Trends in
Ecology & Evolution

CellPress
OPEN ACCESS

Review

Freshwater salinisation: a research agenda for a saltier world

David Cunillera-Montcusí [1,2,*], Meryem Beklioğlu [3], Miguel Cañedo-Argüelles [4], Erik Jeppesen [3,5,6,7], Robert Ptacnik [1], Cihelio A. Amorim [3], Shelley E. Arnott [8], Stella A. Berger [9], Sandra Brucet [10,11], Hilary A. Dugan [12], Miriam Gerhard [13], Zsófia Horváth [14,15], Silke Langenheder [16,17], Jens C. Nejstgaard [9], Marko Reinikainen [18], Maren Striebel [13], Pablo Urrutia-Cordero [19], Csaba F. Vad [14,15], Egor Zadereev [20,21] and Miguel Matias [22,23]

The widespread salinisation of freshwater ecosystems poses a major threat to the biodiversity, functioning, and services that they provide. Human activities promote freshwater salinisation through multiple drivers (e.g., agriculture, resource extraction, urbanisation) that are amplified by climate change. Due to its complexity, we are still far from fully understanding the ecological and evolutionary consequences of freshwater salinisation. Here, we assess current research gaps and present a research agenda to guide future studies. We identified different gaps in taxonomic groups, levels of biological organisation, and geographic regions. We suggest focusing on global- and landscape-scale processes, functional approaches, genetic and molecular levels, and eco-evolutionary dynamics as key future avenues to predict the consequences of freshwater salinisation for ecosystems and human societies.

Highlights

The global acceleration of freshwater salinisation due to human activities such as agriculture, resource extraction, and urbanisation and its amplification by climate change is unequivocal. Although research in this field is growing, there are key aspects at the ecological and evolutionary levels that remain unaddressed.

Increasing salinisation is a problem as it can increase the stress or mortality of freshwater organisms, leading to a loss of diversity and/or functionality of freshwater ecosystems but also the services and benefits to human societies that they provide.

We identify the main gaps of recent research and suggest a research agenda to facilitate future research efforts in order to achieve a more comprehensive understanding on freshwater salinisation.

A global increase in salinity

Salinity, the concentration of dissolved salts in water, is one of the key environmental parameters shaping aquatic biodiversity worldwide [1]. The global trend in salinisation of freshwater ecosystems [i.e., freshwater salinisation (FS); Box 1] caused by anthropogenic activities (e.g., agriculture, water and resource extraction, application of road de-icers, climate change [2]) has the potential to change the structure and functioning of aquatic communities as well as the benefits that we obtain from aquatic ecosystems, understood as **ecosystems services** (see Glossary) or nature's contributions to people (e.g., crops, water, climate regulation [3–7]). Moreover, FS has direct economic costs and may pose risks to human health (e.g., rise in lead concentrations in drinking water [8,9]). The scientific interest in FS has increased during the last two decades [4,9–11], but major knowledge gaps still exist. Here, we review recent literature on FS (Box S1 in the supplemental information online) to identify main knowledge gaps (Figure 1) and propose a research agenda (Table 1 and Table S1 in the supplemental information online) aiming to stimulate future research.

Current knowledge gaps

The current understanding of the impacts of FS is limited from both ecological and evolutionary perspectives. For example, there is limited focus on the functional, spatial, and trophic consequences of FS and only a few long-term studies exist (but see [12,13]). FS research also suffers from geographic bias, with only a handful of regions being studied (see later). Furthermore, FS can be a result of different types of salts or compounds [4,14] that may trigger complex chemical or biological interactions [10]. Such complexity hinders the development of a common theory of the consequences and impacts of salinisation that might affect the genetic [15], physiological [16], community [17], or ecosystem [4,18] levels of biological organisation. Building a common

[1]WasserCluster Lunz - Biologische Station GmbH, Lunz am See, Austria
[2]Freshwater Ecology, Hydrology and Management Group (FEHM), Section of Ecology, Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain
[3]Limnology Laboratory, Department of Biological Sciences and Centre for Ecosystem Research and Implementation, Middle East Technical University, Ankara, Turkey
[4]Serra Húnter Fellow, Freshwater Ecology, Hydrology and Management group (FEHM), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Institut de Recerca de l'Aigua (IdRA), Universitat de Barcelona, Barcelona, Spain

Box 1. The problem of freshwater salinisation

Many anthropogenic activities are increasing the quantities of salts and ions entering aquatic systems, generating a widespread salinisation of freshwaters [9,10,20]. Maintaining the osmotic equilibrium between internal fluids and the external media (e.g., freshwaters, estuaries, seawater) is critical for the survival of aquatic organisms [9,142]. Therefore, salinity is one of the main drivers of adaptation, speciation, and community assembly in aquatic systems [92,128]. When an external process (e.g., agriculture leading to salt-polluted surface runoff) changes the ion concentrations and ratios of the external media, the organisms need to regulate their internal ion concentrations accordingly. However, this ion regulation capacity (i.e., osmoregulation) has a limit and comes with an energetic cost and if surpassed or maintained in the long term it can compromise the performance of organisms by causing stress or mortality [10,17,142]. Some organisms have become more efficient or developed strategies to cope with such stress and are therefore better able to cope either with salinity fluctuations or with a rise in ionic concentration in the water [80,91]. However, a rise in the ion concentration of freshwaters (i.e., freshwater salinisation) can also affect other conditions of the habitat where organisms live, as the acidification of streams [49], the mobilisation of toxic metals through ion exchange [14], the facilitation of invasion of saltwater species [35], and/or the interference with the natural mixing of lakes [70]. In the end, these changes impact the performance of organisms and change the conditions of the previous freshwater habitat. This process can lead to the loss of species and the alteration of community assemblages [17], ecosystem functionalities [39], regional species pools [57], even pH changes at the continental or global scales [49], among many other consequences. However, all these impacts not only concern organisms and ecosystem functioning, but they also have an effect on freshwater ecosystem services and their contribution to humanity [4,7] with a direct impact on social and economic aspects such as potabilisation costs, infrastructure corrosion, fisheries collapse, and human health [9,21]. Therefore, the problem of freshwater salinisation spans a wide range of areas and impacts different levels of organisation that must be considered in order to properly frame it (see Figure 1 in main text). Its interacting impacts at spatial, temporal, and multiple scales make freshwater salinisation a complex topic. However, this should not prevent us from taking action and trying to understand it, since human activities are rapidly exacerbating the impacts related to freshwater salinisation [11,14,34,49].

framework around such a global challenge is mandatory, based on future scenarios of salinisation and **water scarcity** [2,19]. However, the limitations and inherent complexity of FS are still hindering our ability to assess its extent and consequences [9,20] and to effectively manage it [21,22].

Geographical coverage

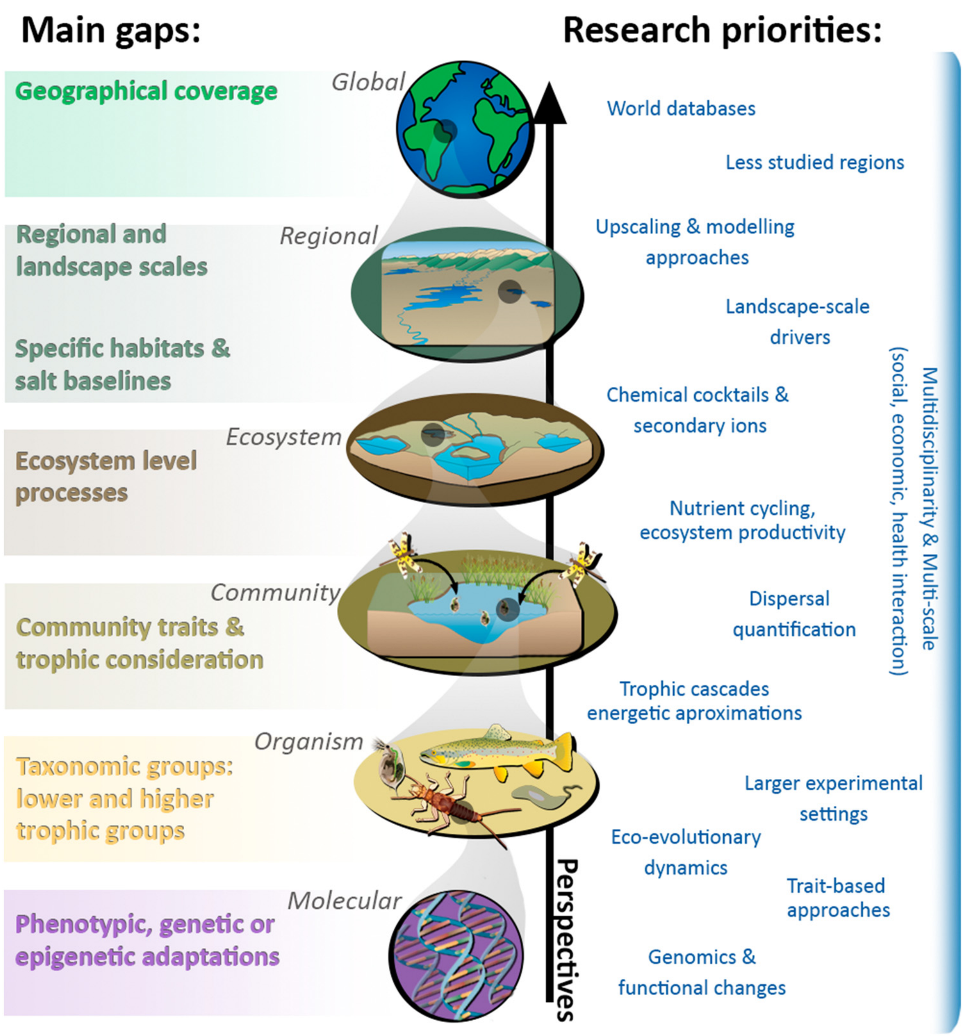
Most of the currently available studies and datasets on FS come from North America, Australia, and Europe [5] (Figure 2), where strong impacts of salinisation occurred in the past [23,24] due to industrialisation and intensive agriculture. There, salinisation is still ongoing (e.g., abandoned mines [25], coal extraction [26]) even if current regulations have slowed it down in many cases [27]. In contrast, FS has been poorly studied in South America, Africa, and Asia (Figure 2), which is worrying as these are the continents where FS drivers are intensifying. For example, irrigation, industrial, and/or resource extraction activities contributing to FS have become increasingly widespread and are expected to expand in countries with poor environmental regulations following a reallocation of industrial activities [28,29]. Due to the unbalanced geographic coverage of the available studies, it is difficult to representatively identify FS hotspots (e.g., seawater intrusion coupled with wastewater discharges could be leading to severe salinisation in Bangladesh [30–32]). Another research gap concerns salinisation caused by climate change and its interactive effects with other drivers of salinisation [19,33], a topic that has been almost exclusively studied in North America, Australia, and Europe (Figure 2). For example, FS amplified by water scarcity [19] is particularly important in arid and semi-arid regions (e.g., the Mediterranean, Middle East, and Central Asia, as highlighted by [3,19,34,35]), but limited datasets are available from these climatic regions [1,10,20]. Additionally, there is a geographical bias in the studied drivers of FS (Figure 2). For example, road de-icing has received great attention in North America [17,36,37] but in comparison, it has been largely neglected in Europe [38].

Specific habitats

Rivers/streams and lakes have received most of the attention in FS research [39,40], while **small water bodies** (e.g., ponds, small shallow lakes, temporary streams) have been largely ignored [30,31,41] (Box S1 in the supplemental information online). These habitats play a key role for

[5]Department of Ecoscience and WATEC, Aarhus University, Aarhus, Denmark
[6]Sino-Danish Centre for Education and Research (SDC), Aarhus, Denmark
[7]Institute of Marine Sciences, Middle East Technical University, Mersin, Turkey
[8]Department of Biology, Queen's University, Kingston, Ontario, Canada
[9]Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Department of Plankton and Microbial Ecology, Zur alten Fischerhuette 2, 16775 Stechlin, Germany
[10]Aquatic Ecology Group, University of Vic, Central University of Catalonia, Vic, Catalonia, Spain
[11]Catalan Institution for Research and Advanced Studies (ICREA), Barcelona, Spain
[12]Center for Limnology, University of Wisconsin—Madison, Madison, WI, USA
[13]Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky University Oldenburg, Schleusenstrasse 1, 26382 Wilhelmshaven, Germany
[14]Institute of Aquatic Ecology, Centre for Ecological Research, Budapest, Hungary
[15]Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven, Belgium
[16]Department of Ecology and Genetics/ Limnology, Uppsala University, Norbyvägen 18D, 75236 Uppsala, Sweden
[17]Department of Ecology and Genetics/ Erken Laboratory, Uppsala University, Norra Malmavägen 45, 761 73 Norrtälje, Sweden
[18]Air Pollution & Climate Secretariat (AirClim), Första Långgatan 18, 413 28 Gothenburg, Sweden
[19]Department of Biology/Aquatic Ecology, Lund University, Ecology building, SE-223 62 Lund, Sweden
[20]Institute of Biophysics, Krasnoyarsk Scientific Centre, Siberian Branch, Russian Academy of Sciences, 660036, Akademgorodok 50/50, Krasnoyarsk, Russia
[21]Siberian Federal University, 79 Svobodniy Ave, 660041, Krasnoyarsk, Russia
[22]Museo Nacional de Ciencias Naturales, CSIC, Madrid, Spain
[23]Biodiversity Research Chair, MED – Mediterranean Institute for Agriculture, Environment and Development. Universidade de Évora, Évora, Portugal

*Correspondence: david.cunillera@dcm.cat (D. Cunillera-Montcusí).



Trends in Ecology & Evolution

Figure 1. Biases and gaps in current salinization literature across scales (left). Main proposed research priorities based on these gaps and following the proposed research agenda (right). Note that the listed research priorities can be applied to different scales. Multidisciplinary priorities are considered to affect several scales. Small images and icons were freely downloaded from IAN Image Library.

biodiversity and ecosystem services [42], are one of the most abundant freshwater habitats in the world [43], and are particularly sensitive to drought or water abstraction and, therefore, salinisation [4,44].

Composition and relative ion concentrations

Salinisation effects depend on ion composition and concentrations, both in terms of background salinity and the '**chemical cocktails**' of ions created by anthropogenic activities [14,45]. The combination of different ions (e.g., Na^+, K^+, Cl^-, CO_3^{2-}, SO_4^{2-}) and the mobilisation of other elements or ions (e.g., Cu, Mn, Zn, Sr, NH^{4+}, PO_4^{3-}) can lead to extremely different and complex habitat-specific consequences [10,14,46]. The interrelationships between these consequences and the chemical, biological, and geological properties of an environment are termed the **freshwater salinisation syndrome** [10,14]. Also, FS needs to be considered in terms of relative

Glossary

Chemical cocktails: novel and variable combinations of anthropogenically enhanced compounds that are found together. These compound mixtures are considered novel because of their elevated concentrations relative to natural baseline conditions and due to the anthropogenically enhanced transport, formation, and transformation in the environment.

Eco-evolutionary dynamics: an integrative field of research that focuses on how ecological change influences evolutionary change, how evolutionary change influences ecological change, and how those two pathways (eco-to-evo and evo-to-eco) sometimes may influence each other.

Eco-hydrological models: mechanistic models into which ecological and hydrological information is integrated and which, based on climatic scenarios, can predict future scenarios.

Ecosystems services: the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life, maintaining biodiversity, production of goods, life-support functions, and intangible aesthetic and cultural benefits.

Epigenetic adaptations: adaptations to a stressor or a phenomenon that changes the final outcome of a locus or chromosome without changing the underlying DNA sequence.

Freshwater salinisation syndrome: the complex interrelationships between salts ions and chemical, biological, and geological parameters and their consequences for nature, society, and the environment. The increase in ionic concentrations derives from pollution, human-accelerated weathering, and/or saltwater intrusion.

Metapopulation and metacommunity: a set of local populations or communities linked by dispersal of multiple potentially interacting individuals or species.

Oligohaline systems: systems within freshwater range that have lowest salinity, mostly in terms of chloride concentrations, as, for example, high mountain snowmelt-fed streams or rivers. General classification of saline waters is not homogenous between inland, estuarine, or marine ecosystems. Based on [141], freshwater would be between 0.02 and 1.0 g/l.

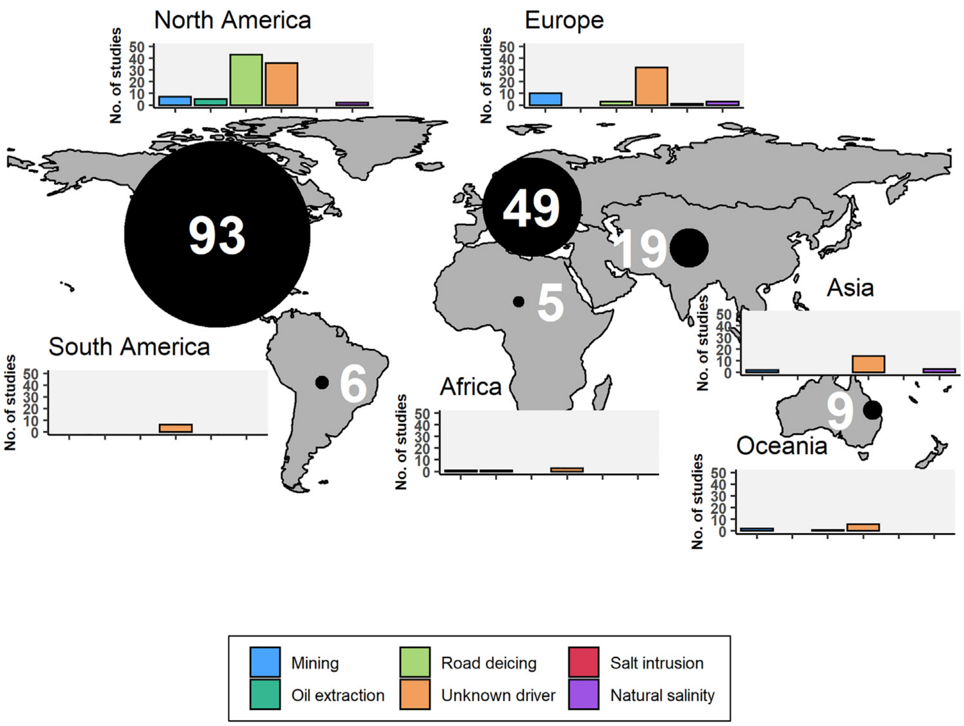


Figure 2. Global representation of studies on salinisation from 2017 to 2021 considering the causes of salinity changes in the studied systems (bar plot colours), including mining, road de-icing, salt intrusion, and oil extraction (e.g., fracking). Studies that did not specify the drivers of salinisation are included in the category 'unknown driver' and those targeting systems with already high salinities due to natural causes (e.g., primary salinisation or saline inland waters) are included in the category 'natural salinity'. Circle size and white numbers correspond to the total number of studies conducted on each continent. See database in Table S2 in the supplemental information online.

Regime shifts: the change of the state of some ecosystems that, for certain environmental conditions, have different alternative stable states, separated by an unstable equilibrium that marks the border between the 'basins of attraction' of the states. A change in the external conditions (e.g., increase in salinity) can generate these shifts from one state (e.g., clear waters dominated by macrophytes) to a different one (e.g., turbid waters dominated by phytoplankton).
Small water bodies: those small lentic water bodies that have received less attention either due to their small size (less than 10 ha) or their shallow depth, despite their unique value. Also, systems that periodically dry out (e.g., lotic or lentic) are included in this category.
Water scarcity: understood here as the decrease in water availability related to direct withdrawal, excessive use, and changes in rainfall and evapotranspiration induced as a consequence of global change.

changes in salt concentrations. For example, a small change in salinity can severely impact the aquatic communities of natural **oligohaline systems** (e.g., high mountain streams) as these have evolved under stable and low ion concentrations [34,36]. However, to date FS research has mainly focused on sodium and chloride [9] while increases of ion concentrations relative to natural conditions have been mostly ignored [47]. This limits our ability to capture the real consequences of FS. For example, aquatic animals that inhabit calcareous catchments could be less sensitive to salinisation due to an ameliorating effect of carbonates, which are also increasing in freshwaters [48,49], on chloride toxicity. This phenomenon has been related to the rise in Ca concentration in body fluids, which reduces membrane permeability, decreasing the passive diffusion of chloride [50–52]. Also, background salinity concentrations can lead to adaptation, resulting in intraspecific differences in the salt sensitivity of aquatic organisms [53,54].

Regional and landscape scales

Although salinity is known as a major driver of regional community structure and spatial beta diversity [55,56], the consequences that FS can have at large spatial scales are still to be understood. Land use alterations (e.g., urbanisation, agriculture [49]) can change regional processes such as dispersal and impact regional species pools. However, FS has rarely been studied from a **metapopulation and metacommunity** perspective [57,58]. FS alters habitat suitability, which translates to altered connectivity between inhabitable patches. In addition, it modifies dispersal and trait selection in water bodies, with consequences for less tolerant keystone species and for the regional pool [59–61]. Thus, it is reasonable to assume that metacommunity dynamics can be significantly affected by FS.

Ecosystem level processes

Responses at species level have received much attention [16,62,63] and often been used to set policy recommendations (e.g., [27,64]), which therefore fail to capture complex interactions (e.g., FS can affect the grazing potential of zooplankton because of changes in the dominance of different groups [65]). However, ecosystem-level responses, including ecosystem functions and services, have been rarely assessed [4,24] (Box S1 in the supplemental information online). Organic matter decomposition is the most studied ecosystem function [66], for which interactive effects of salinization with warming and drought have also been explored, implying an additive decrease in decomposition [67,68]. Less is known about salinity effects on biogeochemical cycles, such as nitrogen processing [69] or the carbon cycle [4]. Although the effects of FS on most physico-chemical processes that are relevant at the ecosystem level remain unknown, recent studies have shown alterations in lake stratification [70,71] and changes in greenhouse gas (GHG) production (e.g., methane) [72]. Finally, in spite of the documentation of salinity-induced **regime shifts** in shallow lakes [73,74], explicit tests of the potential of FS to drive shifts and the thresholds between alternative stable states (e.g., macrophyte-dominated clear waters and phytoplankton-dominated turbid waters) are missing. This gap of knowledge on the functional consequences of FS hinders the development of valid **eco-hydrological models** to predict the impact of FS under different future scenarios. Overall, a more holistic perspective regarding the impacts of salinisation is strongly needed, not only at the ecosystem functioning (e.g., induced rise in GHG emissions, increased nitrogen loads) but also at the ecosystem services level [9].

Community level

FS impacts at community level have been intensively studied. However, the current literature mainly addresses community structure (e.g., species richness or composition [25,75,76]). Functional aspects related to trait diversity, food web structure, and trophic dynamics remain poorly explored. Some studies have reported significant declines of functional diversity of river and stream invertebrates due to FS [77,78], but specific information on which traits could be affected by FS and how this can impact ecosystem functioning is still scarce [79,80]. Also, few studies have quantified the effects of FS on food webs (e.g., isotopic analyses [40,79], trophic structure [74,81,82]).

Taxonomic groups

Recent studies have mostly focused on aquatic invertebrates [83,84], (63 on macroinvertebrates and 46 on zooplankton; Figure 3). Despite their key role for ecosystem functioning (e.g., nutrient cycling), microorganisms have received less attention (30; Figure 3). The same holds true for higher trophic levels such as birds (1), fish (16), amphibians (18), and reptiles (2 studies; Figure 3) [85–87]. The narrow focus on certain taxonomic groups prevents a proper assessment of the risks that FS poses to global biodiversity.

Genetic and molecular levels

Few studies have investigated the role of adaptations (e.g., phenotypic, genetic, or **epigenetic adaptation** [88]) to salt stress. The same is true for the interplay between ecological and evolutionary processes (i.e., **eco-evolutionary dynamics** [89]) in the context of FS. For example, the effects on performance of species within the community (e.g., predation efficiency, stressor cross-tolerance) are still not fully elucidated. Salinity is a strong evolutionary pressure [90–92], but short- or mid-term adaptations can result in a cost for species fitness [84]. These adaptive costs add

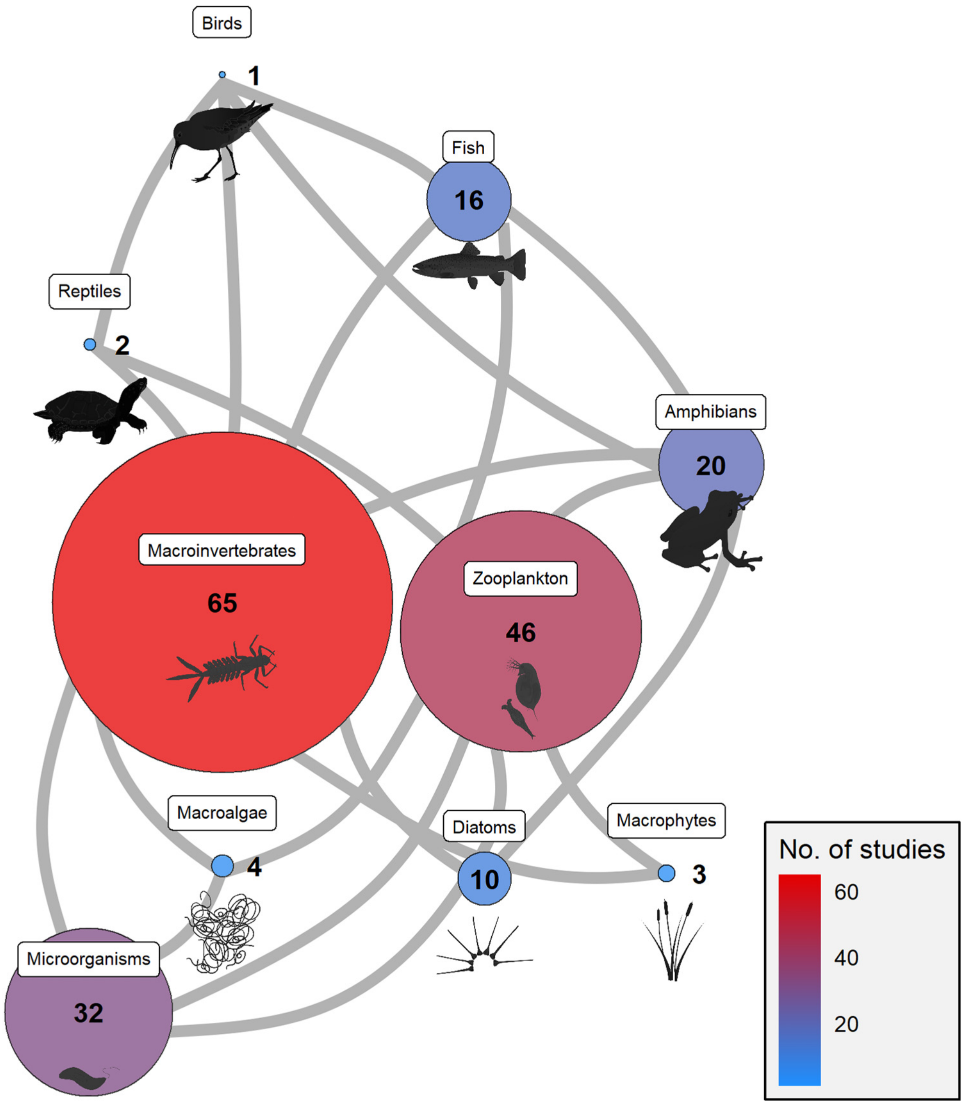


Figure 3. Number of salinisation studies with focus on specific organisms during 2017–2021. Organisms are divided into major groups defined by the focus of each study and they do not always respond to a taxonomic classification (e.g., zooplankton includes Rotifera, Cladocera, and Copepoda, while microorganisms similarly include a number of unicellular taxa, including phytoplankton and bacterial communities in general). Note that an individual study may contribute to several groups. Grey lines are illustrative of the possible trophic connections among the different groups. Organism silhouettes were freely downloaded from IAN Image Library. See database in Table S2 in the supplemental information online.

pressure to aquatic communities exposed to salinisation, potentially leading to loss of genetic diversity [93]. Such information is of key importance to effectively manage salinised ecosystems to ensure mitigation strategies success (e.g., loss of genetic diversity compromising recovery [94,95]).

A research agenda

To facilitate and stimulate future research on FS, we present a research agenda that includes the most urgent knowledge gaps to be addressed (Figure 1 and Table 1). The proposed agenda spans across perspectives.

Table 1. Main agenda priorities (three for each category) for salinisation research to target main gaps and biases, summarising the main discussed ideas of the current manuscript from global, regional, local, temporal, multiscale, and multidisciplinary perspectives[a]

Global
Main focus on: 1. Collecting information from less studied regions (e.g., differences between biogeographic regions, different responses due to climatic properties). 2. Creation of databases with salinity and biological data (e.g., use water quality and biomonitoring data that usually include salinity measured as electrical conductivity). 3. Analyse freshwater salinisation causes, consequences, and dynamics at large spatial scales (e.g., continental, freshwater salinisation increase in more drought-prone regions).
Some suggested approaches: ➢ Gathering salinisation and biological information and building region-wide databases and research networks. Establishing a common methodological framework to generate harmonised data in the future (e.g., report salinity in the same units). ➢ Developing wide-scale approximations to assess extent of salinity consequences (e.g., contribution to greenhouse gas emission of salinised freshwaters). ➢ Partnership at international-level projects with countries understudied that often have small research budgets.
Regional
Main focus on: 1. Community salinity thresholds (i.e., salinity ranges at which there is a drastic change in species composition). 2. Environmental tracking and impact of freshwater salinisation on colonisation–extinction dynamics (e.g., metacommunities) and regional biodiversity. 3. Basin level characteristics (e.g., geology) favouring or buffering freshwater salinisation and modulating its impacts on biodiversity and ecosystems. Basin-wide consideration of salinity dynamics (e.g., upstream–downstream processes).
Some suggested approaches: ➢ Quantification of land uses (e.g., impervious surfaces, crops) using satellite imagery and geographic information systems. ➢ Coordinated experiments across regions with different land uses and climatic conditions (e.g., GLEON salinity experiments, among others). ➢ Large-scale mesocosms experiments[b] for determining salinity thresholds for species extinction and colonisations.
Local
Main focus on: 1. Impact of freshwater salinisation on the less-studied trophic levels (e.g., primary producers, microbial loop, plankton, higher trophic levels) and cascading effects on ecosystem functioning (e.g., bottom-up control, top-down control). 2. Species traits related to salinity tolerance with implications for ecosystem functions. 3. Adaptation to salinisation and consequences for eco-evolutionary dynamics (e.g., species adaptations increase population fitness with an effect on ecosystem functions).
Some suggested approaches: ➢ eDNA, genomic composition of total (DNA) and active (RNA) diversity, (Meta)genomics, (Meta)transcriptomics.[b] ➢ Compound-specific stable isotopes or energetic and metabolic perspectives. ➢ Larger experimental infrastructures (allowing for replicability and for including multiple trophic levels).[b]
Temporal
Main focus on: 1. Long-term datasets or long-term trends analysis (e.g., new experiments or previous databases). 2. High-frequency data, including relevant metrics (e.g., salinity, temperature, water flow). 3. Regional adaptations of the species pool to background salinities (e.g., genetic/phenotypic adaptations from different populations/communities between impacted or nonimpacted regions).
Some suggested approaches: ➢ Paleolimnological data to understand the effect of past salinisation events and capture long-term changes linked to human activities (e.g., road-salt usage, industrialisation). ➢ Combined analysis of time-series data and experimentation (i.e., short-term trajectories). ➢ High-frequency automated monitoring of small-scale ecological responses to salinity changes.
Multiscale and multidisciplinary perspectives and disciplines
Main focus on: 1. Chemical cocktails (e.g., metal ions, salt ions, nutrients), their relationship with geomorphological processes, and their impact on trophic processes and trophic structure. 2. Multiple stressors' effects on community structure and function within the context of freshwater salinisation.

(continued on next page)

3. Effects of salinization on **ecosystem services** and/or nature contributions to people and human health risks.
Some suggested approaches: ➢ Building networks and joint meetings across different disciplines. ➢ Interdisciplinary projects combining ecological, social, health, and economic perspectives (e.g., economic, health, or social assessment of freshwater salinization impacts for human societies based on its ecological impacts). ➢ Citizen science as a tool to engage multiple stakeholders.

[a]Each perspective is an approximate 'level' at which the processes and methods could be analysed and not a restrictive separation.

Local perspective

More information on primary producers (e.g., phytobenthos or phytoplankton) is clearly needed, especially as they constitute a key component in aquatic systems . A simultaneous consideration of multiple trophic levels is also of key importance to better understand how top-down and bottom-up processes change as a response to FS. Changes in salinity are generally accompanied by changes in the trophic state of ecosystems, with possible implications for primary producers [96]. These changes are to some extent triggered by top-down control due to the loss of consumers (e.g., zooplankton, fish [97,98]), which may foster phytoplankton blooms, although it is still unclear how strong this top-down control might be at varying salinity levels [17,99]. Salinisation can also alter bottom-up control. For example, mobilisation of base cations, changes in pH, and the alteration of biogeochemical processes can increase the mobilisation of nutrients (e.g., dissolved inorganic nitrogen and soluble reactive phosphorus [96]). The interaction between increased salinity and other nutrients can trigger compositional changes in primary producers [100] with consequences at higher trophic levels [65,101]. Field tests and ecosystem level manipulations may benefit the understanding of such processes [102].

The highest trophic levels constitute another key component to focus on the local perspective. Existing knowledge on toxicological and individual responses of fish, amphibians, and birds [17,86,103] must be applied to assess salinity-triggered changes in their trophic interactions (e.g., changes in predation rates). At community level, top-down effects (e.g., loss of keystone species due to salinisation [104]) and trophic cascades are receiving increasing attention [79,105]. However, a complete understanding of these interactions as well as more trophic or energetic approaches (e.g., energy fluxes across the food web [40,79]) needs further attention. Similarly, behavioural responses (e.g., boldness, cerebral lateralisation) to FS need to be assessed [106,107]. Finally, FS has been shown to alter host–parasite interactions but the information is limited to a few studies and should be further investigated [108]. The trophic consequences of FS on natural systems are complex to assess, but use of mesocosm experiments can help to assess them [97,109]. In addition, use of compound-specific stable isotopes or energetic perspectives (e.g., fatty acids analysis [110]) can help us to understand the response of trophic food webs to FS under experimental and field conditions.

For the lowest trophic levels (e.g., bacteria, fungi), changes in their communities either in the species composition and/or their activity induced by FS can modulate ecosystem functions and drive processes related to GHG production. Denitrification [69,111], methane production [112], but also dissolved organic carbon, detrital processing, and decomposition [39,68] are key aspects linked to microbial activity that need further attention. Molecular methods used to assess microbial diversity, linking it with functionality, can help to analyse these processes [76]. The few available studies on FS consequences for microorganisms have focused on community composition [113]. Although assessing microbial diversity or composition is relevant, its functional activity is key at the ecosystem level [69]. Therefore, the link between composition and activity should be further explored by analysing genomic composition of total (DNA) and active (RNA) diversity, which can help to identify the more active processes and the taxonomic groups involved in them (e.g., comparison of DNA- and RNA-based sequencing, marker genes such 16S or 18S rRNA, metagenomics and metatranscriptomics).

As shown for other stressors [114], trait-based approaches can be useful tools to obtain a more mechanistic understanding of how FS impacts the structure and function of freshwater communities [75] since they focus on the functional roles of species within the ecosystem rather than their identities (e.g., litter decomposition [39]). Traits associated with tolerating osmotic stress, such as short lifespan, high number of generations per year, dormancy, plastron respiration, or ovoviviparity, might be beneficial for coping with FS (see traits listed in [59,115]). Furthermore, body size and mobility should also be considered, especially when assessing dispersal dynamics or connectivity [57,59].

Regional perspective

Many of the drivers and processes that modulate FS have an effect at the catchment or watershed scales [10,14,49] or even at larger spatial scales [33,116]. Accordingly, landscapes undergoing salinisation can have very large spatial extents (e.g., the Murray-Darling Basin, the Aral Sea Basin, or the Konya Closed Basin), with changes in the regional species pools. This can modify colonisation–extinction dynamics and/or favour the spread of salt tolerant, generalist species or invasive species [61,117]. Habitat connectivity plays a key role in environmental tracking (i.e., adaptation to environmental change at the community level) and therefore in either buffering (e.g., population maintenance due to mass effect) or favouring community differentiation (e.g., change in species pool) [57–59]. At the same time, connectivity may also contribute to negative impacts of FS by propagating it from a main source (e.g., basin-wide effects [118]) and this must therefore be considered since changes in the upstream chemical composition can be exported across a whole river catchment [119,120].

Salinity gradients linked to the natural features of the landscape (e.g., geology, natural drought, land uses) can drive evolutionary adaptations [38,121]. Consequently, background salinity (i.e., salinity levels at which communities have evolved) is relevant when addressing responses to human-driven salinization. Shifting background salinity in naturally oligohaline systems represents a major threat, especially in naturally oligohaline systems (e.g., road de-icers in mountain regions [36,38]), inducing biodiversity loss and an alteration of biogeochemical interactions, species pools, and ecosystem functioning [10,17]. Quantification of regional-scale features accounting for both human and natural salinity drivers (e.g., land use, geology, climate, hydrology) seems essential at this level. Besides, there is a clear need for proof-of-principle experiments accounting for regional-scale processes (e.g., mesocosms with gradients of salinity and connectivity coupled with different regional species pools).

Global perspective

More complete global databases [5,49], also including biological datasets, could provide a better overview of the salt concentrations at which aquatic communities undergo significant changes (e.g., thresholds representing sharp decreases in species richness [122]). Many limnological studies and monitoring programmes not focusing on FS do, however, include electrical conductivity and biological data. Gathering such information (covering both temporal and spatial scales) and building region-wide databases (see some examples [49,116]) are a priority for gaining a global perspective on FS and enabling forecasting of its impacts at a planetary scale. Furthermore, knowledge on how FS affects physico-chemical and ecosystem processes would help to improve and develop ecohydrological models (fed with remote sensing or high-frequency monitoring data). Although related to a more local perspective, such information might be upscaled and used to assess the consequences of salinity changes at larger spatial and temporal scales (e.g., continental, future scenarios). For example, salinity could be assessed via satellite or drone, which can be used to apply already developed salinity indices or together with other proxies (e.g., hydrology, land use, impervious surface [123]), which later could be related to ecosystem metrics (e.g., nutrients, carbon decomposition) or biogeochemical processes (e.g., GHG production, pH). This would help to quantify the extent of salinity as well as its contribution to GHG emissions and to predict future scenarios [2]. Although they sound promising, such approximations still need to be developed. Similarly, data gathering based on citizen science projects, where salinity levels can be obtained by general public participation and reported remotely, remains to be explored but might be valuable to build extensive databases as seen in other disciplines [124,125]. Assessing the extent of FS is central for setting a global management and policy agenda, as has been done for climate change [2].

One of the most important steps for advancing our knowledge on FS is to focus on vulnerable and less-studied regions. There are many regions of the world where severe salinisation of water bodies is likely to occur, but it is hard to prove it due to lack of data (e.g., India [126]). Besides, assessing and monitoring human activities in understudied regions could also be beneficial to feed global databases. This can be attained by promoting international-level projects that will foster salinity research in countries with small research budgets. In this regard, affordable methods, which can be obtained worldwide and centralised to decrease total costs (e.g., satellite-based assessment, eDNA, gene expression quantification), must be developed as well as partnerships with bigger institutions having bigger infrastructure to decrease sample-processing costs.

Temporal perspective

To address the existing knowledge gaps related to the temporal dynamics, long-term datasets related to salinisation impacts are essential for understanding the long-term consequences of FS [127]. Accounting for time is also highly relevant from an adaptive and evolutionary point of view [91]. Here, adaptation of selected species to long-lasting FS impacts may be central for posterior remediation and for comprehending the eco-evolutionary dynamics of salinity changes [61,128]. Generalist and salinity-tolerant species benefit from the release on competition and predation pressures of saline systems [80,129], as reported in, for example, potash mining-impacted streams [119]. Evolution linked to such processes has traditionally been related to geological time scales [91,121]. However, there is accumulating evidence on rapid evolution, now considered an important response of species to environmental change [130,131]. Thus, eco-evolutionary dynamics [132] are likely to be a main driver of community assembly in salinised habitats. However, as human-mediated salinisation may differ from natural salinisation at the chemical level [14], it may also require different evolutionary mechanisms. The lack of long-term datasets should not preclude anticipating the long-term consequences of salinisation. Alternative approaches using combined analysis of time-series data, paleolimnology [133], and experimentation (i.e., short-term trajectories) could help to elucidate such trends [134]. Furthermore, high-frequency monitoring can aid in capturing small-scale ecological responses to FS that are otherwise missed in standard monitoring programmes [134]. High-frequency real-time monitoring can be used to derive ecosystem metabolism [135] or to provide early warning signals for harmful cyanobacterial blooms [136]. However, such methodologies still need to be implemented in FS studies.

Multiscale and multidisciplinary perspectives

More interdisciplinary research should be conducted to obtain, for example, a complete picture of how agriculture modifies the salinity of freshwater ecosystems, its consequences, and how these can be managed; such a picture can only emerge from interaction among experts (e.g., edaphologists, hydrologists, ecotoxicologists, farmers, policy makers, among others). Building networks across different disciplines would represent a step forward in the development of conceptual models, global monitoring, and data analysis and for a successful management of FS. Considering simultaneously ecological, economic (e.g., infrastructure damaging, economic costs), social (e.g., water potability), and political (e.g., regulations or thresholds) facets is especially relevant to generate anticipation, mitigation, and remediation strategies. In the same line, studies on interrelated impacts at chemical, geological, and biological levels must be also pursued [10,14,49]. Implementing a combination of techniques and perspectives in both experimental facilities and later in the field can contribute to a better understanding of more complex relationships [137–139].

Concluding remarks: a saltier world

Salinisation is one of the greatest threats to global freshwater ecosystems and their associated biodiversity, as well as to societal well-being, as it is expected to impact the quality and provisioning of water and related ecosystem services across the globe. This challenge needs to be addressed by a joint and focused effort from the scientific community working at different scales, involving also stakeholders and local practitioners. The implications of salinisation at the ecological and evolutionary levels for freshwater ecosystems will change their biodiversity and functioning and, thereby, affect human societies relying on them at both economic and health levels. Here, we have conceptualised a research agenda outlining the way forward (Table 1 and see Outstanding questions). Research focused on filling knowledge gaps would contribute to significantly advancing and concomitantly developing better management strategies (e.g., nature-based solutions) as well as to raising the general awareness of the problem [1,140].

Acknowledgments

We want to specially thank Anne Mette Poulsen for her valuable editions on the manuscript and to the two reviewers and the editor who helped to improve its quality. This manuscript was inspired by the discussion groups of the AQUACOSM-plus webinar series on Grand Challenges in Aquatic Ecology. This work is part of the AQUACOSM and AQUACOSM-plus projects that have received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement Nos 731065 and 871081. D.C.M., M.B., E.J., R.P., S.A.B., M.G., Z.H., S.L., J.C.N., M.R., and C.F.V. were supported by the H2020 EU-funded project AQUACOSM-plus (no. 871081). D.C.M., M.B., S.A.B., and J.C.N. were supported by the H2020 EU-funded project AQUACOSM (no. 731065). M.B. and E.J. were supported by the TÜBITAK program BIDEB2232 (project 118C250). M.B. and S.B. were supported by the H2020 EU-funded project PONDERFUL (no. 869296). Z.H. and C.F.V. were supported by the NKFIH-471-3/2021 project. Z.H. was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. P.U-C. was supported by the Swedish Research Council Formas (grant: 2020-01825). M.M. was supported by the Grant RyC-2016-19348 funded by MCIN/AEI/10.13039/501100011033 and by ESF 'Investing in your future'.

Author contributions

D.C-M., M.B., M.C-A., E.J., R.P., and M.M. formed the core writing team linked to the AQUACOSM-plus grand challenges world café discussion group. C.A.A., S.E.A., S.A.B., S.B.R., H.D., M.G., Z.H., S.L., J.C.N., M.S., P.U-C., C.F.V., and E.Z. participated in the AQUACOSM-plus grand challenges world café discussion group and also contributed to the more advanced versions of the manuscript.

Declaration of interests

No interests are declared.

Supplemental information

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2021.12.005.

References

1. Reid, A.J. *et al.* (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873
2. IPCC (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. In *Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press
3. Rounsevell, M. *et al.* (2018) *The IPBES Regional Assessment Report on Biodiversity and Ecosystem Services for Europe and Central Asia*, Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem services

Outstanding questions

How can we promote research in less-studied regions and build global networks optimising research costs and methodologies? Developing and promoting cheaper, affordable methods is needed.

How does salinisation interact with other global change drivers such as warming, habitat destruction, or invasive species? Are the effects of these negative drivers interactive or additive?

Could the currently available databases, where biological information as well as electrical conductivity are often reported, be used to build wider-scale databases or long-term datasets? Data collection is still needed from many regions of the world. Citizen science projects may be key to complement such databases.

How are landscape-scale alterations reflected in the composition and functioning of local habitats? How far can salinisation impacts be transmitted across connected systems? Identification and quantification of the main regional drivers of salinisation are necessary to reveal mechanisms beyond regional community patterns.

Can remote sensing be used to predict freshwater salinisation at local and regional scales? Could this be implemented to identify and monitor unknown impacted sites? Such tools still need to be tested and properly developed.

How are ecosystem-level processes affected by freshwater salinisation? Can this lead to shifts in alternative stable states? Do compositional changes affect community functioning? Consideration of microbial activity and gene expression can help to assess changes in ecosystem-level processes and which functions might be more sensitive.

How does salinisation of freshwaters modulate food web structure and functioning? How are energetic fluxes impacted? What are the impacts of freshwater salinisation on the microbial loop? The trophic consequences of freshwater

4. Herbert, E.R. *et al.* (2015) A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. *Ecosphere* 6, 1–43
5. Thorslund, J. and Van Vliet, M.T.H. (2020) A global dataset of surface water and groundwater salinity measurements from 1980 – 2019. *Sci. Data* 7, 1–11
6. Zhao, Q. *et al.* (2021) Increasing anthropogenic salinisation leads to declines in community diversity, functional diversity and trophic links in mountain streams. *Chemosphere* 263, 127994
7. Díaz, B.S. *et al.* (2018) Assessing nature's contributions to people. *Science* 359, 270–272
8. DeVilbiss, S.E. *et al.* (2021) Freshwater salinization increases survival of *Escherichia coli* and risk of bacterial impairment. *Water Res.* 191, 116812
9. Cañedo-Argüelles, M. (2020) A review of recent advances and future challenges in freshwater salinization. *Limnetica* 39, 185–211
10. Kaushal, S.S. *et al.* (2021) Freshwater salinization syndrome: from emerging global problem to managing risks. *Biogeochemistry* 154, 255–292
11. Dugan, H.A. *et al.* (2017) Salting our freshwater lakes. *Proc. Natl. Acad. Sci. U. S. A.* 114, 4453–4458
12. Ermakhanov, Z.K. *et al.* (2012) Changes in the Aral Sea ichthyofauna and fishery during the period of ecological crisis. *Lakes Reserv. Res. Manag.* 17, 3–9
13. Bäthe, J. and Coring, E. (2011) Biological effects of anthropogenic salt-load on the aquatic fauna: a synthesis of 17 years of biological survey on the rivers Werra and Weser. *Limnologica* 41, 125–133
14. Kaushal, S.S. *et al.* (2019) Novel 'chemical cocktails' in inland waters are a consequence of the freshwater salinization syndrome. *Philos. Trans. R. Soc. B* 374, 20180017
15. Venâncio, C. *et al.* (2019) Sensitivity of freshwater species under single and multigenerational exposure to seawater intrusion. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180252
16. Dobry, E. *et al.* (2021) The effect of salinity fluctuation in freshwater streams on the fecundity of post-diapause *Chironomus dilutus*. *Ecotoxicology* 30, 224–230
17. Hintz, W.D. and Relyea, R.A. (2019) A review of the species, community, and ecosystem impacts of road salt salinisation in fresh waters. *Freshw. Biol.* 64, 1081–1097
18. Sauer, F.G. *et al.* (2016) Effects of salinity on leaf breakdown: dryland salinity versus salinity from a coalmine. *Aquat. Toxicol.* 177, 425–432
19. Van Vliet, M.T.H. *et al.* (2017) Quality matters for water scarcity. *Nat. Geosci.* 10, 800–802
20. Jeppesen, E. *et al.* (2020) Salinization increase due to climate change will have substantial negative effects on inland waters: a call for multifaceted research at the local and global scale. *Innovation (N. Y.)* 1, 100030
21. Cañedo-Argüelles, M. *et al.* (2016) Saving freshwaters from salts. *Science* 351, 914–916
22. Schuler, M.S. *et al.* (2019) Regulations are needed to protect freshwater ecosystems from salinization. *Philos. Trans. R. Soc. B* 374, 20180019
23. Schulz, C.-J. and Cañedo-Argüelles, M. (2019) Lost in translation: the German literature on freshwater salinization. *Philos. Trans. R. Soc. B* 374, 20180007
24. Hart, B.T. *et al.* (2003) Ecological risk to aquatic systems from salinity increases. *Aust. J. Bot.* 51, 689–702
25. Vendrell-Puigmitja, L. *et al.* (2021) Effects of an hypersaline effluent from an abandoned potash mine on freshwater biofilm and diatom communities. *Aquat. Toxicol.* 230, 105707
26. Timpano, A.J. *et al.* (2018) Seasonal pattern of anthropogenic salinization in temperate forested headwater streams. *Water Res.* 133, 8–18
27. European Commission (2000) *Directive 2000/60/EC. Establishing a Framework for Community Action in the Field of Water Policy*, European Commission PE-CONS 3639/1/100 Rev 1
28. International Energy Agency (2021) *The Role of Critical Minerals in Clean Energy Transitions*, IEA
29. WWF (2020) *Living Planet Report 2020 - Bending the Curve of Biodiversity Loss*, WWF
30. Ayers, J.C. *et al.* (2017) Salinization and arsenic contamination of surface water in southwest Bangladesh. *Geochem. Trans.* 18, 1–23
31. Hossain, L. *et al.* (2018) Evaluation of present and future wastewater impacts of textile dyeing industries in Bangladesh. *Environ. Dev.* 26, 23–33
32. Dey, S. and Islam, A. (2015) A review on textile wastewater characterization in Bangladesh. *Resour. Environ.* 5, 15–44
33. Olson, J.R. (2019) Predicting combined effects of land use and climate change on river and stream salinity. *Philos. Trans. R. Soc. B* 374, 20180005
34. Gozlan, R.E. *et al.* (2019) Status, trends, and future dynamics of freshwater ecosystems in Europe and Central Asia. *Inland Waters* 9, 78–94
35. Zadereev, E. *et al.* (2020) Overview of past, current, and future ecosystem and biodiversity trends of inland saline lakes of Europe and Central Asia. *Inland Waters* 10, 438–452
36. Arnott, S.E. *et al.* (2020) Road salt impacts freshwater zooplankton at concentrations below current water quality guidelines. *Environ. Sci. Technol.* 54, 9398–9407
37. Kaushal, S.S. *et al.* (2005) Increased salinization of fresh water in the Northeastern United States. *Proc. Natl. Acad. Sci. U. S. A.* 102, 13517–13520
38. Niedrist, G.H. *et al.* (2021) Salinization of Alpine rivers during winter months. *Environ. Sci. Pollut. Res.* 28, 7295–7306
39. Entrekin, S.A. *et al.* (2019) Multiple riparian – stream connections are predicted to change in response to salinization. *Philos. Trans. R. Soc. B* 374, 20180042
40. East, J.L. *et al.* (2017) Aquatic food-web structure along a salinized dryland river. *Freshw. Biol.* 62, 681–694
41. Brucet, S. *et al.* (2012) Effects of temperature, salinity and fish in structuring the macroinvertebrate community in shallow lakes: implications for effects of climate change. *PLoS One* 7, e30877
42. Xu, X. *et al.* (2020) Wetland ecosystem services research: a critical review. *Glob. Ecol. Conserv.* 22, e01027
43. Downing, J.A. *et al.* (2006) The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* 51, 2388–2397
44. Siddig, A.A.H. *et al.* (2020) Drought may amplify the impacts of salt pollution in pond ecosystems: an experimental exploration. *Fundam. Appl. Limnol.* 194, 1–9
45. Schuler, M.S. and Relyea, R.A. (2018) A review of the combined threats of road salts and heavy metals to freshwater systems. *Bioscience* 68, 327–335
46. Mooney, T.J. *et al.* (2020) Elevated magnesium concentrations altered freshwater assemblage structures in a mesocosm experiment. *Environ. Toxicol. Chem.* 39, 1973–1987
47. Le, T.D.H. *et al.* (2021) Invertebrate turnover along gradients of anthropogenic salinisation in rivers of two German regions. *Sci. Total Environ.* 753, 141986
48. Kaushal, S.S. *et al.* (2017) Human-accelerated weathering increases salinization, major ions, and alkalinization in fresh water across land use. *Appl. Geochem.* 83, 121–135
49. Kaushal, S.S. *et al.* (2018) Freshwater salinization syndrome on a continental scale. *Proc. Natl. Acad. Sci. U. S. A.* 115, E574–E583
50. Soucek, D.J. *et al.* (2011) Influence of water hardness and sulfate on the acute toxicity of chloride to sensitive freshwater invertebrates. *Environ. Toxicol. Chem.* 30, 930–938
51. Mount, D.R. *et al.* (1997) Statistical models to predict the toxicity of major ions to *Ceriodaphnia dubia*, *Daphnia magna* and *Pimephales promelas* (fathead minnows). *Environ. Toxicol. Chem.* 16, 2009–2019
52. Orr, S.E. *et al.* (2021) Physiological plasticity and acclimatory responses to salinity stress are ion-specific in the mayfly, *Neocloeon triangulifer*. *Environ. Pollut.* 286, 117221
53. Sala, M. *et al.* (2016) Chloride and sulphate toxicity to *Hydropsyche exocellata* (Trichoptera, Hydropsychidae): exploring intraspecific variation and sub-lethal endpoints. *Sci. Total Environ.* 566–567, 1032–1041
54. Jeremias, G. *et al.* (2018) Transgenerational inheritance of DNA hypomethylation in *Daphnia magna* in response to salinity stress. *Environ. Sci. Technol.* 52, 10114–10123

salinisation should be assessed by complementary approaches.

Which traits are affected by salinization and why? Identifying the main traits related to salinization is key in cross-continental comparisons and can give a more mechanistic understanding of freshwater salinisation impacts.

Can ecological responses measured at small temporal scales and high-frequency tools be used to detect physiological stress and other early warning signals of destabilisation of biological communities?

55. Horváth, Z. *et al.* (2016) Wind dispersal results in a gradient of dispersal limitation and environmental match among discrete aquatic habitats. *Ecography* 39, 726–732
56. Vad, C.F. *et al.* (2017) Wartime scars or reservoirs of biodiversity? The value of bomb crater ponds in aquatic conservation. *Biol. Conserv.* 209, 253–262
57. Sinclair, J.S. and Arnott, S.E. (2018) Local context and connectivity determine the response of zooplankton communities to salt contamination. *Freshw. Biol.* 63, 1273–1286
58. Huynh, M. and Gray, D.K. (2020) Can dispersal buffer against salinity-driven zooplankton community change in Great Plains' lakes? *Freshw. Biol.* 65, 337–350
59. Gutiérrez-Cánovas, C. *et al.* (2019) Do all roads lead to Rome? Exploring community trajectories in response to anthropogenic salinization and dilution of rivers. *Philos. Trans. R. Soc. B* 374, 20180009
60. Piscart, C. *et al.* (2011) Are salinity tolerances of non-native macroinvertebrates in France an indicator of potential for their translocation in a new area? *Limnologica* 41, 107–112
61. Kefford, B.J. *et al.* (2016) Salinized rivers: degraded systems or new habitats for salt-tolerant faunas? *Biol. Lett.* 12, 1–7
62. Veselý, L. *et al.* (2017) Salinity tolerance of marbled crayfish *Procambarus fallax f. virginalis*. *Knowl. Manag. Aquat. Ecosyst.* 418, 21
63. Lopatina, T. *et al.* (2021) Threshold concentrations of the road salt for adverse effects on females and resting eggs of cladoceran *Moina macrocopa*. *Aquat. Ecol.* 55, 283–297
64. Canadian Council of Ministers of the Environment (2003) Canadian water quality guidelines for the protection of aquatic life: chloride. In *Canadian Environmental Quality Guidelines*, CCME
65. Li, Y. *et al.* (2020) Toxic *Microcystis* reduces tolerance of *Daphnia* to increased chloride, and low chloride alleviates the harm of toxic *Microcystis* to *Daphnia*. *Chemosphere* 260, 127594
66. Canhoto, C. *et al.* (2021) Salt modulates plant litter decomposition in stream ecosystems. In *The Ecology of Plant Litter Decomposition in Stream Ecosystems* (Swan, C.M. *et al.*, eds), pp. 323–345, Springer International Publishing
67. Almeida Júnior, E.S. *et al.* (2020) Combined effects of freshwater salinization and leaf traits on litter decomposition. *Hydrobiologia* 847, 3427–3435
68. Gonçalves, A.L. *et al.* (2019) Leaf litter microbial decomposition in salinized streams under intermittency. *Sci. Total Environ.* 653, 1204–1212
69. Macêdo, W.V. *et al.* (2019) The effect of cations (Na+, Mg2+, and Ca2+) on the activity and structure of nitrifying and denitrifying bacterial communities. *Sci. Total Environ.* 679, 279–287
70. Wiltse, B. *et al.* (2020) A reduction in spring mixing due to road salt runoff entering Mirror Lake (Lake Placid, NY). *Lake Reserv. Manag.* 36, 109–121
71. Sibert, R.J. *et al.* (2015) Cultural meromixis: effects of road salt on the chemical stratification of an urban kettle lake. *Chem. Geol.* 395, 126–137
72. Chamberlain, S.D. *et al.* (2020) Effect of drought-induced salinization on wetland methane emissions, gross ecosystem productivity, and their interactions. *Ecosystems* 23, 675–688
73. Jeppesen, E. *et al.* (2007) Salinity induced regime shift in shallow brackish lagoons. *Ecosystems* 10, 47–57
74. Brucet, S. *et al.* (2010) Factors influencing zooplankton size structure at contrasting temperatures in coastal shallow lakes: implications for effects of climate change. *Limnol. Oceanogr.* 55, 1697–1711
75. Setubal, R.B. *et al.* (2020) Effects of functional diversity and salinization on zooplankton productivity: an experimental approach. *Hydrobiologia* 847, 2845–2862
76. Hu, Y. *et al.* (2018) Low recovery of bacterial community after an extreme salinization-desalinization cycle. *BMC Microbiol.* 18, 1–12
77. Zhao, Q. *et al.* (2020) Decadal patterns of anthropogenic salinisation in typical mountain streams in northeastern China: increased rates and sources. *Chemosphere* 246, 125789
78. Muresan, A.N. *et al.* (2020) Structural and functional responses of macroinvertebrate communities in small wetlands of the Po delta with different and variable salinity levels. *Estuar. Coast. Shelf Sci.* 238, 106726
79. Vidal, N. *et al.* (2021) Salinity shapes food webs of lakes in semiarid climate zones: a stable isotope approach. *Inland Waters* 11, 476–491
80. Velasco, J. *et al.* (2019) Effects of salinity changes on aquatic organisms in a multiple stressor context. *Philos. Trans. R. Soc. B* 374, 20180011
81. Golubkov, S.M. *et al.* (2018) Food chains and their dynamics in ecosystems of shallow lakes with different water salinities. *Russ. J. Ecol.* 49, 442–448
82. Castillo, A.M. *et al.* (2018) Exploring the effects of salinization on trophic diversity in freshwater ecosystems: a quantitative review. *Hydrobiologia* 807, 1–17
83. Hills, K.A. *et al.* (2019) Species of freshwater invertebrates that are sensitive to one saline water are mostly sensitive to another saline water but an exception exists. *Philos. Trans. R. Soc. B* 374, 20180003
84. Coldsnow, K.D. *et al.* (2017) Rapid evolution of tolerance to road salt in zooplankton. *Environ. Pollut.* 222, 367–373
85. Zhang, Y. *et al.* (2019) The responses of stream fish to the gradient of conductivity: a case study from the Taizi River, China. *Aquat. Ecosyst. Health Manag.* 22, 171–182
86. Evans, T.G. and Kültz, D. (2020) The cellular stress response in fish exposed to salinity fluctuations. *J. Exp. Zool. Part A Ecol. Integr. Physiol.* 333, 421–435
87. Ho, W.C. and Zhang, J. (2018) Evolutionary adaptations to new environments generally reverse plastic phenotypic changes. *Nat. Commun.* 9, 1–11
88. Hendry, A.P. and Green, D.M. (2017) Eco-evolutionary dynamics in cold blood. *Copeia* 105, 441–450
89. Pallarés, S. *et al.* (2016) Aquatic insects dealing with dehydration: do desiccation resistance traits differ in species with contrasting habitat preferences? *PeerJ* 2016, 1–19
90. Pallarés, S. *et al.* (2017) Aquatic insects in a multistress environment: cross-tolerance to salinity and desiccation. *J. Exp. Biol.* 220, 1277–1286
91. Latta, L.C. *et al.* (2012) The evolution of salinity tolerance in *Daphnia*: a functional genomics approach. *Ecol. Lett.* 15, 794–802
92. Medina, H. *et al.* (2007) Micro-evolution due to pollution: possible consequences for ecosystem responses to toxic stress. *Chemosphere* 67, 2105–2114
93. Des Roches, S. *et al.* (2021) Conserving intraspecific variation for nature's contributions to people. *Nat. Ecol. Evol.* 5, 574–582
94. Le, T.D.H. *et al.* (2019) Predicting current and future background ion concentrations in German surface water under climate change. *Philos. Trans. R. Soc. B Biol. Sci.* 374, 20180004
95. Haq, S. *et al.* (2018) Episodic salinization and freshwater salinization syndrome mobilize base cations, carbon, and nutrients to streams across urban regions. *Biogeochemistry* 141, 463–486
96. Moffett, E.R. *et al.* (2020) Cascading effects of freshwater salinization on plankton communities in the Sierra Nevada. *Limnol. Oceanogr. Lett.* Published online December 5, 2020. https://doi.org/10.1002/lol2.10177
97. Gutierrez, M.F. *et al.* (2018) Salinity shapes zooplankton communities and functional diversity and has complex effects on size structure in lakes. *Hydrobiologia* 813, 237–255
98. Zadereev, E.S. *et al.* (2021) The effect of salinity and nutrient load on the ecosystems of selected lakes in the South of Siberia. *J. Sib. Fed. Univ.* 14, 133–153
99. Mangadze, T. *et al.* (2017) Use of diatom communities as indicators of conductivity and ionic composition in a small austral temperate river system. *Water Air Soil Pollut.* 228, 428
100. Melero-Jiménez, I.J. *et al.* (2020) The limit of resistance to salinity in the freshwater cyanobacterium *Microcystis aeruginosa* is modulated by the rate of salinity increase. *Ecol. Evol.* 10, 5045–5055
101. Oliveira, R. *et al.* (2021) Salt pulses effects on in-stream litter processing and recovery capacity depend on substrata quality. *Sci. Total Environ.* 783, 147013
102. Tiwari, A. and Rachlin, J.W. (2018) A review of road salt ecological impacts. *Northeast. Nat.* 25, 123–142
103. Baberschke, N. *et al.* (2021) Ion-rich potash mining effluents affect sperm motility parameters of European perch, *Perca fluviatilis*, and impair early development of the common roach, *Rutilus*. *Sci. Total Environ.* 752, 141938

104. Cuthbert, R.N. *et al.* (2019) Combined impacts of warming and salinisation on trophic interactions and mortality of a specialist ephemeral wetland predator. *Freshw. Biol.* 64, 1584–1592
105. Hintz, W.D. and Relyea, R.A. (2017) A salty landscape of fear: responses of fish and zooplankton to freshwater salinization and predatory stress. *Oecologia* 185, 147–156
106. Leite, T. *et al.* (2019) Does short-term salinization of freshwater alter the behaviour of the Iberian barbel (*Luciobarbus bocagei*, Steindachner 1864)? *Sci. Total Environ.* 651, 648–655
107. Ilmain, J.K. and Searle, C.L. (2020) The effects of parasite exposure on mortality from aquatic contaminants, carbaryl and elevated salinity, in a freshwater crustacean. *J. Plankton Res.* 42, 394–397
108. Selbach, C. *et al.* (2020) Hidden parasite diversity in a European freshwater system. *Sci. Rep.* 10, 1–14
109. Bray, J.P. *et al.* (2019) Biological interactions mediate context and species-specific sensitivities to salinity. *Philos. Trans. R. Soc. B* 374, 20180020
110. Couturier, L.I.E. *et al.* (2020) State of art and best practices for fatty acid analysis in aquatic sciences. *ICES J. Mar. Sci.* 77, 2375–2395
111. Huang, J. *et al.* (2020) Microbial responses to simulated salinization and desalinization in the sediments of the Qinghai–Tibetan lakes. *Front. Microbiol.* 11, 1–15
112. Dupuis, D. *et al.* (2019) The influence of road salt on seasonal mixing, redox stratification and methane concentrations in urban kettle lakes. *Sci. Total Environ.* 661, 514–521
113. Vander Vorste, R. *et al.* (2019) Microbial and macroinvertebrate communities, but not leaf decomposition, change along a mining-induced salinity gradient. *Freshw. Biol.* 64, 671–684
114. De Castro-Català, N. *et al.* (2020) Unravelling the effects of multiple stressors on diatom and macroinvertebrate communities in European river basins using structural and functional approaches. *Sci. Total Environ.* 742, 140543
115. Piscart, C. *et al.* (2006) The role of salinity in the selection of biological traits of freshwater invertebrates. *Arch. Hydrobiol.* 166, 185–198
116. Estévez, E. *et al.* (2019) Drivers of spatio-temporal patterns of salinity in Spanish rivers: a nationwide assessment. *Philos. Trans. R. Soc. B* 374, 20180022
117. Sowa, A. *et al.* (2020) How does mining salinisation gradient affect the structure and functioning of macroinvertebrate communities? *Water Air Soil Pollut.* 231, 1–19
118. Laceby, J.P. *et al.* (2019) Chloride inputs to the North Saskatchewan River watershed: the role of road salts as a potential driver of salinization downstream of North America's northern most major city (Edmonton, Canada). *Sci. Total Environ.* 688, 1056–1068
119. Ladrera, R. *et al.* (2017) Impact of potash mining in streams: the Llobregat Basin (northeast Spain) as a case study. *J. Limnol.* 76, 343–354
120. Gorostiza, S. and Sauri, D. (2017) Dangerous assemblages: salts, trihalomethanes and endocrine disruptors in the water palimpsest of the Llobregat River, Catalonia. *Geoforum* 81, 153–162
121. Arribas, P. *et al.* (2015) Evolutionary ecology, biogeography and conservation of water beetles in Mediterranean saline ecosystems. *Limnetica* 34, 481–494
122. Pinder, A.M. *et al.* (2005) Occurrence of aquatic invertebrates of the wheatbelt region of Western Australia in relation to salinity. *Hydrobiologia* 543, 1–24
123. Baker, M.E. *et al.* (2019) Impacts of expanding impervious surface on specific conductance in urbanizing streams. *Water Resour. Res.* 55, 6482–6498
124. La Sorte, F.A. and Somveille, M. (2020) Survey completeness of a global citizen-science database of bird occurrence. *Ecography* 43, 34–43
125. Didham, R.K. *et al.* (2020) Interpreting insect declines: seven challenges and a way forward. *Insect Conserv. Divers.* 13, 103–114
126. Bhatia, D. *et al.* (2018) Physicochemical assessment of industrial textile effluents of Punjab (India). *Appl Water Sci* 8, 1–12
127. Ficker, H. *et al.* (2019) Diluting a salty soup: impact of long-lasting salt pollution on a deep Alpine lake (Traunsee, Austria) and the downside of recent recovery from salinization. *Aquat. Sci.* 81, 1–17
128. Coldsnow, K.D. *et al.* (2017) Evolution to environmental contamination ablates the circadian clock of an aquatic sentinel species. *Ecol. Evol.* 7, 10339–10349
129. Arribas, P. *et al.* (2019) Insect communities in saline waters consist of realized but not fundamental niche specialists. *Philos. Trans. R. Soc. B* 374, 20180008
130. Nadeau, C.P. and Urban, M.C. (2019) Eco-evolution on the edge during climate change. *Ecography* 42, 1280–1297
131. Urban, M.C. *et al.* (2016) Improving the forecast for biodiversity under climate change. *Science.* 353, aad8466
132. De Meester, L. *et al.* (2019) Analysing eco-evolutionary dynamics—the challenging complexity of the real world. *Funct. Ecol.* 33, 43–59
133. Valleau, R.E. *et al.* (2020) Effects of road-salt application on Cladocera assemblages in shallow Precambrian shield lakes in south-central Ontario, Canada. *Freshw. Sci.* 39, 824–836
134. Urrutia-Cordero, P. *et al.* (2021) SITES AquaNet: an open infrastructure for mesocosm experiments with high frequency sensor monitoring across lakes. *Limnol. Oceanogr. Methods* 19, 385–400
135. Giling, D.P. *et al.* (2017) Thermocline deepening boosts ecosystem metabolism: evidence from a large-scale lake enclosure experiment simulating a summer storm. *Glob. Chang. Biol.* 23, 1448–1462
136. Wilkinson, G.M. *et al.* (2018) Early warning signals precede cyanobacterial blooms in multiple whole-lake experiments. *Ecol. Monogr.* 88, 188–203
137. Olson, J.R. and Hawkins, C.P. (2017) Effects of total dissolved solids on growth and mortality predict distributions of stream macroinvertebrates. *Freshw. Biol.* 62, 779–791
138. Beermann, A.J. *et al.* (2018) Multiple-stressor effects on stream macroinvertebrate communities: a mesocosm experiment manipulating salinity, fine sediment and flow velocity. *Sci. Total Environ.* 610, 961–971
139. Hall, E.M. *et al.* (2020) Salinity stress increases the severity of *Ranavirus* epidemics in amphibian populations. *Proc. R. Soc. B* 287, 20200062
140. Tickner, D. *et al.* (2020) Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *Bioscience* 70, 330–342
141. Saccò, M. *et al.* (2021) Salt to conserve: a review on the ecology and preservation of hypersaline ecosystems. *Biol. Rev.* 96, 2828–2850
142. Silver, S. and Donini, A. (2021) Physiological responses of freshwater insects to salinity: molecular-, cellular- and organ-level studies. *J. Exp. Biol.* 224, 20