

# How Regime Shifts in Connected Aquatic Ecosystems Are Affected by the Typical Downstream Increase of Water Flow

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## ABSTRACT

All over the world freshwater ecosystems like ponds, ditches and lakes suffer from nutrient-driven regime shifts from submerged plants to dominance by algae or free-floating plants. Although freshwaters are often connected and part of a network, most of our current knowledge on regime shifts comes from studies of isolated ecosystems. The few studies that have assessed the spatial manifestation of regime shifts overlooked the hydrological fact that the water flow through connected waters typically increases in the downstream direction. Here, we use a complex ecosys-

tem model to show that this increase in flow does not lead to spatial differences in ecosystem state. We support these findings with a simple, analytically tractable, nutrient retention model on connected waterbodies. The model shows that all bodies have the same nutrient concentration despite spatial gradients in the flow of water as well as nutrients carried by the water. As a consequence, each connected waterbody is equally vulnerable to a regime shift, implying a regime shift to be system-wide. Furthermore, it appeared that each connected waterbody behaves the same as an isolated waterbody, implying that the vast body of theory on isolated systems, like alternative stable states theory, can still be useful for connected systems. Although these findings are violated when there is heterogeneity in lateral runoff or waterbody characteristics—leading to spatial differences in ecosystem state and therefore to differences in the vulnerability to a regime shift—they show that the typical downstream build-up of water flow does not necessarily lead to differences in ecological state, and thereby provide a basic concept to better understand the ecology of connected freshwaters.

**Key words:** critical transitions; critical nutrient loading; connectivity; landscape limnology; alternative stable states; ecosystem modelling.

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## INTRODUCTION

Due to eutrophication, many of the world's freshwater ecosystems are subject to catastrophic regime shifts (Scheffer and others 2001). Such shifts manifest themselves in different ways depending on the type of waterbody. Shallow-lake ecosystems may switch from a clear-water macrophyte-dominated state to a turbid-water algae-dominated state, often characterized by toxic cyanobacterial blooms (Jeppesen and others 1999). Drainage ditches and ponds may switch from a state dominated by submerged plants to a state dominated by free-floating plants such as duckweed, water fern or water hyacinth (Portielje and Roijackers 1995). These free-floating plants frequently cause dark anoxic underwater conditions severely constraining aquatic life and threatening biodiversity (Janes and others 1996; Verdonshot and Verdonshot 2014).

Over the last decades, ecologists have put considerable effort in understanding and predicting regime shifts. These shifts are often explained from the perspective of alternative stable states (Scheffer and others 2001). An ecosystem possesses alternative stable states when the same external conditions can result in multiple different stable states (Scheffer and Carpenter 2003). This is the case when the system contains positive feedback loops that are strong enough to strengthen a certain ecosystem state, hampering a transition to a contrasting state (Scheffer and others 1993). Such a transition can be triggered by changing external conditions, which push the ecosystem towards a threshold or 'tipping point' (Scheffer 1998). In the case of eutrophication, the threshold level in which a regime shift takes place is referred to as the critical nutrient loading (Janse 1997). For ecosystem restoration, it is of great importance to know the ecosystem's critical nutrient loading. It provides ecosystem managers with a clear target that can easily be communicated (Jaarsma and others 2008), as nutrient reduction is generally considered to be the most effective restoration measure (Sondergaard and others 2007).

Critical nutrient loading is not only relevant to systems that possess alternative stable states such as shallow lakes, but also applies to systems that are not likely to have alternative stable states but still can be subject to abrupt shifts, such as ditches (Van Gerven and others 2015b). The critical nutrient loading of both ditches and shallow lakes was found to depend on system characteristics like water depth, sediment type and water flow (Janse and others 2008; Van Liere and others 2007). These characteristics are important because together with

nutrient loading they affect the nutrient concentration in the water, which in turn determines the ecosystem state, as excessive nutrient concentrations lead to the dominance of free-floating plants or algae (Janse 2005).

Yet, despite the growing theory on regime shifts, it remains largely unclear how regime shifts develop in real aquatic ecosystems. One likely reason is that the vast majority of studies on regime shifts, whether empirical or theoretical, have been performed on isolated systems (Pace and Groffman 1998). However, it is evident that many natural aquatic ecosystems are in close contact with each other and therefore should be regarded as interdependent systems (Soranno and others 2010). The few modelling studies that did consider spatial aspects of regime shifts focused mainly on the effects of connectivity through diffusion, and reported profound implications for the manifestation of regime shifts. For example, Bel and others (2012) and Van de Leemput and others (2015) showed that a regime shift may not be as abrupt as often presumed, but may propagate gradually instead. They also show that diffusion-driven connected ecosystems tend to be in the same state: a local regime shift is either repaired or results in an ecosystem-wide shift. Furthermore, Van Nes and Scheffer (2005) highlight the importance of spatial heterogeneity in environmental characteristics, altering the transient dynamics and allowing for the co-occurrence of alternative stable states. However, these spatial studies did not consider the effects of connectivity through water flow, while aquatic ecosystems are generally part of a catchment, resulting in a hierarchical exchange between systems, from upstream to downstream. The only spatial study we know of that did consider the effect of water flow on regime shifts focused on a chain of lakes (Hilt and others 2011). This study showed that flushing a chain of lakes leads to remarkably different equilibrium states from upstream to downstream, hampering the occurrence of a complete, system-wide shift.

We thus conclude that research studies on regime shifts to date have ignored the hydrological fact that the water flow through connected aquatic ecosystems typically increases in downstream direction. Each system receives water and nutrients from local seepage, precipitation, surface runoff or groundwater (hereafter all together called lateral runoff). This water is transported in downstream direction, giving rise to an increase of water flow from upstream to downstream; the most upstream waterbody receives only its own lateral runoff

water whereas the most downstream waterbody receives also the accumulated runoff water from all upstream waterbodies. The downstream increase in water flow often leads to a downstream increase in nutrient loading, as the water carries nutrients and to a lesser extent also life forms. The implication of this spatial gradient in water flow and nutrient loading for the manifestation of regime shifts is yet to be understood.

In this study, we investigate whether the typical downstream increase of water flow in connected aquatic ecosystems affects the vulnerability to regime shifts. Is each system equally vulnerable to a regime shift or does the vulnerability depend on the system's position in the chain or network? To answer this question, we follow a stepwise approach with increasing complexity. First, we use a simple nutrient retention model to analyse for a chain of connected water bodies how the build-up of water flow and nutrient loading throughout the chain affects the nutrient concentration. Second, we investigate the consequences for ecology in the same chain of waterbodies, using the ecosystem model PCDitch, which can predict the regime shift from dominance by submerged plants to free-floating plant dominance (Janse 1998). Third, we investigate the vulnerability to regime shifts in a more complex spatial configuration, a network of ditches, by applying PCDitch coupled to a spatially explicit hydrodynamic model. In the discussion, we focus on the generality of the results and their applicability to ponds and lakes. Finally, we validate the results with field observations and elaborate on the implications for the management of connected freshwaters.

## METHODS

### Simple Nutrient Retention Model on a Chain of Waterbodies

We used a simple nutrient retention model to describe how the increase of water and nutrient flow

throughout a chain of homogeneous well-mixed water bodies affects the nutrient concentration (Figure 1, Table 1). The model was adopted from Ahlgren (1980). We modified it such that the nutrient retention no longer occurs in the incoming water, but takes place in the waterbody itself, which is, in our view, more realistic.

In the model, each waterbody in the chain has the same water volume  $V$ , the same nutrient retention processes with rate  $r_0$  (zero-order process) and  $r_1$  (first-order process), and the same external nutrient loading  $L_r$  due to lateral runoff with discharge  $Q_r$  and nutrient concentration  $C_r$ . The only aspect that differs is the flow of water; the most upstream body receives no water from other waterbodies, whereas the most downstream body receives all accumulated runoff water. The accumulation of runoff water results in a downstream increase of water discharge  $Q$  and total nutrient loading  $L$ , where  $L$  consists of the lateral runoff loading  $L_r$  and the upstream loading  $L_u$  associated with the inflow from upstream.

The model can be summarized by one equation describing the dynamics of nutrient concentration  $C$  of each waterbody  $i$ :

$$V \frac{dC_i}{dt} = Q_r C_r + (i - 1) Q_r C_{i-1} - i Q_r C_i - r_0 V - r_1 V C_i \quad (1)$$

The nutrient concentrations depend on the lateral runoff loading  $L_r$  (first term at the right hand side), the upstream loading  $L_u$  (second term), the nutrient outflow (third term) and the nutrient retention  $R$  (fourth and fifth term). We determined the waterbodies' final nutrient concentrations by deriving them analytically from equation (1) as well as by running the model until equilibrium. We use the parameter values given in Table 1. The model was run in R (R Core Team 2013), using the deSolve Package (Soetaert and others 2010).

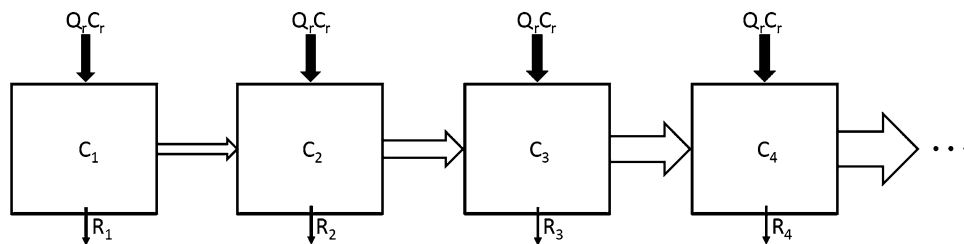


Figure 1. Overview of the simple nutrient retention model, predicting the nutrient concentration  $C$  in a chain of homogeneous well-mixed waterbodies that each have nutrient retention  $R$  and receive water and nutrients by lateral runoff ( $=Q_r C_r$ ), leading to a downstream increase of water and nutrient flow. See Table 1 and equation (1) for symbols and definitions.

### Complex Ecosystem Model on a Chain of Ditches

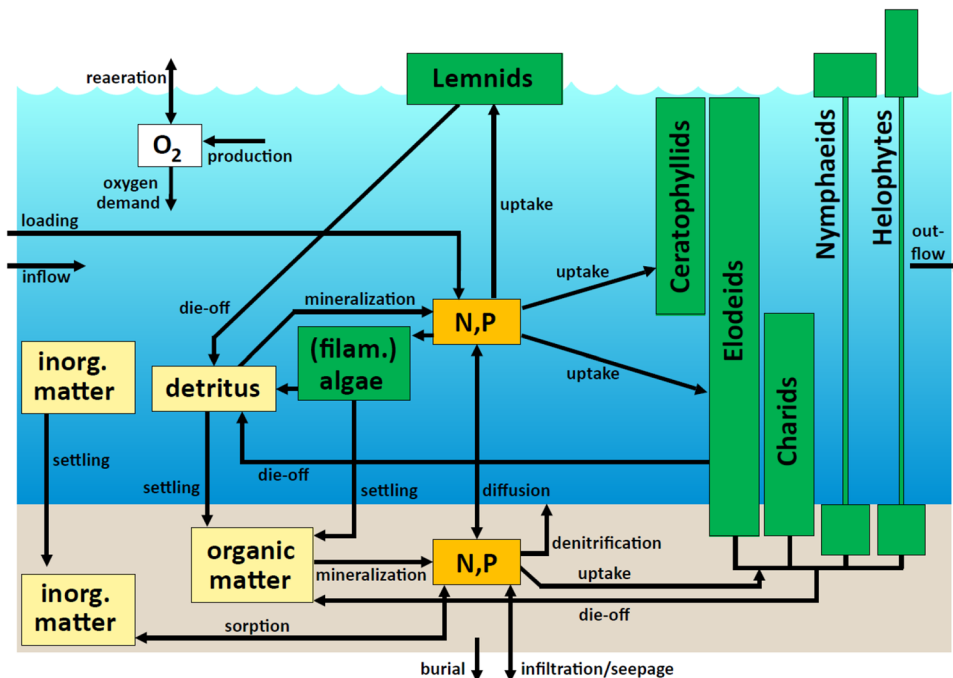
We analysed the same chain of homogenous waterbodies for its ecological state using PCDitch, an ecosystem model for ditches (Janse 1998). Ditches are shallow drainage channels designed to enable agricultural practices. They serve as ecological corridors and support a high biodiversity in which aquatic plants play an important role (Armitage and others 2003). Aquatic plants can promote biodiversity by serving as food or providing shelter to aquatic life, but can also have detrimental effects, in case of highly abundant free-floating plants, by creating dark and anoxic underwater

conditions. Given their important role in the ecological functioning of ditches, PCDitch has a strong focus on macrophytes.

PCDitch simulates the competition of six different plant groups and one group of algae for nitrogen (N), phosphorus (P) and light (Figure 2). To do so, it keeps track of the cycling of N, P and oxygen in the water column and the sediment layer, and thereby accounts for nutrient retention processes such as denitrification and sedimentation followed by burial. The model simulates the interaction of biota with the environment. As such, the nutrient uptake by aquatic plants can be regarded as a form of nutrient retention. The biota can also act as a

**Table 1.** Symbols of the Simple Nutrient Retention Model on a Chain of Waterbodies

Symbol	Description	Formula	Unit	Value
State variables				
$C_i$	Nutrient concentration of waterbody $i$		$g\ m^{-3}$	
Parameters of each waterbody				
$V$	Water volume		$m^3$	50
$Q_r$	Discharge from lateral runoff		$m^3\ d^{-1}$	5
$C_r$	Nutrient concentration of lateral runoff water		$g\ m^{-3}$	5
$r_0$	Zero-order nutrient retention rate		$g\ m^{-3}\ d^{-1}$	0.01
$r_1$	First-order nutrient retention rate		$d^{-1}$	0–0.5
Definitions				
$L_r$	Waterbody's nutrient loading from lateral runoff	$L_r = Q_r C_r$	$g\ d^{-1}$	
$L_{u,i}$	Upstream nutrient loading of waterbody $i$	$L_{u,i} = (i - 1)Q_r C_{i-1}$	$g\ d^{-1}$	
$Q_i$	Total discharge of waterbody $i$	$Q_i = iQ_r$	$m^3\ d^{-1}$	
$R_i$	Nutrient retention of waterbody $i$	$R_i = r_0 V + r_1 V C_i$	$g\ d^{-1}$	



**Figure 2.** Components and processes of the ecosystem model PCDitch, after Janse (1998).

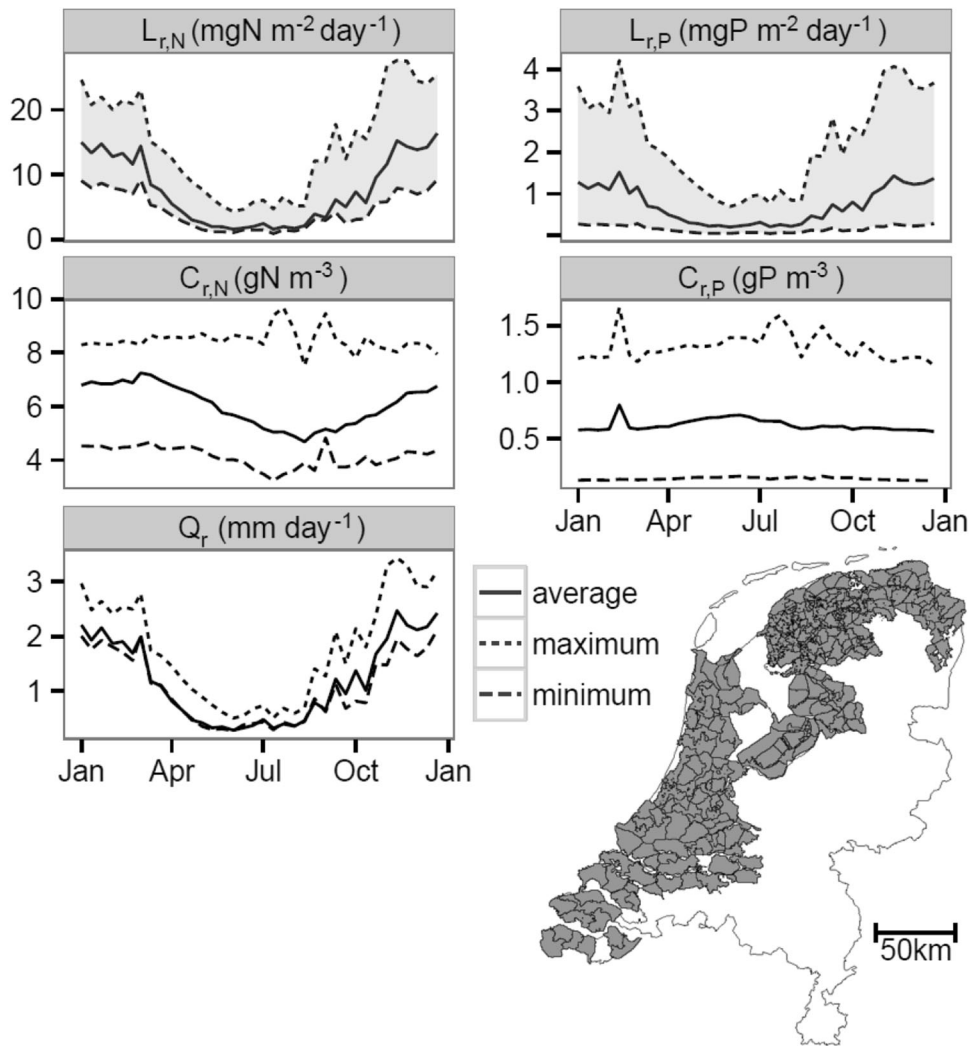


Figure 3. Average, maximum and minimum seasonal runoff in 156 Dutch polders (see map) from 1990 to 2010, calculated with the STONE model (Wolf and others 2005). The runoff nutrient loading  $L_r$  (upper panels), expressed per  $m^2$  runoff area, results from the runoff concentration  $C_r$  (middle panels) multiplied by the runoff discharge  $Q_r$  (lower panel).

source of nutrients, for example, when plants release nutrients due to die-off. In contrast to the PCDitch version used by Kuipers and others (2016), there is no feedback of vegetation on water flow. The model calculates the daily macrophyte abundance, given the imposed water temperature, light intensity, nutrient loading and water flow. PCDitch accounts for seasonality, as it incorporates the phenology of the macrophytes, and simulates the effect of seasonal changes in light intensity and temperature on the biotic and abiotic processes.

As an emergent property, PCDitch predicts the regime shift from dominance of submerged vegetation ('Elodeids' parametrized as *Elodea* spp.) to free-floating plants ('Lemnids' parametrized as *Lemna* spp.) (Van Liere and others 2007). This shift occurs when the nutrient concentration in the water is high enough, requiring the nutrient loading to be sufficient. Note that the other plant groups of PCDitch—the 'Ceratophyllids', 'Charids'

and 'Nymphaeids'—coexist with the 'Elodeids' when the nutrient concentration is low enough. These plant groups do not interfere with the transition from *Elodea* to *Lemna* at which this paper focusses.

To calculate the ecological state in the chain, we ran PCDitch (in R) sequentially from upstream to downstream using the outflow of one ditch as the inflow for the next ditch. We ran PCDitch until seasonal equilibrium (model results that repeat themselves every year) was reached, which took about 20 years in the model. For the process parameters, water temperature and light intensity, we used the settings of the calibrated model (Janse 1998), resembling an 'average ditch' in the Netherlands. For the external input of water and nutrients, we assumed that each ditch in the chain had the same seasonal amount of lateral runoff, for which we took the average seasonal amount in Dutch polders (Figure 3). To convert this amount

expressed as mass per  $\text{m}^2$  watershed to a loading into the ditch, we multiplied it by the total polder area ( $\text{m}^2$ ) and divided it by the area of the ditches ( $\text{m}^2$ ), assuming a ratio of ditch to polder area of 0.023 (Schultz 1992). We assigned each ditch a water depth of 0.5 m and an area of  $100 \text{ m}^2$ , leading to a water volume of  $50 \text{ m}^3$ , which equals the volume used in the simple nutrient retention model.

### Complex Ecosystem Model on a Network of Ditches

We also used PCDitch to analyse the vulnerability of ditches to regime shifts in a more complex spatial configuration: a network of ditches. We chose a network that resembles a typical ditch network in Dutch polder systems; a rectangular network in which parallel 1000 m-long secondary ditches, with a distance of 50 m between them, cross 3 primary 850 m-long ditches every 500 m. The runoff water accumulates in the direction of the polder outlet, located at the end of one of the primary ditches, where it is pumped into the higher-situated nearby river. We assigned each ditch a water depth of 0.5 m and a width of 1 m. These dimensions are common for Dutch polder ditches (Schultz 1992).

We used the 1-D hydrodynamic model SOBEK (Delft Hydraulics 1996) to calculate the water flow in the network. This water flow served as input to calculate the ecological state of each ditch with PCDitch. To establish this coupling of PCDitch with SOBEK, the equations of PCDitch were implemented in DELWAQ (Delft Hydraulics 1995), which took care of the information exchange between SOBEK and PCDitch, and calculated the resulting flow of substances (e.g. nutrients) in the network. To implement PCDitch in DELWAQ, we used a database approach to modelling (DATM) as presented by

Mooij and others (2014), which facilitates the implementation of a model in a new modelling environment (Van Gerven and others 2015a). We verified that the coupling was successful by performing benchmark runs and found that numerical dispersion did not affect the PCDitch–SOBEK results, since decreasing the default calculation time step of 10 min did not alter the model results.

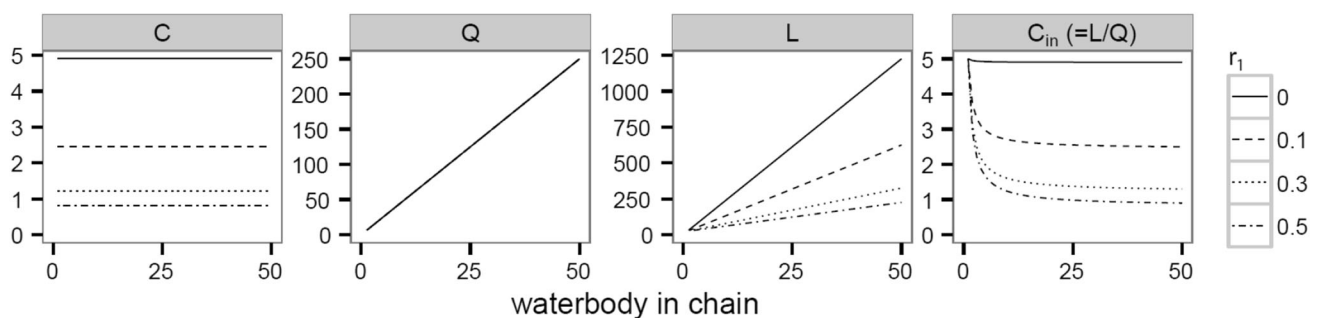
To calculate the ecological state of the network, we ran PCDitch–SOBEK until seasonal equilibrium was reached, which took about 50 years in the model. We assigned the same lateral runoff to each metre of ditch length, again using the average seasonal runoff in Dutch polders (Figure 3). To simulate a regime shift from dominance of submerged plants (*Elodea* spp.) to free-floating plants (*Lemna* spp.), we reran PCDitch–SOBEK while increasing the external nutrient input, by raising the runoff nutrient concentration  $C_r(t)$ .

Finally, we repeated all calculations, but now with spatial variations in ditch characteristics and external nutrient input. The ditch characteristics were varied by doubling the width of the primary ditches, as these ditches are in general wider because they discharge more water. The width of the secondary ditches was kept the same. The lateral nutrient input was varied by randomly changing the nutrient concentration of lateral runoff  $C_r(t)$  of each ditch within plus or minus 30% of its original value, mimicking the natural variations of lateral runoff in Dutch polders (Oenema and others 2005).

## RESULTS

### Nutrient Concentrations in a Chain of Waterbodies

The simple nutrient retention model predicts for a chain of waterbodies that the typical downstream



**Figure 4.** Results of the simple nutrient retention model for different nutrient retention rates  $r_1$  ( $\text{d}^{-1}$ ), showing that each waterbody in the chain has the same equilibrium nutrient concentration  $C$  ( $\text{g m}^{-3}$ ) despite a downstream increase of discharge  $Q$  ( $\text{m}^3 \text{ d}^{-1}$ ) and total nutrient loading  $L$  ( $\text{g d}^{-1}$ ), as well as a downstream decrease of the average concentration of the incoming water  $C_{\text{in}}$  ( $\text{g m}^{-3}$ ).

increase of water and nutrient flow does, on its own, not lead to different nutrient concentrations in the chain (Figure 4). Instead, each waterbody eventually has the same nutrient concentration. This is a rather counterintuitive result, given the downstream increase in discharge and total nutrient loading, and the associated spatial gradient in the average concentration of the incoming water from both upstream waterbodies and lateral runoff (Figure 4). Apparently, the downstream decrease in the average concentration of the incoming water  $C_{in}$  is balanced by the smaller effect of nutrient retention in downstream direction due to the shorter water residence times such that the final nutrient concentration remains the same from upstream to downstream.

This result can be better understood by regarding the analytic solution of the equilibrium concentration  $C^*$  of waterbody  $i$ , which can be derived from equation (1) (Online Appendix A):

$$C_i^* = \frac{Q_r C_r - r_0 V}{Q_r + r_1 V}. \quad (2)$$

Equation (2) shows that the equilibrium concentration depends only on the waterbody's local properties (the lateral input of water  $Q_r$  and nutrients  $C_r$ , water volume  $V$  and nutrient retention rates  $r_0$  and  $r_1$ ), which are the same for each waterbody, explaining the uniform nutrient concentration in the chain. Apparently, under the

assumptions of the model, the equilibrium concentration does not depend on water and nutrient fluxes from upstream, implying that each connected waterbody in fact behaves the same as an isolated waterbody that receives water and nutrients from lateral runoff only.

## Ecological State in a Chain of Ditches

The complex ecosystem model PCDitch predicts that the downstream increase of water and nutrient flow in the chain not only leads to the same nutrient concentration throughout the chain, but also to the same ecological state, as indicated by the uniform abundance of submerged plants (*Elodea* spp.) and floating plants (*Lemna* spp.) (Figure 5). Note that this uniform ecological state changes over time due to seasonality of the imposed conditions (temperature, light intensity and runoff). For the used settings, the waterbodies in the chain are dominated by submerged plants, at the cost of floating plants.

## Ecological State and Regime Shifts in a Network of Ditches

Even in a more complex spatial configuration, a network of ditches, the downstream increase of water and nutrient flow does not lead to spatial differences in the ecological state, as predicted by PCDitch coupled to the 1-D hydrodynamic model

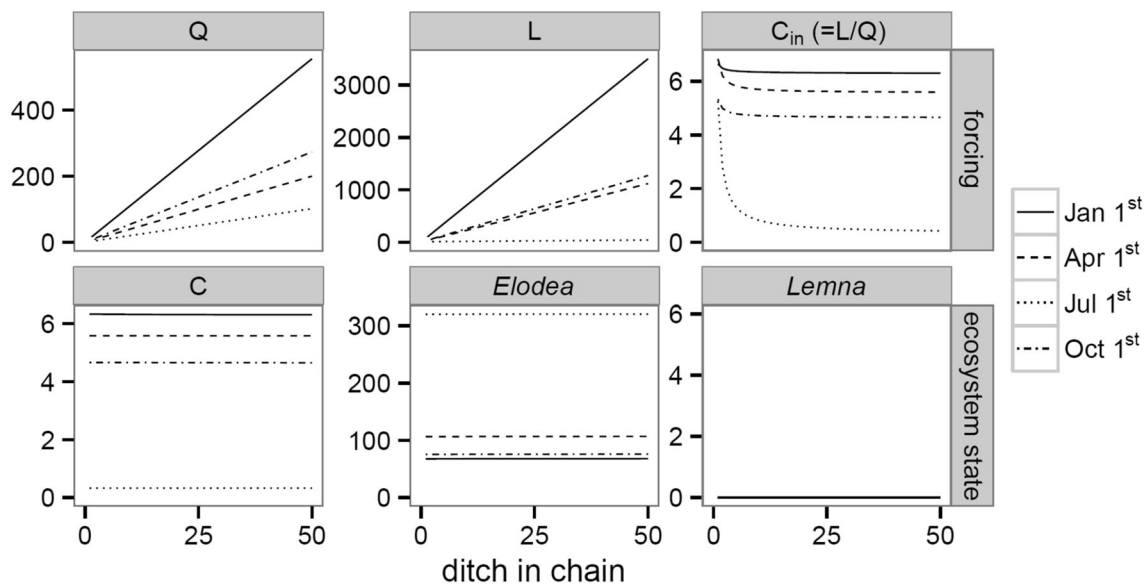
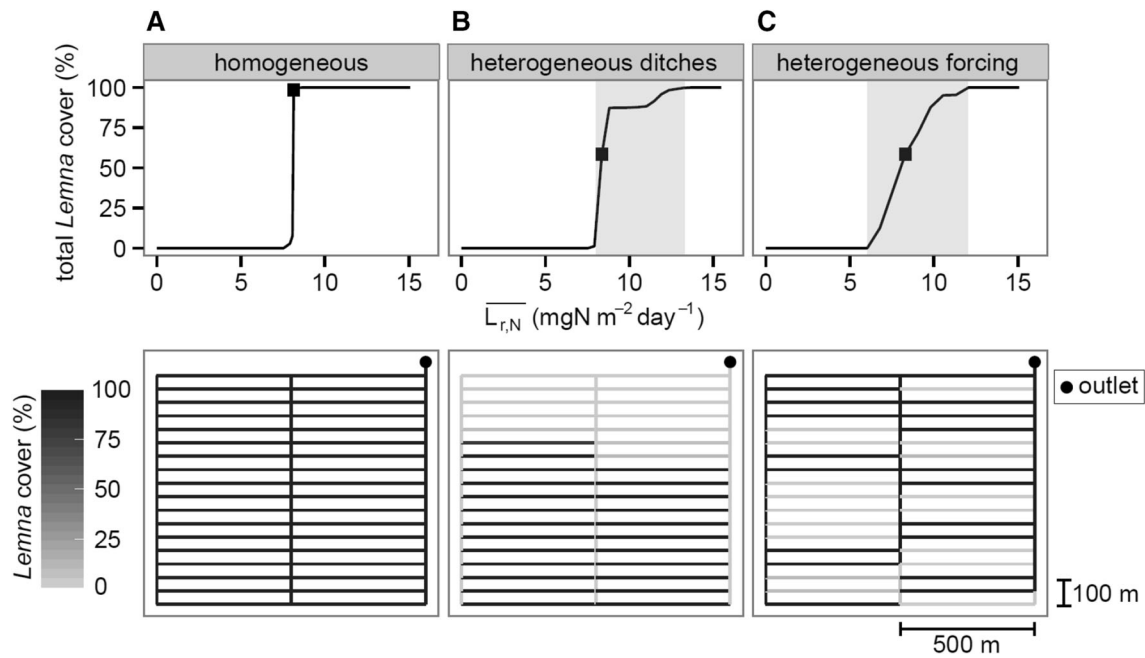


Fig. 5. Results of the complex ecosystem model for different days of the year, showing that each ditch in the chain has the same equilibrium state (*lower panels*)—indicated here by the nitrogen concentration  $C$  ( $\text{gN m}^{-3}$ ) and the plant dry weight ( $\text{g m}^{-2}$ ) of waterweed (*Elodea* spp.) and duckweed (*Lemna* spp.)—despite spatial gradients in the forcing variables (*upper panels*): discharge  $Q$  ( $\text{m}^3 \text{d}^{-1}$ ), total nitrogen loading  $L$  ( $\text{gN d}^{-1}$ ) and average concentration of the incoming water  $C_{in}$  ( $\text{gN m}^{-3}$ ).



**Figure 6.** Results of applying the complex ecosystem model to a network of ditches showing how the network-wide summer-averaged floating-plant cover (*Lemna*) (*upper panels*) depend on the yearly averaged  $N$  loading by lateral runoff  $\overline{L_{r,N}}$  (per  $m^2$  runoff area), in the case of **A** homogeneous ditches with homogeneous runoff, **B** heterogeneous ditches (wider primary ditches) and **C** heterogeneous runoff (runoff concentration to a ditch is randomly varied within  $\pm 30\%$ ). The *gray* areas indicate the network-wide range of critical nutrient loadings. The *lower panels* show the network's *Lemna* coverage for the runoff loadings indicated by the *black squares*.

SOBEK. As a result, each waterbody in the network is equally vulnerable to a regime shift. Therefore, raising the nutrient loading by lateral runoff  $L_r$  leads to a system-wide regime shift, as all ditches in the network switch from dominance of submerged to floating plants at the same loading (Figure 6A).

However, the ditches do have a different vulnerability to a regime shift when accounting for spatial variations in ditch characteristics (wider primary ditches; Figure 6B) or in nutrient loading by runoff (randomly varied runoff; Figure 6C). Then, a regime shift is not system-wide anymore, as each ditch switches to floating plant dominance at a different moment when raising the nutrient loading  $L_r$  by lateral runoff. In addition, the vulnerability to a regime shift now depends on the position of the waterbody in the network. This is illustrated by the case of the widened primary ditches in which the vulnerability to floating-plant dominance not only changes for the widened ditches—it decreases because of a dilution effect—but also changes for the non-widened secondary ditches (Figure 6B). Especially the non-widened ditches close to the polder outlet become less vulnerable, as they receive more water from

the primary ditches and therefore become more diluted.

## DISCUSSION

### Uniform Regime Shifts in Connected Freshwater Ecosystems

Our analyses show that the typical downstream increase of water flow in connected waters does not automatically lead to differences in the vulnerability to a regime shift. Instead, we found that all systems in a chain or network are equally vulnerable to a regime shift, implying a regime shift to be system-wide. This is the case when looking solely at the effect of increasing water flow, in the sense that the characteristics of all waterbodies (such as water depth and sediment type) are the same, and that the increase in water flow is gradual because each waterbody has the same lateral input of water and nutrients by runoff.

We used a simple nutrient retention model to understand this equal vulnerability. This model describes the nutrient concentration in a chain of waterbodies, as the nutrient concentration is of



great importance for the ecological state and thus for the vulnerability to a regime shift. The model shows that the gradual downstream increase of water and nutrient flow leads to the same nutrient concentration throughout the chain. The similar nutrient concentrations can be explained by realizing that the concentration of a waterbody does not change when the waterbody is flushed with water from an upstream waterbody of the same concentration, as is the case in our configuration. This also explains why solving the model equations for equilibrium [equation (2)] shows that each connected waterbody basically behaves the same as an isolated waterbody that receives no water and nutrients from upstream but only from lateral runoff.

### Applicability of the Results to Other Ecosystems

Although we focused in this study on the vulnerability to regime shifts in connected ditches, we expect that our findings also apply to other connected ecosystems like chains or networks of ponds and lakes, also because our findings are explained by the simple nutrient retention model that applies to any waterbody. To be sure, we applied the shallow-lake ecosystem model PCLake (Janse and others 2010) to a chain of lakes and found similar results (not shown here): also in a chain of lakes, each waterbody can be in the same ecological state and therefore has the same vulnerability to a regime shift, despite the downstream increase of water flow. It concerns a regime shift from a clear lake dominated by submerged vegetation to a turbid lake dominated by algae. Even the fact that these algae are transported by the water does not lead to spatial differences in the vulnerability to a regime shift. Furthermore, we checked that the lakes are also equally vulnerable to the backward shift from turbid to clear. Note that this shift occurs at a much lower external nutrient input by runoff because the lakes possess alternative stable states and therefore show hysteresis.

In fact, we expect that any dynamic process-based model that incorporates water, nutrients and biota (for an overview of such models see Janssen and others 2015) can predict that the downstream increase of water flow in connected systems leads to a uniform ecological state, provided that each waterbody has the same process rates, the same characteristics and the same local forcings (for example, lateral input of water and nutrients, temperature, light). Even the size of the waterbodies may differ as long as the local process rates,

characteristics and forcings are the same per  $\text{m}^2$  of waterbody surface.

### Comparison with Other Model Studies

Previous model studies on regime shifts in connected systems ignored the typical downstream increase in water flow, and therefore predicted different results. For example, the model of Hilt and others (2011) on connected systems assumes the water flow to be constant, as it ignores lateral runoff. Their model predicted that flushing a chain of lakes with such a constant water flow leads to profound spatial differences in ecosystem state. The upstream lakes appeared to be more vulnerable to a regime shift from a clear state to a turbid state than the downstream lakes. We expect that our models would under these conditions predict a similar downstream improvement of the ecosystem state, as the nutrient concentration of the flushing water is likely to decrease in downstream direction due to nutrient retention. In reality, lake chains often show an upstream improvement in ecosystem state (Fisher and others 2009; Hillbricht-Ilkowska 2002; Soranno and others 1999). Therefore, Hilt and others (2011) acknowledged that a more realistic prediction requires the consideration of lateral inputs of water and nutrients, as we did in this study.

### Validity of the Results

Our main result—that waterbodies in connected systems are equally vulnerable to a regime shift despite the downstream increase of water flow—only holds true when regarding the simplest conditions. When accounting for spatial heterogeneity in waterbody width or lateral nutrient input by runoff, we found that each connected waterbody displays a different vulnerability, which depends on the position of the waterbody in the chain or network. We found similar results when we varied waterbody characteristics other than width, such as water depth and sediment type. The same holds when spatially varying environmental conditions other than lateral nutrient input such as light intensity or temperature.

In most natural ecosystems, the above-mentioned factors that introduce spatial heterogeneity will be at play. For example, lakes within a chain often have different additional nutrient inputs (related to land use) or distinct depths, leading to differences in nutrient concentrations (Carpenter and Lathrop 2014). Furthermore, connected systems often have a spatial temperature gradient due to local warming or elevation differences. Such spatial gradients, not only related to temperature

but also to other factors, may give rise to a downstream trend in nutrient concentrations. For example, ditches often become wider and deeper in downstream direction, which has a diluting effect and is therefore likely to lead to a downstream decrease in nutrient concentration. As a result, downstream ditches will probably be less vulnerable to a regime shift to free-floating plants. On the other hand, the greater depth of these downstream ditches lowers the light availability for submerged plants, which hampers their growth and thereby increases the vulnerability to free-floating plants. Also, river ecosystems, although not the focus of this paper, often increase in width and depth with distance downstream. Despite the associated diluting effect, many of the world's river systems show an increase of nutrient concentrations from headwaters to the mouth. This is probably related to additional nutrient inputs that vary from being low in the upstream parts to high in the densely populated river deltas.

### Comparison with Field Observations

Based on our findings, one would expect that connected freshwaters located in a fairly homogeneous landscape (in terms of its waterbody characteristics as well as its land use and soil type enabling homogeneous runoff) have a similar ecosystem state. Indeed, field data on nine North American lake chains show a high synchrony in ecosystem state, especially for lakes with short water residence times (Soranno and others 1999). On the other hand, other field studies on seemingly homogeneous landscapes show that ponds connected through overflows show distinct ecosystem states and even a co-occurrence of different states (Cottenie and others 2003; Van Geest and others 2003). However, such a co-occurrence of states may be temporal, like in the Dutch Lake Veluwe where the co-occurrence of a clear water with vegetation and turbid water with algae (Scheffer and others 1994) turned out to be a transition phase of the whole lake to a clear-water state (Van de Leemput and others 2015). Furthermore, in line with our findings, field studies showed that environmental variability can lead to differences in ecosystem state. For example, landscape properties were found to be one of the main causes of the considerable differences in macrophyte vegetation in 50 connected boreal lakes (Mäkelä and others 2004). In addition, we found that due to environmental variability, the position of a waterbody in a chain or network becomes important. This is supported by a study on 71 lakes in Michigan USA,

whose variation in ecosystem state could be largely explained by the position of the lake in the landscape (Martin and Soranno 2006). Furthermore, Carpenter and Lathrop (2014) point at the importance of inter-annual variation in runoff to explain variability in ecosystem state, and illustrated this for 4 lakes of the Yahara chain (Wisconsin, USA).

### Implications for Management of Connected Freshwaters

For ecosystem restoration, it is of great importance to know the critical nutrient loading at which the system shows a swift recovery to a desired state. This critical loading provides ecosystem managers with a clear target that can be easily communicated. However, so far, it is not clear yet how the concept of critical loading should be applied to connected systems.

For connected waters located in fairly homogeneous landscapes, our study shows that the critical nutrient loading can already be predicted by regarding the nutrient loading from lateral runoff only. The other part of the nutrient loading, from upstream waterbodies, may be ignored, as we found that the connected waterbodies tend to behave the same as an isolated waterbody that receives no water and nutrients from upstream but only from lateral runoff. Therefore, the critical nutrient loading can already be estimated with a non-spatial ecosystem model. This approach does not apply to more heterogeneous landscapes. Then, each waterbody has a different vulnerability to a regime shift and also has a different critical nutrient loading. As the vulnerability now depends on the position of the waterbody in the chain or network, the nutrient loading from upstream can no longer be ignored. Therefore, the prediction of the critical nutrient loading becomes much more difficult and requires a spatial modelling approach in which ecology and hydrology are integrated.

### CONCLUSIONS

In this study, we regard connected aquatic ecosystems in their hydrological context, as part of a watershed. We show that the associated downstream increase of water flow, on its own, does not lead to spatial variations in ecology. As a result, all connected waterbodies are equally vulnerable to a regime shift, implying a regime shift to be system-wide. The connected waterbodies turned out to behave the same as an isolated waterbody, implying that the vast body of existing theory on isolated systems can still be of use for connected systems.

Although these findings are violated when there is spatial heterogeneity in lateral runoff or waterbody characteristics, as is often the case in connected aquatic ecosystems, they constitute a basic concept on how hydrology affects the ecology of connected freshwaters.

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