002, Boit and Gaedke 2014). Weighted connectance is the number of links in the whole web relative to the total number of links, in which each link is weighed on the basis of the flux rate (in case of food webs) associated with the link. Weighted connectance has been used before in food web studies (Bersier et al. 2002, Banašek-Richter et al. 2009, Boit and Gaedke 2014), but not yet in the complexity-stability context.

Investigating the relation between weighted connectance and food web stability is interesting for two reasons. First, there is no clear pattern in how unweighted connectance relates to food web stability, even though this relation has been studied for decades. Studies have shown different possibilities (Pimm 1979, Haydon 2000, Chen and Cohen 2001, Dunne et al. 2002) and it would be interesting to see what the weighted version of this relation would add to the complexity-stability debate. Second, it is difficult to predict what the relation between weighted connectance (based on patterns in flux rates) and food web stability (based on patterns in interaction strengths) would be. Interaction strengths are the elements of the Jacobian matrix which is calculated from the system of differential equations that describe food web dynamics (May 1972). These strengths are the per capita fluxes in equilibrium between consumers and resources. Thus, the interaction strengths are derived from the material flux rates, but the relation between flux rate and interaction strength is not one to one: a small flux (small link weight) does not necessarily lead to a weak interaction strength (de Ruiter et al. 1995).

Food web theoreticians emphasize the importance of patterns in interaction strengths to food web stability (de Ruiter et al. 1995, McCann et al. 1998, Neutel et al. 2002, McCann 2012). Studies in which the interaction strengths are derived from empirical information show patterns that are important to stability. McCann et al. (1998) linked food web stability to the occurrence of a few strong links embedded in a majority of weak links. Emmerson and Yearsley (2004) found that the probability of a food web to be stable is larger for interaction strength distributions that are skewed towards weak interaction strengths. De Ruiter et al. (1995) found that the patterning of the interaction strengths is trophic level dependent, and the stabilising effect of such patterns can be understood from its prevention of destabilising strong ('heavy') trophic interaction loops (Neutel et al. 2002).

Different expectations can be formulated on the relation between weighted connectance and stability. From a 'complexity begets stability' point of view (MacArthur 1955), we would expect that an increase in weighted connectance (as a measure of

complexity) would lead to an increase in food web stability. Boit and Gaedke (2014) found that weighted connectance increased during succession and hypothesized that this could “imply an insurance effect enhancing response diversity and robustness against disturbances” (p. 19). However, we could also reason that an increase in weighted connectance might be destabilizing for the food web. An increase in weighted connectance reflects a more even distribution of the fluxes (Ulanowicz 2002, Boit and Gaedke 2014). A more even distribution of fluxes could result in a more even distribution in interaction strengths (which is not necessarily the case, as mentioned above). The loss in skew towards weak interaction strengths could mean a loss of stabilizing interaction strength patterns, because these skewed distributions are associated with stable food webs (McCann et al. 1998, Emmerson and Yearsley 2004). But it might also be possible that a more even distribution in interaction strengths implies that extremely strong links become less strong and in that way prevent destabilising heavy trophic interaction loops (Neutel et al. 2002).

In this study, we will revisit the relation between complexity and food web stability for 15 real soil food webs (Hendrix et al. 1986, Hunt et al. 1987, Andrén et al. 1990, de Ruiter et al. 1993, Neutel et al. 2007). We used the soil food web data to determine the fluxes in terms of the amount of biomass that is transferred from one trophic group to another. Subsequently, we used these fluxes to calculate weighted connectance. Furthermore, these fluxes were used to calculate the interaction strengths and the interaction strength matrices (i.e. the Jacobian matrices, see Methods), cf. de Ruiter et al. (1995), from which we determined food web stability with the diagonal strength metric, s . This measure was introduced by Neutel et al. (2002) and represents the minimal amount of self-damping needed for stability. Thus, similar to the approach of May (1972), we determined food web stability and connectance, with the difference that in our study, food web stability and connectance were based on distributions of fluxes and interactions strengths that were derived from empirical data. To see how the skewness of the distributions of fluxes and interaction strengths was related to weighted connectance and food web stability, we determined skewness with the Gini coefficient (Gini 1912).

Methods

Food web data and fluxes

We used data of 15 real soil food webs, which have been sampled before and described in a number of publications (Hendrix et al. 1986, Hunt et al. 1987, Andrén et al. 1990, de Ruiter et al. 1993, Neutel et al. 2007). Four food webs were sampled on the island of Schiermonnikoog, The Netherlands, and represent a chronosequence of primary succession (Neutel et al. 2007). Each web was originally represented by four food web replications (Neutel et al. 2007), but these were averaged here. Another four food webs were sampled from Hulshorsterzand, The Netherlands, and also represent a chronosequence of primary

succession (Neutel et al. 2007). Again, each web was originally represented by four food web replications (Neutel et al. 2007), but these were averaged here. Three sites (Horseshoe bend in Georgia, USA, Hendrix et al. 1986; Kjettslinge in Uppsala, Sweden, Andrén et al. 1990; and Lovinkhoeve in Marknesse, The Netherlands, de Ruiter et al. 1993) consisted of two treatments (agricultural management practices) and for each treatment the food webs were established. Finally, the present data-set also included the soil food web from the native prairie of the Central plains experimental range (Colorado, USA, Hunt et al. 1987).

Functionally similar species of the food webs were aggregated in groups (Hendrix et al. 1986, Moore et al. 1988, Andrén et al. 1990). The number of trophic groups varied between 12 and 19 (see Table A3.1). These trophic groups form the nodes of the food web, and the links between the groups represent the feeding rates or fluxes of biomass F_{ij} (kg C ha⁻¹ yr⁻¹) from resources j to consumers i . These fluxes were constructed via mass balancing (O'Neill 1969, Hunt et al. 1987, de Ruiter et al. 1993) by using the measured yearly-averaged biomasses of the trophic groups (see Table A3.1), which were assumed to represent equilibrium biomasses B_i , and values from the literature for biomass conversion efficiencies e_i , feeding preferences w_i , and death rates d_i (de Ruiter et al. 1993 and references therein; Neutel et al. 2007).

Food web stability

To determine food web stability, Jacobian matrices, or interaction strength matrices (May 1972), were constructed from the system of generalized Lotka-Volterra differential equations that describe for each food web its dynamics, cf. de Ruiter et al. (1995) and Neutel et al. (2007). The off-diagonal elements, α_{ij} , or the interspecific interaction strengths, represent the per capita effects of species j (i.e. trophic group j) on species i . The effects of consumers j on resources i are given by $\alpha_{ij} = -\frac{F_{ij}}{B_j}$, and the effects of resources i on consumers j are given by $\alpha_{ji} = \frac{e_j F_{ij}}{B_i}$. Non-assimilated biomass was returned to the detritus pool, leading to positive interaction strengths, α_{Di} , of species i on detritus D (see also Supplementary Information of Neutel et al. 2007).

The diagonal elements, α_{ii} , were used to quantify food web stability, cf. Neutel et al (2002). They were defined as $\alpha_{ii} = -sd_i$, where s represents the fraction of deaths caused by density dependence (Neutel et al. 2002). We used s as a measure for stability, which was defined by Neutel et al. (2002) as the minimum value needed for the interaction strength matrix to be stable, i.e. it is the value where the maximum real part of all eigenvalues is equal to zero. The lower the value of s , the 'more stable' the food web is, in the sense that the food web requires less self-damping to remain stable. The diagonal value of detritus, α_{DD} , can be determined directly from the system of differential equations (see Supplementary Information of Neutel et al. 2007). This method only works if the original

interaction strength matrices, with diagonal elements $\alpha_{ii} = 0$ for $i \neq D$, are unstable, which was the case for our 15 food webs.

Connectance, topological and effective connectance per node, and weighted connectance

We determined for each food web unweighted connectance, C , as the number of realized links, L , divided by the total number of possible links, S^2 (Martinez 1991), with S the number of trophic groups in the food web.

We followed the approach of Boit and Gaedke (2014) to determine weighted connectance, which is based on the information theory metrics of Ulanowicz (1997). First, Shannon's formula is used to describe the diversity in flux weights (feeding rates $F_{ij} \neq 0$):

$$H = - \sum_{\substack{i,j \\ i \neq j}} \left(\frac{F_{ij}}{F} \right) \ln \left(\frac{F_{ij}}{F} \right), \quad (3.1)$$

where F is the total sum of fluxes, calculated as the sum of all feeding rates, plus fluxes to detritus from each trophic group caused by egestion or mortality. In theory, the summation holds for $i = j$, but here we exclude this value for i because there are no cannibalistic species in our food webs. Second, the average mutual information A is calculated:

$$A = \sum_{\substack{i,j \\ i \neq j}} \left(\frac{F_{ij}}{F} \right) \ln \left(\frac{F_{ij} F}{\sum_k F_{ik} \sum_m F_{mj}} \right), \quad (3.2)$$

These measures are used to calculate the 'effective connectance per node', m (Ulanowicz 1997):

$$m = \exp \left(\frac{H - A}{2} \right). \quad (3.3)$$

This is the weighted version of link density. A special case is when all links have equal weights. The resulting m is then denoted by m^* , and termed the 'topological connectance per node' (Ulanowicz 1997). Because $H - A$ is actually a sum of Shannon indices (Ulanowicz and Wolff 1991), and because the Shannon index is maximal when all links have equal weights (Shannon 1948), m increases when the flux distribution becomes more even. If links have unequal weights, then $1 \leq m < m^*$ (Ulanowicz and Wolff 1991). The topological connectance per node, m^* , is *not* equal to qualitative link density, L/S (Bersier et al. 2002 use a different weighting of the links, so that their measure of weighted link density is indeed equal to qualitative link density if all links have equal weights).

The criterion of May (1972) states that food webs should be stable if

$$a < \sqrt{SC}, \quad (3.4)$$

where a is the average interaction strength. Ulanowicz (1997) expressed a in terms of m and m^* , and stated that stable food webs (with $m \leq m^*$) should satisfy the following inequality:

$$m < \exp\left(\frac{3 \ln(m^*)}{2\sqrt{m^*}}\right). \quad (3.5)$$

We tested whether the 15 real soil food webs also comply to this inequality.

Finally, weighted connectance, C_w , is obtained by dividing m by the number of trophic groups, S (Boit and Gaedke 2014):

$$C_w = \frac{m}{S}. \quad (3.6)$$

Weighted connectance C_w thus captures how connected the species in a food web are, taking the distribution of the flux weights into account. A skewed flux distribution towards small fluxes (i.e. many small fluxes, few strong fluxes) results in low values for C_w , while a more even flux distribution results in high values for C_w . Because m can vary between 1 and m^* (Ulanowicz and Wolff 1991), and m^* cannot be greater than S (when all species are connected to all species and links have equal link weights), C_w can vary between $1/S$ and 1.

Gini coefficients of fluxes and interaction strengths

Weighted connectance takes the distribution of flux weights into account, but it is also influenced by the number of species and the number of links between species. To determine the skewness (towards weak links) in the distribution of the fluxes and interaction strengths independent of number of species and links, we used the Gini coefficient (Gini 1912). This coefficient is often used in social sciences, mostly to determine the inequality in distribution of income in a society. However, it can be used in other fields as well, including ecology (e.g. Arenas and Fernandez 2000, Wittebolle et al. 2009, Jiang et al. 2013). The Gini coefficient can take values between zero and one, where a (theoretical) value of zero means complete equality (here: all fluxes are of equal size) and a (theoretical) value of one means complete inequality (here: there is only one flux with a non-zero value, all other fluxes are zero). Thus, the higher the value, the more skewed the distribution (towards weak links), i.e. there are only a few links that account for a large proportion of the total sum of fluxes. We used the definition of Sen (1973) to calculate the Gini coefficients for both flux (G_F) and interaction strength (G_I) distributions:

$$G_F = \frac{\sum_{m=1}^S \sum_{n=1}^S |F_m - F_n|}{2S^2 \mu_F}, \quad (3.7)$$

$$G_I = \frac{\sum_{m=1}^S \sum_{n=1}^S |\alpha_m - \alpha_n|}{2S^2 \mu_I}, \quad (3.8)$$

where F_m represents a flux, μ_F is the mean of all fluxes, α_m represents the absolute value of an interaction strength (excluding diagonal values, except the diagonal value for detritus), and μ_I is the mean of all absolute values of interaction strengths (excluding diagonal values, except the diagonal value for detritus).

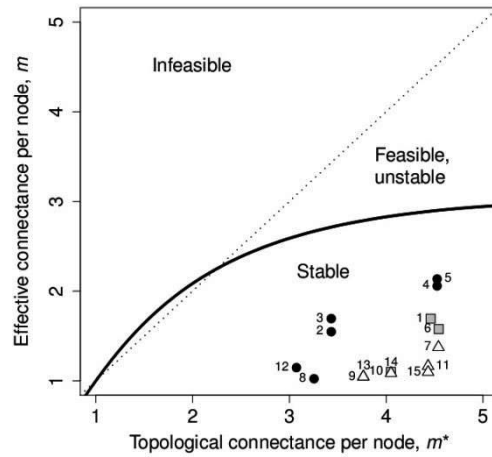


Figure 3.1 Topological connectance per node, m^* , and the effective connectance per node, m , for the 15 real soil food webs. Only values of m that are below the dotted line $m=m^*$ are feasible values. The solid line represents inequality (3.5). Black dots: $s < 0.01$; grey squares: $0.01 \leq s < 0.1$; white triangles: $s \geq 0.1$. Stability and s are inversely related. Label numbers refer to the 15 soil food webs as follows: (1) Central Plains Experimental Range (Hunt et al. 1987), (2) Horseshoe Bend Experimental Farm Conventional Tillage (CT) and (3) No Tillage (NT) (Hendrix et al. 1986), (4) Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and (5) with fertilizer (B120) (Andrén et al. 1990), (6) Lovinkhoeve Experimental Farm Integrated Farming (Int) and (7) Conventional Farming (Con) (de Ruiter et al. 1993), (8)-(11) Schiermonnikoog Primary Succession Stages 1- 4 (Neutel et al. 2007), (12)-(15) Hulshorsterzand Primary Succession Stages 1- 4 (Neutel et al. 2007).

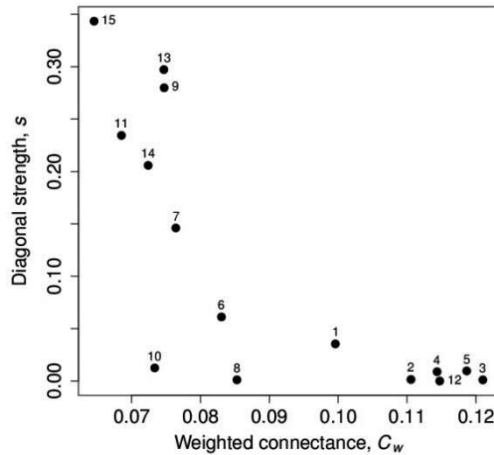


Figure 3.2 Weighted connectance, C_w , and food web stability expressed as diagonal strength, s , for the 15 real soil food webs. Stability and s are inversely related. Label numbers refer to the 15 soil food webs, see legend of Figure 3.1.

Results

We found no relation between unweighted connectance, C , and food web stability expressed as diagonal strength, s , in the 15 real soil food webs (Spearman rank correlation test: $\rho = 0.11$, $P > 0.5$, corrected for 5 ties). There was also no statistically significant relation between the topological connectance per node, m^* , and s (Spearman rank correlation test: $\rho = 0.93$, $0.1 < P < 0.2$). The effective connectance per node, m (i.e. weighted link density), and the topological connectance per node, m^* (i.e. weighted link density where links have equal weights), of the food webs did satisfy the proposed inequality (3.5) of Ulanowicz (1997), as shown in Figure 3.1. Some food webs had a value of m that was very close to the minimum value of 1 (Figure 3.1), that is, these webs had practically one link per node when link weights were taken into account. Both low and high values of stability could occur close to the line $m = 1$ (Figure 3.1).

When connectance was based on the feeding rates, F_{ij} , this weighted connectance, C_w , was negatively correlated with s (Spearman rank correlation test: $\rho = -0.83$, $P < 0.001$; Figure 3.2), i.e. positively correlated with food web stability. Thus, where unweighted connectance and stability did not show any relation at all, the relation between weighted connectance and stability showed an opposite relation from what May (1972) found. The values for weighted connectance (range of C_w between 0.07 and 0.12, median = 0.08) were much lower than the values for unweighted connectance (range of C between 0.16 and 0.23, median = 0.18), implying that the flux distributions of the food webs showed skewed

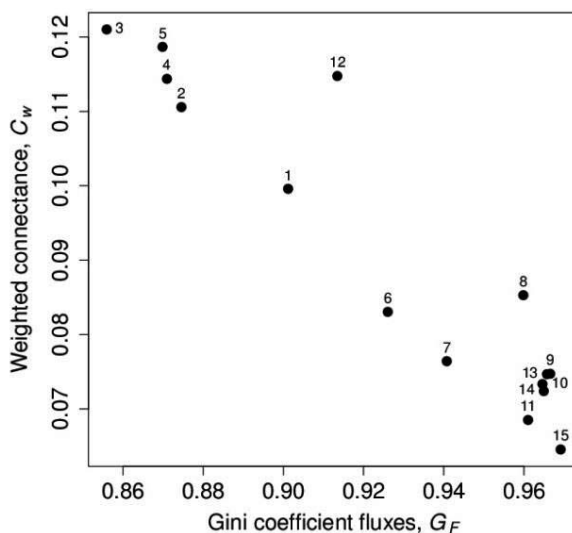


Figure 3.3 Skewness of fluxes expressed as Gini coefficient, G_F , and weighted connectance, C_w , for the 15 real soil food webs. Label numbers refer to the 15 soil food webs, see legend of Figure 3.1.

distributions of many links with small values and only a few links with large values. Figure 3.2 shows that diagonal strength, s , decreased very rapidly for increasing C_w .

The Gini coefficient that we used to express the skewness in the distributions of fluxes, G_F , was negatively correlated with weighted connectance (Spearman rank correlation test: $\rho = -0.90$, $P < 0.001$; Figure 3.3). This is to be expected as weighted connectance, amongst others, takes the skew in distributions into account: the more skewed the data, the lower weighted connectance. The Gini coefficient showed that the flux distributions of the food webs were highly skewed towards small fluxes (see also Table A3.2), because the Gini coefficients of the fluxes for the 15 investigated food webs took values between 0.86 and 0.97 (median = 0.94).

We also found that the Gini coefficient of the fluxes was positively correlated with the Gini coefficient of the per capita interaction strengths, G_I (Spearman rank correlation test: $\rho = 0.58$, $P = 0.03$). The Gini coefficients of these interaction strength distributions were lower (median = 0.77, range = 0.64 – 0.86) than the Gini coefficients of the flux distributions, but still relatively high and indicated that the interaction strength distributions were also highly skewed towards weak interactions (see also Table A3.3).

The Gini coefficients of both the interaction strengths and the fluxes were positively correlated with s (Spearman rank correlation test for G_I and stability: $\rho = 0.60$, $P = 0.02$, Figure 3.4; Spearman rank correlation test for G_F and stability: $\rho = 0.78$, $P < 0.001$), i.e.

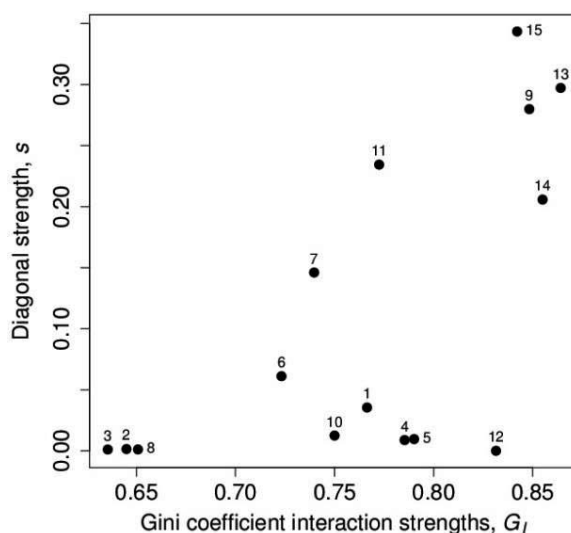


Figure 3.4 Skewness of interaction strengths expressed as Gini coefficient, G_I , and food web stability expressed as diagonal strength, s , for the 15 real soil food webs. Stability and s are inversely related. Label numbers refer to the 15 soil food webs, see legend of Figure 3.1.

negatively correlated with food web stability. Thus, the relations between the Gini coefficients and stability confirm that the higher the skewness of the distribution of either the fluxes or the interaction strengths towards weak links, the lower food web stability.

Discussion

The relation between food web connectance and food web stability has been extensively studied on a wide variety of ecosystems, using empirical and theoretical approaches. The outcomes of these studies gave a scattered picture: some found a positive relation between connectance and stability, others found a negative relation, and some found no relation. In our study, we restricted to soil food webs that were constructed using similar methods (Bersier et al. 2002, Dunne et al. 2002), and in which fluxes and interaction strengths were calculated using the same models as in previous studies (Pimm 1979, Neutel et al. 2007). For these food webs, we did not see any clear pattern of how unweighted connectance relates to food web stability. But we did find a clear positive correlation between weighted connectance and stability. We also found that the more skewed the distribution of fluxes or interaction strengths was towards small fluxes or weak interactions, the less stable the food web was.

When food web complexity is expressed in terms of weighted connectance, our results confirm the notion of ‘complexity begets stability’ (MacArthur 1955), and our results challenge the notion of May (1972) that connectance constrains stability. In the approach of May, unweighted connectance was not dependent on the flux distribution, and food web stability was based on matrices of which the elements were drawn randomly from normal distributions. In real food webs, however, fluxes are not evenly distributed, and distributions of interaction strengths are skewed towards weak interactions (Paine 1980, de Ruiter et al. 1995, McCann et al. 1998, Emmerson and Yearsley 2004, Neutel et al. 2007). The distributions of both our fluxes and interaction strengths were skewed, and this empirical information was used when we calculated both weighted connectance and food web stability. Thus, although we adhered to the approach of May (1972), differences in outcomes can be expected.

Studies on the same soil food webs (Neutel et al. 2002, Neutel et al. 2007) have shown that there is no relation between food web complexity and stability. In these studies, food web stability was based on empirically derived interaction strengths, while complexity was based on number of species and unweighted connectance. In our study, when both stability and connectance are based on observations, a positive relation between complexity (expressed as weighted connectance) and stability emerges. Testing this relation for food webs from other biomes could show whether this result can be generalized.

The present results evokes the question of why there is a positive relation between weighted connectance and stability. The analysis with the Gini coefficients showed that the

more skewed the distribution of either fluxes or interaction strengths was (many weak links, few strong links), the more stable the food web was. Thus, skewed distributions toward weak links seem to be the driving force behind this positive relation. Neutel et al. (2002, 2007) used the same soil food webs and found a negative relation between the maximum loop weight and stability, which together with the present results implies a negative relation between weighted connectance and maximum loop weight. A more even distribution of feeding rates could then prevent heavy loops. However, the precise nature of this relation is not yet clear, as we did not find any relation between the evenness of feeding rates and that of interaction strength.

Interesting here is that we find that very skewed distributions toward weak links are associated with the less stable food webs, while food web theoreticians find that skewed distributions towards weak interactions are associated with stability. Thus, it might be that there is an optimum in skewness. Ulanowicz (1997) also suggested that an extremely skewed link (here, flux) weight distribution towards weak links might make the food web to sparsely connected. He proposed that there is a ‘window of vitality’ (Ulanowicz 2002) in the plane defined by the topological connectance per node m^* and the effective connectance per node m , which is bounded by the line $m = 1$, the line $m = m^*$, and the line defined by inequality (3.5). Ulanowicz (2002) found that 41 observed food webs were positioned within this window of vitality, and that most of the 41 observed webs were relatively far from the ‘edges of chaos’, i.e. were positioned in the middle of the window. All 15 soil food webs that we investigated were also positioned within the window of vitality, but quite a few food webs had values of m that were close to $m = 1$. Based on the hypothesis of Ulanowicz (2002), it might be expected that food webs with m values close to 1 are less stable than food webs with m values that are positioned more in the centre of the window of vitality. This was indeed the case for most food webs, but some food webs actually had very low values for s , i.e. were very stable. These very stable food webs positioned close to the ‘edge of chaos’ might provide clues on what other factors than factors accounted for in weighted connectance are important for food web stability, such as the distribution of weak links in loops (Neutel et al. 2002), or specific biomass ratios between predators and their prey (Brose et al. 2006).

Should we prefer the use of weighted connectance over the use of unweighted connectance? Weighted connectance captures food web properties that are considered to be important for food webs: the number of interacting species, the number of links, and the weights of links. These properties have often been related to food web stability, but separately. Weighted connectance combines these properties, which can be seen as an advantage when one wants to use a summary statistic, or as a disadvantage when actually only one of these properties is relevant to stability. By weighing fluxes, large fluxes are considered to be more important than small fluxes in terms of quantity. But it could be that

the magnitude of a flux is not its most important feature. For example, it has been suggested that weak links can serve as a ‘back-up link’ for species when other links are lost (Paine 1980) and thus a link may be quantitatively redundant, but not functionally. In that case, unweighted connectance would be more suitable to use.

We used weighted connectance here to contribute to the complexity-stability debate, and used empirical information to calculate both weighted connectance, as well as stability. By using realistic distributions of fluxes and interaction strengths, i.e. distributions that are skewed towards weak fluxes and interaction strengths, we confirmed the notion of ‘complexity begets stability’. Using weighted instead of unweighted food web measures can thus shed new light on classical theories, and possibly aid in finding what biological characteristics drive the stability of food webs.

Acknowledgements

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Table A3.1 Biomasses (yearly averages, kg C ha⁻¹ yr⁻¹) for the functional groups of the 15 soil food webs.

	CPER	HSB- CT	HSB- NT	KS- B0	KS- B120	LH- IF	LH- CF	SCH- 1	SCH- 2	SCH- 3	SCH- 4	HUL- 1	HUL- 2	HUL- 3	HUL- 4
Microorganisms															
Bacteria	304	690	440	740	900	245.75	227.5	1.14	4.72	18.75	17.82	3.07	3.85	7.38	9.43
Saprophytic fungi	63	150	160	1500	2300	3.28	2.13	0.03	0.13	0.21	0.29	0.01	0.02	0.18	0.74
Mycorrhizae	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Protozoa															
Amoebae	3.78	50	40	110	34	18.90	11.53	0.01	0.03	0.20	0.35	0.004	0.04	0.03	0.12
Flagellates	0.16	-	-	-	-	0.63	0.53	0.0003	0.004	0.04	0.11	0.0001	0.005	0.006	0.04
Nematodes															
Herbivores	2.9	0.5	0.4	0.18	0.29	0.36	0.19	0.000004	0.003	0.0009	0.0003	-	0.001	0.001	0.00003
Bacteriovores	5.8	1.4	0.46	0.45	0.5	0.36	0.30	0.00006	0.01	0.04	0.07	0.0002	0.010	0.02	0.03
Fungivores	0.41	0.08	0.12	0.2	0.12	0.13	0.08	0.0002	0.004	0.02	0.006	0.0004	0.002	0.02	0.02
Omnivores	0.65	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Predators	1.08	-	-	0.44	0.44	0.06	0.06	0.00003	0.03	0.009	0.005	0.008	0.04	0.05	0.02
Arthropods															
Herbivorous herbage arthropods	-	-	-	0.1	0.14	-	-	-	-	-	-	-	-	-	-
Predatory herbage arthropods	-	-	-	0.15	0.19	-	-	-	-	-	-	-	-	-	-
Herbivorous macroarthropods	-	-	-	0.19	0.19	-	-	-	-	-	-	-	-	-	-

(Continued)

Table A3.1 (Continued)

	C _{PER}	HSB- CT	HSB- NT	KS- B0	KS- B120	LH- IF	LH- CF	SCH- 1	SCH- 2	SCH- 3	SCH- 4	HUL- 1	HUL- 2	HUL- 3	HUL- 4
Microbivorous	-	-	-	0.25	0.25	-	-	-	-	-	-	-	-	-	-
Macroarthropods															
Predatory macroarthropods	-	-	-	0.49	0.49	-	-	-	-	-	-	-	-	-	-
Predatory mites	0.16	0.04	0.2	0.18	0.28	0.08	0.06	-	0.0009	0.02	0.08	-	0.0008	0.02	0.02
Nematophagous mites	0.16	-	-	-	-	0.007	0.004	-	-	0.00008	0.01	-	-	-	0.009
Cryptostigmatic mites	1.68	0.22	0.8	-	-	0.003	0.007	0.00005	0.01	0.02	0.13	0.0004	0.03	0.0008	0.11
Noncryptostigmatic mites	1.36	0.39	0.9	-	-	0.04	0.02	0.0002	0.06	0.07	0.08	0.005	0.06	0.03	0.02
Bacterivorous mites	-	-	-	-	-	0.0003	0.001	-	-	-	0.0005	-	-	-	0.00001
Collembolans	0.46	0.09	0.3	0.17	0.17	0.38	0.47	-	0.002	0.06	0.07	-	0.0378	0.19	0.10
Predatory collembola	-	-	-	-	-	0.008	0.03	-	-	-	0.001	0	0	0.0002	0.007
Annelids															
Enchytraeids	-	0.3	0.1	4.2	3.4	0.21	0.43	-	-	-	-	-	-	-	-
Earthworms	-	20	100	13	13	63.53	-	-	-	-	-	-	-	-	-
Basal groups															
Detritus	3000	8400	6000	22400	32000	2500	2500	4	25	250	2500	4	25	250	2500
Roots	300	200	250	500	700	350	300	225	900	900	675	0	900	900	900

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjetslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (each stage is averaged over four replications) (Neutel et al. 2007), 6 Hulshorsterzand Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (each stage is averaged over four replications) (Neutel et al. 2007).

Table A3.2 Distribution properties of the flux distributions of the 15 soil food webs.

	Nr. of fluxes	Minimum	1 st quartile	median	mean	3 rd quartile	Maximum
CPER¹	56	0.002	0.22	1.43	62.62	13.96	1818
HSB-CT²	32	0.01	0.83	4.92	294.1	185	5471
HSB-NT²	32	0.07	1.44	4.65	344.3	206.5	3894
KS-B0³	58	0.03	0.82	3.28	79.77	11.6	1445
KS-B120³	58	0.007	0.71	3.29	71.67	17.3	1096
LH-IF⁴	58	0.0001	0.02	0.33	118	5.18	2058
LH-CF⁴	56	0.0003	0.02	0.27	46.04	4.58	1606
SCH-1⁵	27	9.41·10 ⁻⁷	0.0001	0.001	8.59	0.02	225
SCH-2⁵	37	0.0001	0.005	0.09	25.45	0.52	900
SCH-3⁵	43	0.00001	0.005	0.08	24.09	0.63	900
SCH-4⁵	52	0.0001	0.008	0.09	16.27	1.02	675
HUL-1⁶	23	0.000003	0.002	0.03	0.77	0.08	12.96
HUL-2⁶	37	0.00002	0.004	0.19	25.47	0.45	900
HUL-3⁶	43	0.00004	0.006	0.15	22.96	0.58	900
HUL-4⁶	52	0.000002	0.007	0.07	19.29	0.81	900

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (each stage is averaged over four replications) (Neutel et al. 2007), 6 Hulshorsterzand Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (each stage is averaged over four replications) (Neutel et al. 2007).

Table A3.3 Distribution properties of the interaction strength distributions of the 15 soil food webs. Absolute values of interaction strengths were taken. The number of positive interaction strengths excludes the diagonal elements α_{ii} for $i \neq D$.

	Nr. of interaction strengths	Minimum	1 st quartile	median	mean	3 rd quartile	Maximum
CPER¹	95	0.0002	0.03	0.29	3.27	3.95	24.70
HSB-CT²	48	0.00009	0.03	1.15	4.49	7.54	20.54
HSB-NT²	48	0.00004	0.12	1.26	5.15	9.01	18.33
KS-B0³	94	0.00003	0.05	0.64	6.59	5.35	65.83
KS-B120³	94	0.00003	0.04	0.76	6.62	5.35	64.80
LH-IF⁴	95	0.000003	0.05	0.46	4.38	6.41	28.60
LH-CF⁴	93	0.000010	0.07	0.31	4.79	6.77	38.64
SCH-1⁵	42	$2.77 \cdot 10^{-8}$	0.02	1.08	4.51	7.98	16.18
SCH-2⁵	60	0.00007	0.04	1.18	16.09	7.10	212.90
SCH-3⁵	71	0.000003	0.08	0.45	5.21	6.82	39.59
SCH-4⁵	87	0.000002	0.09	0.53	7.04	8.61	63.03
HUL-1⁶	36	0.0003	0.06	3.19	24.52	10.66	268.50
HUL-2⁶	60	0.00004	0.06	1.98	30.11	7.16	388.70
HUL-3⁶	71	0.00003	0.04	0.87	16.70	7.59	240.00
HUL-4⁶	87	$5.62 \cdot 10^{-7}$	0.08	0.34	10.25	7.01	168.20

1 Central Plains Experimental Range (Hunt et al. 1987), 2 Horseshoe Bend Experimental Farm Conventional Tillage (CT) and No Tillage (NT) (Hendrix et al. 1986), 3 Kjettslinge Experimental Farm Barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990), 4 Lovinkhoeve Experimental Farm Integrated Farming (Int) and Conventional Farming (Con) (de Ruiter et al. 1993), 5 Schiermonnikoog Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (each stage is averaged over four replications) (Neutel et al. 2007), 6 Hulshorsterzand Primary Succession Stage 1, Stage 2, Stage 3, Stage 4 (each stage is averaged over four replications) (Neutel et al. 2007).

Chapter 4

The impact of bird herbivory on macrophytes and the resilience of the clear-water state in shallow lakes: a model study

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Wolf M. Mooij

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Abstract

Shallow lakes have the potential to switch between two alternative stable states: a clear macrophyte-dominated and a turbid phytoplankton-dominated state. Observational and experimental studies show that in some lakes herbivory by birds may severely decrease macrophyte biomass while in other lakes the removed biomass by herbivory is compensated by regrowth. These contradictory outcomes might arise because of an interplay between top-down control by herbivorous birds and bottom-up effects by nutrient loading on macrophytes. Here, we use the ecosystem model PCLake to study top-down and bottom-up control of macrophytes by coots and nutrient loading. We found that 1) herbivory by birds lowers the critical nutrient loading at which the regime shift occurs; 2) bird impact on macrophyte biomass through herbivory increases with nutrient loading; and 3) improved food quality enhances the impact of birds on macrophytes, thus decreasing the resilience of the clear-water state even further. The fact that herbivorous birds can have a large impact on macrophyte biomass and can facilitate a regime shift implies that the presence of waterfowl should be taken into account in the estimation of critical nutrient loadings to be used in water quality management.

Introduction

Shallow lakes have the potential to switch between two alternative stable states: a clear macrophyte-dominated and a turbid phytoplankton-dominated state (Jeppesen et al. 1990a, Scheffer 1990, Carpenter 2003). This switch can occur in response to gradual changes in external factors, such as nutrient loading, hydraulic loading, or temperature rise (Mooij et al. 2009), or in response to abrupt changes in one of the components of the aquatic food web through biomanipulation (Jeppesen et al. 1990a, Meijer et al. 1999, Mehner et al. 2002). The clear-water state is often preferred by water quality managers because of the associated biodiversity. Macrophytes play an important role in the resilience of the clear-water state (Carpenter and Lodge 1986, Scheffer et al. 1993), because they stabilize this state in multiple ways. For example, they reduce resedimentation of particles from the sediment of the lake (e.g. Horppila and Nurminen 2003). Also, they prevent phytoplankton growth by taking up available nutrients (e.g. van Donk and van de Bund 2002) and provide shelter for zooplankton (e.g. Shapiro 1990).

Whereas it is widely acknowledged that bottom up effects on submerged macrophytes through eutrophication play an important role in regime shifts in lakes, the importance of top-down control by herbivory on the macrophytes themselves remains unclear. Especially the effects of herbivory by waterbirds on submerged macrophytes is debated (Perrow et al. 1997, Marklund et al. 2002). Herbivorous waterbirds, such as coots, swans, and ducks, can visit lakes in large numbers and feed on roots and shoots of submerged macrophytes. Some studies found that herbivory by birds decreased macrophyte biomass severely (Sondergaard et al. 1996, Hilt 2006, Bakker and Nolet 2014), while others found that the removed biomass is compensated by macrophyte regrowth (Mitchell and Wass 1996, Perrow et al. 1997, Hansson et al. 2010). This apparent contradiction may arise from the varying conditions under which these studies have been conducted, such as the macrophyte and the herbivorous bird species under consideration, or the experimental set-up (Perrow et al. 1997, Bakker and Nolet 2014). A recent meta-analysis of all available field studies demonstrated that the impact of herbivorous birds on aquatic plants increases with bird density, offering the first proof that birds systematically reduce macrophyte biomass when present at sufficient densities (Wood et al. 2012). Thus, differences in bird density could possibly explain the differences in experimental outcomes.

However, another explanation for the contradictions in experimental outcomes could be that bottom-up effects through nutrient addition interact with the top-down control on macrophytes by birds. It has been hypothesized that the impact of herbivorous birds on macrophytes varies with the nutrient status of the lake (Perrow et al. 1997, Weisner et al. 1997, Hansson et al. 2010, Bakker and Nolet 2014). Possible mechanisms for this could be that under eutrophic conditions plants have a higher nutrient content relative to their carbon content, making them more preferred food (Bakker and Nolet 2014), and that plants have

less tolerance to grazing due to increased periphyton growth on the macrophytes (Weisner et al. 1997, Hilt 2006). These mechanisms could lead to a higher impact of herbivorous birds under more eutrophic but still transparent conditions.

Another open question is whether the impact of herbivory by waterbirds is limited to a reduction of the standing crop of macrophytes or, alternatively, could eventually lead to a regime shift to the turbid state in lakes (van Donk and Otte 1996, Janse et al. 1998, Hansson et al. 2010, Rip and McCann 2011). Herbivory induced regime shifts can be understood from the key role macrophytes play in stabilizing the clear state. If the grazing impact of herbivorous birds indeed increases under eutrophying conditions, then the largest impact would be close to the tipping point. Thus, in this already vulnerable phase, the resilience of the clear-water phase is decreased even further. However, there are currently no data available to test this hypothesis and therefore we used a modelling approach. A first attempt in this direction was made by Janse et al. (1998), who demonstrated with the ecosystem model PCLake that coot herbivory could indeed have caused the disappearance of macrophytes from restored Lake Zwemlust (The Netherlands) (van Donk and Otte 1996), leading to a shift to the turbid state.

Here, we go one step further by investigating the impact of herbivory on macrophyte biomass and the resilience of the clear-water state along a gradient of nutrient loadings. More specifically, we 1) calculate the effect of herbivorous birds on the critical nutrient loading (CNL) at which the shift from clear to turbid water occurs; 2) determine how the impact of herbivorous birds on macrophyte biomass changes along a nutrient gradient; and 3) investigate how food quality could affect bird impact on macrophytes. We hypothesize that herbivorous birds decrease the CNL by decreasing macrophyte biomass, and that the impact of herbivorous birds will increase with nutrient loading because of improved quality of the macrophytes as food.

Methods

PCLake is a dynamic model based on differential equations that calculates the carbon (for historical reasons expressed as dry weight) and nutrient flows (primarily phosphorus and nitrogen) between the food web compartments in a shallow lake ecosystem. Both the water column and the top layer of the sediment are included in the model. Trophic groups in the water column comprise three groups of phytoplankton (cyanobacteria, diatoms and green algae), planktivorous/benthivorous fish and piscivorous fish. The sediment layer includes settled phytoplankton and zoobenthos. Both water column and sediment layer contain pools for inorganic nutrients and detritus. We use the default setup of PCLake where submerged macrophytes are modelled as one functional group, with a separately modelled shoot and root part (Janse 2005). Macrophyte growth depends on water light conditions and available nutrients in both the water column and the sediment layer.

The model is known to show regime shifts between a clear, macrophyte-dominated state and a turbid, phytoplankton-dominated state when the nutrient loading is either increased (eutrophication) or decreased (re-oligotrophication) (Janse 1997). The critical nutrient loading (hereafter referred to as CNL) at which the shift from the clear-water state to the turbid-water state occurs is higher than the CNL at which the reverse shift occurs. Thus, the model shows hysteresis and alternative stable states for intermediate levels of nutrient loading. In this study, we concentrate on the higher one of the two critical nutrient loadings, that is the CNL during eutrophication.

Herbivorous birds are modelled in PCLake as an external factor that reduces macrophyte biomass, following the approach of Janse et al. (1998). Coots (*Fulica atra*) are taken as a model species. Macrophyte biomass that is ingested but not assimilated by the coots is returned to the water compartment as detritus and freely available nutrients, while the fraction that is assimilated is lost from the system. The amount of macrophyte biomass that is grazed by coots, G (g dry weight $\text{m}^{-2} \text{d}^{-1}$), is modelled with a Holling type II functional response as:

$$G = \frac{qVbg}{10000(h_d + V)} \quad (4.1)$$

with V the macrophyte biomass (g dry weight m^{-2}), q the preference of birds for macrophytes (dimensionless), b the number of coots per ha (a parameter, divided by 10,000 because PCLake uses m^2 as the unit for surface), g the amount of macrophytes grazed per coot (g dry weight coot $^{-1} \text{d}^{-1}$), and h_d the half-saturation constant (g dry weight m^{-2}). We used the standard parametrization of PCLake ($h_d = 5$ g dry weight m^{-2} and $g = 45$ g dry weight coot $^{-1} \text{d}^{-1}$) (Janse et al. 1998).

To investigate the role of food quality, we defined the preference of coots for macrophytes q in two ways. First, we performed the analyses for $q = 1$, thus ignoring the role of food quality. Second, we let q depend on the carbon-to-phosphorus ratio (C:P ratio) of the macrophytes, where low C:P ratios are associated with high food quality, and high C:P ratios with low food quality. If this macrophyte C:P ratio was lower than a reference value (see below), coots were allowed to eat up till 20% more macrophyte biomass than what they would eat when food quality was not taken into account (i.e. when $q = 1$). If the C:P ratio was higher than the reference value, coots were allowed to eat up till 20% less macrophyte biomass. As a reference value, we used for each coot density b the mid-range of all possible macrophyte C:P ratios along the nutrient loading axis when food quality was ignored. This led to the following formula for q when food quality is taken into account:

$$q = \begin{cases} 0.8 & \text{for } \frac{CP}{CP_{ref}} < 0.8, \\ \frac{CP}{CP_{ref}} & \text{for } 0.8 \leq \frac{CP}{CP_{ref}} \leq 1.2, \\ 1.2 & \text{for } \frac{CP}{CP_{ref}} > 1.2. \end{cases} \quad (4.2)$$

with CP the C:P ratio of macrophytes at any particular time step, and CP_{ref} the mid-range reference value. We thus assume that birds eat more (less) macrophytes when macrophyte C:P ratio is lower (higher) than the reference C:P ratio. Moreover, we assume that this change in food intake is proportional to the relative difference between the actual macrophyte C:P ratio and the reference C:P ratio.

We performed a bifurcation analysis with phosphorus (P) loading as the bifurcation parameter (varied between 0.35 and 5 mg P m⁻² d⁻¹). We did this for six different coot densities (b in eq. 4.1): 0, 5, 10, 20, 35, and 50 coots per ha. In the bifurcation analysis, the model was run for 20 years, starting on the lower end of the phosphorus gradient in conditions that represented a clear-water state. Birds were entered in the system after 10 years, and were assumed to be present each year between February 15th and October 15th. Thus, we allowed the birds to be present the entire spring and summer. Additional analysis showed that allowing the birds to be present in winter resulted in only small quantitative differences, and gave similar results qualitatively (not shown). In the 20th year of the simulation, summer averages of chlorophyll-a were measured to determine the impact of herbivorous birds on CNL. At the same moment, summer averages of macrophyte biomass were measured to determine the impact of herbivorous birds on macrophyte biomass. We expressed bird impact as the reduction of macrophyte biomass in scenarios where birds were present, relative to the macrophyte biomass in the scenarios where birds were absent. This measure of bird impact allowed us to compare our results to what was found in field studies (Hansson et al. 2010, Wood et al. 2012).

Results

The critical nutrient loading (CNL) during eutrophication was lower when coots were present, compared to the situation when coots were absent (Figure 4.1). When coots were absent, the CNL was 3 mg P m⁻² d⁻¹. At a density of 10 coots ha⁻¹, CNL was reduced by 18% (CNL=2.3 mg P m⁻² d⁻¹) compared to the CNL when coots were absent; at a density of 35 coots ha⁻¹, CNL was even reduced by 70% (CNL=1 mg P m⁻² d⁻¹), whereas at 50 coots ha⁻¹ there was no stable clear water state. Thus, herbivory by coots enhanced the transition of a clear to a turbid-water state and the higher the density of coots, the more the CNL was decreased.

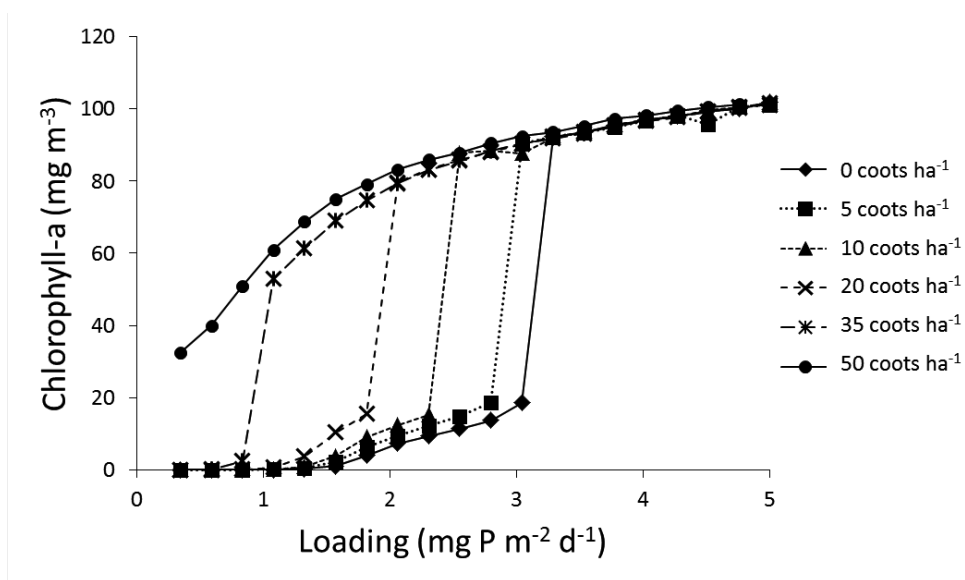


Figure 4.1 Effect of grazing coots on chlorophyll-a along a nutrient loading axis during eutrophication. At a density of 50 coots ha⁻¹, the model predicts that the lake is in the turbid state for all loadings.

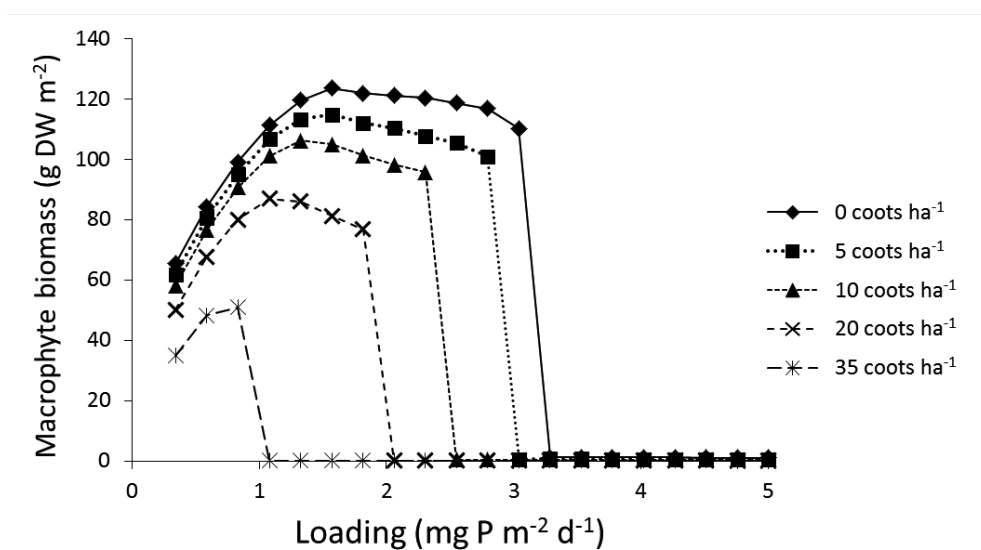


Figure 4.2 Effect of grazing coots on macrophyte biomass along a nutrient loading axis during eutrophication. At a density of 50 coots ha⁻¹ macrophytes were not present for any of the P loadings.

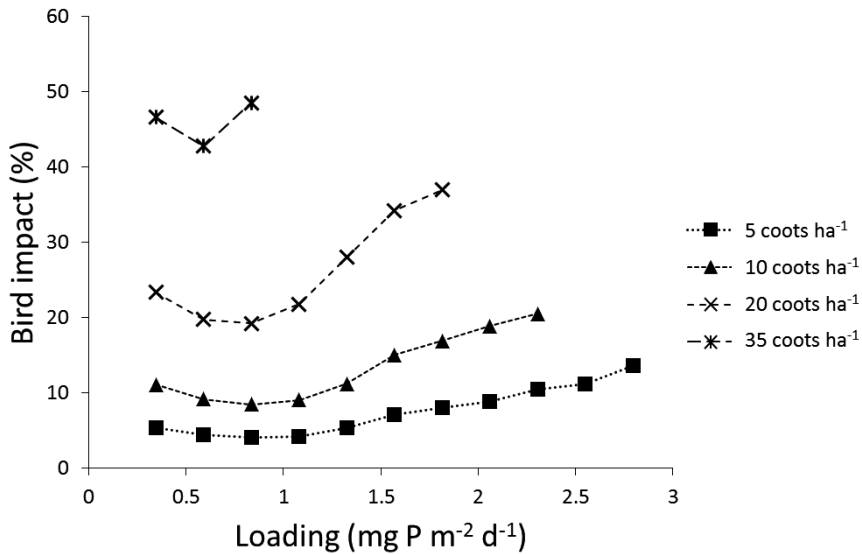


Figure 4.3 The impact of birds, expressed as the percentage decrease in macrophyte biomass relative to macrophyte biomass in absence of birds, under different nutrient conditions during eutrophication. At a density of 50 coots ha⁻¹ macrophytes were not present for any of the P loadings.

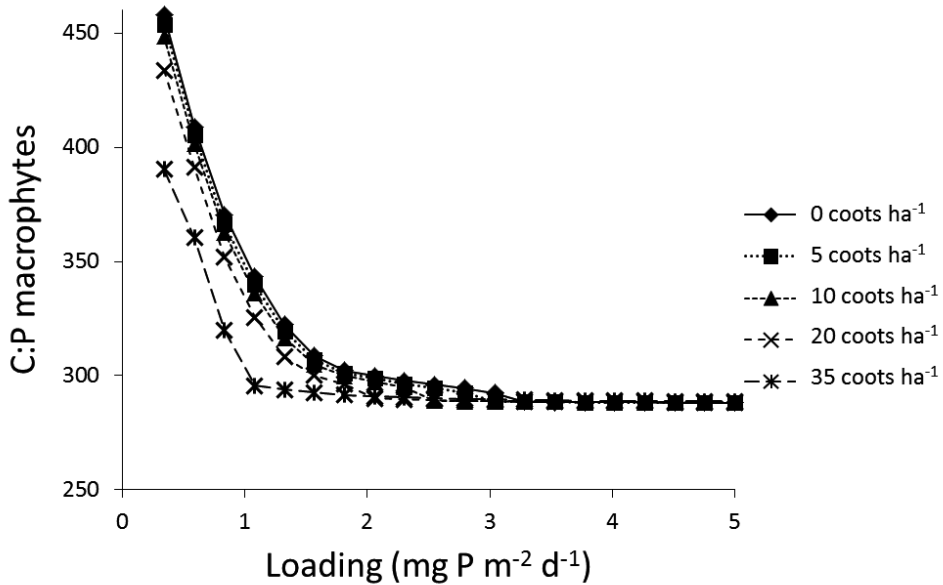


Figure 4.4 C:P ratio of macrophytes decreases with increasing P loading and increasing coot density during eutrophication. At a density of 50 coots ha⁻¹ macrophytes were not present for any of the P loadings.

Macrophyte biomass was lower when coots were present compared to the situation where coots were absent (Figure 4.2). When coots were absent, macrophyte biomass first showed a steep increase with increasing P loading and then slowly decreased until macrophytes practically disappeared at the CNL where the switch to the turbid state occurred. This pattern was repeated when coots were present, but with increasingly lower macrophyte biomass at increasing bird density. This difference in biomass between the scenario with birds compared to the situation without birds becomes more prominent when the CNL is approached (Figure 4.2). Because macrophytes completely disappear at lower CNL with increasing bird densities (see Figure 4.1) the decrease in macrophytes at intermediate nutrient loadings is no longer present in the scenario with 35 coots ha^{-1} . As macrophytes cannot coexist with 50 coots ha^{-1} (Figure 4.1) we do not show the results for this scenario in this and the following analyses.

The impact of grazing coots, expressed as the percentage reduction in macrophyte biomass compared to the situation where coots were absent, was largest at very low nutrient loadings and near the CNL (Figure 4.3). In between these extremes in nutrient loading, the impact of herbivory was smaller (Figure 4.3). Bird impact also increased with coot density for all nutrient loadings: at a density of 10 coots ha^{-1} , bird impact varied between 11 and 19 %, while at a density of 35 coots ha^{-1} , bird impact varied between 43 and 48%.

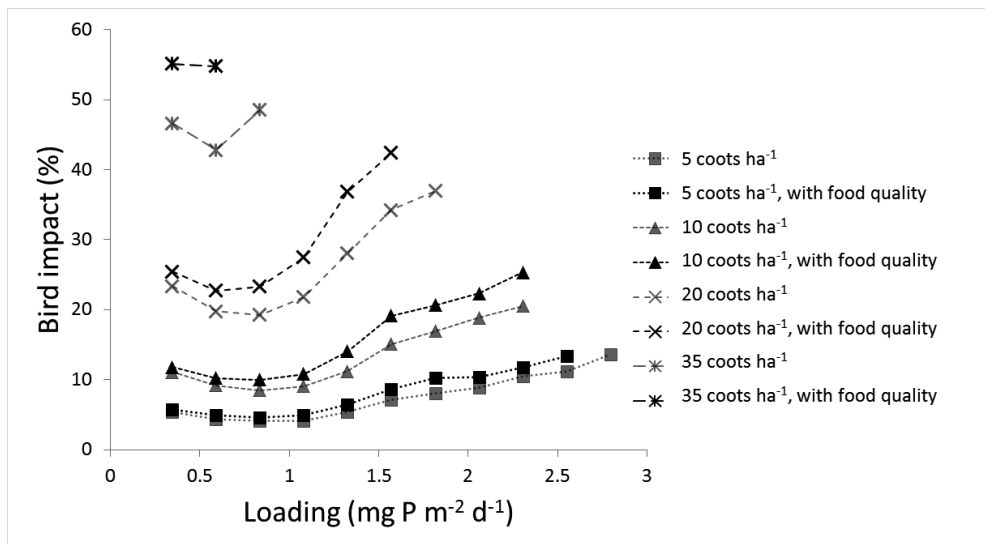


Figure 4.5: Bird impact when food quality is taken into account (q defined as in eq. 4.2, black lines) during eutrophication. Bird impact without food quality ($q = 1$, grey lines) is shown for comparison. At a density of 50 coots ha^{-1} macrophytes were not present for any of the P loadings.

With the preference of coots for macrophytes (q) set equal to one, the quality of macrophytes as food (measured as the C:P ratio) increased with increasing P loading (i.e. macrophyte C:P ratio decreased, Figure 4.4). For the reference value CP_{ref} in eq. 4.2, we took the mid-range of macrophyte C:P ratios along the P loading axis (0.35 - 5 mg P m⁻² d⁻¹). But because the macrophyte C:P ratio decreased with increasing coot density as well, CP_{ref} was defined for each coot density separately. For example, CP_{ref} for a density of 5, 10, 20, and 35 coots ha⁻¹ was equal to 371, 368, 361, and 340 respectively.

When the analyses were performed with coot preference for macrophytes dependent on macrophyte C:P ratio (q defined as in eq. 4.2), we found similar patterns for CNL (not shown), macrophyte biomass (not shown), and bird impact (Figure 4.5) as in the situation where food quality was not taken into account ($q = 1$), but all effects were enhanced. Overall, coots grazed more biomass when their grazing rate was dependent on food quality, which resulted in an even lower CNL compared to the situation when food quality was not taken into account (not shown). At very low P loadings, bird impact was quite similar, especially for the lower coot densities (Figure 4.5). With increasing P loadings the increase in bird impact as a result of improved food quality became more prominent until the CNL was reached.

Discussion

Many field studies and field experiments have been performed to determine the effects of birds on macrophyte biomass. Whereas it has been shown that birds significantly reduce macrophyte biomass at increasing bird densities (Wood et al. 2012), the diversity in experimental set-ups masks the role of environmental factors, such as nutrient loading. Furthermore, it remains unclear whether the impact of birds on macrophyte biomass can induce a regime shift. Here, we used an established ecosystem model, PCLake, to test in a standardized way for different nutrient loadings what the impact of birds is on macrophyte biomass, and whether birds could induce a regime shift from a clear- to a turbid-water state. We showed that: 1) herbivorous birds lower the critical nutrient loading at which the regime shift occurs, implying that at intermediate nutrient loadings birds can trigger a regime shift, 2) bird impact on macrophyte biomass through herbivory increases with nutrient status, and 3) improved food quality can enhance the impact of birds on macrophytes and thereby decrease the resilience of the clear-water state even further.

Previous studies have shown that grazing coots could be responsible for the decreasing stability of the clear-water state in Lake Zwemlust (van Donk and Otte 1996, Janse et al. 1998). By means of the modelling study presented here, we can now generalize this finding for a range of bird densities and nutrient loadings. The range of chosen bird densities during summer that we used in our study (5-50 coots ha⁻¹) encompasses densities as reported from field observations (Lauridsen et al. 1993, Sondergaard et al. 1996, Hilt

2006). When herbivorous birds were added at such densities to the food web, the critical nutrient loading (CNL) during eutrophication was lower than the CNL in the situation where birds were absent. This was true for all bird densities, but the reduction in the CNL became most prominent with increased bird densities. This result fits well with the results of Wood et al. (2012), who found that macrophyte reduction increases with increasing bird density. It might be that in the field, the reduction in CNL is even larger than predicted by PCLake, as grazing birds can have negative effects on the clear-water state via changes in nutrient cycling. For example, they could add allochthonous nutrients through their droppings, thereby contributing to eutrophication directly (Hahn et al. 2008, Chaichana et al. 2010).

In our model study, we saw that bird impact was highest near the critical nutrient loading. At this point, the resilience of the clear-water state becomes very low, even without the extra herbivore pressure on macrophytes. Therefore, herbivory by birds has a synergistic effect with mechanisms that erode the resilience of the system during eutrophication, in particular shading by phytoplankton and periphyton in the case of freshwater lakes (Weisner et al. 1997, Hilt 2006). For very low nutrient loadings, however, bird impact decreased with increasing nutrient loading. This antagonistic effect is most likely caused by the low macrophyte biomass at very low nutrient loadings making the amount of macrophyte biomass that is grazed relatively large compared to the available biomass.

The measure we chose for bird impact, i.e. the relative change of macrophyte biomass compared to the situation without birds, has been used in many field studies with enclosure experiments (e.g. Perrow et al. 1997, Hilt 2006, Hidding et al. 2010). The outcomes of these experiments were extremely variable, with bird impact ranging from zero or a few percent difference to 100% difference (i.e. complete removal; see references in Hansson et al. 2010, Wood et al. 2012). This is probably due to the highly variable experimental set-ups with different bird densities, different lake conditions, and different bird species. Our analyses showed that such a wide range in bird impact (4.1% - 55% or even 100% if we include the herbivory induced turbid state with no macrophytes) is indeed a plausible outcome when we take nutrient status of the lake, bird density and the effects of food quality on grazing rate into account.

The hypothesis of Bakker and Nolet (2014) states that macrophyte food quality would be higher in eutrophic lakes and that birds would therefore increase the proportion of macrophytes in their diets. In support of this hypothesis we showed that along with P loading macrophyte C:P ratio decreases and bird impact increases. But although somewhat less prominent, the increase in bird impact with increasing nutrient load was also visible when we did not take food quality into account. Thus, an increase in food quality is probably not the only cause for an increase in bird impact with increased nutrient loading. It

is important to note that because of the way in which we incorporated food quality (see eq. 4.2), birds were allowed to eat more but also less of macrophytes compared to the reference situation in which food quality was not taken into account. In the scenarios that we analysed, however, birds always ate more macrophytes when food quality was taken into account. It is also interesting to see that macrophyte C:P ratio decreases with increasing coot density as a result of nutrient recycling by grazing. This positive feedback between herbivores and plant quality is known in both aquatic and terrestrial systems (Sturner and Elser 2002, Krumins et al. 2015).

Using a model approach, we could investigate the effects of herbivorous birds on macrophyte biomass and critical transitions in lakes in a systematic way. That is, nutrient loading and coot density were varied in a factorial design and all other aspects were kept constant. In our study we focussed on the effects of nutrient loading and food quality on bird impact on macrophyte biomass. However, herbivorous birds can influence regime shifts in other ways apart from grazing. For example, an effect regularly seen is that grazing birds alter macrophyte species composition, because they prefer certain macrophyte species over others (van Donk and Otte 1996, Hidding et al. 2010, Gayet et al. 2011). Making birds a dynamic factor in the model may also seem a logical extension but is problematic because most waterbirds spend part of their life cycle outside the lake.

The fact that herbivorous birds can have a large impact on macrophyte biomass and can accelerate a regime shift implies that the presence of waterfowl should be taken into account in water quality management scenarios. Complex ecosystem models such as PCLake are frequently applied by lake managers as part of a system analysis to obtain insight in the functioning of their lake, and to estimate the CNL. The concept of CNL provides lake managers with a straightforward dependent variable to steer upon, as the actual phosphorus loading can easily be compared with the CNL, and the concept is simple to communicate to stakeholders. Our study shows that bird density is important to take into account to obtain the most accurate prediction of the CNL. Although we show that the CNL of a lake is negatively affected by grazing birds, controlling their abundance would not bring a sustainable solution: the impact of birds is highest in the domain where the resilience of the lake is already low because of high nutrient loading. While bird management may potentially be part of a set of management measures that can be applied to increase the resilience of the lake, the vulnerability to regime change during eutrophication is primarily a function of the external nutrient loading (Scheffer et al. 1993). Nutrient input reductions should therefore form the basis of any management program aiming at safeguarding the clear water state. Given the freedom of birds to move from one lake to another, when considering the impact of birds, regional (or even larger) scales are important besides local scales.

In summary, in this model study we showed that herbivorous birds can decrease macrophyte biomass in shallow lakes to such an extent that a regime shift from a clear-water state to a turbid-water state is initiated. If birds respond to improved food quality with increased grazing, then the probability of such a shift is even enhanced. Taking a model approach to study the effects of herbivorous birds on macrophytes and the state of the lake reveals that birds should be taken into serious consideration by water quality managers who try to preserve or recover the clear-water state of the lake.

Acknowledgements

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Chapter 5

Food web stability signals critical transitions in temperate shallow lakes

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Abstract

A principal aim of ecologists is to identify critical levels of environmental change beyond which ecosystems undergo radical shifts in their functioning. Both food web theory and alternative stable states theory provide fundamental clues to mechanisms conferring stability to natural systems. Yet, it is unclear how the concept of food web stability is associated with the resilience of ecosystems susceptible to regime change. Here we use a novel combination of food web and ecosystem modelling to show that impending catastrophic shifts in shallow lakes are preceded by a destabilizing reorganization of interaction strengths in the aquatic food web. Analysis of the intricate web of trophic interactions reveals that only few key interactions, involving zooplankton, diatoms and detritus, dictate the deterioration of food web stability. Our study exposes a tight link between food web dynamics and the dynamics of the whole ecosystem, implying that trophic organization may serve as an empirical indicator of ecosystem resilience.

Introduction

Current manifestations of anthropogenic stresses on ecosystems have intensified the need to understand and predict the resilience and stability of ecological systems (Vitousek et al. 1997, Crutzen 2002, Rockstrom et al. 2009). Resilience and stability are topics that have inspired ecologists since the onset of the discipline (Elton 1924, MacArthur 1955), and different theories and conceptual frameworks have developed around these topics, including alternative stable states theory and food web theory.

Alternative stable states theory explains large scale catastrophic shifts in ecosystems - i.e. the ultimate loss of resilience - from positive feedbacks and non-linear interactions among biotic and abiotic key components of the system in relation to external forcings (May 1977, Scheffer et al. 1993, Scheffer et al. 2001). Catastrophic shifts are observed in various ecosystems including peatlands, rangelands, reef systems and shallow lakes, and generally occur unexpectedly (Scheffer et al. 2009). Recent research has identified generic empirical indicators of resilience that might allow to anticipate critical transitions (Scheffer et al. 2009).

Food web theory elucidates which stabilizing mechanisms underlie the complex networks of trophic interactions that are found in nature, looking at the richness, patterning and strength of interactions among species (May 1972, de Ruiter et al. 1995, McCann et al. 1998, Rooney et al. 2006, Neutel et al. 2007). As food webs reflect the flows of energy through a system, their features - including stabilizing properties - are important to ecosystem functions such as carbon and nutrient cycling (Berlow et al. 2004, de Vries et al. 2013). Food webs provide an explicit link between community structure and the maintenance of ecosystem processes.

Although the conceptual frameworks of food webs and alternative stable states are highly influential in modern ecology, they developed independently and catastrophic regime shifts in ecosystems have seldom been explicitly linked to stability properties of complex trophic networks (Ings et al. 2009). Here we test whether indices for stability as defined by food web theory can disclose an impending catastrophic shift in ecosystem state. On one hand, we hypothesize that food web stability and ecosystem stability are inherently linked, considering the key role of food webs in governing the flows of energy through the ecosystem. On the other hand, we ask whether descriptions of food webs contain sufficient information on self-enhancing feedbacks to expose the non-linear behavior of the ecosystem in response to external forcing.

As a model system we use temperate shallow lakes, for which abrupt changes between a submerged macrophyte-dominated state and a phytoplankton-dominated state are empirically well documented (Blindow et al. 1993, Ibelings et al. 2007). In this context shallow lakes are particularly intriguing because many of the feedback loops that keep the

system in each stable state involve the abiotic environment and are therefore not considered in a food web approach to the system (Scheffer et al. 1993).

We use a full scale and well tested dynamic ecosystem model of non-stratifying shallow lakes to simulate a catastrophic regime shift in ecosystem state. The model was originally developed to describe the main nutrient fluxes in Lake Loosdrecht in the Netherlands (Janse et al. 1992, van Liere and Janse 1992), and has since been calibrated with data from more than 40 temperate lakes to obtain a best overall fit, making it suitable for more generalized studies on temperate shallow lakes (Janse et al. 2010). The model has been successful in describing regime shifts in many case studies (van Gerven et al. 2015).

We run the model for a range of nutrient loadings from oligotrophic to hypertrophic conditions and vice versa, to simulate the typical loading history of many shallow lakes in the temperate zone in the second half of the twentieth century (Gulati and van Donk 2002). For each loading level, we run the model until the seasonally forced equilibrium is reached, and obtain the average chlorophyll-*a* concentration to characterize the state of the lake ecosystem; chlorophyll-*a* is one of the most common proxies for water quality used by ecosystem managers. Also, we collect food web data from the ecosystem model to construct material flux descriptions of the aquatic food web at each loading level (Fig. 5.1) (de Ruiter et al. 1993, Moore and de Ruiter 2012).

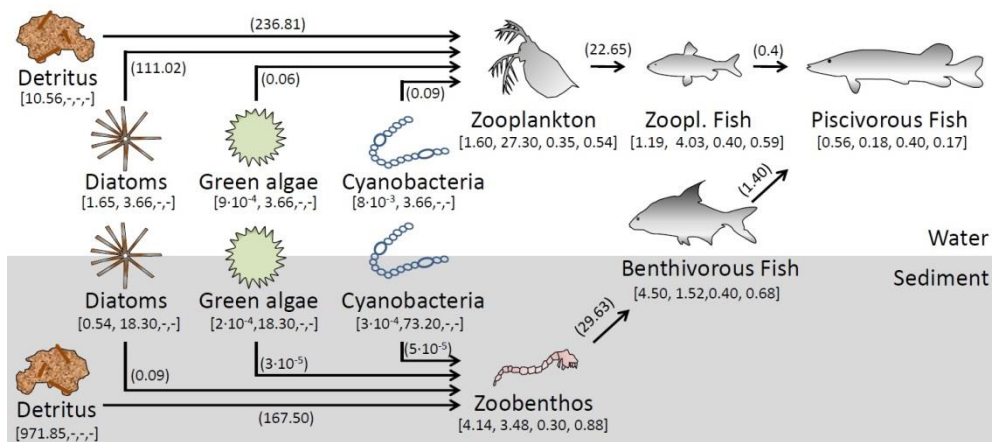


Figure 5.1 Schematic representation of the aquatic food web and the feeding relations. The food web comprises a pelagic and benthic food chain linked by a shared predator. Data (square brackets) used to calculate feeding rates (parentheses) are given in the sequence biomass (g m^{-2}), specific death rate (year^{-1}), assimilation efficiency and production efficiency. Feeding rates ($\text{g m}^{-2} \text{ year}^{-1}$) are given near their respective arrows. Settling, resuspension and reproduction fluxes and flows to the detritus pools are not represented here but were included in the analyses. The data belong to a clear-water state receiving $2.6 \text{ mg P m}^{-2} \text{ d}^{-1}$.

From these food web properties, we estimate the per capita interaction strengths between the trophic groups, using established methods typically used by food web ecologists to describe empirical food webs (de Ruiter et al. 1995, Neutel et al. 2007), based on the principles of May (1972) and Lotka-Volterra type equations (de Ruiter et al. 1995, Moore and de Ruiter 2012). Interaction strengths represent the size of the effects of species on each other's dynamics near equilibrium and define the elements of the (Jacobian) community matrix representation of the food web (May 1972). Food web stability is assessed using the diagonal strength metric (s) (Neutel et al. 2002), being the minimum degree of relative intraspecific interaction needed for matrix stability. Thus, for each level of nutrient loading, we obtain a parameterized (Jacobian) community matrix description of the food web embedded in the ecosystem, and evaluate its stability.

The results of this combined modelling approach show that imminent shifts in ecosystem state during eutrophication and re-oligotrophication are preceded by a destabilizing reorganization of the trophic web. This suggests that trophic organization can serve as an empirical indicator of ecosystem resilience. We show that only few key trophic interactions dictate the decrease of food web stability, particularly among lower trophic level groups, and emphasize the role of destabilizing trophic cascades. Hence, by using a food web approach to ecosystem stability we refine our mechanistic understanding of the biological processes underlying sudden shifts in ecosystem state.

Results

Ecosystem response to nutrient loading.

The bifurcation analysis of the full-scale shallow lake ecosystem model showed the occurrence of alternative stable states between a phosphorus (P) loading of 1.3 and 3.7 mg P m⁻² day⁻¹ (Fig. 5.2a). During eutrophication (Fig. 5.2a, blue line), the macrophyte-dominated clear-water state marked by a low level of chlorophyll-*a* disintegrates abruptly when the critical phosphorus loading is reached, shifting the system to a phytoplankton-dominated state with high levels of chlorophyll-*a*. During re-oligotrophication (Fig. 5.2a, red line) the system lingers in the turbid state until the phosphorus loading is much reduced and the reverse shift back to the clear-water state occurs. The delayed response of chlorophyll-*a* to changes in nutrient loading - i.e. hysteresis - is consistent with many field observations which provide strong empirical evidence for the existence of alternative stable states (Scheffer and Carpenter 2003, Ibelings et al. 2007). An important observation here is that in the clear-water state the average chlorophyll-*a* level hardly responds to eutrophication (Fig. 5.2a), and thus gives no indication for the loss of resilience of the system.

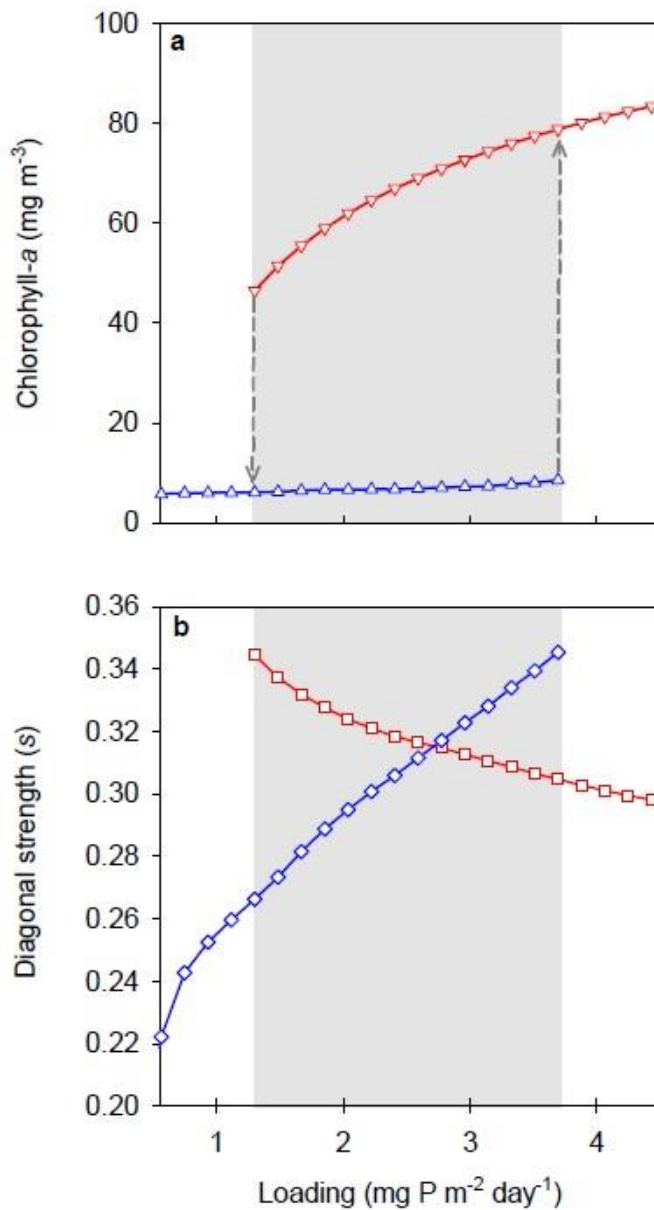


Figure 5.2 Ecosystem and food web response to nutrient loading. (a) The equilibrium concentration (yearly average) chlorophyll-*a* in the water column, as proxy for the ecosystem state, for two initial states: a clear- (blue upward triangles) and a turbid-water state (red downward triangles). (b) Food web stability, represented by the intraspecific interaction needed for matrix stability (*s*) for food webs in a clear- (blue diamonds) and a turbid-water state (red squares). Stability decreases with increasing *s*.

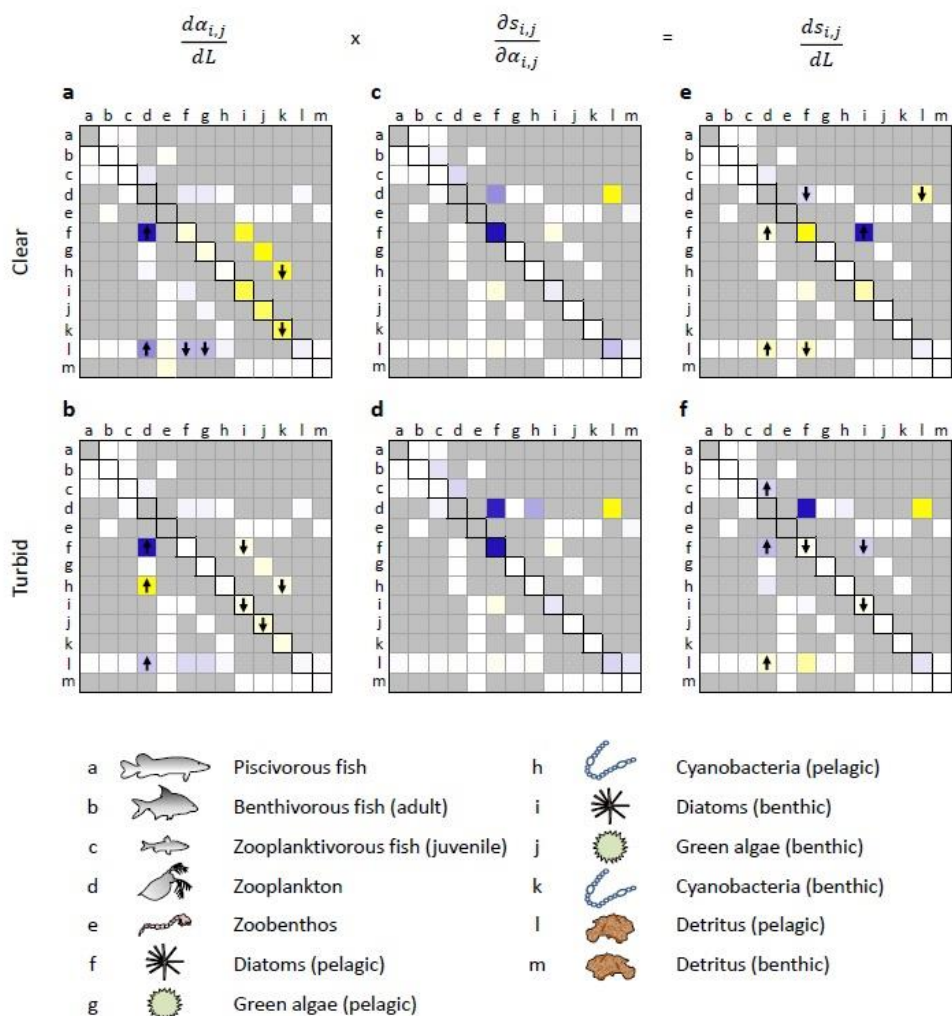


Figure 5.3 Graphical summarization of the changing trophic interactions and their impact on food web stability. The left panels show which interaction terms are impacted by changing nutrient loading. Cell colour indicates whether interaction strength increases (blue), decreases (yellow) or does not change (white) during eutrophication (a) and re-oligotrophication (b). Colour intensity depicts the relative magnitude of change. Arrows indicate whether the change is notably progressive (upward) or descending (downward) towards the regime shift. The middle panels (c,d) show the sensitivity of food web stability to changes in interaction strengths. An increase of interaction strength can have a positive effect (blue cells), negative effect (yellow cells) or no effect (white cells) on stability (and hence an inverse effect on s). The intensity of the colour indicates the relative magnitude of the effect. The right panels show the contribution of each interaction term to the impact of eutrophication (e) and re-oligotrophication (f) on food web stability, which is the product of the foregoing. Colours indicate whether interactions have a positive (blue), negative (yellow) or no effect (white) on stability (and inversely on s).

Food web response to nutrient loading.

We followed the interaction strengths in the trophic web and evaluated food web stability along the eutrophication axis using diagonal strength as an indicator (see methods). We found that with increasing lake productivity (Fig. 5.2b, blue line), destabilizing changes in the food web occurred: decreasing food web stability forebodes the catastrophic shift. This result is not trivial because the ecosystem model and the food web model differ distinctly in structure and shape of the interactions. At the critical nutrient loading, the food web underwent a drastic reorganization to a phytoplankton-dominated configuration, coinciding with a sudden increase of stability (decrease in diagonal strength, from blue to red line in Fig. 5.2b). Intriguingly, we found that during re-oligotrophication (Fig. 5.2b, red line) which is needed for ecosystem recovery, a similar decrease in food web stability was visible, again followed by a sudden re-establishment of stability once the critical nutrient loading for ecosystem recovery was reached. Thus, depending on the trophic organization of the food web, enrichment and impoverishment can both be destabilizing, even though the topology of the web is the same. From an alternative stable states point of view, this can be explained as clear- and turbid-water states each having a basin of attraction that deteriorates towards a tipping point. Hence, we find food web stability to be associated with the resilience of the attracting equilibrium.

Identifying stabilizing and destabilizing interactions.

Food web stability is an aggregated measure with a multitude of underlying processes. We here present an innovative approach to decipher which interactions are primary responsible for the eroding stability during eutrophication and re-oligotrophication. At a given level of nutrient loading, the stability metric s follows directly from the interaction terms in the (Jacobian) community matrix. By varying the strength of each element in the matrix, we calculated the relative sensitivity of s to changes in each specific trophic interaction: $\frac{\partial s}{\partial \alpha_{i,j}}$,

where $\alpha_{i,j}$ is the interaction effect of species j on species i . As such, we reveal the intrinsic dynamics of the food web, i.e. how stability is constrained by the architecture of the food web. Besides the sensitivity, the effect of $\alpha_{i,j}$ on s depends on the actual change of $\alpha_{i,j}$ in response to nutrient loading L : $\frac{d\alpha_{i,j}}{dL}$. Note that changes in interaction strength along the nutrient loading axis may be imposed by forces in the ecosystem that are not explicitly considered in the food web model, such as oxygen dynamics and stoichiometry. Taken together, the following formula can be used to disentangle which and how changing interactions contribute to the weakening of stability (Supplementary Fig. S5.1):

$$\frac{ds}{dL} \approx \sum_i^n \sum_j^n \frac{d\alpha_{i,j}}{dL} \frac{\partial s}{\partial \alpha_{i,j}} \quad (5.1)$$

We found that both during eutrophication (Fig. 5.3a) and re-oligotrophication (Fig. 5.3b) several interactions in the lake food web increased or decreased in strength in response to changing nutrient loading. The majority of these interactions involved zooplankton, benthic and pelagic phytoplankton species or detritus. Most interactions however were unaffected by changing nutrient loading. When we analysed the sensitivity of food web stability to changes in specific interaction strengths, we found that food web stability is sensitive to only a select number of interactions, and that there is just a partial overlap with the interactions that actually changed along the loading axes (Fig. 5.3c, d). As a result, the observed changes in food web stability during eutrophication and re-oligotrophication can be attributed to only a handful of interactions, involving detritus, diatoms and zooplankton (Fig. 5.3e, f). These are interactions of which the strengths change along the eutrophication axis *and* to which food web stability is sensitive. Most destabilizing were the interaction effects between zooplankton and detritus, the effect of pelagic diatoms on detritus, and the effect of pelagic diatoms on themselves relating to sedimentation (Fig. 5.3, Supplementary Fig. S5.2).

We supported these results by calculating the loop weights of all the “trophic interaction loops” in the trophic web along the nutrient loading axis (see methods) (Neutel et al. 2002). We found that, under all conditions, the loop with the highest weight, which is considered the Achilles heel of a trophic network (Neutel et al. 2007), was the omnivorous loop that linked the same three groups: detritus, diatoms and zooplankton (Fig. 5.4). The maximum loop weight increased towards both regime shifts, from either direction of nutrient loading, and was strongly correlated to the amount of intraspecific interaction needed for matrix stability (Neutel et al. 2002) (Fig. 5.5).

We analyzed the biomasses and feeding rates underlying the interactions in the trophic interaction loop that has the maximum weight to disentangle what caused the increase of the loop weight (Fig. 5.4, Table 5.1). We observed that, during eutrophication, the feeding rates increased relatively more than the biomasses. As interaction strengths depend largely on the ratio of feeding rate to population densities (see Methods), this pattern led to an increase in interactions strengths, and hence, in a higher loop weight. Particularly the increase of the interaction effect of detritus on zooplankton, which is the weakest interaction in the loop, contributed to the enhancement of the loop weight (Table 5.1). The regime shift to the turbid cyanobacteria dominated state resulted in an unfavourable climate for zooplankton as their biomass was reduced. The conditions for zooplankton improved however during re-oligotrophication as we observed increasing feeding rates towards the regime shift. The biomasses of the trophic groups were only moderately affected by the reduction of nutrient loading, wherefore the interaction strengths increased along this axis. This time the increase in loop weight was dictated by the effect of zooplankton on diatoms, as the feeding on diatoms increased more than the feeding on detritus (Table 5.1).

Table 5.1 Building blocks of the heaviest loop at different nutrient loadings.

Property	Loading ($\text{mg P m}^{-2} \text{ day}^{-1}$)	Eutrophication		Re-oligotrophication	
		0.5	3.5	4.8	1.3
Loop weight (yr^{-1})		17.25	25.90	18.46	23.62
Biomasses (g m^{-2})					
<i>Zooplankton, d</i>		0.94	1.61	1.18	1.11
<i>Diatoms (pelagic), f</i>		1.41	1.87	3.43	3.53
<i>Detritus (pelagic), l</i>		6.44	10.89	11.15	9.84
Feeding rate ($\text{g m}^{-2} \text{ yr}^{-1}$)					
$F_{f,d}$		58.97	128.62	122.26	157.40
$F_{l,d}$		89.89	249.35	132.31	146.41
F_{total}		148.89	386.85	321.11	344.91
Interaction strengths (yr^{-1})					
$\alpha_{f,d}$		-62.60	-79.68	-103.77	-142.40
$\alpha_{l,f}$		30.87	48.33	26.81	32.68
$\alpha_{d,l}$		2.66	4.36	2.26	2.83

The loop weight is calculated from the interaction strengths: $w = |\alpha_{f,d} \alpha_{l,f} \alpha_{d,l}|^{1/3}$.

Besides rates of the feeding of zooplankton on diatoms and detritus, the total feeding rate of zooplankton is presented, also comprising the feeding on green algae and cyanobacteria.

Discussion

Our results show that a decrease in ecosystem stability coincides with a decrease of food web stability, which supports the prevailing view in food web ecology that non-random patterns of strong and weak trophic interactions confer stability to the ecosystem level (O'Gorman and Emmerson 2009).

From an alternative stable state perspective it may seem surprising that food web metrics can reveal the impending shift without explicitly including the feedbacks through the abiotic environment that are thought to be crucial for regime shifts in lakes, such as shading, provision of refugia and retention of P in the sediment (Scheffer et al. 1993). We resolve this by realizing that the observed webs at each level of nutrient loading are shaped by forces that are not part of the food web model *per se*, implicitly carried over to the food web model during sampling of the food web data. Using expression 5.1, we made a clear distinction between the intrinsic dynamical properties of the food web $\left(\frac{\partial s}{\partial \alpha_{i,j}}\right)$ and the changes in interaction strengths driven by the changing nutrient loading to the ecosystem $\left(\frac{d\alpha_{i,j}}{dL}\right)$.

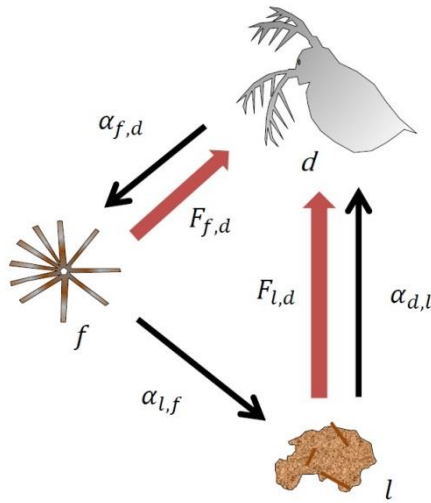


Figure 5.4 Loop with the heaviest loop weight. The omnivorous three link loop with zooplankton (d), pelagic diatoms (f), and pelagic detritus (l) is the heaviest loop in the trophic network. Black arrows indicate the direction of the interaction effect (α). Red arrows indicate the feeding fluxes (F). The top-down effect of zooplankton on diatoms is a negative effect directly resulting from consumption. The effect of diatoms on detritus results from natural mortality of diatoms, and the unassimilated part of diatom consumption by zooplankton. The bottom-up effect of detritus on zooplankton is a positive predation effect.

Equivalently interesting is that the weakening of stability is exposed without explicitly taking non-linear interaction terms into account, as relatively simple Lotka-Volterra dynamics underlie the computation of food web stability. The use of linear interaction terms in food web models greatly eases the estimation of interaction strengths from empirical data (Wootton and Emmerson 2005, Moore and de Ruiter 2012), but has implications for the stability properties of dynamical systems (Holling 1973), potentially hampering a one-to-one mathematical transfer of stability properties from the ecosystem to the food web model. Nonetheless, Lotka-Volterra dynamics have been used in numerous studies to describe empirical food webs and disclose stabilizing patterns of strong and weak links (de Ruiter et al. 1995, Emmerson and Raffaelli 2004, Neutel et al. 2007), and there is mounting experimental evidence that the exposed patterns indeed confer stability to the level of communities (O’Gorman and Emmerson 2009) and ecosystem processes (Rip et al. 2010). It appears that the importance of the patterning of strong and weak trophic links in ecosystems overshadows that of the exact shape of the functional response used to describe the interactions.

Our analyses reveal that only few trophic interactions dictate the deterioration of food web stability, particularly among zooplankton, diatoms and detritus. This is in line with empirical studies on interaction strengths suggesting that most interactions have only a

negligible impact on community dynamics (de Ruiter et al. 1995), and is consistent with alternative stable states theory that regime shifts in ecosystems can be explained from only few key components in relation to external forcing (Scheffer et al. 2001). The interplay between zooplankton and phytoplankton has often been claimed to be pivotal in controlling aquatic ecosystem dynamics and causing alternative stable states (Scheffer 1998).

Zooming in on the interactions that correlated most with stability exposed a destabilizing trophic cascade during eutrophication and re-oligotrophication. In the clear-water state, the ratio of feeding rate to predator biomass increased with productivity through a classic trophic cascade (Oksanen et al. 1981, Carpenter and Kitchell 1996), which resulted in a destabilizing increase of interaction strengths, and hence, a negative productivity-stability relationship. Somewhat paradoxically, another destabilizing trophic cascade occurred during re-oligotrophication, even though the overall productivity was decreasing. A shift in phytoplankton dominance enhanced the trophic transfer efficiency, resulting in an increase in destabilizing interaction strengths. This pattern of shifting dominance during re-oligotrophication, to the detriment of cyanobacteria and the benefit of more edible diatoms and green algae, is consistent with field observations (Jeppesen et al. 2005).

Our finding that most interactions have only a negligible impact on community dynamics does not imply that species are redundant, as extreme changes in interaction strength - e.g. due to species extinctions - can have strong non-linear effects on community

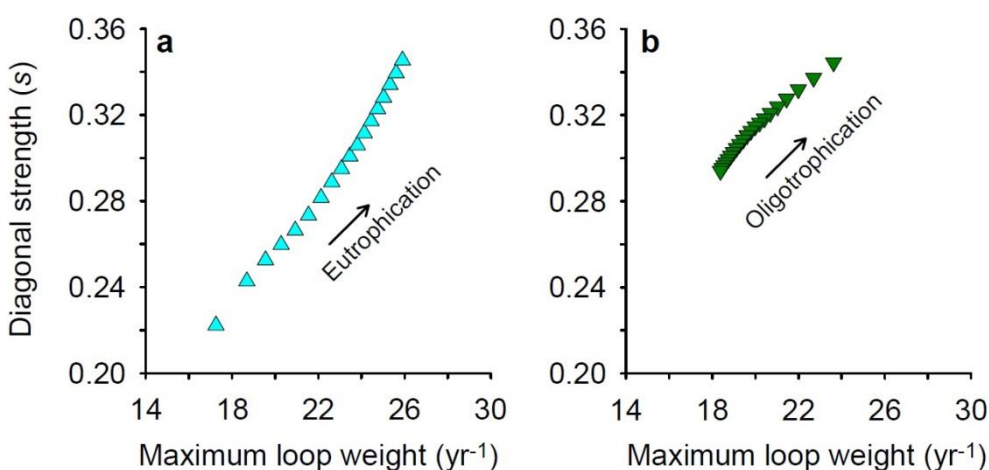


Figure 5.5 Stability versus maximum loop weight. The maximum loop weight (per year (yr^{-1})) shows a positive relationship with intraspecific interaction needed for matrix stability (s) during (a) eutrophication and (b) re-oligotrophication. Food web stability decreases with increasing s .

stability. A next step will be to investigate the synergetic effects of food web manipulations and environmental stress, as it is unquestionable that species extinctions and invasions can have far reaching consequences for ecosystem functioning, of which the introduction of the Nile perch to the world's second largest freshwater system Lake Victoria gives one of the most striking examples (Downing et al. 2012).

Our results indicate that food web stability can be used as an empirical indicator of ecosystem resilience. The established food web methods we used can be turned into a tool for managers to evaluate food web stability on a yearly basis. Food web stability as an early warning signal is of a fundamental different nature than the conventionally used critical slowing down or flickering (Scheffer et al. 2009). Instead, the method is more akin to an alternative generalized modelling approach recently proposed (Lade and Gross 2012), which has the potential advantage of being less dependent on high resolution time series (Dakos et al. 2015). Many of the limitations that have been identified for conventional early warning signals also apply to food web stability (Dakos et al. 2015). For example, food web stability gives no information about the distance to a regime shift, and needs a baseline to be meaningful. To overcome such limitations it has been suggested that the combined use of several independent indicators is needed to confidently disclose an impending regime shift (Kefi et al. 2013). Food web stability can be a valuable addition to the current set of indicators in this respect. We anticipate that paleolimnological reconstructions of food webs (Rawcliffe et al. 2010), and microcosm experiments with multiple nutrient treatments (Hulot et al. 2000), are needed to uncover the true potential and practical limitations of this early warning signal, such as sensitivity to false alarms (Dakos et al. 2015).

By showing that food web stability signals critical transitions in a shallow lake ecosystem we reconcile the conceptual frameworks of food webs and alternative stable states. The food web stability approach laid out here opens up ways to obtain a better mechanistic understanding of the biological processes underlying sudden shifts in ecosystem state, bringing us closer to providing a sound mechanistic basis for predicting ecosystem dynamics in a changing world (Purves et al. 2013).

Methods

Ecosystem modelling.

We used a well-established integrated dynamical model for shallow lakes - PCLake - to simulate a critical transition of a shallow non-stratifying lake (Janse et al. 2010). The model embraces several key ecological concepts including closed cycles of nutrients and matter, benthic-pelagic coupling, stoichiometry, food web dynamics and trophic cascade. The aquatic food web is modelled on the basis of functional groups and comprises four trophic layers. The pelagic and benthic food chains are coupled via a shared predator, reproduction of fish and the settling and resuspension of detritus and phytoplankton.

The model has been calibrated against data of >40 lakes resulting in lake characteristics resembling an ‘average’ shallow lake in the temperate zone (Janse et al. 2010). We used default parameter settings, describing a lake with a mean depth of 2 m, a fetch of 1000 m, a water inflow of 20 mm d⁻¹, a lightly clayish soil, and no wetland zone, and initial values for two contrasting ecosystem states (clear vs. turbid) (Janse et al. 2010).

We ran the model for various phosphorus (P) loadings in the range of 0.1 to 5 mg P m⁻² day⁻¹ in steps of 0.18, starting with either an initially clear- or an initially turbid-water state. The nitrogen loading was consistently kept 10 times the P loading to maintain phosphorus limitation. For each loading the model was run for 20 years to reach seasonally forced equilibrium conditions. Output data of the final year was used to characterize the state of the ecosystem and to compile material flow descriptions of the food web using established food web methods (see below). A more detailed description of the ecosystem model, and the bifurcation analysis with nutrient loading, can be found in (Janse et al. 2010) and references therein.

Material flow descriptions.

For each nutrient loading level, we constructed material flow descriptions of the corresponding food web, following a typical food web approach as presented by (de Ruiter et al. 1993, Moore and de Ruiter 2012). We calculated feeding rates, flows to the detritus pools and reproduction rates from yearly average biomass densities, death rates, prey preferences and energy conversion efficiencies, which we extracted from the ecosystem model. Assuming steady state and the conservation of matter, the production of each population must balance the rate of loss through natural mortality and predation: $F_j = \frac{d_j B_j + M_j}{a_j p_j}$, where F_j is the feeding rate (g m⁻² year⁻¹) of species j , d_j is the specific death rate (year⁻¹), B_j is the average population density (g m⁻²), M_j is the mortality by predation (g m⁻² year⁻¹), a_j is the assimilation efficiency and p_j is the production efficiency (both dimensionless). For the juvenile (zooplanktivorous) fish and adult (benthivorous) fish, the reproduction fluxes were added to the numerator. When a predator feeds on several trophic groups, the prey preferences were included to calculate the feeding rate of predator j on prey species i : $F_{ij} = \frac{w_{ij} B_j}{\sum_{k=1}^n w_{kj} B_k} F_j$, where w_{ij} refers to the preference of predator j for prey i , and n is the number of prey types. The fluxes arising from natural mortality go to the detritus pools, just as the unassimilated fraction of the feeding rate $(1-a_j) \cdot F_{ij}$, representing the biomass that is not actually consumed or is egested. Calculations started at the top of the food chain, as the top predator does not experience predation. The values of the parameters are listed in Supplementary Table S5.1. The parameters are assumed constant for all nutrient loadings. The settling and re-suspension rates of detritus and phytoplankton (g m⁻² year⁻¹) were directly extracted from the ecosystem model. Macrophytes are not consumed directly but as detritus and are therefore only considered as input for the detritus pools.

Food web dynamics

We developed a Lotka-Volterra type food web model that included the same trophic groups as the full ecosystem model, in the form $\dot{X}_i = X_i [b_i + \sum_{j=1}^n c_{i,j} X_j]$ and extensions thereof, where X_i and X_j represent the population sizes of group i and j , b_i is specific rate of increase or decrease of group i , and c_{ij} is the coefficient of interaction between group i and group j . Interaction strengths can be

defined as the partial derivatives of Lotka-Volterra type growth equations in equilibrium and give the elements of the (Jacobian) community matrix representation of our model (May 1972). The interaction effect of predator j on prey i can be expressed as $\alpha_{ij} = \left(\frac{\partial \frac{dX_i}{dt}}{\partial X_j} \right)^* = -c_{i,j}X_i^*$ (a detailed description of all the equations can be found in Supplementary Note 1).

The values of the partial derivatives can be directly derived from the material flow descriptions of the food web, using the criterion developed by May (1972, see also de Ruiter et al. 1995). Here the assumption is that the average annual feeding rate $F_{i,j}$ ($\text{g m}^{-2} \text{ year}^{-1}$) can be expressed as $-c_{i,j}X_i^*X_j^*$ i.e. the death rate of group i due to predation by group j in equilibrium (de Ruiter et al. 1995). Thus, the strength of this interaction can be derived by dividing the feeding rate by the annual average population density of the predator $\alpha_{ij} = -\frac{F_{i,j}}{B_j}$. The opposite (positive) effect of the prey on the predator, as well as the interaction terms resulting from the detrital fluxes, reproduction fluxes and settling and resuspension fluxes, were determined in a similar way (Moore and de Ruiter 2012) (see Supplementary Note 1).

We calculated interaction strengths and constructed (Jacobian) community matrices from the material flow descriptions of the food webs at each loading level for each initial state. A randomization procedure confirmed that the imposed patterns of interaction strengths were non-random, and thus crucial to the stability of the food web (Supplementary Fig. S5.3)(de Ruiter et al. 1995, Neutel et al. 2007).

Calculation of stability.

For the consumers and the phytoplankton groups in the food web, we assume that, for equilibrium conditions, the death rate d_i (year^{-1}) can be split in density-independent death, and density-dependent death: $d_i = (1-s)d_i + sd_i$, where s represents the fraction of the death rate d_i caused by density-dependent mortality (year^{-1}). When taking the partial derivatives of the differential equations to determine the (Jacobian) community matrix, this s will occur on the diagonal of the matrix, representing intraspecific interaction strengths $\alpha_{ii} = -s \cdot d_i$. We followed Neutel et al. (2002, Neutel et al. 2007) and measured stability as the minimum degree of relative intraspecific interaction needed for matrix stability (all eigenvalues having negative real parts), assuming the same value for s for all trophic groups. Food webs that need less intraspecific interference (a smaller value for s) are more stable. There is a close relation between s and the dominant eigenvalue of a matrix without added intraspecific interference (Supplementary Fig. S5.4). The use of s however has the advantage of providing a biological interpretation of stability (Neutel et al. 2007).

Calculation of the maximum loop weight.

The weight of a trophic feedback loop - a closed chain of trophic links - is defined as the geometric mean of the absolute values of the interaction strengths that compose the loop (Neutel et al. 2002, Neutel et al. 2007): $w^{(k)} = |\alpha_{i_1 i_2} \alpha_{i_2 i_3} \cdots \alpha_{i_k i_1}|^{1/k}$, where k is the number of species in the loop. The maximum loop weight gives an approximation of the level of intraspecific interference needed for matrix stability (Neutel et al. 2002).

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Supplementary material

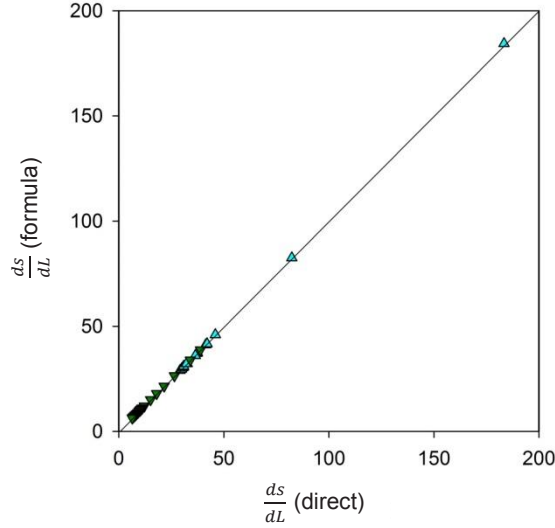


Figure S5.1. Proof of concept of expression 5.1. We show the comparison of the change in matrix stability per unit nutrient loading $\left(\frac{ds}{dL}\right)$ with the sum of the multiplications of the changes in strength and the sensitivities of all individual interactions in the matrix $\left(\sum_i^n \sum_j^n \frac{d\alpha_{ij}}{dL} \frac{\partial s}{\partial \alpha_{ij}}\right)$. We plotted the relation for each step along the loading axis from clear to turbid (turquoise upward triangles), and from turbid to clear conditions (dark green downward triangles).

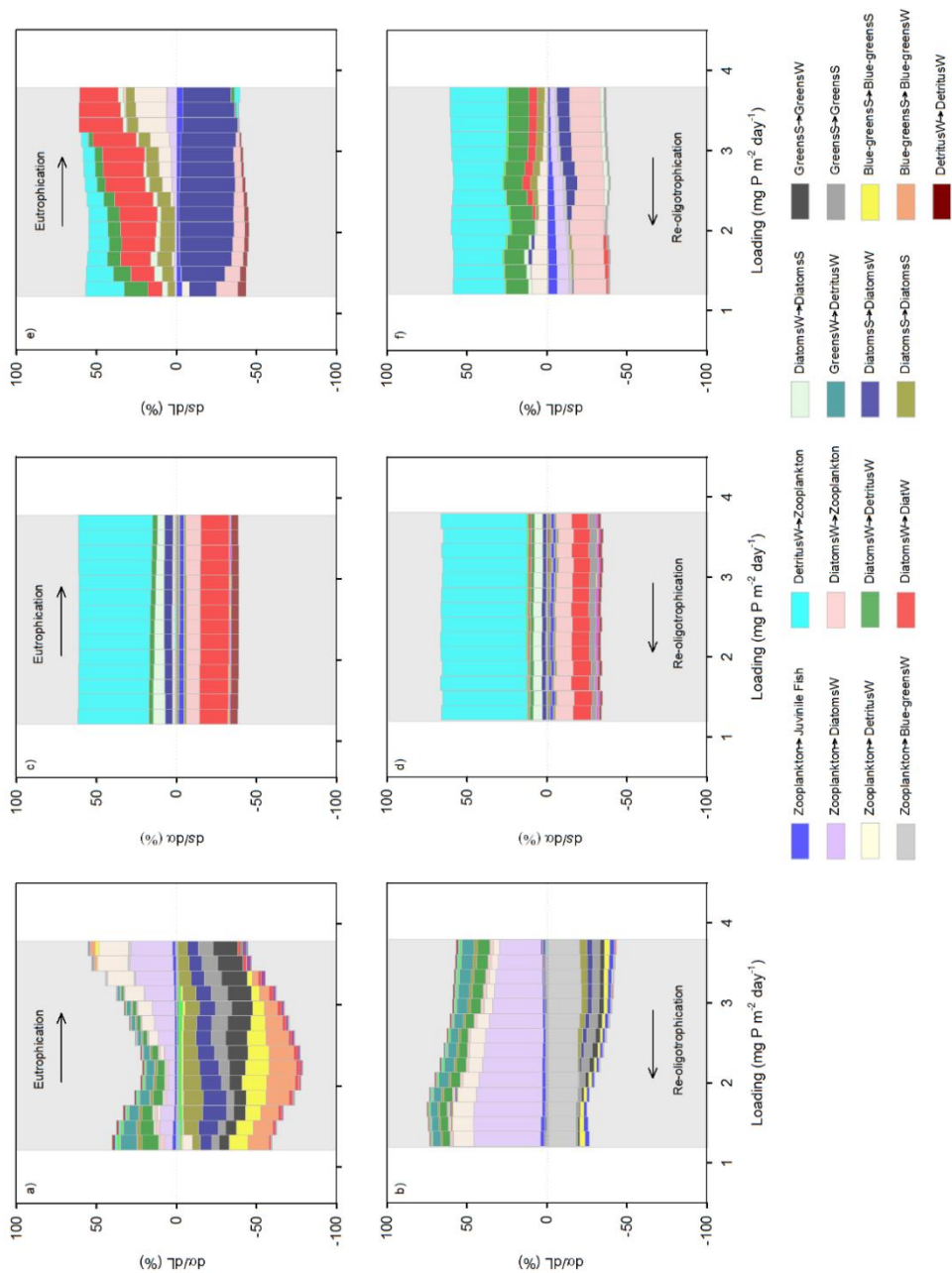


Figure S5.2 (page 88) Elucidating which interactions contribute to the decrease of food web stability. The response of food web stability to nutrient loading depends both on how the strengths of trophic interactions change in response to nutrient loading: $\frac{d\alpha_{i,j}}{dL}$, and the extent to which the stability of the food web is sensitive to those changes: $\left(\frac{\partial s}{\partial \alpha_{i,j}}\right)$. Plotting the relative changes of the interaction strengths per unit change of loading L during eutrophication **(a)** and re-oligotrophication **(b)** reveals that several of the 55 interactions in the food web increase or decrease in strength towards the tipping point. A positive change indicates that the strength of the interaction increases and a negative change indicates that the strength of the interaction is decreasing. Plotting the relative sensitivity of the diagonal strength s to changes in the interaction strengths during eutrophication **(c)** and re-oligotrophication **(d)** reveals that the stability is only sensitive to a select number of interactions, and that the sensitivity is not dependent on the location along the loading axis. The product of the change in strength of each interaction with the sensitivity of s to that interaction strength gives the relative contribution of each interaction to changes in s , during eutrophication **(e)** and re-oligotrophication **(f)**. Only changes in a handful of stabilizing and destabilizing interactions contribute to changes in stability - mainly involving detritus, diatoms and zooplankton. Only relevant interactions are presented in the legend. Phytoplankton species and detritus may appear both in the pelagic and in the sediment layer: they are abbreviated and indicated with ‘W’ if they are in the pelagic, or ‘S’ if they are found in or on the sediment.

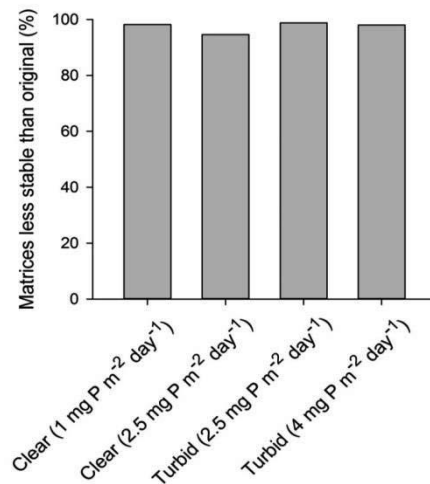


Figure S5.3. Percentage of randomized matrices less stable than original (Jacobian) community matrix representation of the aquatic food web. We randomized the matrices of four lakes differing in their initial conditions or nutrient loading 500 times and compared the stability of the randomized matrices with the stability of the original matrices. Randomization was performed by randomly exchanging pairs of interaction strengths but keeping the pairs as such intact, preserving both the sign structure of the matrix and the overall strength of the trophic interactions relative to the strength of intragroup interference: the randomized matrices have thus a similar structure but lost the pattern that resulted from the ecosystem model.

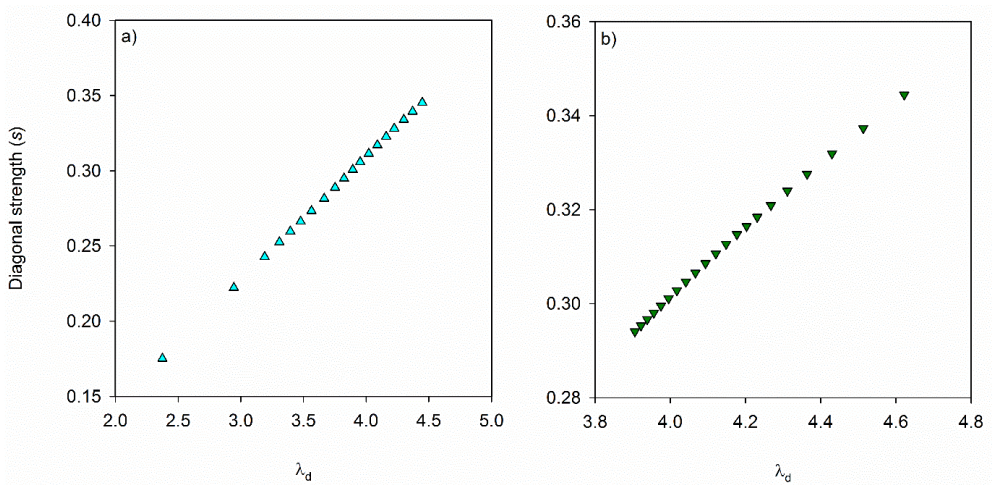


Figure S5.4. Relation between the maximum eigenvalue and the relative intraspecific competition needed for matrix stability. The relation between the maximum eigenvalue λ_d and the relative intraspecific competition s is plotted for each step along the loading axis from **(a)** clear to turbid, and **(b)** from turbid to clear conditions. Unlike the maximum eigenvalue, the level of intraspecific interaction strength s has a biological interpretation as it translates to a loss rate of organisms at steady state relative to the total loss that the system can provide for.

Table S5.1: Overview of the parameters and output of the ecosystem model PCLake used to estimate material fluxes and interaction strengths in the food web.

Class	Trophic group	Unit	Value	Source
Biomass	Piscivorous fish	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Zoopl. fish (juvenile)	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Benth. fish (adult)	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Zooplankton	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Benthos	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Pelagic Diatoms	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Pelagic Green algae	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Pelagic Cyanobacteria	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Pelagic Detritus	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Benthic Diatoms	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Benthic Green algae	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Benthic Cyanobacteria	g m^{-2}	Variable	PCLake simulation – yearly average
Biomass	Benthic Detritus	g m^{-2}	Variable	PCLake simulation – yearly average
Settling flux	Pelagic Diatoms	$\text{g m}^{-2} \text{ yr}^{-1}$	Variable	PCLake simulation – year summation
Settling flux	Pelagic Green algae	$\text{g m}^{-2} \text{ yr}^{-1}$	Variable	PCLake simulation – year summation
Settling flux	Pelagic Cyanobacteria	$\text{g m}^{-2} \text{ yr}^{-1}$	Variable	PCLake simulation – year summation
Settling flux	Pelagic Detritus	$\text{g m}^{-2} \text{ yr}^{-1}$	Variable	PCLake simulation – year summation
Resuspension flux	Benthic Diatoms	$\text{g m}^{-2} \text{ yr}^{-1}$	Variable	PCLake simulation – year summation

(Continued)

Table S5.1 (*Continued*)

Resuspension flux	Benthic Green algae	$\text{g m}^{-2} \text{yr}^{-1}$	Variable	PCLake simulation – year summation
Resuspension flux	Benthic Cyanobacteria	$\text{g m}^{-2} \text{yr}^{-1}$	Variable	PCLake simulation – year summation
Resuspension flux	Benthic Detritus	$\text{g m}^{-2} \text{yr}^{-1}$	Variable	PCLake simulation – year summation
Assimilation eff.	Piscivorous fish	-	0.40	Janse (2005)
Assimilation eff.	Zoopl. fish (juvenile)	-	0.40	Janse (2005)
Assimilation eff.	Benth. fish (adult)	-	0.40	Janse (2005)
Assimilation eff.	Zooplankton	-	0.35	Janse (2005)
Assimilation eff.	Benthos	-	0.30	Janse (2005)
Production eff.	Piscivorous fish	-	0.17	PCLake simulation – overall average
Production eff.	Zoopl. fish (juvenile)	-	0.59	PCLake simulation – overall average
Production eff.	Benth. fish (adult)	-	0.68	PCLake simulation – overall average
Production eff.	Zooplankton	-	0.54	PCLake simulation – overall average
Production eff.	Benthos	-	0.88	PCLake simulation – overall average
Death rate	Piscivorous fish	yr^{-1}	0.22	PCLake simulation – overall average
Death rate	Zoopl. fish (juvenile)	yr^{-1}	4.03	PCLake simulation – overall average
Death rate	Benth. fish (adult)	yr^{-1}	1.53	PCLake simulation – overall average
Death rate	Zooplankton	yr^{-1}	27.3	PCLake simulation – overall average
Death rate	Benthos	yr^{-1}	3.48	PCLake simulation – overall average
Death rate	Pelagic Diatoms	yr^{-1}	3.66	PCLake simulation – overall average
Death rate	Pelagic Green algae	yr^{-1}	3.66	PCLake simulation – overall average
Death rate	Pelagic Cyanobacteria	yr^{-1}	3.66	PCLake simulation – overall average
Death rate	Benthic Diatoms	yr^{-1}	18.3	PCLake simulation – overall average
Death rate	Benthic Green algae	yr^{-1}	18.3	PCLake simulation – overall average
Death rate	Benthic Cyanobacteria	yr^{-1}	73.2	PCLake simulation – overall average
Prey preference	Zoopl. -> Diatoms	-	0.75	Janse (2005)
Prey preference	Zoopl. -> Green Algae	-	0.75	Janse (2005)
Prey preference	Zoopl. -> Cyanobacteria	-	0.125	Janse (2005)
Prey preference	Zoopl. -> Detritus	-	0.25	Janse (2005)
Frac. C fixed in bones	All fish groups	-	0.35	Janse (2005)
Reproduction frac.	Benth. fish (adult)	-	0.026	PCLake simulation – overall average
Ageing fraction	Zoopl. fish (juvenile)	-	0.27	PCLake simulation – overall average

Supplementary Note 1: Differential equations, partial derivatives, and interaction strengths

Consumers

The food web includes five groups of consumers: zoobenthos, zooplankton, piscivorous fish, juvenile benthivorous fish, and adult zooplanktivorous fish. We assume for all consumers that a fraction s of their death rate d_i is caused by density-dependent factors. The equations of zoobenthos, zooplankton, and piscivorous fish are given first, followed by the equations for juvenile benthivorous fish and adult zooplanktivorous fish, which need extra terms for the reproductive fluxes between these two groups.

Zoobenthos, zooplankton, and piscivorous fish

The differential equation of consumer group i is given by:

$$\frac{dX_i}{dt} = -(1-s)d_iX_i - \frac{sd_i}{X_i^*}X_i^2 - c_{i,k}X_iX_k + \sum_j a_i p_i c_{j,i} X_j X_i, \quad (\text{S5.1})$$

where X_i is the biomass of consumer group i , s is the fraction of death rate d_i caused by density-dependent mortality (i.e. our stability metric), $c_{i,k}$ is the consumption coefficient of species X_i being eaten by predator X_k , a_i is the assimilation efficiency, p_i is the production efficiency, and X_j is the biomass of prey j . If group i represents the top predator piscivorous fish, then there is no predation term $-c_{i,k}X_iX_k$.

To determine the Jacobian community matrix, the partial derivative of group i to any other group j is required, evaluated in equilibrium: $\alpha_{i,j} = \left(\frac{\partial \frac{dX_i}{dt}}{\partial X_j} \right)^*$, where the star denotes equilibrium. Taking the partial derivative to predator k gives

$$\alpha_{i,k} = -c_{i,k}X_i^* = -\frac{F_{i,k}}{X_k^*}, \quad (\text{S5.2})$$

where $F_{i,k}$ is the feeding rate of group k on group i , given by $F_{i,k} = c_{i,k}X_i^*X_k^*$. The partial derivative to prey j is given by

$$\alpha_{i,j} = a_i p_i X_i^* = \frac{a_i p_i F_{i,j}}{X_j^*}. \quad (\text{S5.3})$$

Finally, the partial derivative of consumer i to itself is given by

$$\alpha_{i,i} = -sd_i. \quad (\text{S5.4})$$

Juvenile (benthivorous) fish and adult (zooplanktivorous) fish

The differential equations for juvenile and adult fish are the same as for the above consumers, but include extra terms for the ‘exchange’ between juvenile and adult fish.

Additional assumptions are:

- Adult fish lose biomass due to reproduction. This loss in adult fish biomass is added to juvenile fish biomass. The flux from adults to juveniles is independent of juvenile biomass.
- Juvenile fish lose biomass due to juveniles becoming adults. This loss in juvenile biomass is added to adult fish biomass. The flux from juveniles to adults is independent of adult biomass.
- Adult fish do not eat juveniles.

The differential equation of juvenile fish is given by

$$\begin{aligned} \frac{dX_{JF}}{dt} = & -g_{JF}X_{JF} + h_{AF}X_{AF} - (1-s)d_{JF}X_{JF} - \frac{sd_{JF}}{X_{JF}^*}X_{JF}^2 - c_{JF,k}X_{JF}X_k \\ & + a_{JF}p_{JF}c_{j,JF}X_jX_{JF}, \end{aligned} \quad (S5.5)$$

where X_{JF} is the biomass of juvenile fish, g_{JF} is the growth rate of juvenile fish biomass turning into adult fish biomass X_{AF} , h_{AF} is the adult fish biomass loss rate due to reproduction of adults, X_k is the biomass of predator k , and X_j is the biomass of prey j .

Taking the partial derivative to adult fish gives

$$\alpha_{JF,AF} = h_{AF}. \quad (S5.6)$$

The partial derivative to predator k is given by

$$\alpha_{JF,k} = -c_{JF,k}X_{JF}^* = -\frac{F_{JF,k}}{X_k^*}. \quad (S5.7)$$

The partial derivative to prey j is given by

$$\alpha_{JF,j} = a_{JF}p_{JF}c_{j,JF}X_{JF}^* = \frac{a_{JF}p_{JF}F_{j,JF}}{X_j^*}. \quad (S5.8)$$

Finally, the partial derivative of juvenile fish to itself is given by:

$$\alpha_{JF,JF} = -\frac{h_{AF}X_{AF}^*}{X_{JF}^*} - sd_{JF}X_{JF}^*. \quad (S5.9)$$

The differential equation of adult fish is given by

$$\begin{aligned} \frac{dX_{AF}}{dt} = & g_{JF}X_{JF} - h_{AF}X_{AF} - (1-s)d_{AF}X_{AF} - \frac{sd_{AF}}{X_{AF}^*}X_{AF}^2 - c_{AF,k}X_{AF}X_k \\ & + a_{AF}p_{AF}c_{j,AF}X_jX_{AF}. \end{aligned} \quad (S5.10)$$

Taking the partial derivative to juvenile fish gives

$$\alpha_{AF,JF} = g_{JF}. \quad (S5.11)$$

The partial derivative to predator k is given by

$$\alpha_{AF,k} = -c_{AF,k}X_{AF}^* = -\frac{F_{AF,k}}{X_k^*}. \quad (S5.12)$$

The partial derivative to prey j is given by

$$\alpha_{AF,j} = a_{AF} p_{AF} c_{j,AF} X_{AF}^* = \frac{a_{AF} p_{AF} F_{j,AF}}{X_j^*}. \quad (S5.13)$$

Finally, the partial derivative of adult fish to itself is given by:

$$\alpha_{AF,AF} = -\frac{g_{JF} X_{JF}^*}{X_{AF}^*} - s d_{AF} X_{AF}^*. \quad (S5.14)$$

Phytoplankton

The food web includes three types of phytoplankton: cyanobacteria, diatoms, and green algae. These three groups are present in both the water (pelagic) and the sediment (benthic) compartment. For each phytoplankton group, biomass exchange takes place between the water and sediment compartment via settling and re-suspension.

For phytoplankton, we assume that:

- Death rate of phytoplankton in both water and sediment can be split in density dependent and density independent mortality.
- The suspension and re-suspension fluxes are independent of each other, i.e. the settling flux is independent of benthic phytoplankton biomass, and the re-suspension flux is independent of pelagic phytoplankton biomass.
- Phytoplankton in the sediment do not reproduce (no growth rate r).

The differential equation of phytoplankton in the water compartment for group i (iW) is given by:

$$\frac{dX_{iW}}{dt} = -n_{iW} X_{iW} + m_{iS} X_{iS} + r_{iW} X_{iW} - (1-s) d_{iW} X_{iW} - \frac{s d_{iW}}{X_{iW}^*} X_{iW}^2 - c_{iW,k} X_{iW} X_k, \quad (S5.15)$$

where X_{iW} is the biomass of water phytoplankton group iW , n_{iW} is the sedimentation rate of water phytoplankton to sediment phytoplankton, m_{iS} is the re-suspension rate of sediment phytoplankton to water phytoplankton, X_{iS} is the biomass of sediment phytoplankton group i (iS), and r_{iW} is the growth rate.

If group j is sediment phytoplankton (iS), this gives

$$\alpha_{iW,iS} = m_{iS}. \quad (S5.16)$$

If group j is a predator k of group iW , this gives

$$\alpha_{iW,k} = -c_{iW,k} X_k^* = -\frac{F_{iW,k}}{X_{iW}^*}. \quad (S5.17)$$

Finally, the partial derivative of water phytoplankton to itself is given by

$$\alpha_{iW,iW} = -\frac{m_{iS}}{X_{iW}^*} X_{iS}^* - s d_{iW}. \quad (S5.18)$$

The differential equation of phytoplankton in the sediment compartment for group i (iS) is given by:

$$\frac{dX_{iS}}{dt} = n_{iW}X_{iW} - m_{iS}X_{iS} - (1-s)d_{iS}X_{iS} - \frac{sd_{iS}}{X_{iS}^*}X_{iS}^2 - c_{iS,k}X_{iS}X_k, \quad (S5.19)$$

where X_{iS} is the biomass of sediment phytoplankton group iS , and X_k is the biomass of predator k .

Taking the partial derivative to water phytoplankton group iW gives

$$\alpha_{iS,iW} = n_{iW}. \quad (S5.20)$$

The partial derivative to predator k is given by

$$\alpha_{iS,k} = -c_{iS,k}X_k^* = -\frac{F_{iS,k}}{X_{iS}^*}. \quad (S5.21)$$

Finally, the partial derivative of sediment phytoplankton to itself is given by

$$\alpha_{iS,iS} = -\frac{n_{iW}}{X_{iS}^*}X_{iW}^* - sd_{iS}. \quad (S5.22)$$

Detritus

The food web includes two groups of detritus: one in the water compartment and one in the sediment compartment. These groups are linked via suspension and re-suspension flows between the detritus pools. Assumptions for detritus are:

- Detritus receives allochthonous input (optional) (cf. Moore and de Ruiter 2012).
- All biomass lost through mortality in phytoplankton and consumers, both through density-independent and density-dependent causes, is assumed to enter the detritus pools. Depending on whether the species lives in water or sediment, dead material goes to water detritus or sediment detritus, respectively. A fraction of the fish bones is removed from the system.
- The suspension and re-suspension fluxes are independent of each other, i.e. the suspension flux is independent of detritus biomass in the sediment, and the re-suspension flux is independent of detritus biomass in the water.

The differential equation of water detritus is given by

$$\begin{aligned} \frac{dX_{DW}}{dt} = & R_{DW} - n_{DW}X_{DW} + m_{DS}X_{DS} + \sum_i \sum_j (1-a_j)c_{i,j}X_iX_j \\ & + \sum_i (1-s)d_iX_i + \sum_i \frac{sd_i}{X_i^*}X_i^2 - \sum_j c_{DW,j}X_{DW}X_j, \end{aligned} \quad (S5.23)$$

where X_{DW} is the biomass of water detritus, R_{DW} is allochthonous input, n_{DW} is the sedimentation rate of water detritus to sediment detritus, m_{DS} is the re-suspension rate of sediment detritus to water detritus, and X_{DS} is the biomass of sediment detritus.

Taking the partial derivative to sediment detritus, this gives

$$\alpha_{DW,DS} = m_{DS}. \quad (\text{S5.24})$$

The partial derivative to any phytoplankton or consumer group j gives

$$\begin{aligned} \alpha_{DW,j} &= \sum_i (1 - a_j) c_{i,j} X_i^* + (1 - a_k) c_{j,k} X_k^* + (1 + s) d_j - c_{DW,j} X_{DW}^* = \\ &= \sum_i \frac{(1 - a_j) F_{i,j}}{X_j^*} + \frac{(1 - a_k) F_{j,k}}{X_j^*} + (1 + s) d_j - \frac{F_{DW,j}}{X_j^*}, \end{aligned} \quad (\text{S5.25})$$

where X_i is prey biomass eaten by j (this term is absent if group j is phytoplankton), and X_k is predator biomass consuming j (this term is absent if group j is the top predator). If group j does not consume water detritus, then the last term of $\alpha_{DW,j}$ is absent.

Finally, the partial derivative of water detritus to itself is given by

$$\alpha_{DW,DW} = -n_{DW} - \sum_j a_j c_{DW,j} X_j^* = -n_{DW} - \sum_j \frac{a_j F_{DW,j}}{X_{DW}^*}. \quad (\text{S5.26})$$

The equations for sediment detritus are very similar to equations (S5.23)-(S5.26) for water detritus:

$$\begin{aligned} \frac{dX_{DS}}{dt} &= R_{DS} + n_{DW} X_{DW} - m_{DS} X_{DS} + \sum_i \sum_j (1 - a_j) c_{i,j} X_i X_j + \sum_i (1 - s) d_i X_i \\ &\quad + \sum_i \frac{s d_i}{X_i^*} X_i^2 - \sum_j c_{DS,j} X_{DS} X_j, \end{aligned} \quad (\text{S5.27})$$

$$\alpha_{DS,DW} = n_{DW}, \quad (\text{S5.28})$$

$$\alpha_{DS,j} = \sum_i \frac{(1 - a_j) F_{i,j}}{X_j^*} + \frac{(1 - a_k) F_{j,k}}{X_j^*} + (1 + s) d_j - \frac{F_{DS,j}}{X_j^*}, \quad (\text{S5.29})$$

$$\alpha_{DS,DS} = -m_{DS} - \sum_j \frac{a_j F_{DS,j}}{X_{DS}^*}. \quad (\text{S5.30})$$

Chapter 6

Searching for balance

General discussion

6.1 ‘Saving ecosystems’

“We live in a world of wonders.” I think that is why I wanted to ‘save the world’ when I was younger: our planet fascinates me. Nature fascinates me in all its facets: its variety, its colours, its shapes, its inhabitants, its wonders. Over the years, I lost some of my idealism, but I keep the question ‘how can I save the world?’ in mind in almost everything I do. During my studies in ecology, the question became: how can I contribute to ‘saving ecosystems’? With ‘saving ecosystems’ I mean protecting their biodiversity, and functions that facilitate a healthy environment for humans to live in. And finally, in this thesis positioned in the field of theoretical ecology, the question became: how can ecological models help in ‘saving ecosystems’?

6.2 The role of ecological models in ‘saving ecosystems’

I think ecological models can help in ‘saving ecosystems’ in three ways. First, building an ecological model forces us to think of what are the most important processes and the most important components in ecosystems. Interesting about this point is that while science strives for objectivity, what is thought to be important is to a certain extent dependent on the modeller and therefore rather subjective. Moreover, opinions on what is important differ among subfields of ecology. In food web ecology, the most important processes are thought to be the trophic interactions between functional groups. Other processes, for example competition, are assumed to be the indirect result of these feeding interactions. However, a researcher who focusses on how competition affects species populations and communities is more likely to take these processes explicitly into account. Thus, creating a model organizes the thoughts of the modeller about what is important to the world, but limits one’s view by ignoring aspects that are thought to be of lesser importance. To me, this rather subjective aspect of prioritizing what is important and what is not seems a necessary step in developing models. I do not claim that only modelling studies force one to do this, but I do consider it a particular strength of modelling.

Second, by studying the model and interpreting its outcomes, interesting theories and hypotheses can be formulated. What I consider interesting here, is that the model does not necessarily have to be completely realistic, or even realistic at all to be of use. For example, consider the famous predator-prey cycles that arise from the Lotka-Volterra equations. These cycles are often illustrated with rabbits as prey and foxes or lynxes as predator. Many aspects of this trophic interaction are being ignored by the modelling approach taken by Lotka and Volterra, such as the ability for the prey to hide, or interactions with other species or with the environment. Still, the theories that can be formed from such models, even if these models are simplistic or perhaps somewhat unrealistic, give empiricists new

ideas for experiments or observational studies. This is a two-way interaction, because modellers can support theories formed by empiricists.

The third way in how models can help in ‘saving ecosystems’ is that we can use them to predict what will happen to ecosystems in years to come. By running the model for different scenarios, actions can be taken in favour of the scenario with the most desired outcome. For example, the IPCC climate models show us what will happen if we reduce carbon dioxide emissions, and what happens if we do nothing. Of course, the ‘taking actions’ part is beyond the scope of ecology because it involves political and economic interests that are thought to be more important than maintaining a safe environment for humanity; but at least we know what we are heading for under the ‘business as usual’ scenario, as well as various alternative scenarios.

6.3 The ecological models in this thesis

In this thesis, I used two types of models to describe species communities. Being developed within the context of food web ecology, both models cover the whole species community (so more than the single consumer-resource interaction as in the Lotka-Volterra model) living in a specific environment: terrestrial soils and shallow lakes (so less than the whole world as covered by for example the IPCC models). In that sense, they are intermediate in terms of scope and complexity. More specifically, the model that I used for the local stability analysis and the interaction strength matrix approach, i.e. the dynamic system based on generalized Lotka-Volterra equations, focusses on the trophic relations between species and dead organic matter. The model that I used for the bifurcation analysis, i.e. the dynamic model PCLake, also takes other processes, including many abiotic ones, into account. Therefore, I refer to the first model as ‘the food web model’, and the second model as ‘the ecosystem model’ (cf. Chapters 1 and 5). Below, I will discuss different aspects of the food web model and the ecosystem model that are related to the research of this thesis.

6.4 The food web model

A food web model, as used in this thesis, is a dynamic model that describes the network of species (in the scientific literature also referred to as trophic or functional groups) and their feeding relations. The network consists of ‘many species’, by which I mean that the number of species is larger than five. This number makes food web models different from consumer-resource models which typically focus on two, three or sometimes four species. The model is used to construct the so-called interaction strength matrix, meaning the Jacobian matrix of the dynamic system, to evaluate the local stability of the equilibrium.

What I see as a clear advantage of the food web model is that it is a relatively complex model (many species, many interactions), but that it is still relatively easy to parameterize

with data that can be measured relatively easy in the field or in the lab. That this is possible has been shown for terrestrial soil (de Ruiter et al. 1995) and aquatic (Yodzis and Innes 1992) ecosystems. What remains difficult to parameterize are the intraspecific interaction strengths, that is, the effects of species on itself. How should one measure this component of the species' loss rate, and how should it be defined in the model? After going through the literature on interaction strength matrices, I did not find a consensus on how to define the diagonal of the interaction strength matrix that represents these intraspecific interaction strengths. It appears that the common way to define the diagonal is to make an educated guess. The subjectivity in this made me wonder how the various possible choices affect the outcome of the local stability analysis. I addressed this question in chapter 2 by performing a sensitivity analysis for interaction strengths and food web stability. I found that if a single interspecific interaction strength is changed and food web stability is determined along that axis, then the response in stability is affected by the choice of the diagonal. So given a food web matrix, increasing interaction strength x might increase stability for diagonal A, while for diagonal B, increasing the same interaction strength x might decrease stability. This can be a potential problem in theoretical food web studies, for example when one wants to study the importance of weak interaction strengths to food web stability (McCann 2012). This result therefore asks for more research in the processes that underlie density dependent effects. Given the difficulties in measuring density dependence in the field, experiments might give more information about this important process. Until then, I would consider it to be an improvement when the choice for the diagonal elements is taken into serious consideration, which can simply be achieved by performing a sensitivity analysis for the diagonal.

Because interaction strength matrices are now parameterized with real data, results from the past based on 'theoretical matrices' can be compared to outcomes based on 'real matrices'. By theoretical matrices, I mean interaction strength matrices that have been constructed by assigning random values to matrix elements (e.g. May 1972, Yodzis 1981). By real matrices, I mean interaction strength matrices that have been parameterized with empirical data (e.g. de Ruiter et al. 1995, Montoya et al. 2009). Assuming that the latter matrices are indeed more realistic, comparing results based on real matrices to results based on theoretical matrices might tell us more about the mechanisms or structures that shape ecosystems or that preserve their stability. This is what I aimed for in chapter 3. I revisited a classic theory which was based on theoretical matrices and used real matrices instead, to determine the relation between food web stability and food web complexity. I also used a quantitative version of connectance that May (1972) used as a measure for complexity. Quantified food web measures assign more importance to links that represent a large flux from resource to consumer, compared to links that represent small fluxes. Thus, the weight of the fluxes is taken into account. What I found in chapter 3 was that when both interaction

strength matrices and connectance are determined from empirical data, a positive relation exists between complexity (represented by weighted connectance) and stability. I did not find this or any relation between the same matrices and the classic unweighted connectance. So when we consider complex food webs to be webs of which the weights of fluxes are more or less equal to each other, i.e. that have an even flux distribution, then these webs are more stable. Intuitively, that seems plausible to me. If a predator would eat considerable amounts from one resource and only small amounts of other prey, then that appears to me to be a less stable configuration than when the predator eats an equal amount of all its resources. However, studies in network theory show that there are many networks that have stable configurations with skewed distribution towards weak links, including food webs. So my intuition must be wrong. Or maybe I would not have found this positive relation between stability and weighted connectance for another set of food webs. Or maybe the values of weighted connectance I found were extremely low, and maybe one would find other results when the whole spectrum of values of weighted connectance was investigated. My results do not tell me this. What I do know is that by using a weighted version of a food web measure, this gave some surprising results, which sheds new light on a classic theory. And that led to new questions, which might inspire others to come up with new questions. This is, I think, an essential point in science in general.

6.5 The ecosystem model

When I started working with the ecosystem model PCLake, a model that describes the food web of shallow lakes, I first thought it was a better representation of a species community than the food web model. Because PCLake not only takes into account species and their interactions, but also describes the environment and how that interacts with the food web. For example, it takes into account the seasonal cycling of temperature and light dynamics: essential when the model is run over time. Furthermore, not only carbon fluxes are described, but also the cycles of inorganic nutrients such as phosphorus and nitrogen. It encompasses sedimentation and resedimentation, stoichiometry, oxygen dynamics, bioturbation, etcetera.

However, as I started to work with the model, I realised that all this model complexity comes with a cost: it has become a black box. For example, the underlying causes for the regime shift in shallow lakes that the model shows are hard to find, almost as hard as it would be in a real lake, because there are thousands of potential causes, both direct and indirect. The advantage of a modelling approach is that in theory one could actually examine all these thousands of potential causes in a systematic way. Only this would take a very long time. As a side note, compared to the ecosystem model the supposedly less complex food web model still has a level of complexity that it might actually be regarded as a black box as well. For example, if I changed a single interaction strength and watched

what that did to food web stability (Chapter 2), I often could not explain why stability responded to that changing interaction strength in a particular way. For a two species model, such responses in stability to changing parameters or interactions strengths can be analytically resolved, but for an 18 species model, this is practically impossible.

Still, PCLake allows running the model under different scenarios, by which we can test hypotheses and make predictions. In chapter 4, I used PCLake to investigate what the effects of herbivorous birds are on macrophyte biomass and whether these birds have the potential to facilitate a sudden transition, or catastrophic shift, from a clear to a turbid water state. The outcome was that the impact through bird herbivory becomes greater along the nutrient loading axis, and that catastrophic shifts are indeed facilitated by that. In field studies and experimental set-ups with exclosures, this is rather difficult to observe or to test. The difficulty lies in the different circumstances under which field or experimental studies are performed, which can lead to different conclusions regarding the significance of bird herbivory to macrophytes. In this case, but also in general, using a model is a perfect way to do ‘experiments’ under controlled circumstances. For example, the effects of bird herbivory can be tested for any density of birds, in any time of the year, and under all ‘field conditions’. Once all the conditions have been set, they remain the same throughout the analysis: there will be no sudden change in temperature, no sudden outbreak of a disease, or other unexpected disturbances that could disrupt an experiment. That I used an ecosystem model for this particular question was necessary, given the many biotic and abiotic processes that are known to play a role in the critical transitions in shallow lakes.

There are many differences between the ecosystem model and the food web model. For one, these two models differ in how the species interactions are mathematically defined. The food web model employs proportional type I functional responses, while the ecosystem model employs saturating type II and III functional responses. There is also a difference in model complexity, if you express model complexity in terms of number of equations or parameters. Because the ecosystem model also covers abiotic processes, such as light conditions, temperature, and inorganic nutrient flows explicitly, the number of equations (> 60 for state variables only) and parameters (>400) is much higher than in the food web model (maximum number of equations used here was 19, maximum number of parameters was 52). Because there are so many differences between both models, one would expect the mathematical stability properties of both models to be quite different. Yet, we saw in chapter 5 that both models in fact did give comparable results, when used to analyse what happens to the stability of the clear-water state during eutrophication and the stability of the turbid state during re-oligotrophication.

Regarding the use of type I functional response in the food web model, this linear functional response is considered to be not very realistic, because it implies that there is no limit to the amount of resource a consumer can eat (which is taken into account by a

type II functional response). In addition, other factors such as encounter rate at low prey densities or density dependent prey selection (covered by a type III functional response) cause the response of a predator's feeding rate to the number of prey to be nonlinear. So given the somewhat unrealistic assumptions that underlie the type I functional response, are they appropriate to use in food web models? I would say that it depends on the type of analysis that you want to perform. For example, for a time series analysis, I would not recommend to use the food web model with linear functional responses, but to use an ecosystem model instead. However, for local stability analysis the food web model is of value, because I think that it can be seen as a simpler representation of an unknown, more complex model. I think that the results from chapter 5 support this statement. Both the ecosystem model and the food web model show the same result: the stability of the clear-water state decreases under eutrophication. These models are completely different in the (mathematical) way they are defined and in their complexity and yet, decreasing food web stability signalled the critical transition in the lake. So for stability analysis, I would say that generalized Lotka-Volterra models and the interaction strength matrix approach can be used very well to understand how ecosystem states change in terms of their stability (see also 6.6).

6.6 Searching for balance in nature

Throughout this thesis, I have often used the words 'equilibrium', 'balance', and 'steady state'. For me, these words represent the same idea: a state of the system in which nothing changes, where everything remains the same over time. These concepts are convenient from a mathematical point of view, but how do they work in the real world? Is nature in equilibrium, balance, or steady state? From what I learned in this study, I would say: it depends on what time scale you define balance. Suppose that you can observe an ecosystem for an extremely short time span, a fraction of a second, then nothing changes, i.e. the system is in balance. This might continue for a few hours, but already in the time span of a few days, birth and death cause changes in species densities. These changes can still be regarded as relatively small, but in the course of a year, seasons can cause large fluctuations in populations. This is not exactly what I would call a steady state. However, if the time span is increased again and these fluctuations repeat over the years, then I think that most people would refer to this as a balanced system. This is why yearly averages were taken in both the food web model and the ecosystem model approach. If the time span is increased even further, say to decades, then the system is likely to change, for example, through succession or because the environment changed.

Regarding stability of equilibria, I had to make two assumptions in this thesis which are actually contradictory. On the one hand, I assume that over the course of a few years, the system does not change and we can take yearly averages as representing the system's

equilibrium state. However, I made this assumption to explore exactly what I just assumed not to be the case: to see how the system responds to change, for example when a parameter or interaction strength changes. I am not sure how I can justify this apparent paradox. The best defence I can give right now, is that the yearly averages that we see as the equilibrium state of the food web should be regarded as a ‘hypothetical equilibrium’ for which we can ask: if the system would be in this equilibrium, what would its stability be? And if the system does change, which we hypothesize to happen, will the stability of the new ‘hypothetical equilibrium’ be greater or smaller?

6.7 Insights and impacts of my work: final conclusions

As the title of my thesis already suggests, I searched for balance in food webs in each of my research chapters. Overlooking the whole thesis, another search emerges, namely finding a balance between simplicity and complexity in food web and ecosystem models. This search for ‘optimal complexity’ fits well with the concept of the Medawar zone. According to the original interpretation of the Medawar zone (Loehle 1990), this zone represents an optimum in scientific problems that are neither too simple that they produce trivial results, nor too complex that they are insolvable. Thus, the most interesting models fall within the Medawar zone. While I consider the two models that I present in this thesis to lie well within the Medawar zone - that is, they both represent a valuable research tool in their own right as shown in chapter 2, 3, and 4 - they do differ in complexity. The food web model presented in chapters 2 and 3 provides a trackable but quite abstract representation of ecosystems. The ecosystem model presented in chapter 4 gives a more comprehensive view of natural systems, but is more difficult to analyse. In chapter 5 the complexity gap was bridged between both models by using the more complex ecosystem model as a virtual reality on basis of which we parameterized the less complex food web model. The surprising result of this study was that despite the considerable difference in complexity between both models, loss of stability in the food web model signalled an upcoming regime shift in the ecosystem model. Besides being an interesting conclusion in itself, both the predictive power of the food web model and insight in the ecosystem model gained from this combination.

The food web model has a level of complexity that is still insightful. The relatively low number of equations and the matrix format make it comprehensible and allow for deeper analyses on for example stabilizing patterns in interaction strengths (e.g. Yodzis 1981, de Ruiter et al. 1995, Emmerson and Yearsley 2004, James et al. 2015). I can add two insights to this. In chapter 2, I found that the choice of the diagonal affects stability analyses severely when it comes to the results of press perturbations. In chapter 3, I found that incorporating empirical information, i.e. skewed flux and interaction strength

distributions (towards weak links), has a profound influence on the complexity-stability relation.

The food web model is very suitable for explanatory studies. However, it is less suitable for predictive studies in a management context, because it does not take the environment explicitly into account. The ecosystem model (PCLake in this case) does take the environment explicitly into account and is therefore suitable to run under different scenarios, or different environmental conditions. Based on the results of chapter 4, I can therefore predict that the presence of herbivorous birds in shallow lakes can facilitate a regime shift from a clear-water state to a turbid water state. I have touched upon the causes for this (e.g. increased food quality results in increased grazing), but the exact causes are difficult to uncover. The ecosystem model has become a black box due to its level of complexity.

Bringing these two models together, the food web model gained more predictive power. It was coupled to a specific environmental variable, so that (in theory) it can be used as an indicator for catastrophic shifts in lakes. On the other hand, the ecosystem model became more insightful, by using the 'food web theory toolbox' (e.g. interaction strengths, trophic loops) to understand destabilizing patterns of the food web. This brings me to conclude that when searching for balance in ecological systems, there is much to gain from combining models of different complexity in a single coherent analysis.

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Summary

The overall theme of this thesis is the stability of species communities. I investigated the resilience of these systems to disturbances with mathematical models. To this end, the species communities are represented as food webs. A food web is a network of species that are linked via their feeding relations, or trophic interactions. I used two types of models, each with its own type of stability analysis.

The first model I refer to as ‘food web model’. A generalized Lotka-Volterra model is used to describe the dynamics of the species (or trophic groups). With this model, I determined the stability of the food web, assuming it to be in balance. This means that the food web is in equilibrium in the sense that the population abundances do not change over time. The equilibrium biomasses that I used to this end are the yearly-averaged biomasses. Thus, it is possible (and most likely) that population biomasses fluctuate within a year, but when yearly averages are taken, I assume that these averages are equal between years. These yearly-averaged biomasses can then be used for local stability analysis. The Jacobian matrix is determined and evaluated in equilibrium to calculate the maximum real part of all eigenvalues, which is an indicator of stability. The Jacobian matrix is here referred to as the interaction strength matrix, with interspecific (off-diagonal) and intraspecific (diagonal) interaction strengths as its elements.

The second model I refer to as ‘ecosystem model’. In this model, the food web forms the basis and species dynamics are again described by differential equations. In addition, dynamics of ecosystem and abiotic processes such as seasonal fluctuations, bioturbation, light conditions and nutrient flows (other than carbon) are described as well. I used the ecosystem model PCLake, describing the dynamics of a shallow lake, to perform bifurcation analysis. In bifurcation analysis, a parameter is changed along an environmental gradient and the influence on the ecosystem state is measured. PCLake shows a well-known phenomenon in shallow lakes, namely the sudden transition of a clear-water state to a turbid-water state during eutrophication. During oligotrophication, the reverse shift can be seen, but at a lower nutrient threshold than the threshold at which the shift during eutrophication occurred. This phenomena is denoted by several terms, such as ‘catastrophic shift’, ‘hysteresis’, and ‘alternative stable states’.

These two models and two analyses have so far been used and applied independently from each other but are combined in this thesis. In chapters 2, 3 and 4, I used either of these approaches to study food web stability. In chapter 5, both models and methods are combined to study alternative stable states in shallow lakes from two perspectives.

In chapter 2, I looked into how interaction strength matrices are parameterised. Particularly, the diagonal elements, or the intraspecific interaction strengths, are hard to parameterize with empirical data and often random numbers are chosen for these elements. I investigated in this chapter whether the way the diagonal elements are defined had any influence on the outcomes of two types of stability analyses. The first analysis ranked food webs by their stability ('food web A is more stable than 'B'). In the second analysis, a single interspecific interaction strength (off-diagonal element) was varied and the effect on stability was determined. For 11 real soil food webs, four definitions, or 'patterns', for the intraspecific interaction strengths were chosen, based on the ecological literature and the analyses were repeated for these four patterns. The first analysis showed that ranking the 11 food webs by their stability was only weakly influenced by the choice of diagonal pattern. This could imply that interspecific interaction strengths, which were not changed in this analysis, are more important to stability in this type of analysis than the intraspecific interaction strengths. In contrast, the second analysis showed that the response of food web stability to variation in a single interspecific interaction strength was sensitive to the choice of diagonal pattern. Stability could even increase using one pattern, and decrease using another. Thus, for this type of analysis, food web theoreticians should pay extra attention to the diagonal elements, and repeat their analyses for several diagonal patterns to see whether this has any influence on their conclusions.

In chapter 3, I used the food web model and the interaction strength matrix approach to test the relation between food web stability and complexity. Often, unweighted connectance is used to express food web complexity. Unweighted connectance describes the proportion of realized links in the food web and does not take link weights (fluxes or feeding rates) into account. I used here weighted connectance, which does take these link weights into account and also captures the skewness of the distribution of fluxes. I determined both unweighted and weighted connectance of 15 real soil food webs and determined stability via the interaction strength matrices. There was no relation between unweighted connectance and food web stability, but weighted connectance was positively correlated with stability. This last finding challenges the notion that complexity may constrain stability. The positive correlation between weighted connectance and stability implies that the more evenly flux rates were distributed over links, the more stable the webs were. However, the most even distributions of this dataset were still strongly skewed towards small fluxes or weak interaction strengths. Thus, incorporating these distributions with many weak links via weighted instead of unweighted food web measures can shed new light on classical theories.

In chapter 4, I used the ecosystem model PCLake to study the effects of herbivorous birds on macrophytes and the water condition of shallow lakes. Some field studies showed that herbivorous birds had the potential to decrease macrophyte biomass to such an extent

that the lake switched from a clear, macrophyte-dominated state to a turbid, phytoplankton-dominated state. But other studies showed that the loss in macrophyte biomass could be compensated by macrophyte regrowth. A potential explanation for these contradictory outcomes could be that nutrient status of the lake plays a role. By using a model approach, I indeed found that macrophyte biomass decreased most severely in more nutrient rich lakes. This could be due to the improved food quality which, when incorporated in the model, was causing an increased food intake. Through these mechanisms, birds can facilitate a catastrophic shift from the clear-water state to the turbid-water state. The fact that herbivorous birds can have a large impact on macrophyte biomass and can facilitate a regime shift implies that the presence of waterfowl should be taken into account in the estimation of critical nutrient loadings to be used in water quality management.

In chapter 5, I used both the ecosystem model and the food web model to study the transition of a shallow lake from a clear- to a turbid-water state. In doing so, this is the first time that alternative stable state theory is investigated from a food web theory perspective. In food web theory, emphasis lies on trophic interactions and patterns therein, while alternative stable state theory associates the regime shift with changes in non-trophic interactions, such as competition for light and nutrients between macrophytes and phytoplankton. The ecosystem model PCLake was first run for a number of nutrient loadings. For each loading, the model was run until the seasonally-forced equilibrium was reached. The species biomasses of this equilibrium were used to calculate an interaction strength matrix for this nutrient loading, of which the stability was determined. Thus, the stability of the food web was determined along the nutrient loading axis. Prior to both regime shifts caused by eutrophication and oligotrophication, a decrease in food web stability was found. Thus, the decrease in food web stability is a signal for the impending catastrophic shift. Further analysis of the interaction strengths showed that only a few key interactions involving zooplankton, diatoms and detritus, foreboded the deterioration of food web stability. This study exposes a tight link between food web dynamics and the dynamics of the whole ecosystem, implying that trophic organization may serve as an empirical indicator of ecosystem resilience.

As the title of my thesis already suggests, I looked for balance in food webs in each of my research chapters. Overlooking the whole thesis, another search emerges, namely finding a balance between simplicity and complexity in food web and ecosystem models. In chapter 5, we bridged the complexity gap between the two models by using the more complex ecosystem model as a virtual reality on basis of which we parameterized the less complex food web model. The surprising result of this study was that despite the considerable difference in complexity between both models, loss of stability in the food web model signalled an upcoming regime shift in the ecosystem model. Besides being an interesting conclusion in itself, this brings me to conclude that when searching for balance

in ecological systems, there is much to gain from combining models of different complexity in a single coherent analysis.

Samenvatting

In de natuur leven organismen met elkaar samen in levensgemeenschappen, zoals in de bodem, een bos, of een meer. Deze levensgemeenschappen staan regelmatig bloot aan verstoringen, veroorzaakt bijvoorbeeld door ziektes, of door veranderingen in weersomstandigheden of in de omgeving. Over het algemeen kan een natuurlijk systeem tegen een stootje en herstelt het zich weer naar de situatie van voor de verstoring. Deze toestand, waarin de organismen elkaar in evenwicht houden, wordt ook wel de evenwichtssituatie genoemd. Maar het kan ook zijn dat het systeem zich niet herstelt, waarbij bijvoorbeeld soorten wegvallen, of de onderlinge aantalsverhoudingen veranderen.

Bestudering van het herstelvermogen van biologische gemeenschappen is van groot belang, vooral in het licht van klimaatverandering en andere door de mens veroorzaakte verstoringen. Dat kan bijvoorbeeld door een lange periode metingen uit te voeren in bepaalde gebieden, of door een levensgemeenschap in het klein te reproduceren in het laboratorium of in het veld en daar vervolgens experimenten op uit te voeren. Maar je kan de dynamiek van deze systemen ook beschrijven met wiskundige modellen. Met het model kan dan bekeken worden hoe gevoelig de gemeenschap is voor verstoringen.

In werkelijkheid is een levensgemeenschap een complex biologisch systeem dat bestaat uit vele soorten en interacties tussen die soorten en hun omgeving; een wiskundig model daarvan maken is daarom niet eenvoudig. Het is daarbij noodzakelijk om keuzes te maken en de werkelijkheid te vereenvoudigen om tot een hanteerbaar model te komen. Voor de modellen die in dit proefschrift gebruikt worden, gaan we ervan uit dat de interacties tussen predatoren en hun prooi, ook wel trofische relaties genoemd, een belangrijke rol spelen in de dynamiek van de levensgemeenschap. Soorten die eenzelfde manier van leven hebben en gemeenschappelijke prooi en predatoren delen, worden daarbij tot dezelfde groep gerekend, ook wel trofische groepen genoemd. Zo kan de dynamiek van een complex systeem beschreven worden aan de hand van een relatief eenvoudig netwerk van trofische groepen die verbonden zijn door trofische relaties; dit is een voedselwebmodel. Als ook de omgeving in het model meegenomen wordt, spreken we van een ecosysteemmodel. In dit proefschrift wordt met twee methoden de stabiliteit van voedselwebben onderzocht, waarbij de ene methode gebruik maakt van een voedselwebmodel en de andere van een ecosysteemmodel.

Het onderzoek met de eerste methode en het voedselwebmodel kan vergeleken worden met het bestuderen van de stabiliteit van een bouwwerk. Hierbij stel ik de evenwichtssituatie van het voedselweb voor als een gebouw. De constructie en de

materialen van het gebouw vertellen je iets over de stabiliteit van het gebouw. Zo is het ook met het voedselweb: de populatiegroottes en onderlinge verhoudingen kunnen een idee geven van de stabiliteit van het evenwicht. Door de evenwichtssituatie te onderzoeken met wiskundige technieken, kan bepaald worden of het evenwicht stabiel is (oftewel, of de gemeenschap zich kan herstellen na een verstoring). De technieken die hier gebruikt worden zijn 'linearisatie' en 'lokale stabiliteitsanalyse'. Het komt erop neer dat uiteindelijk de stabiliteit van een matrix (een soort tabel) bepaald wordt aan de hand van de zogenaamde 'maximale eigenwaarde'. Alsof je van de bouwtekening alle getallen bij elkaar op- en aftrekt en er uiteindelijk uit deze berekening een getal rolt dat aangeeft of het gebouw stabiel is.

Bij de tweede methode maak ik gebruik van het ecosysteemmodel. In tegenstelling tot het voedselwebmodel beschouwt dit model niet alleen de onderlinge relaties tussen organismen, maar neemt het ook expliciet omgevingsfactoren mee, zoals temperatuur, daglicht, voedingsstoffen, etc. De methode die ik gebruik met dit ecosysteemmodel is te vergelijken met het afspelen van een film. De film begint in een bepaalde situatie, het verhaal ontwikkelt zich, en uiteindelijk eindigt de film weer in dezelfde situatie (een 'alles-komt-weer-goed-scenario'), of in een totaal andere situatie (het 'cliffhanger-scenario'). De film is hier het wiskundige model: startend in de evenwichtssituatie laat je het model runnen door de tijd, en bekijk je hoe de populatiegroottes zich ontwikkelen. Keren ze terug naar hun oorspronkelijke evenwichtssituatie ('alles komt weer goed'), dan is het evenwicht stabiel; als ze uitkomen op een andere situatie, dan is het evenwicht instabiel ('de cliffhanger').

Beide methodes en modellen zijn in de voedselwebecologie tot nu toe apart van elkaar gebruikt om voedselwebben en hun stabiliteit te onderzoeken. Ook in dit proefschrift gebruik ik in hoofdstuk 2 en 3 enkel het voedselwebmodel, en in hoofdstuk 4 enkel het ecosysteemmodel. Maar in hoofdstuk 5 gebruik ik beide modellen en beide methodes om voedselwebstabiliteit te onderzoeken, wat interessante resultaten oplevert.

In hoofdstuk 2 ligt de focus op de matrix waarmee de voedselwebstabiliteit bepaald wordt. Deze matrix heet in de voedselwebecologie de 'interactiematrix'; in de wiskunde staat deze matrix bekend als de 'Jacobi-matrix'. Welke getallen in de interactiematrix staan, hangt af van hoe de vergelijkingen in het model gedefinieerd zijn. De getallen die niet op de diagonaal van de interactiematrix staan, ook wel de 'interspecifieke interactiesterktes' genoemd, geven aan hoe sterk de interactie is tussen twee soorten. Deze getallen zijn goed af te leiden uit de vergelijkingen en achtergrondkennis van het systeem. De getallen op de diagonaal daarentegen, de 'intraspecifieke interactiesterktes', zijn vaak lastiger af te leiden. Meestal worden daarom willekeurige getallen voor de diagonaal gekozen. Vaak wordt dan voorbijgegaan aan het gevolg van deze keuze is op de stabiliteitsanalyse. In dit hoofdstuk definieer ik de diagonaal van interactiematrices behorende bij bodemvoedselwebben op

vier verschillende manieren, en kom tot de conclusie dat de uitkomst van de stabiliteitsanalyse behoorlijk beïnvloed kan worden door de keuze van de diagonaalelementen. Dit geeft aan dat het van groot belang is de gevoeligheid van de stabiliteitsanalyses voor de diagonaalkeuze te testen.

In hoofdstuk 3 kijk ik - weer met het voedselwebmodel - naar de relatie tussen voedselwebstabiliteit en –complexiteit. Deze relatie is in de voedselwebecologie veel onderzocht. Intuïtief zou je denken dat een complexer web, met veel organismen en veel onderlinge interacties, stabiel is, doordat het beter klappen op kan vangen. Er wordt echter vaak gevonden dat er geen relatie, of zelfs een negatieve relatie (hoe complexer, hoe minder stabiel het web) bestaat tussen deze twee voedselwebkarakteristieken. Als maat voor voedselwebcomplexiteit gebruik ik hier een maat voor de onderlinge verbondenheid in het voedselweb, *connectance*: het relatieve aantal bestaande interacties ten opzichte van het aantal mogelijke interacties. In deze studie is er géén relatie tussen voedselwebcomplexiteit en –stabiliteit voor 15 bodemvoedselwebben. Maar als in plaats van *connectance* ‘gewogen *connectance*’ gebruikt wordt, dan is er wel een positieve relatie tussen complexiteit en stabiliteit. Gewogen connectance neemt de zwaarte van de interactie tussen predator en prooi mee. Soms eet een predator veel van prooi A en weinig van prooi B. Bij gewogen connectance telt de eerste interactie dan zwaarder mee dan de tweede. De verdeling van interactiesterktes over het web speelt zo een meer prominente rol. Het meenemen van de verdeling van interactiesterktes in voedselwebanalyses is een recente ontwikkeling, die, zoals hier aangetoond, een behoorlijke invloed kan hebben op de uitkomsten.

In hoofdstuk 4 richt ik me op een aquatisch voedselweb en gebruik ik het ecosysteemmodel (PCLake) om het effect van vogels op de plotselinge omslag in helderheid in meren te bestuderen. Deze omslag is een bekend verschijnsel in de aquatische ecologie: bij een toenemende aanvoer van nutriënten als fosfaat kan een helder meer van het ene op het andere moment veranderen in een troebel meer. Interacties tussen waterplanten, die stabiliserend werken voor de heldere toestand, en plankton spelen hierbij een belangrijke rol. Watervogels als meerkoeten begrazen de waterplanten en zouden zo een omslag naar een troebele toestand kunnen faciliteren. Veldstudies geven hier niet een eenduidig antwoord op, omdat deze zijn uitgevoerd onder verschillende omstandigheden en zo andere factoren (wind, ligging van het meer, klimaat) niet zijn uit te sluiten. Een wiskundig model kan uitkomst bieden, omdat verschillende scenario's met watervogels kunnen worden getest onder constante omstandigheden. Uit deze modelstudie komt naar voren dat meerkoeten onder toenemende fosfaattoevoer meer planten eten, en daardoor inderdaad een omslag naar een troebele toestand faciliteren. Dit resultaat kan van belang zijn voor waterbeheerders die graag willen weten wanneer een meer omslaat van helder naar troebel water, omdat het aangeeft dat herbivorie door watervogels daarbij ook in ogenschouw genomen moet worden.

In hoofdstuk 5 bekijk ik nogmaals de omslag in meren van helder naar troebel water, en weer terug, maar dit keer met beide modellen en beide methodes. Zoals gezegd is het voedselwebmodel gericht op de interacties tussen de organismen. Maar in de mechanismen die ten grondslag liggen aan de omslag van de watertoestand in een meer spelen abiotische factoren (licht, opwelling van bodemmateriaal) een belangrijke rol. De vraag is of het voedselwebmodel en de matrixmethode dan wel gebruikt kunnen worden voor het bestuderen van deze omslag. Als dat het geval is, dan komt er een heel pakket aan wiskundige technieken en ecologische theorieën vrij om dit fenomeen verder te bestuderen. Het ecosysteemmodel PCLake (waarvan bekend is dat het een dergelijke omslag kan modelleren) is hier gebruikt om data te genereren; PCLake fungeert hiermee als een soort virtuele waterwereld. Voor verschillende toevoeren van fosfaat werd PCLake doorgerekend, net zolang tot het meer zich in een evenwichtstoestand bevond. De populatiegroottes en parameters van deze scenario's werden gebruikt in het voedselwebmodel, waarmee via de matrixmethode de mate van stabiliteit bepaald werd langs de nutriëntengradiënt. De uitkomsten van deze analyses laten zien dat voor een toenemende fosfaattoevoer de maximale eigenwaarde toeneemt, wat wil zeggen dat de stabiliteit van het web afneemt. Dit klopt met het idee dat de stabiliteit van de heldere toestand afneemt, net zolang tot deze instabiel wordt en het meer omslaat naar een troebele toestand. Maar het is heel opmerkelijk dat het voedselwebmodel, dat enkel gebaseerd is op trofische groepen en hun onderlinge relaties, deze afname in stabiliteit weet op te pikken, terwijl die is gerelateerd aan factoren die niet expliciet meegenomen worden in dit model.

De resultaten van hoofdstuk 5 laten de meerwaarde zien van het naast elkaar gebruiken van verschillende modellen en methodes. Het voedselwebmodel beschrijft de interacties tussen organismen zonder expliciet de interacties met en invloeden van de omgeving mee te nemen. Het is daardoor minder geschikt om scenario's te testen waarin een omgevingsfactor verandert. In het ecosysteemmodel worden omgevingsfactoren en hun invloed op organismen wel expliciet gemodelleerd, maar dit gaat gepaard met een enorme hoeveelheid aan vergelijkingen en parameters, waardoor het lastig is om de modelresultaten te interpreteren. Door beide modellen te gebruiken, worden deze zwakke punten teniet gedaan. Het voedselwebmodel krijgt een grotere voorspellende waarde (het kan gekoppeld worden aan een omgevingsfactor, hier fosfaattoevoer), terwijl het ecosysteemmodel inzichtelijker wordt (via de matrixmethode, waarmee patronen in interacties nader bestudeerd kunnen worden). In één zin samengevat laat dit proefschrift daarmee zien dat terwijl verschillende wiskundige modellen en technieken gebruikt kunnen worden om diverse vraagstukken in de voedselwebecologie te onderzoeken, de meest interessante resultaten worden verkregen door deze modellen en technieken te combineren in één samenhangende analyse.

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of literature (4.5 ECTS)

- Searching for balance: equilibria and stability of food webs

Post-graduate courses (9.8 ECTS)

- Complexity winterschool; NWO (2011, 2012)
- Theoretical ecology; PE&RC (2012)
- Parameter estimation; PSG Biometris (2013)
- Life history theory; PE&RC (2013)
- Consumer-resource interactions; PE&RC (2014)

Laboratory training and working visits (1.2 ECTS)

- Lake Constance food web; University of Potsdam, Institute of Biochemistry and Biology (2012)

Invited review of (unpublished) journal manuscript (1 ECTS)

- Book: Energetic food webs: biomass build-up, fluxes and models of food webs (2012)

Competence strengthening / skills courses (5.7 ECTS)

- Lecturing; Educational Staff Development (2012)
- Project and time management; WGS (2012)
- Techniques for writing and presenting a scientific paper; WGS (2013)
- Career orientation; WGS (2013)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- Netherlands Annual Ecology Meeting (NERN) (2012)
- PE&RC Day (2012)
- Current themes in ecology (2012, 2014)

Discussion groups / local seminars / other scientific meetings (6.4 ECTS)

- Food web ecology discussion group; organiser (2011-2014)
- Ecological theory and application discussion group (2012-2014)
- Wageningen evolution and ecology seminars (2012-2014)
- NWO Complexity meetings (2012-2014)
- Population studies discussion group; Radboud University (2014)

International symposia, workshops and conferences (5.1 ECTS)

- Netherlands Annual Ecology Meeting (NERN) (2013, 2014)
- Food webs: Science for Impact; Justus Liebig University Giessen (2013)

Lecturing / supervision of practical's / tutorials (8.4 ECTS)

- Wiskunde M 1,2,3 (2011-2014)
- Food web ecology (2013)

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Cover

Image: Piet Mondriaan, Blossoming Apple Tree (*Bloeiende appelboom*), 1912, Gemeentemuseum Den Haag