For quality of life

Tipping points in natural systems

An inventory of types, early warnings, and consequences

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1   Introduction

1.1   Problem statement

The continuing increase of the human population generates a large demand for fresh water, food stuffs, energy, materials, and land. This puts an enormous pressure on natural resources and land use, and it has resulted in a significant increase in the exhaust of pollutants, aerosols, excess nutrients, greenhouse gasses and more. This threatens ecosystem services worldwide. Scientists and environmentalists have discussed ecosystem services already for decades, but only recently have other stakeholders like governments and farmers become much more appreciative of the possible services that ecosystems may provide for humans. Not only do ecosystems provide sources of food and water, but they also deliver a wide variety of other services, like sources of medicine, carbon fixation, or less tangible services like increased human welfare through recreation and discovery. Ecosystem services have been formalized and popularized by the four-year study 'Millennium Ecosystem Assessment' (MA).

It is a major challenge for mankind in the 21st century to deal with the durable protection of ecosystem services, in order to be able to continue making use of them. Nowhere is this more the case then in densely populated riverbed areas, like in India, China, or the Netherlands. The project 'durable development of the green blue space' (KB IV-project "*duurzame ontwikkeling van de groenblauwe ruimte*"), financed by the Dutch ministry of Economic Affairs, Agriculture and Innovation, aims at developing solutions for a durable use and management of the space in the Netherlands, trying to promote the protection of various ecosystem services while maintaining economic (industrial, agricultural) production.

One aspect of this is to obtain an overview of possible threats (or possibilities) to ecosystem services, for instance caused by climate change. A major concept that has arisen the past decades in this context is 'tipping points'. It has been realized that neither ecosystems nor other complex systems, for instance socio-economic systems, are necessarily either static or linearly responding to changes. Instead, they commonly display strongly nonlinear responses to changes (so-called 'drivers'), and not only small responses under large changes ('buffering'), but also large responses under small changes. Furthermore, if the small change is reverted after the response, the system does not necessarily have to be able to revert to the original state it was in before the small change occurred. When this occurs, i.e. the system responds heavily to a small change and is not restored after a restoration of the change, the system is said to have undergone a 'tipping point' or 'regime shift' (there are also other names for it, which we will mention later in this report). The new state into which a system has shifted after the change may not be a desirable one from our point of view. It is therefore important to gain insight in which natural or semi-natural systems what types of tipping points can be expected, and what changes will result in the occurrence of tipping points in these systems.

1.2   Goal and approach

In this report the primary goal is to obtain insight in what types of tipping points there may occur in (semi-)natural systems, especially when they are relevant with regard to the 'durable development of the green blue space'. For that the scientific literature on the subject was screened. The search included mostly ecologically oriented papers in 'Web of Science' and 'Scholar Google' with the term 'tipping point' and/or related terms, including alternative steady state, bistability, resilience, catastrophic, regime shift, early warning, alternate regimes, change-point, priority effect, assembly theory, restoration ecology, threshold, and some related subjects for more background information, including rhizosphere, pedobiology, soil-plant-atmosphere interactions, crop simulation models, and similar terms. Although not a complete overview of all possible tipping points in all possible ecosystems is presented here, it has been attempted to at least obtain an overview that covers the main points on natural systems that may undergo tipping points, and that have relevance for the Netherlands.

1.3   Report set-up

The rest of the report is set-up as followed. We first consider the terminology and theoretical background on tipping points. This includes an overview of methodologies on the detection of tipping points in models, which is rooted in the branch of bifurcation analysis, and in data, which has a strong statistical component. Next, we consider the experimental and (semi-)natural systems in which tipping points have been demonstrated or are likely. This includes also possibilities for tipping points in major components of the climate system, named 'tipping elements'. Finally we consider which ecosystem services may likely be vulnerable to tipping points within a realistic time frame, with some focus on the natural systems that exist in western Europe and the Netherlands.

2 Nederlandse samenvatting

2.1 Inleiding en probleemstelling

De groei van de menselijke populatie leidt wereldwijd en in het bijzonder in Nederland tot een steeds grotere druk op natuurlijke hulpbronnen, ruimte en ruimtegebruik, etc., en tot een steeds grotere uitstoot van afval, CO_2, en andere vervuilende stoffen. Dit dreigt daarmee ook steeds meer te leiden tot belangenverstrengelingen van verschillende belangenhouders, en tot het verlies van functies of systemen die minder bij lijken te dragen aan primaire behoeften. Hierbij valt te denken aan ecosysteemdiensten die geleverd worden door (half-)natuurlijke systemen, zoals waterzuivering, CO_2-opslag, of het welzijn van burgers. Het is dan ook een uitdaging voor de 21ste eeuw om onderzoek te doen hoe creatief om te gaan met de toenemende druk door de menselijke populatie en de mogelijke belangenverstrengelingen van verschillende belangenhouders die dat met zich meebrengt, bv. door systemen meerdere functies tegelijk te laten vervullen. Het KB IV-programma "groenblauwe ruimte" beoogt te onderzoeken hoe, door goed gebruik te maken van de half-natuurlijke terrestrische ('groene') en aquatische ('blauwe') ruimte, hier oplossingen kunnen worden geboden.

Een grote onzekerheid binnen deze vraagstelling wordt echter gevormd door het bestaan van diverse niet-lineaire verbanden tussen de verschillende componenten (economische, sociale, biologische, geologische, chemische en fysische factoren) van de verschillende betrokken systemen. Onderzoek heeft uitgewezen dat er in meerdere natuurlijke en menselijke systemen mogelijke 'kantelpunten' (Eng. '*tipping points*') bestaan: Kleine veranderingen in factoren die van belang voor het systeem zijn, zgn. '*drivers*', kunnen in plaats van lineaire en dus voorspelbare veranderingen in een systeem door de niet-lineariteiten ook leiden tot plotselinge grote veranderingen ('*shifts*' of '*regime shifts*'). Bovendien zijn die veranderingen niet altijd eenvoudig herstelbaar door een omkering in de 'driver'; Er is meer voor nodig om het systeem te herstellen naar de oude toestand.

2.2 Doel

Het project "Hoe voorkomen we dat ecosystemen kantelpunten overschrijden en zodoende belangrijke ecologische diensten verliezen?", afgekort "tipping points" levert bijdragen aan het KB IV-programma "groenblauwe ruimte", hoofdzakelijk met het oog op het bestaan van mogelijke kantelpunten in natuurlijke en half-natuurlijke systemen. Daarbij wordt niet alleen gekeken naar kantelpunten die voor Nederland en West-Europa belangrijk kunnen zijn, maar ook naar kantelpunten die voor andere gebieden van belang zijn. De bijdragen zijn onder meer:
- Inzicht in terugkoppelingen tussen het humane systeem en biofysische processen, vooral klimaatverandering en de effecten van klimaatverandering;
- Het karakteriseren van 'tipping points', en het bestaan van mogelijke tipping points in systemen die belangrijke ecosysteemdiensten leveren;
- Een overzicht van indicatoren voor 'early warning', die aan kunnen geven of een systeem op de korte termijn een tipping point dreigt te ondergaan;
- Daaraan gerelateerd inzicht in de bedreigingen of kansen die dat met zich meebrengt (identificatie van 'zwakke plekken') voor de duurzame ontwikkelingen van ecosysteemdiensten in de groenblauwe ruimte.

Omdat veel half-natuurlijke systemen onder grote invloed van menselijke componenten staan, wordt er tegenwoordig ook veel gedacht in termen van Complexe Adaptieve Systemen (CASsen), waarin deze componenten ook meegenomen worden. Voor de indeling van de groenblauwe ruimte ligt deze keuze nog extra voor de hand, omdat de uiteindelijke indeling van de ruimte ook deels door menselijke factoren wordt bepaald. Dit project is daarom ook zijdelings gekoppeld aan het IPOP CAS-thema binnen de WUR.

2.3   Opzet van het rapport

Het (verder Engelstalige) rapport is als volgt opgezet. Eerst kijken we naar de achtergrond van kantelpunten: Wat zijn het precies, en waar komt het concept vandaan? We behandelen hierbij ook de noodzakelijke wiskundige achtergrond. Daarnaast geven we een overzicht van een aantal typen kantelpunten in modellen, en een klein overzicht van methoden hoe ze in modellen kunnen worden gevonden. Verder kijken we naar statistische methoden voor het detecteren van kantelpunten, inclusief methoden die bruikbaar worden geacht voor 'early warning'. Daarna bespreken we een selectief overzicht van laboratoriumexperimenten waarin kantelpunten zijn aangetoond, gevolgd door observaties in (half-)natuurlijke systemen. Dit omdat kantelpunten op verschillende ruimte- en tijdschalen, variërend van kantelpunten in lokale bodems tot 'tipping elements' in klimaat-subsystemen. Uiteindelijk geven we nog een discussie van welke kantelpunten relevant worden geacht binnen een realistisch tijdsbestek van ca. 100 jaar, met enige focus op West-Europa en de ontwikkeling van de groenblauwe ruimte in Nederland.

3 Tipping points: background

In this chapter we consider the theoretical background of tipping points, namely what they are and what properties they display.

3.1 Concepts

The concept of 'tipping point' comes from the social sciences, and was first coined by Grodzins (1958) in his research on the dynamics in neighbourhoods between Afro-American and Caucasian families. A tipping point is defined as "the critical point in an evolving situation that leads to a new and irreversible development" (Techtarget). Currently, the concept of tipping points has been popularized by Gladwell (2000), and has found its way in many diverse fields of research, like climate change research or economics (Scheffer, 2009). Depending on the context the term 'tipping point' can have slightly different meanings. For instance, in social sciences a tipping point is often referring to events in which previously rare phenomena rapidly become more common. In this report we limit ourselves to the interpretation in the ecological and climatological sciences. Ironically, within ecology and climatology there is a whole spectrum of names (Andersen et al., 2009), such as catastrophic shift (Scheffer et al., 2001a), regime shift (Scheffer et al., 2001b), critical threshold, abrupt change, ecological threshold, break-point, change-point, structural change, climate jump (Yamamoto et al., 1986), observational inhomogeneity, tipping element (Lenton et al., 2008), that more or less describe the same phenomenon: a system can undergo (relatively) rapid, significant, and not easily reversed changes under small changes in a 'driver' (an input in a system, like the inflow of nutrients or climate change).

It is important to first consider that ecological thinking in general has been focussed on the 'resilience' or 'stability' of biological systems, as these systems usually contain many biotic components, which constitutes a large biodiversity. This allows for possibilities for the 'absorption' of disturbances, and as such biodiversity has value for the maintaining of ecosystem services (Elmqvist et al., 2003). Resilience means, that for instance, when rainfall is less than the previous year a rainforest will not instantly disappear. A natural system like a forest may be able to deal with even large disturbances or changes in drivers, which seemingly have little effect on the state of the system. However, it has been realized that ecosystems can be quite complex, adaptive systems, that are characterized by historical dependency, nonlinear dynamics, threshold effects, multiple basins of attraction, and limited predictability (Levin, 1999).

Set off by the seminal paper by Holling (1973), the thinking in terms of 'tipping points' has replaced the assumptions about 'smooth' response functions in natural systems in response to forcing, either induced by anthropogenic processes or otherwise, which has resulted in a large literature where 'stability' is no longer considered to be the norm for biological systems. There exists increasing evidence that suggests that ecosystems often do not respond in a smooth way to gradual change (Gunderson & Pritchard, 2002; Folke et al., 2004, and see the Resilience Alliance, http://www.resalliance.org/). Under some conditions the capacity to 'buffer' disturbances may be 'full' or overstretched. At that point the chances of a 'tipping point' occurring increases dramatically, and the system may seemingly undergo large changes as a result of a small disturbance or change in input, settling into a new state (Scheffer et al., 2009). For instance, in the above example after a tipping point a rainforest may be converted to a grassland. The buffer capacity properties of the new state into which the system has settled also likely differ from the properties of the old state, which means that the responses to disturbances have changed as well. Reverting the system to the old state – the forest – may therefore prove very difficult. The property that it may require much more effort to restore the system to the old state than the effort it took to shift the system to the new state is referred to as 'hysteresis' (which means 'memory').

Tipping points and resilience can hence be seen as two sides of the same medallion. Indeed, it should be observed that the definition of 'resilience' has changed from a more engineering point of view on resilience, based on recovery time, to a more ecological point of view, based on the amount of disturbance which is required to push an ecosystem over its 'ecological threshold' (Groffman et al.,

2006). Tipping points and resilience are both the result of the nonlinearity of natural systems. This nonlinearity is the result of the complexity of natural systems, which are capable of self-organisation. It is important for management purposes to be aware of this, and to get an overview of which systems are prone to undergo 'tipping points' under current, mostly human-induced changes, and to be able to quantify these nonlinearities. Furthermore, the framework even becomes more complex when considering the increase in the human population numbers and the anthropogenic effects on natural systems. As a result also the role of anthropogenic actors is becoming more important. It should be realised that most natural systems are no longer 'natural', but instead they have become semi-natural systems. This is commonly referred to as 'socio-ecological systems' (SESs), which in turn are actually Complex Adaptive Systems (CASs). CASs have properties like nonlinearity, and furthermore show adaptability because of the changing behaviours of 'agents', which may be abstract or actual components of the systems, like human communities. The resilience of a SES may be influenced by such agents (Walker et al., 2004), either in a good or a bad way. Especially in the Netherlands the role of agents should be considered, as there are hardly any natural systems which are not under significant anthropogenic influence in one way or the other.

3.2 Mathematical underpinning

Of course, there would be no observable shift if a system does not have multiple alternative states (Scheffer & Carpenter, 2003), which are 'stable attractors', and that arise because of nonlinear feedbacks in the system (Mayer & Rietkerk, 2004). An alternative stable state, however, does not have to be positive. In fact, it can easily be zero, which is ecologically interpreted as 'extinct', or 'barren'. In practice it means, for instance, that an observed population of species is no longer capable of maintaining itself.

To understand how a tipping point (or shift) can occur in a system, we first need to explain more about the mathematics with regard to stable states. In models, there are in general two types of events that can be indicated by a 'tipping point':
- The first is a shift from one stable state to another state or a transition from one type of behaviour to another under a small change in conditions;
- The second is a shift from one stable state to another state under practically the same conditions, but a change is made in the state variables.

To make it practical, we present below two small and well-known food web models that can be used for demonstrating the possibilities for tipping points.

Example type 1 tipping point

A well-known ecological food web model of two ordinary differential equations known as the Rosenzweig-MacArthur model (Rosenzweig-MacArthur, 1963) is given as:

$$\frac{dX(t)}{dt} = r\,X(t)\left(1 - \frac{X(t)}{K}\right) - \frac{A_{X,Y}\,X(t)Y(t)}{(\kappa + X(t))} \qquad Eq.\,(3.1a)$$

$$\frac{dY(t)}{dt} = y_{X,Y}\frac{A_{X,Y}\,X(t)Y(t)}{(\kappa + X(t))} - RY(t) \qquad Eq.\,(3.1b)$$

In this model $X(t)$ denotes the prey population, and $Y(t)$ denotes the predator population. It describes the growth and decline of the two populations in time. The prey population follows a logistic growth, meaning that growth of the prey population goes fast when the numbers are low, but the growth decreases when numbers are high, and finally there is a 'saturation', known as the 'carrying capacity'. The predator-prey interactions are given as a Holling type II functional response (Holling, 1959), which means, that the predator population cannot consume prey at an infinite rate. The parameters are given in Table 3.1 (Van Voorn et al., 2008; Van Voorn, 2009, and references therein).

Table 3.1: Parameters of the Rosenzweig-MacArthur model (Van Voorn, 2009). This table contains the SI units, the default values, and the ecological interpretation of the parameters. 'Variable' indicates that the parameter can have different values. This will be explored later on.

Parameter	SI units	Value	Meaning
r	s^{-1}	0.5	Prey population specific growth rate
K	$mol(X)\,m^{-3}$	Variable	Carrying capacity for supporting the prey population
$A_{X,Y}$	$mol\,(X)\,mol\,(Y)^{-1}s^{-1}$	0.5	Ingestion of prey by predator per time unit
κ	$mol(X)\,m^{-3}$	9.	Saturation constant of Holling type II functional response
$y_{X,Y}$	$mol\,(Y)\,mol\,(X)^{-1}$	0.4	Conversion efficiency of prey to predator biomass
R	s^{-1}	0.08	Mortality rate of the predator population

Fixing all the parameters as given the system can be evaluated for 'steady states'. These are obtained by setting the equations Eq. (3.1) both to zero. Fulfilling this condition means that the values of $X(t)$ and $Y(t)$ do not change in time anymore, hence it is a 'steady state', i.e., the values remain fixed in time, unless some change in the parameters occurs. For example, we set the given parameter values plus $K = 15$ (ignoring the exact biological interpretation of these values for now), and we obtain the following steady states: $E_0 : X = 0$ and $Y = 0$, $E_1 : X = K = 15$ and $Y = 0$, and $E_2 : X = 6$ and $Y = 9$. The first two solutions E_0 and E_1 indicate extinction of either both populations or the predator population, respectively, while the third solution E_2 indicates that both populations might co-exist.

The question now is how to establish which one of the steady states is the attractor? For that we need to introduce the concept of 'stability', which is determined by a local linearization of the system around the steady state (the 'Jacobian matrix') and calculating the so-called 'eigenvalues' (Guckenheimer & Holmes, 1985; Edelstein-Keshet, 1988; Wiggins, 1988, 1990; Kuznetsov, 2004). We will not explain all the details in this regard (for that, see for instance Van Voorn, 2009, or any good introductory book on theoretical ecology or bifurcation analysis), but it is important to note that the eigenvalues of any steady state give information about the stability of that point. If all eigenvalues are negative, it indicates that all local trajectories will be attracted to the steady state, and hence it can be concluded that the steady state is stable. Vice versa, if not all eigenvalues are negative but some are positive, then the evaluated point is unstable.

In the above case it can be shown (using software for symbolic calculations like Maple, Mathematica, or Matlab) that E_0 and E_1 are unstable, while E_2 is stable. Hence, the positive steady state is stable, and this indicates that the populations of prey and predator will be maintained under constant conditions. As there are no further steady states and there is only one stable steady state, all positive initial conditions will eventually convergence to the same E_2. In other words, the 'domain of attraction' of the steady state E_2 spans the whole of positive solutions. If we plot the values of X versus Y we obtain a so-called 'phase plot'. For completion, we also plot the 'isoclines', the curves along which only one of the two equations Eq. (3.1) equals zero. The phase plot for the Rosenzweig-MacArthur model with the given parameter values plus $K = 15$ is a simple picture, given in Figure 3.1, left upper panel. The left lower panel shows the dynamics in time.

Figure 3.1, right upper panel also shows the phase plot of the model for $K = 25$. The system still has three equilibria, where now $E_2 : X = 6$ and $Y = 11.4$. The eigenvalues show that this positive steady state E_2 is now also unstable. Instead, trajectories evolve to some periodic solution around E_2, which is known as a 'limit cycle'. In time plots this shows up as periodic fluctuations (see right lower panel), like the well-known example of the snowshoe hare and lynx (Elton & Nicholson, 1942). Observe, that a limit cycle is still perceived by many as both 'mathematically stable' and 'biologically stable', as the pattern is repetitive and the populations do not go extinct.
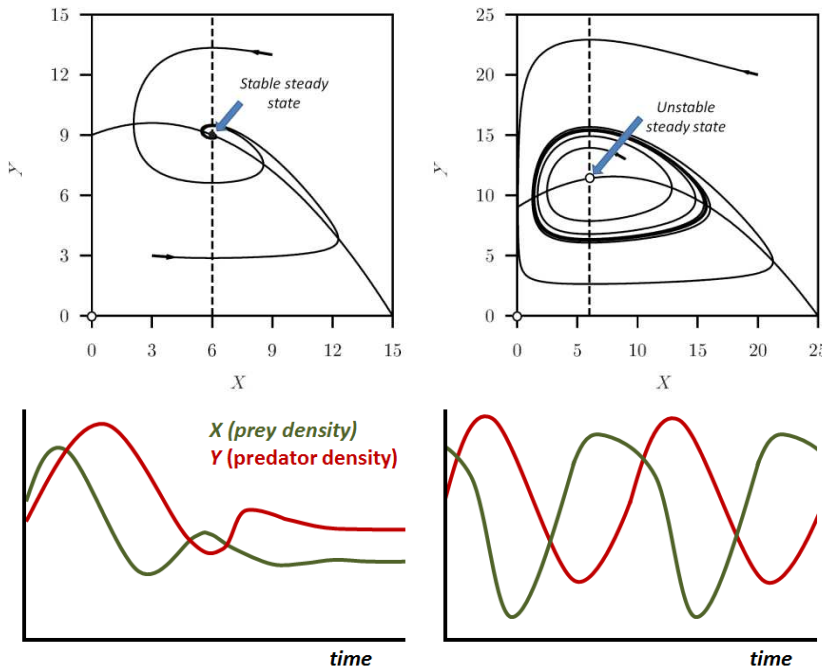
Figure 3.1: Phase plots and time plots of the Rosenzweig-MacArthur model for two parameter settings.
Upper left: Phase plot at $K = 15$. A positive stable state exists. Trajectories eventually lead to this stable state.
Lower left: Time trajectories at $K = 15$.
Upper right: Phase plot at $K = 25$. A positive state exists, but it is unstable. Instead there are periodic solutions.
Lower right: Time trajectories at $K = 25$. This behaviour is periodic.

Apparently there has been a transition in going from the situation in the left panel of Figure 3.1 to the right panel, or put differently, by increasing K from 15 to 25. This transition is a tipping point, and biologically this situation occurs when a system is enriched by nutrients ('eutrophication'). This is the first type of tipping point: A transition is the qualitative behaviour of the system through a bifurcation under parameter change. We will discuss this bifurcation point in more detail in Section 3.4.

Example type II tipping point

There is also a second type of tipping point, and for that we look at another example. We consider a model of two ordinary differential equations much like the Rosenzweig-MacArthur model, but including a so-called 'Allee effect'

$$\frac{dX(t)}{dt} = r\,X(t)\left(1 - \frac{X(t)}{K}\right)\left(\frac{X(t)-Z}{K}\right) - \frac{A_{X,Y}\,X(t)Y(t)}{\left(\kappa + X(t)\right)} \qquad Eq.\,(3.2a)$$

$$\frac{dY(t)}{dt} = y_{X,Y}\,\frac{A_{X,Y}\,X(t)Y(t)}{\left(\kappa + X(t)\right)} - RY(t) \qquad Eq.\,(3.2b)$$

In this model the prey population $X(t)$ is subject to the Allee effect (Allee, 1931; Van Voorn et al., 2007; Kramer et al., 2009) instead of following a logistic growth. In this case the growth of the prey population is not only limited at higher numbers, but also at low numbers. Biologically the effect mimics for instance the difficulties of finding mates at low numbers, or a reduced survival probability because of smaller group sizes. The Allee effect may be either 'weak' or 'strong', depending on the value of the Allee threshold parameter $Z[mol\,(X)\,m^{-3}]$. Observe, that in the limit case $Z \to 0$ the model collapses to Eq. (3.1).

The model displays some new features as compared to Eq. (3.1). It is important to note that for an arbitrary value of $0 < Z < K$ there are now four solutions: three steady states in which the predator population does not exist, namely $E_0 : X = 0$, $E_1 : X = Z$, and $E_2 : X = K$, and the fourth steady state E_3 where both the prey and the predator populations exist. Again, we can determine the stability of each steady state by evaluation of the eigenvalues. It turns out that the system contains two stable steady states, namely the steady state E_3, as in the Rosenzweig-MacArthur model, and E_0. In other words, there is 'bistability'. Both steady states have a 'domain of attraction'. Depending on the initial conditions, the system evolves either to the steady state E_3 (both populations co-exist) or to E_0 (i.e., both populations

go extinct). The two domains of attraction are separated by a so-called 'separatrix' , that splits the state space.

The tipping point that may occur in this case is not a transition in the type of behaviour under parameter change. Instead, under *equal parameter values* a shift may occur from one stable state to another by traversing the separatrix. This might occur because of a sudden change in the size of one or two of the populations, for instance by harvesting of these populations, see Figure 3.2. Observe, that the model Eq. (3.2) also displays other tipping points. We will revisit the model in Section 3.4 for more details.
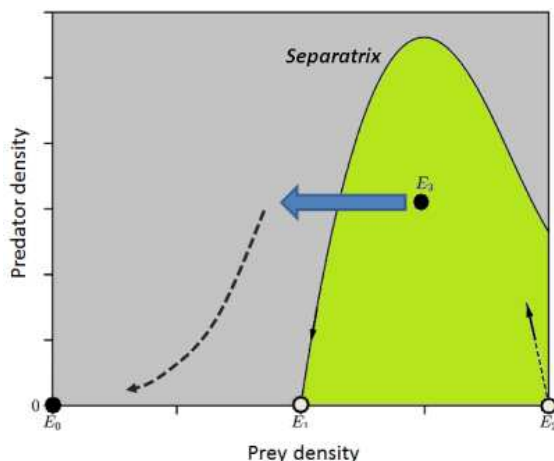

Figure 3.2: Phase plots of the Allee model. Two positive stable states exists, namely the origin E_0 (no prey, no predators), and the internal steady state E_3 (positive prey and predator densities). A 'separatrix' divides the domains of attraction for E_0 (grey area) and for E_3 (green area). Trajectories starting within the green area eventually end up in E_3, while trajectories starting within the grey area eventually end up in E_0. If for some reason a perturbation would occur, e.g., a decline in prey because of human interference, the state of the system might be shifted into the grey area (blue arrow). In that case no further perturbations have to occur for the populations to go extinct.

3.3 Types of tipping points

We recapitulate the above information. In the case of a transition a bifurcation is crossed under parameter change. At a bifurcation a state may lose its stability, becoming unstable, or it may disappear altogether. In the case of a shift a boundary between two domains of attraction (a separatrix) is crossed. This can only happen when there are at least two stable states. The main concepts discussed above are depicted in Figure 3.3.
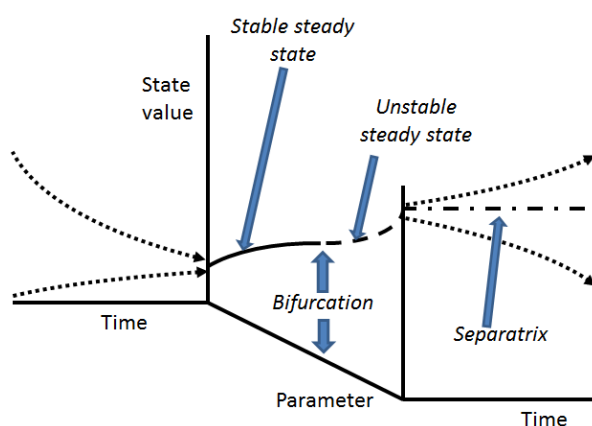

Figure 3.3: Three-dimensional diagram depicting the most important concepts discussed in Sections 3.2 and 3.3. The x-axis depicts forward time, y-axis depicts the parameter, and z-axis depicts the state value (both assumed to be one-dimensional). Starting left at two different initial conditions, we see that both trajectories converge to a stable steady state. Under parameter change, the system undergoes a bifurcation, and the steady state (solid curve) becomes unstable (dashed curve). The steady state itself functions as separatrix and splits the state space into two regions. Trajectories now leave from the steady state, either up- or downwards.

The two types of tipping points can be coupled to the four experimental approaches to locate tipping points that are distinguished (Schröder et al., 2005). These are:
- A discontinuity in the response to a driver (usually some environmental parameter, e.g., K in Figure 3.1);
- A lack of recovery potential after a perturbation (like in Figure 3.2);
- Divergence due to different initial conditions (like the right time panel in Figure 3.3);
- Random divergence (causing a shift much like in Figure 3.2).

The first approach thus corresponds to localizing a bifurcation under parameter variation, while the other three approaches are based on crossing a separatrix. We will discuss the more experimental details in Chapter 5.

3.4   Bifurcation types

Given the scope of this report it goes too far to give an overview of all bifurcation types. Neither will we present a diagram of all types and how they are related. Instead, below we will present an overview of several bifurcations commonly encountered in ecological models, and that are also found in laboratory or field experiments (see Chapter 5). Some of these bifurcations are of higher co-dimension, which means that they are bifurcation points in which several properties of separate bifurcations are combined, and they usually form the origin of these separate bifurcations which can be tracked through parameter space (Kuznetsov, 2004).

Hopf bifurcation – Birth of periodic behaviour

There exist two types of Hopf bifurcations, namely the subcritical and the supercritical (Kuznetsov, 2004). The supercritical Hopf bifurcation is the most commonly encountered, and we focus here on this one. An example of a supercritical Hopf bifurcation has been given when we discussed the Rosenzweig-MacArthur model Eq. (3.1), and Figure 3.1. This bifurcation is a point at which a stable steady state destabilizes. Around the (now) unstable steady state a stable 'limit cycle' occurs. When displayed on a time-axis, the limit cycle appears as regular periodic fluctuations, as was shown in Figure 3.1, lower panels. Mathematically a Hopf bifurcation is characterized by two eigenvalues, which both have zero real parts and non-zero imaginary parts which are each other's counterparts (Kuznetsov, 2004).

A Hopf bifurcation can only occur in a system of at least two state variables. In practice this condition is easily satisfied as even very isolated systems still consist of several 'state variables', of which many remain hidden for the human observer. In population models, the Hopf bifurcation is mostly demonstrated in predator-prey models (Kooi, 2003). It has been coupled strongly to the 'paradox of enrichment' phenomenon (Van Voorn et al., 2008, and references therein). This paradox is observed in models like the Rosenzweig-MacArthur model Eq. (3.1), in which an increase in nutrient or food availability (larger K) paradoxically leads to destabilization of the food chain. Eventually the amplitude of the periodic fluctuation tends to become very large, which makes the probability of extinction through random fluctuations very likely.

Periodic fluctuations under parameter change have been demonstrated to occur in experimental laboratory set-ups (Fussman et al., 2000; see Chapter 5), and the phenomenon is commonly linked to the well-known example of the snowshoe hare and lynx (Elton & Nicholson, 1942).

Transcritical bifurcation – Extinction or invasion criterion

There exist two types of transcritical bifurcations, namely the subcritical and the supercritical (Kuznetsov, 2004). Again, the supercritical type is the most commonly encountered. The transcritical bifurcation often forms a criterion for invasion or extinction of a species (Kooi, 2003). Mathematically it is characterized by having an eigenvalue equal to zero. In a transcritical bifurcation a stable steady state and an unstable steady state collide and exchange their stability properties. In Figure 3.4 phase plots are depicted, illustrating the general idea.
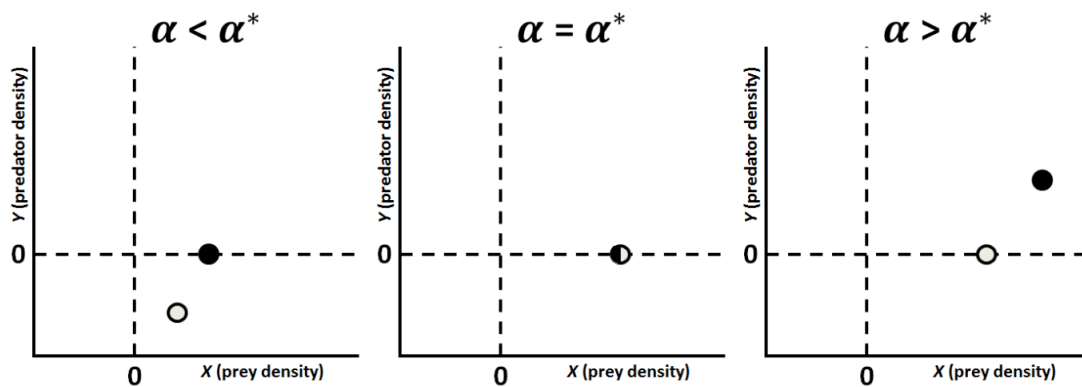
Figure 3.4: Phase plots demonstrating a *transcritical* bifurcation as invasion criterion. Dashed lines are the x- and y-axis. An arbitrary parameter α is varied, e.g., because of anthropogenic influence. *Left panel*: For α smaller than some critical value α^* there exist two steady states, one stable (solid), and one unstable (open). The stable state is a positive prey density, while the predator density is zero. *Middle panel*: For the critical value α^* the two states collide (indicated by a half-open circle). There is thus only one steady state. *Right panel*: After a further increase in α beyond the critical value α^* there is now a positive stable state – the prey and predator populations coexist.

An example of a transcritical bifurcation can be found also in the Rosenzweig-MacArthur model Eq. (3.1), see Figure 3.5. Given the parameter settings from Table 3.1, for values of $6 < K$ the predator population does not exist. At $K = 6$ the steady state has eigenvalue zero, and a new stable state occurs with positive prey and predator populations. This point is thus an invasion criterion for the predator population.

Figure 3.5: One-parameter bifurcation diagram of the Rosenzweig-MacArthur model, plotting the steady state values of the prey and predator densities as function of the carrying capacity (parameter K). For low values of K only the prey population exist in steady state (solid curve). An increase in K results in a stable steady state including the predator population (also solid curve), at a transcritical bifurcation (blue arrow). A further increase in K eventually leads to a supercritical Hopf (red arrow), at which point the steady state destabilizes (dotted curves) and periodic fluctuations occur (maximum and minimum values in solid) – the 'paradox of enrichment' in full effect.

Tangent bifurcation, cusp bifurcation, and hysteresis

The tangent bifurcation is a generalized case of the transcritical bifurcation (Kuznetsov, 2004). Also of this bifurcation there exist a super- and a subcritical type, and again the supercritical type is the biologically more interesting one. As it is the generalized case of the transcritical bifurcation, it is also characterized mathematically by an eigenvalue equal to zero. Compared to the transcritical bifurcation, in a tangent bifurcation the two colliding steady states disappear. In Figure 3.6 phase plots are depicted to illustrate the concept.

Figure 3.6: Phase plots demonstrating a *tangent* bifurcation. Again, an arbitrary parameter α is varied. *Left panel*: For α sma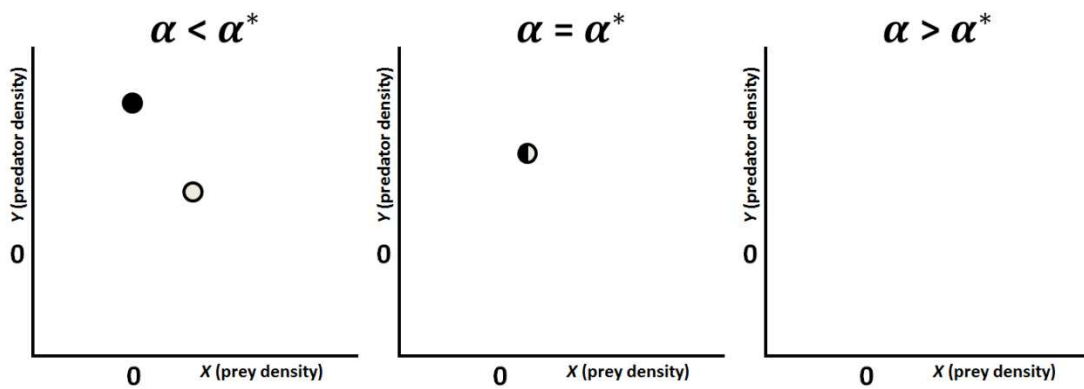ller than some critical value α^* there exist two positive steady states, one stable (solid), and one unstable (open). The prey and predator populations coexist. *Middle panel*: For the critical value α^* the two states collide (indicated by a half-open circle). There is thus only one steady state. *Right panel*: After a further increase in α beyond the critical value α^* there is no stable state left. There may however exist a further attractor.

The tangent bifurcation is best known in the environmental sciences for its role in the phenomenon of 'hysteresis' or memory after a tipping point (Scheffer & Carpenter, 2003). Hysteresis occurs for instance in systems like shallow lakes under variations in phosphorus content. A stable state exists under low phosphorus content (a 'clear' lake), which persists under a mild increase in phosphorus content but rather abruptly disappears after a slight further increase in phosphorus content, giving a 'turbid' state. A small decrease does however not restore the clear state, but instead a much larger decrease is required. This is shown in Figure 3.7. The example about shallow lakes is discussed in more detail in Chapter 5.
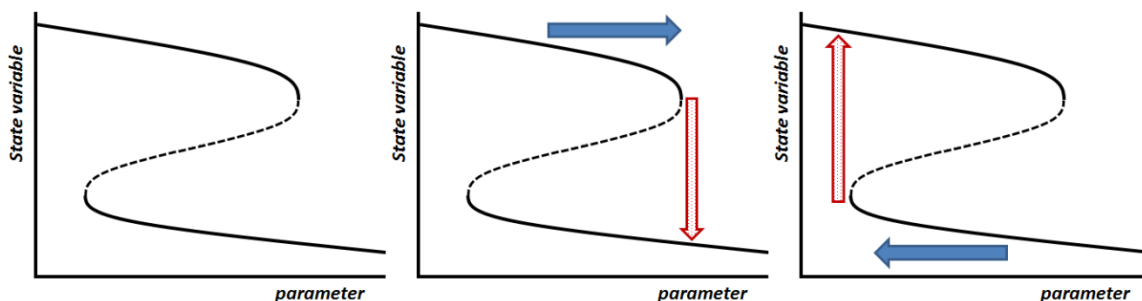

Figure 3.7: One-parameter bifurcation diagram showing *hysteresis*. Solid curves depict stable steady states as function of the parameter, dashed curves the unstable steady state. In a certain range there exist three steady states simultaneously: two stable, and one unstable. Observe, that the state variable is represented as one-dimensional, which is usually not the case. *Middle panel*: A significant change in the parameter value (the 'driver', blue arrow) does not lead to significant changes in the state, until a tangent bifurcation is encountered. Then, a small increase in the parameter value leads to a 'regime shift' as the higher stable state disappears (red arrow). *Right panel*: As the system is now settled in the lower stable state a significant backward change (blue arrow) is required in order to switch the system back to the original higher stable state (red arrow).

What is less known is that the origin of hysteresis is a cusp bifurcation, a bifurcation of higher co-dimension that forms the birthplace for a pair of tangent bifurcations (Kuznetsov, 2004). As the co-dimension is two it means in practice that two parameters need to be varied in order to find a cusp bifurcation. Mathematically a cusp bifurcation is characterized by having one zero eigenvalue, like the tangent bifurcation, but furthermore all other eigenvalues have zero real parts (they may have non-zero imaginary parts, however). In effect, it is the point where two tangent bifurcations come together. A cusp bifurcation is 'born' as the result of an increase in the strength of nonlinear interactions and feedbacks in a system. This is shown in Figure 3.8 (and see Figure 1 in Scheffer et al., 2001a).
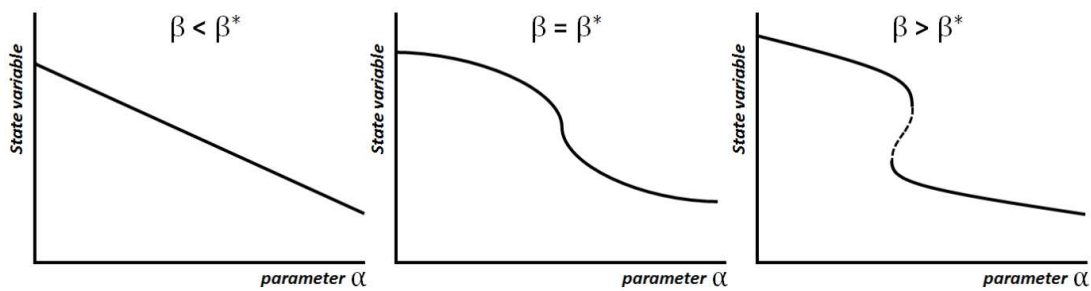
Figure 3.8: One-parameter bifurcation diagram showing the 'birth' of hysteresis in a *cusp* bifurcation. The x-axis still depicts the parameter α, like in Figure 3.7, which may vary. This time also a second parameter describing the strength of certain nonlinearities in the system (β) is involved, which may be manipulated through anthropogenic influence as well. *Left panel*: There is practically no nonlinearity in the system for $\beta \ll \beta^*$. Variations in parameter α have no consequences other than a variation in the value of the steady state. *Middle panel*: As β increases, the nonlinearity of the system increases as well. For $\beta = \beta^*$ a cusp bifurcation occurs, and two tangent bifurcations are 'born' simultaneously. *Right panel*: For $\beta > \beta^*$ the system shows hysteresis. A variation in parameter α may now lead to a regime shift, as depicted in Figure 3.7. Observe, that both α and β can be referred to as 'driver'.

It is not unlikely that nonlinear interactions and feedbacks may appear or increase in strength because of anthropogenic influences. This is in particular to be expected in Complex Adaptive Systems, in which the behaviour of individual agents is a significant part of the system (e.g., groups of humans, companies, nations). Natural systems may have a reasonable capacity to buffer outside random perturbations (resilience), which may be weakened (or enforced, for that matter) by the agents operating in or on that system (Walker et al., 2004). In the above example the parameter α may represent something like the enrichment of the system by nutrient emission, while parameter β represents the influence of the actors on the resilience of the system. As especially in the Netherlands the influence of agents is significant, we can imagine that something like a cusp bifurcation may easily be encountered.

Global bifurcations

All the bifurcations up to now are so-called 'local' bifurcations, which means that they can be detected by looking at local properties only. I.e., the evaluation of the Jacobian matrix (in effect a local linearization around the investigated steady state) and its eigenvalues is sufficient to know if such a bifurcation is encountered and what its properties are. This is not the case for 'global' bifurcations.

An example of a global bifurcation is found in the Allee model Eq. (3.2) that we already introduced. In this model we showed the existence of a tipping point under perturbation. However, when the predator population mortality rate is decreased (parameter R in the model) the system also undergoes a supercritical Hopf bifurcation, leading to periodic cycles, and then a so-called heteroclinic connection. At the heteroclinic connection the saddle steady state E_2 connects to the saddle steady state E_1. After a further decrease in R the domain of attraction of the positive attractor is lost, and both populations go extinct for any initial densities, see Figure 3.9. Because of its counterintuitive nature – the predator mortality rate decreases, yet it results in the extinction of the predator (and the prey) population – this phenomenon has been named 'overexploitation' by Van Voorn et al. (2007).
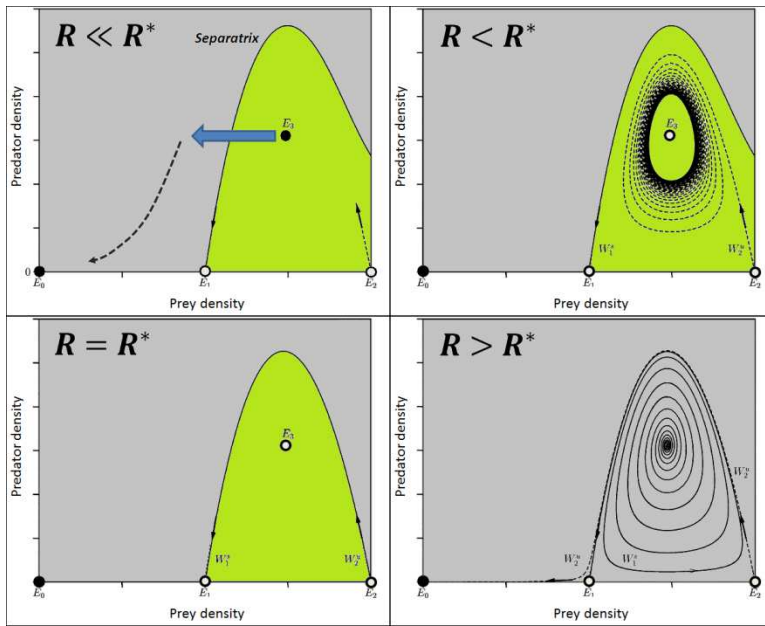
Figure 3.9: Phase plots of the Allee model for different predator mortality rates R (Van Voorn et al., 2007). *Left upper panel*: $R \ll R^*$. Two domains of attraction exist, and a tipping point may occur under perturbations. *Right upper panel*: $R < R^*$. A Hopf bifurcation has occurred, but the two domains of attraction remain. *Left lower panel*: $R = R^*$. A heteroclinic connection between two of the saddle steady states, which lies exactly on the separatrix between the two domains of attraction. *Right lower panel*: $R > R^*$. After the heteroclinic connection the separatrix has disappeared, as has the domain of attraction of the positive state.

As may be apparent from the example, global bifurcations cannot be detected by evaluating local information. Global bifurcations are not based on local properties like specific eigenvalues, but on connections between steady states. Thus, a 'global' view is required on the state space to expose the existence of these connections. Steady states can either connect to themselves – then they are 'homoclinic' connections – or to other steady states – these are 'heteroclinic' connections, like in the above example. Such connections can occur only between unstable steady states and/or limit cycles, or more specifically, 'saddle points' or 'saddle limit cycles' with at least one stable and at least one unstable eigenvalue. In a homoclinic connection the stable part of the steady state connects to the unstable part of itself, in a heteroclinic connection it connects to the unstable part of a second steady state.

Global bifurcations have been found in several ecologically oriented models, for instance in the extended variant of the Rosenzweig-MacArthur model Eq. (3.1), in which also a top-predator population exists that feeds on the predator population. As may be clear from the above example, homo- and heteroclinic connections are interesting, as at first one would not expect saddle steady states to be relevant in a biological context. However, global bifurcations are associated to the disappearance of domains of attraction or the disappearance of or a change in chaotic behaviour. As such, they present tipping points that are very relevant biologically speaking.

In the next Chapter we present a general discussion on the detection of bifurcations in models. Furthermore, we present an overview of statistical methods for the detection of tipping points and for early warning.

4 Early warning indicators and methods for detecting tipping points

In this chapter we consider methodologies for the detection of tipping points in both models and observational data, while real-life examples of tipping points are discussed in Chapter 5. The detection of tipping points in models is strongly related to what is referred to as 'bifurcation analysis', while the detection of tipping points in data is mostly based in statistical theory. It is prudent to specifically consider tipping points in models for various reasons. First of all, tipping point research (or rather bifurcation analysis) developed earlier as model analysis approach than it was used in experimental research. It allows us to conceptually understand how tipping points can occur. Also, although models are always 'incorrect' representations of experimental or field systems, it is attempted to provide models with 'real-life' features for various applications of these models. Any phenomena occurring in the models may also occur in the real systems they represent. Furthermore, in some branches of research, like climatology, models are about the only way of making forward time predictions, as the instrumental record of the Earth's climate system is not long enough to provide a reliable estimate, plus it may also be contaminated by the effects of external forcing (Barnett et al., 2005). Therefore, long control simulations with simulation models without anomalous external forcing are typically used for tipping point detection.

In Section 4.3 stochastic models will be considered. Both system and measurement noise can 'blur' tipping points, but tipping points may still exist and have clear effects. Obviously, with stochastic influences involved the probability of a shift occurring in the system is much larger near a bifurcation or separatrix than when the current system state is far off. In this case also statistical measures may be useful for localizing tipping points. Furthermore, systems that will undergo tipping points may show 'clues' that they are about to shift. Methodologies or indicators that reveal these clues are named 'early warning'. We will discuss the statistical methodologies for tipping point detection and early warning in the Sections 4.4 and 4.5.

4.1 Detection in models – Bifurcation analysis

The most relevant bifurcations have been discussed in Chapter 3, and these can be detected using bifurcation analysis techniques. These consist of the symbolical or numerical analysis of the existing states of a dynamical model, and the qualitative changes they undergo with respect to the system parameters (Guckenheimer & Holmes, 1985; Edelstein-Keshet, 1988; Wiggins, 1988, 1990; Kuznetsov, 2004; Seydel, 2010). Bifurcation analysis is in particular well-suited to analyse systems of limited numbers of ordinary differential equations to locate the existing steady states, including unstable ones, and hence to pinpoint 'tipping points' and 'alternative states'. Techniques and tools have been applied to ecological models (Gwaltney et al., 2007), resulting in the coupling of types of bifurcation to types of asymptotic ecological behaviour (for example, Kooi, 2003).

In general there are a couple of ways to perform bifurcation analysis. There is a division between purely algebraic and numerical methodologies (see Figure 4.1). Algebraic methodologies using symbolical software (e.g., Maple, Mathematica, Matlab) may be sufficient for the analysis of models containing one, two, or three state variable equations. Larger models (i.e., with more than three state variable equations) will necessarily have to be analysed using numerical methods. These methodologies are broadly divided into two groups, namely bifurcation detection via simulation, and detection via continuation. The three approaches vary in philosophy, execution, and results. We will discuss all three of them in more detail below.
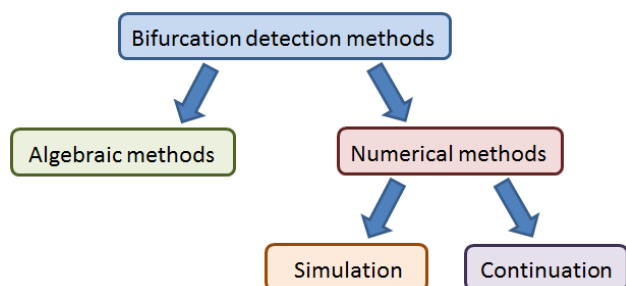
Figure 4.1: Bifurcation detection methods can be roughly divided into algebraic methods, using symbolical calculations, and numerical methods. The latter category is roughly divided into two sub-categories: simulation and continuation. In practice, for maximal results it is best to use a mixture of the three methods.

Algebraic bifurcation detection methodologies

Algebraic methodologies use symbolical software (e.g., Maple, Mathematica, Matlab), and may be sufficient for the analysis of one-, two-, and three-dimensional models. Such an approach has been used extensively in the past to analyse small ecological models as computer power was not available. Currently, algebraic methods are still used in various parts of the mathematical community when smaller models are analysed, and focus on proving things with respect to bifurcations, like the existence of states, or the bounded-ness of the system.

With algebraic analysis, the Jacobian matrix and its eigenvalues are calculated symbolically, i.e., parameters have no values. Many bifurcations are characterized by having one or more zero eigenvalues, or by eigenvalues with zero real parts. Furthermore, often ranges can be found in which parameter combinations indicate the stability of the steady state(s). One particular focus of algebraic bifurcation detection is the use of the so-called 'normal form analysis' for analysing bifurcation points of higher co-dimension. Regular bifurcations can be found by using a linearization of the system, but bifurcations of higher co-dimension require also higher order terms of the Taylor expansion around the bifurcation point before they can be analysed. Observe, that bifurcation points of higher co-dimension are relevant as they are the 'birthplace' of two or more local bifurcations (for instance, in the case of the cusp bifurcation, in which two tangent bifurcations originate). Furthermore, they are often also associated with the existence of global bifurcations in the model.

Simulation bifurcation detection methodologies

Simulation techniques (also known as 'brute force') form the most commonly used approach nowadays for the analysis of ecological models, including bifurcation analysis. If there are no options for using symbolical methods, then simulation is the only option for the calculation of steady states. In short, in simulation bifurcation analysis the analysed model is fixed at some parameter values and some initial conditions, after which time-integration is done. The integration is aimed at letting the system evolve to the attractor, and therefore it should be sufficiently long, otherwise the found results will likely not represent the real attractor values. The parameter is then increased slightly, after which another integration run is made. This procedure is repeated to scan a portion of the parameter space.

Although the method is popular, it is prone to some serious issues:
- It requires a restart every time. Hence, it may take a very long time (not just in the number of integration steps but also in real time) to find a value which is appropriately close to the real attractor. Actually, finding the real attractor values is in practice impossible, as it would require an infinite amount of time to do so. By making a full integration only once, then restarting at the 'old' attractor values after each consecutive small parameter change, this problem is reduced.
- There is a continuous build-up of numerical errors with each integration step. Hence, the longer the integration time, the less accurate the estimation of the state values in general is.
- The method does not allow to detect bifurcations exactly, which is the primary goal of the approach. The asymptotic behaviour becomes more pronounced near bifurcation points because of eigenvalues that are zero (see Section 3.3). Hence, integrations take even longer and longer near bifurcation points before the attractor is appropriately approximated. Bifurcation points are thus 'blurred', not because of noise, but because of the used procedure.

- The method can easily lead to incomplete results. It is, for instance, practically impossible to find a separatrix. However, as separatrices are essential for tipping points of the second type, this is a serious drawback. Furthermore, simulation methods are incapable of detecting global bifurcations.

A clear demonstration of the weaknesses of the simulation approach can be made with regard to the global bifurcation in the Allee model Eq. (3.2). In earlier literature, Kent et al. (2003) reported that "[l]imit cycles are not sustained by the Allee effect; instead both populations collapse to zero over a large region of the predator-prey phase plane." They used a combination of algebraic analysis and simulations, and found that the stable steady state disappears under some parameter conditions. In that case both the prey and predator populations went extinct in the simulations. However, we know from the example in Chapter 3 that these results are imprecise. A limit cycle does occur in the Allee model, as there is a Hopf bifurcation. However, it disappears again because of the heteroclinic connection. The domain of attraction of the positive stable state then disappears and all initial conditions result in extinction of the populations.

Continuation bifurcation detection methodologies

The disadvantages of simulation methods have been pointed out by several authors, who prefer the use of continuation methods (Van Voorn et al., 2007, 2010). Continuation aims at 'tracking' steady states as function of one or more parameters (Khibnik, 1993; Beyn et al., 2002). First a stable steady state should be found via simulation, or a (stable, saddle, or unstable) steady state should be found using algebraic analysis. These steady state values do not have to be exactly right, just as long as they are sufficiently close for techniques to make a successful exact detection of the steady state. A typical approach for locating exact steady states is the use of a Newton-Raphson (NR) method, which is capable of making a very reliable approximation, although other approaches have been suggested as well (for instance, the 'interval' method by Gwaltney et al., 2007). The steady state is then followed under variation in one or more parameter values. This is done by repeatedly making a change in the parameter, then using the NR method again to find the new steady state value. The parameter step is divided into several smaller sub-steps to improve the approximation further by dividing the error over the different sub-steps. Of course, the parameter changes should not be too large, or else the NR method might fail. Most bifurcation software packages thus have an automated variable step size, making large parameter steps to save time when changes are small, and small parameter steps when changes are large.

The important part of the continuation methodologies is however not the tracking of the steady states, but the use of so-called 'test functions' (Seydel, 1997; Beyn et al., 2002; Kuznetsov, 2004; Seydel, 2010). While the steady states are followed through parameter space, various test functions monitor the Jacobian matrix and eigenvalues and, if desired, also other properties of the steady states. These test functions are not trivial because numerical approximations are not exact. For instance, a tangent bifurcation cannot be found by monitoring the eigenvalues for the condition that one of them is zero, as a solution is never really zero numerically. Instead, a test function monitors the partial derivative of the equations with respect to the parameter used for the continuation. A tangent is then detected when the partial derivative switches sign (i.e., makes a curve in parameter space) and some auxiliary conditions are fulfilled.

Software packages for bifurcation analysis like AUTO (Doedel & Oldeman, 2009), CONTENT (Kuznetsov & Levitin, 1997), and MATCONT (Dhooge et al., 2003) contain methodologies for the continuation of steady states (including limit cycles) and test functions for the detection of most local bifurcations, also of higher co-dimension. Furthermore, AUTO has been extended with techniques for the localization and continuation of global bifurcations (Van Voorn et al., 2007; Doedel et al., 2008, 2009; Krauskopf & Riess, 2008). The techniques by Van Voorn et al. (2007) and Doedel et al. (2008, 2009) are based on orthogonal projections of the eigenvectors associated with the eigenvalues of the Jacobian matrices of the steady states that are connected, while Krauskopf & Riess (2008) make use of a Lin's method. However, it is beyond the scope of the report to discuss these methodologies in detail.

4.2   Model analysis and finding tipping points

We have already seen some examples of bifurcations as tipping points and the consequences of their occurrence in models, namely:

- The cusp bifurcation and the birth of hysteresis in a system (Scheffer et al., 2001a; Scheffer & Carpenter, 2003), leading to switches in an aquatic system from one state ('clear') to another ('turbid') that are difficult to reverse (this example is elaborated in Chapter 5);
- The transcritical bifurcation in the Rosenzweig-MacArthur model Eq. (3.1) as invasion boundary for a population (or extinction boundary, when reversing the direction in which the driving parameter changes);
- The supercritical Hopf bifurcation in the Rosenzweig-MacArthur model Eq. (3.1) and the Allee model Eq. (3.2) as point of destabilization, i.e., the stable steady state destabilizes. Instead, a stable limit cycle occurs, indicating periodic oscillations in the populations;
- The heteroclinic connection in the Allee model Eq. (3.2), at which point the domain of attraction of the positive stable attractor disappears together with this stable state. Only one global attractor is left, which in this case means extinction of the involved populations.

It is important to realize that the type of bifurcation is not necessarily related to the kind of changes in the model behaviour as a result of the tipping point. For instance, Van Voorn et al. (2010) analysed several food chain models and found that there was no 1-on-1 coupling between the type of global bifurcation and the ecological results. In some cases a global bifurcation leads to the extinction of species, while in other cases it actually stabilized the food web dynamics. Below we show two more examples of global bifurcations in model studies. Observe, that they are intended to demonstrate the effects of bifurcations in models and some of the techniques to find the bifurcations.

Sub-lethal toxicant concentrations and extinction events

Kooi et al. (2008) studied a model of a freshwater food chain, consisting of nutrient, a prey species, and a predator species. The model study was motivated by results for closed experimental set-ups, containing the mixotrophic phytoflagellate *Cryptomonas*, and the planktonic ciliate *Urotricha furcata*. The system was polluted by low levels of toxicants (the insecticide parathion-methyl, and the herbicide promethyn). Two models were created, in which toxicants either influenced only the prey or both the prey and the predator species. The toxicant is absorbed by the prey from water, while the predator absorbs toxicant from the water and by feeding on the (polluted) prey. Individuals always spend an amount of energy on maintenance, including detoxification (Kooijman, 2009).

As the toxicant is easily absorbed by the different individuals, it is expected that at higher toxicant concentrations the populations disappear. Nevertheless, there is bistability: if a population is sufficiently large, then the toxicant is divided over many different individuals, keeping the intracellular toxicant concentrations per individual low enough to stay sub-lethal. However, the concentrations of the toxicants were kept such, that they would be deemed sufficiently sub-lethal based on standard ecotoxicological tests, which means that individuals do not die from the concentrations in those tests. But even then a population can go extinct when the population size is too small, as maintenance costs for detoxification increase and the reproduction is negatively affected.

The models display a global bifurcation, which is a homoclinic connection (connecting a saddle steady state to itself). The scenario resembles that in the Allee model we already discussed: under change of a parameter first periodic cycles appear (after a Hopf bifurcation), and then the global bifurcation occurs. The parameter in this case is the dilution rate, the rate of in- and outflux of water, that also affects the outflux of toxicant and biomass. The scenario from stable steady state (coexistence of all species) to full extinction occurs under only a slight decrease in the dilution rate (about 0.01 h^{-1}). What is even more dramatic is that such changes in the dilution rate are normal under real-world conditions (i.e., differences in river in- and outflux because of seasonal changes and precipitation). This shows, that even if models,

experiments, or standardized tests seem to suggest that an ecosystem is not qualitatively influenced by pollution, it is possible that the ecosystem in fact is in serious danger, and may collapse under regular and natural variations in inherent system processes, like the flow rate.

Chaotic attractor merging

Not all bifurcations (or tipping points) have to result in negative effects. A different example was found for instance by Van Voorn et al. (2010), who studied a food chain model that has been developed by Letellier & Aziz-Alaoui (2002), and that consists of a prey species, a predator species, and a top-predator species. In this model the top-predator is subject to intraspecific interference, i.e., the top-predator individuals actively spend time on interacting, which results in biomass loss (e.g., by the direct killing of individuals, or by wasting energy through interacting).

The model displays bistability like in the model with toxicants and the Allee model. However, the 'stable states' are not steady states over the full parameter range. Instead, over a large part of the parameter space the stable states are limit cycles, limit cycles of higher period, or even chaotic attractors. It is true that the property of chaos is that an orbit never obtains the exact state twice, otherwise it would be a limit cycle of higher period (in that sense a chaotic attractor is a limit cycle of infinite period). However, the chaos is bounded in state space. Think for instance of the butterfly attractors of the Lorenz equations, which appear after sufficient simulation time, which shows that the chaos is bounded. This means biologically that the species coexist, albeit without being at fixed densities. The Letellier & Aziz-Alaoui-model displays even two different chaotic attractors for a limited parameter range.

Under change in the carrying capacity a global bifurcation can occur in which one of the chaotic attractors disappears, see Figure 4.2.
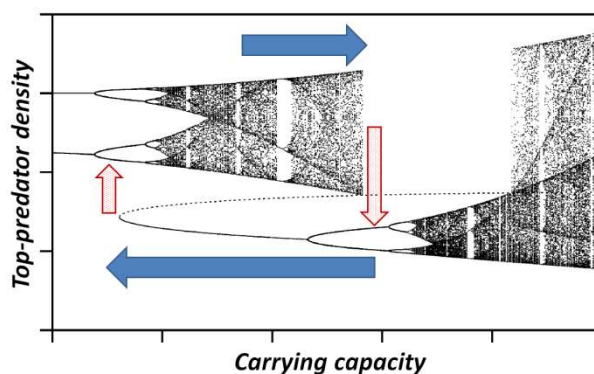

Figure 4.2: One-parameter bifurcation diagram of the Letelllier & Aziz-Alaoui model. Plotted are the extrema, maximal and minimal values of the top-predator. There are clear transitions from limit cycle to chaos under increasing carrying capacity (eutrophication; upper blue arrow), which are local bifurcations. At some point the chaos disappears via a global bifurcation, and the system settles into a limit cycle attractor (right red arrow). A significant decrease in carrying capacity is then possible before the system resettles into the original attractor again.

While the chaotic attractor disappears, a stable limit cycle attractor remains. In that sense this tipping point actually work 'stabilizing', as the chaos is replaced by periodic solutions with a larger domain of attraction. Furthermore, there is hysteresis. Returning the carrying capacity to the original value does not restore the chaotic attractor. Instead, the systems remains in the limit cycle attractor for a significant decrease of the carrying capacity. Under further increase of the carrying capacity there is also another global bifurcation, in which the second chaotic attractor merges with the 'remnants' of the first chaotic attractor to become one chaotic attractor with a larger domain of attraction.

4.3   Tipping points in systems with noise

Thus far we have only considered model systems without explicit spatial structure or stochastic input sources ('openness'). We will come back to spatially explicit systems in real-life example cases discussed in Chapter 5. Here we will focus more on the effects of stochastic events ('system noise') in systems. Noise masks the exact position of bifurcations and separatrices, making it more difficult to find them. But furthermore, noise leads to probabilities of the occurrence of tipping points. This by necessity requires the use of statistical approaches. Therefore in this section we discuss work on the effect of noise on the

masking of tipping points. In the next sections we discuss statistical methods for tipping point detection in data, and early warning methods.

Foob web model with noise

To get an impression of the effect of stochastic events on the occurrence and detection of tipping points, it is helpful to first consider a model of ordinary differential equations that is subject to random input that has been recorded. Kooijman et al. (2007) studied a small, closed and nutrient-limited food web system with random feeding, growing and dying events. These random events are caused by hidden nutrient dynamics, but an important property of their model that separates it from the literature on stochastic simulation models is that it is closed also across random events in order to conserve mass. This property is usually violated in other stochastic models, which unnecessarily obscures model analysis. A second important feature of their model is that the prey biomass is clearly separated into structure biomass and reserves biomass, according to Dynamic Energy Budget theory (Kooijman, 2009). Time scale separation is used for the formulation of the functional response (the description of the feeding relationship).

The deterministic version of the model (i.e., without the noise) displays several standard local bifurcations. A tangent bifurcation exists, indicating bistability. The two alternative states are a positive attractor, and both populations at zero density. Under nutrient enrichment the positive steady state undergoes a supercritical Hopf bifurcation, replacing it with a limit cycle attractor. Under further nutrient enrichment a global bifurcation is encountered, in which the positive attractor disappears. Both species then inevitably go extinct.

The stochastic version of their model very much matches the output of the deterministic version of their model in some parameter ranges, while in other ranges it does not. The mismatches become very pronounced near different local bifurcations that exist in the model. This can be explained by looking at the return time after perturbations, see Figure 4.3.

Figure 4.3: A diagram plotting the return time after a perturbation as function of a bifurcation parameter. At the right-hand side of the diagram is near a local bifurcation, say, a tangent bifurcation. The return time is highest near a local bifurcation, as eigenvalues become smaller and smaller and are exactly zero at a bifurcation point.

An important property of local bifurcations, like the transcritical, the tangent, or the Hopf bifurcation, is that one or more eigenvalues are zero (see Section 3.4). Relatively far away from a local bifurcation eigenvalues will be large. This also means that the return time after a perturbation is small, i.e., after a perturbation the system resettles into the steady state relatively quickly. As a result, stochastic simulation output at a fixed amount of simulation time will not display a large deviation from the output of the deterministic model version. Near bifurcation points, however, the eigenvalues become smaller and approach zero. This also means that the return time grows significantly. As a result also the output of the stochastic model deviates significantly from that of the deterministic model version.

For Hopf bifurcations the mismatch between simulation and deterministic model output already starts to show further away from the bifurcation, as these bifurcations have eigenvalues with zero real parts, but with non-zero imaginary parts. Imaginary parts indicate rotation in phase space. The return orbit after a perturbation has a rotating motion, showing as oscillations of decreasing amplitude, which takes much more time than a straightforward decay towards the steady state. When the return time increases it also

becomes more likely that a new perturbation will occur before the system has resettled to the steady state. This new perturbation may by accident knock the system back close to its steady state, but it is much more likely that it will knock the state even further away from the steady state. Then the return time increases even more because of the oscillatory behaviour. As a result, near a Hopf bifurcation the system will appear to display almost randomly modified periodic oscillations. This obscures the exact location of the Hopf bifurcation.

Impact of noise on bistability

Not only the exact location and effects of bifurcation points are modified by the addition of noise. Guttal & Jayaprakash (2007) studied the effect of noise in environmental parameters (like nutrient input and rainfall) on bistability in ecological systems, including the lake system studied by Scheffer et al. (2001a) and Scheffer & Carpenter (2003), in which switches may occur from one state ('clear') to another ('turbid') that are difficult to reverse. They found that regions in which bistability occurs in the deterministic versions of the studied models were reduced or even disappeared when noise was present. However, when the region of bistability disappears, the system frequently undergoes tipping points.

Their results can be explained as the bistability region has never really disappeared. Instead, the system never evolves to either one of the stable states under stochastic changes, while the separatrix is commonly crossed because of the random perturbations. As their results were obtained by simulations, it requires a new analysis of their studied models to obtain a more precise analysis. Nevertheless, when we combine their results with the ones from the model studied by Kooijman et al. (2007), we can make some interesting observations. First, noise or perturbations in drivers or otherwise 'mask' the position and effects of tipping points, both the ones caused by bifurcations or by separatrix crossings. Second, this does not mean that the bifurcations or separatrices have disappeared. Third, the addition of noise makes the occurrence of tipping points even more likely, certainly in the cases where more than one stable state exists and perturbations result in frequent crossings of the separatrix in the system. Without the noise the system would probably simply settle in one of the stable states, and one might not even realize that bistability or the possibility of a tipping point exists. This leads to our fourth observation, that is, it is not impossible that tipping points are more frequent than we realize. Perhaps under climate change or otherwise systems are more prone to stochastic effects that may result in more frequent tipping points in environmental systems.

4.4 Statistical data analysis methods for finding tipping points

We have seen that tipping points (either resulting from a bifurcation orthe crossing of a separatrix) will not easily be revealed when masked by system noise. In reality things are even more complicated, as there are also other issues, like measurement noise, unobservable states, and measurement scales. Again limiting things to spatially unstructured systems, it is already difficult to ascertain what a 'steady state' is. In most environmental studies data are discretely measured (although there are some notable exceptions, like the continuous monitoring of river water levels) and measured on scales that are subject to temporal changes. When considering the densities of species there are all kinds of observer effects, which obscure the exact 'state' at some time point. How can steady states be detected from data, and extending on that, how can shifts between alternative states be detected?

The exploratory analysis of data with the focus of finding tipping points is certainly not a new field. However, instead of 'tipping points' in general the used terminology is 'change-point detection', especially when it concerns time series of observables. The literature on this point has grown rapidly, hampering any proper overview of the subject and increasing the probability of re-invention of methodologies (Andersen et al., 2009). Rodionov (2005) gives a concise overview of tipping point detection methods primarily used in atmospheric and oceanic studies, which are divided into four classes, based on the type of shifts they are designed to detect, and discusses their strong and weak properties. The lion's share of the change-point detection methodologies is aimed at the detection of shifts in the mean. They mostly test if there is statistical support for the hypothesis that a shift has occurred in the

Table 4.1: Overview of change-point detection methods, mostly applied in climatology and ecology.

Alexandersson (1986): Standard normal homogeneity test

Andersen et al. (2009)

Barnett et al. (2005): Fingerprinting

Basseville & Nikiforov (1993): ARIMA modelling of time series, combined with likelihood ratio test

Breaker (2007): A variant of a simple cumulative sum (CUSUM) method

Buishand (1982): Cumulative deviation test with adjusted partial sums or cumulative deviations

Buishand (1984)

Conners et al. (2002) : Application of Lanzante (1996)

Chu and Zhao (2004): Bayesian analysis

Downton & Katz (1993): Downton-Katz test, looks for shifts in variance

Ducre-Robitaille et al. (2003): Student t-test

Easterling and Peterson (1995): modified version of Solow (1987)

Ebbesmeyer et al. (1991) Average standard deviates compositing method (ASD)

Elsner et al. (2000): Bayesian approach using Gibbs sampling. The MCMC algorithm determines candidate change points, then determines posterior data distributions, ignoring other candidates.

Fath et al. (2003): Use of Fisher information

Francis & Hare (1994): analysis of Alaska salmon catch records using Wei (1990)

Gerstengarbe & Werner (1999): shifted sequential version of Mann-Kendall test

Goossens & Berger (1987): Mann-Kendall test, useful in analysis of abrupt climate changes

Hare & Mantua (2000): Application of PCA (Von Storch and Zwiers, 1999) on 100 biotic and abiotic time series

Karl & Williams (1987): Wilcoxon rank sum, non-parametric test for homogenization of time series

Khaliq & Ouarda (2007)

Kiem & Verdon-Kidd (2010): Mann-Whitney U-test

Lanzante (1996)

Lintz et al. (2011): Response surfaces

Liu et al. (2011): Modified Lepage test

Livina & Lenton (2007): Detrended Fluctuation Analysis (DFA)

Lombard (1987): Wilcoxon rank sum

Lund & Reeves (2002): modified version of Solow (1987)

Lund et al. (2007)

Mantua (2004): Principal Component Analysis (PCA) for regime shift detection

Mauget (2003): Mann-Whitney U-test

Mayer et al. (2006): Use of Fisher information

Nicholls (2011)

Oerlemans (1978)

Pawlowski & Cabezas (2008)

Perreault et al. (2000): Bayesian analysis

Pettitt (1979): Pettitt test

Rebstock (2002): A variant of a simple cumulative sum (CUSUM) method

Robbins et al. (2011): Overview of mean shift testing in correlated data

Rodionov (1994): Application of Basseville & Nikiforov (1993)

Rodionov (2004): STARS, sequential version of partial CUSUM method combined with t-test

Rodionov & Overland (2005): Application of Rodionov (2004)

Rodionov (2006): Prewhitening in climate regime shift detection

Seekell et al. (2011): Conditional heteroscedasticity as a leading indicator

Solow (1987): Two-phase regression technique, tested time series is predicted, time is predictor

Solow & Beet (2005): Vector auto-regressive method

Von Storch & Zwiers (1999): Principal Component Analysis (PCA) for regime shift detection

Wei (1990): Intervention analysis, extension of Auto-Regressive Integrated Moving Average (ARIMA)

Wijngaard et al. (2003): 4 different tests, including Von Neumann ratio test

Yamamoto et al. (1986): Signal-to-noise ratio. A regime shift ("climatic jump") is defined when the signal-to-noise ratio > 1, equivalent to the 95% significance level

Yonetani (1993): Modified Lepage test, sum of squares of standardized Wilcoxon's & Ansari–Bradley's statistics.

Zhang et al. (2009): Mann-Kendall test & modified Lepage test

mean during a time series of observational data. This requires a sufficient number of measurement points for both means. Some methodologies aim for detecting shifts in the variance. They indirectly make use of the property that there are eigenvalues that are near zero close to bifurcation points. The increased return time near a bifurcation point also means that measurements at fixed intervals will show a larger deviation from the mean. Of course, these methods require a sufficient number of measurements while the mean value remains fixed or near fixed, in order to make a reliable estimation of the variance. Finally, there are several methods that work differently.

We do not discuss all the methods reviewed by Rodionov (2005) or that are present in the literature. Instead, in Table 4.1 we provide a tabular overview of selected references in short, among them the ones mentioned by Rodionov (2005). The full references can then be found at the end of this report.

4.5 Early warnings

Many of the change-point detection methods are more or less applicable for the development of methodologies for early warning. Several statistical signals have been suggested to be particularly of use as indicators of non-linear transitions. In the recent literature, rising autocorrelation, steep increases in variance, and extreme changes in the skewness and shifts in variance spectra toward low frequencies have appeared as such indicators, more popularly referred to as methods for 'early warning' (Kleinen et al., 2003; Carpenter & Brock, 2006; Van Nes & Scheffer, 2007; Guttal & Jayaprakash, 2008; Contamin & Ellison, 2009; Scheffer et al., 2009; Brock & Carpenter, 2010).

Many properties that indicate 'early warning' can be understood in terms of separatrices, and bifurcations and their eigenvalues. For instance, Carpenter & Brock (2006) performed Monte Carlo simulations with the model by Carpenter et al. (1999), in which bistability exists. They observed a rising variance in the distribution when the parameter value was near the tangent bifurcation at which the preferred state disappears (also referred to as 'critical slowing down'), and argued that a rising variance is a useful indicator for early warning. The rising variance can be understood when evaluating the eigenvalues of the two stable states, and considering the separatrix that exists in the region of bistability. Nearing the tangent bifurcation the dominant stable eigenvalue decreases to zero and the return time after a perturbation increases significantly, as we have already discussed in Section 4.3. This also means that most of the randomly drawn initial conditions will not have converged near the preferred stable state yet. Furthermore, many initial conditions will not converge to the preferred state but to the alternative state, as the seperatrix is very close to the preferred state when close to the tangent bifurcation. These two properties, the near-zero eigenvalue and the proximity of the separatrix to the preferred state, explain why the distribution of the Monte Carlo sampling shows a wide variability when the sampling is done near a bifurcation.

Another indicator for early warning is changing skewness (Guttal & Jayaprakash, 2008). They studied the model proposed by Guttal & Jayaprakash (2007) and two other models, and calculated the skewness γ in *in silico* generated data from model simulations and in real data on Sahara climate change. The skewness is a scaled third moment, given as

$$\gamma = \int (x - \mu)^3 \, \sigma^{-3} \, P(x) \, dx$$

Here $P(x)$ is the probability distribution, μ is the mean, and σ is the standard deviation. The variable x is assumed to be measured at a certain fixed time point after perturbation. It was found that the skewness changes significantly when approaching a bifurcation point.

It should be noted that all examples entail bistability regimes. The explanation for the changed skewness is therefore strongly related to the one given for the critical showing down. Near a tangent bifurcation the separatrix between the two alternative stable states is very close to one of the stable states. If we consider that perturbations from the close-by stable state are random, it is to be expected that around half of the perturbations increases the state, and around half decreases the state. If the separatrix has a

state value that is only slightly higher than the stable state value, then most of the upper half of the random perturbations will result in crossing the separatrix and will cause a shift away from the stable state (see Figure 4.4). This asymmetry is even magnified by the increased nonlinearity near the tangent bifurcation. Hence, the distribution of the data will show a strong skewness near the tangent bifurcation.
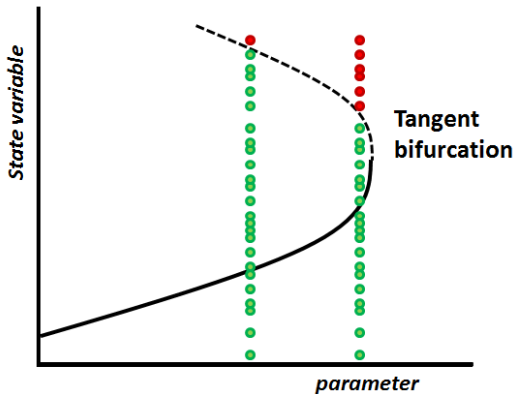

Figure 4.4: Indicators for early warning like critical slowing down and changed skewness can be understood graphically. One of the two alternative stable states (solid) is shown, as is the separatrix (dashed). 25 perturbations, i.e., different initial conditions, divided into two equal groups above or below the mean, are shown for two parameter values: one away from the tangent bifurcation, and one close by. Green perturbations return to the stable state, while red perturbations move away to the alternative stable state. Near the bifurcation there are many red perturbations, all at the same side. This shows up in different statistics as explained in the main text.

Contamin & Ellison (2009) analysed six possible indicators of tipping points in ecological systems, and studied their usefulness for prediction. They furthermore investigated two key properties for the prevention of tipping points, namely the amount of inertia in the system, and the amount of variability intrinsic to the system. Indicators were considered powerful if they are able to detect impending tipping points with adequate 'warning time', so that preventing policy can be implemented. They also found that inherent system noise greatly obscures the reliability and hence utility of the tested indicators, which led them to argue that human decision making plays a primary role in managing ecosystems with regard to avoiding tipping points.

4.6   Synthesis discussion

There are several issues to consider when statistical data analysis with regard to tipping points is performed, which we can roughly put into two categories: statistical issues, and philosophical or modelling issues.

The first statistical issue is that data analysis is prone to false positives (or type I errors, i.e., the null hypothesis is rejected while it should not) and false negatives (or type II errors, i.e., the null hypothesis is false but it is not rejected). For instance, the average standard deviates (ASD) is a method that is known to have an unacceptable false positive rate on auto-correlated data (Andersen et al., 2009). Statistically speaking a method should be preferred that reduces the false positive detection rate. Secondly, ecological time series are in general much shorter (20-40 steps) than climatic or econometric time series (> 100), and can therefore not be used convincingly for robust tests of regime shifts against a null hypothesis (Andersen et al., 2009). A significant exception is formed by limnology studies, which we will discuss in detail in the coming chapter. Thirdly, in turn, the analyses of climatic time series suffer from another problem, namely a deterioration of the test statistics toward the ends of time series in most of the used methods. In order to detect a regime shift with a certain degree of confidence it is necessary to have enough data available (> 10 years) to apply a formal statistical test. In practice, by the time that these data are available, the system may already be close to shifting once again to another state (Rodionov, 2004). This defeats the whole purpose of using statistical methods for regime shift prediction.

There are also some philosophical issues, which are perhaps more important than the statistical issues. In light of the conclusions in Section 4.3 and 4.5 it is important to broaden the scope of early warning indicators, or rather, the application of statistical measures to the analysis of nonlinear processes. First of all, statistically detected change-points (or tipping points) in general give no indications other than those directly based on the data about the origin of the tipping point. In other words, it gives no information about the mechanisms that cause the tipping point(s). Therefore, any policy to prevent the tipping point or to counter its effects is likely to be haphazard. Second, most of the model studies presented thus far

present rather 'clear' cases of tipping points – mostly they present a model with bistability, in which a separatrix separates two domains of attraction that are graphically easily represented. But already in three-dimensional process models bi- or multistability can occur, for which the different domains of attraction can be very complicated. For example, the three-dimensional Rosenzweig-MacArthur model has been shown to have very complicated domains of attraction (Boer et al., 1999, 2001). Noise will undoubtedly obscure the exact morphologies of such domains of attraction in real-life systems.

A proper modelling of the processes of the system behind tipping points may be very helpful in the successful prediction of tipping points (Barnett et al., 2005). However, a serious problem with modelling in general, which also applies to the application of detecting 'tipping points', is the scaling of the system. Most if not all systems are scaled artificially, as scale is something that is induced as variables need to be 'put along a measure bar' (Bierkens et al., 2000). Once variables are measured, an artificial axis is imposed, with a nominal or reference value as origin, upper and lower limits (often physically imposed detection limits), and more than occasionally variables are discretized already for measurement purposes (for the implementation into numerical simulation models variables are practically always discretized). Furthermore, there is the issue of what measurements may be put together (aggregated), both in terms of time and space. We will come back to the discussion on scaling in Section 6.4.

For reasonably well-bounded, homogenized environments with rather clear organizational levels, 'tipping points' are to be expected to be more easily found, or to be less artificial, than in strongly heterogeneous environments that do not have clear boundaries and no clear organizational levels. In his already mentioned paper Holling (1973) actually indicated that tipping points were found easily in limnology, as lakes of all ecosystems typically best approach the conditions under which the classical mathematical theory on steady states holds: lakes are rather homogenized environments, which are relatively closed for mass and energy within their watersheds, and with a lot of buffering from transient changes. On top of that, there are ample data available, including documented man-made disturbances specifically targeting lakes, and which are specific enough to be coupled unambiguously to model parameters or state variables. Another type of environment are chemostats, experimental set-ups that mimic these conditions of homogenized environments, which are (relatively) closed for mass and energy. We will discuss examples of tipping points in experiments or real-life systems on various spatiotemporal scales in more detail in the next Chapter.

5   Tipping points in experiments and natural systems

In this chapter empirical evidence is reviewed from the scientific literature on the detection of tipping points and the results of their occurrence. The systems in which the empirical evidence has been obtained can be divided into different groups based on spatial and/or temporal scale, and whether they have been obtained by manipulation or not. Obviously, small experimental set-ups like chemostat devices allow for proper experimentation, while for large climate-related systems only observational data can be obtained, for they are simple too large, have too large a timescale, and experiments cannot be duplicated anyway. In many cases also models have been used to supplement the research. We consider some of those models and/or their results as well, which may give the reader the impression the results are not 'real'. This is not necessarily so, as models can be very helpful in the interpretation of results.

Some authors have expressed criticism with regard to the subject, for instance, Andersen et al. (2009) observe "there is an apparent gap between the prominence of present theoretical frameworks involving ecological thresholds and regime shifts, and the paucity of efforts to conduct simple tests and quantitative inferences on the actual appearance of such phenomena in ecological data". Of course, one should be careful as well with making such observations, as any lack of empirical support may be because of a number of reasons, including a still existing unawareness with regard to the subject. It may be obvious to the reader that it is almost impossible from a phenomenological point of view to detect a tipping point, as it is the exact point where a system shifts from one state to another. Mathematically we are looking for the boundaries between the domains of attraction of different states (separatrices) or the exact parameter values where a state disappears (bifurcations). In principle it is already difficult or nearly impossible to locate such a point exactly in the parameter or state space of a model (see Chapter 3), let alone in practice, where there are numerous reasons why the exact localization of a tipping point may be hindered, such as accuracy and repeatability of the data, violation of all kinds of assumptions made with regard to the system, and system noise.

One way of looking for indirect evidence of the existence of tipping points is by looking for evidence of alternative stable states. If a system displays alternative stable states, we can safely assume it also displays tipping points when switching between stable states. Schröder et al. (2005) give an overview of experimental evidence for alternative stable states up to 2005. They found 13 experiments that to their judgement clearly showed alternative stable states, with a bias towards laboratory experiments as contrasted to field experiments. This last observation may not be surprising, as laboratory experiments usually entail more rigorously controlled experimental set-ups. They distinguish between four distinct experimental approaches, which mostly correspond to the characteristics of the different types of 'tipping points' as discussed in chapter 3. Of course, tipping points do not necessarily have to be a shift from one stable state to another – as we have seen they can also entail a transition from one type of behaviour to another – but the approach may be useful anyway. The four distinguished approaches (which were already mentioned in Section 3.3) are:
1. A discontinuity in the response to a driver (usually some environmental parameter);
2. A lack of recovery potential after a perturbation;
3. Divergence due to different initial conditions;
4. Random divergence.

Approach 1/ corresponds to localizing a bifurcation under parameter variation, while 2/ corresponds to crossing a separatrix after a change in the state and is an indication of the basin of attraction, and 3/ and 4/ indicate the same as 2/, but now by starting from different initial conditions.

Below we first consider small experiment set-ups which have been used to study tipping points. These experimental set-ups provide an *in vitro* system which sufficiently fulfils various assumptions that are typically made to study ecological systems. Next, we consider studies with observational and field experiment data from various (semi-)natural systems. These are divided into marine, freshwater, and terrestrial systems. We also look at cases in which spatial components are considered explicitly. Observe, that in such a context the term 'tipping point' becomes somewhat ambiguous – while in many systems it is acceptable to assume a certain level of spatial homogeneity and the whole system is 'shifting', in some

systems it becomes a matter 'where' the tipping point is occurring at a certain point in time. Finally, we review data and model study results of large environmental systems. These systems cannot be manipulated experimentally and do not allow for experimental duplications (albeit they are obviously manipulated on a major scale as a result of anthropogenic influences). They can also play a significant role as drivers of other systems on a smaller time and spatial scale, which leads to the interesting notion that a tipping point in a large environmental system may result in a variety of tipping points in other systems as well (a 'cascade'). In Chapter 6 we consider spatially explicit systems.

5.1   Experimental biological set-ups

The detection of tipping points in experimental set-ups has still proven difficult, but shifts to alternative states under changes in system inputs have been reasonably demonstrated. Instead of presenting an exhaustive list, below the focus is on some demonstrative examples.

Tipping points found in experiments

The Allee effect, discussed already in Chapter 3, is one of the commonly considered factors underlying tipping points in natural populations, and therefore we consider here an extinction experiment by Kramer & Drake (2010) centred around the Allee effect. They worked with a small microcosm set-up, including *Daphnia magna* as prey, and *Chaoborus trivittatus* as predator. The set-up was under constant environmental conditions, except that there was a daily food influx. Also a stochastic model describing the two populations was developed and analysed. The Allee effect was revealed in the experiments as populations at lower densities actually showed a substantial negative per capita growth rate, while populations at higher densities showed growth rates similar to predator-free populations. The high variance in the results however did not allow for a solid estimation of the exact Allee threshold (the separatrix responsible for possible tipping points). Nevertheless, the results suggest that indeed an Allee effect, generated by predation or otherwise, may underlie the existence of a tipping point in a food chain system. An overview of empirical evidence for Allee effects in natural populations is given by Kramer et al. (2009), but this is of the scope of this report.

Fussman et al. (2000) studied a predator-prey food chain in a chemostat set-up, consisting of planktonic rotifers (*Brachionus calyciflorus*), feeding on unicellular green algae (*Chlorella vulgaris*), which in turn was limited in its growth by nitrogen. A chemostat is a system closed for mass and the conditions are kept as constant as possible, while the contents of the chemostat is stirred continuously, creating a near homogeneous mixture. Furthermore, there are clear input factors that can be varied experimentally, such as the dilution rate (rate of the in- and outflow) and the amount of nitrogen per volume of inflowing medium. Hence, a model can be developed based on ODEs which in turn can be used to localize behavioural regimes in parameter space, i.e., we can make a reasonable projection about where tipping points occur. Fussman et al. (2000) indeed developed a model and used it to compare the long-term behaviour of the model to the experimental findings. The data consisted of time series of sufficient length (30-120 days) for the system to evolve to a stable state, if any existed. Depending on the settings of the input factors (nutrient content of inflowing medium, dilution rate) the system evolved to a stable state, periodic fluctuating populations (limit cycle), or the populations went extinct, according to the authors due to extreme cycle amplitudes. These results suggest that there is at least a Hopf bifurcation both in the model and in the experimental system, as a Hopf bifurcation explains a transition from a stable steady state to a limit cycle under parameter variation.

In another chemostat experiment by Becks et al. (2005) a food web of three species was studied: a predator ciliate (*Tetrahymena pyriformis*), and two co-existing bacteria (*Pedobacter* and *Brevundimonas*). The dilution rate was varied both between experiments and within experiments. Measurements of population densities were matched to model calculations. The goal of the research was to demonstrate the occurrence of chaos (constantly, a-periodically fluctuating population sizes, but no extinction) in an ecological system. Indeed, chaotic behaviour occurred in the system, which was proven by calculation of the Lyapunov exponents. Inadvertently they also demonstrated the occurrence of

several tipping points. Depending on the dilution rate value, the system displayed stable steady states, stable periodicity, or chaotic behaviour. In some experimental runs during which the dilution rate was varied a clear change from one type of state to another occurred. For instance, the system quickly switched from periodic to a stable steady state when the dilution rate was changed from 0.5 to 0.75 d^{-1} (d is day) halfway during the experiment. Another example is the disappearance of *Pedobacter* at a dilution rate value between 0.75 and 0.9 d^{-1}, indicating at least one transcritical bifurcation existed in the system.

Experimental testing of early warning indicators

In Section 4.4 and 4.5 we discussed statistical measures that may indicate the proximity (or risk) of a tipping point. There is also literature available discussing experiments to test early warning indicators. Drake & Griffen (2010) performed experiments which focus on dynamical phenomena associated with the extinction of populations. They performed a laboratory experiment with *Daphnia magna* in which indeed critical slowing down was found when the population was near extinction. Four statistical indicators (coefficient of variation, autocorrelation, skewness, and spatial correlation) showed evidence of an approaching transcritical bifurcation associated with the extinction of a population around 100 days in advance, which is around 8 generation cycles. A drawback is that the indicators performed only properly after a suitable baseline was established, but on the positive side it seems that the results are general, and can be applied to other species as well.

Veraart et al. (2012) demonstrated critical slowing down experimentally in a chemostat containing photo-inhibited cyanobacterial population. Self-shading of the population is the mechanism which results in bistability under light stress: if the population is large enough then it survives because of self-shading, but if the population is too low it irrevocably goes extinct. In this sense, self-shading is the mechanistic process that creates an Allee effect in the system. Perturbations in the experiment by Veraart et al. (2012) entailed the removal of 10% of the population, i.e., a perturbation of the state variable. The time to recover after such perturbations increased significantly while approaching the critical point in the system, providing experimental evidence that critical showing down indeed is an indicator that there is a large probability of a tipping point occurring.

Although it is difficult to really 'prove' that the observed transitions between types of behaviour or states in the above-mentioned experiments are truly bifurcations, the findings suggest that the mathematical approach of modelling and analysing these models using bifurcation analysis does make sense. It seems that different modes of behaviour do exist, at least in experimental set-ups, and that tipping points marking the transition from one type of behaviour to another do occur under changing drivers. Furthermore, statistical measures seem to provide at least some useful indicators for approaching tipping points. A significant point of criticism is of course is that obtaining these results under tightly controlled laboratory conditions is not the same as obtaining them in the field, or observing them in natural systems. As already pointed out by Schröder et al. (2005) there seems to be a bias toward results obtained under laboratory conditions as compared to field conditions. In the next sections we therefore consider tipping points in observations and experiments under field conditions.

5.2   Tipping points in aquatic systems

In this section we give an overview of the biological systems in which 'tipping points' have been positively identified or for which there is strong evidence that they may undergo tipping points. Albeit being an older paper, Folke et al. (2004) give an overview of evidence for (the possibility of) tipping points in terrestrial and aquatic environments. In this section, we will discuss some of their examples in detail.

As the subject of KB IV is 'green blue space', we are interested in both terrestrial and freshwater systems. However, we also reconsider some demonstrative examples from marine systems, on which we have already discussed some in chapter 3 and 4. We first consider aquatic systems, specifically

freshwater systems. There are a number of arguments why lakes best approach the conditions for classical mathematical theory on steady states based on ODEs. Lakes are reasonably well-bounded, homogenized environments with rather clear organizational levels, that are relatively closed for mass and energy within their watersheds, and with a lot of buffering from transient changes (Holling, 1973). Also, there are historically well-documented cases in which the evolution of the state of the lake can clearly be coupled to anthropogenic influences. Furthermore, because lakes best approach the classical mathematical theory, many examples already exist in the literature. In fact, much of the ecological theory on tipping points and early warnings has been developed based on examples from limnology. Folke et al. (2004) mention examples of tipping points from temperate and shallow lakes, tropical lakes, and wetlands. From the perspective of this report the temperate and shallow lakes are the most interesting ones, and we focus on examples of tipping points in those systems.

Hysteresis under phosphorus changes in lake systems

The phenomenon of hysteresis in lakes is one of the best known examples of tipping points, and has been discussed by Carpenter et al. (1999), Scheffer et al. (2001a), Carpenter (2003, 2005), and Scheffer & Carpenter (2003), among others. The research on temperate lakes has specifically focused on the switches between two states under nutrient enrichment, mostly by phosphorus pollution from non-point sources (Carpenter, 2011). Eutrophication is an over-enrichment of an aquatic system which leads to algal blooms. The algal blooms lead to shading, in turn leading to mortality in rooted aquatic plants, anoxia (oxygen shortage), and fish kills. This state is referred to as 'turbid', while the original state is referred to as 'clear', indicating that algal densities under normal conditions are low and a lot of sunlight reaches the bottom of shallow lakes (Carpenter, 2003), see Figure 5.1 (left).

Eutrophication has been found to be a persistent problem for surface water, not only for biota but also by leading to the loss of quality of drinking water and water recreation. The turbid state therefore provides 'lower' ecosystem services, which is undesirable (Folke et al., 2004, and references therein). After reduction of the phosphorus input some lakes have recovered to the clear state, while others remain in the turbid state because of nutrient cycling. Hence, substantial changes in soil management are needed for the lakes to switch back to the clear state (Carpenter, 2011). For deeper lakes, which have thermal stratification, the mechanisms via which eutrophication works are different, yet they yield similar results. In this case iron-oxygen interactions are important. Oxygen consumption in deep water is low, oxidizing iron, which in turn binds phosphorus. However, eutrophication leads to anoxia, reducing the iron, which in turn releases the phosphorus, leading to a positive feedback on phosphorus concentrations (Folke et al., 2004, and references therein).
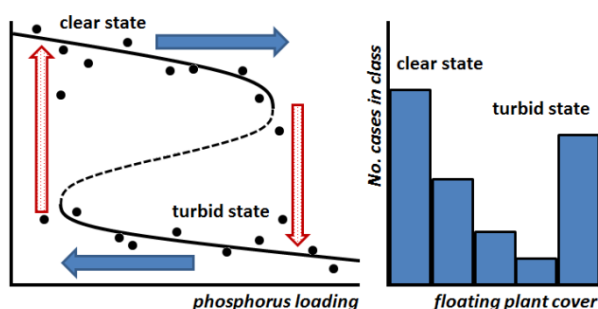

Figure 5.1: Conceptual diagrams of hysteresis in shallow lakes (after Scheffer & Carpenter, 2003). *Left*: A shift from a 'clear' to a 'turbid' state under increase in phosphorus loading. A significant decrease in phosphorus loading is required to restore the lake to a clear state. *Right*: A conceptual reproduction of an inventory of Dutch ditches that revealed a bimodal distribution, indicating a distinction between two states.

The 'lake hysteresis loop' has been found in Dutch lakes also. Scheffer & Carpenter (2003) give an example of Lake Veluwe, in which the percentage of lake area covered by charophytes is plotted as function of the total phosphorus concentration. An increase in the lake first did not lead to any significant loss in the covered area, until higher concentrations of phosphorus (around $0.15 \; mg \; l^{-1}$) where reached. The percentage of covered area then quickly dropped to zero. However, it was required that the phosphorus concentration be reduced below $0.1 \; mg \; l^{-1}$ before any restoration to the old state would occur. This behaviour is corresponding to the existence of two state states, separated by a separatrix. A switch only occurs when the separatrix is crossed because of stochastic fluctuations when it is near one of the stable states, or when the separatrix and one of the stable states disappear together in a tangent

bifurcation under increase of the phosphorus input. Decreasing the phosphorus input does not restore the system to the old state, as the system is now settled in the new state and the separatrix now prevents a switch back the old state. Only when the phosphorus concentration is sufficiently reduced a switch back may occur when the separatrix is crossed because of stochastic fluctuations, or when the separatrix and the new stable state disappear together in a second tangent bifurcation.

Scheffer & Carpenter (2003) also pointed out a hint of the existence of alternative stable states from data of 158 Dutch ditches. A histogram with bin classes based on floating plant cover of the ditches clearly showed a bimodal distribution, with significant maxima in the classes near 0 and near 100 per cent (see Figure 5.1, right). Manipulation field experiments may also reveal the existence of alternative stable states within data of the same system. A bio-manipulation experiment in a turbid English gravel pit induced a shift to a long-term clear state, obtained by a temporary reduction in fish stock. A bio-manipulation experiment in the Dutch Lake Zwemlust resulted in the lake being clear for several years before returning to the turbid state. This might indicate that the induced change was not sufficient to obtain a long-term change.

Food chain reorganization tipping point in lakes

A different way of having a tipping point in lake systems was demonstrated in a convincing, albeit somewhat unethical, bio-manipulation experiment, that was performed by Carpenter et al. (2011). Two lakes were taken, one as reference, and one in which in a 3-year time span slowly the top predator largemouth bass (Micropterus salmoides) was introduced into the ecosystem. Because of the proximity to each other and because of assessments before the disturbance experiment was started the two lakes were assumed to be 'identical'. The introduction of bass in one lake resulted in shifts in the food web. In the 'before' state smaller fish species were dominant. After the addition of bass in a step-wise matter the smaller fish species declined and showed patchy behaviour (from shoaling for protection, which was shown via Fourier analysis of spatial data). Large-bodied zooplankton increased, and cyclic oscillations of zoo- and phytoplankton appeared. An important side note is that body mass plays an important role as a switch for bass from a planktivorous to a pictivorous mode.

Carpenter et al. (2011) argued that for the period after 2008 they expected periods of increased variability, return rates near zero, lag-1 autocorrelations near one, skew-ness far from zero, and shifts in variance spectra toward low frequencies, based on early warning indicators. The data mainly focused on chlorophyll, which responds strongly to food web fluctuations and were measured at very high frequency (every 5 minutes) and precision. In 2009 and 2010 the spectral power shifted to low frequencies in the manipulated lake relative to the reference lake. Carpenter et al. (2011) furthermore argued the importance of time scale: given that the transition is approached slowly and the right variables are sampled frequently (observe, that it is assumed here that chlorophyll is a 'right' variable), warnings may be evident well before the regime shift has completed. Two indicators appeared to be useful based on the data: slowing return rates, and rising variance. Furthermore, a conservative test for nonlinearity was performed by Carpenter et al. (2011) and found to reject the hypothesis of linearity for the manipulated lake, while it did not reject the hypothesis of linearity for the reference lake.

Bistability under toxicant stress

In Chapter 4 we discussed the results of a food chain model by Kooi et al. (2008), in which toxicants affect some or all trophic levels. It shows that under nutrient stress bistability occurs in the system. Under higher population densities the species can survive when the toxicant level *per individual* is sub-lethal *and* the reproduction rate is not hampered too much by the loss of maintenance costs for toxicant handling (Kooijman, 2009). These population-dynamical features are not considered in standard ecotoxicological tests. Furthermore, the model displays a global bifurcation, and under varying dilution rate a scenario similar to that in the Allee model was found.

Van der Heide et al. (2010) used data from experiments to construct a model describing the interactions between seagrass *Zostera marina* and ammonia, and also found bistability in the model. The ammonia levels are lethal to low densities of sea grass, while higher densities of sea grass are able to survive. They argued that the toxic effect may in particular be present in sheltered, eutrophicated estuaries where the mixing of water is poor, creating local high and lethal ammonia densities. Although the model by Van der Heide et al. (2010) is simpler than the one by Kooi et al. (2008) and is based on a simple growth dilution assumption, the results are more or less the same, suggesting that toxicants in freshwater and probably also marine environments can be responsible for tipping points in populations of species. Furthermore, toxicants can pose a threat to species in concentrations that are considered sub-lethal in standardized ecotoxicological tests.

Tipping points in marine systems

There exist several examples of tipping points in marine systems, for instance see Folke et al. (2004) and Petraitis & Dudgeon (2004) for references. Much of the work on tipping points in marine systems is focused on 'depensatory effects', which is actually similar to the Allee effect, but then for aquatic populations of species. Overfishing is an major threat to benthic and ocean food webs, and in turn also for a growing world population, as it is vital to have sustainable food sources. In general it is assumed there exist many depensatory effects that have already caused or may in the future cause the sudden collapse of marine food webs.

Even if the fishing pressure itself does not cause the extinction of a population, the depensatory effects may occur because of other random changes in the system. For instance, a disease may temporarily increase the Allee threshold of a population, which normally would not pose a problem, but under fishing conditions leads to a crossing of the separatrix and consecutive extinction (Hilker, 2010). Climate change is thought to be another driver that may amplify depensatory effects; Wassmann et al. (2011) found a total of 51 reports of documented changes in Arctic marine biota in response to climate change, mostly focussed on the higher trophic levels (sea mammals and fish). However, not in all cases there is convincing evidence that the reported changes are really the result of 'tipping points' and not just gradual changes.

5.3   Tipping points in terrestrial systems

This category is of the most interest with regard to the goal of the project on the management of the green-blue space, in particular when it concerns biological systems that exist in western Europe, like forests, grasslands, heath lands, and obviously agricultural lands. An important remark is that the different examples have different spatiotemporal scales. We mostly ignore this in the below examples, and come back to it in Chapter 6.

Soil hysteresis

One type of terrestrial (sub)system which may be subject to tipping points that is often neglected by ecologists is soil. Yet hysteresis, popularized especially in the context of lake eutrophication, is known to occur in the unsaturated zone of different types of soil, in particular in clay soil. The main driver of the phenomenon is drying and wetting, which is a combination of temperature and evapotranspiration. The observation that the soil water retention does not follow the same curve during drying as it does during wetting but displays a hysteretic pattern was already made by Haines (1930), who wrote that "[t]he individual [soil] cell does not fill or empty by smooth reversible changes but shows two unstable stages at which filling or emptying is completed at a bound". Plots of volumetric water content (in %) as function of the soil suction (in kPa) reveal this 'hysteretic loop', as sketched in Figure 5.2.
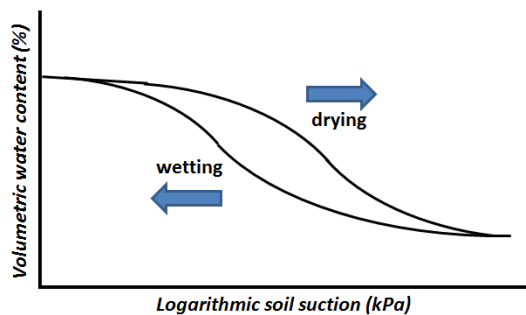
Figure 5.2: Conceptual diagram of hysteresis in soil (after Pham et al., 2005). The relationship between soil suction and volumetric water content of the soil is not equal for wetting (typically in winter, and after strong rainfall) and drying (typically in summer).

Soil hysteresis has been shown to be essential for the generation and recurrence of preferential flow paths (Ritsema et al., 2000). However, the direct characterization of hysteresis in water retention has proven cumbersome, and data on it are scarce. Furthermore, there is an apparent lack of a universally applicable index for the degree of hysteresis (Gebrenegus & Ghezzehei, 2011). Hence, hysteresis is often ignored in unsaturated flow models (Gebrenegus & Ghezzehei, 2011), although there exist several models that include soil hysteresis, for instance, Pham et al. (2005) found 28 soil hysteresis models in the scientific literature. Gebrenegus & Ghezzehei (2011) proposed a generalized index for the degree of hysteresis, that allows for the prediction of the degree of hysteresis and the missing hysteresis branch using only wetting or drying water retention data, but in general the modelling of soil hysteresis seems to remain elusive.

The soil hysteresis seems to be relevant for ecosystem services. The hysteresis in drying and wetting also causes microbial stress, resulting in hysteresis dynamics of carbon and nitrogen mineralization (Groffman & Tiedje, 1988). This may have consequences for the carbon storage capacity of soils under climate change. Zhuang et al. (2008) argued, that the hysteretic soil water characteristics are also influenced by soil organic matter, but that this has been poorly studied thus far. Their results show that organic matter significantly increases water retention in micro-aggregates, and they suggest a positive feedback between water retention and organic matter via increased physical protection of organic matter. This suggests, in turn, that an increase of soil organic matter by biotic activity (e.g., fungi and earthworms) may increase water retention, which in turn may have a positive feedback on organic matter protection, and may ultimately effect vegetation and ecosystem services like carbon sequestration.

Tipping points between ecosystem states

Much of the literature on tipping points in ecosystems is somewhat arbitrary on what exactly are the states between which a switch occurs in a tipping point. For instance, Folke et al. (2004) made an overview of tipping points in different ecosystems, in which they divided reported case studies in different types of ecosystem, such as rainforests, temperate forest, savannahs, etc. However, many of the case studies presented by them and others discuss transitions from one type of ecosystem to another. The distinction between different ecosystems as states of a biogeochemical system makes sense, as there are many feedbacks between biota, and between biota and their geophysical environment. Especially when the feedbacks of a biota-biota type are positive, non-gradual switches between 'states' may be possible.

Indeed, authors like Hirota et al. (2011) distinguish between 'states' as being different ecosystems. In their specific case they distinguish between 'forest', 'savannah', and 'treeless state' for tropical regions. Hirota et al. empirically reconstructed the domains of attraction for these different states, and found that the resilience of the states vary with precipitation. Based on those findings they generated a map with regions where either forests or savannahs are most likely to switch to an alternative state. However, observe that the variation in the data by Hirota et al. is of such magnitude, that there is ample room for alternative interpretations. Rather, their results present a first proxy of how the state of a system depends on inputs like precipitation.

Warman & Moles (2009) give another example of a re-interpretation of the whole ecosystem approach of the concept of alternative stable states. They discuss the tropical region of far North Queensland, in which different ecosystems exist, like tropical rainforests, fire-prone forests, and woodlands. These systems have thus far been studied independently from each other, but Warman & Moles (2009) argue that many characteristics of the vegetation are consistent with those of a complex, dynamic, spatially heterogeneous system which exhibits alternative stable states. As driving mechanism they propose the interaction of vegetation-specific positive feedback loops with the regions' environmental parameters, such as topography, steep humidity gradients and seasonality, which results in the rainforest/fire-prone vegetation mosaic pattern. We will discuss more examples on heterogeneous vegetation patterns in Chapter 6.

Grasslands and rangelands

Terrestrial rangeland ecosystems are vast natural landscapes with species of grass, like tallgrass and shortgrass prairies, desert grasslands and shrublands, woodlands, savannas, steppes, and tundras. They are distinguished from pasture lands primarily by the natural vegetation, as opposed to vegetation which has been planted by people, and rangelands are usually managed by livestock grazing and fire regimes, instead of seeding, irrigation, and fertilizer use. Rangelands have been analysed in detail by several authors already before the 1980s. Rangeland systems are interesting case studies with regard to 'tipping points' for several reasons. The complexity of the system is often limited in terms of the number of species (usually one herbivore, one or a few dominant plant species), the environmental heterogeneity tends to be limited, and movement of animals is controlled, which are conditions that comply with the assumptions behind differential equation modelling. Also, there is a large and increasing number of observations and experiments on pasture and range systems in many parts of the world (Noy-Meir, 1975). Furthermore, grazing systems are important types of ecosystems for mankind: millions of people in rangelands depend directly on livestock for their livelihoods, while the management of these systems still seems to be covered in controversy (Gillson & Hoffman, 2007).

In the absence of fires rangelands tend to become overgrown by trees and shrub species, possibly eventually even turning into forests. Van Langevelde et al. (2003) argued that the balance between trees and grasses in savannahs is dominated by herbivory and fire, which is based in the positive feedback between 'fuel load' (grass biomass) and fire intensity. This is a possible tipping point for grassland ecosystems: a switch from a grass state to a forested state. Anderies et al. (2002) developed a stylized model to consider also economic factors that determine the resilience of a managed fire-driven rangeland system. The important driver in their model is the grazing pressure, which determines in which of three regimes the system settles: a fire-dominated, a grazing-dominated, or a shrub-dominated rangeland. Economic costs of the different regimes were considered, specifically with a focus on economic factors that can reduce the resilience of a system by driving the desirable configuration to the edge of the basin of attraction.

A second possible tipping point in grasslands is the switch from a vegetation state to a barren desert state. Once the system is settled into the desert state it is difficult to restore the vegetation state. The desertification of semi-arid rangeland regions is a major issue with regard to the large economic dependence of many people on the rangeland ecosystem services. Different drivers behind desertification have been proposed. Livestock grazing is often considered to be the most important factor for desertification, especially by small ungulates like goats and sheep. Other candidates as driver are changes in climate, in particular prolonged and recurrent droughts. O'Connor & Roux (1995) considered data from a time series of 23 years of the Karoo, South-Africa. They concluded that variability in rainfall mostly had direct influence on plant species densities, but sheep grazing on longer-lived plant species became more important over longer time periods. Brown et al. (1997) studied long-term data from south-eastern Arizona. Three components in the Chihuahuan Desert ecosystem were documented to show changes: precipitation, vegetation (resulting from changes in precipitation), and animal populations (resulting from changes in the vegetation). The 20-hectare test site used in the study was fenced to keep

out grazers and hence to exclude the effects of grazing. Still changes were observed, which were argued to be the result of shifts in the regional climate.

Rietkerk & Van de Koppel (1997) proposed a more mechanistic explanation for desertification occurring under grazing, based on a model focussing on the plant-soil interactions when vegetation density is low. Vegetation growth in arid and semi-arid systems is mostly limited due to the limitation of water, while erosion plays an important secondary role: if there is no vegetation, then the soil is eroded more quickly, making it even more difficult for new vegetation to establish itself. Hence, there seems to be a positive feedback because of plant-soil interactions: a flourishing plant life usually means a well-developed network of roots and soil biota, which prevents erosion effects. The model study by Rietkerk & Van de Koppel (1997) demonstrates how these positive feedbacks between plants and soil can result in the occurrence of bistability in semi-arid systems.

Rainforests

Tipping points can also occur within a terrestrial ecosystem, i.e., a situation in which a switch from one state to another occurs, but the system more or less appears to remain unchanged at an aggregated level. For instance, O'Dowd et al. (2003) investigated the invasion by the alien crazy ant *Anoplolepis gracilipes* in a rainforest ecosystem of a tropical oceanic island. The ant affected the ecosystem at least at three trophic levels: ants foraging on canopy trees resulted in high population densities of host-generalist scale insects and growth of sooty moulds, leading to canopy dieback and even death of canopy trees. Despite this non-gradual change, the ecosystem as such does not switch to a 'state' that is visually differentiable from what people in general would name a rainforest.

In general it is believed that rainforests are important for at least two reasons. First, they have a large role in de carbon cycle, if not as 'lungs' of the Earth, then at least as one of the world's largest natural carbon storages. The loss of major areas of rainforest in the previous and coming decades is considered to be very problematic for this reason. Second, rainforests hold a very rich biodiversity. It is not unlikely that there are many more possible tipping points within the rainforest state, that leave the appearance of a 'rainforest' more or less intact, but in the meanwhile entail perhaps large changes in trophic food web structures, like in the example by O'Dowd et al. (2003).

Temperate forests

Many reported tipping points within temperate forests describe switches from dominance of one species to a dominance of a different species. A classic example is provided by Holling (1978), who discusses the switch from a state of dominance by spruce (*Picea* spp.) and fir (*Abies* spp.) to a dominance by aspen (*Populus* spp.) and birch (*Betula* spp.) in boreal forests in North America. These forests experience distinctive outbreaks of western and eastern spruce budworm (*Choristoneura occidentalis* and *Choristoneura fumiferana*, resp.) every 40-60 years, that can extent over areas of thousands of square kilometres (Holling, 1978; Folke et al., 2004). These insects defoliate the spruce and fir, which are then replaced by mainly aspen and birch. However, over a period of 20 to 40 years, selective browsing by moose shifts the forest back to the original state of spruce and fir dominance (Folke et al., 2004).

Antonovsky et al. (1990) developed a mathematical model for the case of balsam fir and eastern spruce budworm, and considered two extreme cases: either the pest only feeds on young trees, or it feeds on old trees. In the version of their model in which the pest predates on old trees only the pest is continuously present. However, in the version in which the pest predates on young trees only a sort of Allee effect and a global bifurcation occur. Similar to the Allee model, after the global bifurcation both the tree and budworm populations go extinct. Of course, in reality there will be re-invasion of the cleared area by outside trees, and it may explain why pest outbreaks disappear together with most of the spruce and fir, and how they are replaced by other tree species.

Peterson (2002) studied the transition of pyrogenic longleaf pine (*Pinus palustris*) savanna to mesic oak (*Quercus* spp.) forest in northeast Florida using a model consisting of some cells, making it 'semi-spatial'. In the absence of fire oaks are the 'better competitors' that eventually outgrow pines. However, the area is subject to regular fire. There are several positive feedbacks in the competition between pine and oak. Both young and mature longleaf pines can survive ground fires, while mature longleaf pines also shed needles that provide good fuel for ground fires. On the other hand, young oaks are intolerant of fire, while mature oaks shed leaves that work as 'fire delay'. Because of logging and other reasons the area of pines has been reduced to 5% of the original are, and Peterson studied three possible fire strategies to switch part of the area that has been overgrown by oak back to pine.

Arctic and sub-arctic systems

An example of a tipping point in arctic systems is presented by Zimov et al. (1995). They compiled the results of simulation models, experiments, and literature and concluded that there has been a switch from moss-dominated tundra to grass-dominated steppe in cold areas. General circulation models suggest that the Pleistocene environment in Beringia was colder than the present, with wetter soils. This in turn suggests that the steppe-like vegetation and dry soils in Beringia must be the result of something other than an arid macroclimate.

Zimov et al. (1995) suggested that important factors in the system are trampling and grazing by herbivores. Grasses can better deal with trampling and grazing than mosses, and they reduce soil moisture more effectively because of high evapotranspiration. On the other hand, under low grazing pressure the mosses create ideal wet conditions for themselves, outcompeting the grasses. The model by Zimov et al. displayed two possible states: under low grazing the system is in a 'mossy' state, while under high grazing the system is in a 'grassy' state. The authors furthermore suggest that over-effective human hunting has led to mass extinction among large herbivores at the end of the Pleistocene, which in turn has led to a decrease in grazing and a switch of large cold areas to a moss state.

5.4 Tipping points in the climate system

The highest level at which we consider the concept of tipping points is at the global climate level. The climate system is a composite system consisting of five major interactive adjoint components: atmosphere, hydrosphere (oceans included), cryosphere, lithosphere, and biosphere. The atmosphere, hydrosphere, cryosphere and biosphere act as cascading systems linked to each other (and human systems) by complex feedback processes. Major natural external forcing on the climate is the result of gravity and solar radiation, and because of the constant forcing, the subsystems of the climate system are actually never really in equilibrium with each other. The past 100-200 years the anthropogenic influence on the system starts to become another dominant forcing of the climate systems.

Tipping points are a 'hot topic' especially in the context of climate change. The term 'tipping point' in the context of climate change was first mentioned by James Hansen in 2005, who stated that ''we are on the precipice of climate system tipping points beyond which there is no redemption'' (Russill & Nyssa, 2009). The awareness about possible tipping points in climate systems is however already older. Lockwood (2001) reviewed work on abrupt climate changes and oscillations, and explicitly mentioned that the climatic system "is viewed as a dissipative, highly non-linear system […] and, as such, should be expected to have some unusual properties". He lists several rapid climatic changes have occurred in the past 1000 years.

Past climate tipping points and glacial-interglacial cycles

A research item within oceanography and climate research that has received considerable attention is the existence of a repeating cycle in glacial and interglacial periods in the Pleistocene. Around 8 separate consecutive glacial-interglacial periods are distinguished (Augustin et al., 2004). The cycle became apparent from Vostok ice boring data published by Petit et al. (1999), who plotted the promillage of

deuterium ("heavy water") as function of the ice depth, which resulted in a 'sawtooth'-like pattern (for a stylized representation of their publication, see Figure 5.3). The depth of analysed ice cores scales with backward time: the deeper the ice, the older it in general is.
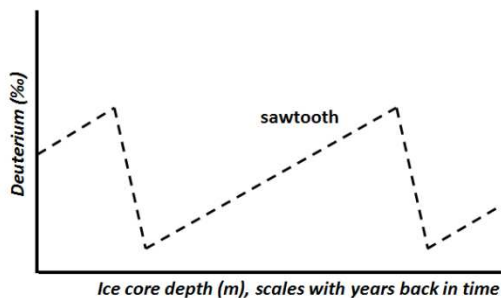

Figure 5.3: Conceptual diagram of the Vostok ice core data by Petit et al. (1999). The data follow a rather pronounced 'sawtooth'-like pattern. The data are obtained by ice boring and analysing the content of the gas bubbles enclosed in the ice. Observe that the x-axis is a reversed time scale, as in general deeper ice samples were formed further back in time. The periodic changes in deuterium content seem to match very well to the glacial-interglacial cycle of the Pleistocene.

It is now generally accepted that the sawtooth pattern in the ice is also followed by the fluctuations in carbon dioxide and global temperature during the Pleistocene the past million year or so. An interesting point is now how this cycle came about. Part of the explanation may be given by Oerlemans (1980), who already proposed a "switch-like" behaviour in the global temperature on a physical basis. The Earth's axis is slightly titled, and furthermore the planet follows an elliptical orbit. Because of the titled axis and the eccentricity there exist so-called Milankovic cycles. Oerlemans suggested that there exists a positive feedback between the amount of land area covered by ice and snow and the Earth's global temperature: ice reflects much of the incoming heat from the sun, leading to a further cooling down, and hence to a further genesis of ice. In a sense, the Earth system is switching between an 'icy' state and an 'ice-free' state.

Two points of criticism can be raised with regard to this explanation. First, alternative explanations are possible, and indeed have been presented. Second, is that the switch between the icy and ice-free states does not seem to exist beyond one million years in the past, nor is it clear what will happen to it in the future in light of anthropogenic pressures. Although this may be because of lack of data, one has to be critical on what drives the system behind the switch. Maybe despite the current anthropogenic pressures the Milankovic cycle is dominant enough to force the switch and a new Ice Age will arrive, but maybe it is not and the climate system will switch to a new regime. This also depends on the existence of other tipping points in lower systems to which the global climate system connects. We will discuss some more on that later on.

Historical climate tipping points

It is now widely accepted that also in historically recent climate history a tipping point has occurred, namely in the North Pacific Ocean in the winter of 1976-77. Subsequent research has suggested that also several other tipping points have occurred. Hare & Mantua (2000) analysed 31 climatic and 69 biological time series in the period of 1965 to 1997 for evidence of tipping points. They reported there is also evidence for a tipping point in 1989 in some components of the North Pacific ecosystem. These tipping points are most pronounced in data from the North Pacific and Bering Sea. Hare & Mantua (2000) argue that this may be due to a stronger nonlinearity in the response to environmental forcing, which may be related to the 'size' of the marine ecosystems of the North Pacific and Bering Sea in terms of biological components. They furthermore suggest to focus on monitoring the North Pacific and Bering Sea ecosystems for an earlier identification of tipping points than that is possible from monitoring climate data alone.

Future climate tipping points

More tipping points in the climate system are expected to occur, perhaps in the near future. Lenton et al. (2008) organized a workshop "Tipping Points in the Earth System" and brought together leading experts, in order to identify which tipping points would be most crucial with regard to climate change. They

defined the term 'tipping element' to indicate through which mechanisms these tipping points may occur and how they may be avoided (or enhanced) by human interference. Furthermore, to fulfil the conditions of a tipping element the time horizon has to be within a period of a 100 years. The following 'tipping elements' were identified with great confidence: Melting of the Arctic summer ice, melting of the Greenland ice sheet, melting of the West Antarctic ice sheet, a switch in the Atlantic thermohaline circulation, a switch in the behaviour of El Niño, a switch in the Indian summer monsoon, switches in the Sahara/Sahel and the West African monsoon, dieback of the Amazon rainforest, and a biome switch in the boreal forests. Less certain tipping elements were: A switch in Antarctic bottom water, a biome switch in the tundra, melting of permafrost, the release of marine methane hydrates, ocean anoxia, and the occurrence of an arctic-European hole in the ozone layer. Lenton et al. (2008) indicated that their list differs from the one composed by the IPCC (2007).

Collapse of the Atlantic Thermohaline Circulation

The most important 'tipping element' that has been established in the contemporary scientific literature, and which bears significant relevance for western Europa in particular, is the possible collapse of the Atlantic Thermohaline Circulation (THC; also named Meridional Overturning Circulation). Ocean water circulates at the ocean surface from the Gulf of Mexico to the Arctic seas, then sinks and returns to the Gulf of Mexico at large ocean depth. The ocean thermocline circulation is driven by water density gradients created by heat and freshwater inlet. The Atlantic THC is of specific interest for the Netherlands, as the current mild climate stems primarily from the moderating influence of the THC passing through the North Sea. Any significant change in the Atlantic THC may have a severe impact on the climate in Western Europe. Research shows that the THC-system may cross a tipping point within a limited time frame of around 10 years under human-induced changes in drivers, which would have a significant impact on primary ocean productivity and on the climate, and thus indirectly on many other relevant aspects for the Netherlands, such as agricultural productivity and the management of sea flood protection.

The THC-research is heavily founded in modelling, in particular the GENIE-1 model. The GENIE-1 model (Grid Enabled Integrated Earth system model; Lunt et al., 2006; Ridgwell et al., 2007; http://www.genie.ac.uk/) is a numerical simulation model containing the following components: A standard two-dimensional diffusive model for surface fluxes of heat and moisture; a three-dimensional, non-eddy-resolving (ocean eddy's are swirlings of fluid and the reverse current which occur after the passing of the flow of an obstacle, which can vary between 10 and 500 km in diameter), frictional geostrophic model; a three-dimensional, non-eddy-resolving, stationary wave atmosphere model; a simplified land-surface scheme (MOSES); a two-dimensional sea-ice model; ocean biogeochemistry; a marine sediment interaction model; and an ice-sheet model for (de)glaciation.

The suggestion that there are likely two stable regimes for flow of the Atlantic THC, namely one in which there is ocean circulation (simply indicated as "on"), and one in which there is advective spin down (indicated by "off"), dates back to Stommel (1961). The shift from one regime to the other depends primarily on the size of the influx of freshwater. GENIE-1 has been used for a systematic search for bistability of the THC by Lenton et al. (2007), who found that the bistability property is very robust. As a result of a collapse of the Atlantic THC there is a further increase in influx of freshwater at the southern boundary, leading to a reduction in the density gradient between North and South, which amplifies the "off"-state. The regime in which the system is settled into depends on the initial conditions, and currently the system is "on". However, paleoclimatological research has indicated that the THC has been shut "off" at times (Lenton et al., 2009). The potential collapse of the THC has been inferred from data (Bryden et al., 2005), while models in general suggest that a tipping point exists, but there is disagreement about the proximity (Rahmstorf et al., 2005), and there are some model studies that disagree about the possibility of a regime shift (e.g., Latif et al., 2000). Knutti & Stocker (2002) argued, that the sensitivity of the ocean circulation to perturbation rapidly increases when approaching a tipping point, and that as a result this will severely limit the predictability of the future climate. However, considering the amount of uncertainty, Yohe et al. (2006) argue that the likelihood of an Atlantic THC-collapse somewhere within

the next 200 years is roughly two-thirds, and furthermore argue that waiting another 30 years without acting upon this knowledge will in all cases considered increase the odds of a collapse considerably.

Working Group 1 of the Intergovernmental Panel of Climate Change (IPCC, 2007) gave a low (less than 10%) probability of collapse in the Atlantic THC this century, but this claim has been challenged by Lenton et al. (2009). They argued that the models used to obtain this expert assessment have been subjectively tuned to mimic the current state of the system, without paying much attention to past climate states (which would make it a case of over-fitting). Instead, Lenton et al. (2009) performed a rigorous model study including automated methods for observational data assimilation, and they concluded based on the averaging of outcomes of many models that anthropogenic climate forcing leads to a robust weakening of the THC and increases the probability of crossing a tipping point. According to the study by Lenton et al. (2009), the tipping point in the THC will occur because of freshwater forcing which becomes too large by the melting of large packages of sea ice on a relatively short time scale under the increase of global temperature, pushing the ocean circulation to the "off"-setting. The tipping point is furthermore predicted based on Greenland ice core paleotemperature data that have been analysed using Detrended Fluctuation Analysis (Livina & Lenton, 2007).

Climate tipping point cascades

As already mentioned, in general it is assumed that the atmosphere, hydrosphere, cryosphere and biosphere act as cascading systems linked to each other (and human systems) by complex feedback processes. The behaviour of the total climate system therefore cannot evidently be derived from the behaviour of the components studied in isolation (Higgins et al., 2002). Tipping points in one of the components may very well lead to tipping points in another component (and vice versa), having a snowball effect. Higgins et al. (2002) argue that the interactions between the thermohaline circulation and climate illustrate one emergent property of coupling ocean and atmospheric circulation.

Another example is atmosphere–biosphere interactions, that lead to multiple stable states in the Sahel region of West Africa. Foley et al. (2003) discuss that two tipping points can be shown for this region in the data. The first tipping point occurred around 5500 years ago, when a sudden switch from a vegetation-rich Sahara to desert occurred. Foley et al. furthermore argue that the Milankovic cycle cannot in itself explain this shift. Therefore the switch much be explained from interactions between components in the system. Their hypothesis is based on the existence of nonlinear feedbacks between vegetation and atmosphere. They also claim that in very recent history a second tipping point has occurred, in 1969, with the onset of a 30-year drought in the Sahel.

The above-mentioned view on tipping point cascades does not entail a spatially explicit view. However, Rietkerk et al. (2011) offer an extended view on the linking of components in the climate system, including emergent behaviour from spatially explicit systems in which local interactions between biota play an important role. We will discuss more on this in the next Chapter, in which we consider spatially explicit systems.

6 Spatially explicit systems and tipping points

It is hypothesized that tipping points also play an important role in spatially heterogeneous dynamical systems, yet it has proven difficult to find them in such a context. Most of the work done on tipping points thus far has been limited to models or systems, either in a laboratory or in the field, that are spatially homogeneous or near homogeneous (see previous chapters). Recently more and more the discussion is emerging what the concept of 'tipping point' actually entails in a spatial heterogeneous context, like for example the (Dutch) 'green-blue space'. What is a tipping point in the context of land-use systems, heterogeneous landscapes, or agro-economic systems? Here we broaden the scope to include existing work on spatially explicit modelling in an attempt to address this issue.

6.1 Mathematical tools

There exist several mathematical frameworks in which spatially explicit systems can be described. They are briefly discussed below.

Cellular automata

Cellular automata (CAs) are spatially explicit numerical models. They consist of (squared or hexagonal) cells, and each cell is in one of a limited number of (discrete) states. A famous CA is Conway's Game of Life (Gardner, 1970), in which cells are either in a 'dead' state or a 'living' state. Each iteration step some or all neighbouring cells are checked, in fact mimicking local interactions. A few simple, fixed rules on if a cell 'dies', 'stays alive', or 'procreates' are considered in all these evaluations. We will expand on CAs in the next Section.

Spatially explicit differential equations

Ordinary differential equations, of which we already have seen many examples in this report, assume a homogeneous mixing of the densities of the various state variables. To have spatially explicit descriptions of the densities of the state variables, like the various species densities, one has to resort to other mathematical descriptions, like partial differential equations (PDEs), reaction-diffusion equations (Fisher, 1937; Skellam, 1951; Drury & Candelaria, 2008), and integrodifference equations (Kot & Schaffer, 1986; Drury & Candelaria, 2008). In these formulations one or more state variables have not only a temporal but also a spatial index, which indicates position. Diffusion from higher to lower densities is usually included also. PDEs, etc. are even more difficult to solve than ODEs, and need to be approximated numerically. A popular method for this is finite differences, and the whole model is then implemented as some sort of cellular automaton (see above), but with continuous state variables in each cell.

Agent-based models & Complex Adaptive Systems

Agent-based models (ABMs, Gilbert, 2008; Macal & North, 2010) are numerical descriptions of Complex Adaptive Systems (CASs), systems that are adaptable and open to outside influences. The key element of ABMs is that they consist of autonomous agents, that interact with each other and the environment, and that can adapt their behaviour according to events. ABMs are powerful tools, but the number of options of behavioural patterns can easily be daunting to modellers and non-modellers alike. CAs can be viewed as simplified ABMs, but the agents may be on fixed locations (depending on the modelled quantities), the rules may be non-adaptable, and the openness and stochastic fluctuations may be reduced to zero.

The research on ABMs is an expanding scientific field, but it is still in an infant stage. They offer a promising route to the modelling of SESs, but there are serious limitations in terms of utility and validation that have to be overcome.

6.2   Emerging properties and tipping points

ABMs and CAs are well-known for their emergent properties, properties that appear while they have not been included *a priori* in the model. It is mostly because of these emergent properties that these types of models have been gaining in popularity for use in sociological and ecological sciences.

Patterns from discrete states

The Game of Life and other CAs are capable of producing various types of patterns ('pattern formation'), that can be fixed in space, or moving, and very dynamical in time, see Figure 6.1.
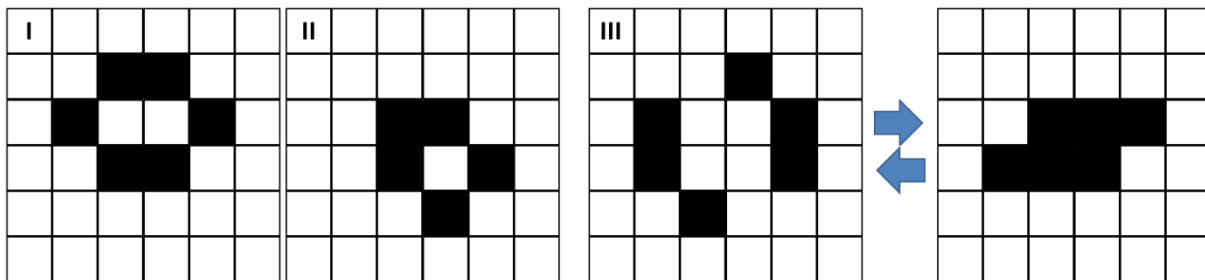

Figure 6.1: Some spatially fixed patterns from the Game of Life. *Left* (I): A 'beehive'. *Middle* (II): A 'boat'. *Right* (III): A 'toad', a period-2 pattern, which means that if in the one iteration it has the one shape, then in the following iteration it has the second shape, and so on. There are numerous more patterns that are fixed in space, of period 2 or more, or moving through the grid.

Many of these (time-dynamical) patterns also exist in various areas of nature, for instance snowflake formation, patterns on seashells, or the stripes of zebra's (Murray, 1988). The evolution of the patterns in CAs often strongly depends on the initial 'seeding', i.e., the states that the different cells have at the initiation of the simulation – this is called 'path dependency'. However, also changes in the parameter settings of a CA, if there are any parameters, may show transitions in the types of patterns that evolve. Such transitions can then be thought of as 'tipping points'. Imagining that different patterns can be perceived as landscape or land use types in one way or another, tipping points in a spatial context could arise through local state perturbations (cells that change their state randomly) or changes in the settings of parameters that have some sociological, economical, or biophysical interpretation.

In spite of this promising line of thought, it should be noted that there some drawbacks to CAs. One issue is a lack of 'mass' balance: in the Game of Life cells die or are born, but there is no global conservation of biomass. This is of course not an issue when the cell states would represent a less physical quantity, like votes ('yes' or 'no'), for example. Second, the meaning of a discrete 'state' is somewhat arbitrary. In the Game of Life, a cell is either living or dead, but it has no biomass as such. The interpretation of cell states, however, is essential.

Patterns from continuous states

The implementations to numerically approximate reaction-diffusion equations are much like CAs, except that the cells have continuous state values. Pattern formation can occur also in these systems, already when only two components (state variables) are considered. The work of Turing (1952) shows, that a single cell (which in in effect an ODE) may be in a stable steady state. However, under diffusion this state may destabilize, which is counter-intuitive, as diffusion is mostly associated with having a equalizing effect.

This destabilization occurs in so-called activator-inhibitor systems. One component stimulates the production of both components, while the other components inhibits their production. A change in parameter can lead to a Hopf bifurcation, having an effect much like in an ODE, namely periodic waves appear, or it can lead to a Turing bifurcation. After this latter bifurcation has occurred, typically striped or

hexagonal patterns appear. Under certain conditions also bistability can exist, in which case one or the other pattern occurs, depending on the initial conditions. Hence, tipping points exist in spatially explicit systems. However, at present there does not seem to be a rigorous overview of bi- and multistability, and bifurcations and patterns in reaction-diffusion models of more than two state variables, let alone it is clear what the socio-ecological interpretations are of emerging patterns or of tipping points.

6.3 Example studies

Examples in which transitions between spatial patterns in SESs have been demonstrated sufficiently stem from spatial ecology, for instance as listed by Rietkerk et al. (2004). In their Table 1 they explicitly mention vegetation patterns that appear in different ecosystems. We discuss them briefly below.

Arid and semi-arid ecosystems

Spatially vegetation patterns in arid and semi-arid ecosystems can be classified based on observational means like aerial photographs. Patterns are named like 'bands', 'labyrinths', 'spots', 'stripes', and 'gaps' (like 'spots', but then soil spots on a vegetation 'background' instead of vice versa), on various scales (between 1 and a 100 meter). Patterns have been studied for instance by Klausmeier (1999), who reported that vegetation forms regular stripes on hillsides, while it forms irregular mosaics on flat ground. Furthermore, he argued that the regular patterns on hillsides emerged from Turing-like instabilities. The stripes on hillsides are then explained as sloping ground is necessary for resource redistribution, where vegetation stripes develop along elevation contours. However, this hypothesis has been contested (Barbier et al., 2006). Other hypothesized driving factors apart from topography have been proposed, such as differential infiltration and underground moisture gradients. For instance, HilleRisLambers et al. (2001) argue that slope and underlying heterogeneity are not essential conditions for pattern formation, but instead patterns are generated based on the positive feedback between plant density and local water infiltration coupled with the spatial redistribution of runoff water.

Water is a scarce resource in arid and semi-arid regions, for which there is both competition and facilitation. On the long range the different plant individuals compete for water, while in the vicinity plant individuals facilitate each other for water uptake. Water infiltration into vegetated ground is faster than into bare soil, which leads to a net displacement of surface water into vegetated patches. This hypothesis seems to be supported by observations, for example, measurements in southwest Niger showed that soil water recharge was effectively homogeneous with respect to vegetation cover (i.e., the patterns do not arise as a result from 'imposed' input patterns in water recharge), but the stock half-life under cover was found to be approximately twice that of bare areas (Barbier et al., 2008). However, Gilad et al. (2007) came up with a more nuanced point of view. They argue that the water uptake by plant roots depletes the water resource, and hence there exists a trade-off between the increase in water infiltration and the uptake of water by plants.

The vegetation pattern formation can be explained by considering the plant-soil system as a reaction-diffusion system, in which there is lateral diffusion of water and plants (via propagation). The 'cells' in the system have been modelled as squared vegetation patches of variable density (HilleRisLambers et al., 2001; Rietkerk et al., 2002), in which case the model is a spatially extended version of the model proposed and analysed by Rietkerk & Van de Koppel (1997), which we discussed in Chapter 5.3, or alternatively as individual plant units (Barbier et al., 2008). During raining water partly infiltrates the soil, while the remainder runs off as surface water, outside the reach of the vegetation. The infiltrated water will also partly diffuse outside of the reach of the roots of the vegetation, but the higher the root density, the better the capacity to 'bind' water to the vegetative patch (up to a certain asymptotic maximum). The PDE-based models are capable of reproducing the different kinds of vegetative patterns on a scale of 400 by 400 metres under different amounts of rainfall. More importantly, on slopes the models reproduce the vegetation bands as noted by Klausmeier (1999).

According to the model results, changes in rainfall under climatic change can be a driver of tipping points in arid and semi-arid regions. However, Rietkerk et al. (2002) also point out a second important driver. Grazing by livestock is a principal land use in these areas. Localized grazing, especially by goats and sheep, can easily lead a greater exposure of soil, which in turn increases erosion, while the grazing also prevents re-establishment of vegetation. Counter-intuitively but appearing as an emergent property from the models, relatively homogeneous grazing can lead to spatially heterogeneous vegetation patterns. Kéfi et al. (2007) analysed in more detail how vegetation patterns in arid ecosystems change under different grazing pressures, using both a modelling approach and field data from Mediterranean countries. A conceptual graphical diagram of a tipping point in (semi-)arid areas is given in Figure 6.2.
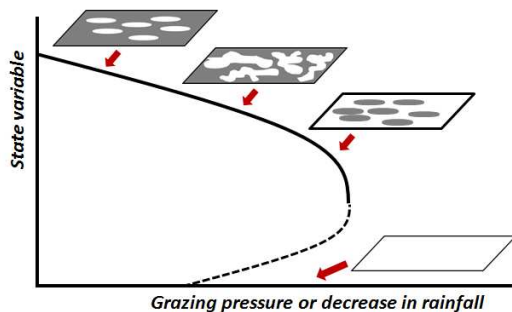

Figure 6.2:Graphical representation of a tipping point in vegetation patterns under change in an environmental or anthropogenic parameter like grazing pressure or a decrease in rainfall, adapted from Rietkerk et al. (2004). The vegetation patterns change gradually, until a bifurcation point is encountered and the vegetation disappears. Re-establishment of the vegetation is hampered, and a significant backward change in the parameter is required before system restoration is possible.

These observations have also led to the idea that spatial patterns might provide useful indicators (early warning) for an increased risk of a tipping point occurring (Kéfi et al., 2011; Konings et al., 2011). Kéfi et al. (2007) found that with increasing grazing pressure the data showed consistent deviations from power laws, and suggested that this is an indicator for early warning. Again, this can be explained by considering the eigenvalues of the stable state. Far away from a bifurcation there is usually one dominant stable eigenvalue that dictates the attraction to the steady state. However, when approaching the bifurcation the dominance of this one eigenvalue disappears as it starts to approach zero. In essence, the deviation from the power law is similar to the rise in variance near a bifurcation. Konings et al. (2011) focussed on modelling the timescales to understand the response of patterned vegetation systems to drought. There results suggest changes in pattern morphology as a result of shifts in annual rainfall may take around 4-5 years to show.

At any rate, the research suggests that tipping points may occur under climatic change and changes in grazing pressure. When the system starts to approach a tipping point this may be observed from changes in vegetation patterns, but not immediately. This means that policy on preventing desertification in countries with arid and semi-arid land use have to take these things into account. Of course, whether or not such policies are devised and also properly executed by locals is a different issue. Furthermore, the research suggests some approaches on how to restore vegetation in arid or semi-arid areas. Indeed, Pueyo et al. (2009) for instance considered the restoration of vegetation in semi-arid regions in Spain. They introduced 'nurse' shrubs (*Suaeda vera*) that had a significant effect on the local facilitation of the vegetation by water and nutrient retention, and suggested the use of nurse plants as general treatment for the restoration of semi-arid regions.

Savannahs

Vegetation patterns similar to those in arid and semi-arid regions are found in savannahs. In this case, however, the component of interest is not water but nutrients. Lejeune et al. (2002) observed the common existence in Africa and South America of patches of trees on a 'background' of grass under humid yet nutrient-poor conditions. Furthermore, they argue it is not likely that these patterns are

imposed from pre-existing nutrient distributions, and have to arise from plant-plant interactions. They developed a kinetic equation describing vegetation density and with two-dimensional diffusion of this vegetation. Locally the vegetation facilitate each other in nutrient adsorption, but globally there is a shortage of nutrients and thus competition for this resource. The model can be analysed using bifurcation analysis by taking a Fourier expansion and applying nonlinear analysis techniques, which results in a set of two ODEs. Tipping points exist in the model that can explain the emergence of different patterns.

It is interesting to note there also appear to be alternative hypotheses on the savannah pattern formation. For example, Wiegand et al. (2006) hypothesized a cyclical succession between open savannah and 'woody dominance', based on a 'honeycomb model' (consisting of hexagonal cells). The cycles are driven by a highly variable rainfall in time and space, and inter-tree competition. They argue that moisture is still the most limiting resource for savannahs. Furthermore, they also argue that savannahs are likely to be unstable on a smaller spatial scale, while they are persisting on a larger spatial for millennia. As rain cells can be as small as 1 square kilometre, and several rainfalls are needed on the same spot for germination of woody plants, the events under which germination occur are more or less random.

Scanlon et al. (2007) used CAs describing global-scale water constraints and local-scale facilitation. They obtained similar savannah vegetation patterns as Lejeune et al. (2002). Furthermore, they compared model outcomes with high-resolution satellite data over a regional rainfall gradient in the Kalahari desert. Tree canopy cover ranged from 4 to 65%. They found that the observed power law distributions in tree canopy cluster sizes can arise from the global-scale water constraints and local-scale facilitation. Furthermore, this did not entail any 'threshold behaviour'. Scanlon et al. (2007) argue, that there is no physically based mechanism for the propagation of disturbances, and that the Kalahari is currently not at risk of any tipping point, other than due to global properties through vegetation-climate interactions, as was discussed by Foley et al. (2003) for the Sahel region (see Section 5.4). The discrepancies between the findings by Scanlon et al. (2007) and Lejeune et al. (2002) may be explained from differences in the modelling approach and the studied system.

Peat bogs

Bogs or mires are wetlands that accumulate acidic peat, a deposit of dead plant material (often mosses like *Sphagnum*). As such, they generally function as net carbon sinks. Bogs occur where the ground surface is acid, as a result from acidic ground water or because water is derived from precipitation only. Via a positive feedback mosses further acidify the ground surface by taking up cations such as calcium and magnesium and releasing hydrogen ions, creating more ideal circumstances for themselves.

Peatlands display spatial vegetation patterns. Swanson & Grigal (1988) used a stochastic simulation model to explain the formation of flark-and-string patterns in bogs, i.e., linear ridges oriented perpendicular to the slope, separated by wetter zones ('flarks') that are more sparsely vegetated. In the model hummocks (knolls above the general surface level) and hollows (ground depressions) are responsible for the pattern formation, as hummocks impede water flow across the bog, while a lower water table increases the probability of a hummock forming. In the model by Swanson & Grigal (1988) a critical minimum surface slope and a sufficient hampering of the water supply are required to produce the patterning.

Paleoecological studies have indicated that peatland ecosystems may be subject to tipping points because of bistability. One state is open treeless bogs, the other is bog woodlands. Both the switch from open to woodland and from woodland to open has been reported. Eppinga et al. (2009a) suggested that the pattern formation and the bistability might be related and developed a model including both local and long-range interactions between *Sphagnum*, vascular plants, and the local environment. They identified several positive feedbacks in the system, that may explain the occurrence of bistability in the system, and were able to reproduce different patterns that were previously only explained separately (Eppinga et al., 2009b). Nutrients and hydrology were found to be important as structuring mechanisms.

7 Discussion & conclusion

In the previous chapters various aspects of tipping points have been discussed: what they are (Chapter 2), what properties they display (Chapter 3), and how they can be found in models and data (Chapter 4). Also, many literature examples of tipping points in experiments and in field situations have been presented, at different spatiotemporal scales, both for systems that are considered spatially homogeneous (Chapter 5) and spatially explicit (Chapter 6), where it should be observed that one can consider the same system in different ways. Considering all the above-mentioned information in regard to applying it to the green-blue environment, in particular with regard to the Netherlands:

- How relevant is the concept of 'tipping points' for the (Dutch) green-blue environment?
- Are there great risks involved in the coming decades in the (further) development of the (Dutch) green-blue environment, specifically with regard to 'tipping points'?
- If yes, what scenarios are there and what possibilities are there to reduce such risks?
- Are there possibly beneficial effects to be expected from 'tipping points', or can we think of win-win scenarios in this regard?

Answering these questions requires both data for detection and process understanding, and an adequate modelling framework for insight and scenario development. A preliminary inventory of possibilities of tipping points can be made, with specific regard to the Netherlands. Then several modelling considerations are discussed, which also give relevant criteria for data.

7.1 Tipping point risks in the Netherlands

An inventory is given here of systems in which tipping points may be expected to exist and that may be of significance for the development of the Dutch 'green-blue space' in the coming decades. Observe, that this list is by no means complete, but rather gives an initial impression.

Possible tipping points in soil food webs

The acidification of soils in the later decades of the 20th century has been shown to result in significant shifts of species in forest and grassland ecosystems. Acidification has, for instance, resulted in shifts in bacterial- and fungi-dominated food webs (J. Faber, personal communication). Liming has been a popular management approach to increase the pH of soils, but this has not resulted in the restoration of the pre-acidification conditions (for instance, Kreutzer, 1995). In how far this really represents a tipping point remains to be seen. One critical point is that liming is not the same as changing an environmental parameter in a model, and may have additional unwanted or unobserved effects. Furthermore, in order to have a tipping point one has to show there are alternative states – any shift in species composition may also simply be the result of pH tolerances of different species.

'Desertification' of the Veluwe

In Chapters 5 and 6 examples have been discussed of how grazing by large herbivores can drive the occurrence of tipping points. For instance, tipping points from vegetation states to barren states can occur in semi-arid and arid systems under grazing pressure, while switches from mosses-to-grasses have occurred in the Pleistocene under grazing pressure.

It seems that the formation of sandy, barren regions at the Veluwe may also be a result of over-grazing by sheep (Ryan Teuling, personal communication). The general thought seems to be that grazers produce manure that enrich the soil. However, the conditions resemble those in (semi-)arid systems: not nutrients but water is the limiting factor for vegetation growth. Future research may reveal more about the underlying processes, and what can be done to prevent land degradation without having to force the grazers away.

Soil carbon storage capacity

The carbon dioxide exhaust from anthropogenic activities is significant. Soils are important for the storage of carbon. In particular forests play an important role in the Earth's carbon balance: two-thirds of the forest carbon is stored in its soil, where much is protected against turnover in soil aggregates and chemical complexes (Simard & Austin, 2010). Changes in forest soil food webs because of climate change or human interference may lead to significant reductions of this carbon storage function.

Also in grassland and agricultural soils carbon is stored and protected by soil aggregates and chemical complexes. Earthworms contribute significantly in this service by being a key component in the formation of these components. In agricultural soils this service is seriously hampered because of the significant earthworm mortality that results from tillage, while tillage also exposes the deeper layers in which carbon has been stored to weathering and microbial degradation. Experiments in which tillage is no longer performed have shown rising earthworm densities and improved soil services (J. Faber, personal communication).

Also here we have to be critical: earthworm densities increase again after tillage is abandoned, hence it appears that the soil system has not been subjected to any tipping point. Nevertheless, large-scale erosion has occurred, for instance in agricultural lands in former Soviet-states. It remains to be seen what can be done about that, and the conditions seem to resemble those of the barren desert state after a tipping point has occurred in (semi-)arid systems.

Possible carbon release through loss of peat bogs

Peat bogs also play an important role in carbon storage. Peat bogs have a low rate of carbon storage, and therefore this storing process has thus far been neglected in carbon cycle models (Kleinen et al., 2012). Indeed, on a shorter timescale of decades peat bogs are not relevant as carbon storing sink. However, substantial peat deposits have already accumulated since the last Ice Age. It is therefore relevant to ensure that peat bogs are not 'disturbed' too much as that they release much of this accumulated carbon.

As discussed in Section 6.3, peat bog systems display bistability between open bogs and bog woodlands. The switches from one state to the other are accompanied by rapid changes in decomposition rates and carbon sequestration (Eppinga et al., 2009a). Plant growth in peatlands is limited by water stress, both by too high and too low water levels (Eppinga et al., 2009b). Hence, waterlogging and desiccation are both threats that should be considered, as the hydrology is one of the two major drivers behind peat bog vegetation pattern formation, next to eutrophication.

7.2   Modelling considerations

The example studies mentioned in Section 6.3 show that the concept of 'tipping points' can exist in a spatially explicit environment, which is one criterion for the application of the concept in the framework of the green-blue space. However, one important issue with regard to this application is 'scale'. There are various spatial, temporal, and organizational scales at which we can look at the concept. One can ask at which scale a tipping point may occur, and what it means at other scales.

Different scales, and meanings of scale

From a modelling viewpoint the concept of 'scale' is very important, albeit it is in the end an artificial concept and may give rise to modelling artefacts. 'Scale' is a more difficult concept than most people realize. Different things are meant when the term 'scale' is used, which makes the concept even more confusing. Scale can be interpreted as 'the scale at which processes occur'. Scales can be tangible when it concerns time or space, but they can also be more abstract when organizational scales are concerned.

'Scale' can also concern the properties of data. Bierkens et al. (2000) distinguish three scale aspects of scale. The first aspect, 'extent', is the result of the fact, that measurements have an upper and lower boundary. Within the extent measurements are often made in discontinuous intervals, for instance, time series are often not data of continuous time, but measurements with a certain fixed time interval between two consecutive measurements. It is commonly assumed that a measurement of an observed attribute (state variable, input, …) is the average value within the interval, which is the second aspect distinguished by Bierkens et al. (2002), although there are more sophisticated approaches to determine the value of an attribute within an interval, like 'kriging'. The third aspect is 'coverage', the ratio between extent and support for the extent. For example, when measurements are made every hour for one second only, the coverage is only 1/3600 seconds. In practice the attributes of many environmental systems have an even worse coverage.

But we are primarily concerned here with the 'scale' in a spatiotemporal sense. When concerning ourselves with something like the green-blue space, we have to wonder at which scale processes are to play a role in the possible occurrence of tipping points. Rietkerk et al. (2011), for instance, argue that tipping points do not have to be the result of positive feedbacks on large spatial scales, as they are typically considered in climate change scenarios (as was discussed in Section 5.4). Tipping points may also be the result of positive feedbacks on small spatial scales (1-100 m), as was demonstrated in the systems discussed in the previous Section. Rietkerk et al. (2011) argue that so-called 'cross-scale links' couple the different spatiotemporal scales, and that a tipping point on a 'lower' level may also drive a tipping point at a 'higher' level instead of vice versa. Furthermore, they point out that most climatological research ignores the low-level spatiotemporal scales.

Spatiotemporal scales and homo- and heterogeneous patterns

The coupling of spatiotemporal scales may potentially lead to serious confusion over what patterns are. Heterogeneities at lower scales may either show as or result in homogeneities at higher scales, and vice versa. An example is given by Lantz et al. (2010), who classified air-photos to examine vegetation characteristics (cover and patch size) across a latitudinal gradient which is frequently mapped as homogeneous vegetation. However, Lantz et al. (2010) argued that it exhibits significant heterogeneity on a finer scale. Along the same line we can consider the vegetation pattern formation in (semi-)arid areas, that demonstrates how the soil can be homogeneous, while plant-plant and plant-soil interactions lead to heterogeneities in the vegetation patterns. However, if we 'zoom out' and look differently at the vegetation pattern, it may be perceived as homogeneous again, much like a curtain with a fixed pattern may be perceived as homogeneous. On the other hand, heterogeneities in the soil may be 'masked' by the vegetation, perhaps because the soil properties that are heterogeneously distributed are not the most important limiting factor for vegetation growth. 'Zooming out' to a higher scale, the landscape may be perceived heterogeneous again, if the vegetation at a larger scale displays heterogeneous patterns.

Both in the modelling and the data acquisition and analysis methodologies it is of paramount importance to consider this scale issue.

Landscape processes

Extending on this, the concept of tipping points has not yet led to major insights when it comes to landscapes, the spatiotemporal scale of choice when it comes to the green-blue space. On the landscape level several important processes can be distinguished. Potentially a soil in a landscape can be rather homogeneous, while there are geophysical gradients, like dominant water flows, temperature gradients, and three-dimensional curvatures and shapes (hills, caverns, etc.). It is not trivial to evaluate how and when a landscape has settled into a form of steady state.

Not everybody is even convinced that landscape systems settle into stable states often. Phillips (2011) argues, that apparent 'steady states' are often actually the emergent outcome of two simple principles: gradient selection and threshold-mediated modulation. The first principle means that geomorphic

features associated with gradient-driven flows persist and grow relative to other features and pathways. The second principle entails that there are inherent limits on system development, restricting state space for most if not all geomorphic systems. Phillips (2011) does not contest that there may be valid or useful steady state assumptions for Earth surface systems, but argues that the assumption is over-used commonly.

Complex Adaptive Systems and organizational scales

As previously argued, agro-systems and other SESs are formed in part because of anthropogenic actions and interactions, or the results of these actions and interactions, in particular with regard to the coming decades. It therefore makes sense to include these anthropogenic actions and especially interactions in the models concerning the potential risks of tipping points in the green-blue space. This suggests that a modelling approach with regard to these systems should probably be along the lines of Complex Adaptive Systems (CASs).

The existence of different spatiotemporal scales and the existence of 'cross-scale links' between them seems to be an important issue for the more naturally developed landscapes. On the other hand, the agents that perform actions and interactions in SESs are not necessarily very clearly organized in a spatiotemporal sense. Instead, different organizational scales exist. Institutes like 'nations' and 'companies' still have some physical limitations in a spatiotemporal sense, but institutes like 'internet', 'cyberspace', or 'people's networks' are mostly non-physical, except perhaps for the physical contact nodes that are required for interactions, like mainframes or schools.

An intriguing example is desert formation. While vegetation patterns may arise as a result from local facilitation and global competition between plants, overgrazing seems to be a primary reason for the disappearance of vegetation in (semi-)arid regions and the consecutive erosion (see the previous Section). The overgrazing seems to be the result of an increasing land use by humans, who keep their livestock in these regions, but also in general the landscape is increasingly dominated by human actions. Policies devised with the primary goal of restoring the vegetation in (semi-)arid regions seem to be unsuccessful, i.e., a tipping point has occurred that appears to have resulted in a new 'state' that is persistent, and it is difficult to restore the system to its old state.

The question in the example of desert formation now is, what this tipping point actually entails. If it is geo- or biophysical in nature, then a strategy like devised by Pueyo et al. (2009) may very well be successful in restoring the vegetation in semi-arid regions. However, if the tipping point has a more sociological origin, this may not be enough. The organizational scales of the system may be of importance. For instance, it is not unthinkable that the nature of the agent-dominated system is such, that an easy restoration is prevented. Even if desert formation has occurred, it does not mean that local or non-local people will start the analysis of the problem by re-evaluating their own actions and objectives. Instead, people are often prone to put the blame to events or institutes that they have, or claim to have, no control over, or to other people. But even if individual people change or have a motivation to change their behaviour and objectives, there still exist different social structures that may also prove rigid. E.g., (semi-)nomadic people are often aggregated into 'cabals', where elders have a dominant opinion. Solving a problem like desertification thus may mean more than observing a tipping point in, e.g., vegetation patterns, especially in strongly human-influenced systems. The organizational scales of these systems might be equally or even more important than the spatiotemporal scales.

7.3   Considerations for future research

It may be clear to conclude that with this review we are not at the end point, but rather at the beginning on research on tipping points in the Dutch green-blue space. Several courses of actions for future research can be considered to extent the research.

First, although in the literature there appears to be a rising awareness that most natural and semi-natural systems behave (highly) nonlinear and may display alternative stable states, it is in practice not trivial to find convincing examples of these alternative states that do not allow for any alternative explanation, let alone allow for a robust risk analysis or policy evaluation. Also, even if a system displays a nonlinear or non-gradual response to input changes, this does not mean that alternative stable states exist. For this there need to be sufficiently strong and dominating positive feedback mechanisms present in the system. In the end there is no *a priori* reason to assume that alternative steady states exist in the investigated system (although this obviously depends on the scale at which one evaluates the system), and the "burden of proof is carried by [the] scientist investigating a given system" (Schröder et al., 2005), yet the number of cases presented in this report suggest that the possibility for 'tipping points' cannot be ignored. Furthermore, even if the Dutch green-blue space is not at risk of tipping points, there might be possibilities to induce them purposely for beneficial goals. One possibility to proceed in this regard is to systematically approach experts on various natural and half-natural systems and interview them if they have ever encountered observations that might lead someone to suspect the existence of a tipping point in a certain system.

Second, for the concept of 'tipping points' to be applicable for the green-blue space, an explicit spatial framework is required on the landscape level. For that it needs to be clear what is a landscape as 'state', and what natural and semi-natural systems can produce different types of landscapes (or perhaps better: different states). In general, a landscape is assumed to be an end state result of geophysical forces, biological interactions, and human interference. However, as different spatiotemporal and organizational scales are involved, it is doubtful in how far a system really settles in a stable state. Furthermore, it is almost impossible for various reasons to perform large-scale experiments to assess the possibilities for 'tipping' from one state to another. Hence, a solid conceptual and modelling framework is required to address this issue.

Third, the influence of anthropogenic forces is such in the Netherlands, that it is almost impractical to obtain answers with significant credibility with regard to tipping points and their effects without considering these forces. Hence, it seems almost unavoidable to adopt a more CAS-like approach in the research with regard to this subject.

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