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Freshwater ecosystem services resilience in a changing world

Ana Paula Portela

1. CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal
2. Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Rua do Campo Alegre s/n, 4169–007 Porto, Portugal
3. BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal
4. CE3C - Centre for Ecology, Evolution and Environmental Changes, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

* Corresponding author: apportela@fc.ul.pt

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ABSTRACT

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Healthy freshwater ecosystems provide essential ecosystem services to society such as clean water. However, freshwater ecosystems are degraded, and freshwater biodiversity is severely threatened due to anthropogenic impacts and stressors. Climate change interacts with existing stressors and may compromise the resilience of freshwater ecosystems and their services in the future. Here the aim is to review advances in assessing freshwater ecosystem services and their resilience to environmental change. This work reviews the ecosystem services provided by freshwaters, the conceptual background on ecological resilience, and examples on the resilience of freshwater ecosystems and their services. Examples from African lakes, the Pantanal wetland in Brazil and the Murray-Darling Basin riparian forests in Australia are used to understand the resilience of freshwater ecosystem services to recent and ongoing climate changes and disturbances. This work illustrates the diverse responses of freshwater socio-ecological systems to environmental change and highlights examples of declining resilience of freshwater ecosystems and their services due to climate change and extreme events. However, a high degree of uncertainty still surrounds the identification of regime shifts and future ecosystem trajectories. Research is needed to understand the dynamics of freshwater socio-ecological systems and ensure resilient ecosystems and societies.

KEY WORDS: biodiversity, nature's contributions to people, rivers, lakes, and riparian ecosystems

RESUMO

Resiliência dos serviços de ecossistema aquáticos num mundo em alteração.

Os ecossistemas de águas interiores saudáveis prestam serviços de ecossistema essenciais à sociedade, como a água potável. No entanto, estes ecossistemas encontram-se degradados e a biodiversidade dos mesmos ameaçada devido a impactos antropogénicos. As alterações climáticas interagem com as pressões existentes e podem comprometer a resiliência dos ecossistemas de águas interiores e dos seus serviços no futuro. O objetivo é analisar os avanços na avaliação dos serviços de ecossistema de água doce e a sua resiliência às *alterações ambientais. Neste trabalho apresenta-se uma revisão dos serviços de ecossistema prestados pelas águas interiores, o enquadramento conceptual da resiliência ecológica e exemplos sobre a resiliência dos ecossistemas de água doce e dos seus serviços. Os exemplos de lagos africanos, da zona húmida do Pantanal no Brasil e das florestas ripícolas da bacia do rio Murray-Darling na Austrália são utilizados para compreender a resiliência dos serviços dos ecossistemas de água doce às alterações e perturbações climáticas recentes e em curso. Este trabalho ilustra a diversidade de respostas dos sistemas socio-ecológicos de água doce às alterações ambientais, realçando exemplos preocupantes de declínio da resiliência dos ecossistemas de água doce devido às alterações climáticas e por eventos extremos. No entanto, subsiste um elevado grau de incerteza quanto às mudanças de estado destes ecossistemas e às suas trajetórias futuras. A investigação da resiliência dos sistemas socio-ecológicos associados às águas interiores é necessária para compreender as suas dinâmicas e garantir ecossistemas e sociedades resilientes no futuro.*

PALAVRAS CHAVE: *biodiversidade, contribuição da natureza para as pessoas, rios, lagos, ecossistemas ripícolas.*

INTRODUCTION

Healthy freshwater ecosystems provide essential ecosystem services to society, including vital resources such as clean water. However, freshwater ecosystems are degraded, freshwater biodiversity is threatened, and an estimated 4.4 billion people globally lack access to safe drinking water (Greenwood et al., 2024). Rapid global changes including a growing human population, increasing demand for natural resources, urbanization, and intensification of agriculture have led to a focus on the exploitation of provisioning services, often at the expense of other essential services, particularly regulating services (Brauman et al., 2020). Climate change is already interacting with anthropogenic pressures and stressors, increasing the likelihood of large, potentially irreversible ecosystem changes that can have significant impacts on ecosystem services and human well-being (Forzieri et al., 2022). Thus, one of the major challenges of sustainability in the 21st century is to protect and restore ecosystems to ensure the flow of ecosystem services to society, both today and in the future (United Nations, 2022). This challenge is perhaps nowhere more pressing than in freshwater ecosystems. The strong interdependence and feedback between natural and human systems within freshwaters make them crucial social-ecological systems (Dunham et al., 2018). The ecosystem services linked to freshwater ecosystems include basic human needs and underpin social and economic well-being (Falkenmark & Wang-Erlandsson, 2021). Therefore, ensuring the resilience of freshwater ecosystem services is of significant societal and policy interest.

This work aims to provide an overview of the ecosystem services supplied by freshwaters, their resilience under global change and identify implications for management. First, I focus on the definition of ecosystem services, provide an overview of freshwater ecosystem services and discuss current limitations in their assessment. Second, I discuss the definition of resilience, the mechanisms that underpin it, and evaluate the resilience of freshwater ecosystem services to environmental changes using examples from African lakes, the Pantanal wetland in Brazil and the Murray-Darling Basin riparian forests in Australia. Third, I discuss implications for the resilience of freshwater socio-ecological systems under global change.

I. FRESHWATER ECOSYSTEM SERVICES

Definition of ecosystem services

The ecosystem services concept has been crucial in mainstreaming the link between ecosystems and human societies in research and policy. The concept and its associated theoretical framework have evolved greatly since it was first coined (Ehrlich & Ehrlich, 1981), particularly in two critical moments associated with the development of international science-policy interfaces. The first was the Millennium Ecosystem Assessment, supported by the United Nations and the Convention on Biological Diversity which mainstreamed the concept of ecosystem services leading to an exponential growth of the literature (Braat & de Groot, 2012; Gómez-Baggethun et al., 2010). The second was the establishment of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) in 2012 to create a science-policy platform for biodiversity comparable to the Intergovernmental Panel on Climate Change (Díaz et al., 2015). The Millennium Ecosystem Assessment defined ecosystem services simply as the benefits people obtain from ecosystems (Millennium Ecosystem Assessment, 2005). IPBES expanded this concept into Nature's contributions to people defined as all the contributions, positive and negative, of living nature (diversity of organisms, ecosystems, and their ecological and evolutionary processes) to people's quality of life (Díaz et al., 2018). The change aimed at addressing criticisms faced by the ecosystem services concept related to the lack of recognition of diverse values of nature, the role of culture in shaping relationships between people and nature and concerns about nature's commodification (Díaz et al., 2018). The introduction of nature's contributions to people initiated an intense debate about its novelty and value within the ecosystem services research and practice community (Kadykalo et al., 2019). It is beyond the scope of this work to address this debate. Here, this is considered a natural evolution of a field aiming to understand relationships between nature and people. The term ecosystem service is used for consistency with a large part of the referenced literature.

Freshwater ecosystem services

Freshwater ecosystem services are all those services and benefits generated by freshwater ecosystems and the interactions of land and water in ecosystems such as forests, agricultural lands, riparian areas, wetlands and water bodies (Grizzetti et al., 2016). The definition is much broader than that of hydrologic services, which focuses on the way terrestrial ecosystems affect freshwater resources through ecohydrological processes in landscapes (Brauman, 2015). By recognizing the interactions between land and water and the processes within freshwater ecosystems, the definition of freshwater ecosystem services can better reflect the ecosystem functions and services that are relevant to freshwater management.

The ecosystem services and benefits provided by freshwater ecosystems span all categories including provisioning or material contributions, regulating, and cultural or non-material contributions (Table 1; Aylward et al., 2005; Díaz et al., 2018). The initial MEA and the national assessments focused solely on hydrological services or were based on expert knowledge. Recently, there has been an increasing interest in the freshwater scientific community to contribute to the area of ecosystem services mainly by reviewing and updating the knowledge for some freshwater organisms including riparian vegetation (Riis et al., 2020), macrophytes (Thomaz, 2023), freshwater bivalves (Zieritz et al., 2022), aquatic fungi (Seena et al., 2022), freshwater fish (Holmlund & Hammer, 1999) and freshwater ecosystems namely lakes (Heino et al., 2021; Sterner et al., 2020), intermittent rivers (Datry et al., 2018; Pastor et al., 2022) and dry rivers (Nicolás Ruiz et al., 2021), small streams (Ferreira et al., 2022), wetlands (Xu et al., 2020).

Difficulties in assessment

The concept of ecosystem services has gained traction in freshwater science as evidenced by the reviews and studies published recently. However, the actual assessment of the supply and demand of freshwater ecosystem services provided by these ecosystems remains challenging. In previous studies on ecosystem services, less than 5% of indicators on supply and less than 1% of monetary valuation estimates were related to freshwater ecosystems (Egoh et al., 2012; Maes et al., 2012; Van der Ploeg et al., 2010). In studies specifically quantifying river ecosystem services, three or fewer ecosystem services were evaluated on average (Hanna et al., 2018). The most frequently assessed ecosystem services are recreation and tourism, water supply, water quality, habitat provision and erosion prevention (Hanna et al., 2018), however overall, the regulation and provision services were assessed more frequently. These trends reflect the lack of development of ecosystem services methods specifically targeting freshwater ecosystems (Riis et al., 2020). A review on riparian vegetation notes that the assessment of ecosystem services provided by different vegetation types remains based on expert

Table 1. Ecosystem services provided by freshwater ecosystems. The classification of services provided follows the CICES v5.2 (Haines-Young, 2023). The column on Section makes the correspondence between the nomenclature adopted in CICES and the IPBES Nature's Contribution's to People framework. The examples provided for each freshwater ecosystem are based on the literature and represent the most identified ecosystem services associated with each ecosystem. These freshwater ecosystems may provide additional ecosystem services; however, they are not considered as relevant in the literature. *Serviços de ecossistema prestados pelos ecossistemas de água doce. A classificação dos serviços de ecossistema segue a CICES v5.2 (Haines-Young, 2023). A coluna relativa à Secção faz a correspondência entre a nomenclatura adotada pela CICES e pelo IPBES no quadro das Contribuições da Natureza para as Pessoas. Os exemplos identificados para cada ecossistema de água doce baseiam-se na literatura e representam os serviços de ecossistema mais frequentemente associados a cada ecossistema. Esses ecossistemas de água doce podem fornecer outros serviços de ecossistema que não foram mencionados aqui devido à sua menor relevância na literatura atual.*

Section	Division	Group	Class	Rivers	Lakes	Riparian ecosystems
				(Grizzetti et al., 2019; Maltby et al., 2011)	(Heino et al., 2021; Sterner et al., 2020)	(Riis et al., 2020)
Provisioning / Material	Biomass	Wild animals (terrestrial and aquatic) for nutrition, materials or energy	Wild animals (terrestrial and aquatic) used for nutritional purposes	Fisheries, bivalves	Fisheries	
		Wild plants (terrestrial and aquatic) for nutrition, materials or energy	Fibres and other materials from wild plants for direct use or processing (excluding genetic materials)			Thatching, wickerwork
			Wild plants (terrestrial and aquatic, including fungi, algae) used as a source of energy			Fuel for heating
			Wild plants (terrestrial and aquatic, including fungi, algae) used for nutrition	Edible freshwater macrophytes		Wild berries and herbs
	Genetic material from all biota (including seed, spore or gamete production)	Genetic material from plants, algae or fungi	Higher and lower plants (whole organisms) used to breed new strains or varieties			Crops wild relatives
	Water	Surface water used for nutrition, materials, or energy	Freshwater surface water used as an energy source	Hydropower production	Hydropower production	
			Surface water for drinking	Drinking water	Drinking water	
			Surface water used as a material (non-drinking purposes)	Industry, navigation, agriculture	Industry, navigation, agriculture	
Regulation	Regulation of baseline flows and extreme events	Regulation of baseline flows and extreme events	Buffering and attenuation of mass movement			Landslide
		Erosion control	Control of water erosion rates			Erosion control
		Hazard mitigation	Fire protection	Fire protection		Reduce frequency, spread or magnitude of fires
		Hydrological cycle and water flow regulation	Regulation of peak flows	Flood regulation		Mitigation of extreme flows
			Regulation runoff and base flows	Flow regulation		Flow regulation

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Section	Division	Group	Class	Rivers	Lakes	Riparian ecosystems
	Regulation of physical, chemical, biological conditions	Atmospheric composition and conditions	Regulation of chemical composition of atmosphere and oceans, including maintaining rainfall patterns through evapotranspiration at the sub-continental scale		Climate Regulation	Carbon sequestration by vegetation
		Atmospheric composition and conditions	Regulation of temperature and humidity, including ventilation and transpiration at local scales	Local climate regulation		Evaporative cooling by trees
		Lifecycle maintenance, habitat and gene pool protection	Pollination			Pollination
		Lifecycle maintenance, habitat, and gene pool protection	Maintaining or regulating nursery populations and habitats or breeding grounds (Includes gene pool protection)	Maintenance of nursery populations		Providing habitats
		Pest and disease control	Disease control			Habitats for native pest control agents
		Water conditions	Regulation of the chemical condition of freshwaters by living processes	Water purification	Water purification	Removal of nutrients in runoff
	Transformation of biochemical or physical inputs to ecosystems	Mediation of waste, toxics and other nuisances by non-living processes	Dilution or transport of wastes by freshwater and marine ecosystems	Dilution of wastewater		
		Mediation of wastes or toxic substances of anthropogenic origin by living processes	Bio-remediation by micro-organisms, algae, plants, and animals	Water purification	Nutrient and pollutant retention by macrophyte beds	Filtration and storage of particles, nutrient removal
Cultural/ Non-material	Intellectual and representative interactions with natural environment	Direct, in-situ and outdoor interactions with living systems that depend on presence in the environmental setting	Elements of living systems that enable aesthetic experiences	Areas of natural beauty, ornamental use of freshwater pearls, fishes		Areas of natural beauty
			Elements of living systems that enable scientific investigation or the creation of traditional ecological knowledge	Science and education		Sites of specific scientific interest, sites used for conservation
			Elements of living systems that are resonant in terms of culture or heritage			Heritage, sites of cultural importance
		Indirect, interactions with living systems	Elements of living systems used for entertainment or representation outside the setting concerned	Artistic productions		Artistic productions

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Section	Division	Group	Class	Rivers	Lakes	Riparian ecosystems
	Physical and experiential interactions with natural environment	Direct, in-situ and outdoor interactions with living systems that depend on presence in the environmental setting, i.e. broadly recreational activities	Elements of living systems that enable activities promoting health, recuperation or enjoyment through passive or observational interactions	Wildlife tourism	Wildlife tourism	Wildlife tourism and ecotourism
		Physical and experiential interactions with natural environment	Direct, in-situ and outdoor interactions with living systems that depend on presence in the environmental setting, i.e. broadly recreational activities	Angling and water sports	Angling and water sports	Sports activities
	Spiritual, symbolic and other cultural interactions with natural environment	Elements of living systems that are indirectly appreciated and have significance for people without their presence in the environmental setting.	Elements of living systems that have spiritual or religious meaning	Religion		Totemic species or settings of religious interest
			Elements of living systems that have symbolic meaning, capture the distinctiveness of settings or their sense of place	Sense of place		Species, habitats, or landscapes that can be used as symbols
		Other biophysical characteristics of species or ecosystems that are appreciated in their own right by people	Elements or features of living systems whose contemporary existence or conservation is important to people			Wilderness areas
		Other biophysical characteristics of species or ecosystems that are appreciated in their own right by people	Elements or features of living systems whose inter-generational existence or conservation is important to people.			Bequest

knowledge and that we have little information for intermediate vegetation types (Riis et al., 2020). A study on large lakes mentioned that quantification was limited to ecosystem services with commercial value due to a lack of data (Sterner et al., 2020). The scale of supply of ecosystem service often makes assessments challenging as many water ecosystem services depend on processes occurring across scales from the watershed to the habitat. Cultural services are challenging to assess in freshwater as well as other ecosystems. The multitude of notions and non-material benefits grouped into this category, which range from aesthetic to moral, leads to a focus on services with more tangible effects namely recreation and tourism (Kadykalo et al., 2019; Small et al., 2017). The role of culture in influencing the values beneficiaries attribute to ecosystem services remains poorly studied despite influencing how different groups prioritize services and manage ecosystems (Kadykalo et al., 2019; Small et al., 2017).

II. RESILIENCE OF FRESHWATER ECOSYSTEM SERVICES

Definition of resilience

The term resilience has been used in the ecological, and social sciences literature and by broader society in a variety of ways. Generally, resilience is associated with the ability to recover to a previous good state from a disturbance, trauma or pressure (Cambridge Advanced Learner's Dictionary & Thesaurus, 2024). This meaning aligns closely with the definition of engineering resilience in the ecological literature, which is which refers to the rate at which a system returns to the reference condition following a perturbation (Pimm, 1984; Van Meerbeek et al., 2021). There is an additional definition in the ecological literature which emphasises the ability to absorb disturbance and remain in the same state. Ecological resilience refers to the magnitude of disturbance that can be absorbed before the system changes its structure by changing the variables and processes that control behaviour, i.e., the ability of the system to remain in the same domain of attraction or stable state (Holling, 1973; Van Meerbeek et al., 2021). Thus, engineering resilience generally focuses on dynamics within a stable state while ecological resilience focuses on dynamics across different stable states.

Resilience is mostly perceived as a positive aspect, however, resilience may be a positive or negative property depending on whether a given stable state is desirable in a given management context (Standish et al., 2014). Ecosystems degraded by anthropogenic activities may be as resilient or even more so than ecosystems in a better state (Durance et al., 2016; Standish et al., 2014). In these cases, resilience is a negative property, designated as unhelpful resilience, that keeps ecosystems in an undesirable state posing a management challenge (Standish et al., 2014). Regime shifts may be largely irreversible or require large amounts of energy or disturbance to shift the system to a more desirable stable state (Folke et al., 2004). The reversibility of regime shifts depends on the strength of the dominant system feedback.

Resilience mechanisms: What brings about resilience?

Resilience can be measured at the various levels of biological organization, from population to community to ecosystem (Donohue et al., 2016; Oliver et al., 2015). However, the ability to maintain ecosystem structure and functioning and ensure the stability of ecosystem service supply is essential for ecosystem management under environmental change (Oliver et al., 2015).

The resilience of ecosystem functioning and services depends on the nature of the service, abiotic and biotic factors, and the social and governance context. This ability is shaped by the spatial and temporal scales of disturbance, and by species-to-landscape level mechanisms, including intraspecific diversity, community functional diversity and redundancy, food web complexity, and landscape heterogeneity (Gutiérrez-Cánovas et al., 2021; Oliver et al., 2015; Standish et al., 2014). Diversity, particularly functional diversity, is expected to contribute to resilience by stabilizing ecosystem functioning in the face of disturbance through compensatory dynamics or insurance effects of redundancy (de Bello et al., 2021).

Some freshwater ecosystem services directly arise from biodiversity, at the species, taxonomic group, community or ecosystem level, such as fisheries (Brooks et al., 2016; Lynch et al., 2023). However, the relationship between biodiversity and ecosystem services is often more complex and multi-layered (Mace et al., 2012). Biodiversity may have a regulating role in key ecosystem processes, be a final ecosystem service, or a good (Mace et al., 2012). Biodiversity may be a factor controlling the ecosystem processes underpinning ecosystem services, for instance, higher biodiversity is associated with increased ecosystem functions (Mace et al., 2012). Biodiversity may also be a final service in instances where diversity contributes to goods and services, such as benefits to wild medicines and bioprospection arising from genetic diversity (Mace et al., 2012). Biodiversity itself may also be valued by humans due to its conservation or cultural value, where maintaining the diversity of wildlife, or charismatic species is considered important for recreational, educational, religious, or spiritual reasons (Mace et al., 2012).

For many ecosystem services, the contribution of biodiversity is not well defined and the evidence on biodiversity effects is mixed (Cardinale et al., 2012). The effects of biodiversity depend on the ecosystem service, whether supply or benefit is analysed, spatial scale, and on the type of linkage considered (e.g., spatial, functional, or management) (Ricketts et al., 2016). For many services, there isn't sufficient data to evaluate the relationship between biodiversity and the service (Cardinale et al., 2012). For provisioning services, service supply depends on the abundance or yield of harvested species which may or may not increase with biodiversity (Ricketts et al., 2016). For a small number of ecosystem services current evidence runs counter to general expectations, showing no relationship or negative effects of biodiversity (Cardinale et al., 2012). For instance, tree stem density, biomass, and age may have negative effects on freshwater provision through increased evapotranspiration. Nevertheless, these attributes may improve other services such as atmospheric regulation (Harrison et al. 2014).

While the evidence on the relationship between biodiversity and ecosystem services has grown it remains a critical challenge to understand how various biodiversity facets contribute the resilience of ecosystem services under environmental change.

Resilience of freshwater ecosystem services

Although an increasing number of studies reference resilience, a comprehensive understanding of ecosystem resilience, including the resilience of ecosystem services, is still lacking (Strickland et al., 2024). Few studies have measured the stability of ecosystem functions or services (Donohue et al., 2016; Oliver et al., 2015; Strickland et al., 2024). The concept of resilience is often referenced as an objective for ecosystem management or sustainable development; however, it is frequently not quantified or operational (Lloret et al., 2024). The numerous definitions of resilience applied in the realms of natural and social sciences and the diversity of indices to assess resilience even within the natural sciences have contributed to this lack of coherent global understanding (Lloret et al., 2024; Runge et al., 2025). In freshwaters, the resilience and alternative states of lake ecosystems have contributed with key references to the resilience scholarship (Carrier-Belleau et al., 2022). However, it is still unclear how widespread are regime shifts in freshwaters and challenging to find evidence of the resilience of freshwater ecosystem services.

I carried out a literature search and screening for peer-reviewed articles that studied freshwater ecosystem services resilience using Web of Science (Clarivate™, Web of Science™) to examine the current state of the literature. A search for topics "freshwater" AND "ecosystem services" AND "resilience" returned 145 results (Clarivate™, Web of Science™, 1 April 2025). Of these 102 articles were considered potentially relevant and the full text was analysed to understand the objectives and how they examined the resilience of freshwater ecosystem services. The articles considered irrelevant included studies focusing on marine, coastal, brackish water ecosystems, artificial water bodies, and presentations of special issues or projects. Five additional articles were not evaluated due to lack of access to the full text. Of the relevant articles almost, half were theoretical or conceptual including reviews, synthesis, perspectives, and conceptual frameworks. A few observational studies measured resilience at the level of biotic communities (Burthe et al., 2016; Feio et al., 2015). Some studies examined the resilience of local populations in relation to their dependence on ecosystem services, focusing on social contexts and governance without quantitatively measuring resilience (Komugabe-Dixson et al., 2019; Kosamu et al., 2022). One study directly connected changes in habitat for fish populations with variability in current and future spatiotemporal patterns of recreational fishery services (Cline et al., 2022). However, this example lacks metrics that connect to engineering or ecological resilience definitions. The small number of studies addressing resilience and freshwater ecosystem services, diverse methodologies and lack of operational use of resilience concepts hinder a systematic review or meta-analysis.

Therefore, the following sections present narrative examples from different freshwater ecosystems displaying diverse responses of socio-ecological ecosystems to environmental changes and disturbances. Although this a qualitative assessment, it enables a broader discussion about the resilience of freshwater socio-ecological systems and how close they are to tipping points and regime shifts.

African lakes

The great African lakes hold an estimated 25% of the world's liquid surface freshwater. African lakes contribute to the livelihoods of millions of people as well as national economies. Some lakes experience fluctuations in water levels as well as dry-out periods which impact the livelihoods of local communities (Ogutu-Ohwayo et al., 2016). The increasing exploitation of lake resources during the past century has led to habitat loss and degradation, introduction of exotic species, pollution from agricultural, industrial and urban runoff (Kafumbata et al., 2014; Ogutu-Ohwayo et al., 2016). These stressors are likely to be aggravated by climate change (Mutanda & Nhamo, 2024). The loss of ecosystem services has profound implications for the local communities which rely heavily on the flow of ecosystem services from the lakes for food security and employment.

In Lake Naivasha in Kenya population growth caused riparian vegetation degradation, high nutrient, sediment loads and increasing water abstraction for agriculture and industry (Mutethya & Yongo, 2021; Renaut & Owen, 2023). The lake levels have decreased because of the increasing water demand for a growing horticultural industry and population and it has become eutrophic due to nutrient inputs (Renaut & Owen, 2023). The introduction of non-native fish may have contributed further to alteration of the lake's trophic state (Mutethya & Yongo, 2021). The lake levels have recovered following drought and its ecosystem services have remained resilient due to groundwater recharge from aquifers and the establishment of commercial fisheries around non-native fish species (Harper et al., 2011; Kafumbata et al., 2014; Mutethya & Yongo, 2021).

Lake Chilwa in Malawi on the other hand is showing signs of declining resilience (Kafumbata et al., 2014). The lake experiences significant inter- and intra-annual variations in water levels including severe lake level recessions and complete drying associated with droughts (Kambombe et al., 2021). The lake recovered from desiccation; however, it has a negative water budget and the wetland area is decreasing due to deforestation and agricultural expansion (Kambombe et al., 2023; Njaya et al., 2011). Fisheries are strongly dependent on lake levels, declining in periods of lake recession and requiring three to four years to recover after a severe recession (Rebelo et al., 2011; Njaya et al., 2011). Since fishing may contribute up to half of income for local populations, lake recessions have a significant impact on local livelihoods (Njaya et al., 2011). During dry periods, communities turn to other activities leading to increased exploitation of exposed land for agriculture, livestock grazing, and wetland birds (Kafumbata et al., 2014; Njaya et al., 2011). The loss of income leads to migration of fishermen while women and children are left with minimal resources in a context of increasing conflicts for the exploitation of resources (Nagoli & Chiwona-Karltun, 2017).

Lake Chad in West Africa, in the conjunction of Chad, Cameroon, Nigeria and Niger, is considered to have shifted to an alternative ecosystem state since this once-large lake has shrunk by more than 90% since the 1960s splitting into two pools (Bouchez et al., 2016; Leblanc et al., 2011). The dramatic change in the lake is attributed to declines in precipitation and streamflow associated with climate change as well as water abstraction for agriculture in the tributaries (Pham-Duc et al., 2020). The lake is a source of freshwater and natural resources for two million people on the lakeshore and over ten million further afield (Lake Chad Basin Commission, 2016; Riebe & Dressel, 2021). The decline of lake levels reduced ecosystem services supply, namely water supply, crop production, livestock production, and fisheries (Okpara et al., 2016; Riebe & Dressel, 2021). This has led to food insecurity and loss of income for local communities which migrate within the lake and change their activities, often leading to conflicts due to competition for limited resources (Okpara et al., 2016). The instability and unemployment caused by the declines of Lake Chad are believed to have contributed to the increasing the influence of the armed group Boko Haram in the region (Owonikoko & Momodu, 2020).

The three African lakes presented here provide three examples of various levels of resilience of ecosystem services. Lake Naivasha retained resilience thanks to groundwater recharge, while Lake Chilwa is in a downward spiral with declining capacity to provide ecosystem services (Kafumbata et al., 2014). Lake Chad is considered to have passed a critical threshold into another state that cannot provide adequate ecosystem services to communities, contributing to large-scale conflicts in the region (Bouchez et al., 2016; Kafumbata et al., 2014). In all three examples, local communities are strongly dependent on the ecosystem services provided by the lakes and thus food security and livelihoods are highly sensitive to variability and shifts in the natural systems. This is exacerbated by the lack of adequate human responses, particularly institutional responses that mitigate impacts on local communities (Kafumbata et al., 2014).

The Pantanal Wetland in Brazil

The Pantanal is the world's largest freshwater wetland and a UNESCO World Heritage Site occupying an area of 140 000 km^2 mostly in Brazil (90% [Pott & Pott, 2004; UNESCO, 2025]). The Pantanal is a seasonal floodplain in the upper Paraguay River basin alternating between flooded and dry phases which influence the ecosystem functioning, biodiversity and local communities' lifestyles (Pott & Pott, 2004). The landscape is a mosaic of flooded and non-flooded grasslands, forests, savannahs, and permanent and temporary water bodies hosting high species diversity (Pott & Pott, 2004). The main source of income is traditional extensive cattle grazing, where local communities move the cattle along flooding gradients to graze using fire to manage vegetation and promote the growth of native grasses (Tomas et al., 2024). Fisheries are the second most important activity as riverside communities move through the canals and lakes to find fishing grounds (Tomas et al., 2024). Agriculture, hydroelectric developments and climate change pose major threats to the Pantanal ecosystem (Thielen et al., 2020; Wantzen et al., 2024). The Pantanal is prone to wildfires during the dry season and fires started by human activities get out of control often (Pott & Pott, 2004). In 2020 the Pantanal experienced the worst drought in 60 years leading to massive fires that burned nearly four million hectares (Ferreira Barbosa et al., 2022; Laboratório de Aplicações de Satélites Ambientais, 2021; Libonati et al., 2020). In 2024 drought conditions fuelled large fires again burning more than 2 million hectares (Laboratório de Aplicações de Satélites Ambientais, 2021). Recent studies estimate that at least 16.952 million vertebrates were killed by the 2020 fires (Tomas et al., 2021). Recurrent fire may eliminate fire-sensitive species increasing the dominance of fire-prone species (Libonati et al., 2020; Pott & Pott, 2004). However, the full-scale impacts of the extreme events of 2020 and 2024 remain largely unknown requiring additional monitoring to understand Pantanal's resilience (Tomas et al., 2021). The large fires raised awareness about the need to implement integrated fire management policies prompting the approval of state legislation to regulate fire use (Tomas et al., 2021). However, severe fire legislation that criminalises fire use by traditional communities may risk local ecosystems since cattle ranchers and farmers turn to exotic grass species (Garcia et al., 2021; Tomas et al., 2019). Overall, we still require further research to understand the socio-ecological resilience of the Pantanal especially in the long-term.

Riparian forests of the Murray-Darling Basin in Australia

The Murray-Darling Basin is the largest freshwater basin in Australia spanning one million square kilometres of south-eastern Australia across the states of New South Wales, Queensland, South Australia, Victoria and the Australian Capital Territory (Murray-Darling Basin Authority, 2023b). The basin is responsible for 40% of Australia's agricultural production and it is home to more than two million people (Murray-Darling Basin Authority, 2023a). The ecosystems are valued nationally and internationally supporting tourism and recreation and hold cultural value for indigenous populations (Murray-Darling Basin Authority, 2023a). This region experienced a multi-year drought between 2000-2009 known as the Millenium Drought (van Dijk et al., 2013). The Millenium Drought was the most severe on record for SE Australia and, together with high water demand, led to a water availability of less than 40% of the historical average (van Dijk et al., 2013). The river ecosystems and the agriculture in the Murray-Darling Basin were severely affected by this drought, and people faced higher electricity prices and water use restrictions (van Dijk et al., 2013). The drought and water abstraction caused the dieback of iconic floodplain species along the river (Harris et al., 2018). The river red gum forests (*Eucalyptus camaldulensis*) showed reductions in canopy cover and mortality, particularly in higher-density forest areas (Harris et al., 2018). The recovery of these forests is hindered by declines in recruitment due to lower flooding frequency associated to river regulation, increasing salinity of soil and water (Mac Nally et al., 2011).

The drought and tree dieback caused severe declines in freshwater ecosystem services. Aesthetic values, pollination, timber, carbon storage, nutrient cycling, erosion and water quality regulation all suffered significant reductions (van Dijk et al., 2013). The losses in water ecosystem services caused by the Millennium Drought required an estimated expenditure of 810 million AUD to mitigate ecosystem services losses and to implement adaptation measures (Banerjee et al., 2013). Riverbanks receded, slumped and in some cases collapsed as the water decreased leading to the need to develop a hazard mitigation plan (Banerjee et al., 2013). Seven years after the drought one-third of the watersheds in the state of Victoria had not fully recovered to pre-drought runoff levels (Peterson et al., 2021). These trends suggest that the socio-ecological system has passed a tipping point, from a social and political perspective if not from an ecological perspective.

III. RESILIENCE OF FRESHWATER ECOSYSTEMS AND SERVICES UNDER GLOBAL CHANGE

According to the latest assessment of planetary boundaries, the freshwater boundary has already been transgressed (Richardson et al., 2023). This evaluation is supported by an increase in land area where blue (streamflow) and green water (soil moisture) levels deviate from pre-industrial reference conditions (Porkka et al., 2024). Another concerning indicator is the increase in freshwater blooms in lakes since the 1980s (Ho et al., 2019). Broadly the trajectories of freshwater ecosystems and their services under climate change are expected to depend on whether ecosystems are energy or water-limited systems (Campbell et al., 2022). In energy-limited systems in higher latitudes and mountains the increasing temperature promotes range shifts, increasing competition and possibly excluding cold-adapted species (Nilsson et al., 2012; Perry et al., 2012). Aquatic and riparian cold-water animal species are already experiencing population declines (Durance & Ormerod, 2007; Rogers et al., 2020). In water-limited systems, such as those in the Mediterranean climate, increasing water limitation will promote environmental filtering, declines in functional diversity and shifts toward more conservative strategies (Portela, Durance, et al., 2023a). Obligate riparian and drought-sensitive plant species are expected to decline and annual species to increase in semi-arid rivers (Perry et al., 2012; Stromberg et al., 2012). These trends may represent significant departures from the current ecosystem status and functional diversity levels. The ecosystem services expected to be most affected include water provisioning, fisheries, and many regulation services such as climate change mitigation and water quality regulation (Campbell et al., 2022; Portela, Durance, et al., 2023b). Since functional diversity underpins ecosystem functioning and stability we also expect changes from current baselines of ecosystem resilience (Biggs et al., 2020).

The examples discussed in this work illustrate declines in freshwater ecosystem services, erosion of resilience in socio-ecological systems as well as the uncertainty surrounding the identification of regime shifts and future trajectories. Clear examples of loss of resilience and regime shifts are still rare and mostly associated with lake systems, as exemplified here by Lake Chad. A study of LTER sites in the US over 40 years finds limited evidence of lasting regime shifts in freshwater and forest ecosystems (Campbell et al., 2022). This may be because many of these LTER sites are still experiencing conditions similar to their historical climate space (Campbell et al., 2022). It is also hypothesised that shallow lakes are more prone to regime shifts whereas running waters are more resilient (Durance et al., 2016). However, the observational or experimental evidence available on the resilience of freshwater ecosystems and their services remains limited. Many studies discuss resilience and associated topics in the introduction or discussion, but do not aim to quantify it (Carrier-Belleau et al., 2022). This prevents a comprehensive, systematic assessment of the resilience of freshwater ecosystems and their services globally or comparatively. While the freshwater resilience research continues to evolve, there are examples of warning signs of loss of resilience particularly in response to extreme climate events and disturbances.

Disturbances such as drought, fire, hurricanes, and ice storms appear to be pushing socio-ecological systems near or beyond tipping points and towards new stable states. Disturbances across land and water can impact and destabilise freshwater ecosystems and their services (Crausbay et al., 2020; Falkenmark & Wang-Erlandsson, 2021). The Millenium Drought in Australia, the Paranal fires, and the recurrent drying in Lake Chilwa are examples of recurring or prolonged extremes that may be overwhelming the capacity of socio-ecological systems to recover and sustain ecosystem services. Furthermore, extreme events can cause legacy effects in key attributes of ecosystem functioning, where declines in ecosystem productivity and streamflow last several years following the event (Peterson et al., 2021; Portela, Gonçalves, et al., 2023). However, their effects may not be fully evident at short time scales. A watershed scale experiment at a LTER site suggests initial recoveries of ecosystem functions following disturbance do not preclude later regime shifts as other disturbances impact recovery trajectories (Jackson et al., 2018). Climate extremes and other disturbances may be as important or even more so than changes in average climate for the resilience of freshwater ecosystems in the future.

The resilience of the socio-ecological systems is also modulated by social systems including community and institutional dynamics as shown by the examples presented here. The Millennium Drought illustrates how high water consumption and river regulation contribute to the decline of riparian forests and their limited recovery. The examples from African lakes and the Australian Millennium Drought offer a stark contrast on institutional dynamics. In Lake Chad the lack of institutional responses has contributed to unemployment, conflicts, and instability in the region as the livelihoods of the people strongly depend on ecosystem services provided by or connected to the lake. In the Australian Drought the stronger institutional capacity allowed the implementation of several measures to mitigate and adapt to the effects of the event, even if at a significant cost. The loss of water-resilience has been linked with broader social dynamics including armed conflicts, uprisings, and even the collapse of ancient civilizations (Falkenmark & Wang-Erlandsson, 2021). These connections are still debated and difficult to ascertain due to the complexity of social systems. Nevertheless, the communities most affected by loss of freshwater ecosystem services are undoubtedly those that depend the most on ecosystems. Then, social structures at individual, community and institutional levels shape the capacity to adapt or replace ecosystem services with technological solutions or grey infrastructure thus mediating the resilience of freshwater social-ecological systems (Falkenmark et al., 2019).

The resilience of freshwaters to climate change, compounding disturbances and stressors is still unclear and emerging, thus further research is needed the resilience of ecosystems and their services. First, we need to address the basic gaps in the assessment of freshwater ecosystem services and their linkages with biodiversity. Second, we need to improve our understanding of resilience, identifying alternative stable states and tipping points in freshwaters, especially in running waters. To that end, we need long-term studies and monitoring as well as retrospective studies to understand the response of ecosystems to past and ongoing changes and identify potential tipping points. Third, we need to enhance our understanding of the roles of social dynamics in modulating resilience and to include multidisciplinary perspectives in evaluating freshwater ecosystem services and resilience.

CONCLUSION

In conclusion, this work illustrates diverse responses of freshwater socio-ecological systems to environmental changes, highlighting warning signs of declining resilience due to climate change and altered disturbance regimes. The examples highlight how significant the consequences for social systems can be as well as the role of social structures in mediating resilience. However, a high degree of uncertainty still surrounds the identification of tipping points, regime shifts, and future ecosystem trajectories. The responses of freshwater ecosystems to climate change, multiple disturbances and stressors are still emerging. Predicting the dynamics of these critical socio-ecological systems in the future requires long-term studies directly examining resilience. Research on the resilience of freshwaters is essential to ensure they continue providing critical ecosystem services to society, thereby fostering resilient communities.

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