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Modeling water quality in the Anthropocene: directions for the next-generation aquatic ecosystem models☆

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"Everything changes and nothing stands still" (Heraclitus). Here we review three major improvements to freshwater aquatic ecosystem models — and ecological models in general — as water quality scenario analysis tools towards a sustainable future. To tackle the rapid and deeply connected dynamics characteristic of the Anthropocene, we argue for the inclusion of eco-evolutionary, novel ecosystem and social-ecological dynamics. These dynamics arise from adaptive responses in organisms and ecosystems to global environmental change and act at different integration levels and different time scales. We provide reasons and means to incorporate each improvement into aquatic ecosystem models. Throughout this study we refer to Lake Victoria as a microcosm of the evolving novel social-ecological systems of the Anthropocene. The Lake Victoria case clearly shows how interlinked eco-evolutionary, novel ecosystem and social-ecological dynamics are, and demonstrates the need for transdisciplinary research approaches towards global sustainability.

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☆ Please note that the term 'Anthropocene' is not formally recognized by the U.S. Geological Survey as a description of geologic time.

The challenge of sustainable development

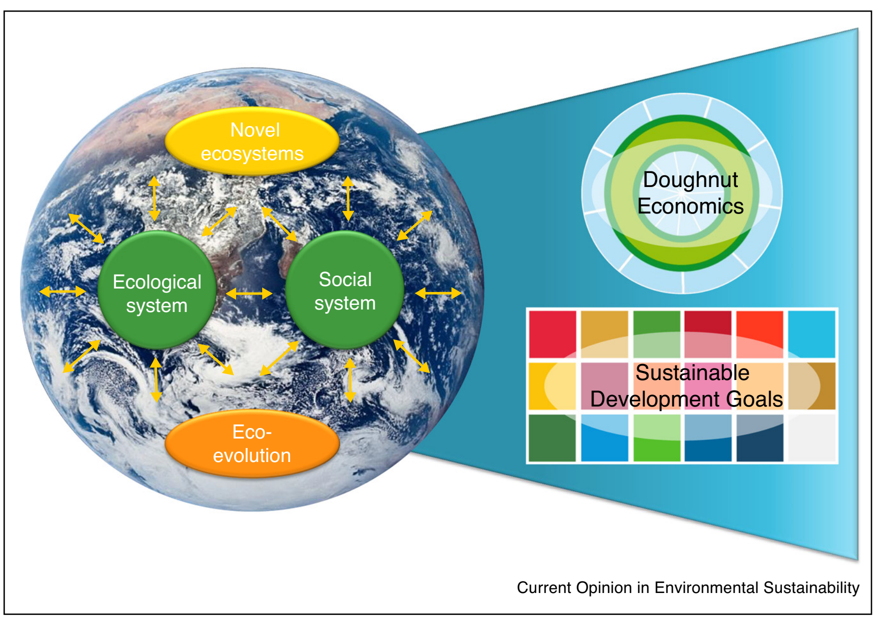
"Earth provides enough to satisfy every[one's] needs but not every[one's] greed" (Mahatma Gandhi)

Since the dawn of history, humans have tried to improve the quality of their lives through technological innovation, scientific development and social organization. After World War II, this 'progress' culminated in what is known as 'the great acceleration'. Hence, we now live in the 'Anthropocene', defined by a globally measurable impact of human activities on system Earth [1,2], and we are transgressing planetary boundaries [3,4]. To meet human needs within the means of the planet, Kate Raworth [5,6] recently presented the 'Doughnut Economics' framework. Doughnut Economics specify *"a safe and just space for humanity"* [5] in terms of eleven fundamental human needs that together provide a social foundation and nine aspects of global environmental change that provide an ecological ceiling. Essential human needs and planetary boundaries are also covered by the UN Sustainable Development Goals [7,8]. Both frameworks provide targets society should strive for in its quest for a safe and just future (Figure 1) but leave the question how to get there unanswered [9]. Consequently, we require scenario analyses to provide decision makers with feasible pathways to a sustainable future, that meet *"the needs of the present without compromising the ability of future generations to meet their own needs"* [10].

Mathematical models are essential tools to capture our knowledge of numerous and intricate causal relations between human activities and environmental impacts and to translate them into scenarios for sustainable development [11–14]. The power of scenario analyses has been clearly shown by the work of the IPCC. They define multiple greenhouse gas emission scenarios and make projections for global temperature development under each scenario that are now widely used in policy making [15]. More recently, IPBES was established as the biodiversity and ecosystem focused analogue of IPCC [16–18]. Within the domain of IPBES, we here focus on freshwater aquatic ecosystems and aim for scenario output on water quality [19,20]. Freshwater aquatic ecosystems were instrumental to the formulation of the ecosystem concept [21–23], are seen as 'sentinels of climate change' [24] and provide many essential ecosystem services to humanity [25]. Therefore, freshwater aquatic ecosystem models can strongly contribute to sustainable development.

State-of-the-art aquatic ecosystem models vary enormously in complexity. Lumped models comprising one or two non-linear differential equations [26] or even a

Figure 1



The challenge of sustainable development.

Doughnut Economics and UN Sustainable Development Goals provide a search image for a safe and just future for the inhabitants of spaceship Earth by meeting human needs within the means of the planet. In this study we present reasons and means to include eco-evolutionary, novel ecosystem and social-ecological dynamics in aquatic ecosystem models as water quality scenario analysis tools for sustainable development. Throughout this study we refer to Lake Victoria as a microcosm of the evolving novel social-ecological systems that are typical of the Anthropocene (Box 1).

single statistical relation [27] represent the 'simple' end of this complexity spectrum [28]. They aim to generate insight in the dominant responses of the system to the dominant stress factors. Such models have been applied successfully to many important ecosystems on Earth, as well as to societal [29], medical [30,31] and psychological [32] dynamic systems. On the 'complex' end of the spectrum are integrated ecological models [33] that link multiple ecosystems [34] and can be applied in ecological management [35], and models that zoom in on ecological detail (e.g. individual-based models) [36], make projections on shorter timescales [37] or combine simple models with goal functions (e.g. structural dynamic models) [38]. Rather than arguing for the superiority of one of these approaches, we see considerable complementarity and redundancy among them and argue that we can exploit such model diversity to get a more complete picture of the systems under study [39].

Most aquatic ecosystem models use a combination of correlations, patterns and cause-and-effect relations, with process-based models most explicitly covering the latter [40]. PCLake is a well-studied and well documented example of a process-based aquatic ecosystem model. Originally developed for shallow lakes only [41], the model now also applies to ditches [42] and deep lakes [43], and a wetland version is under construction [44]. In the scientific domain, PCLake has been successfully linked to theories on alternative stable states [28], competition [45] and food web dynamics [46]. In the applied domain, the model has been embedded in 1D, 2D and 3D hydrodynamical drivers [47] and multiple modeling frameworks [48], used to assess climate change impacts on lake ecosystems [49], used to provide ecological dynamics for modeling contaminant distributions in aquatic systems [50], and successfully applied to a much wider range of lake ecosystems in different climate zones than the model was originally intended for [51,52].

Here we present three major challenges to improve the applicability of aquatic ecosystem models — and ecological models in general — for supporting sustainable development in this time of global environmental change (Figure 1). The first challenge arises from the notion that if societal change leads to environmental change, this will ultimately lead to adaptive responses in organisms and species through eco-evolutionary dynamics [53]. Secondly, because each species solves the 'adaptive puzzle' in a unique way, or may go extinct, this will lead to new species interactions and novel ecosystem dynamics [54]. Thirdly, not only ecosystems but also societies show nonlinear and sometimes hysteretic responses to stress, leading to complicated social-ecological dynamics [55,56]. These challenges are logically arranged along an axis of complexity that ranges from single individuals to whole societies. In this paper we review each of these challenges and refer to Lake Victoria as an iconic example of how eco-evolutionary, novel ecosystem and social-ecological dynamics interact (Box 1).

Box 1 The case of Lake Victoria.

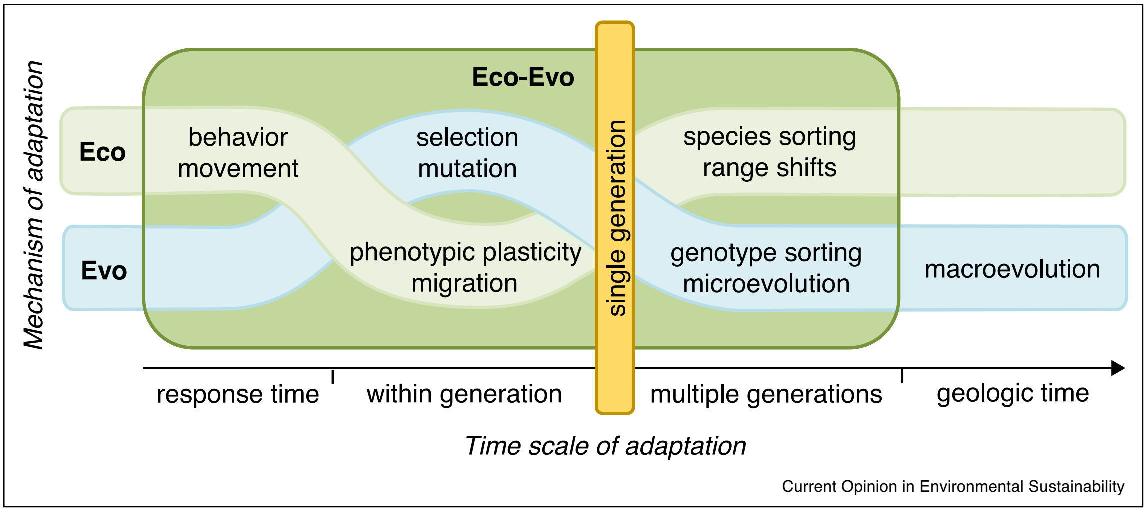
In the 1980s, the concurrent effects of the introduction of Nile perch (*Lates niloticus*) [78] and eutrophication caused Lake Victoria's ecosystem to shift dramatically [79] through various of eco-evolutionary adaptations (Figure 2). Hundreds of endemic haplochromine species went extinct [80,81], Nile perch became dominant, and other native species, such as the cyprinid dagaa (*Rastrineobola argentea)* claimed a new place in the food web (Figure 3). These two anthropogenic processes — species introductions and eutrophication — transformed the ecosystem's functioning and structure [82]. This led to new evolutionary pathways for the surviving native species. Surviving haplochromine cichlids have evolved and adapted their morphology, diets and mating [83]. Different species appear to have solved the 'adaptation puzzle' in a unique way [84], thus altering the flow of nutrients and matter through the food web [82]. Societies have adapted to the novel ecosystem's new resources, building an important export industry on Nile perch — creating new and different job opportunities as well as infrastructure and land-uses in the wider watershed [85]. In turn, ever-evolving societal needs are shaping the dynamics of Lake Victoria's ecosystem, through fishing pressure, coastal development and further land-use changes that influence the nutrient loading of the lake [85] (Figure 4). Lake Victoria is a microcosm of the evolving novel social-ecological systems that are typical of the Anthropocene (Figure 1): it has become more populated, and through trade and technology, is increasingly connected to the broader world as well as to its own resources, accelerating rates of change, as well as increasing the vulnerability of peoples to global trade and to resource collapse [86]. Sustainable development for Lake Victoria implies understanding the dynamic and evolving nature of social-ecological systems and boundaries of social needs — as opposed to seemingly fixed limits to resources or thresholds to Earth system dynamics — keeping in balance the rates and directions of changes of human needs with those of ecosystem functioning.

Eco-evolutionary dynamics

> *"Nothing in biology makes sense except in the light of evolution"* (Theodosius Dobzhansky)

Adaptation is an essential and admired property of life and hence we need to consider it when we aim for understanding and projecting future life [57]. It involves both ecological and evolutionary mechanisms. Recent studies convincingly show that time scales of evolutionary adaptation overlap with ecological time scales, leading to eco-evolutionary dynamics [53,58,59] (Figure 2). Yet the majority of state-of-the-art aquatic ecosystem models largely ignore adaptation through ecological processes. A partial exception to this is that many models put emphasis on plasticity of organisms in their stoichiometry with a focus on flexible carbon to phosphorus and carbon to nitrogen ratios [60–62]. However, most models ignore many other well-known ecological adaptive responses,

Figure 2



Eco-evolutionary dynamics.
Biological systems have two fundamentally different mechanisms to adapt to changing environmental conditions: through ecological or evolutionary adaptation. Within the ecological domain, organisms can respond at different time scales through behavior and phenotypic plasticity to changing local conditions, or evade those changing conditions by movement or migration. Communities of species can respond to changing local conditions through species sorting, or evade those conditions by range shifts. None of these responses requires evolution through a shift in the genetic makeup of organisms or species but most of these responses create new selection regimes and can thus lead to microevolution. This microevolution can then in turn invoke new ecological responses leading to eco-evolutionary dynamics. The case of Lake Victoria (Box 1) exemplifies such intertwined eco-evo strands, where different components of the social-ecological system's intergenerational ecological adaptation influences the social-ecological system's other components. For instance, the Nile perch boom - a multi-generational range shift - resulted in behavioral changes, the exploitation of available phenotypic plasticity, migration and hybridization in the surviving haplochromine cichlid species, potentially accelerating their microevolution [68]. The combination of haplochromines' microevolution and plasticity in terms of diet and diurnal behavior coincided with the cyprinid dagaa's trophic niche shift and expansion of its population. Water-quality changes, shifts in fish-species compositions and trophic roles also influence species sorting in phytoplankton and zooplankton communities. From the increasing fishing pressure to the creation of an economy and infrastructure around international trade that followed the Nile perch boom, we can follow the eco-evolution of the economic system.

such as inducible defenses [63] or behavioral responses [64] to the presence of predators. Maybe even more importantly, adaptation of organisms to changing conditions through evolutionary mechanisms and their interaction with ecological processes in eco-evolutionary dynamics is mostly ignored despite the empirical evidence of their importance [65–67].

There are multiple ways to build adaptation and eco-evolutionary dynamics into process-based ecological models. Trait-based models incorporate adaptation by making a specific trait a state variable that is affected by the adaptive process [69]. For example, Bruggeman and Kooijman [70] defined a four-parameter phytoplankton model that minimizes physiological detail, but includes a sophisticated representation of community diversity and inter-specific differences. Trait-based models can cover both phenotypic plasticity and evolutionary dynamics in the average trait value of a population [71]. Individual-based models instead focus on trait variation by modeling a sample of individuals that represents standing phenotypic or genetic variation [72,73]. A fundamental difference between trait-based and individual-based models is that in the latter evolution can be an emergent property, whereas in trait-based models the course of evolution is prescribed by the fitness function built into the model [36,74].

Life on Earth has shown remarkable resilience by overcoming no less than five mass extinction events [75]. Therefore, there is no reason to doubt the adaptive potential of nature to overcome the ongoing sixth mass extinction event [76]. At the geologic time scale (e.g. millions of years and longer, Figure 2 right hand side), macroevolution can be expected to counteract the current ongoing mass extinction and restore global biodiversity to pre-extinction levels. In contrast to this, at short time scales (e.g. days and shorter, Figure 2 left hand side) ecological processes such as differences in algal buoyancy leading to surface layers of algal blooms [37] or variable stoichiometry will dominate [77]. At the time scale of human generations (e.g. decades, Figure 2 center), however, eco-evolutionary dynamics come into play and will determine the survival, distribution and abundance of species for human generations to come and thereby the feasibility of goals set by the Sustainable Development Goals or Doughnut Economics. Eco-evolutionary dynamics should therefore be included in models for scenario analyses to reach these goals.

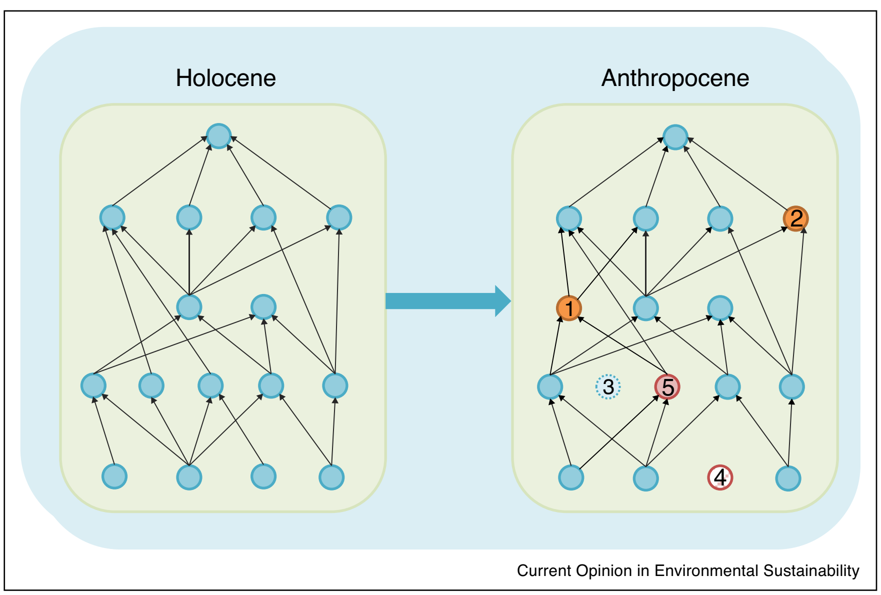
Novel ecosystem dynamics

> *"There are more things in heaven and earth, Horatio, than are dreamt of in your philosophy"* (William Shakespeare)

Adaptations to, and extinctions because of, environmental change will necessarily break up existing species interactions and create new ones [87]. For example, sudden changes such as dam construction can obstruct migration and lead to eco-evolutionary dynamics in the alewife-zooplankton system [88]. Slower environmental changes, such as climate change, may result in trophic mismatches in lakes [62] and create new species interactions due to range shifts [89,90]. Another important factor altering species interactions is that of exotic species, here defined as species of which the dispersal capacity is augmented by human activity [91,92]. Exotic species may become invasive because they are better direct or indirect competitors [93], can benefit from disturbance, secrete novel chemicals, are released from their natural enemies [94], or alternatively, because they carry their natural enemies with them, which are lethal for the native species they compete with [95]. This myriad of new species and traits leads to novel ecosystems, with unique configurations and functioning [54] (Figure 3). Here we define novel ecosystems as the human-modified, engineered or built ecosystems typical of the Anthropocene.

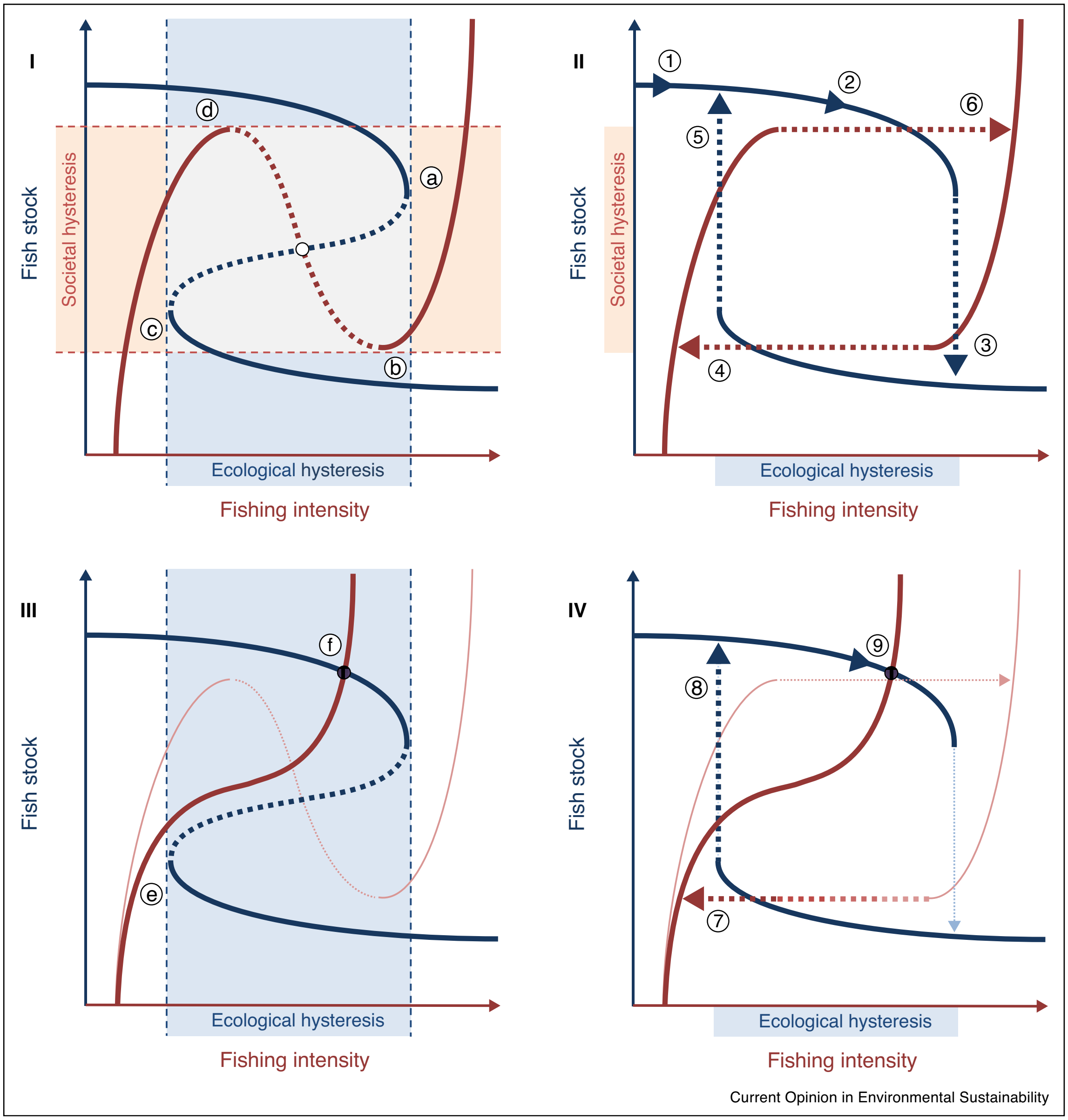
There are multiple ways to incorporate novel-ecosystem dynamics into models. Models such as PCLake automatically cover shifts in phenology and mismatches that may arise because the life-history and phenology of all the model's functional groups are temperature-dependent, with differential response curves [49]. As stated earlier, however, many other adaptive eco-evolutionary mechanisms are not covered by the model. And even more importantly, the process of species extinction and invasion itself is not dynamically modelled. The impact of invasive species is difficult to capture in models given the stochasticity in when and where they arrive and in whose company [96]. Once this information is known, the incorporation of specific invasive species, or even whole new functional

Figure 3



Novel ecosystem dynamics.
Species interactions in food webs evolved under the relatively stable conditions of the Holocene and will drastically change due to rapid global environmental change in the Anthropocene. For example, species invade (1), potentially replacing other species (2), go extinct (3), have differential phenotypic responses leading to a trophic mismatch (4), or adapt by exploiting a new resource (5), all leading to novel ecosystem dynamics. In the case of Lake Victoria (Box 1), the Nile perch represents an introduced species with a new position in the food web (1), the introduced Nile tilapia outcompeted native haplochromine cichlid species (2), swaths of benthivorous haplochromines went extinct (3), some surviving zooplanktivorous haplochromines evolved changes in the morphology of their mouths and adapted to different foods (4) and finally, dagaa started eating bigger prey in response to environmental changes (5). Please note that we did not aim to mimic the trophic position of each of these examples from Lake Victoria in the abstract food web shown in the figure.

Figure 4



Social-ecological dynamics.

Hypothetical response of fish stocks to fishing intensity and vice versa in a coupled social-ecological system inspired by Box 1 in [107]. Panels I and II depict social-ecological cycles of unsustainable fishery, panels III and IV depict sustainable fishery. Blue lines refer to the dynamical properties of the ecological system and red lines to the dynamical properties of the societal system. Panels I and III show isoclines with stable equilibria as solid lines and unstable equilibria as dashed lines. Panels II and IV show only the stable parts of the isoclines as solid lines and the catastrophic transitions between them as dashed arrows. Because of strong positive feedbacks, both the societal and ecological stability landscapes exhibit hysteresis (shaded zones in panel I). Different from Box 1 in [107] we focus on the situation where: the unregulated fishing intensity is higher than the ecological tipping point (panel I gap a) thus taking the system from its pre-fishery abundance (panel II arrow 1) through a seemingly healthy fishery with little impact on stock size (panel II arrow 2) towards a catastrophic shift resulting in an exhausted fish stock (panel II arrow 3); the exhaustion of the fish stock is deeper than the societal tipping point (panel I gap b) thus invoking a regulated fishery (panel II arrow 4); the regulated fishing intensity is lower than the ecological tipping point for the fish stock to recover (panel I gap c) thus resulting in a recovery of the fish stock (panel II arrow 5); the abundance of the recovered fish stock is higher than the societal tipping point (panel I gap d) leading to deregulation of fishing intensity (panel II arrow 6); then the deregulated fishing intensity is once again higher than the ecological tipping point leading to an endless limit cycle of overexploitation, regulation, recovery and deregulation. To break this cycle, the societal response to ecological collapse (panel IV arrow 7) should not only impose a reduction in fishing intensity that allows the fish stock to recover (panel III gap e) but also reduce or eliminate the hysteresis in the societal response and maintain regulation after stock recovery (panel IV arrow 8) thus creating a sustainable fishery at high stock levels (panel III point f, panel IV point 9). In Lake Victoria (Box 1), since the introduction of Nile perch, fishing intensity has increased (going from points 1 to 2 in panel II), risking the collapse of the stock (going from point 2 to 3 in panel II). To avert this groups, would require specific but potentially simple model adjustments [97]. The optimization technique employed in the BLOOM II model of phytoplankton dynamics is of particular interest when it comes to novel community dynamics [98]. Instead of specifying specific species, this model defines the range of potential species. At any moment in time, the actual species composition is chosen from this range based on an optimization goal such as biomass maximization.

Recognizing the emergence of novel ecosystems will stimulate a new approach to ecosystem management and modeling. Until recently, the dominant view in ecological restoration was that we should try to preserve as much of the biodiversity and natural areas on Earth that developed during the relatively stable climate of the Holocene and were still in place at the onset of the great acceleration [99]. Within this paradigm, it seemed logical to focus our ecosystem and landscape models on nature as it once was. A full appreciation of the changes taking place in the Anthropocene has given rise to a radically different view on ecological restoration [100] and the emergence of the concept of novel ecosystems [54]. Novel ecosystems are part of the human environment and niche, including urban, suburban, and rural areas [101,102], but also arise where most endemic species have gone extinct, whether or not due to, but in any case followed by, invasions of exotic species [103]. In the absence of natural analogs, models might serve as virtual realities of what might be possible within novel ecosystems.

Social-ecological dynamics

> *"We use nature because it's valuable, but we lose nature because it's free"* (Pavan Sukhdev)

Rooted in the seminal work of Holling [104], it is now well established that ecological systems show non-linear responses to stress factors, with the possibility of alternative stable states [26]. This notion led to the term 'ecological resilience' to denote critical stress levels beyond which systems undergo a regime shift, which differs from the concept of 'engineering resilience', which focuses on return time to a single equilibrium [105]. In water quality management ecological resilience translates into 'critical nutrient load' identification [51,106]. Processes in society also show non-linear and hysteretic responses to stress. Recently, Hughes *et al.* [107] pointed out that while human exploitation defines the stress ecosystems experience, the deteriorated ecosystem state will be perceived as a stress factor by society (Figure 4). Taking an example from fisheries, Hughes *et al.* postulate that a coupled non-linear social-ecological system may move through a cycle of four states (panels I and II in Figure 4). This cycle may repeat itself, or be broken through prudent management, reshaping the societal stability landscape (panels III and IV in Figure 4). By including social-ecological dynamics in our models, and considering social-ecological resilience, we might be able to develop more realistic and encompassing management scenarios for pathways towards sustainability [108].

Hysteretic responses of dynamical systems arise from positive, self-reinforcing feedback loops. Such feedback loops can be revealed and studied through feedback diagrams to identify the dominant system components and their qualitative interactions (Figure 1 in [109]). Subsequently, minimal dynamic models can qualitatively capture specific feedback loops for bifurcation analysis. Alternatively, more complex models may combine all interactions considered to be important, as PCLake does for lake ecosystems. Such integrated models still enable bifurcation analysis, though with more effort [106]. These three approaches are also valuable in studying social-ecological systems. For example, Downing combines connections across society, fisheries and limnology in feedback diagrams for Lake Victoria, showing how the Nile perch fishery may go through the four phases in Figure 4 [86]. Figure 4 depicts social-ecological interactions arising from minimal dynamic models. Examples of more complex models that include social-ecological interactions can be found in IMAGE-GNM [110], MARINA [111] or VEMALA [112]. Society has long been embedded in models as a measure of impact on the environment. More recently, through the ecosystem service framework, some models cover the different uses of the environment by societies. Ultimately, to close the social-ecological feedback loop, models should incorporate the dynamic and varying needs of societies that shape these uses of ecosystem services and drive impacts on the environment. [113]. Coupled human-environment system models [114], hybrid modeling that combines a system dynamics with an agent-based approach [115] and dynamic modeling of ecosystem services and their socio-economic valuation [116] seem promising ways to include those mutual social-ecological dynamics.

As stated in the introduction, Sustainable Development Goals and Doughnut Economics aim to meet human needs within the means of the planet, and models are

(Figure 4 Legend Continued) situation, and find a stable social-ecological equilibrium (point 9 in panel IV), responses to stock decline must be found in societal dynamics (shape of the red isoclines). One such initiative might be ecolabeling aimed to reduce over fishing of Nile perch by effectively removing the role of middlemen in the fishing-boat to filleting factory transaction. If successful, this would allow tighter responses in harvesting and pricing of the fish to eliminate perverse incentives to fish more when stocks go down. It has been argued however, that such an initiative will only be effective if the sustainable fishing method in itself outcompetes other, unsustainable fishing methods [86].

an essential tool to capture the mutual causal relations between human activities and environmental impacts. While some claim that we are about to model all life on Earth in a single coherent model [117], we would like to advocate a view on future model development for understanding social-ecological systems that is inspired by biodiversity. Within this view each model develops and should be judged within the context of its niche. Just as natural biodiversity is characterized by complementarity and redundancy among coexisting species, we believe it is useful to maintain a healthy level of model diversity and to employ the concept of ensemble runs [118] to allow social-ecological models to compete, show their fitness and evolve into newer versions [39].

Concluding remarks

> *"We [do these] things, not because they are easy, but because they are hard"* (John F. Kennedy)

The evolution of models so far illustrates that combining fields of knowledge is more than an additive process because combined process dynamics can lead to emergent properties. The question is then: how do we design satisfactory models to understand the dynamics of even relatively narrow questions of water quality? We suggest that a fundamental part of the answer lies in recognizing the subjectivity of all scientific approaches and methods, from the questions asked, to the variables chosen to observe and measure, through a myriad of assumptions and perceptions. To constrain subjectivities, one can first provide explicit contexts to the modeling questions: what time and space scales do they delineate? and then triangulate across fields of study to co-produce the knowledge behind the model design [119]. The exercise is a process of transforming multidisciplinarity to transdisciplinarity. The study by Downing *et al.* [86] for instance, where a team of ±40 scientists co-designed a shared understanding of the social-ecological system of lake Victoria – generalized to the level of the whole lake in the post Nile perch boom era – took time and pushed most, if not all, contributors outside their comfort zones, into the comfort zones of their colleagues. The product is neither a final nor an absolute representation of Lake Victoria's social ecological system. It nonetheless represents more than the sum of its parts, and is a useful building block in the design of future research questions and models.

It is difficult to predict what tools for water quality scenario analysis will look like in, say, a decade from now. America's politicians, scientists, engineers, workers and taxpayers were determined and able to put humans on the Moon, and return them safely to Earth, within the seven year deadline set by John F. Kennedy in late 1962 [120]. Scenario analysis and computer simulation played an important role in this electrifying achievement, which confronted humans with a picture of the Earth we live on. This was the start of a growing understanding of the uniqueness and fragility of system Earth. Here we make a plea for incorporating eco-evolutionary, novel ecosystem and social-ecological dynamics in aquatic ecosystem models as part of the contemporary global challenge to balance human needs with planetary boundaries. It is an intriguing question whether the scientific method can handle this added model complexity and can produce models for scenario analysis which meet the requirements of model understanding and model uncertainty to make them suitable as decision support tools. We will never know if we don't try.

> *"It always seems impossible until it's done"* (Nelson Mandela)

Conflict of interest statement

Nothing declared.

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