Making eco logic and models work

An integrative approach to lake ecosystem modelling

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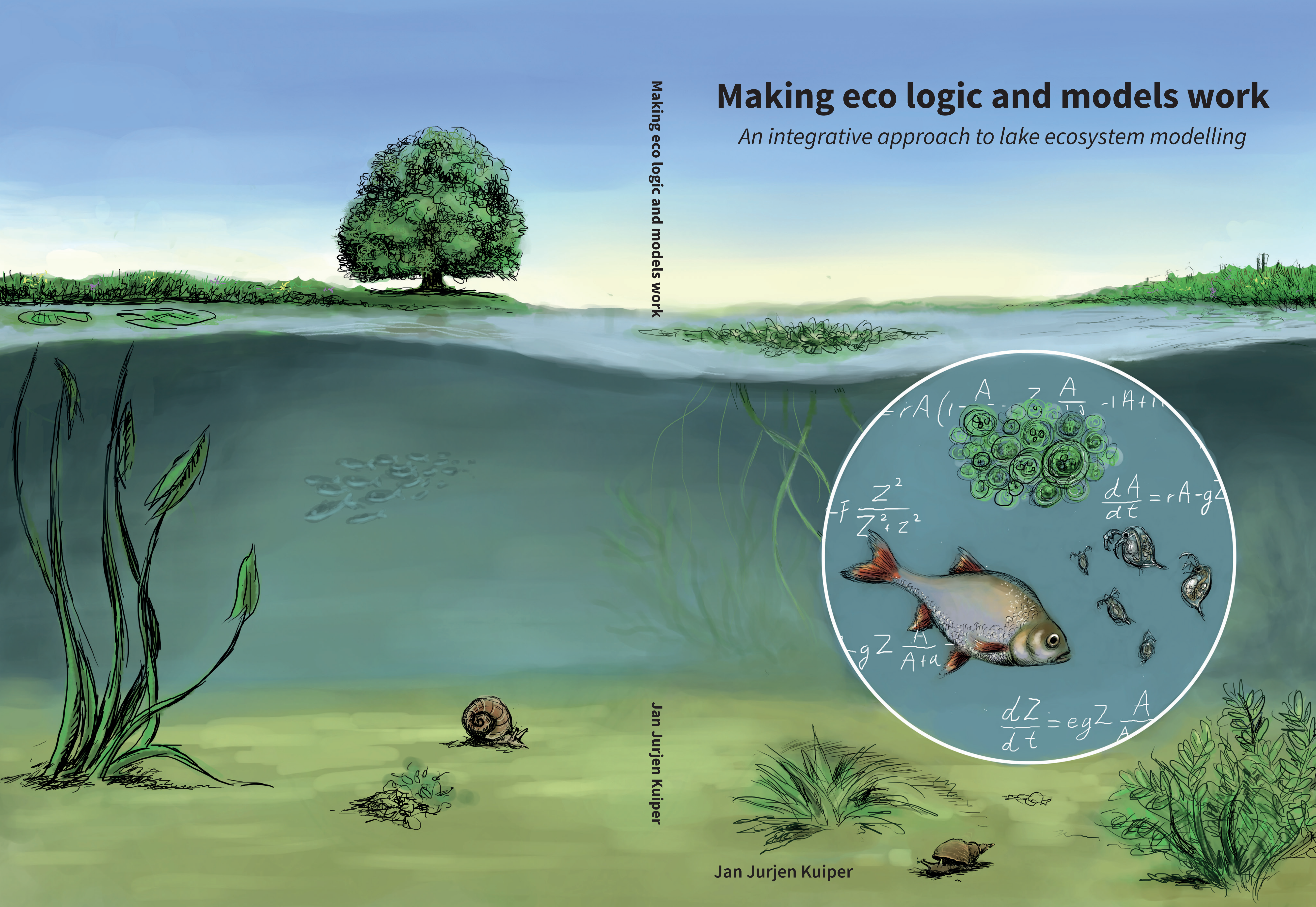

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Chapter 1

General introduction

1.1 A personal note

“There are these moments in life that change the way you look at the world. About one decade ago I had such a moment when I was hiking along a beach in the heart of Corcovado national park in Costa Rica. This peninsula is renowned for being among the places on earth with the highest biodiversity and I found myself happy to work there as a volunteer. I have always been intrigued by nature - as a kid you could often find me sitting on my knees observing pond life - yet the natural beauty I encountered during that walk was purely amazing. But what struck me most was witnessing the piles of human waste that had been washed up on the shore, especially since I was in the absolute middle of no-where (the nearest town was 50 km away, and it took me a 2 hour 4WD ride through the jungle, 30 minutes by boat and a 3 hour hike to get where I was). Shampoo bottles, lighters, flip-flops and drinking bottles were everywhere, and some of them I found deep inside the rainforest. It was then when I fully realised that humans are dominating this planet, affecting even the most remote places.”

1.2 The main challenge of our time

If humanity continues to use more of the natural systems than what these systems can provide for, resulting changes in our physical environment will remain to pose large risks on many societies (Meadows et al., 1972; Rockström et al., 2009). For example, by extracting fossilized carbon from the earth’s crust at a rate much higher than the rate at which the biosphere can sequestrate carbon, we allow the atmospheric CO2 concentration to rise and the global climate to change (Schneider, 1989). Already we are subjected to increasing temperatures and more frequent extreme weather events (Blunden and Arndt, 2016; IPCC, 2013; Van den Hurk et al., 2014). Indeed, it has recently been postulated that climate change related droughts were a major impetus for the civil war in Syria which is currently lacerating the Middle East (Kelley et al., 2015). Ultimately, the rise of CO2 in the atmosphere may lead to so called Large-Scale Discontinuities, such as substantial reduction of the North Atlantic Meridional Overturning Circulation or the complete deglaciation of the Greenland and West Antarctic ice sheets, which are conceivably the biggest cause for climate concern (Lenton et al., 2008; Smith et al., 2009). Other planetary boundaries that we probably have exceeded already include the loss of biodiversity and disruption of the Nitrogen and Phosphorus cycles (Rockström et al., 2009; Steffen et al., 2015). More than forty years ago it was predicted that growth of the human ecological footprint was unlikely to be stopped until after the sustainable limits had been exceeded due to delays in global decision making (Meadows et al., 1972; Randers, 2012). Indeed, only recently world leaders have started to recognize lowering the human ecological footprint as being one of the most critical challenges of our time. For example, in December 2015 - the warmest year ever recorded - 195 countries adopted a new climate agreement (the ‘Paris Agreement’), committing themselves to stop global warming below 2 ^{0}C (UNFCCC, 2015). Moreover, the leader of the Catholic Church, Pope Francis, presented an encyclical completely devoted to ecology and environmentalism, which he - for the first time in history - addressed to every person on the planet, followers and non-followers alike (Pope Francis, 2015). How societies can and should reform to circumvent the detrimental consequences of anthropogenically induced global environmental change is still largely an open question however (Hatfield-Dodds et al., 2015).

1.3 Responsibilities of environmental research

Global sustainability problems are sometimes referred to as ‘messy’ or ‘wicked’ because they are multidimensional, value-laden and originate in complex adaptive systems with numerous interactions and interdependencies at different scales (Verweij et al., 2006). In fact, they cannot be seen as single problems as they result from a combination of multiple interacting problems (Meadows et al., 1972). Because science is all about making the world more intelligible, there is an apparent role for scientists in supporting human societies to resolve these complex issues. However, the traditional way of knowledge production, which is curiosity driven, taking place within academic institutions and societies, and structured by scientific disciplines, appears to be insufficient, as sustainability problems typically fail to respond to non-integrative monodisciplinary approaches (Jones et al., 2010). In fact, what is called for is a post-modern science that is able to support decision makers in times when interests are conflicting, uncertainty is high and decisions are urgent (Funtowicz and Ravetz, 1993; Hessels and van Lente, 2008). In democracies, decision makers typically respond to constituencies which push their short-term profit interests, thereby imposing a great responsibility on scientists to elucidate and represent the long term interests (Safina, 1999). Indeed, we see that the science system is changing, whereby knowledge is increasingly being produced in the context of its application and by pan-disciplinary research teams (Hessels and van Lente, 2008). Along this path we see that science is becoming more predictive. Enabling decision makers and ecosystem managers to foresee the consequences, costs and benefits of future policies and management actions is probably decisive in designing successful routes towards sustainability. The most common way of predicting is by projecting our current understanding into the future using mechanistic models (Pace, 2001).

1.4 Models for understanding and prediction

In daily life humans are constantly turning experiences into judgements, assumptions and guesses in order to respond swiftly to novel circumstances, and generally these generalizations tend to be accurate (Gigerenzer and Brighton, 2009). In science, experience-based generalizations are referred to as ‘hypotheses’, and in the pursuit of truth we aim to falsify such generalizations by means of carefully designed experiments. Yet, certain issues are so complex that we cannot grasp them by performing (thought) experiments only, for example when we want to understand or predict the dynamics of complex dynamic ecosystems that are perturbed by human actions. In those cases mechanistic modelling may provide a solution, helping to gain experience with complex or counterintuitive phenomena, and turning experiences into predictions of future conditions. Models provide a logical structure that enables synthesizing various types of knowledge and data into an integrated view of the system it portrays. By manipulating the model we can identify the most important processes and components, and learn about the relationships between processes and model outputs (Carpenter, 2003). This is particularly useful when we have some understanding of the structure and dynamics of a system but only little data. Yet, when there is empirical data to confront the model with, we may be able to confirm that the essential mechanisms needed to reproduce observed system dynamics are indeed accounted for. If that is the case and there is enough confidence, we may continue with making quantitative predictions about how a system reacts when it is perturbed under given scenarios.

1.5 Shallow lakes

Small and shallow lakes are the most abundant of the ~117 million lakes in the world >0.2 ha (Verpoorter et al., 2014), and provide crucial ecosystem services for human wellbeing (Millennium Ecosystem Assessment, 2005). For example, lakes typically have a *source* function, e.g. of food products, a *sink* function, e.g. of waste water, and a *storage* function, e.g. of surplus water when connected rivers are about to burst their banks. Due to the high surface-to-volume ratio, shallow lakes have a relatively high turnover of nutrients and matter, as the water column is easily mixed and light is able to penetrate through the majority of its volume. As a result small and shallow lakes are relatively important components of global carbon and nutrient cycles; the greenhouse gasses sequestrated and emitted by lakes make a significant contribution to the total budgets (Bastviken et al., 2011; Raymond et al., 2013). Other reasons why these lakes are important for society is that they provide a critical habitat for all kinds of biota, and have important aesthetic, cultural and recreational values (Millennium Ecosystem Assessment, 2005). From a scientific point of view, lakes are particularly interesting because they have relatively well-defined boundaries, making them fairly simple, isolated and stable study objects, wherefore they are sometimes referred to as ‘microcosms’ (Forbes, 1887; Fussmann, 2008). Hence, some of the most basic concepts in ecology, such as food web dynamics and ecosystem ecology, were first described by limnologists (Forbes, 1887; Lindeman, 1942). Somewhat paradoxically, lakes are also renowned for the interactions across their boundaries, as they have been put forward as sentinels of changes in terrestrial and atmospheric processes in their catchment (Rinke et al., 2013; Schindler, 2009; Williamson et al., 2008). Because lakes are depressions in the landscape they accumulate runoff via drainage ditches, canals and rivers and thereby integrate the effects of human developments in their catchment. Moreover, because of the fast turnover of energy and matter, the changes imposed on the system become rapidly visible at the level of the whole ecosystem (Adrian et al., 2009).

1.6 The main stressors on lakes

Freshwater ecosystems are among the most impacted systems on the planet (Janse et al., 2015; WWF, 2014). An important reason is that on average the human population density near freshwater ecosystems is relatively high; human settlements have emerged near lakes to exploit their ecosystem services since the onset of human development (de Sherbinin et al., 2007). A second important reason is that, as described above, lakes integrate the effects of anthropogenic changes in their surrounding environment (Williamson et al., 2008). At the global scale increasing nutrient availability is one of the most dominant stress factors to lakes (Hasler, 1947; Smith, 2003), causing widespread eutrophication and resulting in a ‘green soup’ of toxic cyanobacteria and anoxic conditions (Correll, 1998; Gulati and Van Donk, 2002). The main sources of nutrients are sewer systems and agricultural runoff. Other harmful substances entering lakes via runoff include micro-plastics (Quik et al., 2015), pharmaceuticals (Van Donk et al., 2015), pesticides, herbicides and other chemicals (e.g. Van Wijngaarden et al., 2005). Another major force acting on lakes is anthropogenic climate change, including global warming and the increase of extreme weather conditions (Mooij et al., 2005). Hence, higher temperatures boost cyanobacterial growth (Paerl and Huisman, 2008), and especially lakes in arid regions suffer from low water levels and high salinity (Jeppesen et al., 2015; Rodríguez Díaz et al., 2007). Some lakes have already dried up completely (Jeppesen et al., 2009). An indirect effect of global warming is increasing input of organic carbon from wetlands and terrestrial systems, which reduces water transparency and subsidizes the aquatic food web (Lischke et al., 2014). A different source of stress comes from modifications of the food web, particularly by overexploitation. Removal of top-predators such as pike and zander can have a strong cascading effect on lower trophic levels of the food web (Carpenter et al., 1985; Estes et al., 2011). Also the introduction or invasion of non-native species can have significant impact on lake functioning. Typical examples of exotic species include Dreissena mussels, whose presence can have a large effect on transparency (Holland et al., 1995), and the red swamp crayfish, which can greatly frustrate the establishment of aquatic plant communities (Van der Wal et al., 2013). Besides inducing the above mentioned changes in external forcings and the food web, humans tend to alter the physical characteristics of lakes: surrounding marsh areas are converted into agricultural land, natural banks are turned into steep concrete banks and the water table is regulated by dams and wires for e.g. water storage or flood control (Kong et al., 2016; Sollie et al., 2008). These modifications may corrode the resilience of the system to withstand and recover from stress (Janse et al., 2008).

1.7 Lake response to stress

There are several ways in which lakes can respond to increasing anthropogenic pressure (Fig. 1). Lakes may, for example, respond gradual or even linear to changing environmental conditions (Fig. 1a). Such a response implicates that the system has no capacity to absorb stress, but has the advantage of providing a clear signal of change, which can be easily measured by water quality managers. Lakes may also respond non-linearly to changing conditions (Fig. 1b), or even show abrupt transitions, in which case stress does not seem to have much impact until a large change becomes apparent (Fig. 1c). This latter response indicates that the lake has a certain potential to withstand changes in external conditions, which creates possibilities for economic exploitation of the source or sink functions of lakes.

At the same time however, this resilience obscures the underlying environmental change, and without obvious warnings ecosystem managers might not anticipate an imminent regime shift. Such a shift will be particularly problematic when it is ‘catastrophic’, which means that when the lake is pushed over a threshold, positive feedbacks cause a self-propagating shift to an alternative regime (Fig. 1d). This alternative regime has its own resilience, which makes that a reduction of stress does not automatically lead to recovery - a phenomenon known as hysteresis. This implicates that for intermediate stress levels the system can linger in two contrasting states, whereby the prevailing state depends on the foregoing conditions (Fig. 1d). Clearly, the presence of alternative stable states and hysteresis agitates ecosystem management, although generic statistical early warning signals for catastrophic regime shifts are being developed (Dakos et al., 2015). In the most severe case, the shift to the alternative state is irreversible, e.g. when certain key species become (locally) extinct (Fig. 1e).

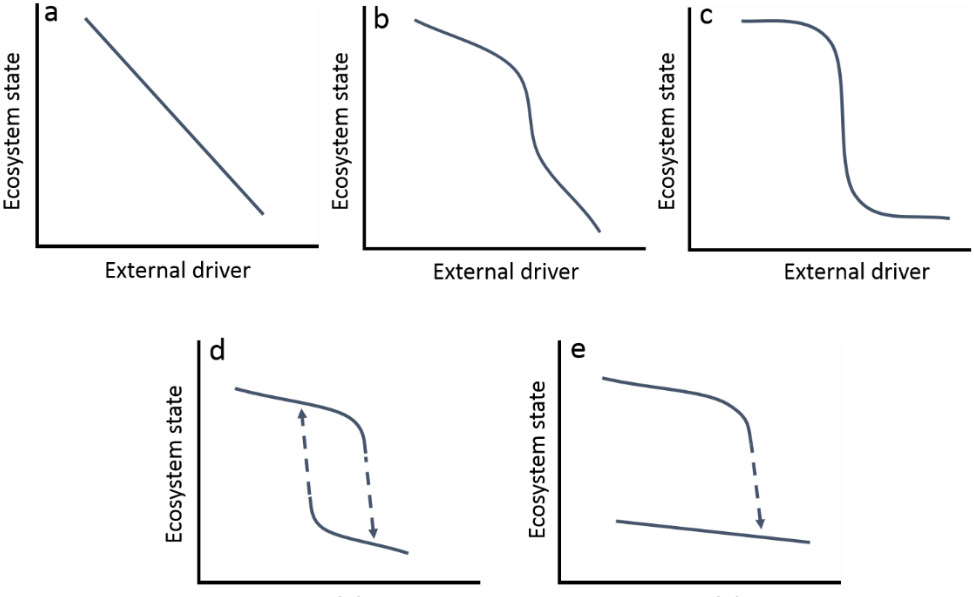

Figure 1 Possible responses of lakes to changing environmental conditions: (a) linear, (b) nonlinear, (c) threshold-like, (d) threshold-like with hysteresis, (e) threshold-like with irreversible change (solid lines, stable; dashed lines, regime shift).

1.8 Positive feedbacks in Shallow Lakes

Shallow lakes have provided some of the clearest examples of alternative stable states in nature (Scheffer et al., 2001). From the 1950’s onwards, numerous shallow lakes in temperate zone have switched from a clear water state with submerged plants into a turbid state dominated by phytoplankton and cyanobacteria following excessive pollution by nutrients

(Gulati and Van Donk, 2002; Scheffer et al., 1993). Even though tremendous management effort has been devoted to lake restoration ever since, mainly through the reduction of external nutrient inputs, many lake ecosystems appear to linger in the turbid water state and show only moderate signs of recovery (Hanson et al., 2016). The basic ingredient for a catastrophic regime shift are positive feedbacks (Fig. 2), and the most prominent feedbacks in shallow lakes involve the interaction between submerged vegetation and turbidity (Scheffer, 1990). Aquatic plants are capable of enhancing their own growing conditions through a positive feedback with water clarity (Scheffer, 1989; Van Donk and Van de Bund, 2002). For example, aquatic plants are able to suppress phytoplankton growth by being strong competitors for nutrients and via the excretion of allelopathic substances (Mulderij et al., 2005; Sondergaard and Moss, 1998). Moreover, they provide habitat for zooplankton which graze on phytoplankton (Scheffer, 1999). As a result, the aquatic plants prevent phytoplankton from blocking the sunlight, which is particularly important during the start of the growing season when aquatic plants germinate and need the light to reach the sediment. Water transparency is even further increased by the capacity of aquatic plants to reduce the resuspension of solids, e.g. by reducing flow velocities (Madsen et al., 2001), and to stabilize the sediment with their roots (Horppila and Nurminen, 2003). A second positive feedback loop involves the abundance of fish. Piscivorous fish which need clear water conditions for hunting, such as pike, also have a positive impact on water clarity by imposing top-down control on benthivorous and zooplanktivorous fish species which promote turbid conditions (Scheffer, 2004). Benthivorous fish, such as bream and carp, cause resuspension of sediments as they forage (Breukelaar et al., 1994), while zooplanktivorous fish release the phytoplankton from the grazing pressure of zooplankton (Scheffer, 2004). These feedbacks enable the system to resist changes in external environmental conditions, i.e. they underlie the emergence of alternative stable states (Scheffer, 1989). For example, during eutrophication, increasing inputs of external nutrients will initially not lead to major changes in the state of the lake. Although the abundance of aquatic plants will increase, the transparency of the water remains high. When the input of nutrients continues to increase, however, the clear water state is becoming saturated, and when the critical nutrient loading is exceeded, the aquatic plants lose their primacy. At that point, the exact same positive feedback loops that first kept the system in its clear state start to operate in the exact opposite direction, thereby propelling the lake to the contrasting phytoplankton dominated state. These feedbacks now give rise to the resilience of the turbid state, making moderate nutrient reductions ineffective. Having an estimate of the critical nutrient loading is of great importance to lake ecosystem managers as comparison with the actual nutrient loading provides crucial insight in which restoration measures are effective, and which ones are not (Jaarsma et al., 2008).

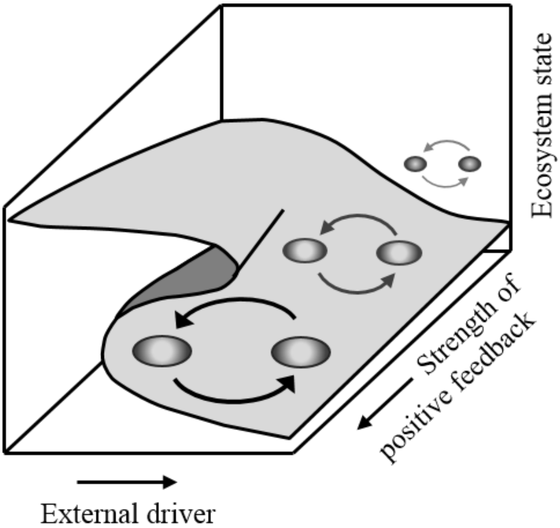

Figure 2 The strength of positive feedbacks and the emergence of alternative stable states and hysteresis in lakes (figure adapted from Scheffer 2009).

1.9 Complex problems require complex models

The foundation of our understanding of alternative stable states in ecosystems has been laid by so called minimal dynamical models consisting of only a few equations. These models show that a few positive feedback loops in lakes are sufficient to cause the catastrophic behaviour that has been observed in the field (Scheffer, 1990, 1989; Scheffer et al., 1993). In fact, it is largely attributable to these minimal dynamical models - as they are fully tractable and easy to communicate - that alternative stable states theory has become an integral part of water quality management in the Netherlands (Jaarsma et al., 2008). Despite their elegance however, the direct application of minimal dynamical models in water quality management can be tricky, because these models are by definition highly abstract representations of reality and are not intended to produce quantitative estimates that can be tested against field data. Alternatively, water quality managers may apply more complex or integrated ecosystem models which provide more explicit representations of our current quantitative understanding of the causes and consequences in lake ecosystems. Such models allow for integrating various different sources of data, and for analysing the relative importance of different processes. Subsequently this information is turned into quantitative projections and can be used for scenario analysis (Evans, 2012). However, because comprehensive models are hard to develop, maintain and communicate, there are only a few models readily available to scientists and lake ecosystem managers (Janssen et al., 2015). An example of an integrated ecosystem model for shallow lakes in the temperate regions is PCLake, which aims to integrate the main processes both in terms of biotic and abiotic variables.

1.10 The integrated ecosystem model PCLake

PCLake is basically a set of coupled ordinary differential and auxiliary equations describing the most important biotic and abiotic components of non-stratifying shallow lakes (Janse, 1997). The biota in PCLake are modelled on the basis of functional groups (Fig. 3). The primary producers are represented by three groups of phytoplankton ('diatoms', 'green algae' and 'cyanobacteria') and submerged plants. The remaining food web consists of zooplankton, zoobenthos, planktivorous fish, benthivorous fish and piscivorous fish. The abiotic components in the pelagic and in the sediment are detritus, inorganic material, dissolved phosphorus, ammonium and nitrate. All organic components are modelled in terms of dry-weight (DW), nitrogen (N) and phosphorus (P). An important result of this explicit stoichiometry is that the nutrient-to-dry-weight ratios of the organic components are variable. Other ecological key concepts covered by the model are: closed nutrient cycles, seasonal succession, food-web dynamics, trophic cascade and benthic-pelagic coupling. The main inputs to the model are: physical dimensions (depth and fetch), water inflow and outflow, nutrient loading, temperature, irradiance, initial values of the biota (composition of the food web), sediment characteristics and loading history. Optionally a marsh module can be attached to the model. A complete description of the model is presented by Janse (2005). PCLake shows great resemblance with PCDitch, its sister model for drainage ditches and linear water bodies (Van Liere et al., 2006). The main difference is that PCDitch focusses on the competition between different groups of plant species, while PCLake focusses on the trophic interactions in the food web (Janse, 1998).

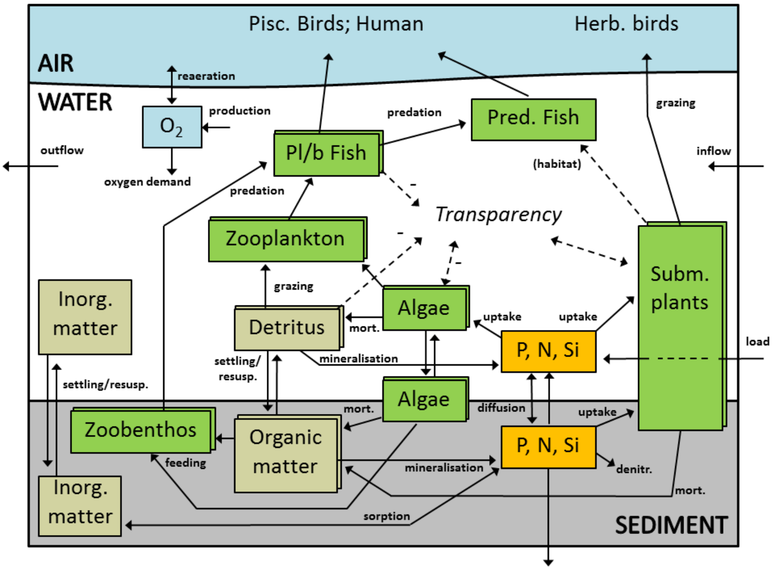

Figure 3 Schematic representation of PCLake with the most important biotic and abiotic components. Arrows depict mass fluxes, dotted arrows depict 'empirical' relations.

1.11 A small history of PCLake and its salient features

PCLake has originally been developed to describe the nutrient cycles of Lake Loosdrecht in the Netherlands as part of the WQL project (Water Quality research Loosdrecht Lakes; Janse and Aldenberg, 1990; Janse et al., 1992). The WQL project was basically a comprehensive system analysis aimed at understanding the mechanisms of the eutrophication process, and evaluating the effect of recovery measures (Fig. 4). Back then, the project was unique because of its size, duration and integrated nature: it included monitoring of a large set of physical, chemical and biological variables, both in situ and by remote sensing, lab experiments and ecosystem modelling (Van Liere et al., 1992). The project ran from 1979 to 1990 and resulted in the publication of more than 130 scientific papers (Van Liere, 1992). Although >100 aquatic ecosystem models have been in existence in since the WQL project, many of these models are seldom if ever used or cited in the peer-reviewed literature (Trolle et al., 2012). However, PCLake has stood the test of time as a quarter century after its first introduction it is still actively used in water quality management and is even one of the most cited lake ecosystem model in the literature (Trolle et al., 2012). This raises the question which features of the model underlie its success. The first success factor is arguably that the model is a direct product of a fully-fledged system analysis. As such, water quality managers can easily use the model as a quantitative framework for setting up their own system analysis, as many relevant components and processes are provided for. PCLake has been used to analyse the dynamics of several lakes in the Netherlands, including the Reewijk Lakes (Janse et al., 1993), Lake Zwemlust (Janse et al., 1998) and the Loenderveense Plassen (Witteveen+Bos, 2010). Also lakes outside the Netherlands have been analysed, including Lake Engelsholm (Trolle et al., 2014) and Lake Arreskov (Nielsen et al., 2014) in Denmark and lake Chao in China (Kong et al., 2016). A second important reason is that the model shows alternative stable states as an emergent property. PCLake is one of the few tools available for water quality managers that can be used to estimate the critical nutrient loadings of a shallow lake. This capability also makes the model popular among scientists; it is quite unique that a complex model with a fair amount of realism can be linked so easily to important theoretical concepts such as stability, resilience and alternative stable states. As such, researchers use the model as a virtual playground to study how specific processes, feedbacks or ecological concepts relate to the occurrence of alternative equilibria. The use of PCLake for this purpose was greatly enhanced by a multi-lake calibration exercise using data from more than 40 lakes with the aim of obtaining a best overall fit (Aldenberg et al., 1995; Janse et al., 2010). The result is that PCLake by default describes an ‘average’ shallow lake, making the model suitable for generalized studies on temperate shallow lakes. For example, Janse et al. (2008) used the model to study how general lake features, such as depth, fetch and sediment type determine the resilience of shallow lakes. Likewise, PCLake has been used to evaluate the importance of rising temperatures (Mooij et al., 2009, 2007) littoral–pelagic coupling (Sollie et al., 2008), allochthones carbon (Lischke et al., 2014), tube-dwelling invertebrates (Holker et al. 2015) and herbivory by birds (Van Altena et al., 2016). Summarizing, it may be concluded that PCLake embodies the right order of complexity: simple enough to maintain a connection with ecological theory and sufficiently complex to link up with the daily practice of ecosystem managers. This is in line with Constanza and (Sklar 1985) and Fulton (2001) who analysed numerous models in a wide range of fields and concluded that models of intermediate complexity score highest on their metric for ‘effectiveness’ (Hannah et al., 2010).

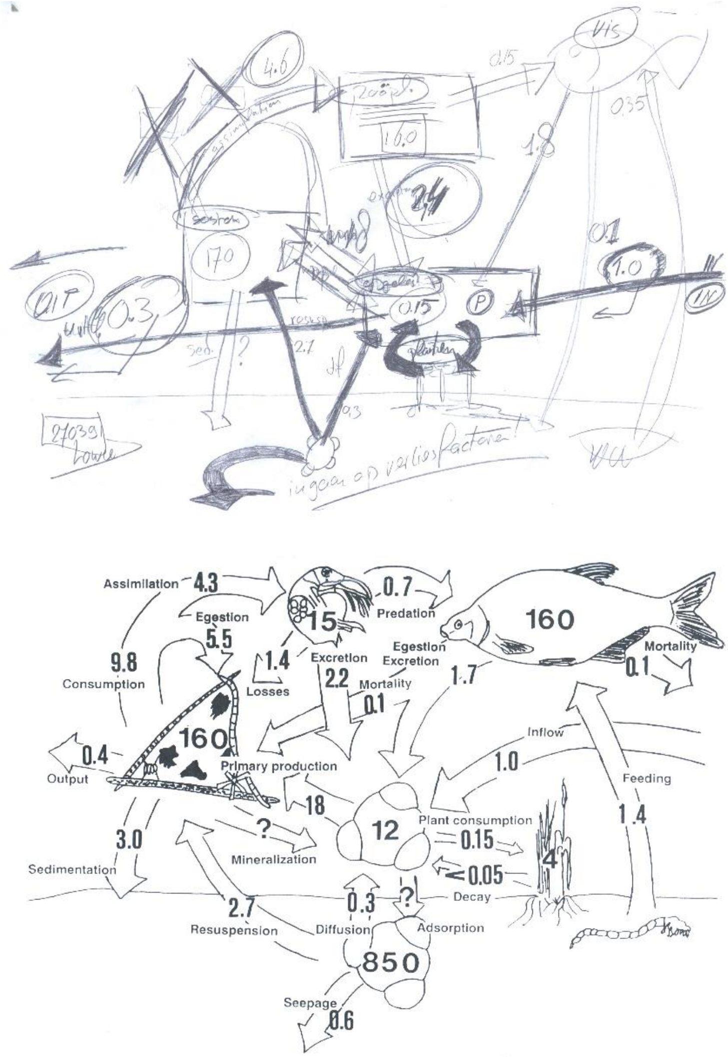

Figure 4 Drawings of the most important biotic and abiotic components in Lake Loosdrecht, focussing on estimates of the phosphorus contents and the phosphorus flows between components. These drawings were made during the WQL project and formed the basis of the PCLake model. The upper drawing is produced by Lowie van Liere, Jan Janse and Eddy Lammens on March 27, 1991. The lower graph is presented in Van Liere and Janse (1992).

1.12 The Water Framework Directive and the need for systems analyses

The Water Framework Directive (WFD, European Union 2000) is European legislation which commits all water managers in the EU to achieve a good ecological status in fresh waters, with the next audit in 2021 and the final audit in 2027. By emphasizing the ecological state rather than chemical parameters or external forcings, the WFD aims for re-establishment and sustainable use of ecosystem services, including the purifying capacity of ecosystems and the provision of habitat for biodiversity (Gaalen et al., 2015). The WFD requires member nations to monitor the current state of their water bodies, set restoration targets and implement measures to meet these targets. These targets and proposed measures are reported in river-basin management plans, which have a term of 6 years. The first management cycle has just ended (2009-2016) and revealed that water quality managers face serious challenges. In the Netherlands, for example, only 3 percent of the regional water bodies is currently in a good ecological state (Gaalen et al., 2015). Many water bodies remain highly productive due to persisting high nutrient loading, making them linger in a turbid phytoplankton dominated state or enter a monocultural and densely vegetated state (Lamers et al., 2012; Smolders et al., 2006). A recent ex-ante evaluation of the second cycle of river-basin management plans carried out by the Netherlands Environmental Assessment Agency (PBL) indicated that the proposed measures are not sufficient for reaching the ecological targets (Gaalen et al., 2015). Consequently, there is currently a major impetus for water quality managers to take additional restoration measures and to re-evaluate their targets. Managers are increasingly aware that every system is unique (n=1) and that successful implementation of the WFD calls for a tailored integrated assessment and modelling approach (Rekolainen et al., 2003). As such, water quality managers have a need for quantitative tools which enable them to (1) diagnose why the ecological status of a given system is not sufficient, (2) identify controlling variables, (3) formulate effective and cost-efficient management measures and (4) predict the effect of (combined) measures on the ecological state (Van Geest et al., 2009). The aquatic ecological scientific community has been, and remains challenged by the need to put this approach into practice (Basset, 2010).

1.13 The assignment

The ecosystem model PCLake has the potential to become the backbone of the many integrated systems analyses that are called for by the WFD. Unfortunately, relatively few water quality managers are familiar with the model, and the ones that do use the model increasingly have questions about the scope of the model and its limitations. It is also worrying that the development of the model seems to have stalled as there have been no major developments in the last couple of years. Taken together, this made the Dutch Foundation for Applied Water Research (STOWA) decide to initiate and fund a research project with the overall aim of increasing the usefulness and the validity of PCLake, and to increase the confidence in the model among water quality managers. This project became a collaboration between the Netherlands Institute of Ecology (NIOO-KNAW), Wageningen University & Research centre (WUR), the Netherlands Environmental Assessment Agency (PBL) and Witteveen+Bos, a private engineering company. The core of the research project consisted of a large number of case studies on Dutch lakes and two parallel running PhD-studies: one focussing on PCDitch (Van Gerven, 2016), and one focussing on PCLake (this thesis). Four objectives were identified as important pillars of the overarching project:

- To make the models more accessible;
- To make improvements to the models;
- To increase our understanding of the models as well as the ecosystems they portray;
- To explore new applications in lake ecosystem management.

1.14 Thesis outline

In **chapter 2**, I present the Database Approach To Modelling (DATM), which we developed to make models more accessible. The idea of DATM is that mathematical equations are stored in a database, independently of programming language and software specific formulations. The advantage here is that the database provides structure and overview, which facilitates understanding of the mathematical formulations, also by non-modellers. To run the model in a given framework the information in the database is automatically translated, augmented and compiled into a working model version. Thereby the model becomes available in many different software frameworks, and it becomes easy to switch between frameworks to exploit their joint set of tools and analysis. To exemplify the approach we use the simple Lotka-Volterra predator-prey equations and to demonstrate its usefulness we apply DATM to the complex PCLake model.

In **chapter 3**, I discuss the consequences of calibration for improvement of complex ecosystem models. Ecosystem models aiming to describe higher level variables such as water transparency are by definition crude simplifications of reality. Consequently, calibration at an aggregated level is often performed to align the individual components in such way that the model as a whole adequately describes the dynamics at the ecosystem level. As such, any missing dynamics can still be covered by the model, albeit indirectly. An important consequence is that once calibration has been performed, any model ‘improvement’ in the form of adding new components can bring the model ‘out of balance’ as it may lead to double counting with the implicit components. This same notion has consequences for sharing and reusing model components within the community of ecosystem modellers. We exemplify this line of reasoning by expanding PCLake with filter-feeding zoobenthos, which are always present in the lakes modelled by PCLake, but were until yet not explicitly covered by the model.

In **chapter 4**, I scrutinize the relation between complex ecosystem models and empirical food web models. Both modelling paradigms are used by scientists to improve our understanding of how stability is conferred to complex ecosystems although it is largely unclear how insights from these different fields can be aligned. We treat PCLake as a virtual reality from which we can sample 'empirical' information to parameterize a food web model which can be analysed for its stability. This allows us to study food web stability along the eutrophication gradient, knowing that PCLake will show a regime shift when a critical nutrient loading is reached. This strategy allows us to bring together the important theoretical frameworks of food web theory and alternative stable states theory and test them against each other. As such, we aim to increase our understanding of the biological mechanisms underlying the deterioration of food web stability in shallow lakes.

In **chapter 5**, I continue to analyse the extent to which models of a different form can describe the same natural phenomenon, and hence, how these models can be used for a better understanding of such natural phenomenon. We zoom in on the influence of the self-limitation and functional response terms rather than on the number of equations. Using classical extensions of the famous Lotka-Volterra equations we analyse the consequence of changing a system with a sophisticated functional response term (e.g. Holling type II or III) into a system with a simpler functional response term while maintaining equilibrium densities and material fluxes. We are interested in the extent to which stability properties of a complex system can be reflected by a simpler system. These insights may help resolve the question under which conditions empirical data can be linked to mathematical models to estimate the stability properties of real ecosystems.

In **chapter 6**, I present a new application of PCLake. Whereas PCLake is usually applied in the context of ecosystem restoration of turbid phytoplankton dominated lakes, we explore here how the model can be used once the clear water state has returned and an aquatic plant community has re-established. Dense stands of aquatic plants can be noxious and easily cause nuisance, and hence the removal of plants is an emerging management issue. Yet, because water plants are so crucial for stabilizing the clear water state, the removal of plant biomass can potentially instigate a critical transition back to the turbid water state. There is only limited empirical and theoretical understanding of how harvesting of submerged plants affects ecosystem functioning. Using PCLake, we evaluate the impact of harvesting for different nutrient loadings, and analyse the importance of mowing intensity and timing.

It is safe to say that to grasp the complexity of nature, and predict its response to environmental change, scientists need to conduct interdisciplinary studies and integrate different approaches. However, in search for understanding, scientific research often zooms in on a certain problem to expose more detail instead of integrating and synthesizing knowledge to show how higher level features arise. In the studies presented in this thesis I deliberately aimed at taking an integrative approach to gain insight in the functioning of complex ecosystems by connecting theories, models, modelling frameworks, methods and even experts from different fields. In **chapter 7**, I reflect on the added value of the integrated nature of the different studies presented in this thesis, and end with a personal note on integrative research.

As stated before, the studies presented in this thesis were part of a larger research project with the overall aim of increasing the usefulness and the validity of PCLake and its twin model PCDitch, and to enhance the confidence in the models among water quality managers. In **chapter 8**, we present a synopsis of the overarching collaborative research project on PCLake and PCDitch by describing the setup and the most important achievements of the project and discussing some remaining challenges and future directions.

Chapter 2

Serving many at once: How a database approach can create unity in dynamical ecosystem modelling

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&

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Abstract

Simulation modelling in ecology is a field that is becoming increasingly compartmentalized: while models based on differential equations can all be formulated in the universal language of mathematics, they are integrated and analyzed through a variety of frameworks, each with different user-interfaces, integration-options, spatial settings and components. These frameworks have produced myriads of models that are incompatible, not because of the fundamental ecological processes they describe, but because of framework-induced differences in the code. This has led to a dilemma: while the existing diversity of models and model-analyses is undoubtedly much needed, it can seldom be effectively used because of the time and energy involved in learning and mastering more than a single framework. In this way, many models have become locked into their frameworks, and scientific expertise has narrowed down to the scale of the framework.

Here we propose a Database Approach To Modelling (DATM) to create unity in dynamical ecosystem modelling with differential equations. In this approach the storage of ecological knowledge to be incorporated in the model is independent of the language and platform in which the model will be run. To create an instance of the model in a certain platform, the information in the database is translated and augmented with the language and platform specifics. This process is automated so that a new instance can be created each time the database is updated. We describe the approach using the simple Lotka-Volterra model and exemplify it with the complex ecosystem model for shallow lakes PCLake (and sister model PCDitch) which we automatically implement in the frameworks OSIRIS, GRIND for MATLAB, ACSL, R, DUFLOW and DELWAQ. A clear advantage of working in a database is the overview it provides. This facilitates the customization of the model code and the comparison of multiple versions. The most remarkable spin-off of the DATM approach is in the benefits that emerge from the interactive use of multiple frameworks in a single study, and even within a single analysis, facilitating the path to ecosystem-based approaches to modelling. The simplicity of the approach only adds to its elegance.

Introduction

Since the onset of ecological simulation modelling based on differential equations - in the sixties and seventies of the last century - attempts have been made to bring conceptual unity through the development of modelling frameworks. In the field of aquatic ecology, such frameworks include the widely used DELWAQ – a library of water quality and ecology models developed by Delft Hydraulics (Delft Hydraulics, 1995; Deltares, 2013), as well as the Computational Aquatic Ecosystem Dynamics Model (CAEDYM) – a library of ecological process sub-models (Hipsey et al., 2007), AQUASIM (Reichert, 1994), the Dutch Waterboards' DUFLOW framework (Spaans et al., 1989) and the recently developed FABM – Framework for Aquatic Biogeochemical Models (http://fabm.sourceforge.net). Each of these frameworks is internally consistent, intuitive and well suited to answer the ecological questions it was designed for (Clemmens et al., 1993; Gal et al., 2004), and all are based on the same basic mathematical principles underlying the differential equations. Nonetheless, because these frameworks were developed independently, they all have their own sets of implementation requirements, language and coding specifications, spatial configuration options as well as boundary conditions and forcing function specifications, etc. A user must therefore invest a considerable amount of effort to master any given framework, which in turn reduces the number of frameworks that any single user can master. The choice of framework to be used for any given project is thus primarily based on its availability, owned licenses, user experience and developer familiarity. This in turn leads to models being locked into their given frameworks, a narrowing-down of scientific expertise to the framework-scale and to the proverbial 're-invention of the wheel' – i.e., the inefficient redevelopment of existing tools for each framework, rather than a more productive cross-pollination of approaches to analyze models across frameworks, institutions, disciplines and scientists (Leavesley et al., 2002; Mooij et al., 2010; Trolle et al., 2012). We are confronted with the paradoxical situation that, while there is unity within each framework, there is no unity at the level of the ecological models.

Here we propose a method to bring unity at the level of the ecological module, with the idea that many of the existing frameworks will continue to coexist, and that, taken together, they provide the user with a wide and rich array of tools for model analysis. We coin this method a 'Database Approach To Modelling' (DATM). We developed this approach for the ecosystem model for shallow lakes PCLake, and its twin model for linear waters PCDitch. However, our approach is in no way limited to these models. In fact, it applies to all models based on differential equations and probably even beyond. We here show how one can automatically link these models to a wide variety of frameworks, including OSIRIS (Mooij and Boersma, 1996), GRIND for MATLAB (available on http://www.sparcs-center.org/grind.html), ACSL (Mitchell and Gauthier, 1976), R (R Development Core Team, 2008), DUFLOW (Spaans et al., 1989) and DELWAQ (Deltares, 2013). Note that the latter two frameworks are spatially explicit and therefore are formulated in terms of partial differential equations (PDE's), whereas implementations of an ecological model (e.g. PCLake) in the general purpose frameworks are a set of ordinary differential equations

(ODE’s). We will show that with DATM we can overcome this difference, and translate a single code either in a set of ODE’s in a general purpose framework or as the ecological component of a set of PDE’s in these spatially explicit frameworks. In the latter case, these ecological components are then merged by the frameworks with the advective and diffusive transport of matter to get the full PDE. Please note that in its current form, DATM does not provide the spatial configuration of the model, this has still to be entered at the level of the framework.

To explain the principles of DATM, we use as an example the classical Lotka-Volterra equations. These equations represent the earliest use of coupled differential equations in ecology (Lotka, 1920; Volterra, 1931, 1926). With this example, we show how knowledge of quite a few framework-specific details is necessary to implement even this simplest of models in some of the most widely used mathematical frameworks. From experience, we have learned how implementing more complex models in more specific frameworks takes a considerable effort, which is why we propose to automate this process: an essential component of DATM is the set of translators developed to automatically convert the database definitions of a given model into a working implementation in a specific framework. Conceptually, we argue that the overview and insight that arises when the model definition is stored in the database, conveniently displayed in tables and accessed through queries, facilitates model development and understanding.

Methods

DATM is based on the notion that ecological models are essentially rooted in mathematics. Here, we focus on models based on the mathematical concept of coupled differential equations. The dynamic systems represented by these equations have a universal mathematical notation. As an example, the Lotka-Volterra predator-prey equations can be read and understood by all in the following form:

$$dV/dt = r\,V - a\,V\,P \qquad \textit{eq. 1a}$$

$$dP/dt = a\,e\,V\,P - d\,P \qquad \textit{eq. 1b}$$

with state variables V for prey and P for predator; parameters r for autonomous growth rate of the prey; a the attack rate of the predator on the prey, e the conversion efficiency of the predator and d the autonomous death rate of the predator. This system is in this form fully defined and ready for simulation for a given set of parameters r, a, e and d and initial conditions $V_{t=0}$ and $P_{t=0}$. Our central point is that this mathematical notation for complex simulation models is sufficient to achieve unity and transparency in ecological modelling.

As shown in the above example, the set of coupled equations 1a and 1b must be augmented with information on the interpretation of the various identifiers that are used in the model. As a minimum description, the identifiers must belong to a certain class (e.g. state variable, parameter); represent a specific component of the system (e.g. prey, predator); have units (e.g. biomass, number of individuals), and (initial) values. In scientific papers that document smaller models, such as the Lotka-Volterra model, this information is often organized in tables, with either a shared table for all identifiers or separate tables per class of identifiers. Given the number of identifiers in the more complex water quality models, we choose to work with separate tables for each class of identifiers. For the Lotka-Volterra model such tables could look like (note the ‘s’ prefix to identifiers of state variables):

Table 1: state variables

Identifier	*description*	*dimension*	*initial value*
sV	prey density	biomass V	(some number)
sP	predator density	biomass P	(some number)

for the states,

Table 2: parameters

identifier	*description*	*dimension*	*value*
r	prey growth rate	time^{-1}	(some number)
a	predator attack rate	$\text{time}^{-1} \cdot \text{biomass P}^{-1}$	(some number)
e	predator efficiency	$\text{biomass P} \cdot \text{biomass V}^{-1}$	(some number)
d	predator death rate	time^{-1}	(some number)

for the parameters, and

Table 3: derivatives

identifier	*description*	*dimension*	*equation*
dV	prey derivative	$\text{biomass V} \cdot \text{time}^{-1}$	$dV = r \cdot sV - a \cdot sV \cdot sP$
dP	predator derivative	$\text{biomass P} \cdot \text{time}^{-1}$	$dP = a \cdot e \cdot sV \cdot sP - d \cdot sP$

for the derivatives. Extra columns with additional information, such as the references for the parameter values, can be added, of course, until all relevant information is stored in the tables. We thus reach a full documentation of the model in a set of linked tables; i.e., in a database.

To create an instance of the model for a certain framework, the information in the database is translated and augmented to meet the specification of running it in the chosen framework. For instance, the following code would provide a running version of the above model in MATLAB (Fig. 1):

```
Box 1: Implementation of the Lotka-Volterra equations in MATLAB

function LotkaVolterra_ode45

% set initial values
sV_0 = 10;
sP_0 = 10;

% integrate the model
options = odeset('RelTol', 0.0001, 'NonNegative', [1 2]);
[t, x] = ode45(@LotkaVolterra, [0 20], [sV_0 sP_0], options);

% show the results
plot(t, x);
legend('sV', 'sP');

****************

% define the model
function dx = LotkaVolterra(t, x)

% set parameters
r = 1;
a = 0.05;
e = 0.4;
d = 0.5;

% copy x to states
sV = x(1);
sP = x(2);

% calculate derivatives
dV = r * sV - a * sV * sP;
dP = a * e * sV * sP - d * sP;

% copy derivatives to x
dx(1, 1) = dV;
dx(2, 1) = dP;
```

To run it in Mathematica, one would need a script like this:

```
Box 2: Implementation of the Lotka-Volterra equations in Mathematica

(* define the model *)
ode = {
  sV'[t] == r sV[t] - a sV[t] sP[t],
  sP'[t] == a e sV[t] sP[t] - d sP[t]
};

(* set parameters *)
par = {r -> 1, a -> 0.05, e -> 0.4, d -> 0.5};
```

```
(* set initial values *)
ic = {sV[0] == 10, sP[0] == 10};

(* set run time *)
t0 = 0; t1 = 20;

(* integrate the model *)
eqns = ode~Join~ic;
sol = NDSolve[eqns /. par, {sV[t], sP[t]}, {t, t0, t1}];

(* show the results *)
Plot[{sV[t], sP[t]} /. sol, {t, t0, t1}]
```

While for R, one would need a script like this:

```
Box 3: Implementation of the Lotka-Volterra equations in R

# define the model
LotkaVolterra <- function(times, states, parameters){
  with(as.list(c(states,parameters)), {
    dV <- r * sV - a * sV * sP
    dP <- a * e * sV * sP - d * sP
    list(c(dV, dP))
  }
)}

# set parameters
parameters <- c(r = 1, a = 0.05, e = 0.4, d = 0.5)

# set initial values
states <- c(sV = 10, sP = 10)

# set run time
times <- seq(from = 0, to = 20)

# integrate the model
library("deSolve")
results <- ode(states, times, LotkaVolterra, parameters, method="ode45")

# show the results
plot(results)
```

Note that each of these implementations needs information that controls the simulation such as the integration method and time step (t-int) and the time interval over with the model is run (t-end). This essential information is specified in an additional table in the database:

Table 4: information controlling the simulation

model	*integration method*	*t-int*	*t-end*
LotkaVolterra	ode45	0.1	20

Additionally, tables can be included that hold input time series data for forcing functions, or data for calibration or validation. Simultaneously with the translation of the model code, the data are translated to the format set by the different frameworks.

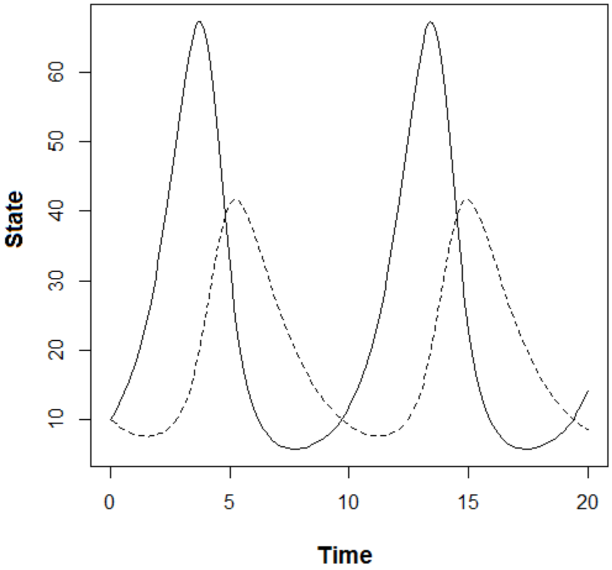

Figure 1 Typical model output for the Lotka-Volterra example presented in Boxes 1-3. The solid line shows the dynamics of prey density V, the dashed line the dynamics of predator density P.

To apply the approach, we implemented the Tables 1-4 in a Microsoft Excel Workbook as Worksheets (see Appendix A). We would like to stress that any program that can hold tables could be used. We chose Excel because it is widely available, and most people are familiar with it. Microsoft Access is an alternative that might provide a more rigid control of the database, but fewer people have experience with it. A freeware alternative would be LibreOffice, which also has the advantage of being easily portable to Mac, Linux and Windows.

Using Excel Macros and Visual Basic for Applications (VBA), we wrote translators that turn the information provided in Tables 1-4 into the working scripts provided in Boxes 1-3 (the code of the translators can be found in Appendix B and the code they produce in Appendices C1-3). Again, these translators can be written in any language that easily handles tables, records, and text strings such as R, Python or PERL. We chose VBA because it is embedded in Excel. The validity of these translators can be checked by comparing the results of benchmark runs against each other. These not only show the (dis)similarity in model outcomes, but also give an indication of the performance of the model under study in each framework. Thereafter, the model can be analyzed with the tools provided by each framework (e.g. the “paranal” function for sensitivity analysis in GRIND for MATLAB). DATM therefore provides easy access to existing tools of analysis in various frameworks, without providing these tools itself.

We have applied the methodology described above to implement the ecosystem models for shallow lakes PCLake (Janse et al., 2010, 2008) and for shallow linear waters PCDitch (Janse and Van Puijenbroek, 1998; Van Liere et al., 2006) in the frameworks OSIRIS, ACSL, GRIND for MATLAB, R, DUFLOW and DELWAQ. PCLake and PCDitch are integrated ecological models to study the main nutrient and food web dynamics of shallow lakes and ditches in response to eutrophication and associated restoration measures (See Mooij et al., 2010 for a comparison with other water quality models). Both models are frequently used in both water quality management and for scientific investigations. For brevity, we will only refer to PCLake in the results, since its implementation is technically equivalent to that of PCDitch.

Results

PCLake is about two orders of magnitude more complex than the Lotka-Volterra model. It has 104 state variables and approximately 400 parameters. Instead of calculating the right hand sides of the differential equations directly, it uses near 1500 intermediate variables to calculate components that are used in the 104 differential equations. PCLake also includes a set of equations that are calculated before running the simulation to make sure that the initial values of the states obey certain basic biological rules (e.g. stoichiometric constraints) when initial values are provided only for dry-weight values but not for N and P. These equations also set the initial composition of the sediment. The PCLake database therefore consists of five instead of four tables: 1) Simulation information, 2) States, 3) Parameters, 4) Initial equations, 5) Dynamic equations (calculation of auxiliaries and derivatives). The last table could have been split into two tables but with experience we find that we get a better model-overview when auxiliaries and the derivatives are in a single table. We refer to Appendix D for the definition of each table of the PCLake implementation in DATM and for a comparison with the Lotka-Volterra example.

Tables 1-4 show the minimal record structure for each table in the Lotka-Volterra example. For PCLake in DATM, we added a column to each table to number the identifiers, and a column to provide additional information per identifier. The table approach also allows one to enter multiple input vectors for initial values of states and of parameters. By adding variables to the simulation table that specify which input vector is used in a given simulation, one can compare model runs for various initial values and/or parameter sets. This approach can be extended to the column in which the model equations are specified. Different columns then characterize multiple versions of the model in a single table. The version of the equations to be used can then be specified in the simulation table. This allows for a straightforward comparison of runs for different model equations and even for different model structures where, for example, certain state variables and associated fluxes are added or switched off. DATM thus facilitates sensitivity analyses on both parameters and model structure.

The Lotka-Volterra example only contains the addition (+), multiplication (*) and equality (=) mathematical operators, but more complex models can include power (e.g. ^), relational operators (e.g. >) and logical operators (e.g. AND), as well as conditional statements (e.g. IF-THEN-ELSE). Operators and statements have distinct implementations in the dominant multi-purpose computer languages such as C++ and FORTRAN. The difference is usually in the syntax (e.g. '&&' in C++ is '.and.' in FORTRAN), though sometimes operators do not have their equivalent in all languages (e.g. the power-operator is missing in C++). Furthermore, some frameworks have their own computer languages, such as DUFLOW, where modules are written in the language DUPROL. Table 5 contains a complete list of translations used in PCLake and PCDitch.

All operators except '=', '+' and '*' and all standard mathematical functions are given a unique text-based identifier in the database. These unique identifiers of operators and functions are then translated into an automated search-and-replace operation. For this reason, a correct translation into any specific language can only be guaranteed if operators cannot be confused with parts of names of other identifiers. In the same way, the names of identifiers, state variables, parameters or intermediate variables must be completely unique, i.e. they should not be contained in the name of any other identifier. Each identifier in the database is therefore preceded and followed by a unique symbol. We propose to use the underscore, since it has no specific meaning in mathematics and enhances the readability of the equations.

Table 5: translations of conditional statements, logical operators and mathematical functions from the database to each of the six modelling platforms.

FRAMEWORK	OSIRIS	GRIND	ACSL	R	DUFLOW	DELWAQ
Language	*C++*	*MATLAB*	*ACSL*	*R*	*DUPROL*	*FORTRAN*
_IF_	(blank)	if	IF	if	if	if
THEN	?	(cr)	THEN (cr)	{ (cr)	{ (cr)	then (cr)
ELSEIF	:	(cr) elseif	(cr) ELSEIF	(cr) } else if	(cr) } else if	(cr) else if (cr)
ELSE	:	(cr) else (cr)	(cr) ELSE (cr)	(cr) } else { (cr)	(cr) } else { (cr)	(cr) else (cr)
ENDIF	(blank)	(cr) end	(cr) ENDIF	(cr) }	(cr) }	endif
_EQ_	==	==	.EQ.	==	==	==
_NE_	!=	~=	.NE.	!=	!=	/=
_GE_	>=	>=	.GE.	>=	>=	>=
_LT_	<	<	.LT.	<	<	<
_GT_	>	>	.GT.	>	>	>
_LE_	<=	<=	.LE.	<=	<=	<=
TRUE	1	true	.TRUE.	1	1	1
FALSE	0	false	.FALSE.	0	0	0
AND	&&	&&	.AND.	&&	&&	.and.
_OR_	||	||	.OR.	||	||	.or.
FLOOR	floor	floor	INT	floor	int	floor
COS	cos	cos	COS	cos	cos	cos
SIN	sin	sin	SIN	sin	sin	sin
TAN	tan	tan	TAN	tan	tan	tan
ACOS	acos	acos	ACOS	acos	acos	acos
ASIN	asin	asin	ASIN	asin	asin	asin
ATAN	atan	atan	ATAN	atan	atan	atan
EXP	Exp	exp	EXP	exp	exp	exp
MIN	Min	min	MIN	min	min	min
MAX	max	max	MAX	max	max	max
_LN_	log	ln	LOG	log	ln	log
POW	pow	(blank)	(blank)	(blank)	(blank)	(blank)
_^_	,	^	**	^	^	**

(blank)=no entry, (cr)=new line

The database format prescribes that all the right hand terms for a given identifier are given on a single line; we therefore used the following style:

left hand term = _IF_ condition 1 _THEN_ right hand term 1 _ELSEIF_ condition 2 _THEN_ right hand term 2 _ELSE_ right hand term 3 _ENDIF_

For C-based languages, this can be easily translated into a conditional expression using the ternary operator “? :”:

left hand term = condition 1 ? right hand term 1 : condition 2 ? right hand term 2 : right hand term 3

or translated into the more traditional “IF-THEN-ELSE” construct:

```
IF condition 1 THEN
    left hand term = right hand term 1
ELSE
    IF condition 2 THEN
        left hand term = right hand term 2
    ELSE
        left hand term = right hand term 3
    ENDIF
ENDIF
```

and variations thereof.

Another small obstacle towards generality is the absence of a power operator in C-based languages. Power functions such a^b are entered in the database with a combination of both styles:

POW (a _^_ b)

which can easily be translated into in C++:

pow(a, b)

or in FORTRAN:

(a ** b)

(note the essential parenthesis).

As demonstrated in the implementations of the Lotka-Volterra model in MATLAB, R and Mathematica, the model code is preceded and followed by certain statements that bridge the code defining the model *sensu stricto* and the framework. What information should be provided – or omitted – depends on the specific framework; some frameworks make use of a graphical user interface that is difficult to circumvent (e.g. DUFLOW). The spatial capabilities of DELWAQ and DUFLOW prescribe that the corresponding simple single cell modules for hydrology and transport available in PCLake should be excluded during translation, as these processes are taken care of by these frameworks. Note that the integration between the ODE process formulations provided by DATM and the PDE process formulations of the framework is taken care of by the framework. To enable integration with an existing water quality model, process modules formulated as ODE’s can be stored in a repository in both DUFLOW and DELWAQ. The DATM translator simply adds another model to these repositories. For spatially-explicit frameworks that lack such build-in facilities for the incorporation of water quality models formulated as ODE's, a more customized integration is necessary, given that any framework should have some formal entry point for these equations. As of yet, however, we do not have experience with such frameworks. Some details about the richer structure of the implementation of PCLake (and PCDitch) in the different frameworks can be found in Appendix E.

After solving the inevitable errors that are reported by the compiler or interpreter, it is essential to check that the newly translated code functions correctly. An effective first step is to calculate the value of each identifier (all parameters, initial states, intermediate variables and derivatives) at t = 0 and compare these values with a control set. This dump output at t=0 is also very useful in studying the main and side effects of changes to the code and is therefore a standard asset of the approach that we advocate.

Secondly, benchmark simulations of varying complexity reveal the proper functioning of conditional statements and forcing functions. This is clearly shown as we overlay time plots from two different frameworks (Fig. 2a, b). Of course, small differences remain because of machine rounding of errors and small differences arising from numerical integration. However, these differences are several orders of magnitude smaller than the ecological range of each state and therefore not visible when we plot the outcome of all frameworks for a given state against each other over this full range (Fig. 3). Such benchmark runs also demonstrate the runtime performance, which can be an important criterion for the choice of a framework. Obviously, one is limited in such runs to a model setup that can be handled by all the frameworks that participate in the test.

One should take into consideration that most platforms support different routines for numerical integration that do not need to be the same and thus influence both the accuracy of the model output and the runtime performance. Moreover, the difference between compiled languages (e.g. C++, FORTRAN) and scripting languages (e.g. R, MATLAB) can be misleading. While scripting languages generally have the advantage of supporting more compact code, powerful libraries, shorter interactive development cycle and interactive graphics and statistics, compiled languages are usually much faster and, in some sense, offer more freedom. For complex models a hybrid implementation is a sensible option, thereby making use of the advantages of both concepts. For example, for the current implementation of PCLake in the R environment, the model equations are not actually translated into R, instead they are solved in C++ (cf. Soetaert et al., 2010). To do so, R compiles the in C++ coded model equations into a .DLL and invokes this .DLL to numerically integrate the model. Note that while both the OSIRIS and the R implementation use C++ code, this is not exactly the same code because each framework has its own exact specification of the function call to the C++ routine with the ecological process formulations of PCLake. So, while the DATM translators for OSIRIS and R have much in common, there are subtle differences to meet the exact requirements of each framework.

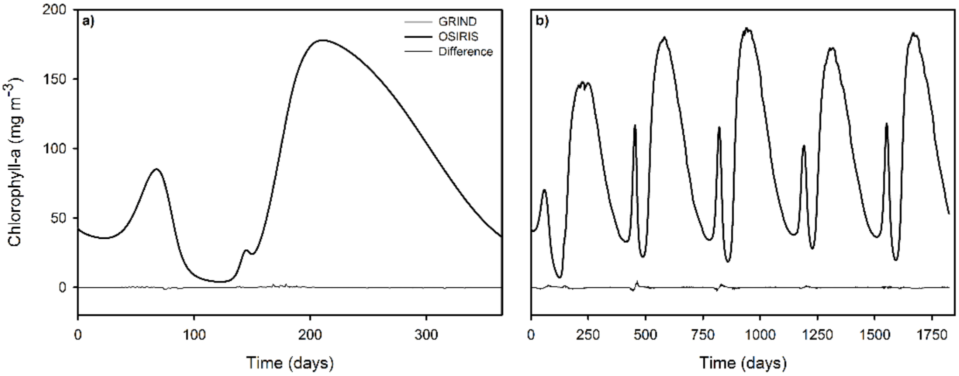

Figure 2 PCLake benchmark simulation output for chlorophyll-a produced by two different frameworks (OSIRIS and GRIND for MATLAB resp.), for a ‘simple’ 1-year simulation (a) and a ‘complex’ multi-year simulation (b) whereby the system is exposed to time series of meteorological forcing, hydrological forcing and transport of matter (e.g. nutrient loading). Also the difference between the simulations is plotted, showing that the output series of the two frameworks are almost identical.

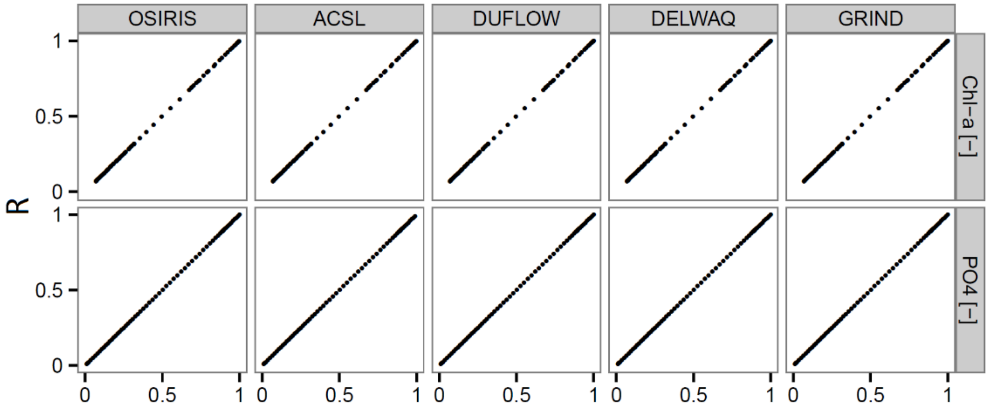

Figure 3 Illustrative example showing the successful translation of PCLake to different frameworks, whereby the output of the R application is compared with the output of OSIRIS ACSL, DUFLOW, DELWAQ and GRIND for MATLAB respectively, with chlorophyll-a and soluble reactive phosphorus in the pelagic as the dependent variable. Please note that both axis are normalized by dividing each value by the maximum value.

Discussion

The DATM approach we here present allows *ecology* to take precedence over *informatics*. We achieve this by formulating the model in the fundamental and universal language of mathematics, and by systematically complementing this mathematical notation with the necessary metadata. The translators create a seamless bridge between the mathematical formulation of the model in the database and the framework-specific implementations.

Experience gained during years of development of PCLake was the main driver behind the development of DATM. PCLake was initially developed in the ACSL framework (Mitchell and Gauthier, 1976), which served as an excellent platform for model development, but where license costs limited the distribution of the model. As this distribution-bottleneck hindered wider use of the model, version 4.08 of PCLake was translated to DUFLOW, a framework that also allows spatial configurations of the model (Jeuken et al., 1999). To further respond to user needs, this version was then translated into DELWAQ and OSIRIS (Mooij et al., 2010). Each translation involved first distinguishing model- from framework-code, and then translating the framework code. Although these translations were semi-automated, each translation represented a big time investment, in which only a few scientists, undaunted by the complexity of the model and specifics of the different frameworks, could effectively carry out the translations and verifications. These efforts monopolized energy away from further model application, analysis and development. The universal mathematical notation we here advocate greatly simplifies the translation process, and makes it much more dynamic and robust at the same time. This allows for direct translation of a new model version in the framework of choice, thereby greatly facilitating the process of model development. Typically, the time needed to develop and test a new translator varies between a few hours for a simple model like the Lotka-Volterra equations to a week for a complex model like PCLake for any given framework.

The erstwhile barriers to framework-switching have led to each framework developing more complex modules to accommodate the growing scope of simulation models. These developments not only make the underlying ecological processes and assumptions more difficult to access, but also require the user to select more options and provide more detail. These developments can in turn reduce the in-depth understanding of the model. Paradoxically, this form of model-framework co-evolution leads to a necessary simplification of a model to make it graspable and useful for ecological theory (Scheffer and Beets, 1994; Van Nes and Scheffer, 2005a), whereas the purpose of adding complexity to the framework ought to be to uncover more complex processes in models.

The diversity of analysis tools available across frameworks can greatly enhance our scientific understanding of any given ecological model. In that sense, the database is used to specify where to go, while the different translators and associated frameworks represent ways to get there. One could take route-planning software as a metaphor: the user gives a final destination whereupon the route-planner proposes alternative routes depending on the type of transport one prefers (i.e. bus, train, car, walking, airplane etc.). To explore the ecological code in detail one should go ‘by foot’ (e.g. using GRIND for MATLAB), while for fast simulation runs an ‘airplane’ would be more convenient (e.g. OSIRIS). Before entering the territory of spatial complexity of the system with frameworks like DUFLOW and DELWAQ, it might be useful to perform an in-depth analysis of the ecological part of the model in a 0D context. Here, we can exploit the potential of DATM to translate a single code to either a set of ODE’s for a general purpose framework of the required ecological component or the PDE’s of a spatially explicit water quality modelling framework. To study the asymptotic behaviour of PCLake, translators for bifurcation programs such as MatCont (Dhooge et al., 2003) and AUTO (Doedel et al., 2007) are planned. For the *most* optimal use of the capabilities offered by the different frameworks, however, proper frameworks-specific user knowledge will always be a prerequisite. For the more simple analysis that are provided by most frameworks, however, DATM allows one to stick to the framework one is familiar with and is not forced to learn a new framework.

Experience teaches that DATM also facilitates model simplification by making use of the very existence of a database: providing a clear overview of all model equations and the possibility to label them (e.g. code for spatial dimensioning, hydrology, integration, or user-interface). By means of queries, groups of model equations can easily be identified, grouped and then switched off or simplified. Because columns can be easily duplicated, one can specify multiple versions of the model concurrently in a single table, and then specify which version of the equations is used in a specific simulation. For example, one can easily compare how different types of functional response functions affect model outcome. By "experiments in model structure", DATM is a relatively straightforward tool for assessing model structural uncertainty in addition to input and parameter uncertainty, which is seldom examined (Mooij et al., 2010). DATM thus also potentially allows for model structure optimization, whereby different model structures can be rapidly assessed as part of an optimization process and the most optimal structure is selected (Recknagel et al., 2008). Completing the columns with the necessary meta-information has the additional advantage of contributing to ‘good modelling practice’ by improving communication among those working with the model (Scholten et al., 2007).

There is increased need for community-based approaches to ecosystem modelling, in order to bring together the knowledge and expertise of ecologists across fields and methodological approaches (Mooij et al., 2010, Trolle et al., 2012). The DATM approach we present here is ideal for building community based approaches: indeed, using a common language (mathematics) and grammar (DATM + translation platform) makes the cross-pollination of ideas and expertise between frameworks, institutes, disciplines and approaches both easier and more attractive. This is not restricted to the field of aquatic ecosystem modelling, as other scientific disciplines can also benefit from a standardized and easily understandable formulation of processes and equations (Jeltsch et al., 2013), allowing one to explore more complex questions in a multidisciplinary setting, and enhancing the interaction with environmental management (Scholten et al., 2007). Additionally, the structure provided allows for easy reuse of pieces of code and processes, thereby preventing ‘reinventions of the wheel’ (Mooij et al., 2010). To further promote model development, we strongly encourage

DATM initiatives to be released under the GNU General Public License (http://www.gnu.org/licenses/gpl-3.0.txt), or the GNU Lesser General Public License (http://www.gnu.org/licenses/lgpl-3.0.txt) so that open sharing of common versions of models is guaranteed.

Emphasis on the model rather than on the framework has an added educational value: teachers can focus on the ecological principles of interest and students can rely on their existing mathematical knowledge to access these principles instead of being first subjected to an often superficial crash-course in a framework's implementation specifics. Our approach thus also makes the model more directly manipulatable by students, irrespective of their framework experiences, and ensures their understanding of model dynamics is based on the ecological model, rather than confounded by framework options. In fact, the Lotka-Volterra DATM example that we presented here and provide as a digital appendix can be of direct use in an educational context.

It is necessary to store the equations in the correct order in the database. With this we mean that each variable must be assigned a value before it is used in the assignment of another variable (in other words, it must first be used as a left hand term before it is used as a right hand term). Some frameworks such as GRIND for MATLAB and ASCL do this sorting automatically, but others do not have this facility. To stay compliant with the latter frameworks, the statements should be ordered already in the database. Fortunately, most compilers or interpreters do provide the user with warning messages accompanied by helpful information when the sequence is violated. Yet, one of the disadvantages of code generators (and other top-level structures which hide implementation details) is that they can make debugging difficult. This is remedied by an iterative procedure, where the user edits and tests the generated code temporarily and then goes back to the table, which gives just another argument for readable code and proper indentation.

We do not claim that our approach is unique in all respects. For instance, both the ECOBAS (http://www.ecobas.org/ecobas/index.html) and SED-ML (http://sed-ml.org/) initiative aim at creating unity in dynamical modelling. ECOBAS provides an overview of ecological models with their metadata and references to the models themselves. SED-ML provides a unifying language for the implementation of dynamical models. DATM balances between those approaches by providing the actual models, but with a focus on the mathematics of the model instead of the informatics. The idea to implement the complete model in a database resembles the design concept of the modelling framework SMART (Kramer and Scholten, 2001). The current version of SMART, however, does not allow translating and exporting models to other frameworks, whereas this is a key-feature of DATM. Automated code translators are already in use at the level of individual frameworks (e.g. SMILE, Muetzelfeldt and Massheder, 2003), although mostly for simpler models. Moreover, there are important advances in establishing a community-based framework for aquatic ecosystem models aiming at unity at the framework level, i.e. the Framework for Aquatic Biogeochemical Models (FABM) (Trolle et al., 2012). A number of the advantages mentioned here are also covered by FABM, such as easy inclusion of new variables and equations, and automatically incorporating different physical assumptions in 0D-3D. DATM complements such efforts - i.e., DATM may also translate models into the FABM framework - thereby providing unique abilities to address some of the challenges and opportunities that remain in the field of aquatic ecosystem modelling (Mooij et al., 2010).

At the onset of this project, our humble aim was to maintain long-term availability and use of PCLake and PCDitch. Happily, this work produced a remarkable and unexpected spin-off: with DATM we have acquired the ability to interactively use multiple frameworks in a single study and even within a single analysis. This dynamic shift in framework use, and more importantly in ecological simulation model analyses, will likely represent a cornerstone in the further development of ecological modelling. As illustrated with the Lotka-Volterra model and the use of Excel and VBA, the ingredients need not be exotic for the pudding to be tasty.

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Supplementary Information

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http://www.sciencedirect.com/science/article/pii/S136481521400108X

Chapter 3

The weak link between ecosystem models and real ecosystems: Reflections on the consequences for model calibration and improvement

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Abstract

Ecosystem models aiming to describe higher level variables such as total phosphorus and water transparency will always remain a crude simplification of reality regardless of the detail that is included. This weak link between model and reality implies that it will be impossible to accurately parameterize each of the model components on basis of empirical data. A calibration at an aggregated level will allow to get the individual components of the model aligned such that the model as a whole is adequately describing the dynamics of the lake at the ecosystem level. As such, any dynamics observed in the field which is not explicitly part of the model may still leave an impact on the model during calibration by modifying the functionality of the components that are included. This occurs if the included parameter or component is in fact a lumped parameter combining several processes. These missing dynamics are then thus still covered by the model, albeit indirectly. An important consequence is that once calibration has been performed, any model 'improvement' in the form of adding more components explicitly may bring the model 'out of balance' as it may lead to double counting with the implicit components. Without recalibration such an intended improvement would be an impairment instead. We exemplify this line of reasoning with the integrated ecosystem model PCLake, which we expanded with a filter feeding benthos group. These species are always present in the ecosystems PCLake simulates, but were until yet not dealt with explicitly in the model itself but implicitly included in the lumped parameters describing grazing on phytoplankton.

Introduction

Dynamical models have long been recognized as useful tools for ecosystem managers to elucidate ecosystem complexity and perform simulation experiments to predict the effects of measures (e.g. Evans 2012). By definition, all ecological models are drastic simplifications of reality, and designing a model that is both realistic and useful is a challenging task. There is no general agreement among ecologists about what an ecosystem model should look like, as modellers have to find a balance between the aim of the study, the available knowledge, the available data, the theory on which the model is based on and their personal preferences (Janssen et al., 2015; Mooij et al., 2010). As a result, many different coexisting modelling paradigms have developed (for examples see Otto and Day 2007). These paradigms range from strategic mini-models based on a few differential equations (e.g. Scheffer et al. 2001) to elaborate systems of differential equations describing the main functional groups and abiotic components of an ecosystem (e.g. Janse et al. 2008; Janse et al. 2010). Another important distinction is between unstructured models where biota are described in a single quantity, often carbon, and structured models that take for each component the age or stage structure (e.g. matrix population models, Caswell 2001), size structure (e.g. physiologically structured population models, Roos and Persson 2001), nutrient storage (e.g. Droop 1974), energy storage (e.g. dynamic energy budgets, Nisbet et al. 2000), stoichiometry (e.g. Sterner and Elser 2002) or trait distributions (e.g. Litchman and Klausmeier 2008) into account. While models that focus on a single structural aspect can be developed as extensions of unstructured models using matrix and partial differential notations, models that look at more than one structural aspect are better implemented as agent-based models (DeAngelis and Mooij, 2005). Out of this wealth of approaches, we discriminate two different philosophies on how models are rooted in reality. One focuses primarily on individual characteristics and works toward the ecosystem level, while the other focusses on the ecosystem level and works down to individual characteristics.

The individual-based philosophy embraces a reductionist view that the behaviour of an ecological system can be understood as the sum of its constituent parts, that is, from rules governing the behaviour of elements at lower hierarchical levels (Anderson, 2005). The point of departure is that if all essential elements are identified, analysed and properly described as mathematical equations with values based on ‘first principles’, the correct dynamics at the higher level will emerge naturally once the elements are assembled (Grimm and Berger, 2016). Or as sometimes stated by proponents of this view: “The rest is bookkeeping”. Hence, during model development there is much emphasis on structural realism and getting the components right. Parameters values are estimated by fitting equations to data from the field, from experimental data, or derived from the literature. Many commonly used process-based ecosystem models, such as the lake models DYRESM-CAEDYM (Hipsey et al., 2007) and SALMO-OO (Recknagel et al., 2008), have a flexible structure, and come with a process-library from which an instance of the model can be assembled. Note that these lake models have a strong physical and chemical focus and hence are largely based on fundamental laws of these respective fields - the first principles - so that process rates can be determined empirically with great precision. However, especially for the ecological components it is difficult to obtain proper values for all parameters, in which case parameters of lower level functions may be calibrated so that higher level outputs better match field observations. According to the individual-based philosophy, calibration should be kept to a minimum, as information about the individual characteristics may get lost or distorted during the calibration process and problems with model structure may be masked (e.g. Anderson 2005; Mitra et al. 2007; Anderson and Mitra 2010). To safeguard tractability and reduce propagation error, several modelling approaches, such as physiologically structured population models (PSPMs) and dynamic energy budget (DEB) models, focus on certain parts of the ecosystem, instead of providing a full representation of all relevant features (Nisbet et al., 2000; Roos and Persson, 2001). This allows them to being so closely linked to fundamental physiological principles that they do not need to be calibrated. While being hailed for their contribution to scientific understanding, an apparent downside is that these models generally do not address higher level variables such as water transparency, chlorophyll-a or total ecosystem productivity, while predictions for exactly these variables are of crucial importance to ecosystem managers.

Alternatively, we identify a more pragmatic view which is focussed on the ecosystem level, i.e. the higher level variables. Also here the wish exists to include the essential processes and causalities, but in this view it is acknowledged more explicitly that the apparent complexity of nature makes a one-to-one relation between model and reality practically impossible, particularly for aggregated variables. Moreover, it is acknowledged that model development is path-dependent, as choices made in one step constrain the choices that are available in the subsequent steps of development (Grimm and Berger, 2015). From this perspective, there is no *a priori* reason to assume that the assembly of individual characteristics will automatically result in a proper description of the higher level dynamics. However, premised on the need of ecosystem managers to have operational models that describe exactly these higher level dynamics, a solution is found in model calibration at the ecosystem level (Janssen and Heuberger, 1995; Rastetter et al., 1992). The information present in field observations and the uncertainty in the *a priori* parameter distributions are used to align the individual components in such a way that the model as a whole does an adequate job describing and predicting the dynamics at the ecosystem level. Hence, the idea is that the *a posteriori* parameter values contain not only information on what is empirically known about a given model component, but also how this component should behave in concert with the other model components so as to produce the correct higher level output. The premise of non-uniqueness of parameter values is also reflected in the Bayesian view on modelling, which assumes a natural variability of parameters and makes use of this to estimate the uncertainty in model output. In Bayesian parameter estimation, *a posteriori* parameter ranges are based on *a priori* parameter ranges (from previous knowledge) and weighted by the degree of concordance of model outputs with observations (e.g. Reckhow and Chapra 1983; Hilborn and Mangel 1997; Reichert and Omlin 1997; Omlin and Reichert 1999). The distinction between *a priori* and *a posteriori* parameter values acknowledges that the meaning of a parameter also depends on the model context, e.g. because parameters can be different in different environments, or because a parameter is in fact a ‘lumped’ parameter combining different processes. One could state provocatively that during calibration “one makes the components slightly wrong to make the whole right”. Calibrated ecosystem models have been criticized for being ‘overparameterized’ (Brun et al., 2001), suffering from ‘non-uniqueness’ (Reichert and Omlin, 1997) and for having ‘dysfunctional components’ (Anderson and Mitra, 2010). At the same time these calibrated ecosystem models often have great value in an applied management context (e.g. Janse, 2005). Once there is confidence that the model is capable of describing the right dynamics at the ecosystem level, experiments such as robustness analysis can be used to understand how the individual components act together and explain the dynamics (Grimm and Berger, 2015). This approach is thus exactly opposite to the more individual-based bottom-up approach as described above.

While we see the tension between those two modelling philosophies as a healthy stimulus for the development of the field of predictive ecology, we also observe that it leads to insidious misunderstanding, particularly since ecological models are increasingly being shared, reused, coupled to other models and developed by grass-root initiatives (Robson, 2014; Trolle et al., 2012). Nowadays it can easily occur that a modeller adhering to the first philosophy adopts an existing model that has been developed following the second philosophy. This entails the risk of the modeller trying to improve the original model by introducing missing functionalities without properly acknowledging the far-reaching consequences of a previous calibration, assuming that the validity of the model can be enhanced directly. A second risk emerges when the model is blindly coupled to other models, or when the model is disassembled into separate modules to be included in process-libraries and used in other models (e.g. Hu et al. 2016). In a recent study Beecham et al. (2016) coupled an established food web model (Ecopath), which is originally based on assumptions of mass balances in equilibrium, to a spatial and temporal explicit ocean model (GOTM-ERSEM). The authors concluded that before the coupled model was able to produce useful outputs some fundamental changes had to be made to the ecological formulations. We here thus stress that risk of misinterpretation, when the integrity of a calibrated model and the coherence of its components are not properly acknowledged. Although this all may sound trivial for some, we wonder whether all modellers who start working with an existing model take the time to examine the caveats for its operation, or to acquaint themselves with the original philosophy underlying its development. A fortiori, the review of Arhonditis and Brett (2004) revealed that even basic guidelines for ‘good modelling practice’, including performing a decent sensitivity and uncertainty analysis, are not followed in many modelling studies.

The aim of this paper is to exemplify what happens when a new individual level component is added to an established ecosystem model. We focus on a specific model for shallow lakes named PCLake (Janse et al., 2010, 2008). This model was developed to evaluate the impact of eutrophication on water transparency and chlorophyll-a concentration under various management scenarios and calibrated against a dataset of 43 lakes. In a recent multi-model ensemble study using an independent dataset, PCLake came out as the best model out of a set of three tested aquatic ecosystem models (Trolle et al., 2014). The apparent success of the model has attracted many new users, and since its development in the early eighties of the past century, the model has been applied in a much wider context than the eutrophication studies for which the model was originally developed and calibrated. These applications include studies on climate change (Mooij et al., 2007; Nielsen et al., 2014), the impact of marsh zones (Sollie et al. 2008), water level fluctuations (Kong et al., 2016) and the impact of allochthonous carbon inputs to lakes (Lischke et al., 2014). Moreover, the model was used in studies that zoom in on a specific component of or process in the ecosystem, such the effect of herbivory (Van Altena et al., 2016). When confronted with the model, experts in each of these fields of research rightfully question the way specific components or processes are implemented in the model. For instance the outcomes of the model for climate change studies will critically dependent on the way temperature dependencies of various biological processes are implemented in the model (Mooij et al., 2009). These dependencies might have received less attention during the original model development because they played a smaller role in eutrophication studies. Moreover, these experts note omissions in the model components, in particular within their particular field of interest. This often results in a request to change or expand the model so that it more rightfully captures our contemporary view on the structure and functioning of aquatic ecosystems.

A good example is the request to explicitly include filter-feeding tube dwelling zoobenthos (chironomids) in the model as part of a larger study on the importance of these organisms for the functioning of aquatic ecosystems (Hölker et al., 2015). Chironomids are not explicitly modelled in the standard version of PClake as not much information about this species group was available during its initial development. When entered in the model as a new group, comparison of the ‘improved’ model with output of the original model shows that chironomids have a huge impact on ecosystem functioning. From a mechanistic point of view this is logical: if one adds a turbo (the additional filtering capacity of chironomids) to a diesel engine, its power (its capacity to keep the water transparent) will increase considerably. However, for a calibrated ecosystem model, there is an important caveat in the reasoning here. Although their importance was not understood at that time, it is safe to assume that chironomids were commonly present in the lakes that have been used for calibration of PCLake. We postulate that during calibration the impact of chironomids was entered in the components which were present in the original model, for instance in zooplankton functionalities. In other words, after calibration the zooplankton grazing rate became a ‘lumped parameter’ that also implicitly included the filtering capacity of chironomids (and hence the earlier statement that during calibration components are distorted to make the whole right). This means that before the higher level outputs of PCLake are improved by introducing chironomids, we first need to nullify the implicit modelling of chironomids by the zooplankton module during a re-calibration of the model. This notion strongly opposes the individual-based view on ecological modelling that assumes that components can be left unchanged in future model versions, or even ported to other models, once they are properly established.

To exemplify the above reasoning, we redo the calibration procedure for PCLake without and with chironomids and show how the zooplankton grazing rate in PCLake should be changed in response to the inclusion of chironomids in the model as presented by Holker et al., (2015). Moreover, we check whether calibrating only the zooplankton grazing rate is sufficient to make the addition of chironomids to the model an improvement to the overall fit of the model.

Methods

Model description

PCLake is essentially a large set of coupled ordinary differential equations describing both the water column and the sediment top-layer (10 cm) of a temperate shallow lake, including the most important biotic and abiotic components (Fig. 1). The primary producers are represented by submerged macrophytes and three species of phytoplankton. The food web is completed by zooplankton, detritivorous macrozoobenthos, zooplanktivorous fish, benthivorous fish and piscivorous fish. Abiotic components include detritus, inorganic material, dissolved phosphorus, ammonium and nitrate. All organic groups are modelled as dry-weight, nitrogen and phosphorus. Besides 60 differential equations, the model consists of >1000 auxiliary equations, of which quite a few are used to compile additional output, such as ‘Secchi depth’ and ‘chlorophyll-a’. Furthermore, the model comprises >300 parameters, which can be classified into input factors, process parameters, physical constants and conversion factors. The most important inputs to the model are fetch, water inflow, nitrogen and phosphorus loading and the sediment characteristics including the loading history. Optionally, a wetland module can be included, consisting of 42 state variables and an additional 35 parameters. A full description of PCLake is presented in Janse (2005).

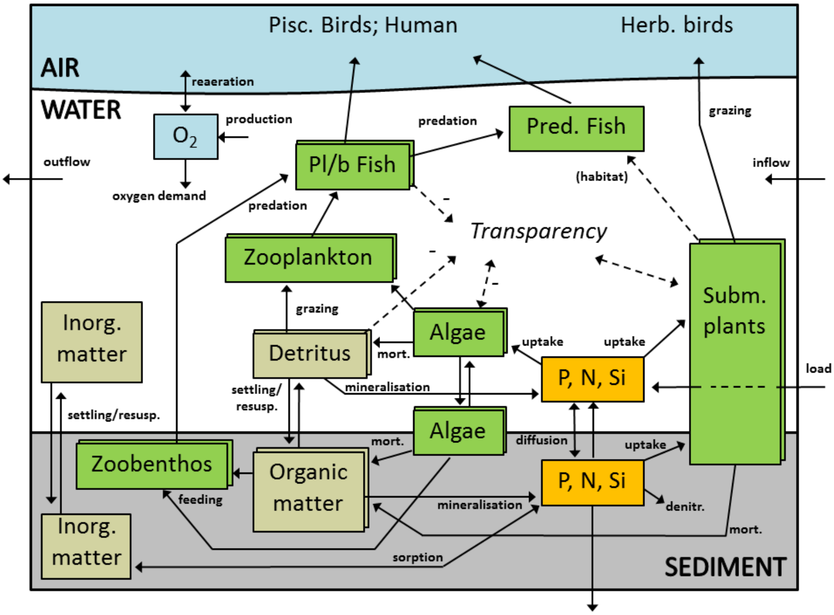

Figure 1 A graphical overview of the model structure of PCLake (modified after Janse 1997). Boxes depict (lumped) state variables and the arrows depict interactions. Chironomids are not included in the default version of the model. For a full description of PCLake see Janse (2005).

Development and calibration of PCLake

PCLake is originally the product of large multidisciplinary research program on the eutrophication and restoration of the Loosdrecht Lakes in the Netherlands (Janse and Aldenberg, 1990; Janse et al., 1992). This WQL project ran from 1979 to 1990 and resulted in the publication of more than 130 scientific papers (Van Liere, 1992). It was unique in terms of its size, duration and integrated nature: it included lab experiments, monitoring of physical, chemical and biological variables and processes, both in situ and by remote sensing, and ecosystem modelling (Van Liere et al., 1992). The model predicted correctly that the proposed reduction of the external nutrient loading would not prevent phytoplankton blooms from occurring, and pointed to some likely mechanisms underlying this failure (Van Liere and Janse, 1992). Rising interest in the occurrence of alternative equilibria in shallow lakes triggered an extension of the model with macrophytes and predatory fish to cover both the current turbid state and the desired vegetated clear water state. Indeed, PCLake proved to be able to predict critical regime shifts between a clear and turbid state in response to changing nutrient loading (Janse, 1997). The scope of PCLake was extended to an analysis of the critical nutrient loading and the factors influencing a regime shift. In this context, simulations were performed on the effects of biomanipulation (Janse and van Liere, 1995) and the influence of marsh zones (Janse et al., 2001). To make the model fit for this purpose, a multi-lake calibration exercise was carried out following the Bayesian approach of parameter estimation and uncertainty analysis (Janse et al., 2010). The aim was to obtain a best overall fit for the whole set of lakes, rather than achieving an optimal fit for one specific lake at the expense of others, making the model suitable for generalized studies on temperate shallow lakes (Janse 2005).

This Bayesian exercise was based on 43 lakes for which both input factors and observations were known. Each lake was defined as a certain combination of input factors, including depth, fetch, marsh area, water inflow, infiltration or seepage, sediment characteristics, external nutrient loading, inflow concentrations of inorganic suspended matter and the intensity of fishery. Furthermore, for each lake there was a set of data available that could be compared with the main output variables of the model, that is, higher level variables that typically have the attention of ecosystem managers. These were chlorophyll-a, transparency (Secchi depth), vegetation coverage and the concentrations of N and P in the water column. Simulations with PClake were carried out for these lakes for a grid-based sample of 7 varying parameters that were both uncertain and most sensitive according to the previously performed sensitivity analysis, while 4 other parameters were coupled to these parameters with a proportional relationship. The maximum filtering rate of zooplankton (referred to as cFiltMaxZoo in PCLake) was one of the selected parameters (see for more details Janse et al. 2010). To keep computational time reasonable, no other parameters were varied and each of the 7 parameters could take 3 different values from an *a priori* uncertainty distribution, resulting in 2187 unique combinations and hence 94041 different simulations. The fit of each run was assessed by comparison of the model output with the observations. The residuals were based on the natural logarithms of the measured and simulated values after adding a ‘minimum significant difference’ (ε). The residuals were squared to obtain the fit function $Phi_{i,j}$ for every parameter combination i and every dependent variable j.

$$Phi_{i,j} = [LOG(y_{j,\,meas} + \varepsilon_j) - LOG(y_{j,\,sim} + \varepsilon_j)]^2$$

This implies that each variable is given a comparable weight as the large differences in ranges (e.g. chlorophyll-a in mg m^{-3}, P-total in mg P l^{-1}, vegetation coverage in %) are corrected for. The value of $Phi_{i,j}$ is 0 when the fit of a variable is perfect and when the fit worsens the value of $Phi_{i,j}$ increases. The Phi’s for all variables and lakes were combined (summed over variables and averaged over lakes) to give each parameter combination a measure of the ‘overall’ fit for all the available data (Phi_{total}). The best run, that is, the parameter combination which produced the lowest Phi_{total}, was selected, and the corresponding parameter values used as a default set to describe an ‘average’ shallow lake in the temperate zone. The total set of runs with their ‘weights’ was used to estimate the uncertainty range around the optimal. A full description of the sensitivity analysis, calibration and uncertainty analysis of PCLake is presented by Janse et al. (2010).

Description of the Chironomid module

In the original PCLake model filter-feeding benthic invertebrates such as chironomids are not included as a functional group. A recent study by Holker et al., (2015) reviewed much of the existing evidence available on the functional role of chironomids in the aquatic environment. Although many details are still unknown, the authors come to the conclusion that chironomids are important ecosystem engineers that alter multiple ecosystem functions, and acknowledge that limnologists have long overlooked their importance. To emphasize their message, the authors extended the PCLake model with a chironomid module. The aim of this model exercise was not to provide a precise description of chironomid dynamics, nor was it the explicit aim to improve the validity of the model. Rather the exercise was meant as a preliminary attempt to estimate the importance of chironomids at the ecosystem level. Hence, the module was not calibrated and validated with field data. The growth equations were broadly adapted from the existing zooplankton and zoobenthos modules in PCLake. The chironomids filter-feed on phytoplankton and detritus in the pelagic and are assumed to have a higher nutrient to biomass ratio compared to their food, striving to maintain an 'optimal' nutrient to biomass ratio by assimilating nutrients with a greater efficiency than carbon. The nutrient assimilation efficiencies are made dependent on the (variable) nutrient to dry weight ratios of the food. Also they are able to increase their respiration when the P or N content become too low (extra utilization of carbohydrates), and lower their phosphorus excretion (as P is retained in the body). Their egested matter (detritus and nutrients) is assumed to be retained in the sediment layer, while the excreted nutrients return to the water column. Chironomids are preyed upon by benthivorous fish, with increased resuspension as a result. A more detailed description of the chironomid module and a list of parameter values can be found in Holker et al., (2015).

The optimal filtering rate of zooplankton with and without Chironomids

In this study we analysed the relationship between the filter-feeding capacity of zooplankton and the fit of PCLake to five ecosystem-level variables of 43 lakes, and inspected how this relationship is influenced by the presence of chironomids in the model. To do so, we re-established the methods described by Janse et al. (2010) to calculate the overall model fit $\text{Phi}_{\text{total}}$. Subsequently, we determined the relation between the value of the maximum filtering rate of zooplankton (cFiltMaxZoo) and $\text{Phi}_{\text{total}}$, with and without the inclusion of the chironomid module as presented by Holker et al., (2015). We varied the cFiltMaxZoo from 1.5 to 6 in steps of 0.5 ($\text{l mg}^{-1}\ \text{d}^{-1}$) while keeping all other parameters at their default value, and for each value of cFiltMaxZoo we calculated the $\text{Phi}_{\text{total}}$.

Software

We reprogrammed the calibration procedure in the free software environment 'R' (R Core Team, 2015). To run PCLake in R, we used the Database Approach to Modelling (DATM; Mooij et al., 2014) to generate a C++ version of the model from the database wherein the most up-to-date model equations of PCLake are stored. In R we compiled the C++ code into a .DLL using the GNU C++ compiler in R-tools. This .DLL is then invoked by R for numerical integration, for which we used the deSolve package (Soetaert et al., 2010). Several different integration routines were applied to minimize runtime. First the fastest routine was tried (VODE) and the output checked for failures, e.g. when a run is aborted or produces empty output. If failures occurred the program automatically switched to a more robust, but slower integration routine, in the order of DASPK, Euler 0.003 (day) and Euler 0.002 (day). To enhance the runtime even further we divided the simulation runs over four processor cores, and invoked four additional cores using multithreading.

Results

Analysis of the relation between cFiltMaxZoo and the Phi_{total} for the default version of PCLake, that is, the version without chironomids, reveals that the best fit for all 43 lakes is achieved when cFiltMaxZoo has a value of 3.5 l mg^{-1} day^{-1} (Fig. 2). For a higher or a lower value of cFiltMaxZoo the overall model fit deteriorates. Repeating this analysis after the introduction of the chironomid group shows that shape of the relationship between cFiltMaxZoo and Phi_{totol} is qualitatively quite comparable with that of the original model without chironomids, but that there are two important quantitative differences (Fig. 2). The first is the location of the optimum value of cFiltMaxZoo which is lowered by ~25% to a value of ~2.6 l mg^{-1} day^{-1}. This confirms our expectation that when the chironomids are explicitly modelled, the filtering capacity of zooplankton has to be reduced quite drastically for the model to achieve the new optimum fit. The second is that Phi_{total} is increased, which indicates that the structural improvement of the model by introduction of a functional group that is present in the ecosystem deteriorates the model performance, and that lowering the cFiltMaxZoo is not sufficient to completely compensate for this.

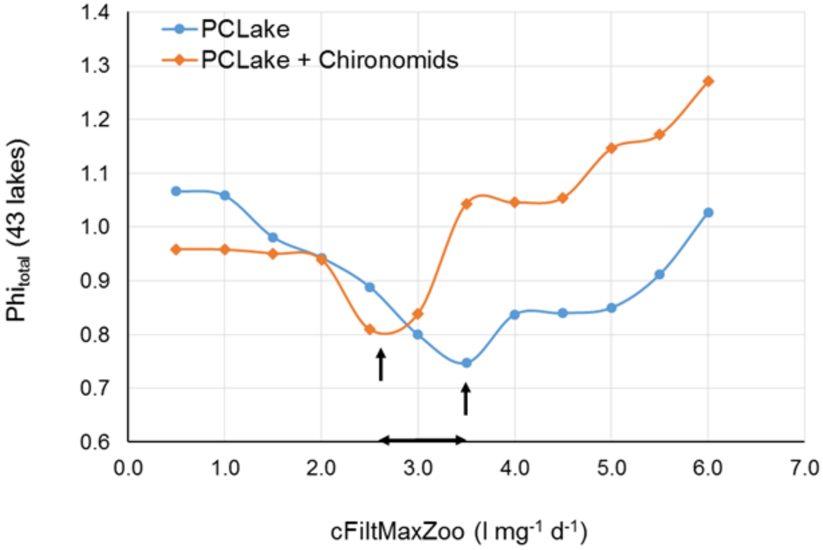

Figure 2 The overall fit (Phi_{total}) for the 43 Lake dataset is plotted for different values of the maximum filtering rate of the zooplankton (cFiltMaxZoo) for the default PCLake version (blue bullets) and the extended model where a chironomid group is added (orange diamonds). This figure shows two important phenomena: (i) inclusion of the chironomid group lowers the optimum filtering rate of zooplankton and (ii) slightly worsens the overall model fit, as the average Phi_{total} increases when chironomids are included.

Discussion

Our results indicate that adding a missing component to a model that has been calibrated previously with the intention of improving the model's predictive capability, will in fact not automatically lead to improvement, and can effectively lead to a loss of predictive power. Instead, first the existing components that have been influenced by a previous calibration should be improved by means of a new calibration before increased predictive power can be achieved. The same holds when an existing but dysfunctional component is replaced by a more realistic component (Anderson and Mitra, 2010). While this main conclusion of our study may sound trivial to those having experience with calibrated ecosystem models, we believe that it is important to make this message explicit for those who are less familiar with these types of models. While the activity of developing and changing dynamical models used to be restricted to a small group of experts that oversaw every aspect of the modelling process, we are now moving to a situation where the modelling community is rapidly expanding and diversifying, while at the same time models are increasingly reused and shared (Trolle et al., 2012). Hence, it is not obvious anymore that this new community of modellers comprehends the limitations of the model they work with (Robson, 2014).

This notion also has implications for the coupling of ecological (sub)models to more physically oriented models. Premised on the need for a multidisciplinary and integrated approach to solve complex environmental problems, there is a rising interest in coupling models from different disciplines. This practice is facilitated by recent technological developments such as the Framework for Aquatic Biogeochemical Modelling (FABM; Bruggeman and Bolding, 2014), the Modular System for Shelves and Coasts (MOSSCO; Nasermoaddeli et al., 2014), the Database Approach to Modelling (DATM; Mooij et al. 2014) and Couplerlib (Beecham et al., 2016). This movement seems to have its roots in the earth-system sciences, which has a longer and successful tradition with coupling different models. It is important to note that the models used in earth sciences (e.g. climate, hydrological and soil-erosion models) are almost exclusively physically or chemically oriented, which means that modellers are 'blessed' with a rich array of first principles to build their models on. Consequently, researchers in these fields are likely to adhere a reductionistic philosophy, comparable with the individual-based philosophy in ecological modelling referred to in the introduction. The confusion arises when the biology kicks in, which is arguably more of a 'grey' science (Smart, 1963), and the different philosophies may get mixed-up. For example, PCLake has recently been re-programmed into a modular structure to establish a coupling with the FABM framework, to facilitate a dynamic link with complex hydrodynamic models (Hu et al., 2016). As a result, with one push of a button, the zooplankton module of PCLake can now be exported and incorporated into other integrated models. Our calibration analysis presented here shows the effect of model calibration on the properties of zooplankton in the model, and highlights the need to take the history of this module into account before it is reused. Technological developments like the ones mentioned above are almost exclusively documented in the literature as success stories, whereby often much emphasis is put on the technological hurdles that have been taken, while relatively little attention is devoted to the ecological limitations and caveats. As such, the impression may arise that henceforward it is possible to compose new models forthwith, and that these are instantaneously suitable for tackling complex environmental issues. We here warn for the potential risks associated with unscrupulous swapping of submodules (Flynn, 2005).

The most straightforward way for modellers to circumvent the above mentioned problems is to acquaint themselves with the philosophy that is underlying a model, and to stick to that philosophy. For the individual-based philosophy, the way forward seems clear yet infinite: continue to improve model components until, one day, accurate predictions at the ecosystems level may be reached (Purves et al 2013). For the ecosystem-oriented approach, the way forward is not less troublesome as practicing the initial philosophy implies that the whole model has to be calibrated each time its structure is updated with a new functionality. While both these paths may seem as hard as the works of Hercules, distinguishing these different philosophies is probably better than mixing them in a hybrid strategy.

It is important to realize, however, that the above reasoning primarily applies to situations where the specific aim is to make quantitative predictions at the ecosystem level that closely match the dynamics observed in the field. Many models are primarily used for exploratory purposes, and in those cases qualitative or relative results will be sufficient to improve our understanding of ecosystem components. In fact, many of the individual-based modelling approaches are not developed to predict higher level outputs, but to explain certain ecological phenomena from first principles. The study of Holker et al., (2015) provides a clear example of an ecosystem-oriented model that is not used for accurate prediction of ecosystem level dynamics, but merely for identifying poorly understood yet crucial processes. Importantly, in such case calibration is not necessary *per se* as long as the results are interpreted as a sensitivity rather than a scenario analysis. A more comprehensive analysis of the impact of chironomids at the ecosystem level could have been to first calibrate the whole model including the chironomids, and thereafter erase the chironomid group again from the new model. In that way the erstwhile implicit modelling of chironomids by the zooplankton module is first nullified during the calibration, after which the removal of chironomids will give a more nuanced picture of how much impact this species had on ecosystem functioning.

The prospect of performing rigorous calibration every time the structure of the model is changed will definitely cause for reluctance among modellers. Indeed, we observed that no major changes to the structure of PCLake have been made since its previous calibration documented in Janse et al., (2010). At the same time we acknowledge that many of the erstwhile technological and practical barriers to calibration have disappeared, or are disappearing rapidly. For example, the computational power of modern day computers makes that runtime performance is becoming less of an issue, while the advent of the free ‘R’ programming environment enables every modeller to use established automated calibration routines. Initiatives like DATM, which allows for easy switching between different software environments, further stimulate the use of the advanced calibration routines by providing easy access to the different options that are available among the different software environments (Van Gerven et al., 2015a). Finally, we see that more data are becoming available at a fast rate, thanks to data sharing initiatives like the Global Biodiversity Information Facility (GBIF; Faith et al., 2013), and legislation, such as the Water Framework Directive (European Union, 2000), forcing ecosystem managers to monitor and report ecological variables.

At the same time it is important to note that calibration is not a holy grail, and it should be exercised with care. A study of Mitra et al., (2007) provides a noteworthy example of a model that is able to reproduce ecosystem level dynamics in a satisfying way, yet merely because one flaw in the model is compensated by another flaw. In the short term the model is therefore able to perform well, even though the erroneous allocation of energy in the food web happening in the background can potentially lead to serious mistakes in the long run. This brings us to the question how much we may distort individual components in order to make the whole model right. As models are ought to be explicit representations of our understanding of the system, we at least should stay within certain bounds of the *a priori* uncertainty distribution for each parameter as advocated by the Bayesian approach (Janse et al., 2010). Moreover, while the behaviour of each submodel may not be as good as it could be, it is arguably important that they should be in agreement with the gross characteristics of the particular component. (Flynn, 2005). To check this, several methods have been developed to scrutinize the behaviour of submodels and to analyse how they act in concert (Grimm and Berger, 2015; Van Nes and Scheffer, 2005a). Such analyses should become integral parts of 'good modelling practice' of ecosystem models. Furthermore, commonly used ecosystem models like PCLake should be accompanied with a tailored calibration protocol, safeguarding the model from becoming dysfunctional during further development and facilitating continued model improvement.

While we here explicitly discriminate between the behaviour of model components and the behaviour of the model as a whole (e.g. measured in chlorophyll-a or transparency), we have to acknowledge that there is still a level that is even higher, that is, the threshold levels of various environmental forcings. One of the attractive aspects of PCLake for scientists and water quality managers alike is that it shows a nonlinear response to changing nutrient inputs and hysteresis, implicating that the model shows alternative stable states. Knowing at which level of environmental forcing an ecosystem will shift from one stable state to a contrasting stable state is crucial for ecosystem managers, as the effectiveness of many management strategies will depend on the state of the system relative to this tipping point, i.e. how resilient the system is to change. This non-linear behaviour of PCLake is an emergent property of the model, and because empirical observations of regime shifts are scarce (and unknown for most of the 43 lakes used to calibrate PCLake), we cannot calibrate a model directly on the location of the tipping points along an axis of environmental forcing (e.g. nutrient loading). Nevertheless, the emergence of the alternative stable states is influenced by the results of the calibration exercise as it is currently performed, albeit indirectly. We assume that the model can reasonably predict the tipping points if it can reasonably reproduce high-level variables in a variety of lakes from both clear and turbid states. As a result, improving the model with e.g. chironomids will influence the exact position where a regime shift occurs, even if the model is properly recalibrated to ecosystem-level parameters.

The question thus arises how we need to deal during model improvement with emergent features we cannot calibrate. The answer will depend on how PCLake is used. If PCLake is used to predict the critical nutrient loading of a specific lake ecosystem, the procedure does not differ from a regular scenario study and good modelling practice (Scholten et al., 2007). First the improved model has to be parameterized for the system under study in order to reproduce the observed behaviour. Subsequently the process of validation is key, using an independent dataset. Preferably this is a dataset which includes a regime shift, although we already acknowledged that in most cases this will not be the case. When validation indicates that the model is sufficiently capable of reproducing the observed dynamics at the ecosystem level, the user may have gained enough confidence in that the model indeed comprises the right processes and feedbacks to predict the critical nutrient loading during scenario analysis, while acknowledging that the prediction will always have a fair amount of uncertainty. For the other main purpose of PCLake, whereby PCLake is used as a virtual reality to scientifically study how regime shifts come about, the focus is generally on qualitative and relative impacts. Hence, the exact quantitative prediction of the location of a regime shift does not really matter that much, and a re-calibrated model will be equally useful for this purpose.

We conclude that although the potential of models in science and for management is enormous, and that complex ecological models take a central position in contemporary science, the weak link between models and ecosystems makes successful development of ecosystem models a delicate affair. The only way forward for the field of ecological modelling is to become even more community-based and open-source (Rose, 2012). In this new setting a wider pool of experts is better able to scrutinize model structure and application, discuss limitations and appropriate use, and educate and support newcomers (Robson, 2014; Trolle et al., 2012). Yet, to make this a successful enterprise we have to acknowledge that different philosophies are underlying ecological models, and that these philosophies are neither right nor wrong, but have profound implications for ecological modelling.

Acknowledgements

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Chapter 4

Food-web stability signals critical transitions in temperate shallow lakes

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Abstract

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

Introduction

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

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

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

Although the conceptual frameworks of food webs and alternative stable states are highly influential in modern ecology, they developed independently and catastrophic regime shifts in ecosystems have seldom been explicitly linked to stability properties of complex trophic networks (Ings et al., 2008). Here we test whether indices for stability as defined by food-web theory can disclose an impending catastrophic shift in ecosystem state. On one hand, we hypothesize that food-web stability and ecosystem stability are inherently linked, considering the key role of food webs in governing the flows of energy through the ecosystem. On the other hand, we ask whether descriptions of food webs contain sufficient information on self-enhancing feedbacks to expose the non-linear behavior of the ecosystem in response to external forcing.

As a model system we use temperate shallow lakes, for which abrupt changes between a submerged macrophyte-dominated state and a phytoplankton-dominated state are empirically well documented (Blindow et al., 1993; Ibelings et al., 2007). In this context shallow lakes are particularly intriguing because many of the feedback loops that keep the system in each stable state involve the abiotic environment and are therefore not considered in a food-web approach to the system (Scheffer et al., 1993).

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

We run the model for a range of nutrient loadings from oligotrophic to hypertrophic conditions and vice versa, to simulate the typical loading history of many shallow lakes in the temperate zone in the second half of the twentieth century (Gulati and Van Donk, 2002). For each loading level, we run the model until the seasonally forced equilibrium is reached, and obtain the average chlorophyll-*a* concentration to characterize the state of the lake ecosystem; chlorophyll-*a* is one of the most common proxies for water quality used by ecosystem managers. Also, we collect food-web data from the ecosystem model to construct material flux descriptions of the aquatic food web at each loading level (Fig. 1) (de Ruiter et al., 1993; Moore and de Ruiter, 2012).

From these food-web properties, we estimate the per capita interaction strengths between the trophic groups, using established methods typically used by food-web ecologists to describe empirical food webs (de Ruiter et al., 1995; Neutel et al., 2007), based on the principles of May (May, 1972) and Lotka-Volterra type equations (de Ruiter et al., 1995; Moore and de Ruiter, 2012). Interaction strengths represent the size of the effects of species on each other's dynamics near equilibrium and define the elements of the (Jacobian) community matrix representation of the food web (May, 1972). Food-web stability is assessed using the diagonal strength metric (s)(Neutel et al., 2002; Van Altena et al., 2014), being the minimum degree of relative intraspecific interaction needed for matrix stability. Thus, for each level of nutrient loading, we obtain a parameterized (Jacobian) community matrix description of the food web embedded in the ecosystem, and evaluate its stability.

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

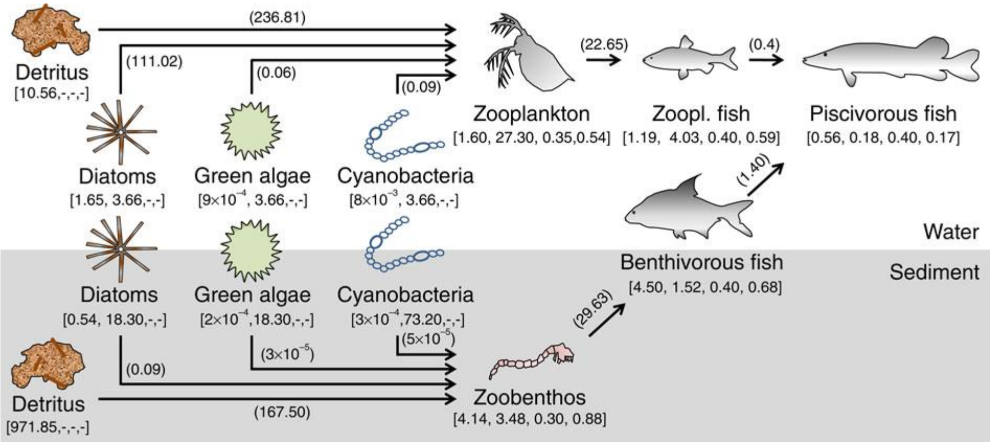

Figure 1 Schematic representation of the aquatic food web and the feeding relations. The food web comprises a pelagic and benthic food chain linked by a shared predator. Data (square brackets) used to calculate feeding rates (parentheses) are given in the sequence biomass (g m^{-2}), specific death rate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

Results

Ecosystem response to nutrient loading.

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

Food-web response to nutrient loading.

We followed the interaction strengths in the trophic web and evaluated food-web stability along the eutrophication axis using diagonal strength as an indicator (see methods). We found that with increasing lake productivity (Fig. 2b, blue line), destabilizing changes in the food web occurred: decreasing food-web stability forebodes the catastrophic shift. This result is not trivial because the ecosystem model and the food-web model differ distinctly in structure and shape of the interactions. At the critical nutrient loading, the food web underwent a drastic reorganization to a phytoplankton-dominated configuration, coinciding with a sudden increase of stability (decrease in diagonal strength, from blue to red line in Fig. 2b). Intriguingly, we found that during re-oligotrophication (Fig. 2b, red line) which is needed for ecosystem recovery, a similar decrease in food-web stability was visible, again followed by a sudden re-establishment of stability once the critical nutrient loading for ecosystem recovery was reached. Thus, depending on the trophic organization of the food web, enrichment and impoverishment can both be destabilizing, even though the topology of the web is the same. From an alternative stable states point of view, this can be explained as clear- and turbid-water states each having a basin of attraction that deteriorates towards a tipping point. Hence, we find food-web stability to be associated with the resilience of the attracting equilibrium.

Identifying stabilizing and destabilizing interactions.

Food-web stability is an aggregated measure with a multitude of underlying processes. We here present an innovative approach to decipher which interactions are primary responsible for the eroding stability during eutrophication and re-oligotrophication. At a given level of nutrient loading, the stability metric s follows directly from the interaction terms in the (Jacobian) community matrix. By varying the strength of each element in the matrix, we calculated the relative sensitivity of s to changes in each specific trophic interaction: $\frac{\partial s}{\partial \alpha_{i,j}}$, where $\alpha_{i,j}$ is the interaction effect of species j on species i. As such, we reveal the intrinsic dynamics of the food web, i.e. how stability is constrained by the architecture of the food web. Besides the sensitivity, the effect of $\alpha_{i,j}$ on s depends on the actual change of $\alpha_{i,j}$ in response to nutrient loading L: $\frac{d\alpha_{i,j}}{dL}$. Note that changes in interaction strength along the nutrient loading axis may be imposed by forces in the ecosystem that are not explicitly considered in the food-web model, such as oxygen dynamics and stoichiometry. Taken together, the following formula can be used to disentangle which and how changing interactions contribute to the weakening of stability (Supplementary Fig. 1):

$$\frac{ds}{dL} \approx \sum_{i}^{n} \sum_{j}^{n} \frac{d\alpha_{i,j}}{dL} \frac{\partial s}{\partial \alpha_{i,j}} \qquad (1)$$

We found that both during eutrophication (Fig. 3a) and re-oligotrophication (Fig. 3b) several interactions in the lake food web increased or decreased in strength in response to changing nutrient loading. The majority of these interactions involved zooplankton, benthic and pelagic phytoplankton species or detritus. Most interactions however were unaffected by changing nutrient loading. When we analysed the sensitivity of food-web stability to changes in specific interaction strengths, we found that food-web stability is sensitive to only a select number of interactions, and that there is just a partial overlap with the interactions that actually changed along the loading axes (Fig. 3c, d). As a result, the observed changes in food-web stability during eutrophication and re-oligotrophication can be attributed to only a handful of interactions, involving detritus, diatoms and zooplankton (Fig. 3e, f). These are interactions of which the strengths change along the eutrophication axis *and* to which food-web stability is sensitive. Most destabilizing were the interaction effects between zooplankton and detritus, the effect of pelagic diatoms on detritus, and the effect of pelagic diatoms on themselves relating to sedimentation (Fig. 3, Supplementary Fig. 2).

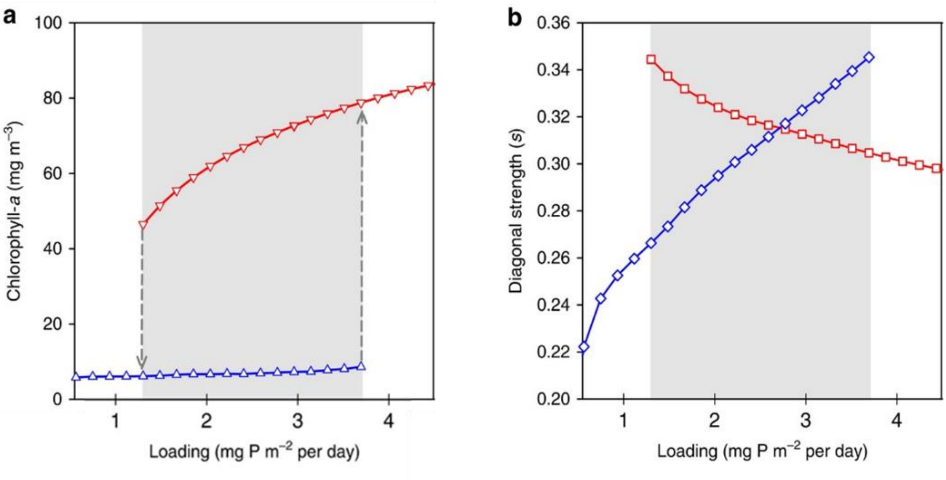

Figure 2 Ecosystem and food-web response to nutrient loading. (**a**) The equilibrium concentration (yearly average) chlorophyll-*a* in the water column, as proxy for the ecosystem state, for two initial states: a clear- (blue upward triangles) and a turbid-water state (red downward triangles). (**b**) Food-web stability, represented by the intraspecific interaction needed for matrix stability (*s*) for food webs in a clear- (blue diamonds) and a turbid-water state (red squares). Stability decreases with increasing *s*.

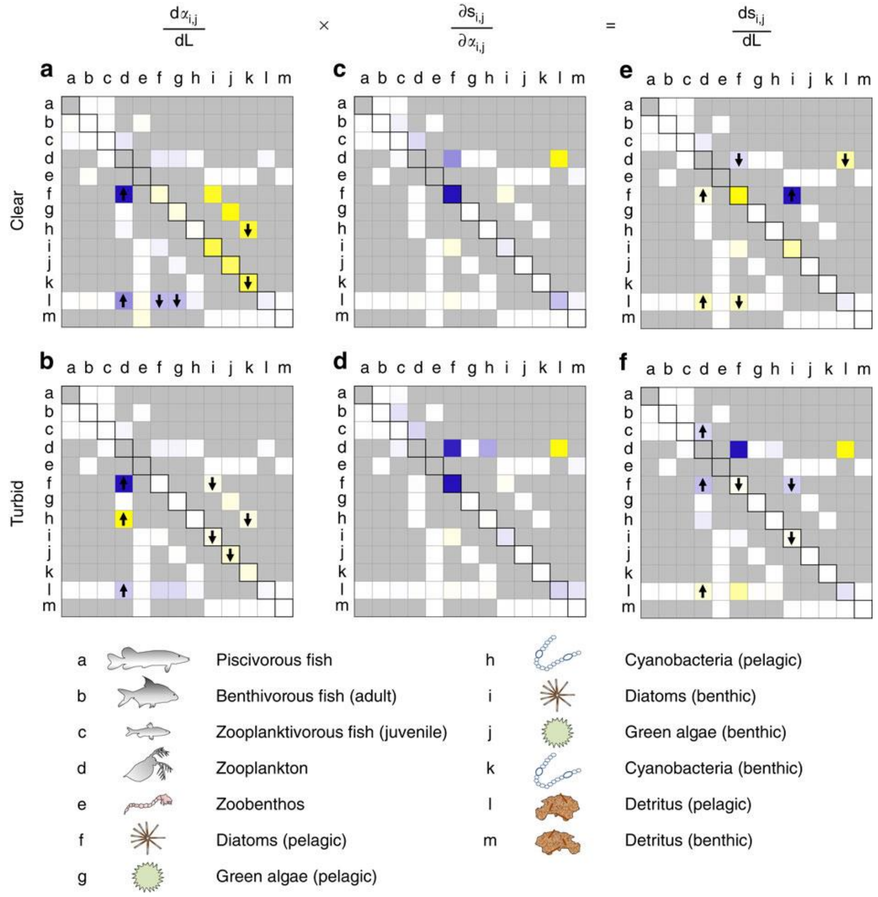

Figure 3 Graphical summarization of the changing trophic interactions and their impact on food-web stability. The left panels show which interaction terms are impacted by changing nutrient loading. Cell colour indicates whether interaction strength increases (blue), decreases (yellow) or does not change (white) during eutrophication (a) and re-oligotrophication (b). Colour intensity depicts the relative magnitude of change. Arrows indicate whether the change is notably progressive (upward) or descending (downward) towards the regime shift. The middle panels (c,d) show the sensitivity of food-web stability to changes in interaction strengths. An increase of interaction strength can have a positive effect (blue cells), negative effect (yellow cells) or no effect (white cells) on stability (and hence an inverse effect on s). The intensity of the colour indicates the relative magnitude of the effect. The right panels show the contribution of each interaction term to the impact of eutrophication (e) and re-oligotrophication (f) on food-web stability, which is the product of the foregoing. Colours indicate whether interactions have a positive (blue), negative (yellow) or no effect (white) on stability (and inversely on s).

We supported these results by calculating the loop weights of all the “trophic interaction loops” in the trophic web along the nutrient loading axis (see methods) (Neutel et al., 2002). We found that, under all conditions, the loop with the highest weight, which is considered the Achilles heel of a trophic network (Neutel et al., 2007), was the omnivorous loop that linked the same three groups: detritus, diatoms and zooplankton (Fig. 4). The maximum loop weight increased towards both regime shifts, from either direction of nutrient loading, and was strongly correlated to the amount of intraspecific interaction needed for matrix stability (Neutel et al., 2002) (Fig. 5).

We analyzed the biomass densities and feeding rates underlying the interactions in the trophic interaction loop that has the maximum weight to disentangle what caused the increase of the loop weight (Fig. 4, Table 1). We observed that, during eutrophication, the feeding rates increased relatively more than the biomass densities. As interaction strengths depend largely on the ratio of feeding rate to population densities (see Methods), this pattern led to an increase in interactions strengths, and hence, in a higher loop weight. Particularly the increase of the interaction effect of detritus on zooplankton, which is the weakest interaction in the loop, contributed to the enhancement of the loop weight (Table 1). The regime shift to the turbid cyanobacteria dominated state resulted in an unfavourable climate for zooplankton as their biomass was reduced. The conditions for zooplankton improved however during re-oligotrophication as we observed increasing feeding rates towards the regime shift. The biomass densities of the trophic groups were only moderately affected by the reduction of nutrient loading, wherefore the interaction strengths increased along this axis. This time the increase in loop weight was dictated by the effect of zooplankton on diatoms, as the feeding on diatoms increased more than the feeding on detritus (Table 1).

Table 1 | Building blocks of the heaviest loop at different nutrient loadings.

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

The loop weight is calculated from the interaction strengths: $w = |\alpha_{f,d} \cdot \alpha_{l,f} \cdot \alpha_{d,l}|^{1/3}$.
Besides rates of the feeding of zooplankton on diatoms and detritus, the total feeding rate of zooplankton is presented, also comprising the feeding on green algae and cyanobacteria.

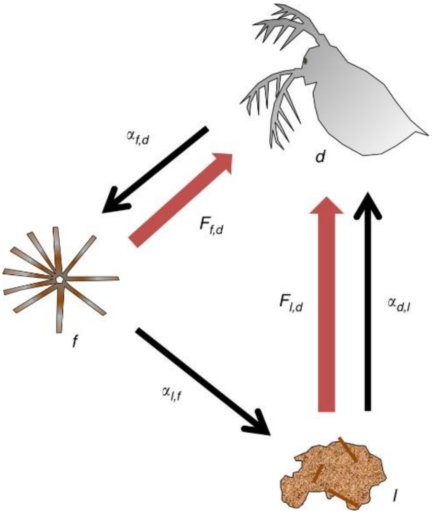

Figure 4 Loop with the heaviest loop weight. The omnivorous three link loop with zooplankton (*d*), pelagic diatoms (*f*), and pelagic detritus (*l*) is the heaviest loop in the trophic network. Black arrows indicate the direction of the interaction effect (*α*). Red arrows indicate the feeding fluxes (*F*). The top-down effect of zooplankton on diatoms is a negative effect directly resulting from consumption. The effect of diatoms on detritus results from natural mortality of diatoms, and the unassimilated part of diatom consumption by zooplankton. The bottom-up effect of detritus on zooplankton is a positive predation effect.

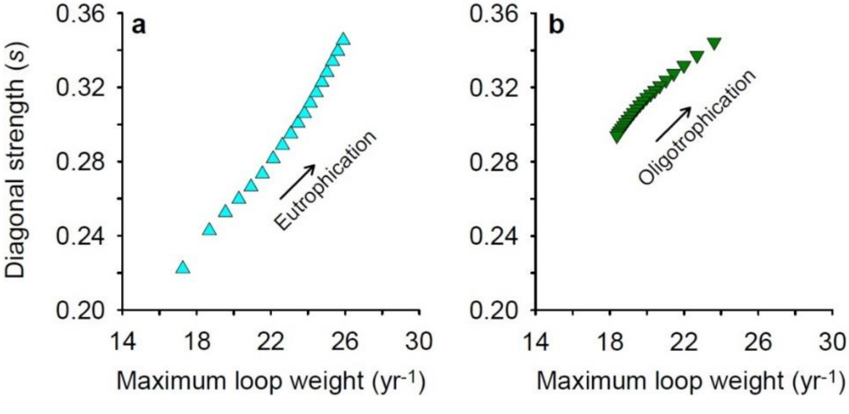

Figure 5 Stability versus maximum loop weight. The maximum loop weight (per year (yr^{-1})) shows a positive relationship with intraspecific interaction needed for matrix stability (s) during (a) eutrophication and (b) re-oligotrophication. Food-web stability decreases with increasing s.

Discussion

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

From an alternative stable state perspective it may seem surprising that food-web metrics can reveal the impending shift without explicitly including the feedbacks through the abiotic environment that are thought to be crucial for regime shifts in lakes, such as shading, provision of refugia and retention of P in the sediment[6]. We resolve this by realizing that the observed webs at each level of nutrient loading are shaped by forces that are not part of the food-web model *per se*, implicitly carried over to the food-web model during sampling of the food-web data. Using expression 1, we made a clear distinction between the intrinsic dynamical properties of the food web ($\frac{\partial s}{\partial \alpha_{i,j}}$) and the changes in interaction strengths driven by the changing nutrient loading to the ecosystem ($\frac{d\alpha_{i,j}}{dL}$).

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

Our analyses reveal that only few trophic interactions dictate the deterioration of food-web stability, particularly among zooplankton, diatoms and detritus. This is in line with empirical studies on interaction strengths suggesting that most interactions have only a negligible impact on community dynamics(de Ruiter et al., 1995), and is consistent with alternative stable states theory that regime shifts in ecosystems can be explained from only few key components in relation to external forcing (Scheffer et al., 2001). The interplay between zooplankton and phytoplankton has often been claimed to be pivotal in controlling aquatic ecosystem dynamics and causing alternative stable states (Scheffer, 2004).

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

Our finding that most interactions have only a negligible impact on community dynamics does not imply that species are redundant, as extreme changes in interaction strength - e.g. due to species extinctions - can have strong non-linear effects on community stability. A next step will be to investigate the synergetic effects of food-web manipulations and environmental stress, as it is unquestionable that species extinctions and invasions can have far reaching consequences for ecosystem functioning, of which the introduction of the Nile perch to the world's second largest freshwater system Lake Victoria gives one of the most striking examples (Downing et al., 2012).

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

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

Methods

Ecosystem modelling.

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

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

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

Material flow descriptions.

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

Food-web dynamics

We developed a Lotka-Volterra type food-web model that included the same trophic groups as the full ecosystem model, in the form $\dot{X}_i = X_i\left[b_i + \sum_{j=1}^{n} c_{i,j}X_j\right]$ and extensions thereof, where X_i and X_j represent the population sizes of group *i* and *j*, b_i is specific rate of increase or decrease of group *i*, and c_{ij} is the coefficient of interaction between group *i* and group *j*. Interaction strengths can be defined as the partial derivatives of Lotka-Volterra type growth equations in equilibrium and give the elements of the (Jacobian) community matrix representation of our model (May, 1972). The interaction effect of predator *j* on prey *i* can be expressed as $\alpha_{ij} = \left(\frac{\partial \frac{dX_i}{dt}}{\partial X_j}\right)^{*} = \frac{-c_{i,j}X_i^{*}X_j^{*}}{X_j^{*}}$ (a detailed description of all the equations can be found in Supplementary Note 1).

The values of the partial derivatives can be directly derived from the material flow descriptions of the food web, using the criterion developed by May[10,](de Ruiter et al., 1995). Here the assumption is that the average annual feeding rate $F_{i,j}$ (g m^{-2} $year^{-1}$) can be expressed as $-c_{i,j}X_i^{*}X_j^{*}$ i.e. the death rate of group *i* due to predation by group *j* in equilibrium[11]. Thus, the strength of this interaction can be derived by dividing the feeding rate by the annual average population density of the predator $\alpha_{ij} = -\frac{F_{i,j}}{B_j}$. The opposite (positive) effect of the prey on the predator, as well as the interaction terms resulting from the detrital fluxes, reproduction fluxes and settling and resuspension fluxes, were determined in a similar way (Moore and de Ruiter, 2012) (see Supplementary Note 1).

We calculated interaction strengths and constructed (Jacobian) community matrices from the material flow descriptions of the food webs at each loading level for each initial state. A randomization procedure confirmed that the imposed patterns of interaction strengths were non-random, and thus crucial to the stability of the food web (Supplementary Fig. 3)(de Ruiter et al., 1995; Neutel et al., 2002).

Calculation of stability.

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

Calculation of the maximum loop weight.

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

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Supplementary material

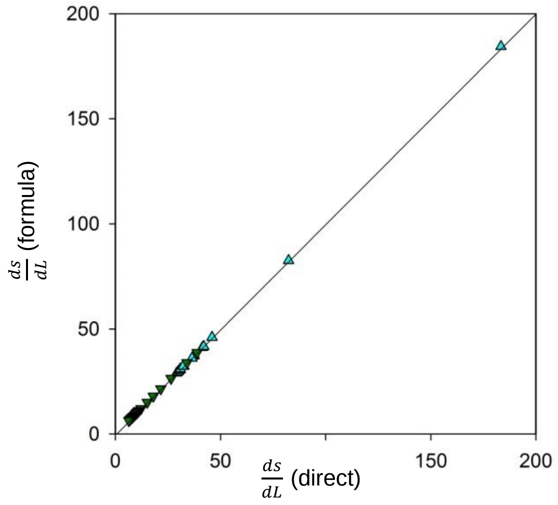

Figure S1 Proof of concept of expression 1. We show the comparison of the change in matrix stability per unit nutrient loading $\left(\frac{dS}{dL}\right)$ with the sum of the multiplications of the changes in strength and the sensitivities of all individual interactions in the matrix $\left(\sum_i^n \sum_j^n \frac{d\alpha_{i,j}}{dL} \frac{\partial s}{\partial \alpha_{i,j}}\right)$. We plotted the relation for each step along the loading axis from clear to turbid (turquoise upward triangles), and from turbid to clear conditions (dark green downward triangles).

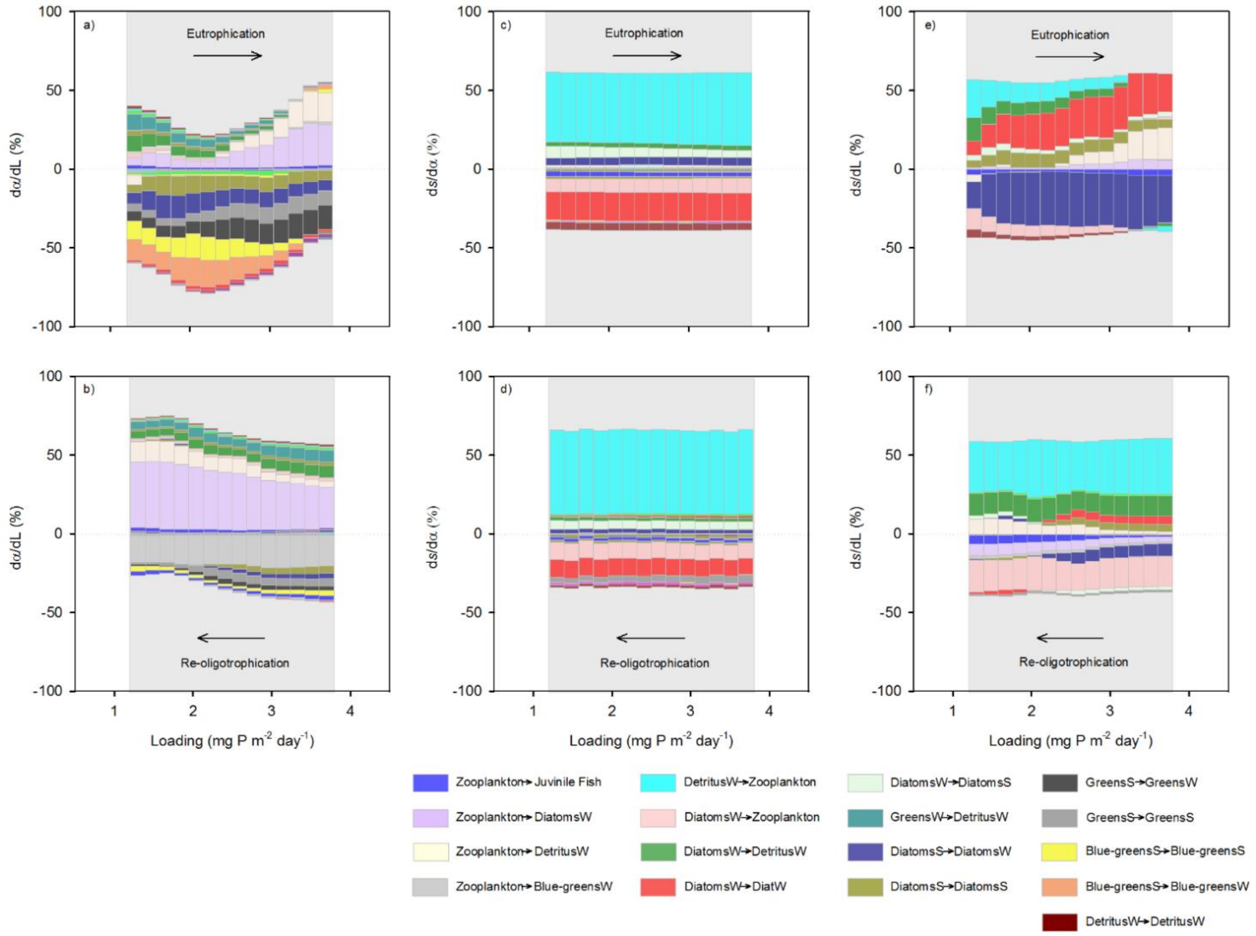a)
b)
c)
d)
e)
f)
Eutrophication
Re-oligotrophication
dα/dL (%)
ds/dα (%)
ds/dL (%)
100
50
0
-50
-100
1
2
3
4
Loading (mg P m^{-2} day^{-1})
Zooplankton→Juvinile Fish
Zooplankton→DiatomsW
Zooplankton→DetritusW
Zooplankton→Blue-greensW
DetritusW→Zooplankton
DiatomsW→Zooplankton
DiatomsW→DetritusW
DiatomsW→DiatW
DiatomsW→DiatomsS
GreensW→DetritusW
DiatomsS→DiatomsW
DiatomsS→DiatomsS
GreensS→GreensW
GreensS→GreensS
Blue-greensS→Blue-greensS
Blue-greensS→Blue-greensW
DetritusW→DetritusW

Figure S2 Elucidating which interactions contribute to the decrease of food web stability. The response of food web stability to nutrient loading depends both on how the strengths of trophic interactions change in response to nutrient loading: $\frac{d\alpha_{i,j}}{dL}$, and the extent to which the stability of the food web is sensitive to those changes: $\left(\frac{\partial s}{\partial \alpha_{i,j}}\right)$. Plotting the relative changes of the interaction strengths per unit change of loading L during eutrophication **(a)** and re-oligotrophication **(b)** reveals that several of the 55 interactions in the food web increase or decrease in strength towards the tipping point. A positive change indicates that the strength of the interaction increases and a negative change indicates that the strength of the interaction is decreasing. Plotting the relative sensitivity of the diagonal strength s to changes in the interaction strengths during eutrophication **(c)** and re-oligotrophication **(d)** reveals that the stability is only sensitive to a select number of interactions, and that the sensitivity is not dependent on the location along the loading axis. The product of the change in strength of each interaction with the sensitivity of s to that interaction strength gives the relative contribution of each interaction to changes in s, during eutrophication **(e)** and re-oligotrophication **(f)**. Only changes in a handful of stabilizing and destabilizing interactions contribute to changes in stability - mainly involving detritus, diatoms and zooplankton. Only relevant interactions are presented in the legend. Phytoplankton species and detritus may appear both in the pelagic and in the sediment layer: they are abbreviated and indicated with 'W' if they are in the pelagic, or 'S' if they are found in or on the sediment.

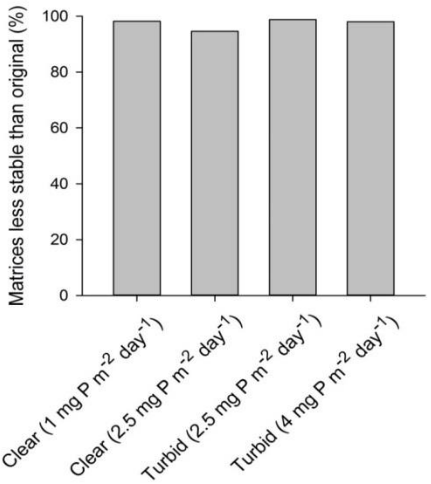

Figure S3 Percentage of randomized matrices less stable than original (Jacobian) community matrix representation of the aquatic food web. We randomized the matrices of four lakes differing in their initial conditions or nutrient loading 500 times and compared the stability of the randomized matrices with the stability of the original matrices. Randomization was performed by randomly exchanging pairs of interaction strengths but keeping the pairs as such intact, preserving both the sign structure of the matrix and the overall strength of the trophic interactions relative to the strength of intragroup interference: the randomized matrices have thus a similar structure but lost the pattern that resulted from the ecosystem model.

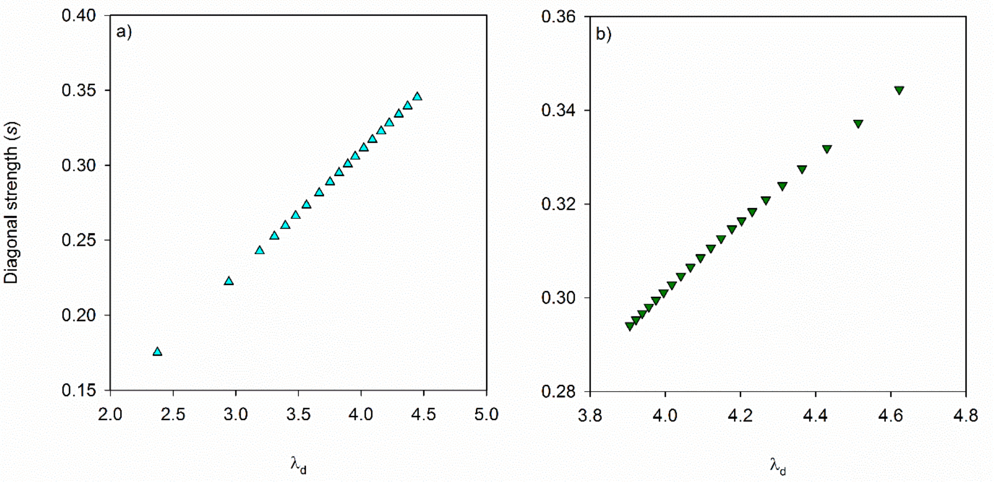

Figure S4 Relation between the maximum eigenvalue and the relative intraspecific competition needed for matrix stability. The relation between the maximum eigenvalue λ_d and the relative intraspecific competition *s* is plotted for each step along the loading axis from **(a)** clear to turbid, and **(b)** from turbid to clear conditions. Unlike the maximum eigenvalue, the level of intraspecific interaction strength *s* has a biological interpretation as it translates to a loss rate of organisms at steady state relative to the total loss that the system can provide for.

Table S1: Overview of the parameters and output of the ecosystem model PCLake used to estimate material fluxes and interaction strengths in the food web.

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

(Continued)

Table S1 *(Continued)*

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

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

Consumers

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

Zoobenthos, zooplankton, and piscivorous fish

The differential equation of consumer group i is given by:

$$\frac{dX_i}{dt} = -(1-s)d_iX_i - \frac{sd_i}{X_i^*}X_i^2 - c_{i,k}X_iX_k + \sum_j a_ip_ic_{j,i}X_jX_i, \tag{S1}$$

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

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

$$\alpha_{i,k} = -c_{i,k}X_i^* = -\frac{F_{i,k}}{X_k^*}, \tag{S2}$$

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

$$\alpha_{i,j} = a_ip_iX_i^* = \frac{a_ip_iF_{i,j}}{X_j^*}. \tag{S3}$$

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

$$\alpha_{i,i} = -sd_i. \tag{S4}$$

Juvenile (benthivorous) fish and adult (zooplanktivorous) fish

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

Additional assumptions are:

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

The differential equation of juvenile fish is given by

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

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

Taking the partial derivative to adult fish gives

$$\alpha_{JF,AF} = h_{AF}. \tag{S6}$$

The partial derivative to predator k is given by

$$\alpha_{JF,k} = -c_{JF,k}X_{JF}^* = -\frac{F_{JF,k}}{X_k^*}. \tag{S7}$$

The partial derivative to prey j is given by

$$\alpha_{JF,j} = a_{JF}p_{JF}c_{j,JF}X_{JF}^* = \frac{a_{JF}p_{JF}F_{j,JF}}{X_j^*}. \tag{S8}$$

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

$$\alpha_{JF,JF} = -\frac{h_{AF}X_{AF}^*}{X_{JF}^*} - sd_{JF}X_{JF}^*. \tag{S9}$$

The differential equation of adult fish is given by

$$\frac{dX_{AF}}{dt} = g_{JF}X_{JF} - h_{AF}X_{AF} - (1-s)d_{AF}X_{AF} - \frac{sd_{AF}}{X_{AF}^*}X_{AF}^2 - c_{AF,k}X_{AF}X_k + a_{AF}p_{AF}c_{j,AF}X_jX_{AF}. \tag{S10}$$

Taking the partial derivative to juvenile fish gives

$$\alpha_{AF,JF} = g_{JF}. \tag{S11}$$

The partial derivative to predator k is given by

$$\alpha_{AF,k} = -c_{AF,k}X_{AF}^* = -\frac{F_{AF,k}}{X_k^*}. \tag{S12}$$

The partial derivative to prey j is given by

$$\alpha_{AF,j} = a_{AF} p_{AF} c_{j,AF} X_{AF}^* = \frac{a_{AF} p_{AF} F_{j,AF}}{X_j^*}. \tag{S13}$$

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

$$\alpha_{AF,AF} = -\frac{g_{JF} X_{JF}^*}{X_{AF}^*} - sd_{AF} X_{AF}^*. \tag{S14}$$

Phytoplankton

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

For phytoplankton, we assume that:

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

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

$$\begin{aligned}\frac{dX_{iW}}{dt} = -n_{iW} X_{iW} + m_{iS} X_{iS} + r_{iW} X_{iW} - (1-s) d_{iW} X_{iW} - \frac{sd_{iW}}{X_{iW}^*} X_{iW}^2 \\ - c_{iW,k} X_{iW} X_k,\end{aligned} \tag{S15}$$

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

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

$$\alpha_{iW,iS} = m_{iS}. \tag{S16}$$

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

$$\alpha_{iW,k} = -c_{iW,k} X_k^* = -\frac{F_{iW,k}}{X_{iW}^*}. \tag{S17}$$

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

$$\alpha_{iW,iW} = -\frac{m_{iS}}{X_{iW}^*} X_{iS}^* - sd_{iW}. \tag{S18}$$

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

$$\frac{dX_{iS}}{dt} = n_{iW}X_{iW} - m_{iS}X_{iS} - (1-s)d_{iS}X_{iS} - \frac{sd_{iS}}{X_{iS}^*}X_{iS}^2 - c_{iS,k}X_{iS}X_k, \tag{S19}$$

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

Taking the partial derivative to water phytoplankton group iW gives

$$\alpha_{iS,iW} = n_{iW}. \tag{S20}$$

The partial derivative to predator k is given by

$$\alpha_{iS,k} = -c_{iS,k}X_k^* = -\frac{F_{iS,k}}{X_{iS}^*}. \tag{S21}$$

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

$$\alpha_{iS,iS} = -\frac{n_{iW}}{X_{iS}^*}X_{iW}^* - sd_{iS}. \tag{S22}$$

Detritus

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

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

The differential equation of water detritus is given by

$$\begin{aligned}\frac{dX_{DW}}{dt} &= R_{DW} - n_{DW}X_{DW} + m_{DS}X_{DS} + \sum_i\sum_j(1-a_j)c_{i,j}X_iX_j \\ &\quad + \sum_i(1-s)d_iX_i + \sum_i\frac{sd_i}{X_i^*}X_i^2 - \sum_j c_{DW,j}X_{DW}X_j,\end{aligned} \tag{S23}$$

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

Taking the partial derivative to sediment detritus, this gives

$$\alpha_{DW,DS} = m_{DS}. \tag{S24}$$

The partial derivative to any phytoplankton or consumer group *j* gives

$$\begin{aligned}\alpha_{DW,j} &= \sum_i \left(1 - a_j\right) c_{i,j} X_i^* + (1 - a_k) c_{j,k} X_k^* + (1 + s) d_j - c_{DW,j} X_{DW}^* = \\ &= \sum_i \frac{\left(1 - a_j\right) F_{i,j}}{X_j^*} + \frac{(1 - a_k) F_{j,k}}{X_j^*} + (1 + s) d_j - \frac{F_{DW,j}}{X_j^*},\end{aligned} \tag{S25}$$

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

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

$$\alpha_{DW,DW} = -n_{DW} - \sum_j a_j c_{DW,j} X_j^* = -n_{DW} - \sum_j \frac{a_j F_{DW,j}}{X_{DW}^*}. \tag{S26}$$

The equations for sediment detritus are very similar to equations (S23)-(S26) for water detritus:

$$\begin{aligned}\frac{dX_{DS}}{dt} &= R_{DS} + n_{DW} X_{DW} - m_{DS} X_{DS} + \sum_i \sum_j (1 - a_j) c_{i,j} X_i X_j + \sum_i (1 - s) d_i X_i \\ &+ \sum_i \frac{s d_i}{X_i^*} X_i^2 - \sum_j c_{DS,j} X_{DS} X_j,\end{aligned} \tag{S27}$$

$$\alpha_{DS,DW} = n_{DW}, \tag{S28}$$

$$\alpha_{DS,j} = \sum_i \frac{\left(1 - a_j\right) F_{i,j}}{X_j^*} + \frac{(1 - a_k) F_{j,k}}{X_j^*} + (1 + s) d_j - \frac{F_{DS,j}}{X_j^*}, \tag{S29}$$

$\alpha_{DS,DS} = -m_{DS} - \sum_j \frac{a_j F_{DS,j}}{X_{DS}^*}$.

$$\alpha_{DS,DS} = -m_{DS} - \sum_j \frac{a_j F_{DS,j}}{X_{DS}^*}. \tag{S30}$$

Chapter 5

Sampled equilibrium solutions and the predictability of ecosystem stability along a gradient of environmental stress

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Abstract

The ecosystems of the world are experiencing unprecedented levels of environmental change. Consequently, there is increasing societal demand for mathematical models that help to understand and predict imminent regime changes in ecosystem state. Such models may be parameterized with empirical information such as biomass densities and feeding rates of species. Interestingly, models of different form can be developed to describe the same empirical information. In this study, we are interested in the extent to which the stability properties of a more complex model system along a gradient of environmental stress can be reflected by a simpler model system that is built upon the same biomass densities and energy fluxes. Specifically, we use classical minimal dynamical models to analyze the consequence of changing a system with non-proportional interaction terms into a system with simpler linear interaction terms, while maintaining the equilibrium densities. The insights obtained here may help resolve the question under which conditions empirical data can be linked to mathematical models to estimate the stability properties of real ecosystems.

Introduction

The current period in geological time can be characterized by the large influence that humans have on the natural world, for which it is coined the Anthropocene (cf. Crutzen, 2002). All over the earth ecosystems are experiencing stress due to e.g. land conversion, climate change, overexploitation and pollution (Millenium Ecosystem Assessment, 2005). Consequently, ecosystems change both in structure and function, and hence so do the services they deliver to human societies (Rockström et al., 2009). Changes in ecosystem state are particularly troublesome when they are abrupt and nonlinear (Scheffer et al., 2001). A fundamental question from society to ecologists is whether dynamic models can be developed that describe and help predict the resilience and stability of natural ecosystems under anthropogenic stress (Clark et al., 2001; Evans, 2012).

The modelling of species interactions often forms the first step in analyzing more complex behaviour of ecosystems. As such, the seminal work by Alfred Lotka (1920) and Vito Volterra (1926), who independently of each other discovered the cycles that arise in a set of coupled differential equations representing consumers and resources, forms the foundation for innumerable ecological models that have been developed since. The Lotka-Volterra (LV) model is one of the earliest models in mathematical ecology, and represents the simplest model of predator-prey interactions. It is based on linear per capita growth rates, interaction rates and mortality rates. Taking the LV equations as a starting point, we distinct three dominant modelling approaches (or schools) that have developed to study ecosystem stability but differ noticeably from each other.

The first approach we highlight is the thorough analysis of small sets of differential equations, which are referred to as ‘simple’ or ‘minimal’ models. This strategy is built upon the observation that the addition of ‘simple’ ingredients to LV equations, such as non-proportional interaction terms, can have large and surprising effects on model outcome (Wangersky 1978; Fig. 1, top right). One of the most famous examples comes from Rosenzweig and MacArthur (1963), who replaced the linear interaction term of the original LV model with a Holling type 2 functional response, and included logistic growth in the dynamics of the resource. Their observation that increasing resource density tends to destabilize the system led to the formulation of the ‘paradox of enrichment’ (Rosenzweig, 1971). Minimal dynamical models are typically used to show the workings of certain mechanistic principles in a pure and controlled way (Scheffer and Beets, 1994). A particular merit is that they allow for studying bifurcations that reveal qualitative changes in the long-term dynamics of the model along a gradient of environmental change (e.g. productivity in the Rosenzweig-MacArthur example). As such, minimal dynamical models help to unveil which ingredients are minimally required to evoke phenomena that are qualitatively similar to phenomena observed in real life (Scheffer, 2004), thereby providing an essential theoretical foundation for studying ecosystem stability in nature. A downside is that they are not intended to give quantitative descriptions of the system under study. The included mechanisms are typically represented at a very abstract level and the connection with the empirical world is generally rather loose. The usefulness of this type of models for making detailed predictions of the stability of real world ecosystems is therefore criticized (Evans et al., 2013).

A second type of modelling we distinguish is the linking of multiple Lotka-Volterra type equations to form a web of interacting species (Fig. 1, bottom left). Hence, the important theoretical results on stability that were obtained by entering non-linear terms did not make the Lotka-Volterra equations with linear terms obsolete. Rooted in the work of Gardner and Ashby (1970) and May (1972), general n-species Lotka-Volterra (GLV) systems with linear functional response interaction terms continue to play an important role in food web ecology. These seminal studies laid down a theoretical framework suggesting that more 'complex' systems, in terms of the number of species and the frequency of interactions, tend to be less stable. This challenged the dominant idea that complexity 'begets' stability (sensu MacArthur 1955), and has set the agenda for a long lasting and ongoing debate about the relationship between complexity and stability (McCann, 2000). Conforming to May (1972; 1973), numerous studies used the Jacobian matrix approach to identify which non-random food web structures are the building blocks of (locally) stable food webs (Moore and de Ruiter, 2012). The Jacobian matrix is calculated in equilibrium, after which the stability of those equilibria can be determined. Importantly, GLV type equations allow for local stability analysis of empirical food webs, as they can be parameterized fairly easily with readily available empirical information as long as equilibrium conditions are assumed (de Ruiter et al., 1995, 1993). Analyses of empirical food web models have yielded important insights in which stabilizing structures are prevalent in nature and hence should be maintained (Emmerson and Yearsley, 2004; Neutel et al., 2002). Yet, a consequence of merely focussing on trophic interactions is that non-trophic interactions are mostly ignored and that physical and environmental processes are usually not explicitly modelled as part of the system (Berlow et al., 2004; Sonia Kéfi et al., 2012). This, in combination with the focus on local stability, makes that empirical food web models are seldom analysed in the context of changing environmental conditions, and are difficult to apply by ecosystem managers.

A third dominant modelling strategy is that of complex simulation models, which include both of the aforementioned extensions and are thus complex in terms of the number of interactions and the nature of these interactions (Fig. 1, bottom right). Besides being used to describe the long-term, asymptotic behaviour of a dynamical system, complex ecosystem models are often applied to describe relative short-term transient dynamics. Unlike the empirical food web models, complex ecosystem models do not map all trophic interactions present in the ecosystem. Instead, they typically focus on capturing only those components, whether biotic or abiotic, which are considered key for successfully describing higher level variables of the ecosystem. Nonetheless, these models usually do allow for, or even require integrating large amounts of empirical information, including high frequency time series of external forcings. Together these characteristics make that complex simulation models can have a multitude of functions in both science and ecosystem management (e.g. Janssen et al. 2015; Weijerman et al. 2015). For example, scenario analysis allows ecosystem managers to evaluate the stability of a specific ecosystem along a gradient of environmental stress. A typical example is given by the ecosystem model PCLake, which consists of more than 60 differential equations and more than 300 parameters (Janse et al. 2010). PCLake is frequently applied by water quality managers to identify the 'critical' nutrient loading of a shallow lake ecosystem and to evaluate the effectiveness of potential management measures (Janse, 1997). The critical nutrient loading is the nutrient loading that triggers a regime shift from a clear state to a turbid phytoplankton dominated state, or vice versa (Scheffer, 1990). An evident downside of the complexity of these comprehensive models is that it goes at the costs of mathematical tractability, and hence, scientific understanding (Scheffer and Beets, 1994). It is oftentimes difficult to interpret the output of complex simulation models and to grasp the causality in the underlying processes, making it difficult to link up with theoretical ecology.

The three modelling strategies presented here are not exhaustive, as there are various other approaches that, for example, do not use ordinary differential equations, such as agent-based models and partial differential equation models (Janssen et al., 2015; Mooij et al., 2010). Neither are they completely demarcated, as there are many forms of hybrid models presented in the literature, e.g. in the form of extended minimal dynamical models that represent simplified food webs (e.g. McCann et al. 1998; Rooney et al. 2006). Nevertheless, we acknowledge that in a broad sense these approaches embody three complementary paradigms that each have produced a wealth of knowledge about the stability of ecosystems. An inherent disadvantage of having co-existing paradigms, however, is that understanding how the insights produced by one paradigm fit in with the insights resulting from another paradigm can be troublesome (e.g. Thompson et al. 2012), even when both are fed with empirical information from one and the same ecosystem. For example, a fundamental yet largely unresolved question is how the local stability of an empirical food web, as determined by the Jacobian matrix approach, relates to resilience of ecosystems susceptible to regime change (Hannah et al., 2010). The few studies that have established series of empirical food web models along gradients of e.g. productivity (Neutel et al., 2007) and grazing (Andres et al., 2016) were not able to use their results to preview potential nonlinear ecosystem responses to environmental change. An apparent complicating factor is that food web stability is often analysed using models with linear interaction terms, while regime shifts are mostly studied with models that employ nonlinear interaction terms.

Recently Kuiper et al. (2015) presented a new approach to bridge the gap between complex consumer-resource models with linear and with nonlinear interaction terms. While the historical trend has been to add complexity to consumer resource models, Kuiper et al. started at the complex side and worked from there towards simpler models. More exactly, the authors used the complex PCLake model as a virtual reality in which observations were made to parameterize a Lotka-Volterra 'blueprint' of the aquatic food web, which they could then analyze for its local stability. Hence, while both the ecosystem model and the food web model describe the same food web, the food web model is much simpler as it excludes all abiotic processes and uses linear interaction terms instead of more complex non-linear interaction terms. Subsequently, they used PCLake to simulate two catastrophic regime shifts: one from clear to turbid water during eutrophication and one from turbid to clear water during re-oligotrophication. They found that the stability of the food web model decreased towards both regime shifts. This remarkable result raises the question how exactly stability properties of the ecosystem model are transferred to the food web model. In other words, for a system of consumer resource interactions in equilibrium, is it the exact shape of the interactions (e.g. type-1 vs. type-2 functional response), or is the patterning of interactions in the network (e.g. degree of omnivory, connectance etc.) that is decisive in determining the stability properties? Given the complexity of PCLake and the produced food web models it is difficult to answer these questions.

In the present study, we address the question how stability properties are transferred when models with linear interaction terms are parameterized on basis of the output of consumer resource models with nonlinear interaction terms along an environmental gradient. Instead of using complex models, we will use three extensions of the Lotka-Volterra models that are classics in ecology, and of which the stability properties are mathematically fully understood. Specifically, we would like to know whether in such relatively small systems of consumer resource interactions the equilibrium solutions along an environmental gradient carry intrinsic information about the dynamical stability and upcoming regime shifts in the system.

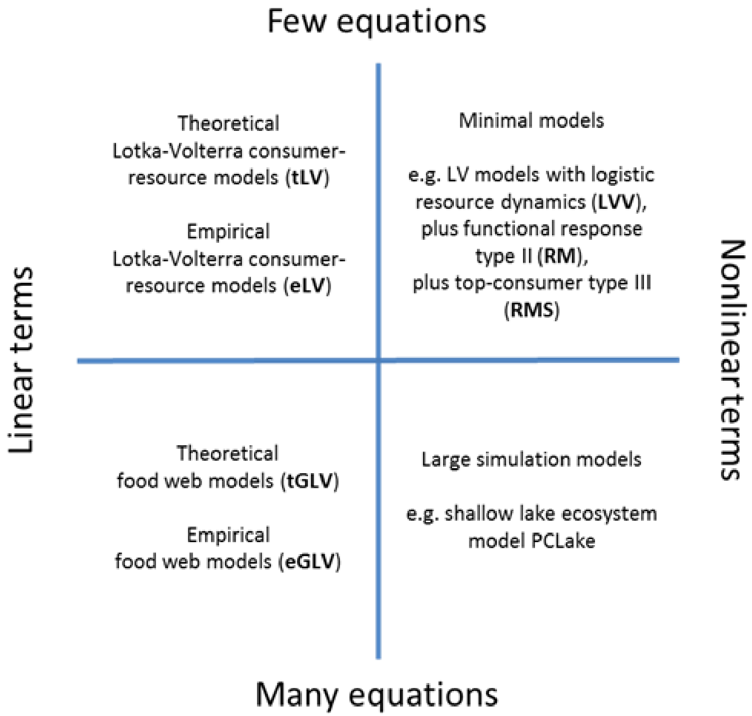

Figure 1 Overview of two types of complexity in models of consumer resource interactions. Horizontally, a distinction is made between models with linear interaction terms and those with non-linear interaction terms. Theoretical ecology focuses on the mathematical comparison between simple Lotka Volterra type of models (tLV or eLV) and their counterparts with nonlinear interaction terms (e.g. LVV, RM and RMS). Vertically, a distinction is made between models with typically two or three equations that can be thoroughly analyzed mathematically and more empirically oriented models that contain as many compartments as is deemed necessary to represent the natural system under study. The stability-diversity debate originates in a comparison between tLV with few interactions and tGLV or eGLV type of models consisting of a web of interactions. While the historical trend has been to add complexity to consumer resource models, we claim that there is much to win by starting at the complex side and work from there towards simpler models, to identify the least amount of information needed to disclose the stability properties of complex ecosystems.

Methods

The models

In this study we focus on three key extensions of the classical Lotka-Volterra (LV) consumer-resource model (Box 1a and 2a). The original LV model contains proportional growth and death rates of resource and consumer, respectively, and a proportional interaction term between consumer and resource. Please note that within the ecological setting of this paper we will refer to consumer-resource models with proportional growth, loss and interaction terms as having ‘linear equations’, and refer to models that have non-proportional terms as ‘non-linear’ equations (cf. Arditi and Michalski 1996). This usage of the term linear does not comply with the mathematical definition of what constitutes a linear and a nonlinear equation. According to this mathematical definition the classical Lotka-Volterra equations are nonlinear because the interaction term involves the multiplication of two states, irrespective whether this interaction is proportional to both states, or not. We parameterize all models for algae and zooplankton, and, therefore, identify the resource as A and the consumer as Z.

The first logical extension of the original LV model we consider is the inclusion of negative density dependence in the resource so as to prevent unbounded growth in absence of the consumer. A classical formulation of negative density dependence is the logistic equation (Verhulst, 1845). Hence, we replace the linear growth term rA in the resource with a the non-linear logistic term rA(1-A/K), and refer to this extension as the Lotka-Volterra-Verhulst (LVV) model (Box 3a).

A second logical extension is the realization that consumers approach a maximum intake rate at high resource levels. This can for instance be achieved by replacing the linear interaction term of the Lotka Volterra model gZA with a non-linear Holling type 2 functional response gZA/(A+a) (Holling, 1959), which in turn is mathematically equal to Michaelis-Menten kinetics (Michaelis and Menten, 1913). The combination of both extensions, logistic growth in the resource and a Holling type 2 functional response, results in the aforementioned Rosenzweig-MacArthur (RM) model (Rosenzweig and MacArthur, 1963) (Box 4a).

A third straightforward extension stems from the realisation that above a given threshold density, the consumer itself might become an attractive resource for a top-consumer. Such prey switchting responses in the top-consumer can be modelled with a sigmoid Holling type III functional response of the top-consumer, which is a specific case of a Hill function (Hill, 1910). A Rosenzweig MacArthur (RM) model with a Hill function in the loss term of the consumer was analysed by Scheffer et al. (2000). We will further refer to this model as the Rosenzweig-MacArthur-Scheffer (RMS) model. In the RMS model a nonlinear Holling type III loss term of the consumer $FZ^2/(Z^2+z^2)$ is added to the linear loss term of the LV model mZ. To fully comply with the formulation used by Scheffer et al. (2000) a constant influx of the resource is also added, thus mimicking chemostat dynamics (Box 5a).

Each of these models is mathematically fully analyzed through bifurcation analysis for their stability properties and described in the theoretical ecological literature (e.g. Rosenzweig and MacArthur 1963; Scheffer et al. 2000). The stability properties range from neutrally stable (LV), always stable (LVV), for some parameter values stable, for others unstable (RM) and for some parameter values showing alternative stable states (RMS).

The equilibria of the models along an environmental gradient

For the LV model (Box 2a), the LVV model (Box 3a) and the RM model (Box 4a), but not for the RMS model (Box 5a), explicit expressions of the equilibria are available. The LVV, the RM and the RMS model contain the carrying capacity K of the resource and can therefore be analyzed along an environmental gradient representing eutrophication. Please note, however, that K does not appear in the equilibrium expressions of the resource for the LVV and RM model. Numerical analysis shows that the equilibrium density of the resource is dependent on the carrying capacity for the RMS model. The RMS model is intended for analysis along another gradient, namely that of consumption of the consumer by a top-consumer expressed in parameter F. For easy comparison with the RMS model as it is described in literature, we therefore choose to present the analysis for F in the main results, and present the analysis for K in the online supplementary material.

The Jacobian elements of the original models

Symbolic expressions for the elements of the Jacobian matrix J, that is, the matrix with the derivatives of the model equations for each of the state variables, can be found for each of the models, including the RMS model for which no expressions for the equilibria are available (Box 2a, 3a, 4a and 5a). Comparison of the expressions of the Jacobian matrix with the model equations show that some of these elements should always be zero. This holds for element J(1,1) of the LV model and element J(2, 2) of the LV, LVV and RM model.

The linearization

In the linearization, each of the nonlinear growth, interaction and loss terms in the LVV, RM, RMS models, is replaced by a single parameter. Because the original LV model is already linear, it is not affected by linearization (Box 2b). The resulting linearized models are identified with an apostrophe: LVV’ for the linearized Lotka-Volterra-Verhulst model (Box 3b), RM’ for the linearized Rosenzweig-MacArthur model (Box 4b) and RMS’ for the linearized Rosenzweig-MacArthur-Scheffer model (Box 5b). To maintain a link with the original model, and to allow an analysis of the linearized models along the same environmental gradients against which the original models can be analyzed, we expressed the linear parameters r’, g’ and F’ in terms of the original parameters r, K, g, a, F and z, and the equilibrium densities A* and Z*. By doing so, we guarantee that the equilibrium densities of the original models LVV, RM and RMS are by definition equal to those for their linearized counterparts LVV’, RM’, and RMS’.

The Jacobian of the linearized model

After linearizing each model, we again derived the elements of the Jacobian matrix J’ (note the apostrophe). We first did this in terms of the new parameters r’, g’ and F’ and thereafter reformulated each element of that matrix in terms of the original parameters r, K, g, a, F and z. This allows for a one to one comparison of J and J’ (Box 2b, 3b, 4b and 5b). This comparison shows that J(1, 1) and J’(1, 1) are different for all three models (LVV, RM and RMS) while elements (J1, 2) and J’(1, 2) are equal for all models (LVV, RM and RMS). Element J(2, 1) and J’(2, 1) are equal for the LVV model but not for the RM and RMS model. Finally, element J(2, 2) and J’(2, 2) are equal for the LVV and the RM model but not for the RMS model.

Box 1a States and parameters of the original Lotka-Volterra (LV), Lotka-Volterra-Verhulst (LVV), Rosenzweig-MacArthur (RM) and Rosenzweig-MacArthur-Scheffer (RMS) models:

	Description	Unit
A	Resource	Resource unit
Z	Consumer	Consumer unit
r	Maximum growth rate resource	Time^{-1}
K	Carrying capacity resource	Resource unit
g	Maximum intake rate consumer	LV and LVV model: consumer unit^{-1}·time^{-1}; RM and RMS model: resource unit·consumer unit^{-1}·time^{-1}
a	Half saturation consumer on resource	Resource unit
l	Resource loss rate	Time^{-1}
e	Consumer-resource conversion efficiency	Consumer unit·resource unit^{-1}
F	Maximum intake rate top-consumer	Consumer unit·time^{-1}
z	Half saturation rate top-consumer on consumer	Consumer unit
m	Consumer loss rate	Time^{-1}

Box 1b States and parameters of the linearized Lotka-Volterra (LV’), Lotka-Volterra-Verhulst (LVV’), Rosenzweig-MacArthur (RM’) and Rosenzweig-MacArthur-Scheffer (RMS’) models:

	Description	Unit
A’	Resource	Resource unit
Z’	Consumer	Consumer unit
r’	Growth rate resource	Time^{-1}
g’	Intake rate consumer	Time^{-1}
F’	Intake rate top-consumer	Time^{-1}

Box 2a Differential equations, equilibria and elements of the Jacobian matrix J for the original Lotka-Volterra (LV) model

$$\frac{dA}{dt} = rA - gZA - lA$$

$$\frac{dZ}{dt} = egZA - mZ$$

$$A^* = \frac{m}{eg}$$

$$Z^* = \frac{r-l}{g}$$

$$J_{1,1} = r - gZ^* - l = \frac{1}{A^*}\frac{dA^*}{dt} = 0$$

$$J_{1,2} = -gA^* = -g\frac{m}{eg} = \frac{m}{e}$$

$$J_{2,1} = egZ^* = eg\frac{r-l}{g} = e(r-l)$$

$$J_{2,2} = egA^* - m = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0$$

Box 2b Differential equations, parameters, equilibria and elements of the Jacobian matrix *J'* for the linearized Lotka-Volterra (LV') model

$$\frac{dA'}{dt} = r'A' - g'Z'A' - lA'$$

$$\frac{dZ'}{dt} = eg'Z'A' - mZ'$$

$$r' = r$$

$$g' = g$$

$$A'^* = A^*$$

$$Z'^* = Z^*$$

$$J'_{1,1} = r' - g'Z'^* - l = r - gZ^* - l = \frac{1}{A^*}\frac{dA^*}{dt} = 0 = J_{1,1}$$

$$J'_{1,2} = -g'A'^* = -gA^* = J_{1,2}$$

$$J'_{2,1} = eg'Z'^* = egZ^* = J_{2,1}$$

$$J'_{2,2} = eg'A'^* - m = egA^* - m = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0 = J_{2,2}$$

Box 3a Differential equations, equilibria and elements of the Jacobian matrix J for the original Lotka-Volterra-Verhulst (LVV) model:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) - gZA - lA$$

$$\frac{dZ}{dt} = egZA - mZ$$

$$A^* = \frac{m}{eg}$$

$$Z^* = \frac{r\left(1 - \frac{A^*}{K}\right) - l}{g}$$

$$J_{1,1} = r\left(1 - \frac{A^*}{K}\right) - r\frac{A^*}{K} - gZ^* - l$$

$$J_{1,2} = -gA^*$$

$$J_{2,1} = egZ^*$$

$$J_{2,2} = egA^* - m = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0$$

Box 3b Differential equations, parameters, equilibria and elements of the Jacobian matrix J' for the linearized Lotka-Volterra-Verhulst (LVV') model:

$$\frac{dA'}{dt} = r'A' - g'Z'A' - lA'$$

$$\frac{dZ'}{dt} = eg'Z'A' - mZ'$$

$$r' = r\left(1 - \frac{A^*}{K}\right)$$

$$g' = g$$

$$A'^* = A^*$$

$$Z'^* = Z^*$$

$$J'_{1,1} = r' - g'Z'^* - l = r\left(1 - \frac{A^*}{K}\right) - gZ^* - l = \frac{1}{A^*}\frac{dA^*}{dt} = 0 = J_{1,1} + \frac{rA^*}{K}$$

$$J'_{1,2} = -g'A'^* = -gA^* = J_{1,2}$$

$$J'_{2,1} = eg'Z'^* = egZ^* = J_{2,1}$$

$$J'_{2,2} = eg'A'^* - m = egA^* - m = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0 = J_{2,2}$$

Box 4a Differential equations, equilibria and elements of the Jacobian matrix *J* for the original Rosenzweig-MacArthur (RM) model:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) - gZ\frac{A}{A + a} - lA$$

$$\frac{dZ}{dt} = egZ\frac{A}{A + a} - mZ$$

$$A^* = \frac{am}{eg - m} \qquad Z^* = \frac{\left(r\left(1 - \frac{A^*}{K}\right) - l\right)(A^* + a)}{g}$$

$$J_{1,1} = r\left(1 - \frac{A^*}{K}\right) - r\frac{A^*}{K} - gZ^*\frac{a}{(A^* + a)^2} - l$$

$$J_{1,2} = -g\left(\frac{A^*}{A^* + a}\right)$$

$$J_{2,1} = egZ^*\frac{a}{(A^* + a)^2}$$

$$J_{2,2} = eg\frac{A^*}{A^* + a} - m = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0$$

Box 4b Differential equations, parameters, equilibria and elements of the Jacobian matrix *J’* for the linearized Rosenzweig-MacArthur (RM’) model:

$$\frac{dA'}{dt} = r'A' - g'Z'A' - lA'$$

$$\frac{dZ'}{dt} = eg'Z'A' - mZ'$$

$$r' = r\left(1 - \frac{A^*}{K}\right) \qquad g' = \frac{g}{(A^* + a)}$$

$$A'^* = A^* \qquad Z'^* = Z^*$$

$$\begin{aligned} J'_{1,1} = r' - g'Z'^* - l = r\left(1 - \frac{A^*}{K}\right) - g\frac{Z^*}{(A^* + a)} - l = \frac{1}{A^*}\frac{dA^*}{dt} = 0 \\ = J_{1,1} + r\frac{A^*}{K} + gZ^*\frac{a}{(A^* + a)^2} - g\frac{Z^*}{(A^* + a)} \end{aligned}$$

$$J'_{1,2} = -g'A'^* = -g\frac{A^*}{(A^* + a)} = J_{1,2}$$

$$J'_{2,1} = eg'Z'^* = eg\frac{Z^*}{(A^* + a)} = J_{2,1}\frac{A^* + a}{a}$$

$$J'_{2,2} = eg'A'^* - m = eg\frac{A^*}{(A^* + a)} - m = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0 = J_{2,2}$$

Box 5a Differential equations, equilibria and elements of the Jacobian matrix J for the original Rosenzweig-MacArthur-Scheffer (RMS) model:

$$\frac{dA}{dt} = rA\left(1 - \frac{A}{K}\right) - gZ\frac{A}{A+a} - lA + lK$$

$$\frac{dZ}{dt} = egZ\frac{A}{A+a} - mZ - F\frac{Z^2}{Z^2 + z^2}$$

$$no\ explicit\ expression\ for\ A^*$$

$$no\ explicit\ expression\ for\ Z^*$$

$$J_{1,1} = r\left(1 - \frac{A^*}{K}\right) - r\frac{A^*}{K} - gZ^*\frac{a}{(A+a)^2} - l$$

$$J_{1,2} = -g\left(\frac{A^*}{A^* + a}\right)$$

$$J_{2,1} = egZ^*\frac{a}{(A^* + a)^2}$$

$$J_{2,2} = eg\frac{A^*}{A^* + a} - m - 2FZ^*\frac{z^2}{(Z^{*2} + z^2)^2}$$

Box 5b Differential equations, parameters, equilibria and elements of the Jacobian matrix *J’* for the linearized Rosenzweig-MacArthur-Scheffer (RMS’) model:

$$\frac{dA'}{dt} = r'A' - g'Z'A' - lA' + lK$$

$$\frac{dZ'}{dt} = eg'Z'A' - mZ' - F'Z$$

$$r' = r\left(1 - \frac{A^*}{K}\right) \qquad g' = \frac{g}{(A^* + a)} \qquad F' = \frac{FZ^*}{(Z^{*2} + z^2)}$$

$$A'^* = A^* \qquad Z'^* = Z^*$$

$$J'_{1,1} = r' - g'Z'^* - l = r\left(1 - \frac{A^*}{K}\right) - g\frac{Z^*}{(A^* + a)} - l = J_{1,1} + r\frac{A^*}{K} + gZ^*\frac{a}{(A^* + a)^2} - g\frac{Z^*}{(A^* + a)}$$

$$J'_{1,2} = -g'A'^* = -g\frac{A^*}{(A^* + a)} = J_{1,2}$$

$$J'_{2,1} = eg'Z'^* = eg\frac{Z^*}{(A^* + a)} = J_{2,1}\frac{A^* + a}{a}$$

$$\begin{aligned} J'_{2,2} = eg'A'^* - m - F' = eg\frac{A^*}{(A^* + a)} - m - \frac{FZ^*}{(Z^{*2} + z^2)} = \frac{1}{Z^*}\frac{dZ^*}{dt} = 0 \\ = J_{2,2} + 2FZ^*\frac{z^2}{(Z^{*2} + z^2)^2} - \frac{FZ^*}{(Z^{*2} + z^2)} \end{aligned}$$

Analysis

Due to the simplicity of the models used here we have symbolic analytical expressions for the elements of the Jacobian of both the non-linear and the linear version of the models. This allows us to study the impact of the linearization on stability in analytical terms. More specifically, we calculated equilibrium densities and material fluxes for each model along an environmental gradient: K for the LVV, RM models and F for the RMS model. We also analysed K for the RMS model but present the results as online supplementary material. We then used these values, as if they were observations taken from the virtual reality of the models with nonlinear terms and used them to parameterize the models with the linear terms along the same environmental gradient. Both the linear and the nonlinear versions thus describe the same biomass densities and material fluxes. We then analysed the stability properties of the non-linear and the linear models along the environmental gradients under study. To simplify comparison with the literature we used the same parameters values as were used by Scheffer et al. (2000). Their parameters were inspired by algae-zooplankton dynamics and are shown in the legends of the figures.

Results

Lotka-Volterra-Verhulst model

The equilibrium density of the resource in the LVV model is not dependent on the carrying capacity because the loss rate of the consumers does not depend on K and therefore its R* (cf. Tilman 1982) is constant over the environmental gradient (Fig. 2a, line A*). Instead, the increasing productivity of the system ends up in increasing biomass of the consumer (Fig. 2a, line Z*). The LVV model goes through a predator invasion threshold (or transcritical bifurcation) at K = 0.64 and is stable for higher carrying capacities, first as a sink and thereafter as a damped oscillation (Fig. 2b). The only parameter of the LVV model that is linearized is the resource growth rate r' (Box 3b) and this parameter increases with increasing carrying capacity (not shown). The linearized version of the LVV model (denoted as LVV') also shows a transcritical bifurcation at a corresponding value of K but thereafter shows the type of neutral stability that is typical for LV models with only linear terms (Fig. 2b).

Rosenzweig-MacArthur model

Also in the RM model, the equilibrium density of the resource is not dependent on the carrying capacity because the loss rate of the consumer does not depend on K and therefore their R* is constant over the environmental gradient (Fig. 2c, line A*). And again, the increasing productivity of the system ends up in increasing biomass of the consumer (Fig. 2c, line Z*). The RM model goes through a transcritical bifurcation at K = 1.02, and shows a stable equilibrium thereafter, first as a sink and thereafter as a damped oscillation (Fig. 2d). At a value of K = 2.65 a supercritical hopf bifurcation occurs and the model shows stable limit cycles as its dynamic behavior at higher carrying capacities. This is the famous 'paradox of enrichment' that states that increasing the carrying capacity of the resource tends to destabilize consumer-resource interactions. During linearization of the RM model, two parameters are linearized, namely the resource growth rate r' and the interaction term g' (Box 4b). However, of this two, only the resource growth rate increases with increasing carrying capacity (not shown). The interaction term g' stays constant because it contain as its only variable the resource concentration, which itself does not depend on the carrying capacity. The linearized version of the RM model (denoted at RM') also shows a transcritical bifurcation at a corresponding value of K but thereafter shows the type of neutral stability that is typical for LV models with only linear terms (Fig. 2d).

Rosenzweig-MacArthur-Scheffer model

Finally in the RMS model, the equilibrium density of both the resource and the consumer is dependent on the consumption rate of the top-consumer F (Fig. 2e, line A*) or the carrying capacity K (Fig. S1a, line A*). The pattern that the increasing productivity of the system ends up only in increasing biomass of the consumer has been lost (Fig. S1a, line A*) and the models shows a more complex response of resource and consumer abundance to enrichment or top-consumer consumption rate. Namely, the RMS model shows alternative stable states with critical transitions at F = 0.2408 and F = 0.076 (Fig. 2f). In addition to these saddle node bifurcations, the system shows a supercritical hopf bifurcation at F = 0.2404. As a result, the system shows limit cycles with increasing amplitude at lower values of F. When the amplitude becomes large enough, the system will shift to the other state in a homoclinic bifurcation. For more details on this aspect of the model see Scheffer et al. (2000).

In line with the LVV and RM model, the RMS model first goes through a transcritical bifurcation when increasing K (Fig S1a, K = 1.0), and shows a stable equilibrium thereafter. At a value of K = 3.39, however, a saddle-node bifurcation occurs and the equilibrium densities of resources and consumers suddenly switch to a different level, lower for the resource and higher for the zooplankton (Fig. S1a). At decreasing carrying capacity, this switch takes place at a lower value of K = 3.12 and hence the system shows hysteresis and alternative stable states also for K. In addition to these alternative stable states, the system shows a supercritical hopf bifurcation at K = 3.89 and the model shows stable limit cycles as its dynamic behaviour at higher carrying capacities (Fig. S1b).

During linearization of the RMS model, three parameters are linearized, namely the resource growth rate r', the interaction term g' and the consumption rate by the top-consumer F' (Box 5b). Each of these linearized parameters changes with increasing top-consumer consumption rate or carrying capacity. The linearized version of the RMS model (denoted at RMS') shows damped oscillations for any value of top-consumer abundance (Fig 2f). Importantly, the linearized RMS' model does not show alternative stable states. When increasing K, the model does show the transcritical bifurcation at the value of 1.0 but thereafter only shows damped oscillations for higher values of the carrying capacity (Fig. S1b). This different behaviour of the RMS' model compared with the LVV' and the RM' model can be explained from the chemostat dynamics that were build in the resource equation of the RMS model.

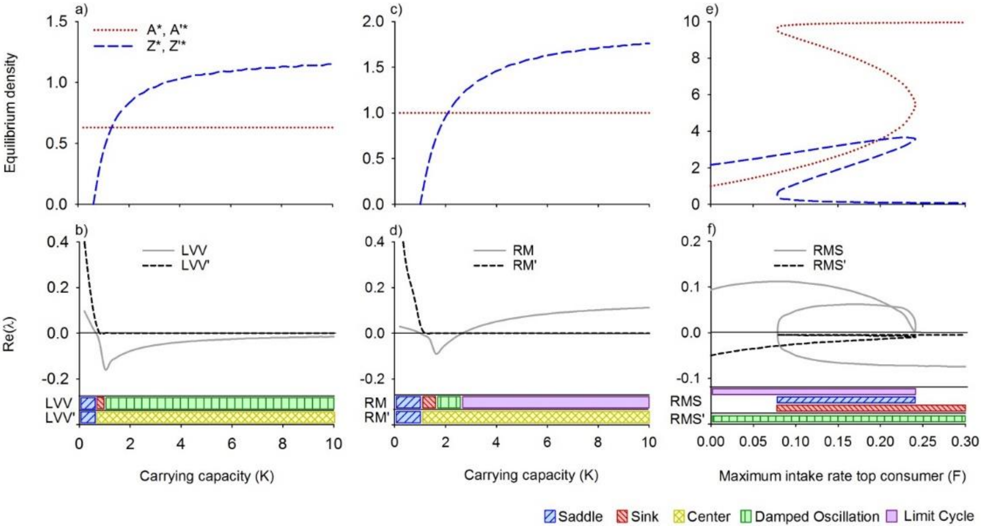

Figure 2 Equilibrium density and the maximum real part of the eigenvalues (Re(λ)) of the original and the linearized (') Lotka-Volterra-Verhulst (a-b), Rosenzweig MacArthur (c-d) and the Rosenzweig-MacArthur-Scheffer (e-f) models along an environmental gradient (bifurcation axis). Also the mode of behavior along the gradient is depicted. Parameters are $r = 0.5$, $K = 10$ (panels e and f only), $g = 0.4$, $a = 0.6$, $l = 0.01$, $e = 0.6$, $m = 0.15$ and $z = 0.5$.

Discussion

When models are constructed to mimic the dynamics of biological systems, critical choices have to be made about which processes to include and how these processes are formulated. With respect to these choices it is important to understand their consequences for detecting the stability of the natural systems in relation to ongoing global environmental change. Our main result is that changing nonlinear terms in simple models of consumer resource interactions into linear ones, while maintaining the equilibrium densities and consequently the flux of the mass, has a strong impact on the stability properties of the model system. Although transcritical bifurcations were maintained during the transfer, the hopf and saddle-node bifurcations were lost. Especially the latter is important for ecosystem managers that wish to anticipate and prevent abrupt regime shifts.

This result contradicts with the observations made by Kuiper et al. (2015) who used the complex ecosystem model PCLake as a virtual reality in which they sampled information to parameterize an 'empirical' food web model that contained linear interaction terms. They found that stability of the simpler 'empirical'food web model decreased in the direction of where the full ecosystem model showed a critical transition. The complexity of PCLake makes a clear understanding of what exactly happens during the transfer of stability properties troublesome. This triggered us to perform the current study for minimal dynamical models that have a much simpler network structure and of which the impact of the transfer on the Jacobian matrix can be studied analytically.

We can only speculate on what causes the apparent contradiction between the results presented here and the study of Kuiper et al. (2015). So far, we focussed on what is lost during the transfer, namely the nonlinear terms. It appears that for a model like PCLake, which contains a more realistic food web description compared to the minimal dynamical models used in this study, the organization of biomass densities and mass fluxes contains enough information for the food web model to capture the stability pattern of the whole system. Hence, apparent patterns in the trophic organization, such as feedback loops, connectivity and the distribution of weak and strong links, change along the gradient, and are present in both the ecosystem model and the 'empirical' food web model. This is consistent with the dominant view among food web ecologists that stability is woven by non-random structures in complex webs (Moore et al., 1993; Polis, 1998). But by showing here that for simpler models the shape of the interaction used is decisive, the question arises how many realistic patterns should be there to ensure that the calculated stability measure is not an artifact of the shape of the interaction that is chosen, and which nonlinear interaction terms have to be included to capture the stability properties of the system. We see much potential in the continuation of the work of Neutel et al. (2007) and Andres et al. (2016) who established series of empirical food web models along an environmental gradient in real ecosystem. Such analyses could be repeated for ecosystems that are known to show abrupt regime shifts, like shallow lakes and peatland ecosystems (Moore and de Ruiter, 2012; Scheffer et al., 2001), for example by performing mesocosm experiments (Moss et al., 2004) or by making or paleoecological reconstructions of food webs (Rawcliffe et al., 2010). Alternatively, Hannah et al. (2010) call for a more comprehensive description of the structure of food webs in the designs of the next generation ecosystem models to address the insights on stability from food web theory.

Yet it may be that food web theory just does not provide an ideal framework for studying ecosystems in the context of environmental change, as models of food webs are primarily developed to understand the internal structure as it is, rather than to predict how this structure is affected by external change. Hence, it may be more worthwhile to continue developing the conventional methods for predicting the nonlinear dynamic behavior of ecosystems, i.e. using large simulation models or statistical models that detect generic early warning indicators in time series (Boettiger et al., 2013; Evans et al., 2012). But what is it then that makes these tools suitable for prediction making?

For complex ecosystem models the argument is that they are (i) process based and (ii) contain sufficient *a-priori* knowledge of the forms and time scales of interactions in the system to essentially predict the possibility of regime shifts. After parameterization with field data and a proper validation procedure the modeller may be able to make sensible predictions using scenario analysis (Robson, 2014). A typical example is given by the PCLake model, which is the product of a comprehensive multidisciplinary research project on the functioning of Lake Loosdrecht in the Netherlands (Van Liere et al., 1992). Later, the model was calibrated with data from more than 40 temperate lakes to obtain a best overall fit (Janse et al., 2010). As a result, PCLake is able to predict regime shifts for a range of shallow lake systems, although fine-tuning may still be necessary (Van Gerven et al., 2015a).

For the statistical early warning signals the clue is that they don't require any a-priori system knowledge at all, as the indicators for critical transitions, such as critical slowing down and flickering, are generic and hence can be detected for all dynamical systems given that sufficient data is available to distill the hidden patterns (Dakos et al., 2015).

Unfortunately, both these methods are not a panacea for making accurate predictions in ecosystem management. Early warning indicators may produce false alarms (Boettiger and Hastings, 2012) and certain regime shifts may not be preceded by any warning sign (Hastings and Wysham, 2010). Complex models in turn are generally difficult to operate and validate (Scheffer and Beets, 1994), while their uncertainty is high and often ignored (Arhonditis and Brett, 2004; Beck, 1987). A strategy that has been proposed to overcome the weaknesses of a single modelling approach is to exploit the diversity of modelling approaches (*sensu* Janssen et al. 2015), e.g. by applying them side by side within one integrated environmental assessment (Logan, 1994; Weijerman et al., 2015).

In nature we often see that the interfaces between biotopes, such as riparian zones and estuaries, are exciting places, as there is a lot of heterogeneity and diversity in these ecotones (e.g. Tockner and Stanford 2002). Inspired by this, we argue that there is much to win by scrutinizing the interface between different modelling paradigms, like we endeavor in the present study. Only then can we truly consolidate insights generated by different modelling paradigms and understand how empirical data can be linked to mathematics to predict the stability of real ecosystems.

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Supplementary Information

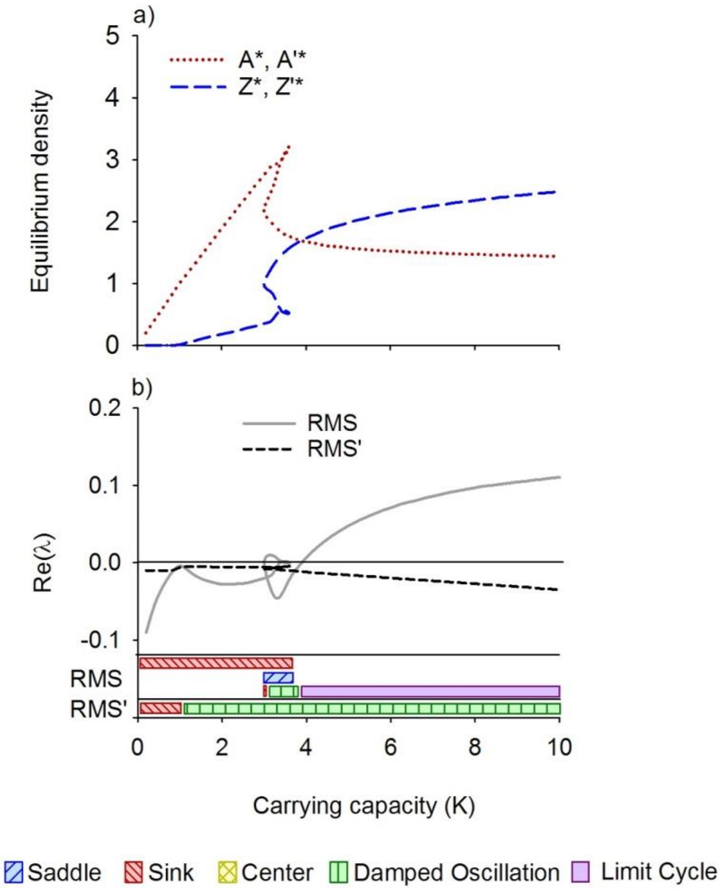

Figure S1 Equilibrium density (a) and the maximum real part of the eigenvalues (b) of the original and the linearized (‘) Rosenzweig-MacArthur-Scheffer (RMS) model along a gradient of increasing carrying capacity (K). Also the mode of behavior along the gradient is depicted. Parameters are r = 0.5, g = 0.4, a = 0.6, l = 0.01, e = 0.6, m = 0.15, F = 0.05, and z = 0.5.

Chapter 6

Mowing submerged macrophytes in shallow lakes with alternative stable states: Battling the good guys?

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Abstract

Submerged macrophytes play an important role in maintaining good water quality in shallow lakes. Yet extensive stands easily interfere with various services provided by these lakes, and harvesting is increasingly applied as a management measure. Because shallow lakes may possess alternative stable states over a wide range of environmental conditions, designing a successful mowing strategy is challenging, given the important role of submerged plants in stabilizing the clear water state. In this study, a detailed aquatic ecosystem model is used to explore the consequences of mowing, in terms of reducing nuisance and ecosystem stability, for a wide range of external nutrient loadings, mowing intensities and timings. Additionally, we use the model to estimate how much phosphorus is removed, and evaluate the long-term effect of harvesting. Our model indicates that mowing can temporarily reduce nuisance caused by submerged plants in the first weeks after cutting, particularly when external nutrient loading is fairly low. When the modelled lake is more eutrophic, the risk of instigating a regime shift increases. This risk can be tempered by mowing halfway the growing season when the resilience of the system is highest, as our model showed. Up to half of the phosphorus entering the system can potentially be removed along with the harvested biomass. As a result, prolonged mowing can prevent an oligo- to mesotrophic lake from becoming eutrophic to a certain extent, as our model shows that the critical nutrient loading where the lake shifts to the turbid state can be slightly increased.

Introduction

Shallow lake ecosystems depend on the presence of submerged aquatic plants (macrophytes) for good water quality and high biodiversity (Carpenter and Lodge, 1986; Heimans and Thijsse, 1895; Jeppesen et al., 1998). There is a positive feedback between aquatic plants and water clarity, through which the plants enhance their own growing conditions (Scheffer, 2004; Van Donk and Van de Bund, 2002). Such self-stabilizing mechanism causes a tendency of the system to resist changes in external environmental conditions, i.e. it promotes a clear water state within the context of alternative stable states in lakes (Scheffer, 2004).

During the second half of the twentieth century, submerged macrophytes disappeared from many shallow lakes in temperate regions because of external nutrient loading from mainly anthropogenic sources (Gulati and Van Donk, 2002; Körner, 2002). Lakes switched from a clear-water state, dominated by macrophytes, to a turbid-water state with few plants, prone to harmful cyanobacterial blooms (Carpenter et al., 1999; Scheffer et al., 1993). For many years since, tremendous management effort has been devoted to the restoration of aquatic plant communities, mainly through the reduction of external nutrient loading, especially phosphorus (P) (Cullen and Forsberg, 1988; Hilt et al., 2006; Jeppesen et al., 2005). Although lakes in the turbid state may also be resilient to changes in external environmental conditions (Hosper, 1998), reduction of external nutrient loading is effective in the long run (Jeppesen et al., 2005), and many of the impacted lakes have recovered or are now recovering to a clear-water state with submerged macrophytes (Gulati and Van Donk, 2002; Sondergaard and Moss, 1998).

Almost inevitable, the return of aquatic plants is accompanied by nuisance caused by these plants (e.g. van Donk 1990). The nutrient availability in restored lakes is generally still rather high, which in combination with improved light conditions allows for rampant growth of rooted macrophytes (Lamers et al., 2012). These dense stands of aquatic plants cause nuisance to boaters, swimmers and anglers, and impact other functions and services such as the retention and discharge capacity of the lake (Anderson, 2003; Van Nes et al., 1999). As a result, current management practices are more and more focusing on the reduction of aquatic plants, even though the re-establishment of an aquatic plant community is still considered a prerequisite for the long-term success of lake restoration measures (Van Nes et al., 2002). In many rapidly developing countries nuisance growth of aquatic plants is also readily apparent (Van Ginkel, 2011). There, the increased availability of nutrients stimulates plant growth in precedence of a regime shift to a phytoplankton dominated state – a part of eutrophication which also occurred in the temperate lakes before the submerged macrophytes disappeared *en mass* during the last century (Hasler, 1947).

A common response to excessive growth of submerged macrophytes is mechanical cutting and harvesting. Though cost- and labor-intensive, this option is generally preferred over biological control by e.g. grass carp or the use of herbicides (Hilt et al., 2006). However, when lakes have alternative stable states, defining a sustainable mowing regime is challenging, given the important role of macrophytes in stabilizing the clear water state. Theory predicts that when a critical, in practice unknown, amount of vegetation is removed, positive feedbacks propel the system to the turbid state with phytoplankton dominance (Scheffer et al., 1993; Van Nes et al., 2002). When less vegetation is removed, on the other hand, the system may show a swift recovery back to the vegetated equilibrium state, undoing the impact of mowing. Van Nes et al. (2002) applied two dynamic aquatic plant models of different complexity to analyze the response of aquatic plant populations to harvesting and concluded that it may be almost impossible to maintain vegetation biomass at any desired intermediate level. Consequently, Van Nes et al. (1999, 2002) suggest it may be more fruitful to assign just a few key functions to entire lakes, than to pursue a compromise between conflicting destinations. In most cases however, lake managers do not have the luxury to divide functions over different lakes, also due to legal obligations, such as the Water Framework Directive (European Union, 2000).

A potentially viable option is to aim for a temporal relief of nuisance following a discrete mowing event. When this period of relief coincides with the moment users are relying on the services provided by the lake, mowing can be convenient despite eventual recovery to the vegetated equilibrium state. Van Nes et al. (2002) did not consider the temporal aspects of mowing in their plant modelling study, as they assumed continuous cutting strategies for simplicity. Yet it remains a tall order for water quality managers to estimate the amount of plant volume that can be safely removed, and predict the period of relief of nuisance after mowing. The numerous field and laboratory studies that have investigated the response of macrophytes and phytoplankton to harvesting (e.g. Engel 1990; Nichols and Lathrop 1994; Barrat-Segretain and Amoros 1996; Morris et al. 2003; Bal et al. 2006; Morris et al. 2006) did not bring general applicable insights as the results were ambiguous. Moreover, lake managers in NW Europe often lack experience as submerged macrophytes were missing for a long time, while formal decision support schemes are basically absent (Hilt et al., 2006). We argue that there is a need for an integrated analysis to obtain a better understanding of the general consequences of plant removal in relation to trophic state and ecosystem resilience.

In this research we use a comprehensive dynamic ecosystem model - PCLake - to study the effect of mowing on shallow lake ecosystems with alternative stable states. This model describes the main nutrient and food web dynamics of a non-stratifying shallow lake in response to eutrophication and re-oligotrophication (Janse and van Liere, 1995; Janse, 1997), including many feedback mechanisms and processes that have been associated with plants and alternative stable states in lakes. Firstly, we evaluate how the impact of mowing depends on the trophic status of the lake (i.e. external nutrient loading), mowing intensity and timing of mowing during the growing season. We express the effect of mowing both in terms of remaining plant cover, and in terms of days without nuisance caused either by macrophytes or cyanobacteria. This exercise also allows us to evaluate under which conditions mechanical cutting of macrophytes results in a critical regime shift to the alternative turbid state. Secondly, we use the model to obtain quantitative estimations of the amount of P that can be removed from the system via harvesting of macrophytes. Removal of P may help to remediate eutrophication effects in the lake, and potentially can be recovered for sustainable reuse. Finally, we explore the long term impacts of mowing to analyze whether mowing is a measure that also can be applied to help prevent undesired eutrophication effects in shallow lakes.

Methods

Model description

General features

PCLake consists of a number of coupled ordinary differential equations and auxiliary equations which describe the most important biotic and abiotic components of both the water column and the sediment top-layer of a non-stratifying shallow lake (Janse 1997; see Online Resource 1 for a schematic overview of the model). By putting equal emphasis on the biotic and abiotic components, the model is unique in its kind (Janssen et al., 2015). All organic components are modelled in dry-weight (DW), nitrogen (N) and phosphorus (P). An important stoichiometric consequence is that the nutrient-to-dry-weight ratios of the organic components are variable. Other key ecological concepts covered by the model are: closed nutrient cycles, benthic-pelagic coupling, food-web dynamics and trophic cascade. PCLake has been calibrated with data from more than 40 temperate lakes to obtain a best overall fit, making the model suitable for more generalized studies on temperate shallow lakes (Janse et al., 2010).

Alternative stable states

The PCLake model shows a nonlinear response to changing nutrient loadings, similar to examples studied in the field (Janse, 1997). Lakes with a low external nutrient loading are in the clear-water macrophyte-dominated state with low chlorophyll-*a* concentrations. Lakes that receive a high external nutrient input reside in a turbid phytoplankton dominated state. In between, a fairly abrupt shift between the contrasting states takes place. The *critical nutrient loading* for a shift from a clear to a turbid state during eutrophication (CNL_{eu}) is at a much higher value than the critical nutrient loading where the reverse switch takes place, back to clear conditions during re-oligotrophication (CNL_{oligo}). Hence, at intermediate loading levels both the clear-water state and the turbid water state can exist as alternative stable states and the prevalent state depends on the foregoing conditions - a phenomenon known as hysteresis. Between the critical nutrient loading values, strong perturbations, such as discrete mowing events, may instigate a regime shift from one state to the other (Janse et al., 2008). Classical alternative stable states theory predicts that a lake is more vulnerable to disturbances closer to a tipping point, while the time it takes to recover from a perturbation increases (Van Nes and Scheffer, 2007).

Macrophytes

The submerged macrophytes in PCLake represent Waterweeds in general (*Elodea* spp.). Waterweed species are non-native in NW Europe and they are often among the first macrophytes to return after restoration measures have been taken (Heimans and Thijsse, 1895; Immers et al., 2015; Perrow et al., 1997; Pot and ter Heerdt, 2014). They are documented to cause nuisance by their mass development and are subject to mowing management (Hilt et al., 2006; Zehnsdorf et al., 2015). In PCLake, the growth of the submerged macrophytes (Fig. 1) is dependent on nutrient availability, temperature and under-water light availability. Plants take up phosphate, ammonium, and nitrate from both water column and soil pore water to achieve optimal P:biomass and N:biomass ratios (c.f. Droop 1974). Ammonium is preferred, but when the ammonium concentration is low, the plants switch to nitrate uptake. The available light for primary production forms a gradient with depth (Lambert–Beer's law) and is controlled by the light intensity at the water surface, which is set by a seasonal sine curve (based on long-term averages for Dutch solar irradiance), and by the light attenuation by the plants themselves (self-shading), phytoplankton, detritus and inorganic matter in the water column as well as background extinction. It is assumed that the growing season starts when a critical spring water temperature (9°C) is reached. This happens in mid-April, given the long-term averaged seasonal water temperature in Dutch lakes. The growing season ends half September onwards, when part of the above-ground biomass is allocated to the below ground biomass, and the mortality of the plants is raised for two weeks such that 30% of the original biomass survives, i.e. the over-wintering parts.

A mowing function is available in PCLake, which requires defining a date when the mowing event takes place, the duration of the mowing event and a mowing intensity (i.e. fraction of the biomass that is removed). The mowing intensity is independent of the duration of the mowing event: a natural logarithm is used to calculate the amount of biomass that is removed per day: $h = -ln(1.0–f)/p*V$, where h is the harvested biomass (g m^{-2} day^{-1}), f is the intensity (-), p is the duration (days) and V is the total aquatic plant biomass in the lake (g m^{-2}). We applied a 'clean' mowing strategy throughout this study, whereby all biomass is removed from the lake. We did briefly consider potentially harmful side effects of mowing however, including enhanced resuspension and incomplete removal of plant material from the water column, but present these findings as an appendix as they did not affect the conclusions of our main analyses (see Online Resource 2).

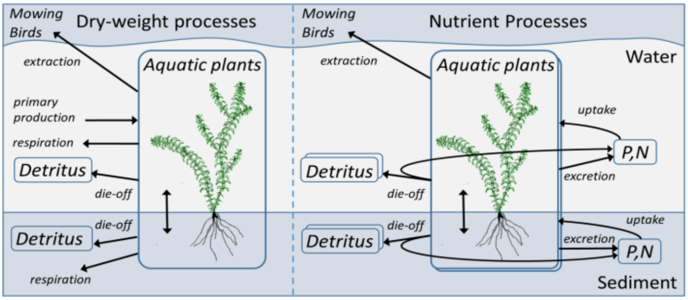


Figure 1 Basic processes of the aquatic plants in PCLake. The modelled processes are nutrient uptake, production, respiration and nutrient excretion, mortality, grazing by birds and mowing. The nutrient processes are modelled both in phosphorus and nitrogen. Herbivory by birds was not considered in this study. The figure is adapted from Janse (2005).

Implementation

We used default parameter settings describing a lake that is representative for many shallow lakes in the temperate zone, with a mean depth of 2 m, a 1000 m fetch, a water inflow of 20 mm d^{-1} (100 day residence time), a lightly clayish soil (30% dry matter, of which 10% organic matter, and 10% lutum), no infiltration or seepage and no surrounding wetland area (c.f. Janse et al. 2010). The N:P ratio of the external nutrient loading was set at 13, i.e. the estimated average N:P ratio for agricultural runoff in the Netherlands (Wolf et al., 2003). In this set-up, the calculated CNL_{eu} and CNL_{oligo} values are 1.6 and 0.9 mg P m^{-2} d^{-1} respectively. To run simulations we used a C++ compiled version of the PCLake model called from GRIND for MATLAB (Mooij et al., 2014).

Model simulations

Nutrient loading, mowing intensity and timing

To study the impact of mowing on the lake we varied three parameters of the model: (1) external nutrient loading, (2) mowing intensity and (3) timing of the mowing. We first focused on the interplay between the first two. We simulated different combinations of external P loading, ranging from 0.7 to 1.7 in steps of 0.05 (mg m^{-2} d^{-1}), and mowing intensity, ranging from 0 to 0.9 in steps of 0.1 (-). We did not consider P loadings above 1.7 mg m^{-2} d^{-1} as the modelled lake then resides in the turbid water state without macrophytes. Each simulation was started from a clear water state and we ran the model for 20 years before starting the mowing procedure to ensure the lake to be in (seasonal) equilibrium. The initialization period was followed by three succeeding years where a mowing event took place. We considered three years to include the effect of mowing on the biomass in the next year (Kimbel and Carpenter, 1981). Each of the mowing years comprised one discrete mowing event, taking place on July 1st. This is in compliance with the guidelines provided by Rijkswaterstaat, responsible for the management of the main waterways and water systems in the Netherlands, who discourage mowing during the avian breeding season (Rijkswaterstaat, 2012). The duration of the mowing event (*p*) was kept at the default value of 10 days in all of these and subsequent cases. Next, we repeated the foregoing simulations, but this time focusing on different combinations of mowing intensity and timing. Again the mowing intensity ranged from 0 to 0.9 in steps of 0.1, while the mowing dates ranged from June 1st to September 1st in steps of 7 days. We performed this analysis for three different nutrient loading settings (0.8, 1.1 and 1.4 g P m^{-2} d^{-1}, respectively).

To evaluate the effects of the mowing actions we analyzed the summer average (June 10th to September 15th) vegetation cover and total and cyanobacterial chlorophyll-*a* concentration in the final year of the simulations. In the model, the vegetation cover increases linearly with the dry weight (DW) of submerged plants until 200 g DW m^{-2} is reached and the cover is 100%. Also, we calculated the days with nuisance during the peak of the holiday season (beginning of July until the end of August) caused by either submerged water plants or cyanobacteria. We presumed that water plants cause nuisance when they cover more than 40% of the area. For the cyanobacteria, we followed the Dutch cyanobacteria protocol and took 12,5 mg m^{-3} cyano-chlorophyll as a limit above which nuisance occurs (Nationaal Water Overleg, 2012). Short-time human exposure to concentrations higher than this value can cause skin rashes or gastrointestinal sickness, and this risk should be communicated to bathing guests.

Additionally, we zoomed in on one intermediate nutrient loading (1.3 mg P m^{-2} d^{-1}) and present the within-season dynamics of the vegetation cover and chlorophyll-*a* in response to several different mowing intensities, to also obtain a more detailed view on the dynamics of the lake.

Nutrient removal by harvesting

We kept track of the amount of P stored in aquatic plant biomass which was harvested from the system in the final (third) year of mowing, to evaluate the potential to impoverish the lake. The amount of P removed from the system via harvesting provides an indication of the P that can potentially be recovered for reuse. In addition, we calculated the relative removal of P, that is, the ratio of P in the harvested biomass to the total amount of P added to the system via external loading. The relative removal thus allows to assess the extent to which harvesting may contribute to the closing of the P cycle.

Prolonged mowing and the resilience to nutrient loading

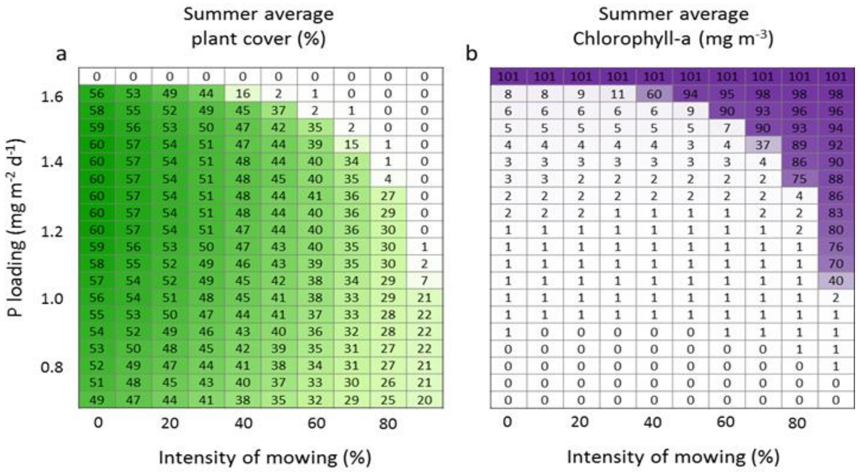
We used PCLake to analyze whether harvesting of macrophytes has the potential to forestall eutrophication effects in the long run. More precisely, we analyzed how repeated annual harvesting changes the CNL_{eu} of the lake, that is, the amount of external nutrient loading the lake can withstand without switching to a phytoplankton-dominated turbid state. Following Janse et al. (2008), we calculated CNL_{eu} values for different combinations of mowing intensity and timing, for which we took the same ranges as presented in the foregoing analysis. For each combination the model was evaluated for P loading rates ranging from 0.1

to 4 mg P m^{-2} day^{-1} in steps of 0.1. Each simulation started with a clear and oligotrophic lake. The summer average Secchi depth (m) after 20 years was used to evaluate the state of the lake, to determine which P loading is the CNL$_{eu}$. Previous analyses have shown that the ratio of Secchi depth to lake depth is a suitable response variable to determine the CNL$_{eu}$ (c.f. Witteveen+Bos 2010; Lischke et al. 2014): above a ratio of 0.5 the lake is defined as clear, while below this ratio the lake is defined as turbid. Mowing took place in each of the 20 years and comprised one discrete mowing event lasting the standard 10 days.

Results

Nutrient loading and mowing intensity

The model shows that the summer average plant cover can be reduced by mowing (Fig. 2a). When external nutrient loading is low, plant cover shows an almost linear decrease with increasing mowing intensity. At high nutrient loadings however, mowing can trigger a regime shift to an alternative state with high phytoplankton concentrations (Fig. 2b). The mowing intensity that leads to a regime shift shows a nonlinear relationship with nutrient loading; the critical mowing intensity decreases sharply when the external loading approaches the critical nutrient loading (1.61 mg m^{-2} d^{-1}). In the vicinity of the critical nutrient loading, a mowing intensity of >30% is sufficient to trigger a collapse.



	0		20		40		60		80	
	0	0	0	0	0	0	0	0	0	0
1.6	56	53	49	44	16	2	1	0	0	0
	58	55	52	49	45	37	2	1	0	0
	59	56	53	50	47	42	35	2	0	0
	60	57	54	51	47	44	39	15	1	0
1.4	60	57	54	51	48	44	40	34	1	0
	60	57	54	51	48	45	40	35	4	0
	60	57	54	51	48	44	41	36	27	0
	60	57	54	51	48	44	40	36	29	0
1.2	60	57	54	51	47	44	40	36	30	0
	59	56	53	50	47	43	40	35	30	1
	58	55	52	49	46	43	39	35	30	2
	57	54	52	49	45	42	38	34	29	7
1.0	56	54	51	48	45	41	38	33	29	21
	55	53	50	47	44	41	37	33	28	22
	54	52	49	46	43	40	36	32	28	22
	53	50	48	45	42	39	35	31	27	22
0.8	52	49	47	44	41	38	34	31	27	21
	51	48	45	43	40	37	33	30	26	21
	49	47	44	41	38	35	32	29	25	20

0		20		40		60		80	
101	101	101	101	101	101	101	101	101	101
8	8	9	11	60	94	95	98	98	98
6	6	6	6	6	9	90	93	96	96
5	5	5	5	5	5	7	90	93	94
4	4	4	4	4	3	4	37	89	92
3	3	3	3	3	3	3	4	86	90
3	3	2	2	2	2	2	2	75	88
2	2	2	2	2	2	2	2	4	86
2	2	2	1	1	1	1	2	2	83
1	1	1	1	1	1	1	1	2	80
1	1	1	1	1	1	1	1	1	76
1	1	1	1	1	1	1	1	1	70
1	1	1	1	1	1	1	1	1	40
1	1	1	1	1	1	1	1	1	2
1	1	1	1	1	1	1	1	1	1
1	0	0	0	0	0	1	1	1	1
0	0	0	0	0	0	0	0	1	1
0	0	0	0	0	0	0	0	0	1
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0

Figure 2 Combined effects of mowing intensity and nutrient loading on summer average plant coverage (**a**) and chlorophyll-*a* (**b**) in the final year of the simulations. Mowing starts on July 1st.

Zooming in on the seasonal dynamics clearly reveals the time window where plant cover is reduced due to mowing lasting for at least several weeks (Fig. 3a). It also shows that, apart from the average plant cover, the maximum plant cover reached during the growing season is also lowered with increasing mowing intensity. A detailed look reveals the importance of considering three succeeding years: the 90% mowing treatment triggers a regime shift, which only becomes apparent in the second and third year, when the plant community collapses and phytoplankton blooms start to occur (Fig. 3b).

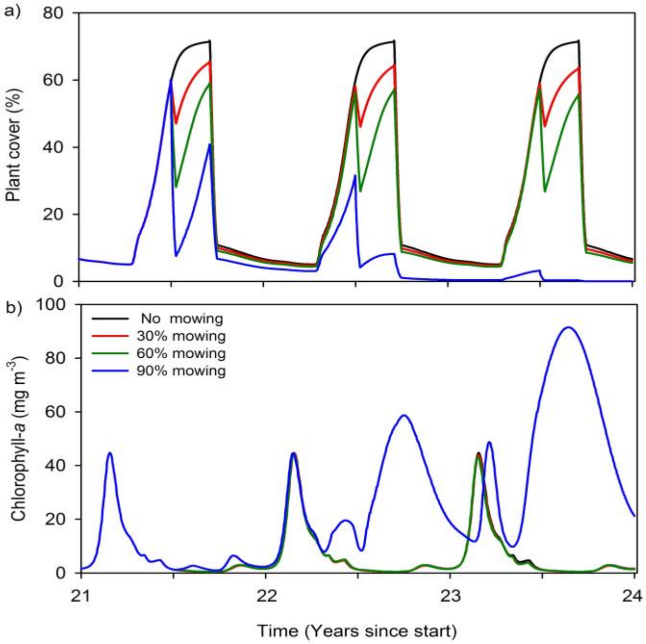


Figure 3 Effects of mowing on July 1st on summer average plant coverage (**a**) and chlorophyll-*a* (**b**) in three succeeding years for a lake receiving 1.3 mg P m^{-2} day^{-1}.

An important question is how the response of the ecosystem to mowing translates to nuisance experienced by lake users. Our approach illustrates that there is a sharp boundary between nuisance caused by macrophytes and nuisance caused by cyanobacteria when the nutrient loading is high (Fig. 4a-c). On the other hand, when the nutrient loading is fairly low (<1 mg m^{-2} day^{-1}), mowing can create conditions where hardly any nuisance is experienced during the peak of the summer holiday season (Fig. 4c), given that a substantial fraction of the submerged macrophytes is removed (>50%).

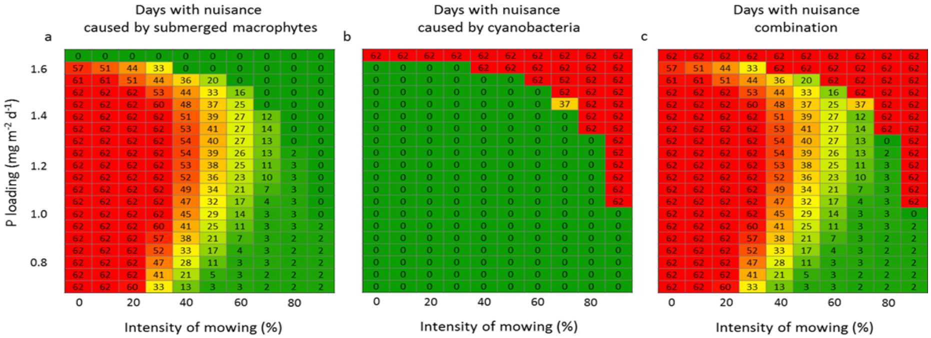
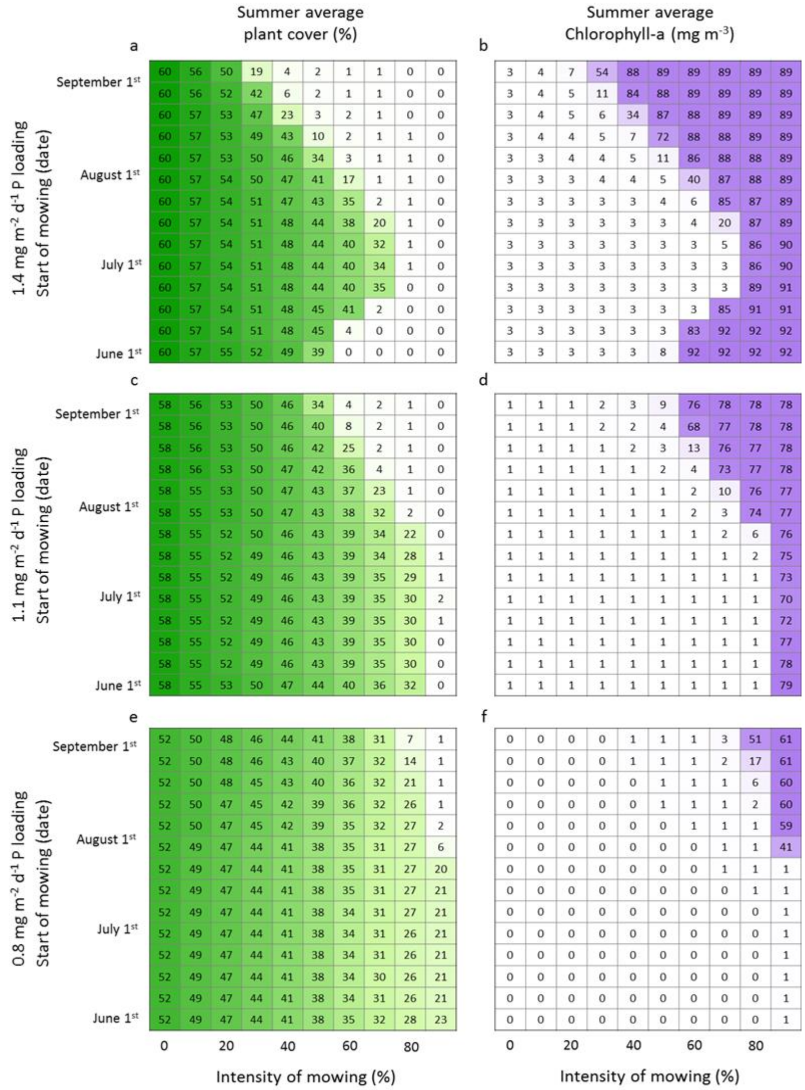


Figure 4 Combined effects of mowing intensity and nutrient loading on days with nuisance caused by plants (**a**), cyanobacteria (**b**) or both plants and cyanobacteria (**c**) during July and August (peak of the holiday season in the temperate region) in the final year of the simulations. Mowing starts on July 1st.

Timing of mowing

The impact of harvesting varies during the growing season (Fig. 5), particularly when the external nutrient loading is high (Fig. 5a-b) and the lake is susceptible to a regime shift (Fig. 2a-b). When the nutrient loading is high, the modelled lake is most vulnerable in late summer, when harvesting a fraction of 40% is sufficient to instigate a regime shift to the phytoplankton dominated state. To a somewhat lesser extent, also mowing in early summer eases a shift to the turbid state. The resilience of the modelled lake is highest during mid-summer, as up to 80% of the vegetation can be removed, resulting in a halving of the summer average plant cover (Fig. 5a-b). The timing of mowing is not particularly important when the external nutrient loading is low (Fig. 5e,f). Large fractions of the plant biomass can be removed almost the entire growing season without risking a regime shift, allowing to reduce the summer average plant cover up to 40%.



a

September 1st	60	56	50	19	4	2	1	1	0	0
	60	56	52	42	6	2	1	1	0	0
	60	57	53	47	23	3	2	1	0	0
	60	57	53	49	43	10	2	1	1	0
	60	57	53	50	46	34	3	1	1	0
August 1st	60	57	54	50	47	41	17	1	1	0
	60	57	54	51	47	43	35	2	1	0
	60	57	54	51	48	44	38	20	1	0
	60	57	54	51	48	44	40	32	1	0
July 1st	60	57	54	51	48	44	40	34	1	0
	60	57	54	51	48	44	40	35	0	0
	60	57	54	51	48	45	41	2	0	0
	60	57	54	51	48	45	4	0	0	0
June 1st	60	57	55	52	49	39	0	0	0	0

b

September 1st	3	4	7	54	88	89	89	89	89	89
	3	4	5	11	84	88	89	89	89	89
	3	4	5	6	34	87	88	89	89	89
	3	4	4	5	7	72	88	88	89	89
	3	3	4	4	5	11	86	88	88	89
August 1st	3	3	3	4	4	5	40	87	88	89
	3	3	3	3	3	4	6	85	87	89
	3	3	3	3	3	3	4	20	87	89
	3	3	3	3	3	3	3	5	86	90
July 1st	3	3	3	3	3	3	3	3	86	90
	3	3	3	3	3	3	3	3	89	91
	3	3	3	3	3	3	3	85	91	91
	3	3	3	3	3	3	83	92	92	92
June 1st	3	3	3	3	3	8	92	92	92	92

c

September 1st	58	56	53	50	46	34	4	2	1	0
	58	56	53	50	46	40	8	2	1	0
	58	56	53	50	46	42	25	2	1	0
	58	56	53	50	47	42	36	4	1	0
	58	55	53	50	47	43	37	23	1	0
August 1st	58	55	53	50	47	43	38	32	2	0
	58	55	52	50	46	43	39	34	22	0
	58	55	52	49	46	43	39	34	28	1
	58	55	52	49	46	43	39	35	29	1
July 1st	58	55	52	49	46	43	39	35	30	2
	58	55	52	49	46	43	39	35	30	1
	58	55	52	49	46	43	39	35	30	0
	58	55	52	49	46	43	39	35	30	0
June 1st	58	55	53	50	47	44	40	36	32	0

d

September 1st	1	1	1	2	3	9	76	78	78	78
	1	1	1	2	2	4	68	77	78	78
	1	1	1	1	2	3	13	76	77	78
	1	1	1	1	1	2	4	73	77	78
	1	1	1	1	1	1	2	10	76	77
August 1st	1	1	1	1	1	1	2	3	74	77
	1	1	1	1	1	1	1	2	6	76
	1	1	1	1	1	1	1	1	2	75
	1	1	1	1	1	1	1	1	1	73
July 1st	1	1	1	1	1	1	1	1	1	70
	1	1	1	1	1	1	1	1	1	72
	1	1	1	1	1	1	1	1	1	77
	1	1	1	1	1	1	1	1	1	78
June 1st	1	1	1	1	1	1	1	1	1	79

e

September 1st	52	50	48	46	44	41	38	31	7	1
	52	50	48	46	43	40	37	32	14	1
	52	50	48	45	43	40	36	32	21	1
	52	50	47	45	42	39	36	32	26	1
	52	50	47	45	42	39	35	32	27	2
August 1st	52	49	47	44	41	38	35	31	27	6
	52	49	47	44	41	38	35	31	27	20
	52	49	47	44	41	38	35	31	27	21
	52	49	47	44	41	38	34	31	27	21
July 1st	52	49	47	44	41	38	34	31	26	21
	52	49	47	44	41	38	34	31	26	21
	52	49	47	44	41	38	34	30	26	21
	52	49	47	44	41	38	34	31	26	21
June 1st	52	49	47	44	41	38	35	32	28	23
	0		20		40		60		80	

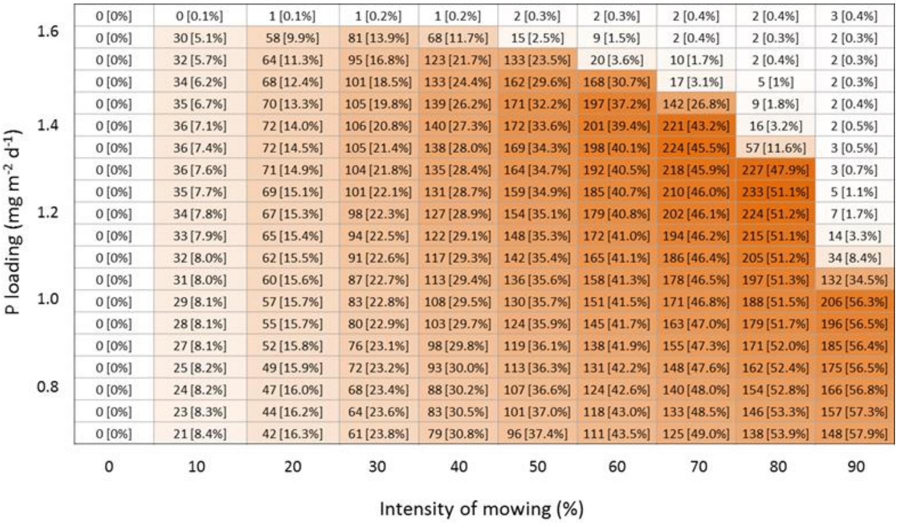
f

September 1st	0	0	0	0	1	1	1	3	51	61
	0	0	0	0	1	1	1	2	17	61
	0	0	0	0	0	1	1	1	6	60
	0	0	0	0	0	1	1	1	2	60
	0	0	0	0	0	0	1	1	1	59
August 1st	0	0	0	0	0	0	0	1	1	41
	0	0	0	0	0	0	0	1	1	1
	0	0	0	0	0	0	0	0	1	1
	0	0	0	0	0	0	0	0	0	1
July 1st	0	0	0	0	0	0	0	0	0	1
	0	0	0	0	0	0	0	0	0	1
	0	0	0	0	0	0	0	0	0	1
	0	0	0	0	0	0	0	0	0	1
June 1st	0	0	0	0	0	0	0	0	0	1
	0		20		40		60		80	

Figure 5 Combined effects of mowing intensity and mowing date on summer average plant coverage and chlorophyll-*a* in the final year of the simulations, for three different nutrient loadings: 1.4, 1.1 and 0.8 mg m^{-2} day^{-1}, respectively.

Nutrient removal by mowing

The amount of P harvested from the lake during a mowing event increases with mowing intensity and nutrient loading, and is highest close to the point where mowing leads to a regime shift, reaching a maximum of almost 230 mg P m^{-2}. The relative removal of P increases with mowing intensity and can be as high as 58%. However, the relative removal decreases with increasing nutrient loading. The associated dry-weight of the harvested plant biomass is presented in Online Resource 3.



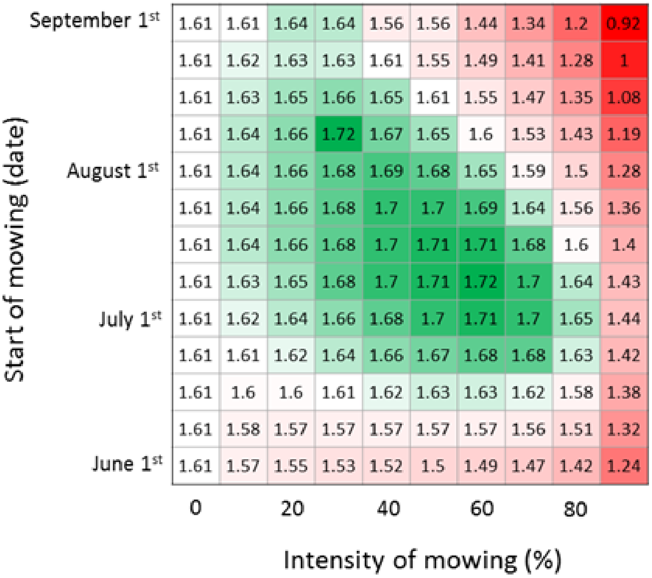
P loading ($mg\ m^{-2}\ d^{-1}$)	0	10	20	30	40	50	60	70	80	90
	0 [0%]	0 [0.1%]	1 [0.1%]	1 [0.2%]	1 [0.2%]	2 [0.3%]	2 [0.3%]	2 [0.4%]	2 [0.4%]	3 [0.4%]
1.6	0 [0%]	30 [5.1%]	58 [9.9%]	81 [13.9%]	68 [11.7%]	15 [2.5%]	9 [1.5%]	2 [0.4%]	2 [0.3%]	2 [0.3%]
	0 [0%]	32 [5.7%]	64 [11.3%]	95 [16.8%]	123 [21.7%]	133 [23.5%]	20 [3.6%]	10 [1.7%]	2 [0.4%]	2 [0.3%]
	0 [0%]	34 [6.2%]	68 [12.4%]	101 [18.5%]	133 [24.4%]	162 [29.6%]	168 [30.7%]	17 [3.1%]	5 [1%]	2 [0.3%]
	0 [0%]	35 [6.7%]	70 [13.3%]	105 [19.8%]	139 [26.2%]	171 [32.2%]	197 [37.2%]	142 [26.8%]	9 [1.8%]	2 [0.4%]
1.4	0 [0%]	36 [7.1%]	72 [14.0%]	106 [20.8%]	140 [27.3%]	172 [33.6%]	201 [39.4%]	221 [43.2%]	16 [3.2%]	2 [0.5%]
	0 [0%]	36 [7.4%]	72 [14.5%]	105 [21.4%]	138 [28.0%]	169 [34.3%]	198 [40.1%]	224 [45.5%]	57 [11.6%]	3 [0.5%]
	0 [0%]	36 [7.6%]	71 [14.9%]	104 [21.8%]	135 [28.4%]	164 [34.7%]	192 [40.5%]	218 [45.9%]	227 [47.9%]	3 [0.7%]
	0 [0%]	35 [7.7%]	69 [15.1%]	101 [22.1%]	131 [28.7%]	159 [34.9%]	185 [40.7%]	210 [46.0%]	233 [51.1%]	5 [1.1%]
1.2	0 [0%]	34 [7.8%]	67 [15.3%]	98 [22.3%]	127 [28.9%]	154 [35.1%]	179 [40.8%]	202 [46.1%]	224 [51.2%]	7 [1.7%]
	0 [0%]	33 [7.9%]	65 [15.4%]	94 [22.5%]	122 [29.1%]	148 [35.3%]	172 [41.0%]	194 [46.2%]	215 [51.1%]	14 [3.3%]
	0 [0%]	32 [8.0%]	62 [15.5%]	91 [22.6%]	117 [29.3%]	142 [35.4%]	165 [41.1%]	186 [46.4%]	205 [51.2%]	34 [8.4%]
	0 [0%]	31 [8.0%]	60 [15.6%]	87 [22.7%]	113 [29.4%]	136 [35.6%]	158 [41.3%]	178 [46.5%]	197 [51.3%]	132 [34.5%]
1.0	0 [0%]	29 [8.1%]	57 [15.7%]	83 [22.8%]	108 [29.5%]	130 [35.7%]	151 [41.5%]	171 [46.8%]	188 [51.5%]	206 [56.3%]
	0 [0%]	28 [8.1%]	55 [15.7%]	80 [22.9%]	103 [29.7%]	124 [35.9%]	145 [41.7%]	163 [47.0%]	179 [51.7%]	196 [56.5%]
	0 [0%]	27 [8.1%]	52 [15.8%]	76 [23.1%]	98 [29.8%]	119 [36.1%]	138 [41.9%]	155 [47.3%]	171 [52.0%]	185 [56.4%]
	0 [0%]	25 [8.2%]	49 [15.9%]	72 [23.2%]	93 [30.0%]	113 [36.3%]	131 [42.2%]	148 [47.6%]	162 [52.4%]	175 [56.5%]
0.8	0 [0%]	24 [8.2%]	47 [16.0%]	68 [23.4%]	88 [30.2%]	107 [36.6%]	124 [42.6%]	140 [48.0%]	154 [52.8%]	166 [56.8%]
	0 [0%]	23 [8.3%]	44 [16.2%]	64 [23.6%]	83 [30.5%]	101 [37.0%]	118 [43.0%]	133 [48.5%]	146 [53.3%]	157 [57.3%]
	0 [0%]	21 [8.4%]	42 [16.3%]	61 [23.8%]	79 [30.8%]	96 [37.4%]	111 [43.5%]	125 [49.0%]	138 [53.9%]	148 [57.9%]

Intensity of mowing (%)

Figure 6 The amount of P (mg m^{-2} $year^{-1}$) extracted from the system via harvesting of plant biomass during the last year of mowing, for different combinations of external nutrient loading and mowing intensity. The orange color indicates the quantity. The relative removal, that is, the ratio of P in the harvested biomass to the total amount of P added to the system via external loading, is presented between squared brackets (%).

Prolonged mowing and resilience

Our model exercises show that in the long run repeated mowing is able to enhance the resilience of the clear water state to nutrient loading for a wide range of mowing intensities and mowing dates, as it leads to an increase (max. 7%) of the critical nutrient loading (CNL_{eu} > 1.61 mg P m^{-2} d^{-1}; Fig. 7). Mowing during July and August in combination with an intermediate mowing intensity is most beneficial for enhancing the CNL_{eu}. Mowing in early-summer or in late-summer can lead to a reduced resilience to nutrient loading (CNL_{eu} < 1.61 mg P m^{-2} d^{-1}).



Start of mowing (date)	0		20		40		60		80	
September 1st	1.61	1.61	1.64	1.64	1.56	1.56	1.44	1.34	1.2	0.92
	1.61	1.62	1.63	1.63	1.61	1.55	1.49	1.41	1.28	1
	1.61	1.63	1.65	1.66	1.65	1.61	1.55	1.47	1.35	1.08
	1.61	1.64	1.66	1.72	1.67	1.65	1.6	1.53	1.43	1.19
August 1st	1.61	1.64	1.66	1.68	1.69	1.68	1.65	1.59	1.5	1.28
	1.61	1.64	1.66	1.68	1.7	1.7	1.69	1.64	1.56	1.36
	1.61	1.64	1.66	1.68	1.7	1.71	1.71	1.68	1.6	1.4
	1.61	1.63	1.65	1.68	1.7	1.71	1.72	1.7	1.64	1.43
July 1st	1.61	1.62	1.64	1.66	1.68	1.7	1.71	1.7	1.65	1.44
	1.61	1.61	1.62	1.64	1.66	1.67	1.68	1.68	1.63	1.42
	1.61	1.6	1.6	1.61	1.62	1.63	1.63	1.62	1.58	1.38
	1.61	1.58	1.57	1.57	1.57	1.57	1.57	1.56	1.51	1.32
June 1st	1.61	1.57	1.55	1.53	1.52	1.5	1.49	1.47	1.42	1.24

Figure 7 Effect of prolonged (long term) mowing on the CNL_{eu} (mg P m^{-2} d^{-1}), i.e. the amount of nutrient input the lake can withstand without shifting to the turbid water state, for different combinations of mowing intensity and timing (start of the mowing procedure). The colors indicate whether mowing leads to an increase (green) or decrease (red) of the critical nutrient loading (default 1.61 mg m^{-2} day^{-1}).

Discussion

Temporal relief of nuisance

Our modelling study shows that mowing can result in a temporal reduction of plant cover for a range of nutrient loadings and mowing intensities. These reductions of plant cover can reduce nuisance for up to several weeks, especially when the mowing intensity is fairly high and the external nutrient loading is low or moderate. Our model thus indicates that mowing can facilitate multi-usage of shallow lake ecosystems. At lower intensities mowing also reduces the summer average plant cover, but this may be not sufficient to actually reduce nuisance as the remaining cover still exceeded the threshold level, which we fixed at 40%. Our model analyses indicate that it is difficult to design a convenient mowing strategy when the external nutrient loading is high; the attraction of the alternative equilibrium is so strong that a rather small reduction in plant volume may be sufficient to trigger a shift to phytoplankton dominance. Interestingly, our results elucidate that a reduction of external nutrient loading alone is not an effective measure to drive back nuisance caused by aquatic plants (Fig. 4), which emphasizes the need for mowing. Because the risk of inducing a regime shift by mowing increases with external nutrient loading, the successfulness of mowing to reduce macrophyte nuisance goes hand in hand with the reduction of external nutrient loading.

The importance of timing of mowing

Our model analyses indicate that the highest reductions of plant biomass can be achieved by mowing in mid-summer, while mowing in late summer appears to be least recommendable. The latter is not just because the peak of the holiday season (and thus recreational usage) is in mid-summer, but also because the risk of inducing a regime shift increases when mowing is conducted later in the growing season. In our model, mowing late in the growing season provides the aquatic plants with little opportunity to regain biomass before the growing season ends. As a result, the macrophytes start the competition with phytoplankton in the following spring on their back foot, which eases a shift to phytoplankton dominance (Scheffer 2004, P. 280). Mowing too early in the growing season also bears a certain risk of triggering a regime shift, as our study showed, particularly when the external nutrient loading is high. We hypothesize that this is because the *inter*-specific competition with phytoplankton in early June is still rather strong, and setting back the submerged macrophytes favors phytoplankton growth. At the peak of the growing season, on the other hand, the *intra*-specific competition among macrophytes becomes more controlling, and mowing reliefs this intraspecific competition. Hence, the net growth rate of the macrophytes directly after mowing relates positively to mowing intensity (e.g. Fig. 2: the net growth rate after 30% and 60% mowing is 0.017 and 0.022 day^{-1}, respectively). This compensatory growth is not sufficient however to compensate for the entire loss of biomass, as plant cover does not recover to pre-harvesting levels (Fig. 2).

The effect of timing on the impact of mowing may be different in field situations, particularly when the macrophyte community comprises growth forms that - unlike e.g. *Elodea canadensis* - produce overwintering organs (Scheffer 2004, p.279). Hence, in case of propagule forming macrophyte species such as several *Potamogeton* and *Myriophyllum* species, these propagules may have already been formed when harvesting takes place late in the growing season, wherefore the impact on the next growing season is much smaller. Harvesting earlier in the season would then be an effective way to reduce the potential for macrophyte plant growth in the succeeding year, as that would prevent the formation of propagules (Wade, 1990). Interestingly, a reduction of plant volume in the succeeding year is generally considered as a positive result of harvesting (e.g. (Dall'Armellina et al., 1996), while our modelling study hints that this strategy is not without risks when lakes have alternative stable states and the external nutrient loading is high.

Restrictions to harvesting

In our model study we harvested fractions of the macrophytes to levels that may be unfeasible in real field situations. For example, there are practical reasons which frustrate harvesting large quantities of aquatic plants, as it is a labor-intensive and expensive activity. A simple calculation learns that for our modelled (circular) lake with a diameter of 1000 m, when receiving 1.2 mg P m^{-2} day^{-1}, a harvesting intensity of 80% implies removing more than 650 tons of fresh biomass in just a short time span, assuming a fresh-weight:dry-weight ratio of 10 (e.g. Boiché et al. 2011; Dorenbosch and Bakker 2011; Online Resource 3). Secondly, local laws and regulations, such as the Dutch flora- and fauna law, may impose restrictions on harvesting intensity and timing. Plants provide habitat and food for many species and it has been reported that significant amounts of fish and macroinvertebrates are removed along with the plants during harvesting (Engel, 1990), which may include protected species. Furthermore, removing large quantities of plants may conflict with the protection of waterbirds that feed on the plants or the fauna living in macrophyte beds. A third reason is that in a field situation it will always be difficult to estimate the amount of aquatic plants that should be present to safeguard a clear water state, forcing lake managers to take a conservative approach when designing their plans. Hence, even though a submerged plant cover as low as 20% may coincide with good water quality (e.g. Portielje and Van der Molen 1998; Yanran et al. 2012), Hilt et al. (2006) advise to take 50% vegetation cover as a rule of thumb, and suggest that remaining stands after harvesting should still cover 50% of the lake. Also the Dutch authorities advise to remove maximally 50% of the plant cover, and even suggests to mow only 10% in case of native plant species (Rijkswaterstaat, 2012).

Spatial heterogeneity

From our analyses it appears that harvesting 10% of the standing crop has only a marginal effect on reducing nuisance. This situation may change however when it is possible and desirable to spatially divide functions over the lake area. By harvesting in such a way that only certain patches are cleared, it may become possible to reduce nuisance locally e.g. in a zone designated for swimming or a channel for navigation. The model we used (PCLake) is not spatially explicit and is therefore no suited to evaluate the effect of a local disturbance by harvesting, as it is intended to provide a general indication of the harvesting pressure the lake can withstand. There is only little known about the effect of spatial heterogeneity on alternative stable states in shallow lakes. Theoretical studies suggest that the potential of local disturbances to instigate an ecosystem-wide regime shift increases with interconnectedness (dispersion) within the system (Van Nes and Scheffer, 2005b), and decreases with spatial heterogeneity (Van de Leemput et al., 2015). These studies thus suggest that alternative stable states are unlikely to persist side by side in lakes which are very homogenous. This means that local mowing becomes risky as over-harvesting has catastrophic consequences for the entire lake, albeit the regime shift may be gradual (Bel et al., 2012; Van de Leemput et al., 2015). When lakes do exhibit spatial heterogeneity e.g. in terms of depth, fetch or sediment composition, the response to a local perturbation becomes much more difficult to predict (Van de Leemput et al., 2015), but this heterogeneity can potentially lead to coexistence of contrasting states. The latter would create opportunities for localized harvesting practices. A follow up step is to couple the ecological modules of PCLake to 2D-hydrodynamic models to analyze harvesting in a spatial hydrodynamic context. This development is still in its infancy however (e.g. Van Gerven et al., 2015a).

Collateral effects

Generally, not all cut plant biomass is removed from the lake due to inefficiency of the harvesting equipment. The fragments that are not collected start to decompose in the water column, thereby releasing nutrients and contributing to the depletion of oxygen which in turn can stimulate internal nutrient loading from the sediment (Hilt et al., 2006). Additionally, cutting machinery may cause resuspension of sediments, which may reduce transparency and stimulate nutrient recycling. These side-effects of mowing are expected to be detrimental to ecosystem functioning (Rijkswaterstaat, 2012), but it is difficult to quantify their true importance in the field. For simplicity reasons, we did not consider the effect of collateral disturbance in our main analyses. Yet, we did briefly look into their relative importance (presented as Online Resource 2), which revealed that, for the modelled circumstances, the effect of collateral damage is marginal. This finding is in line with Carpenter and Gasith (1978) who reported short lived or insignificant effects on the littoral environment after clearing a 0.2 ha patch. Only when a regime shift has already been initiated, our model shows that the collateral effects of mowing stimulate the upheaval (Online Resource 2). A factor we did not consider in this study is that many nuisance species (including *Elodea* spp.) spread by vegetative fragmentation (Hilt et al., 2006). Mowing can stimulate dispersal of non-native nuisance species when fragments are produced that easily ride with the flow and settle at new places (Abernethy et al., 1996). Especially when surrounding lakes or waterways are still free of these exotics, the dispersal capacity of the plant should be taken into consideration.

Nutrient removal and recovery

Because there are nutrients stored in the plant tissue, the removal of submerged plants may help to remediate the detrimental effects of eutrophication, both in the lake where the plants are removed from, and in downstream aquatic ecosystems (Carpenter and Adams, 1977). Our modelling scenarios indicate that the highest amounts of P is extracted from the system when both the external P loading and the mowing intensity are high. The relative removal however, which tells more about the capacity to actually impoverish the system via harvesting, increases with decreasing nutrient loading, maximally reaching 58% in our analyses. The numbers we found are grossly in line with estimations in the literature. For a eutrophic lake with 30% plant cover, Carpenter and Adams (1977) estimated that a relative removal of 37% of the P loading could be established if all plants would be harvested. Conyers and Cooke (1983) reported that a relative removal of 44% could be reached in a mesotrophic lake with 43% plant cover.

Harvested plant tissue can potentially serve as a source of nutrients, instead of only being waste material. The use of aquatic plant biomass to fertilize agriculture fields is an old practice (Roger and Watanabe, 1984), which is still carried out in many parts of mainly the developing world. Recently harvesting aquatic plant biomass has been put forward as a way to close the P cycle (Quilliam et al., 2015). Although excessive growth of macrophytes indicates a local surplus of nutrients, P is a scarce element in many places, leading to phosphate starvation in crops, and global phosphate sources are declining rapidly (Childers et al., 2011; Cordell et al., 2009). The recovery of valuable P thus has the potential to increase the viability of harvesting as a management measure, which is otherwise a costly procedure (Hilt et al., 2006). Currently there is no agreement on how to maximize P uptake and removal by macrophytes (Quilliam et al., 2015). Our model results suggest that it is beneficial for lake managers to reduce the external nutrient loading as much as possible, as that will reduce the possibility of harvesting triggering an unwanted regime shift to a state without macrophytes, and increase the relative removal of P.

Prolonged harvesting

Model analysis of the long-term effects of harvesting suggests that harvesting can potentially be used to prevent nutrient over-enrichment (Fig. 7). It is important to note however that in this analysis harvesting was executed every year, and that we started off with a clear and oligotrophic lake - in the domain where no alternative state is apparent. Because of the latter, almost all macrophytes can be removed at the start of the analysis without risking a shift to the alternative state, as there simply is none. In turn, the removal of macrophytes prevents the accumulation of nutrients in the system, postponing the formation of an alternative equilibrium. What this learns us is that the history of the lake is an important factor to consider. If nutrients have been able to accumulate in the lake prior to the mowing activities, as in our first analyses where we considered lakes in equilibrium, the resilience of the lake to perturbations may have already decreased and fairly small fractions of macrophyte removal may be enough to instigate a regime shift (see Online Resource 4 for an illustrative example). Based on our model analysis we thus argue that it is much harder to use macrophyte removal to impoverish a lake when it is already eutrophic, than to prevent a lake from becoming eutrophic by means of harvesting when it is still oligotrophic, even though the mowing intensities and external nutrient loading levels at the time of mowing may be exactly the same. As many vegetated lakes in NW Europe have only recently recovered from the turbid state, and their sediments are likely still saturated with nutrients, mowing plans should be designed with great care.

Pros and cons of a model approach

Our point of departure is that every water system is unique (n=1), but that there are general mechanisms that are key to the ecological functioning of every lake. PCLake has been developed to include to most important biotic and abiotic processes. Moreover, to strive for generality, the model has been calibrated with data from >40 lakes with the aim to get the best overall fit. Yet, not all processes that may be relevant in the field are included in the model however. For example, we considered only monocultures of *Elodea* spp. while other plant species may contribute differently to ecosystem functioning or respond differently to mowing (e.g. Van Zuidam and Peeters 2012). Therefore, lake managers should be precautious when extrapolating model results to their specific lake systems. For such purpose, a more tailored PCLake study is required, whereby the model is adapted, calibrated and validated for their specific lake (e.g. Witteveen+Bos 2010; Nielsen et al. 2014; Trolle et al.

2014). Rather, the aim of our modelling study is to gain general insight and generating hypotheses. PCLake provides a coherent framework to investigate the effect of mowing within an ecosystem context with alternative stable states, focusing on important aspects such as mowing intensity and external nutrient loading, while keeping other factors constant. The insights that are obtained in this way cannot easily be derived from any other type of study, and are a completion to insights obtained by complementary approaches (Scheffer 2004 p. 313; Janssen et al. 2015).

Conclusions

Our integrated modelling study indicates that harvesting submerged macrophytes can be effective in temporarily reducing nuisance in lakes which are oligo- or mesotrophic, particularly when mowing is executed in mid-summer. Designing a successful mowing strategy becomes less feasible with increasing nutrient loading. Lakes that are more eutrophic are less resilient to perturbations, making relatively small reductions in plant cover sufficient to trigger an unwanted shift to the alternative phytoplankton dominated state. By extracting nutrients from the lake, negative effects of eutrophication may be partially remediated. Our modelling indicates that the largest amounts of P can be recovered close to the tipping point, although the highest removal of P relative to the input of P is realized when the P loading is low. Repeated mowing seems most useful when the lake is still oligotrophic, preventing it from becoming eutrophic, while it appears to be more difficult to use harvesting to impoverish a lake which is already eutrophic, as it is more sensitive to perturbations. These insights provide a basis of more tailored studies on the effects of harvesting in specific lakes systems.

Acknowledgements

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Supplementary Information

Online Resource 1

Schematic representation of PCLake

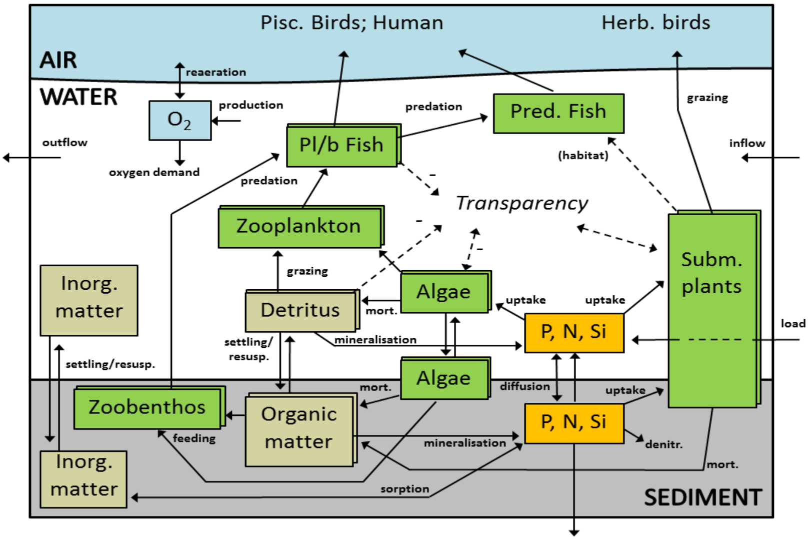

Figure S1 Schematic view of the structure of PCLake. Blocks denote the state variables of the model. Shaded blocks denote compartments modelled in dry weight, phosphorus and nitrogen (and silica in case of diatoms). Arrows denote mass fluxes. Respiration fluxes are not shown. Dotted arrows denote ‘empirical’ relations. The biota in PCLake are modeled as functional groups. The submerged macrophytes are assumed to be homogeneously distributed over the complete water column and are rooted in the sediment. Other groups in the water column are phytoplankton (three groups: ‘diatoms’, ‘green algae’ and ‘cyanobacteria’), zooplankton, planktivorous fish, benthivorous fish and piscivorous fish. The biotic groups in the upper layer of the sediment include the zoobenthos and the settled fractions of the three types of phytoplankton. The abiotic components in the water column and in the sediment are detritus, inorganic material, dissolved phosphorus, ammonium, and nitrate. A full description of the model is presented by Janse (2005). Figure modified after Janse (1997).

Online Resource 2

The importance of collateral disturbance

Although the aim of water managers is to remove cut biomass from the water, part of the plant material is often left in the water due to inefficiency of the cutting machinery. This plant material in the water leads to increased light attenuation and stimulates nutrient recycling, disfavoring the growth of the remaining submerged water plants. Another factor that is potentially detrimental to the remaining vegetation is temporarily enhanced resuspension caused by the mowing procedure. This can for example result from thrust engines on mowing boats that stir up the sediment, or because roots are pulled out from the sediment during the cutting.

In the default version of PCLake only ‘clean’ mowing is considered, whereby all the mown biomass is removed from the system, without additional resuspension. Therefore, we modified the PCLake model equations in such a way that a defined fraction of the clippings remains in the system as detritus. We estimated the fraction to be 20%. Analogous to the detritus resulting from natural mortality, the largest share of this plant material (90%) sinks to the bottom to become part of the detritus pool in the sediment. Furthermore, we developed a function that causes the resuspension of the sediment to increase linearly with mowing intensity, maximally reaching an additional 5 g m^{-2} d^{-1} of resuspended material. The resuspension is only enhanced during the mowing period. We analyzed the effects of these collateral disturbances on the within-season dynamics of the vegetation cover and chlorophyll-*a* for two different mowing intensities (60 and 90% respectively), an intermediate nutrient loading (1.3 mg P m^{-2} d^{-1}) and a single mowing date (July 1st). We compared the results with the default simulations without collateral disturbance caused by mowing.

For the used parameter settings, this analysis reveal no clear sign of collateral damage (Fig. S2a-d). According to our model, enhanced resuspension and remaining of plant material in the water column has a negligible effect when 60% of the submerged plants is cut (Fig. S2a,b), and this is still the case for a mowing intensity of 80% (results not shown). Only when the mowing activity instigates a regime shift, which is the case for a mowing intensity of 90%, the modelled collateral disturbances speed up the regime shift (Fig. S2c,d). Particularly the enhanced resuspension propels the lake faster to the alternative state. A more elaborated (sensitivity) analysis is needed to elucidate the importance of collateral disturbance

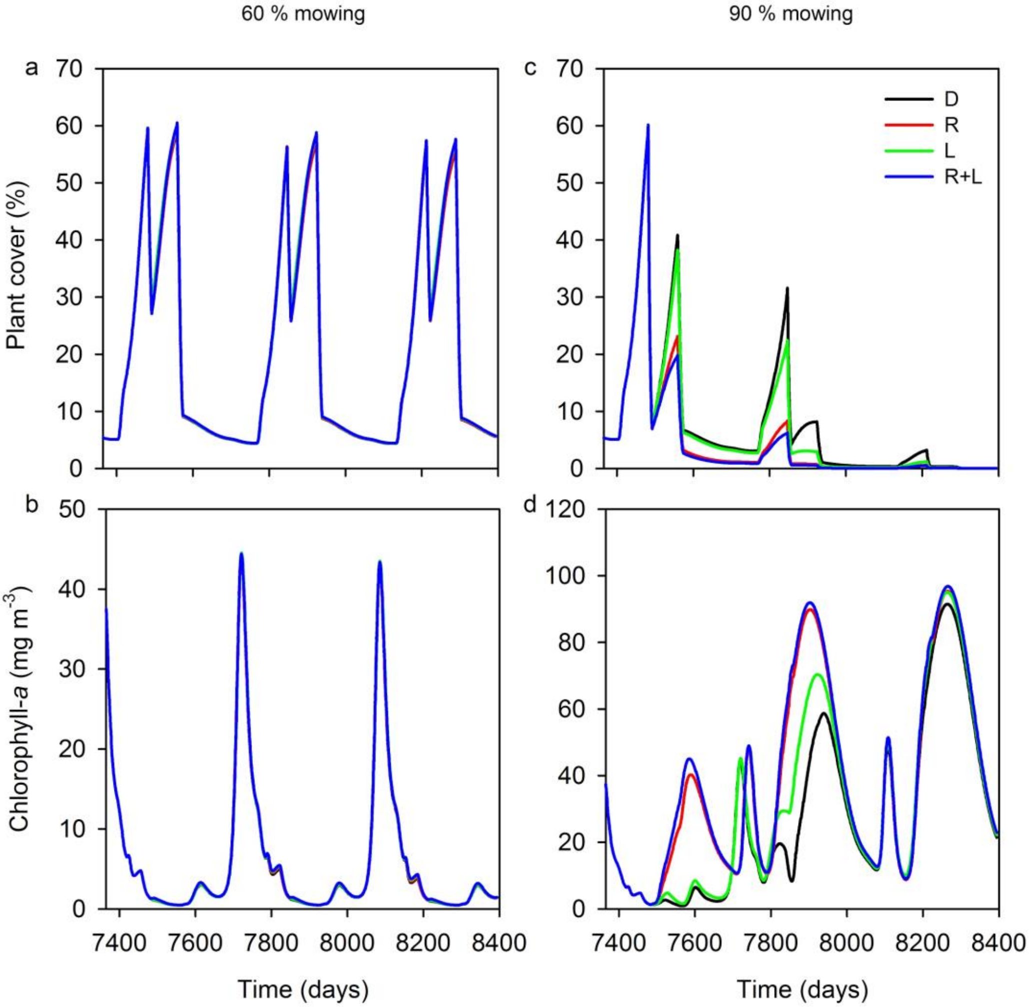

Figure S2 Effects of collateral disturbance caused by the mowing procedure on July 1st the dynamics of plants and phytoplankton in three succeeding years for a lake receiving 1.3 mg P m^{-2} day^{-1}, for 60 percent mowing and 90 % mowing. D is default (black line), R is enhanced resuspension (red line), L is leaving 20 % of the mowed plant biomass in the water column (green line) and R+D is a combination of the latter two (blue line).

Online resource 3

Harvested biomass (dry-weight)

P loading (mg m^{-2} d^{-1})	0	10	20	30	40	50	60	70	80	90
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.6	0.7	0.7
1.6	0.0	9.0	17.6	24.3	20.0	4.2	2.6	0.7	0.5	0.5
	0.0	9.9	19.7	29.2	37.7	40.2	6.0	2.8	0.6	0.5
	0.0	10.6	21.1	31.5	41.6	50.2	51.4	4.9	1.6	0.6
	0.0	11.1	22.2	33.3	44.2	54.3	62.0	42.3	2.7	0.6
1.4	0.0	11.6	23.2	34.7	46.0	56.9	66.4	70.0	4.7	0.7
	0.0	12.0	23.9	35.7	47.3	58.6	68.8	75.8	16.9	0.8
	0.0	12.2	24.4	36.4	48.2	59.6	70.1	78.4	72.5	1.0
	0.0	12.4	24.7	36.7	48.6	60.0	70.7	79.5	81.7	1.4
1.2	0.0	12.5	24.8	36.9	48.7	60.1	70.7	79.8	84.4	2.2
	0.0	12.5	24.7	36.8	48.5	59.8	70.3	79.5	85.1	4.1
	0.0	12.4	24.6	36.5	48.1	59.3	69.7	78.7	84.9	10.1
	0.0	12.3	24.3	36.1	47.6	58.5	68.7	77.7	84.1	40.7
1.0	0.0	12.1	24.0	35.7	46.9	57.7	67.7	76.5	83.0	76.6
	0.0	12.0	23.7	35.2	46.2	56.8	66.7	75.3	81.9	81.7
	0.0	11.8	23.3	34.6	45.4	55.8	65.4	73.8	80.5	82.5
	0.0	11.6	22.9	33.9	44.5	54.6	63.9	72.2	78.9	81.8
0.8	0.0	11.3	22.4	33.1	43.4	53.3	62.3	70.4	77.0	80.3
	0.0	11.0	21.8	32.3	42.3	51.8	60.6	68.4	74.9	78.5
	0.0	10.7	21.2	31.3	41.0	50.2	58.7	66.3	72.6	76.3

Intensity of mowing (%)

Figure S3 Amount of vegetation dry weight biomass that is harvested from the system (g m^{-2} $year^{-1}$). The green color indicates the quantity.

Online Resource 4

Long term vs. short term effects of mowing

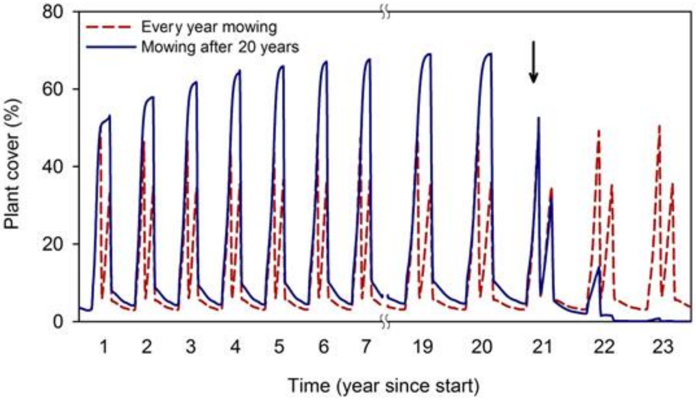

Figure S4 We modelled a lake receiving 1.2 mg P m^{-2} day^{-1} and applied a mowing intensity of 80%. The only difference between the two scenario’s is that in one scenario mowing starts right from the beginning, while in the other scenario mowing starts after twenty years. When mowing is applied directly from the start, the systems moves to an equilibrium situation in which large reductions in plant cover (80%) can be achieved (red striped line). When in the first twenty years no mowing is applied, the system goes to a different equilibrium: after twenty years, when mowing is applied for the first time, the same mowing intensity (80%) instigates a regime shift to the turbid state (blue line). Hence, in the first twenty years nutrients have been able to accumulate in the lake, which lowered the resilience of the lake to perturbations such as mowing.

Chapter 7

General discussion

An integrative approach

The concept of an ecosystem, as coined by Roy Clapham in 1930 (Willis, 1997), is such that one needs an explicit synthesis of biological and physical components of a natural system to understand its dynamics. This makes it obvious that in order to grasp the complexity of nature, and predict its response to human interactions, researchers need to conduct multidisciplinary studies and integrate different approaches. Indeed, there are notions that the scientific system is changing, whereby the old paradigm of knowledge production based on disciplinary science and driven by the autonomy of scientists and academic institutions is superseded, yet not replaced, by a method sometimes referred to as 'mode 2' knowledge production, which is "use-inspired" and takes place in a multidisciplinary setting, largely stimulated by national and international science policies (Hessels and van Lente, 2008; Nowotny et al., 2003; Potì and Reale, 2007). Multidisciplinary research is "hot" and referred to as a "buzzword" (Pain, 2003). At the same time it seems to be "everywhere and nowhere" (Schmidt, 2008), and when using citation patterns as an indicator for multidisciplinarity, only a modest increase over time is observed (Porter and Rafols, 2009). It appears difficult to determine when research is indeed multidisciplinary or integrative, and under which circumstances such an approach actually contributes to enhanced understanding (Jones et al., 2010). Most research follows a reductionist framework, whereby the idea is that a complex systems can be explained in terms of the individual constituent parts and their interactions. Yet, in search for mechanistic explanations, scientific research often zooms in on a certain problem to expose more detail instead of integrating and synthesizing knowledge to show how higher level features arise. As such, reductionism tends to lead to increased specialization and an embranchment of knowledge, and leads to new technologies and methodologies for achieving tighter and tighter control of ever smaller processes (Schlundt, 2011). The overspecialization of disciplines makes it difficult for any one scientist to pull together enough knowledge to actually expose how higher level feature arise from their parts, and it hampers the cross-fertilisation of ideas across disciplines (Anderson and Mitra, 2010; Burton, 1975; Graham and Dayton, 2002). Indeed, has been shown that monodisciplinary research collaborations are more rewarding for scientists than interdisciplinary collaborations (Van Rijnsoever and Hessels, 2011).

These considerations stimulated me to take an integrative approach during my PhD project and to gain insight in the functioning of complex ecosystems by connecting theories, models, modelling frameworks, methods and experts from different disciplines and institutional backgrounds. Below, I reflect on what I consider the added value of this integrated approach for the different studies presented in this thesis. I structure the discussion using the same four themes along which this thesis was organized: *accessibility*, *improvement*, *understanding* and *application*. Each of the four paragraph ends with a single sentence summarising what I consider the essence of each section.

Accessibility

In the conventional way of dynamical modelling, a model is developed and programmed in a certain modelling framework, thereby making use of framework-specific syntax, functions, libraries and user-interfaces (David et al., 2013). As a result of the dependency between model code and modelling framework, the model in its pure form, that is, a set of mathematical equations, is difficult to access and examine independently from the informatics (Lloyd et al., 2011). Particularly for complex models like PCLake, which consists of > 1500 of lines of code, such 'framework invasiveness' poses many drawbacks (Lloyd et al., 2011). The first is that new model users are more or less forced to work with the framework in which the model is programmed. This is inconvenient because it generally takes a considerable amount of time and energy to master a new modelling framework. Moreover, for many frameworks a license fee needs to be paid. These hurdles make that in practice many experienced modellers stick to the modelling framework to which they are already familiar. Also people who are new to the field will tend to choose the framework they have easiest access to, and for which they can get support from experienced users in their direct vicinity. This is a pity, because as a result researchers may not be using the model that is best suited for answering their ecological questions, as it is the framework that largely decides which model can be used (Argent, 2004). Moreover, researchers do not benefit from the large diversity of analyses and tools provided by the many modelling frameworks that are around, e.g. for sensitivity analysis, uncertainty analysis or calibration. Hence, framework invasiveness thereby easily leads to 'reinvention of the wheel' and 'tunnel vision' in aquatic ecosystem modelling (Mooij et al., 2010). Framework invasiveness also hampers the communication about the model in a multidisciplinary research team, particularly with non-programmers such as empiricists, mathematicians and ecosystem managers. Moreover, it frustrates peer-reviewing of model code, whereas stringent criteria for transparency of the logic underlying the model are needed when models are used in the decision making process around delicate and urgent environmental problems such as eutrophication or climate change (Saltelli and Funtowicz, 2014).

When I started working on this research project as a young scientist, I had only very limited modelling experience. Thus, one of my first actions was to look around and talk to colleagues to find out how I could best operate PCLake, and which modelling framework I should learn to master. However, I soon figured out that almost all my colleagues worked with different modelling frameworks and programming languages, which they mastered themselves during previous jobs. Moreover, I found out that PCLake was running in different frameworks: at various moments through time scientists had translated the original source code of PCLake to a new framework, partly by hand and partly automated, and every time this had been a labour intensive exercise. Somewhat problematically, this resulted in PCLake versions that differed slightly from each other, and developments made in one framework were not readily available in another framework. These were important motivations to develop the Database Approach to Modelling (DATM) (**chapter 2**).

The principal aim of DATM is to develop and establish dynamic links between models and model frameworks. DATM allows to embrace diversity without getting lost in technicalities. Interestingly, in my pursuit of integration, the existing link between the model and the framework in which it was developed and programmed first needed to be destroyed. Thereafter the pure model equations could be presented uncluttered in a database, from where an instance of the model for a certain framework can be created automatically. This method enables easy switching between frameworks, thereby allowing to make use of the different analysis methods and tools provided by each framework. But what is even more important here, is that DATM facilitates linking up and collaborating with expert-users of the different modelling frameworks. It is my experience that working with these experts using DATM can bring the analysis of a model to a higher level. Additionally, by providing overview, DATM facilitates collaborations between researchers with different backgrounds. For example, now that informatics do not obscure the matter anymore, empirical ecologists and mathematicians can more easily have in-depth discussions about the representation of specific ecological processes in a model. In fact, establishing multidisciplinary research teams is arguably even essential prerequisite for obtaining a true understanding of the functionality of complex models (e.g. **chapter 3**). It is important that during the development of a method such as DATM the capabilities of expert-users of different frameworks are used throughout the process, for example for the development and the testing of the translators. The involvement of a community of experts, which is expressed by having all their names on the paper (**chapter 2**), contributes to the acceptance of this approach in the scientific community.

Summarizing statement: *"Increased accessibility of ecosystem models greatly enhances the potential for collaboration and interdisciplinary research."*

Model development

Since the onset of the discipline almost half a century ago, the development of ecosystem models has been a bumpy ride (Logan, 1994). Taking off with optimism when computers became widely available to scientists around 1970 (Computer History Museum, 2016), funds became available through 'big science' projects such as the International Biological Program (1964-1974) (Coleman, 2010), and confidence in technology rose to new heights when the moon was conquered in July 1969 during the successful Apollo project (1961-1972) (NASA, 2009), the resulting high expectations were not met in the years to come (Scheffer and Beets, 1994). Apparently, the engineering paradigm that dominated early ecosystem models and the reality of nature did not fully match. As a result, attention moved away from compartment models that described an ecosystem as a connected set of fixed functional groups and resources. Interestingly, both models that took a closer look at nature (e.g. individual based models) and models that took a coarser look at nature (e.g. minimal dynamic models) gained interest and esteem simultaneously. Individual-based models (known as agent-based model in other scientific disciplines) acknowledge what we already know since Darwin, namely that biological systems are shaped by adaptive individual organisms in their struggle for life (Darwin, 1859). These models therefore arguably are a more realistic representation of biological systems than compartment models of functional groups and ideally positions to merge ecological thinking with evolutionary thinking (DeAngelis and Mooij, 2005). But as a trade-off, the ecosystem perspective is lost in most currently existing individual-based models of aquatic ecosystems, with the Atlantis framework as a notable exception (Fulton et al., 2011). Minimal dynamical models, on the other hand, claim that the essential dynamics of the system can be captured in a few nonlinear differential equations. These models have had an important impact on contemporary ecological thinking as can for instance be deduced from the rate at which they are cited (e.g. Scheffer et al. (2001) with over 2400 citations according to Web-of-Science). But, as a trade-off, they are too coarse to be useful in quantitative scenario analysis for ecological management (see also **chapter 5** for a discussion on different modelling approaches).

When theoretical ecologists and ecological modellers argue among themselves how nature should be represented in models, it is not surprising that ecological models are often met with scepticism by empirical ecologists (pers. obs.). They rightfully observe that compartment models of ecological systems such as PCLake differ from their natural counterparts in many ways. Here I would like to zoom in on two important differences. The first major difference lies in the fact that ecosystem models reside in the virtual world as opposed to the real world of natural ecosystems. The other major difference lies in the above mentioned contradiction between the engineering paradigm that forms the basis of ecosystems models based on functional groups and the 'organic paradigm' that sees nature as a highly dynamic and variable conglomerate of an almost infinite number of interacting and reproducing adaptive individuals. These two major axis of difference are depicted in Fig. 1 with PCLake in the lower left corner and real shallow lake ecosystems in the upper right corner. In **Chapter 3**, I worked on the calibration of PCLake with data collected in a set of shallow lakes, thereby crossing the diagonal of the figure back and forth. With the perspective of the empiricists in mind, I find it an intriguing question which of the two axes is hampering us most in the further development of realistic, insightful and applicable tools for ecosystem management.

I note that with the ever increasing computational power (since Apollo 11 landed on the moon, computers have become 1,000,000 times more powerful and Moore's law still holds after 40 years; Moore 1965) and ever increasing internet connectivity (in 1995 1% of humanity was connected, now almost 50%, and 'the-internet-of-things' is about to take off in the same way; http://www.internetlivestats.com/) the difference between reality and the virtual world is rapidly fading away with the movie Jurassic park (1993) as a monument along the way. So, while reality can fade out seamlessly into the virtual world (Fig. 1 towards the lower right corner), the opposite is also true. With modern standards of manufacturing, it would be completely conceivable to develop a physical machine that exactly mimics in the real world the dynamics and outcomes of a computer model such as PCLake (Fig.1 towards the upper left corner). I therefore conclude that while the old commonplace "*PCLake, oh but* *that is JUST a model*" is still heard and factually true, the difference between reality and the virtual world is not the real hurdle obstructing further development of tools for ecosystem management. The real hurdle is in challenging empiricists, theoreticians and modellers alike how to combine a Darwinian view of life as an interactive network of adaptive organisms with the scale and complexity of whole ecosystems in one coherent and feasible scientific framework (Purves et al., 2013).

The research presented in this thesis can contribute to the development of such more 'organic' models of shallow lake ecosystems in several ways. In **chapter 3**, I show that ignoring the weak link between 'engineered' ecosystem models and real 'organic' ecosystems can easily lead to misconceptions during model calibration and development. The Database Approach to Modelling that is presented in **chapter 2** is positioned as a way to port models from one modelling platform to another. But DATM might as well facilitate the transfer of model components developed in the engineering domain to models developed in the organic domain because it reveals the pure mathematical logic of model components. In **chapters 4 and 5**, I develop formal techniques to study the impact of model complexity. This is relevant here because the axis from 'engineered' to 'organic' models is also a complexity axis. Of course, these are just small steps towards more organic models of aquatic ecosystem models. Until these become fully fledged - if they ever will - we need to work the with engineered models of lake ecosystem models such as PCLake and PCDitch, in awareness of their limitations but also of their capability to develop water quality management strategies, as is done in **chapter 6** and the numerous studies with PCLake and PCDitch that are mentioned throughout my thesis.

Summarizing statement: *"For future model development, it is essential that we not only integrate raw knowledge and technology, but also different modes of thinking."*

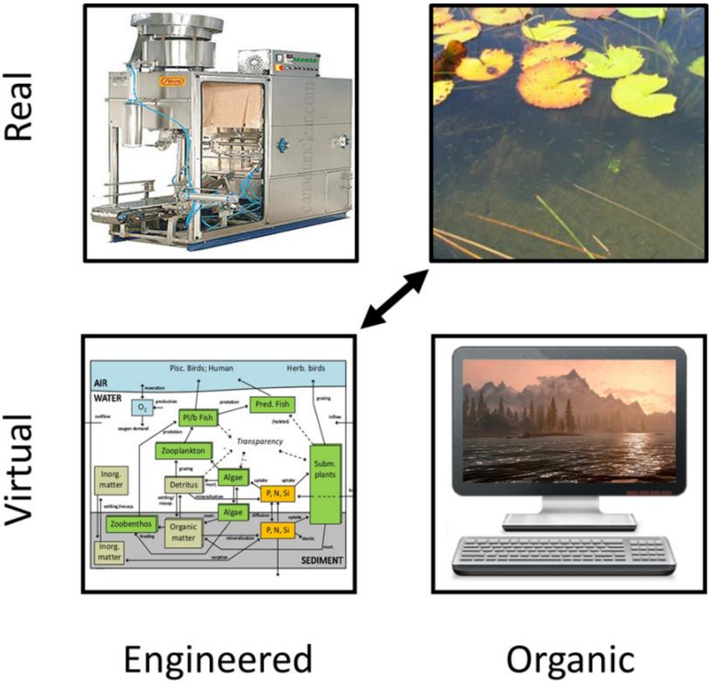

Figure 1 The figure shows four boxes representing (from lower left, clockwise): The PCLake Model, 'The PCLake Machine', The Real Shallow Lake, 'The Model of All Things for Shallow Lakes'. The upper two items represent things in the real world while the lower two items represent things in the virtual world. The left two boxes represent things from the world of engineering, the right two boxes from the natural world. The 'PCLake Machine' should be envisioned as an engineered apparatus, with reservoirs, sensors, pumps, membranes, etc., that performs exactly like PCLake. The 'Model of All Things for Shallow Lakes' should be envisioned as a computer model with the same complexity as real ecosystems (see the Madingly model for an attempt in this direction, Purves et al. 2013). When we apply The PCLake Model to The Real Shallow Lake, we move from lower left to upper right in the figure, while when we calibrated The PCLake Model on basis of data from The Real Shallow Lake we move from upper right to lower left. The figure is meant to show that along this diagonal, we cross two borders: the border that separates the real world from the virtual world and the border that separates the engineered domain from the organic domain. The message is that the main problem in applying PCLake is not in going from the virtual world to the real world and vice versa. The real hurdle is in combining a Darwinian view of life as an interactive network of adaptive organisms with the scale and complexity of whole ecosystems in one coherent and feasible scientific framework. The picture for the PCLake Machine (upper left) pops up as one of the hits when searching for "clear water machine" in Google (Jar filling machine n.d., n.d.). The photo representing the real ecosystem (upper right) was found when searched for "shallow lake" (Spracs Center n.d., n.d.). The image in the lower right corner is a combination of two images: the picture of the virtual lake was found using the query "lake computer game" (Alarra n.d., n.d.), and the drawing of the PC comes from Iconfinder (n.d.). The structure of PCLake (lower left) is modified after Janse (1997).

Understanding

Successful science operates at the frontier that separates what is already known from what is not yet known. This notion is captured in the concept of the Medawar Zone (Medawar, 1967), which is the range of problems which are most likely to produce fruitful results (Fig. 2, left panel). Research on simpler problems (to the left of the Medawar Zone) will only produce trivial results while research on problems that are too ambitious (to the right of the Medawar Zone) are likely to fail. While this conceptual framework is well accepted, considerable disagreement can arise on where the Medawar Zone is located in a given field at a given moment of its scientific development. Here, I apply the concept of the Medawar zone to the topic of this thesis, namely the modelling of shallow lake ecosystems. As stated in the previous section, opinions differ among experts whether models of aquatic ecosystems should be casted as sets of connecting functional groups such as PCLake, as minimal dynamical models that focus on a few dominant nonlinearities in system dynamics or as elaborate models with many individual-based modules such as Atlantis (Fulton et al., 2011). Here I argue that these differences in opinion on where the Medawar zone is located stem from a difference in what defines the benefits that are plotted on the y-axis of figure 2. People with a theoretical inclination aiming for fundamental insight might see more value in simpler models (left hump in the middle panel of figure 2) compared with people who aim at applicability of the model results (right hump in the middle panel of figure 2).

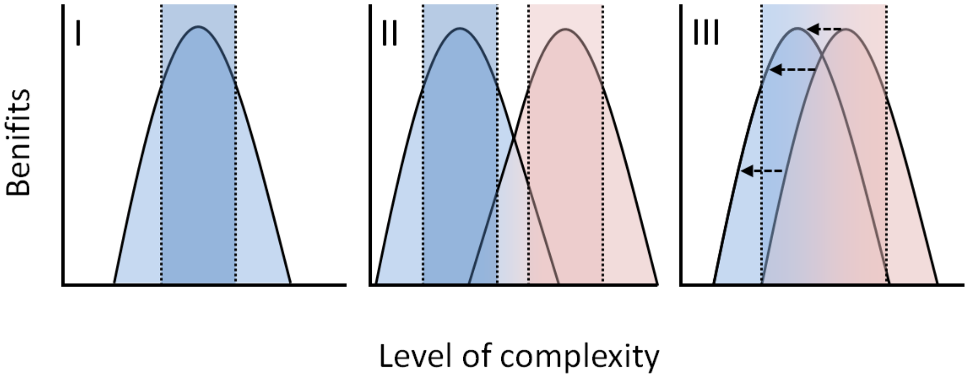

Figure 2 Three representations of the "Medawar zone" when applied to models. The left panel shows the standard representation of the Medawar zone (inspired on Loehle 1990) in which it is assumed that there is a single optimal complexity at which a model produces the most rewarding insights. As simpler and more complex models generally have different strengths and weaknesses and are complementary in the insight they produce, it might be fruitful to apply models of different complexity concurrently within a single study, thereby effectively creating two Medawar zones, each with own optimum (middle panel). Alternatively, by modifying a given model by slightly increasing or decreasing its complexity one can shift the Medawar zone along the x-axis in one coherent analysis (right panel), which has the advantage that one may be better able to scrutinize the costs and benefits of complexity (chapter 4 and chapter 5).

An apparent solution is the application of multiple models of different complexity concurrently within one single study. For example, Mooij et al. (2009) applied PCLake together with a minimal dynamical model of a shallow lake to study the consequences of climate change. However, it may still be difficult to grasp how exactly complementary insights obtained by the different models relate to each other (hence the local minimum in the middle panel of Fig. 2). One way of solving this is to start with a complex model and then make stepwise simplifications so that we start to gradually move along the x-axis of the Medawar plot in such way that it is possible to interpret the results from the different model versions in relation to each other (Fig. 2 right panel). This approach can even be used to explicitly link different theories that build on models of different complexity.

In **chapter 4**, PCLake acts as the complex model. By simplifying PCLake, a generalized Lotka Volterra model with linear interaction terms was created. Fig. 3 shows how this enabled us to link theory on regime shifts with theory on food web dynamics. Research on regime shifts in aquatic ecosystems was initiated on basis of field observations and subsequent whole-lake experiments. Analysis of these observations and experiments resulted in theory on the mechanisms underlying regime shifts in lakes. Finally, this knowledge is formalized in the mathematical equations of models such as PCLake. A comparable chain of knowledge that starts with observations and results in theory and finds its documentation in mathematical models can be described for food web ecology. Both fields of research deal with the stability of ecological systems, but while studies on regime shifts take the abiotic environment and nonlinear interactions explicitly into account (Scheffer et al., 1993) and food web ecology mostly focusses on biotic components of the system and on linear interactions (Moore and de Ruiter, 2012). Because nonlinear interactions and the abiotic environment are considered to be crucial for regime shifts to occur according to prevailing theory, we were interested to see whether stability indices from food web models that ignore these phenomena still signal an upcoming regime shift. This was indeed the case, thereby increasing confidence in both approaches. Because of multiple steps involved in the transfer from PCLake to the generalized Lotka-Volterra models, one might question whether the way we linked both models mathematically automatically resulted in a transfer of the signal. If this were true, it would render our findings as being trivial. We therefore did a comparable analysis, but now for the most simple and well-known models of consumer resource theory **(chapter 5)**. Using comparable methods, we could convincingly show for these simple consumer resource models that going from nonlinear to linear interaction terms greatly altered their stability properties.

Summarizing statement: *"Leaps forward in knowledge production can be achieved by scrutinizing the 'ecotones' of theoretical paradigms."*

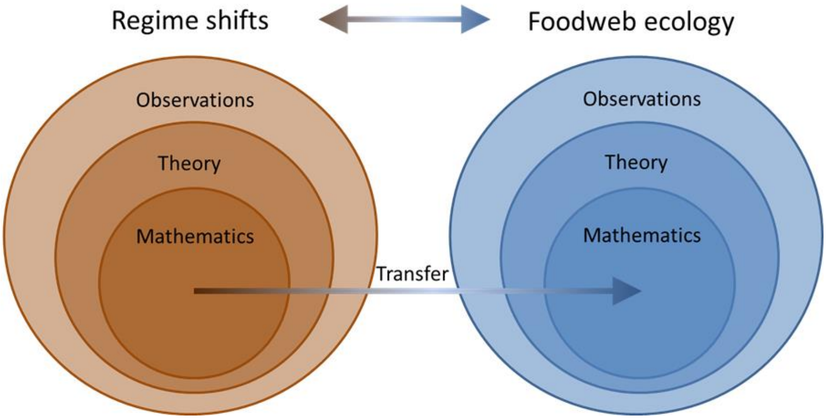

Figure 3 Graphical representation of the approach underlying the study presented in **chapter 4** of this thesis. We start with the notion that each field of research, here regime shifts and food web ecology, are based on their own set of observations from the field and from experiments, have their own theories, and their own mathematical models. We link the fields by transferring information from the more complex model, in our case PCLake, developed in the context of regime shifts to the simpler model, in our case the generalized Lotka-Volterra equations of food web theory. Another way to look at this process is to see the complex model as a virtual reality that is used to develop and parameterize the simpler model.

Application

Shallow lakes provide a clear-cut example of an ecosystem for which management practices are strongly rooted in ecological theory, i.e. alternative stable states theory (Jaarsma et al., 2008; Scheffer, 2004). Concepts such as positive feedback loops, trophic cascades and critical nutrient loading, form the conceptual basis of many management strategies. Minimal dynamical models in particular have had an important role in transferring theoretical insights into ecosystem management, as they are so simple to communicate (Jaarsma et al., 2008; Scheffer, 1990, 1989; Scheffer et al., 1993). Later, large bodies of empirical evidence have been accumulated to reveal how theoretical concepts work out in reality, for example on how biomanipulation by removing benthivorous fish can disrupt ruling positive feedback loops (Bernes et al., 2013). Somewhat problematically, however, most empirical evidence has been obtained from studies on turbid lakes, as most lakes in the temperate zone suffered from eutrophication, and because eutrophied lakes received more attention from water quality managers. Currently, however, a number of lakes have recovered to the desired clear water state, and new management issues emerge that are associated with these new conditions. It now turns out that alternative stable states theory has not been tailored yet to these new conditions, and hence cannot be readily applied to give structure to ecosystem management.

For example, nuisance growth of aquatic plants is an emerging management issue. Yet it is unclear how cutting these plants, which measure is increasingly applied by managers, intervenes with the positive and negative feedback loops that give shape to the alternative stable states in shallow lakes. Theory suggests that harvesting can both undermine and enhance the resilience of the clear water state, depending how it impacts the intraspecific competition among aquatic plants and the interspecific competition between aquatic plants and phytoplankton (Scheffer, 2004).

In **chapter 6**, we elucidate the value of using complex ecosystem models such as PCLake to build an explicit link between ecosystem management and ecological theory. With a mixed team of modellers, empirical scientists and environmental consultants we used PCLake to explore the potential consequences of mowing for water quality. As a result, we could further refine alternative stable states theory, while simultaneously our results provided managers with practical insights in the interdependencies in the system, which they can take into account when designing mowing strategies. Hence, we conclude that complex ecosystem models can be used to reconcile theory and practice.

In chapter 6 we made use of the default setup of PCLake, representing a hypothetical shallow lake in the temperate region, and performed equilibrium analyses to magnify the impact of mowing on the stability properties of the system. Yet the bridge between theory and practice is also existent when PCLake is used as a framework for systems analysis of a specific lake. A nice example is given by the study of Kong et al. (2016) where we used PCLake to study lake Chao in China. First the model was parameterized, calibrated and validated to reconstruct the history of the lake over the past 60 years. We then combined the model output with paleolimnological data to show exactly when in history regime shifts in lake Chao have taken place. Subsequently, we used simulations to elucidate the relative importance of nutrient loading and water table regulation for triggering the regime shifts, and disentangled their interactive effects. By running the model backwards, we were able to verify that the regime shifts were indeed alternative stable states with the associated hysteresis.

Summarizing statement: *“Ecosystem models that are useful both to ecosystem management and the development of ecological theory are in a unique position to bridge the gap between those realms.”*

Integrative science - a personal touch

The integrative approach taken in this thesis goes along well with working with PCLake, which is a model wherein the most important processes in shallow lakes ecosystems are combined to describe higher level phenomena. Also it matched with the design of the overarching research project on PCLake and PCDitch, involving partners from different institutional backgrounds (**chapter 8**). But maybe just as important, or even more important, is that I discovered during the course of this project that the role of being an integrator fits my personality well.

Much of today's science draws on positivism. Assuming that science should be based on facts and should work towards general laws and principles, the system strives for objectivity and avoiding the semblance of subjectivity. As a consequence, the role of the researcher during the process of knowledge development is effaced as much as possible. This is problematic because "interdisciplinarity is first and foremost a state of mind requiring each person to have an attitude that combines humility with open mindedness and curiosity, a willingness to engage in dialogue and hence the capacity for assimilation and synthesis" (OECD 1972, p192). Hence, the role of individual researchers is decisive in determining the success of multidisciplinary research (Whitfield, 2008; Woolley et al., 2010). A different reason why researchers may not be flaunting with their role in pan-disciplinary science is because of the fierce competition for financial resources, in which a tendency to reward personal excellence discourages researchers to unveil their dependence on others. In fact, I postulate that many researchers have incentives to linger in the original 'mode 1 knowledge production' and strive for becoming independent polymaths. In my opinion, this is undesirable, not only because of the urgency of sustainability issues that require a multidisciplinary approach, but mostly because it is obvious that individual accomplishments are easily surpassed by the outcomes of a successful collaboration effort in terms of research output (Cheruvelil et al., 2014). Fortunately, there is increasing body of knowledge about designing productive research collaborations that maximize net benefits for both individuals and the team as a whole (Goring et al., 2014). One important finding is that diversity, in its broad sense, increases both the quality and the quantity of team output. Besides having specialists from different disciplines, there is an important role for a "broker" who facilitates communication and cross-fertilization (Cheruvelil et al., 2014).

In many of the projects presented in this dissertation I took the position of the broker, closely working together with specialists, including programmers, mathematicians, empirical scientists, professional consultants and ecosystem managers. I experienced that these specialists also appreciated and even enjoyed collaboration. Brokers are generally good in pointing specialists to the broad relevance of their work, as specialists may find it hard to zoom out and take a holistic view. Likewise, a broker can help specialists to report their findings in such way that it will appeal to a broad audience. A different aspect of collaboration that was highly appreciated both by me and the people I teamed up with was the joy we had during the work, which brings me to the second precondition for successful teamwork.

Recent studies from MIT and Google on the 'perfect' team revealed that the most successful teams have high average social sensitivity (Duhigg, 2016; Woolley et al., 2010). When things get rough, and it always gets roughs when working on scientific innovation, one needs to know that there will be psychological safety and social support. Social sensitivity has also been referred to as "people skills" or social intelligence, and is the capacity to successfully navigate a full range of social interactions (Albrecht K., 2006; Woolley et al., 2010). An important question is whether the skills needed to become a broker can be learned, or whether they are dependent on someone's personality. Probably it will be both, as in my case my bachelor in "environmental sciences" provided an excellent foundation for this thesis (Bootsma et al., 2014). The social skills needed to operate in multidisciplinary research teams can also be enhanced by workshops and team outings (Cheruvelil et al., 2014). In fact, taking time for social coffee breaks can already form the basis for cross-pollination between scientists from different disciplines (Scheffer, 2014).

Moore's law indicates that technology is developing with an exponential pace (Moore, 1965). And although there is a risk that certain technologies will reinforce the existing pressures on our natural systems, it also sparks hope for technological and societal developments in the opposite direction, i.e. towards sustainable development. During a lecture in 2013, Dennis Meadows, author of the seminal 'limits to growth' report (Meadows et al., 1972), argued that it is too late to tame the great forces of global environmental change, but postulated that on a local scale societies will be able to mitigate and adapt to their consequences. (Scheffer et al., 2015) make a case for creating "safe operating spaces" on a local scale, via management actions aiming at disrupting synergies between different (local) stressors. I postulate here that if we can make such improvements on a local scale, we can also do it on a global scale, even if it can only be achieved by taking the sum of a myriad of local improvements. In this light there is much to expect from the multidisciplinary trends in higher education, as it implies that in the years to come numerous students will graduate that have learned to cooperate in multidisciplinary research teams, and can take the role of broker within such teams (Jacob, 2015). *A fortiori*, many university courses have been completely designed based on the new paradigm of 'Mode 2' knowledge production (Nowotny et al., 2003), implying that university students are subjected to real world learning, carrying out multidisciplinary consultancy projects for a real-life client (Bootsma et al., 2014). Integrated models like PCLake can play an important role in this development. In recent years already many students have learned to operate PCLake in the context of systems analysis of real ecosystems. As a result, when these students leave university, they can immediately and effectively start working on solving the main sustainability challenges of our time, which is clearly a hopeful prospect.

Chapter 8

Synopsis of a collaborative research project on PCLake & PCDitch

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Project set-up

The studies presented in this thesis were part of a larger research project with the overall aim of increasing the usefulness and the validity of PCLake and its twin model PCDitch, and to increase the confidence in the models among water quality managers. This larger research project was a collaboration between the Netherlands Foundation for Applied Water Research (STOWA), the Netherlands Institute of Ecology (NIOO-KNAW), Wageningen University & Research centre (WUR), the Netherlands Environmental Assessment Agency (PBL) and Witteveen+Bos, a private engineering consultancy. The heart of the project consisted of two PhD studies - one on PCLake and one on PCDitch - and about 10 case studies on aquatic ecosystems in the Netherlands. The PhD-projects were complementary in the sense that they focussed on different aquatic ecosystems, and hence different models, but the concepts and tools were sufficiently similar for the researchers to build upon each other's knowledge and progress. The project was joined by a third PhD-project, funded by the Netherlands Organization for Scientific Research (NWO), which focussed on the global application of PCLake with emphasis on China. The PhD studies were important for advancing the scientific development of the models and embedding the progress in the scientific literature. The goal of the case studies was to assess the usefulness of the models in ecosystem management when confronted with empirical data, as a framework for systems analysis, and as a tool for ex-ante evaluations of management measures. The case studies were co-financed by water boards and carried out in close collaboration with ecosystem managers. This setup allowed the project members to study the strengths and weaknesses of the models in real world applications and to experiment with new model developments, while the ecosystem managers benefited directly from the new insights in the functioning of their lakes and the effectiveness of their actions. Over the course of this four year project regular meetings with the project team were held to ensure cross-pollination between all parties involved. In addition, once a year there was a meeting with the sounding board of the project. This sounding board consisted of various stakeholders, including representatives from water boards and consultancy companies in the Netherlands. The first meeting was used to make an inventory of the experiences, questions and wishes of the stakeholders, which provided important input for both PhD-projects and the case-studies.

Major results

Case studies

One of the major achievements of the research project is that, by the time it was finished, practically every water quality manager in the Netherlands has heard about PCLake and PCDitch one way or another. In fact, due to the case studies many water quality managers are now familiar with the models and recognize their importance. The case studies have proved that the models can be applied successfully to various aquatic ecosystems to resolve a variety of management questions. The models have been used to diagnose the problems leading to poor water quality, identify key-processes controlling the systems dynamics, identify viable management options and for *ex-ante* evaluations of these options by predicting their (combined) effect on the ecological state. Exactly these sorts of insights are needed by water quality managers to design effective management strategies to meet the targets of the Water Framework Directive (European Union, 2000). Hence, several of the case studies have already led to changes in the field. For example, at Lake Kardingerplas near the city of Groningen managers have disconnected a helophyte filter as it turned out that during dry spells in the summer the filter became an important source of phosphorus leading to phytoplankton blooms. Moreover, the macrophyte mowing procedures were adjusted, and no cyanobacterial blooms occurred in the first years after the measures were taken. Thus, the case studies clearly showed that, by pointing to effective management measures, modelling studies can lead to more cost-efficient management and that the costs of a modelling study is easily recouped. These economic aspects are important as water management measures are generally very costly and paid for by tax money.

Advancing ecological theory

Several of the scientific studies that have been conceived with the models PCLake and PCDitch contributed to the development of ecological theory. Using these complex ecosystem models as a coherent test-environment, studies were performed to analyse how the emergence of alternative stable states in shallow lakes is controlled by e.g. the input of allochthonous organic matter (Lischke et al., 2014), filter-feeding zoobenthos (Hölker et al., 2015), herbivory by birds (Van Altena et al., 2016), fluctuating water levels (Kong et al., 2016) and the removal of submerged aquatic plants (**chapter 6**). Additionally, Janssen et al. (2014) used PCLake to study the possibility of having alternative stable states in large shallow lakes. Interestingly, PCLake and PCDitch turned out useful for the development of other major theoretical frameworks in ecology, including food web theory (**chapter 4**), consumer resource theory (**chapter 5**), resource competition theory (Van Gerven et al., 2015b), ecological stoichiometry (Van Gerven et al., submitted), and spatial ecology (Van Gerven et al., 2016).

Technological developments

The development of a Database Approach To Modelling (DATM; **chapter 2**) has been a crucial step towards widespread application of PCLake and PCDitch in both scientific studies and ecosystem management. The practical application of DATM has been further shown by Van Gerven et al. (2015). In the extension of DATM, significant technological progress has been made regarding spatial explicit modelling with PCLake and PCDitch. As such, it is now possible to couple the models with the spatially explicit hydrodynamic models SOBEK (http://www.deltares.nl/en/software/sobek) and Delft3D (Deltares, 2014), enabling running simulations in 0D, 1D, 2D or 3D (Van Gerven et al., 2015a). Also, PCLake has been incorporated in the Framework for Aquatic Biogeochemical Models (FABM; Hu et al. 2016), which facilitates the coupling with several hydrodynamic models covered by FABM, including the one-dimensional General Ocean Turbulence Model (GOTM, http://www.gotm.net) and the General Lake Model (GLM, Hipsey et al., 2013), as well as the three-dimensional General Estuary Transport Model (GETM, www.getm.eu). Importantly, these developments make it possible to study alternative stable states in both time and space. For example, Dutch polder systems generally include numerous ditches that are all hydrologically connected, yet to date it remains unclear how spatial heterogeneity impacts the occurrence of regime shifts in these systems (Van Gerven et al., 2016).

The move towards community-based modelling

An important result of the overarching research project is that both the case studies and the scientific collaborations have contributed to the establishment of a large and enthusiastic community of model users, developers and 'ambassadors'. Moreover, the models have been embraced by the international Aquatic Ecosystem Modelling Network (AEMON, Janssen et al. 2015), which has expanded the PCLake-PCDitch community even further. Hence, we may conclude that PCLake and PCDitch are increasingly becoming community-based, and that development now predominantly occurs from bottom up by ad hoc 'grassroots' initiatives (Trolle et al., 2012). The broad community behind the models is arguably one of their major strengths, taking into consideration that many existing aquatic ecosystem models are seldom used or cited (Trolle et al., 2012). A large advantage of the active collaborations within the AEMON community is that PCLake and PCDitch can easily be applied in concert with similar type aquatic ecosystem models during multi-model ensemble studies, providing novel insight in the differences between models and in their uncertainty (Trolle et al., 2014).

International and global applications

In the wake of the PCLake-PCDitch research project, several case studies have been conducted outside of the Netherlands, including cases in Denmark (Nielsen et al., 2014; Trolle et al., 2014), China (Kong et al., 2016) and Greece (Mellios et al., 2015). Given that all countries in Europe have to comply with the Water Framework Directive, there is enormous potential for the application of PCLake and PCDitch, especially for countries in temperate areas. Interestingly, simulations with PCLake have also produced useful insights when the model was applied to lakes outside of the geographic range where the model was calibrated for (Janssen et al., 2014). After implementing some basic modifications, Fragoso et al. (2011) and Kong et al. 2(016) showed that PCLake could even adequately describe the dynamics of tropical lakes. Recently, a start has been made with coupling PCLake to the Integrated Model to Assess the Global Environment (IMAGE, Stehfest et al. 2014) of the Netherlands Environmental Assessment Agency (PBL), which is used for the global assessments of the Organisation for Economic Co-operation and Development (OECD), the Intergovernmental Panel on Climate Change (IPCC), the Intergovernmental Platform on

Biodiversity and Ecosystem Services (IPBES) and others. Hence, in due time PCLake can make an important contribution to the global assessments of the ecological state of the planet.

Education

The models are increasingly used in university courses and at polytechnical universities. During the course of the research project more than hundred Dutch students, attending the Wageningen University MSc course "Models for Ecological Systems" and the HZ University of Applied Sciences MSc course "Aquatic Ecotechnology", gained experience with PCLake and PCDitch and learned about the importance of taking an integrated systems analysis approach in contemporary ecosystem management. Moreover, more than a dozen students at the MSc level gained in-depth experience with the model during internships and major research projects. For example, one student performed an ex-ante evaluation of the development of a large marsh area in Lake Marken in the Netherlands which is currently being constructed.

Outreach

Besides the peer-reviewed articles that have been published in scientific journals and numerous contributions to various workshops, meetings and conferences around the world, the models gained quite some publicity outside the scientific realm. Different media were used to establish communication with stakeholders and the general public, including a website (http://www.stowa.nl/projecten/pclake_en_pcditch), online newsletters, factsheets and articles in non-academic journals. Furthermore, publicity was greatly enhanced by a professionally produced introduction film, which was distributed via various channels of social media (https://www.youtube.com/watch?v=NY0DLSwsP4c).

An example of the "golden triangle"

An implicit yet important result of this research project is that it presents a success story of collaboration within what has been coined the "golden triangle". It is generally assumed that tight university–industry– government relations are needed to stimulate innovation and economic growth of knowledge based societies (Etzkowitz and Leydesdorff, 2000). Inspired by notions such as the "golden triangle", "Triple Helix" and "Mode 2 knowledge production", research policies are increasingly promoting strategic collaborations among organisations of different institutional backgrounds (Hessels and van Lente, 2008; Potì and Reale, 2007). However, it is unclear how exactly such collaborations should be organized for synergy to emerge. In the PCLake-PCDitch research project the collaboration between research institutes, water boards and a private consultancy has shown to be a successful formula for the production of knowledge and for bringing about effective and efficient strategies for ecosystem restoration. An important aspect underlying the success of this project was that some apparent dependencies between the different actors were turned into positive feedbacks. Here we outline how we envision these feedbacks. Knowledge institutes have a positive effect on the consultancy companies, as these companies are allowed to exploit the tools that are developed and largely maintained by scientists. Even though PCLake and PCDitch are free for everyone to use under the LGPL licence (http://www.gnu.org/licenses/gpl-3.0.txt), the consultancy companies commercialize their expertise in applying the models and interpreting their results, which creates a lucrative business model. Yet, an apparent consequence is that these companies are dependent on scientists, for providing them with tools that are approved by the scientific community and for delivering state of the art knowledge on aquatic ecosystem functioning. To ensure that the effect of knowledge institutes on the consultancy companies remains positive, the consultancy companies provide scientists with valuable information on the performance of the models in different field situations, and on the usefulness of models for addressing management questions and supporting the decision making process. The companies can thus be seen as the eyes and ears of the scientists in the field. Also, they ensure that new scientific insights are quickly translated into efficient ecosystem management practices. For water quality managers this all implies that they don't have to become modelling experts themselves, but can hire a consultant from an engineering company, knowing that these companies have access to the latest scientific insights. Moreover, hiring a consultancy company for a competitive rate may be much cheaper than maintaining a sufficient level of knowledge and expertise at the water board. As a result, water quality managers can effectuate great savings in ecosystem management by making a relative small investment in a modelling study, as was shown by our case studies. Hence, the interactions between the consultancy companies and the ecosystem managers are thus generally positive. It is important to note that the market forces can be tamed by the dependency on the research institutions, as knowledge institutes can cease the transfer of knowledge and tools. This trump card allows scientists to secure important long term interests, such as enforcing all players to share knowledge and data, and securing that the models remain open source. An element in the whole process that is pivotal, however, is that some money has to flow from either the consultancy companies or the ecosystem managers to the research institutions to fund their science. We reckon that this is also the most vulnerable element. Fortunately, the research project presented here received financial support by the Netherlands Foundation for Applied Water Research (STOWA), which in turn is funded by all authorities concerned with water quality management in the Netherlands (mainly water boards). The primary aim of STOWA is to provide the water quality managers in the Netherlands with all the knowledge needed to perform their tasks, and STOWA has a long history in setting up collaborations between scientists and ecosystem managers.

Remaining challenges

Although major steps have been taken during the last couple of years, we acknowledge that a model is never perfect and its development never finished, and hence there are a number of new questions, opportunities and requests for improvements. We identified three categories of future model developments.

Changes to the model structure

During scientific collaborations, student projects and interactions with water quality managers in recent years, several suggestions for changes in the model structure have been made, some of them aiming at improving existing modules and others aiming at expanding the functionality of the models to meet new needs. An example of changing an existing module came from a student project where the fish modules were scrutinized. It was concluded that the bioturbation by benthivorous fish in the turbid state is probably too weak in the current version of PCLake, while in the clear water state the rate of bioturbation is probably too strong. Examples of requests for new functional groups include *Dreissena* mussels, *Azolla* species, N-fixing cyanobacteria, Red Swamp crayfish, and periphyton. In addition, requests have been made to develop models for aquatic ecosystems other than shallow lakes and ditches, such as heavily modified waters in urban areas (‘PCCity’), streams and small river systems (‘PCRiver’), brackish lakes and estuaries (‘PCBrack’), and the coupling with chemical fate and toxicological fate models (‘PCToxic’). Provided that justice is done to the coherence of the models (see **chapter 3**), and that the added uncertainty is accounted for, there is a great potential for these model adjustments to become actual improvements. The re-establishment of the original calibration routine in the R modelling environment also enhances this potential (**chapter 3**), although many of the modelling frameworks that have become accessible via DATM will provide even fancier options for calibration (**chapter 2**). Finally, we reckon that for model improvement it is of great importance that datasets gathered under the WFD or in other platforms become readily available for scientists for calibration and validation of the models.

Spatial modelling

Although alternative stable states theory is highly influential in current water quality management, it remains largely unclear how regime shifts come about in real ecosystems. One likely reason for this knowledge gap is that the vast majority of studies on regime shifts, whether theoretical or empirical, have been performed on homogeneous and isolated systems (Van Gerven et al., 2016), while it is evident that many natural aquatic ecosystems are spatially heterogeneous and in close contact with each other (Soranno et al., 2010; Van Gerven et al., 2016). There is thus a large potential for spatial studies with PCLake and PCDitch to contribute to our ecological understanding of heterogeneous aquatic ecosystems, and to reconcile spatial ecology and alternative stable states theory (Van Gerven et al., 2016). However, despite that many technological hurdles have been taken to couple PCLake and PCDitch to spatially explicit hydrodynamic models and run simulations in 1D, 2D and 3D, some essential follow-up steps are still needed before the models are fully operational in a spatial context. For example, they need to undergo a process of thorough validation in space and time before they can be used for making reliable quantitative predictions in ecosystem management. Yet, such validation is generally troublesome due to a lack of datasets that cover both space and time. The fish species in PCLake pose extra difficulties as their behaviour in space is complex. Other modelling methods may be more suitable for such cause, such as Individual Based Modelling (IBMs, DeAngelis and Mooij 2005). A combination of approaches may bring a solution. On the positive side, the unstoppable advance of drones, satellites and high frequency monitoring buoys provides a huge potential for more remote sensing and hence an increase in spatial data.

Graphical user interface

Thanks to DATM (**chapter 2**) it has become possible to run PCLake and PCDitch in various different modelling frameworks. Most of these modelling frameworks however use scripting for input/output handling and visualization, and hence require the model user to master some basic programming skills. Model developers and more advanced users favour that way of working as it gives them freedom to develop their own customized tools and analyses. Less advanced users, however, may be better off with a so called Graphical User Interfaces (GUIs) for input/output handling and visualisation as such devices would clearly simplify operating the model. Currently the easiest option to run PCLake and PCDitch is via Microsoft Excel and some pre-programmed VBA macros. With some basic guidance new users can run successful simulations after a few hours of practice. Yet, no official helpdesk is existing, and nor are there comprehensive manuals available. If a user runs into a persisting error, there is no other option than to contact more experienced users or to abandon the exercise. In fact, this has led to various failed attempts to successfully apply PCLake or PCDitch. Hence, there is an increasing call for more user-friendly modelling software, comprising a fool proof GUI, which gives access to only some basic model features. Although shielding large parts of the model code goes at the cost of functionality and insight, it can make it much easier to control the models and can prevent errors stemming from inexperience to occur. Such software development also paves the road for serious gaming. Gamification is a powerful way of informing stakeholders, students and civilians about aquatic ecology and the difficulty of managing ecosystems that provide many yet contrasting services.

The way forward: oil that makes the wheels turn

The potential for PCLake and PCDitch to make a difference in ecosystem management has never been this large. Yet, now that the PCLake-PCDitch project that is reported here has ended, the question emerges how the above-mentioned developments can be realised, new innovations can be sparked and the continuity of the models can be guaranteed. The models are open source under the LGPL license, and hence they are basically ‘owned’ by everyone. This has great advantages, as it allows the models to be widely employed both in science and in ecosystem management, but it also implicates that the responsibility for the models is diffuse. We can discriminate two major forces that currently bring about model developments: the market forces of supply and demand, and the power of the enthusiastic and dedicated “grassroots” community of ecosystem modellers. The first is boosted by the need of water quality managers to meet their WFD goals and primarily takes place in the context of “the golden triangle”. The latter is mainly driven by scientific curiosity and the wish of scientists to develop useful knowledge and contribute to a better world. Undoubtedly these forces hold the potential to drive many essential model developments. We here postulate however that in order to optimally exploit the potential of the models, some coordination and bundling of efforts is essential. There is an apparent need for a ‘spider in the web’, broker, ‘greaser’, or ‘model coordinator’ who funnels the energy in the community and streamlines developments. Such a person can bring added value by facilitating the establishment of strategic partnerships within the community, and by guiding and aligning new development to prevent “re-inventions of the wheel” (Mooij et al., 2010). Until yet these type of activities were carried out by the members of the just finished research project on PCLake and PCDitch.

For a full-time model coordinator, we identified the following tasks:

- To be the main contact person for all stakeholders, including new users, and to maintain contact with other consortia and initiatives, whether or not relating directly to aquatic ecosystem modelling.
- To set up a more formal community of practice, based on an online platform for sharing ideas and helping each other out. It is also important that workshops, user meetings and symposia are organized which will facilitate cross-pollination of ideas. PCLake and PCDitch can be seen as “freemium” software, as they are free to use, and some basic assistance is provided for via the community of practice. Yet, when more advanced help is needed payment is required. This can be done in kind, or via the commercial route of supply and demand by buying advice from an experienced user.
- To keep track of the challenges, opportunities, needs and developments in water quality management and the field of aquatic ecosystem modelling, and identify funding opportunities, such as open calls for research proposals. Subsequently, the coordinator can search for shared interests among stakeholders, establish liaisons and initiate strategic partnerships. Also supply and demand can be identified and brought together to stimulate model development.
- To align existing developments or even steer developments in a direction where they will be most effective. Moreover, it is important that during model development the coherence of the models remains intact, and as such, the coordinator should signal developments heading in the wrong way.
- To ensure that new developments are disclosed and communicated, and hence become available for the whole community to be used. This includes development of the source code, input/output handling, documentation and training materials. The model coordinator should also secure that developments and insights remain freely accessible (open access, open source).

To ensure that the relationship between government-industry-science remains balanced, it is important that a model coordinator stands above all stakeholders, which could be achieved by operating under the wing of a non-profit organisation such as the Netherlands Foundation for Applied Water Research (STOWA). The participating stakeholders together form a steering committee, so that their stakes are clearly known by the coordinator. We envision that the most fruitful approach to funding a model coordinator is when all stakeholder commit themselves to pay an annual remittance. Given the major challenges associated with achieving the WFD objectives that lay ahead, we imagine that the highest impetus to realise this development comes from the water boards, the more because of the significant savings that can be achieved when a well-functioning model contributes to selecting the most efficient and cost-effective WFD measures.

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Summary

A principal aim of ecologists is to identify critical levels of environmental change beyond which ecosystems undergo radical shifts in their functioning. Dynamical ecosystem models are tools that can help ecologists to understand complex systems, and turn this understanding into predictions of how these systems respond to external changes. This thesis revolves around PCLake, an integrated ecosystem model of shallow lakes, which is used by both scientists and water quality managers to understand and predict abrupt regime shift in shallow lake ecosystems. **Chapter 1** of this thesis presents a general introduction. First the urgency of global environmental change is stressed, along with the responsibility of science to support human societies resolving sustainability issues. Subsequently the argument is made that dynamical models are highly useful tools for obtaining a better understanding of complex systems and for turning this understanding into predictions. The introduction continues with a short review of the important features of shallow lake ecosystems, highlighting that they provide numerous important ecosystem services to human societies, but also showing that lakes are among the most impacted ecosystems on the planet. Thereafter, the most important stress factors to lakes are presented, along with different ways of how lakes may respond to stress. Then the shallow lake ecosystem model PCLake is introduced, which can be used to study and predict the response of lakes to stress. Also the European Water Framework Directive (WFD) is introduced, and it is argued that there is huge potential for PCLake to help ecosystem managers reach their WFD targets. Finally the overarching research project is introduced where this thesis is part of. The broad aim of the overall project was to increase the usefulness of PCLake, and its sister model PCDitch, in contemporary science and ecosystem management. The project involved a collaboration between the Netherlands Foundation for Applied Water Research (STOWA), the Netherlands Institute of Ecology (NIOO-KNAW), Wageningen University & Research centre (WUR), the Netherlands Environmental Assessment Agency (PBL) and Witteveen+Bos, a private engineering consultancy. The heart of the project consisted of two PhD studies, one on PCLake and one on PCDitch, and quite a few case studies on aquatic ecosystems in the Netherlands. Four objectives were identified as important pillars of the overarching project: (1) to make the models more *accessible*, (2) to make *improvements* to the models, (3) to increase our *understanding* of the models as well as the ecosystems they portray and (4) to explore new *applications* of the models in lake ecosystem management. The chapters of this thesis follow from these four pillars.

In **chapter 2**, the Database Approach To Modelling (DATM) is introduced, which is invented to make dynamic models more *accessible*. The idea of DATM is that the mathematical equations of a model are stored in a database independently of program language and software specific information. From the database, the information can be automatically translated, augmented and compiled into working model code of various different modelling frameworks (software programs). This procedure allows for easy switching between frameworks, which facilitates the collaboration between modellers. It also makes it possible to exploit the joint multitude of the tools and analysis provided by the different frameworks. An additional advantage is that working in a database provides structure and overview, which makes it easier for modellers and non-modellers to grasp the mathematical formulations. We describe the approach using the simple Lotka-Volterra predator prey model and exemplify it with the complex model PCLake.

In **chapter 3** we reflect on the weak link between ecosystem models and real ecosystems and discuss the consequences for calibration and *improvement* of PCLake. The apparent weak link between a model and reality implies that it will be merely impossible to accurately parameterize all individual model components on basis of empirical data. A solution is oftentimes found in model calibration at an aggregated level, whereby the components are aligned in such a way that together they do an adequate job in describing those ecosystem level variables that are relevant to ecosystem managers, such as total productivity and water transparency. By doing so, any missing dynamics may still be accounted for, albeit indirectly, by modifying the functionality of the components that are explicitly included. An important consequence is that once calibration has been performed, any model 'improvement' in the form of adding more components may bring the model 'out of balance' as it may lead to double counting with the implicit components. To exemplify this line of reasoning the PCLake model was expanded with a filter feeding zoobenthos group. These species are always present in the shallow lakes simulated by PCLake, but were until yet not dealt with explicitly in the model itself but implicitly included in the zooplankton grazing rate during previous calibration. To elucidate how the zooplankton grazing is changed by the explicit inclusion of filter feeding benthos, the original calibration routine was re-established using data from more than 40 lakes. Indeed, it turned out that, to maintain a good fit, the zooplankton grazing rate needs to be lowered. Nevertheless, the analysis showed that calibrating only the zooplankton grazing rate is not sufficient to make the addition of chironomids an improvement to the overall fit of the model.

In **chapter 4**, the relation between complex ecosystem models and empirical food web models is scrutinized. Both modelling paradigms are highly influential in modern ecology as both food-web theory and alternative stable states theory help scientists *understand* how stability is conferred to complex ecosystems. Unfortunately, it is largely unclear how the concept of food-web stability is associated with the resilience of ecosystems susceptible to regime change, and hence how insights from these different fields can be aligned. In this study we treat PCLake as a virtual reality from which we can sample 'empirical' information to parameterize a food web model, following traditional food web methods. Accordingly, the food web model can be analyzed for its stability using the Jacobian matrix approach. We repeated this exercise along the eutrophication gradient, knowing that PCLake will show a regime shift when a critical nutrient loading is reached. By doing so, we show that impending catastrophic shifts in shallow lakes are preceded by a destabilizing reorganization of interaction strengths in the aquatic food web, and obtain insight in the biological interactions underlying regime shifts in shallow lake.

The results of chapter 4 raise the question how exactly stability properties of the ecosystem model are transferred to the empirical food web model. In other words, for a system of consumer resource interactions in equilibrium, is it the exact shape of the functional response of the interactions (e.g. linear vs. nonlinear), or is the patterning of interaction strengths in the network (e.g. degree of omnivory, connectance etc.) that is decisive in determining the stability properties of the system? Given the complexity of PCLake and the produced food web models it is difficult to answer these questions. **In chapter 5**, the extent to which models of a different form can describe the same natural phenomenon is further addressed. We zoom in on the influence of the functional response terms rather than the number of equations. Using three classical extensions of the famous Lotka-Volterra equations we analyze the consequence of changing a system with a sophisticated functional response term (e.g. Holling type II or III) into a system with a simpler functional response term while maintaining equilibrium densities and material fluxes. We are interested in the extent to which stability properties of a complex system can be reflected by a simpler system. Our main result is that changing nonlinear terms in simple models of consumer resource interactions into linear ones, while maintaining the equilibrium densities and the transfer of mass, has a strong impact on the stability properties of the model system. Although transcritical bifurcations (species extinction/invasion thresholds) are maintained after changing the shape of the interaction terms, the so called hopf and saddle-node bifurcations were lost. Especially the latter is important for ecosystem managers that wish to anticipate and prevent abrupt regime shifts. These results give new insight into when empirical data can be linked to mathematical models to estimate the stability properties of real ecosystems.

In **chapter 6**, a new *application* of PCLake is presented. Although PCLake is predominantly applied in the context of ecosystem restoration of turbid phytoplankton-dominated lakes, this study focusses on the clear water state after the reestablishment of aquatic plant dominance. Dense stands of aquatic plants easily cause nuisance, and hence the removal of aquatic plants is an emerging management issue. Yet, because aquatic plants play an important role in stabilizing the clear water state, the removal of plant biomass can potentially trigger a critical transition back to the turbid water state. Currently there is only limited empirical and theoretical understanding of how harvesting of aquatic plants affects ecosystem functioning, which frustrates effective and efficient ecosystem management. With PCLake the impact of harvesting is evaluated, in terms of reducing nuisance and ecosystem stability, for a wide range of external nutrient loadings, mowing intensities and timings. Additionally, the model is used to estimate how much phosphorus is removed from the system during harvesting. The results show that mowing can temporarily reduce nuisance caused by aquatic plants in the first weeks after plant removal, particularly when external nutrient loading to the system is fairly low. When the external loading increases also the risk of triggering a regime shift increases. This risk can be reduced by mowing halfway the growing season when the resilience of the system appears to be the highest. The model shows that up to half of the phosphorus entering the system can potentially be removed along with the harvested aquatic plant biomass.

During the course of the studies presented in this thesis I deliberately established collaborations with experts from different disciplines (mathematicians, computer programmers, empiricists and ecosystem managers), allowing me to take an integrative approach, connecting theories, models, modelling frameworks, methods and even the different experts. In **chapter 7**, I reflect on what I consider the added value of this integrated approach for the different studies presented in this thesis. This general discussion is structured along the same four themes that gave structure to the thesis: accessibility, improvement, understanding and application. I stress for example that ecosystem models that are used both in ecosystem management and for the development of ecological theory are in a unique position to bridge the gap between those realms. Moreover, I argue that by scrutinizing the 'ecotones' of different theoretical frameworks we can make important steps forward in our understanding of how nature may work and at what level of complexity we can model it best. Finally I discuss the human component in research teams, including my own role within the research collaborations I took part of.

In **chapter 8**, a synopsis is presented of the overarching research project on PCLake and PCDitch. The many case studies that were carried out on shallow lakes in the Netherlands proved that PCLake and PCDitch can be used in ecosystem management to identify effective management measures, and hence they proved that modelling studies can contribute to more cost-efficient ecosystem management. The scientific studies contributed to the development of several important ecological theories, including food web theory, consumer resource theory, resource competition theory and, of course, alternative stable states theory. Furthermore, several important technological developments have been made. For example, it is now possible to connect PCLake and PCDitch to spatial explicit hydrodynamical models, and hence run PCLake and PCDitch in 0D, 1D, 2D and 3D. Finally, and most importantly, a large enthusiastic and dedicated community of programmers, ecologists, consultants and water quality managers has been established, ensuring that the models will now be applied on a large scale and will contribute to a better world.

Samenvatting

Veel ecosystemen op onze aarde zijn aan verandering onderhevig onder invloed van menselijk handelen, waarbij de natuurwaarde meestal afneemt. Soms gaat dit geleidelijk, maar veranderingen kunnen ook abrupt en grootschalig zijn. Een belangrijke taak van ecologen is het begrijpen van deze grote abrupte verandering en het voorspellen bij welke milieudruk ze plaatsvinden. Dynamische modellen helpen onderzoekers daarbij. De essentie van een dynamisch model is dat ecologische processen in de natuur worden gevat in wiskundige formules. Door met de formules te gaan rekenen kan een onderzoeker het ecosysteem beter leren begrijpen, bijvoorbeeld door de samenhang van meerdere ecologische processen te ontrafelen. Maar belangrijker nog, het stelt de onderzoeker in staat wat-als vragen te stellen. Wat gebeurt er als de temperatuur met twee graden wordt verhoogd? De onderzoeker kan met een model voorspellen wat de toekomst ons gaat brengen. In dit proefschrift staat het waterkwaliteitsmodel PCLake centraal. Door grootschalige eutrofiering in de jaren zestig en zeventig van de vorige eeuw zijn veel meren in een groene soep verandert, met daarin blauwalgen die gevaarlijk kunnen zijn voor de gezondheid van mens en dier. PCLake is ontwikkeld om de eutrofiering en het ecologisch herstel van ondiepe meren beter te begrijpen en te voorspellen. Het model laat net als de werkelijkheid zien dat de overgang van helder naar troebel water onder invloed van meststoffen vaak abrupt verloopt. Ook laat het zien dat ecologisch herstel lastig is, en dat het kantelpunt waarbij het meer weer helder wordt bij een veel lagere meststoffenbelasting plaatsvind dan waarbij het systeem troebel werd. De wetenschappelijke theorie die dit verklaart is de theorie van de alternatieve stabiele toestanden, en als onderzoeksinstrument wordt PCLake gebruikt om deze theorie verder uit te bouwen. Maar ook voor waterkwaliteitsbeheerders is een modeltoepassing interessant. Volgens Europese wetgeving, de Kader Richtlijn Water (KRW), moet de ecologische kwaliteit van het oppervlaktewater in heel Europa uiterlijk in 2027 weer zo goed als mogelijk zijn. Daarbij wordt het evalueren van doelen en maatregelen door beheerders in toenemende mate gedaan op basis van systeembegrip. PCLake is bij uitstek geschikt om beheerders te helpen systeembegrip te krijgen, en effectieve beheersmaatregelen te selecteren die nodig zijn om troebele meren weer helder te krijgen. Maar ondanks de grote potentie van PCLake in het beheer wordt het model nog maar beperkt ingezet. De Stichting Toegepast Onderzoek Waterbeheer (STOWA) heeft daarom een onderzoeksproject in het leven geroepen waar voorliggend proefschrift onderdeel van uitmaakt. Vier verschillende aspecten van het modelleren met PCLake staan centraal in dit onderzoek: het ontsluiten van het model, het verbeteren van het model, het uitbouwen van ecologische theorie, en het uitwerken van een nieuwe toepassing in het waterkwaliteitsbeheer. In **hoofdstuk één** van dit proefschrift geef ik een algemene introductie en introduceer ik deze vier pijlers.

In **hoofdstuk twee** wordt een werkwijze gepresenteerd waarmee de toegankelijkheid van dynamische modellen zoals PCLake wordt vergroot. We hebben deze werkwijze de ‘Database Approach to Modelling’ genoemd (DATM). Normaliter wordt de toegankelijkheid van een ingewikkeld computermodel zoals PCLake grotendeels bepaald door het simulatieplatform (software) waarin het model beschikbaar is. In pure vorm is PCLake weliswaar een coherente set van gekoppelde differentiaalvergelijkingen, in de praktijk zijn deze vergelijkingen ingebed in een computercode van honderden programmeerregels die ervoor zorgen dat de vergelijkingen kunnen worden opgelost en het model kan worden aangestuurd. Een gevolg hiervan is dat het voor eenieder moeilijk is om ecologie en informatica van elkaar te scheiden. Ook zorgt het ervoor dat iemand die het model wil gebruiken gedwongen wordt om te werken met het specifieke simulatieplatform waarvoor het model geprogrammeerd is. Iemand kan dus niet vrij kiezen voor het simulatieplatform dat het beste aansluit bij het doel van de modelleerexercitie, of het simulatieplatform waar hij of zij al ervaring mee heeft. Deze drempels hebben ons ertoe aangezet DATM te ontwikkelen. Het idee van DATM is dat de differentiaalvergelijkingen van een model in een database bewaard worden, los van enige programmeercode die software specifiek is. Om het model te draaien in een specifiek simulatieplatform worden de vergelijkingen via een automatische vertaler omgezet naar computercode die ingelezen kan worden door het betreffende platform. Met behulp van DATM is het nu mogelijk om PCLake te draaien in een groot aantal simulatieplatformen, inclusief ‘R’, MATLAB en SOBEK (laatstgenoemde wordt veel gebruikt in het waterkwaliteitsbeheer). DATM zorgt er dus voor dat iedereen gebruik kan maken van zijn favoriete simuleeromgeving en dat ecologen en wiskundigen de vergelijkingen kunnen inspecteren zonder te worden gehinderd door een voor hun onbekende programmeertaal.

In **hoofdstuk drie** worden de gevolgen van kalibratie voor de doorontwikkeling en verbetering van complexe ecosysteemmodellen zoals PCLake beschouwd. Door de tijd heen is het lastig gebleken om nieuwe kennis toe te voegen aan PCLake en één van de achterliggende oorzaken is het feit dat het model in een eerder stadium is gekalibreerd. Een model is per definitie een versimpeling van de werkelijkheid; niet alle processen die in de natuur een rol spelen zijn in het model opgenomen. Daarnaast zijn de processen die wel in het model aanwezig zijn niet altijd met grote nauwkeurigheid beschreven, doordat de kennis die daarvoor nodig is ontbreekt. Om het hele model toch zo goed mogelijk overeen te laten komen met het ecosysteem zoals geobserveerd in het veld, kan men onzekere parameters gaan schatten aan hand van deze velddata door middel van kalibratie. Voor PCLake is velddata van 43 verschillende meren gebruikt om 7 onzekere parameters zo te schatten dat het model een relatief goed resultaat geeft bij elk van deze 43 meren. Het is echter belangrijk om te realiseren dat het mogelijk is dat een deel van de functionaliteit van de processen die wel in het veld maar niet in het model aanwezig zijn door middel van de kalibratieoefening toch wordt ondergebracht bij processen die wel expliciet in het model zijn opgenomen. Neem als voorbeeld muggenlarven in het sediment. Tot voorkort was daar maar weinig over bekend, maar het is nu duidelijk dat deze muggenlarven een aanzienlijke invloed hebben op de waterkwaliteit doordat ze het water filteren om aan voedsel te komen. Muggenlarven zitten niet in PCLake, maar watervlooien wel, en die filteren het water ook. Het kan goed zijn dat tijdens het kalibratieproces de filtercapaciteit van de watervlooien iets te hoog werd afgesteld om het ontbreken van de muggenlarven te compenseren waardoor het model als geheel alsnog in staat is om de dynamiek van het ecosysteem in voldoende mate te voorspellen. Als nu in een later stadium alsnog muggenlarven worden toegevoegd aan het model, met de intentie om het model te verbeteren door een ontbrekende groep toe te voegen, zal er dubbeltelling ontstaan van de filtercapaciteit aanwezig in het systeem. Om het model te verbeteren moet dus wederom het hele model opnieuw gekalibreerd worden. Dit is belangrijk om te realiseren in een tijd waarin modelcode door een steeds bredere en diffusere modelleergemeenschap wordt gebruikt, doorontwikkeld en gekoppeld aan andere modelcode.

In **hoofdstuk vier** gebruiken we PCLake voor de ontwikkeling van wetenschappelijke theorie. Al sinds de jaren negentig van de vorige eeuw speelt de theorie van alternatieve stabiele toestanden een belangrijke rol in het wetenschapsveld van de aquatische ecologie. In toenemende mate wordt deze theorie ook in andere disciplines toegepast om de stabiliteit van ecosystemen te onderzoeken. Stabiliteit verwijst hierbij naar de milieudruk die een ecosysteem aankan voordat er een kantelpunt wordt gepasseerd waarbij een abrupte verandering optreedt. Deze theorie richt zich vaak op specifieke niet-lineaire interactieprocessen die een positieve terugkoppeling veroorzaken; positieve terugkoppeling is het belangrijkste ingrediënt voor het ontstaan van kantelpunten. En veelal zijn niet-levende factoren van belang, zoals het doorzicht van het water en de aanwezigheid van schuilplaatsen voor prooidieren. Een ander belangrijk theoretisch raamwerk in de ecologie dat zich richt op de stabiliteit van ecosystemen is de theorie van voedselwebben. Deze theorie richt zich voornamelijk op het levende deel van een ecosysteem, waarbij het gaat om trofische interacties: ‘eten en gegeten worden’. Ecologen willen weten hoe het komt dat voedselwebben in de natuur vaak stabiel lijken te zijn, in de zin dat deze netwerken van organismen in staat blijken om een klap op te vangen zonder dat ze als een kaartenhuizen in elkaar zakken. Ze proberen te achterhalen welke patronen in het netwerk van interacties stabiliserend werken, waarbij er veel aandacht is voor de sterkte van de interacties tussen soorten. Ecologen maken daarbij vaak gebruik van wiskundige modellen die het niet-levende deel van de natuur buiten beschouwing laten en die uitgaan van proportionele (lineaire) functionele responsie interactietermen. Hoewel de theorie van voedselwebben en van alternatieve toestanden beide iets kunnen zeggen over stabiliteit in ecosystemen, is het nog grotendeels onduidelijk hoe ze zich ten opzichte van elkaar verhouden. In hoofdstuk vier brengen we daar verandering in. We gebruiken PCLake om een omslag van helder naar troebel te simuleren door de externe nutriëntenbelasting stapsgewijs te verhogen. Vervolgens monsteren we “empirische” data uit de virtuele werkelijkheid van PCLake en maken met behulp van die data voedselwebmodellen, zoals een voedselwebecoloog dat ook zou doen. Vervolgens kunnen we de stabiliteitseigenschappen van de voedselwebmodellen analyseren en naast de stabiliteitseigenschappen van het uitgebreidere PCLake model leggen. Wat blijkt is dat we de stabiliteit van de voedselwebmodellen afneemt in de richting van het kantelpunt. Er is dus een relatie, en dat is opmerkelijk omdat een heel aantal van de abiotische factoren, die volgens de theorie van de alternatieve toestanden belangrijk zijn, niet expliciet zijn opgenomen in de voedselwebmodellen. Een belangrijke implicatie hiervan is dat de relatief eenvoudig te meten voedselwebstabiliteit kan dienen als waarschuwingssignaal. Ook betekent het dat er een heel pakket aan methodes en inzichten uit de voedselwebtheorie vrijkomt om kantelpunten verder te bestuderen.

In **hoofdstuk vijf** duiken we nog verder in de theoretische ecologie en stellen we de vraag hoe realistisch een wiskundig model moet zijn om de stabiliteitseigenschappen van een echt ecosysteem te kunnen beschrijven. In deze studie focussen we op het belang van het gebruik van proportionele functionele responsie interactietermen tegenover niet-proportionele termen. We gebruiken daarvoor zogenaamde minimodellen. Deze bestaan slechts uit twee differentiaalvergelijkingen en staan verder af van de realiteit dan uitgebreidere ecosysteemmodellen zoals PCLake. Daar staat tegenover deze minimodellen wel volledig wiskundig te doorgronden zijn. We gebruiken verschillende klassieke predator-prooi modellen uit de literatuur, zoals het beroemde Rosenzweig-MacArthur model. Ieder model bevat niet-proportionele functionele respons termen. Voor elk model rekenen we de evenwichtswaarden uit langs een gradiënt van toenemende milieudruk. Vervolgens bekijken we wat er gebeurt als we de niet-proportionele interactietermen in deze modellen ombuigen tot proportionele interactietermen terwijl de evenwichtswaarden die de modellen beschrijven wel gelijk blijven. Voor zowel de originele als de versimpelde minimodellen berekenen we vervolgens de stabiliteitseigenschappen in het evenwichtspunt langs de hele gradiënt van toenemende milieudruk. Hoewel de originele en versimpelde minimodellen dus dezelfde evenwichtswaarden hebben, blijkt uit deze analyse dat de stabiliteitseigenschappen danig van elkaar verschillen. Dit resultaat is in tegenspraak met de resultaten uit het vorige hoofdstuk. Kennelijk is bij minimodellen de aard van de interactieterm (functionele respons) doorslaggevend, terwijl het er op lijkt dat in realistischere modelsystemen de organisatie van de interactietermen in een netwerk het belang van de specifieke vorm van de interactietermen overschrijdt. Deze inzichten helpen ons verder bij het correct voorspellen van naderende kantelpunten met behulp van wiskundige modellen.

In **hoofdstuk zes** wordt een nieuwe toepassing van PCLake voor het waterkwaliteitsbeheer gepresenteerd. Omdat gedurende lange tijd het grootste deel van Nederlandse meren eutroof en troebel was, is PCLake dusver hoofdzakelijk gebruikt in de context van ecologisch herstel. Hoewel ecologisch herstel veelal een proces is van lange adem, zijn er steeds meer voorbeelden van meren waar het water weer helder is geworden. Echter, de combinatie van verbeterd doorzicht met een bodem die nog wel verzadigd is met meststoffen heeft vaak explosieve plantengroei tot gevolg. En hoewel in een plas vol woekerende waterplanten de kans op giftige blauwalgen minder aanwezig is, kunnen de waterplanten zelf ook voor veel overlast zorgen. Vooral recreanten zoals zwemmers, vissers en plezierrvaarders ondervinden hinder van planten. Een logische oplossing wordt gevonden in het verwijderen van waterplanten met behulp van een maaiboot. Maar omdat waterplanten een belangrijke rol spelen bij het in stand houden van een heldere toestand, kan het hele systeem weer omslaan naar een troebele toestand als teveel waterplanten worden verwijderd.

Omdat de Nederlandse wateren zolang troebel zijn geweest is er nog weinig ervaring met het maaien en daarmee een gebrek aan kennis over de beste aanpak. In dit hoofdstuk hebben we PCLake ingezet om inzicht te krijgen in het effect van maaien op het ecologisch functioneren van een meer, waarbij we specifiek gekeken hebben naar de intensiteit en de timing van het maaien.

PCLake is een voorbeeld van een geïntegreerd model, een instrument waarin wetenschappelijke kennis uit verschillende domeinen bijeen komt en dat gevoed kan worden met een groot aantal empirische datastromen. In **hoofdstuk zeven** bediscussieer ik het belang van een integratieve aanpak in de wetenschap, en in de milieuwetenschappen in het bijzonder. Ik bediscussieer vervolgens hoe ik zelf een integratieve benadering heb toegepast in mijn onderzoek en belicht een aantal resultaten die dankzij deze aanpak tot stand zijn gekomen. Verbinden is daarbij het kernthema. Een mooi voorbeeld is de DATM werkwijze, waarbij we de diversiteit aan verschillende simulatieplatformen hebben omarmd. Door snel te kunnen switchen tussen simulatieplatformen kunnen we gebruikmaken van de voordelen die de verschillende simulatieplatformen te bieden hebben, en kan eenvoudig worden samengewerkt met experts uit verschillende disciplines uit binnen- en buitenland. Door DATM is PCLake een echt gemeenschapsmodel geworden.

Dit promotieonderzoek gericht op PCLake stond niet op zichzelf. Het was onderdeel van een breder onderzoeksprogramma waarvan ook PCDitch onderdeel was. PCDitch is het zustermodel van PCLake en modelleert de ecologie van lijnvormige wateren zoals sloten en kanalen. Een promotietraject gericht op PCDitch liep parallel aan het projectonderzoek dat in dit proefschrift gepresenteerd wordt. Ook onderdeel van het brede onderzoeksprogramma waren tiental casestudies waarbij de modellen getoetst werden in de praktijk. De casestudies werden aangedragen en co-gefinancierd door waterkwaliteitsbeheerders (vooral waterschappen) en werden uitgevoerd door het ingenieursbureau Witteveen+Bos. Zo ontstond een breed onderzoeksprogramma waarin samenwerking tussen wetenschap, waterschap en bedrijfsleven centraal stond. In **hoofdstuk acht** geef ik een overzicht van de opzet van het gehele onderzoeksprogramma en de belangrijkste resultaten die het onderzoeksprogramma heeft voortgebracht. Tevens identificeer ik een aantal stappen die nog gezet kunnen worden om PCLake en PCDitch nog waardevoller te laten worden voor het waterkwaliteitsbeheer. Immers, een model is nooit af. Er komt steeds meer kennis en vragen van waterschappers en beheerders veranderen continu – evenals de wereld om ons heen.

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About the author

Jan Jurjen Kuiper was born on May 14th 1987. He grew up in the Frisian countryside, the Netherlands, together with two brothers and one sister. First in the tiny village Mantgum, and later in the less tiny village Stiens, nearby the city of Leeuwarden. The junior classes of the secondary school he took at the Piter Jelles Haydnstraat in Leeuwarden. He continued his secondary school at the Piter Jelles Montessori in the same city, where he was an active member of the party committee. At the age of eighteen, in 2005, Jan took a gap year prior to entering university. He spent half a year working in a restaurant on Ameland, one of the Frisian Islands in the Waddensea. The second half of the year he spent backpacking in Central America. Upon his return he started his bachelor studies in Environmental Sciences at Utrecht University. During his bachelor he was a board member of the student association STORM and member of the study program committee. For his bachelor thesis he explored the possibilities for large scale clean energy production on the Afsluitdijk, a large dam in the Netherlands separating lake IJselmeer from the Waddensea. He continued his education at the same university and completed his master in Ecology & Natural Resource Management. During his major research project he studied the capacity of peatlands to sequestrate CO_2, under the supervision of Dr Bjorn Robroek. His minor research project took place at the Netherlands Environmental Assessment Agency (PBL), where he studied the relation between river regulation and the biodiversity in floodplain wetlands, under the supervision of Dr Rob Alkemade and Dr Jan Janse. Both research projects resulted in a first-author publication in a peer-reviewed scientific journal. Dr Jan Janse nominated him for a PhD position at the Department of Aquatic Ecology of the Netherlands Institute of Ecology (NIOO-KNAW) in Wageningen, where he continued to be his supervisor. The daily supervision was taken care of by Prof. Dr Wolf Mooij. The supervision team was completed by Dr Jeroen de Klein from the Aquatic Ecology and Water Quality Group at Wageningen University. The results of Jan’s PhD research are presented in this thesis. In his spare time Jan likes to go out into nature and to spend time with friends and family. Jan currently lives in Utrecht together with his girlfriend.

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PE&RC Training and Education Statement

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

Review of literature (4.5 ECTS)
- Turbulent times for shallow lake ecosystems

Writing of project proposal (4.5 ECTS)
- Modelling the functioning of shallow lake ecosystems in the Anthropocene

Post-graduate courses (4 ECTS)
- Critical transitions in nature and society; SENSE (2014)
- Consumer resource interactions; PE&RC (2016)

Invited review of (unpublished) journal manuscript (2 ECTS)
- Hydrology and Earth System Sciences: Natural stochasticity vs. management effort: use of year-to-year variance for disentangling significance of two mutually confounding factors affecting water quality of a Norwegian cold dimictic lake.
- Basic and Applied Ecology Facilitation vs. competition: does interspecific interaction affect drought responses in Sphagnum?

Deficiency, refresh, brush-up courses (3 ECTS)
- C++ for Biologists; CEES (2012)

Competence strengthening / skills courses (1.5 ECTS)
- Project and time management; WGS (2015)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.1 ECTS)
- PE&RC Introduction weekend (2012)
- PE&RC Mid-term weekend (2014)
- PE&RC Last-year’s weekend (2014)

Discussion groups / local seminars / other scientific meetings (4.5 ECTS)
- PE&RC Food Web Ecology discussion group (2012-2015)

International symposia, workshops and conferences (11.3 ECTS)
- SEFS; oral presentation; Munster, Germany (2013)
- Food webs symposium; oral presentation; Giessen, Germany (2013)
- Limnologia AIL conference; oral presentation; Santander, Spain (2014)
- Shallow lakes conference; oral presentation; Antalya, Turkey (2014)
- ASLO; oral presentation; Granada, Spain (2015)

Lecturing / supervision of practicals / tutorials (3 ECTS)
- Modelling ecological systems (2012-2014)

Supervision of 3 MSc students
- Modelling Markermeer with PCLake
- Investigating the fish in PCLake
- Mowing of submerged macrophytes

Colophon

The research presented in this thesis was conducted at the Department of Aquatic Ecology at the Netherlands Institute of Ecology (NIOO-KNAW), and the Aquatic Ecology and Water Quality Management Group at Wageningen University.

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