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A perspective on water quality in connected systems: modelling feedback between upstream and downstream transport and local ecological processes

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Food production for a growing world population relies on application of fertilisers and pesticides on agricultural lands. However, these substances threaten surface water quality and thereby endanger valued ecosystem services such as drinking water supply, food production and recreational water use. Such deleterious effects do not merely arise on the local scale, but also on the regional scale through transport of substances as well as energy and biota across the catchment. Here we argue that aquatic ecosystem models can provide a process-based understanding of how these transports by water and organisms as vectors affect – and are affected by – ecosystem state and functioning in networks of connected lakes. Such a catchment scale approach is key to setting critical limits for the release of substances by agricultural practices and other human pressures on aquatic ecosystems. Thereby, water and food production and the trade-offs between them may be managed more sustainably.

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Introduction

Food production for a growing world population relies on application of fertilisers and pesticides on agricultural lands [1]. However, these substances threaten surface water quality and thereby endanger valued ecosystem services such as food production, drinking water supply and recreational water use. Insight in current and future functioning of aquatic ecosystems at a local, regional and global scale is therefore of high societal relevance [2]. The focus of research on aquatic ecosystem functioning has shifted over the years. The earliest scientific studies in the field of aquatic ecology – such as the seminal work of Forbes [3] – argued that organisms in lakes live in remarkable isolation from the surrounding land. The current scientific view, however, is that the ecological functioning of lakes can only be understood if we take their connectedness with the surrounding watershed and the agricultural practices therein into account [4]. Obviously, the hydrological network supplies lakes with water and nutrients, thereby determining its residence time and trophic status [5•]. Less obvious – but potentially of crucial importance – is that the local ecological state of lakes feedback on other lakes in the network, with the possibility for a domino effect in water quality along the network [6••]. Here we argue that in addition to being connected through water flow, aquatic ecosystems exchange energy, substances and biota through organismal behaviour. Both water flow and organismal behaviour are vectors that are modified by human pressures [7•]. Specifically, we establish how both vectors influence mass transport processes at the catchment and subcatchment scale between lake ecosystems. Furthermore, we examine how such processes translate into modelling a connected waterscape using aquatic ecosystem models (AEMs). The latter is essential for the identification and setting of catchment-wide pollution limits for managers to ensure sound water quality while maintaining human benefits of the landscape and waterscape (e.g. food production, drinking water supply). Here we choose to focus in on the spatial scale of the catchment as it is the spatial scale where water management of local, regional, and even continental institutions [8] and its legislation [9] should be put into practice. Moreover, it is a relatable and graspable spatial scale for stakeholders [10] where their daily lives, regional food production and land use takes place [11••].

Vectors of connectedness

Water flow and organism flow are two major vectors determining the connectedness of lakes within catchments, therewith accounting for the transport of energy, substances and biota (Figure 1). The degree of transport affects ecosystem state and functioning in networks of connected lakes. We now will assess these two major vectors in relation to transport of energy, substances and biota.

Water flows: transport of energy

The speed of water flow has consequences for the transport of both kinetic and thermal energy through the catchment (Figure 1a), therewith selectively removing specific groups of organisms from lakes and potentially affecting ecological states. The speed of water flow affects the kinetic energy which is especially relevant for uprooting of macrophytes [12] or for flushing of phytoplankton [13] and free-floating plants [14]. In contrast, organisms may also mediate kinetic energy by obstructing the water flow. For example, aquatic vegetation causes flow impedance, leading to a reduction of potential washout of aquatic organisms downstream [15]. Another form of energy transport is found in the transport of thermal energy. Inflow of water of a different temperature may have far-reaching ecological effects due to the disruption of natural stratification and ice cover regimes downstream [16]. Stratification determines the redistribution of dissolved substances (nutrients, oxygen) [17], and therefore has a decisive impact on the composition of the ecological community in lake systems [18]. Water heat transfer is strongly impacted by its clarity, which is largely driven by the biomass accumulation of phytoplankton [19]. Through increasing human use of the cooling and heating capacity of water, water systems are increasingly thermally polluted and oxygen depleted [20], which has the potential to make ecologically relevant changes [21] to downstream lakes.

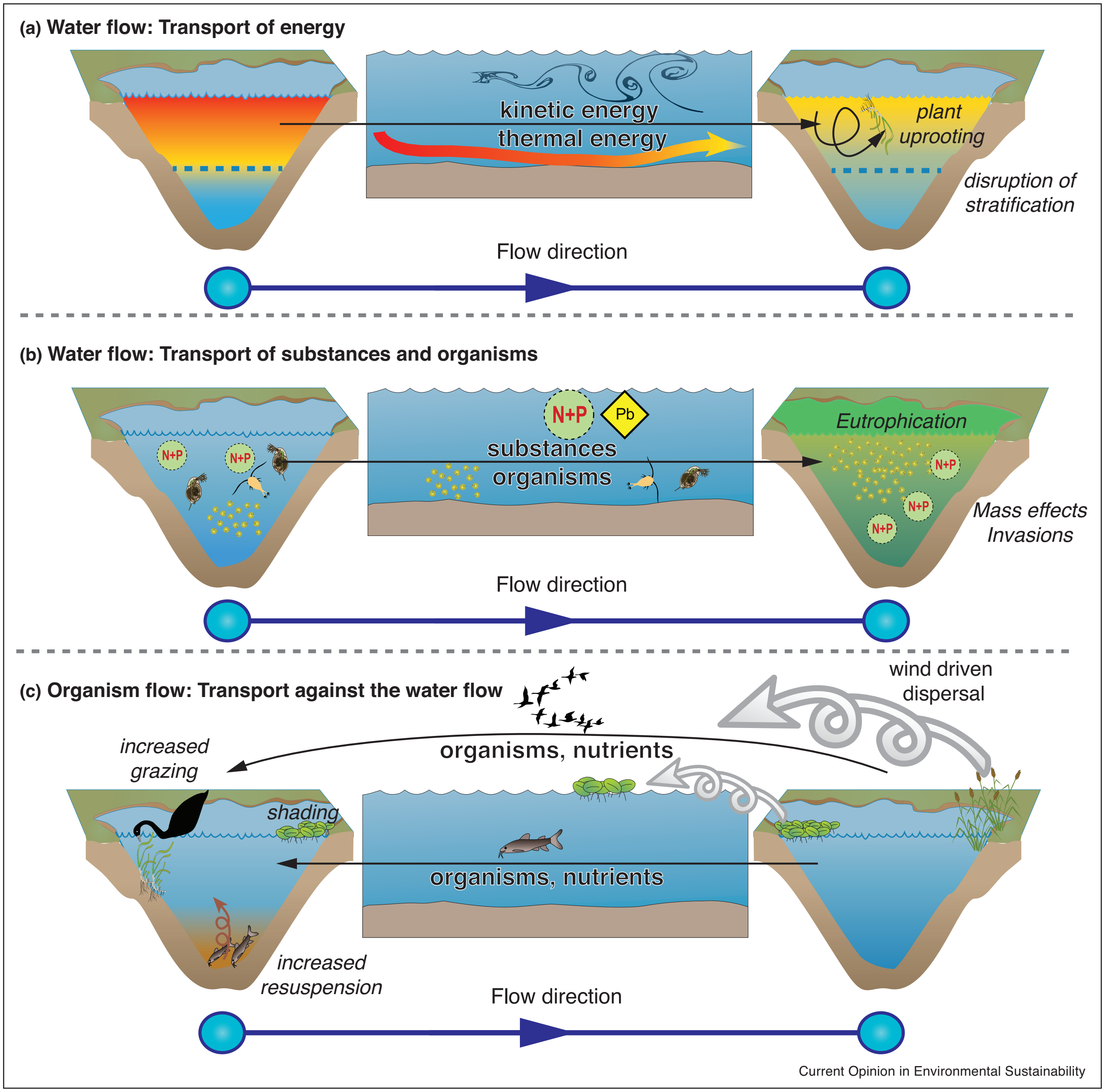
Water flows: transport of substances

Water flows are a key vector for the transport of a whole range of dissolved and suspended substances (Figure 1b). Most relevant in an ecological context are nutrients (primarily phosphorus and nitrogen) and pollutants (e.g. pesticides, heavy metals, pharmaceuticals and microplastics) and sediments [22–24]. Influx of these substances to lakes impact local ecosystem dynamics (i.e. biomass build-ups, toxic effects) and are included in several AEMs (e.g. [25,26•]). When these substances are transported by the water flow downstream the catchment, they can also impact connected lake systems in turn. Some inert substances – such as chloride – are likely to reach downstream systems via relative simple pathways, being a product of the inflowing load and the dilution by the water flows throughout the network (i.e. mass balance calculations) [27]. Non-inert particle transport becomes more complex, as the simple dilution function no longer holds once ecological feedback impact the adhesion, diffusion, uptake or release of substances [28]. For example, nutrients undergo such an ecological feedback, as all biotic groups actively use them in different amounts for biochemical processes, thereby indirectly impacting nutrient retention of lakes. Hence, if an increase or decrease of nutrient input modifies an upstream ecological state (e.g. from macrophyte to phytoplankton domination) the nutrient retention capacity of a system will change due to a changed ecological configuration (e.g. [29•,30]). When lakes are connected, this will, in turn, affect nutrient flows between lakes and can trigger a domino effect of changes in ecological states [6••]. Similar principles may hold for other pollutants, as they are known to trigger state changes [31] and the resulting changed ecological configuration may also lead to notably different retention, uptake and adsorption rates, and even impact the half-life of various substances and their bioaccumulation rate [32]. Lakes, and reservoirs especially, may serve as basins of selective retention within the hydrological network due to their (relatively) long water residence times [33], but depending on physiochemical and ecological conditions they may also selectively release substances [34].

Water flows: unidirectional transport of biota

Similar to the transport of substances, organisms may be transported along with the water flow. This transport of planktonic organisms can cause changes in an ecosystem state when: (a) the inflow of organisms is sufficiently great to displace local communities (mass effect, Leibold 2004), or (b) the organism entering the system is competitively superior (invasion). With mass effects, the inflow of organisms essentially overwhelms the local community, thereby changing ecological configurations directly [87,88]. Invasive species are clear examples of

Figure 1



Schematic figure illustrating different cases of connectedness of aquatic systems through flows of water and organisms, including examples of the associated ecological effects (italic): **(a)** the transport of energy through water flow may impact adjacent aquatic systems by transport of thermal energy that impacts stratification regimes and kinetic energy able to cause uprooting of vegetation; **(b)** transport of substances and planktonic organisms by water flow may cause eutrophication and mass effects or invasions of organisms from the upstream system; **(c)** actively moving organisms (e.g. fish, birds) or overland dispersal through wind can transport organisms (e.g. free floating plants and plant propagules) and nutrients against the dominant flow direction and even to hydrologically unconnected systems.

competitively dominant groups of organisms that even in small numbers – may become dominant in a system [35]. For example, invasion by a diatom algal species (didymo) in New Zealand has had massive impact on the ecological state of lake systems by changing them into phytoplankton dominated systems [36•]. Likewise, ecosystem engineers that modify their existing habitat (e.g. Dreissenid mussels) cause strongly different ecological configurations [37] and become dominant, whilst only arriving in small numbers. When species coming in via water flow are not directly invasive, their numbers are often very small compared to the already present population densities. Inflow of (non-invasive) organisms from upstream sources will become the dominant process determining the state of a lake ecosystem at short residence times (less than a few days) [38]. When residence times become longer, the internal processes of the system will become increasingly important for the ecological outcome in relation to the transport flux [39].

Organisms flows: bi-directional movement

Organism flows can also be bi-directional, allowing organisms to move from downstream to upstream locations and transporting both themselves as well as substances [40,41]. Some aquatic organisms are capable of moving against water flow (i.e. fish), whilst other partially aquatic organisms (e.g. amphibians, insects, birds and crayfish) may move and disperse overland by active motion. Lastly, wind may transport propagule or floating sessile organisms (i.e. free floating plants, algal scums [42]) against the flow. Active movement of organisms is inherently behaviour driven, and may take place at levels of spatial scale far greater than the local ecosystem [43,44]. While only selected groups of organisms are capable of such bi-directional transport, there is ample evidence for the importance of this in cross-ecosystem nutrient transport [45]. The substance transport by organism movement will largely consist of the nutrients that form the building blocks of their biomass, though fish as well as birds are also known to transport seeds, propagules and pathogens of other organisms upstream [46,47]. Meanwhile these organisms can have key impact on the local ecosystems where they are located, for example, fish [48]. This bi-directional movement is ecologically relevant when it either constitutes a large flow of mass of organisms (mass effect) or a large amount of substances causing upstream enrichment. The relative magnitude in terms of biomass of organisms via overland transport tends to be limited. Hence, its importance needs to be seen either through the lens of guanotrophy – the enrichment of systems through organism feces from elsewhere [49] – or in light of new species that massively impact ecological processes (i.e. grazing and/or vandalism by crayfish [50]). The latter also applies for bi-directional movement within the hydrological network, which may be relevant when the organisms moving upstream modify their habitat, for example, increased bioturbation by benthivorous fish [51].

Humans as transport modifiers

Humans have greatly modified the transport of energy, substances and biota all over the world directly and by affecting the water and organisms that carry them [52]. These changes may be aggravated by global climate change through altered water flows and permanent or periodical range shifts of organisms [53,54]. Some human-induced transports are intentional because they form part of the global food production chain, while others are side effects such as the accidental introduction of invasive species through ballast water [55]. Surface waters have always been important routes for trade and travel, thereby attracting human settlement and agricultural production but putting stress on aquatic ecosystems. Moreover, locally humans actively use the aquatic environment as a source of food (fisheries, aquaculture), thereby creating a cross-ecosystem flow of mass from the aquatic to the terrestrial system. On regional and local scales humans put great pressure on aquatic ecosystems in agricultural and urbanised areas by the application of fertiliser and pesticides, disposal of industrial and human waste, and withdrawal of water for multiple uses (*cf.* crop irrigation, drinking water production, industrial cooling and energy production). Management efforts aim to set critical limits to these practices to sustain continued delivery of a wide range of ecosystem services [56•]. Such approaches often aim to shield natural areas from waste loads and water extraction – with mixed success. It proves to be even harder – if not impossible – to shield natural areas from invasive species, potentially leading to an invasional meltdown [57].

Discussion

Assessing critical limits to anthropogenic pollution loads not just on the scale of a water body [58] but on the scale of the entire catchment poses an important next step in safeguarding the ecosystem services of water for human use [59]. Catchment-level hydrological and chemical water and substance transport modelling is a well-developed field (for an extensive review see Ref. [60••]). Currently, these models tend to ignore the ecological feedback on water quality or incorporate them as fixed retention coefficients [59]. Ecological processes are well-known to be relevant for nutrient retention [61]. Moreover, there is strong evidence for potentially unexpected outcomes of ecological quality at larger spatial scales (also see Macrosystems ecology [62]) due to local ecological feedback causing, for example, cascading collapse of ecological states [63]. Hence, incorporating AEMs into or onto catchment level transport models is required to: (a) determine the limits to anthropogenic pollution loading to surface waters including ecological feedback, (b) maximize retention capacity along the water network to minimize downstream impacts and integrate this into downstream mitigation management [64]. Here we identified the need of incorporating the effect of water and organism flow on mass transport into connected aquatic ecosystem models.

The easiest starting point in integrating catchment scale transport models and AEMs is to use the outcome of transport models as input to the AEMs. Resulting hydrological, substance and (where possible) organism flows from transport models are used to feed the AEM. Studies using this approach are already being applied [65,66] and advocated as ways to model any lake on earth

[4]. The next step will be to include ecology as an inherent system property in transport models, advocating for ecology as a driving factor modifying flows of water, substances and energy. When using models, technically this is not different from existing work which couples hydrodynamic flow models to AEMs at scales of individual lakes [67,68,42]. Recent work has shown though, that spatial structure in hydrological systems not necessarily causes heterogeneity in water quality [14,69]. In cases where variations in the flow of water are proportional to the amount of substances it carries, the loading of each segment in terms of the inflowing concentration will be invariant throughout the network and the resulting ecology and water quality will be spatially homogeneous (Figure 2a). In reality, however, water flow and the amount of substances they carry will often be decoupled.

Figure 2

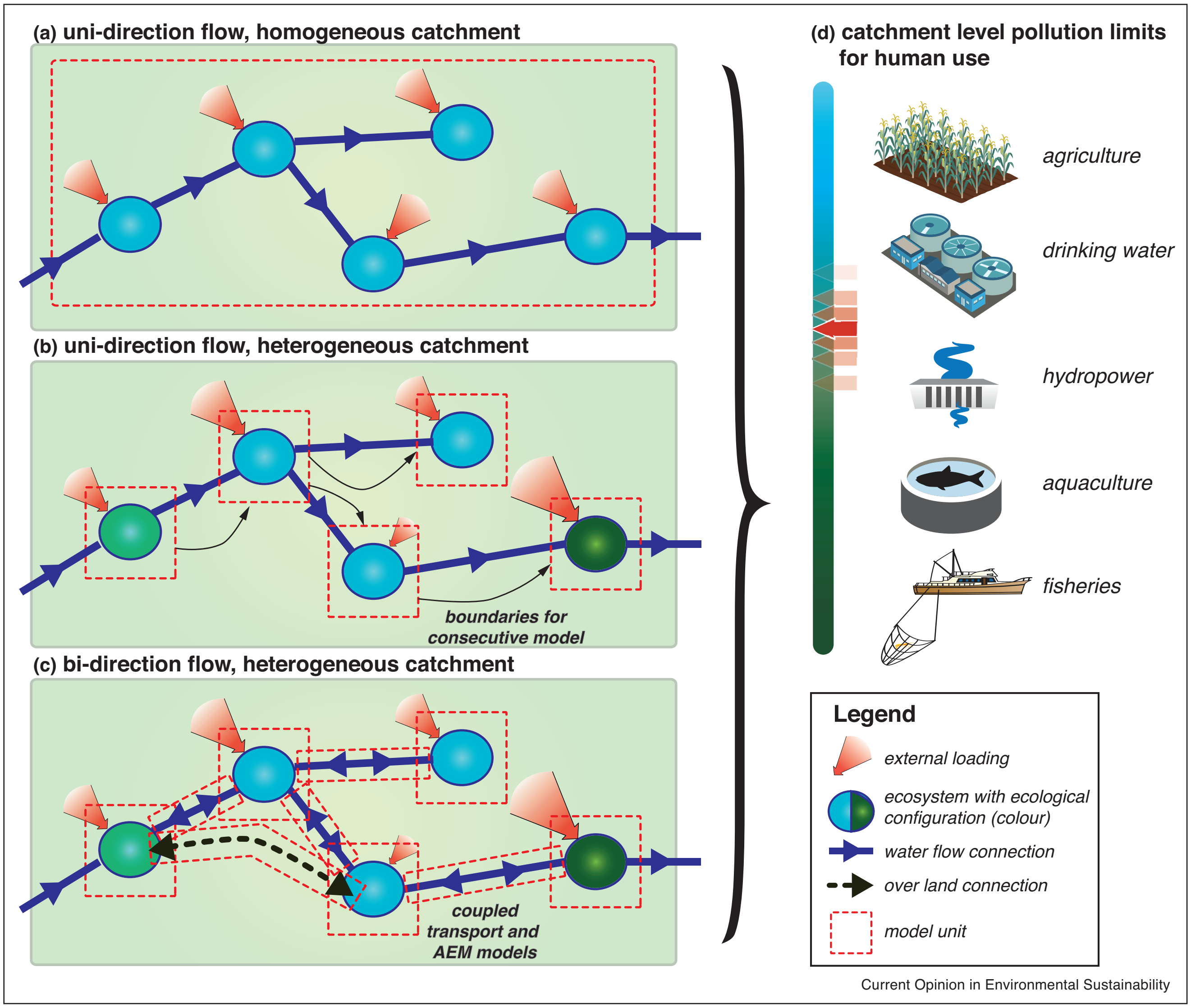


Illustration of the varying complexity of models needed to model catchment scale networks of lakes (nodes) facilitating the setting of catchment level pollution limits. The illustrated catchment network includes different levels of environmental heterogeneity in external loading (red arrows) and ecological configuration (colour of lake nodes) under unidirectional and bi-directional flows. **(a)** illustrates a catchment in which the environmental conditions are similar throughout and flow is unidirectional, allowing for a single AEM unit to be used to predict ecological state (red dotted box). **(b)** Illustrates a landscape with heterogeneous loading and ecological configuration, thereby requiring explicit AEMs for each of the lake nodes. As flow is unidirectional, the outgoing flows of energy, substances and organisms may be used as boundary forcings on the consecutive AEM (black arrows). In the case of **(c)**, bi-directional flows of both water (blue arrows) and overland transport by organisms (black dotted arrow) exist. This makes it necessary to run fully coupled transport (both water and organismal) and ecosystem models, accounting for the transfer of energy, substances and organisms at every time step of the model run. In **(d)** we show that each of these modelling approaches can be used to set catchment level pollution limits that impact a variety of human land and water uses. Different management approaches can lead to a change in catchment level pollution, and thereby maintain or limit ecosystem services.

This decoupling can be caused by different parts of the network having inherently different surrounding landscapes that impact them (e.g. land use intensity), or by having inherently different properties themselves (e.g. depth, ecological configuration) (Figure 2b). This has important consequences for where in the network water quality problems will arise and which water quality measures will be effective.

Modelling ecological quality of a network of connected systems in a spatial context is not synonymous with coupled models. When a network is dominated by unidirectional water flow, sequential modelling of every single system with its inflows of water, organisms and substances will suffice. The outflow from the first modelled system may be used as part of the inflow for the consecutive system in the network. Such an approach has been used previously in connected models [70,6••]. Once flows become bi-directional though, either due to water flow inversion (due to human activity or water table changes at the downstream location) or active movement of organisms (Figure 2c), this approach will no longer suffice. In this case, a fully coupled hydrodynamical and ecological model will be needed, where water flow, substances and organisms are actively exchanged at each point in time between the different systems in the modelled network. When organismal behaviour leads to overland transport, a movement model of organism behaviour including its habitat selection will be required [71]. For example, grazing by birds on aquatic vegetation can lead to a state shift [72]. As the local habitat loses its food source, the birds will move to a new habitat, but by doing so they alleviate grazing pressure from the first system. This means that all aquatic systems, as well as the movement of birds, would have to be modelled conjointly to be able to predict the resulting ecological quality of the systems in the catchment.

Modelling ecological quality of a network of connected systems in a spatial context is worthwhile given that feedback from one system to the next are important drivers of the resulting state of the next system. The inherent issue with this statement is that many ecological processes and changes in ecological configuration are non-linear, making it hard to predict when flows are going to make relevant differences. Moreover, teleconnections [73] between systems can lead to small changes in one system causing a catastrophic collapse over a much larger spatial distance, for example Ref. [43]. To a large extent, the importance of explicitly modelling the ecology as a modifier of the transport across local aquatic system boundaries and its importance on a catchment level is an open scientific question and is likely to depend on a combination of uptake, residence and transport times and the strength of connections between local systems [74]. Knowledge of how and when ecological feedback are relevant to take into account is vital, not just for science, but also for the management of our aquatic systems and their surrounding landscape, especially in a rapidly changing world [75•].

Towards catchment scale models for application

The bridge between what science provides – knowledge of studied systems – and what society demands – global scenarios in the face of the Anthropocene – can be built from both sides: upscaling the local perspective and downscaling the global perspective. Here we advocate to take both spatial approaches simultaneously, while acknowledging that the tools to model all aquatic ecosystems in full detail in one coherent model are not yet available and may never become available. Irrespective of the approach, a simple spatial schematization is a key prerequisite. We suggest to start from a simple node-link schematization as is common in (sub-) catchment modelling [23], with each node representing a lake system and links representing transport corridors (Figure 2). Different node level characteristics in terms of local heterogeneity (Figure 2a versus b) and unidirectionality versus bidirectionality in links (Figure 2b versus c) will determine the need for linking transport models and AEMs explicitly. More complex watershed models and delineations would be the next step forward (e.g. [76]). Starting simple, with node-link setups, and only making explicit linkages between transport models and AEMs when bidirectional transport occurs and is relevant to explain model outcomes (and errors therein) in spatially complex configurations.

Examples of catchment transport models [76,23] and AEMs [26•] are plentiful in literature. Both offer potential for the development of catchment models that adequately account for ecological feedback, and thereby allow for scenario analysis for management. PCLake is a clear example of a model that fits in the upscaling perspective. Developed to study phosphorus loading in a specific lake in the Netherlands [58], it has now been applied far outside of its calibration domain to study eutrophication [77,78,42,68,79], but also all sorts of other management practices that were not originally foreseen [80,81,32] and has now been applied in spatial context [82,66,69]. Such upscaling was enabled through technical innovation [82–84] and a collaborative network of scientists (for more of such examples see Refs. [85,86•]). The perspective of downscaling processes is well represented through the evolution of the VEMALA model applied for Finnish catchments. The model started off as a catchment model with a spatially developed explicit lake network description and simple calibrated lake-specific retention coefficients [5•]. Through ongoing development, these coefficients have now been replaced with an ecological process-based submodel (VEMALA v3 [64]). The model is currently being used (a) to provide fractions of bioavailable nutrient input to the inland and marine water bodies [64] and (b) to assess the effect of the retention in the catchment to inform spatial planning of mitigation measures in hopes of meeting Marine Strategy Framework Directive (MSFD) goals for the Baltic Sea.

Worldwide, waterscapes provide essential services to humanity but face threats, ranging from invasive species to eutrophication. Such threats to aquatic ecosystems can be local, but often act on a regional scale because of the inter-waterbody transport of energy, substances and biota by water and organisms as vectors. Understanding and predicting these exchanges in a catchment context with process-based AEMs will help to manage aquatic ecosystems, set policy targets at the catchment scale and continue to benefit from the services that ecosystems provide. To exemplify this in the context of the water–food–energy nexus, fertiliser and pesticide application for food production leads to the eutrophication and toxification of aquatic ecosystems. The resulting local degradation of surface water quality and altered ecosystem state and functioning will result in a lower retention and removal of nutrients and pollutants in networks of connected lakes, thereby threatening the use of water for irrigation (endangering food production) and aggravating eutrophication problems downstream. These processes involve multiple feedback loops and spatial differentiation in the sources and flows of water, energy, substances and biota. Spatially explicit AEMs on (sub-) catchment scale can help to get a grip on such complex interactions and are key to setting critical limits to the release of substances to aquatic ecosystems by human practices such as agricultural food production.

Conflict of interest statement

Nothing declared.

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