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Multiple riparian–stream connections are predicted to change in response to salinization

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Secondary freshwater salinization, a common anthropogenic alteration, has detrimental, lethal and sub-lethal effects on aquatic biota. Ions from secondary salinization can become toxic to terrestrial and aquatic organisms when exposed to salinized runoff that causes periodic high-concentration pulses. Gradual, low-level (less than 1000 ppm salinity) increases in salt concentrations are also commonly documented in regions with urbanization, agriculture, drilling and mining. Despite widespread low-level salt increases, little is known about the biological and ecological consequences in coupled riparian–stream systems. Recent research indicates lethal and even sub-lethal levels of ions can subsidize or stress microbial decomposer and macroinvertebrate detritivores that could lead to alterations of three riparian–stream pathways: (i) salinized runoff that changes microbial decomposer and macroinvertebrate detritivore and algae performance leading to changes in composition and processing of detrital pools; (ii) riparian plant salt uptake and altered litter chemistry, and litterfall for riparian and aquatic detritivores and their subsequent enrichment, stimulating decomposition rates and production of dissolved and fine organic matter; and (iii) salt consumption in salinized soils could increase riparian detritivore growth, decomposition and dissolved organic matter production. Subsidy–stress and reciprocal flows in coupled riparian–stream connections provide frameworks to identify the extent and magnitude of changes in detrital processing from salinization.

This article is part of the theme issue 'Salt in freshwaters: causes, ecological consequences and future prospects'.

1. Introduction

An increase in one of the four cations (Mg^+, Ca^+, K^+, Na^+) and anions (HCO_3^-, CO_2^{3-}, SO_2^{4-}, Cl^-) has resulted in global freshwater and watershed salinization [1–4]. Human activities that include salts added or immobilized from road deicing [5,6], urban infrastructure that leach ions [7], irrigation and fertilizers from cultivated crops [8–10], soil erosion [11–13], mining [14,15] and drilling (i.e. resource extraction, [16–19]), and rising sea levels and drought [3] result in widespread and gradual salinity increases [2,20]. Dissolved salt concentrations are measured as salinity (salt concentration (mg l^{-1})), total dissolved solids (TDS; mass of all dissolved solids (mg l^{-1})) and conductivity (ability to conduct electrical current (EC) (μS cm^{-1})). For context, major ions vary naturally by orders of magnitude across regions from local geology and precipitation but are typically under 1000 mg l^{-1} salinity (seawater—35 000 mg l^{-1} [20]). In temperate regions, road salting, urbanization, discharged treated wastewater and agriculture lead to intermediate elevated levels (100–500 mg l^{-1} TDS) and highly elevated concentrations (greater than 500 mg l^{-1} TDS [21,22]) that can have detrimental effects on aquatic organisms according to the USA and

Australian water quality regulators. Irrigation, treated and discharged wastewater, resource extraction and climate change (i.e. rising sea levels/drought) are also common causes of salinization in neotropical, arid and semi-arid regions [1,23–25]. Drought and irrigation practices can reduce stream and groundwater flow to concentrate ions [26,27]; resource extraction exposes more rock to weathering [20], adds roads or impervious surfaces near extraction sites and risks accidental release or improper treatment of disposal or produced wastewater (e.g. hydraulic fracturing of shale to get oil and gas) that can elevate salinity to intermediate and high levels in nearby freshwaters [16,18,28]. In fact, chloride concentrations across much of the world surpass or are predicted to surpass the only aquatic life chloride criterion of 120 (Canada [29]) and 230 mg l^{-1} Cl (USA [1,30]).

Salts are essential biochemical micronutrients used for cellular signalling and energy metabolism for microbes and invertebrate animals [31,32]. Salt micronutrients occur in very low concentrations in autotrophs and can limit consumer growth [33]. However, salinization (i.e. increasing salt concentrations) can impair freshwater biological communities via sub-lethal (e.g. growth, reproductive and feeding and assimilation changes) and lethal effects [34]. Excess ions, often 2–4 orders of magnitude above ambient concentrations or 2000 µS cm^{-1} EC (or approx. 1280 mg l^{-1} TDS) that result in ion and osmotic imbalances between microbes and macroinvertebrates and their environment [35]. This ion stress could result in mortality from the increased energy expenditure and investment in morphological structures that are required to maintain homeostasis [23,36–39]. Whereas aquatic and terrestrial fungal activity may not show measureable changes until intermediate or highly elevated salinities occur and thus buffer ecosystem effects [40–42]. However, the mechanisms responsible for the biological response remain uncertain [35,43,44] and ion concentrations below those that result in species loss (e.g. 192 mg l^{-1} TDS, [45]) can still fail to be protective of aquatic life by changing organism performance (i.e. growth, emergence and resource consumption) and associated ecosystem processes [34,46,47]. A better understanding of how sub-lethal increases in ion concentrations impact freshwater biota, communities and ecosystem function is needed [46]. If sub-lethal salinization changes freshwater productivity or other functions, then ion, ion mixtures and concentration-specific management protocols may need to be re-evaluated and new standards set (e.g. [48]).

Biological responses to watershed salinization can include more salty soils [49], altered aquatic and terrestrial detritivore activity [50,51], changes in or mortality of riparian plant communities [15,52] and greater mortality rates of terrestrial and aquatic plants and animals into the detrital pool [11,53,54]. Because over 95% of all fixed carbon in a watershed becomes part of the detrital pool (brown web) changes in riparian soil and vegetation alter aquatic detrital processing [55,56]. Beyond leaves, detritus includes dead wood, fine particulate organic matter (FPOM) and dissolved organic matter (DOM) and dead organisms all colonized by fungi, bacteria and often algae. Riparian detrital inputs to adjacent aquatic systems are impacted by terrestrial microbial decomposer (bacterial and fungal) and macroinvertebrate detritivore (i.e. soil macrofauna and shredders) activity and plant chemistry [57]. In aquatic systems, riparian inputs, retention and microbial decomposers (i.e. fungi and bacteria) and detritivore physiology (i.e. growth, respiration and osmoregulation processes) mediate decomposition rates [58–60]. Microbial-conditioned detritus (i.e. leaves, wood and FPOM) is often the dominant energy source for aquatic detritivores. These same detritivores are sensitive to oxygen and ion changes; thus, detrital-based ecosystems are predicted to exhibit measurable changes from salinization [50,61–63]. If increased low-level salinization changes the quantity and quality of detritus by reducing fungal and bacterial enzymatic activity and production, or by changing microbial community identity, then changes would probably occur in the macroinvertebrate detritivore consumption and assimilation [64]. Subsequent changes in processing rates and possible shifts in community composition could have measurable effects on detrital processes that support secondary production in downstream [65,66] and riparian habitats through the transformation and transfer of energy across riparian and stream boundaries (i.e. reciprocal flows [67,68]). Cumulatively, riparian–stream changes could alter energy flow that supports watershed diversity and production.

2. Predicted detrital alterations from salinization

We review how elevated common salt concentrations could change key detrital linkages in and across the riparian–stream interface, although most pathways have not been tested and even fewer linkages among pathways have been established. Three main pathways (figure 1) predicted to change with salinization are: pathway 1 (PW1) salt runoff changes microbial decomposer [41,62] and macroinvertebrate detritivore [50,69] and algae [70] performance that could lead to changes in the composition and processing rates of detrital pools; pathway 2 (PW2) riparian plant salt uptake [71], altered litter chemistry [72] and litterfall for riparian and aquatic detritivores and their subsequent enrichment (e.g. senesced leaves, insects or corpses) could stimulate decomposition rates and production of DOM and FPOM; and pathway 3 (PW3) direct consumption of salts in salinized soils could increase riparian detritivore growth [51], decomposition and DOM production [73].

(a) Pathway 1: direct salt inputs and salty runoff could alter the osmoregulation of aquatic organisms to change microbial decomposers and detritivore growth

Direct inputs (e.g. waste water treatment) and runoff with elevated salts (*direct input and runoff (1)*) could increase or decrease the energy required for *osmoregulation (2)* (figure 1; PW1). For example, low-level increases in ions in freshwater result in a less hypotonic environment for ion-limited freshwater organisms, thus reducing energy expenditures associated with osmoregulation [23,38,43]. However, once ion limitations are met and external salt inputs continue to rise, more energy is predicted to go towards osmoregulation, which could reduce biological performance down the falling limb of the perturbation gradient [74].

When salts enter the riparian zone, they leach from riparian soils and enter stream systems to increase water salinity, EC and TDS values [75]. The detrital responses to salinization in streams are not well studied [46,50,76,77]. Based on the few studies conducted, relatively high levels of water salinization (greater than 500 mg l^{-1} TDS) may have lethal or sub-lethal detrimental effects on fungi [41,78–80] and bacteria [23] that

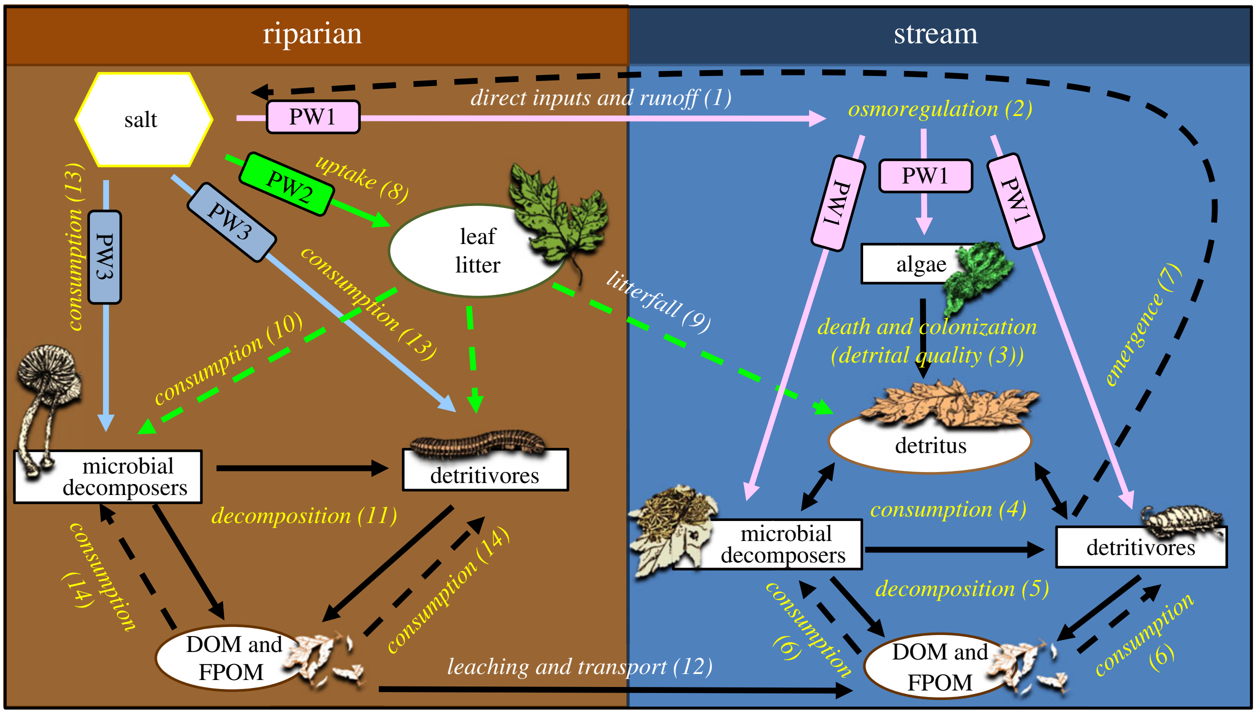

Figure 1. Riparian–stream interactions that could be altered by salt additions. Direct pathways are solid lines, indirect pathways are dashed, shapes are pools and arrows are processes. Hexagons represent inorganic salt pools. Circles represent detrital pools. Squares represent living biotic pools. White text represents abiotic processes, yellow text represents biotic processes. Numbers next to text are for reference to the specific processes connecting pools. Pathway 1 (PW1: pink arrows) demonstrates how salts can impact stream detrital processing through direct salt inputs and runoff (*runoff (1)*) and subsequent increased stream salinity that may impact osmoregulation of aquatic biota (microbial decomposers, detritivores and algae) (*osmoregulation (2)*); the quality of detritus (*detrital quality (3)*), aquatic biota consumption of detritus and associated microbial decomposers and algae (*consumption (4)*) also interact to mediate the amount and quality of detritus (double-headed arrows). Decomposition of detritus (*decomposition (5)*) changes the quality and quantity of fine particulate (FPOM) and dissolved organic matter (DOM) that is consumed (6) by microbial decomposers and detritivores to then influence the timing and emergence (7) of aquatic insects. Pathway 2 (PW2: green arrows) demonstrates how salts may indirectly impact detrital processing from plant uptake of salt in riparian systems (*uptake (8)*). The resulting salt-enriched plant tissue and leaf litterfall (*litterfall (9)*) are then deposited to aquatic or terrestrial systems, which impact terrestrial biota (microbial decomposers and detritivores) by altering consumption (*consumption (10)*) and decomposition in riparian systems (*decomposition (11)*). Altered consumption and decomposition of leaf litter changes the quantity and quality of FPOM and DOM that can enter stream systems (*leaching & transport (12)*). Pathway 3 (PW3: blue arrows) demonstrates how salt can directly impact terrestrial detrital processing by increasing salt consumption by microbial decomposers and detritivores (*consumption (13)*) and then alters their growth and decomposition (*decomposition (14)*) and the subsequent generation and quantity of FPOM and DOM input to riparian and stream systems (*leaching and transport (12)*) or consumption by terrestrial microbial decomposers and detritivores (*consumption 14*). Lastly, these three pathways may ultimately impact microbial decomposers and detritivore emergence timing and quantity (*emergence (7)*) that generates positive or negative feedback loops between riparian and stream systems. Drawings by Natalie Clay.

could alter diversity and function in currently unpredictable ways [41,81]. Rising salinity can increase fungal sporulation supporting the hypothesis that fungi allocate more energy to reproduction in the presence of some salts, in this case HCO_3^- [82]. Conversely, rising salinity from NaCl may also induce fungal sporulation for some species and a decline in extracellular cellulolytic activity in others [41,83]. The effects of low-level salinization are even less understood [69]. If salinization is lethal to microbial decomposers (e.g. greater than 2000 mg l^{-1} salinity, [84]), then detritivores most likely also suffer from ion stress, thus increasing the amount, changing the composition of and reducing the quality of the detrital pool, for example, from more allochthonous to more autochthonous (*detrital quality (3)*). Detrital quality, defined by the interactions among chemical and microbial colonization and composition and detritivores (figure 1, double arrows), would decline resulting in more recalcitrant leaf litter and possibly harmful blue-green algae [85], making detritus less palatable and nutritious for detritivores and thus indirectly slowing *consumption* (*4*) and *decomposition* (*5*) [60,86]. Severe soil salinization that results in the decline in riparian vegetation would reduce detrital inputs and increase light in the stream channel. Together, algae would probably increase and serve as the basis of consumer production [87]. In naturally saline streams, diatoms and cyanobacteria that dominate as producers tend to be less palatable to the aquatic consumer and that can reduce trophic diversity [87,88].

Algae also influence detrital quality and quantity because they occur along with fungi and bacteria in biofilms on most substrates that when exposed to rising salts could alter decomposition by stimulating microbial enzymatic activity [89–92]. Algal photosynthetic activity can be reduced by elevated salt concentrations (e.g. approx. 14 000 mg Na l^{-1}), and respiration can decline at low salt concentrations (3–14 mg Na l^{-1}) [70]. Moderate salinity levels (260–1000 mg l^{-1}) can promote algal growth and even harmful algal blooms [85,93,94], but higher concentrations (e.g. 2260 mg l^{-1}) may induce osmotic stress and reduce growth [84]. Microbial responses to salinization may vary taxonomically, *Chlamydamonas reinhardtii*, display reduced cell density, growth and photosynthesis when exposed to extremely high NaCl (1160–17 400 g l^{-1}) and even greater declines in performance when exposed to $NaHCO_3$ (840–12 600 g l^{-1}) [95]. By contrast, some green algae, cyanobacteria and fungi can respond to osmotic stress, induced at much lower concentrations, by increasing osmoprotective carbohydrates. For example, at NaCl treatments above 2299 mg l^{-1} [96,97] less diverse and more saline-tolerant diatom communities shifted to or were correlated with greater salinity [10,98]. As with other biota, microbes differ in their ability to adapt to salinity, so allocation to reproduction, growth and community composition and/or nutritional element composition are expected to change with ion type, concentrations and their interactions [99,100]. Natural and experimental gradients in the concentrations of several ions in freshwaters are needed to predict and test these changes [101].

Macroinvertebrate detritivores selectively feed on detrital biofilms, particularly different algal [102] and fungal species [103,104] that often confer lower litter carbon : nitrogen : phosphorus (C : N : P); therefore, we predict lower detritivore consumption of less palatable food resources for growth when salts reduce biofilm activity. Litter type could mediate the magnitude of the functional response; more labile litter could support even greater alterations in detrital processing [81]. Because decomposition generates FPOM and DOM production, resource recycling (*consumption* (*6*)) would also decline [105,106], cumulatively causing a decline in secondary production [61,107] and insect *emergence (7)* [108,109]. Lethal and sub-lethal salt concentrations may result in an aquatic community indicative of impaired aquatic life and will surely result in a limited capacity to process organic matter [110].

However, salt concentrations that do not induce osmotic stress could induce a subsidy response that stimulates detrital processing up to a threshold [74]. Growth optima, which can provide a mechanistic explanation for subsidy–stress dynamics, are observed for both environmental conditions (e.g. temperature), and elemental resources [74,111,112]. If the presence of salt optima, whereby energy expenditure for osmoregulation is relieved, can be predicted across phylogeny, salt type growth optima would provide a needed framework to predict microbial population, community and ecosystem responses to rising salts across concentration gradients. If microbial decomposers are tolerant to rising salt concentrations, but the same concentrations reduce detritivore growth and abundance, then *consumption (4)* may or may not decline at the system-level and the impacts to the detrital processing could increase from greater microbial decomposer activity [41] or decline from a loss of a dominant detritivore species or altered biotic interactions [100,113]. Mounting evidence suggests that even relatively low-level increases at similar concentrations across different salt types can alter macroinvertebrate performance and has even been measured as changes in macroinvertebrate communities and associated traits [114,115]. Therefore, low-level salt increases to relatively low concentrations not only directly affect macroinvertebrate community structure indicative of impaired aquatic life [116,117], but rises could also lead to altered detrital processing [50,98,118].

How rising salinities affect freshwater systems have been tested in micro/mesocosms with manipulated water salt concentrations (e.g. [69,119–123]), and/or by measuring salts in stream observational field studies (e.g. [14,50,114,124,125]). These studies demonstrate four principle results for how salinization could alter detrital processing. First, microbial and macroinvertebrate detritivores can display negative or positive growth responses depending on ion concentrations, rate of increase and identity (PW1, *osmoregulation* (2)). *Detrital quality (3)* could then change to alter the microbial decomposer and detritivore *consumption* (*4*) [50,69]. Second, fungi and macroinvertebrates display variable thresholds at which they show signs of stress [23]. Third, microbial biofilms change. Finally, algae bloom in some salts and not others. Changes in consumption and growth would probably alter overall *decomposition (5)* depending on the magnitude and directional responses by the microbial decomposers and detritivores.

(b) Pathway 2: riparian plants can become salt-enriched and may change the quality and quantity of detrital inputs for terrestrial and aquatic detritivores

Ion identity and concentration in riparian soils may change the quantity and quality of organic matter available to the riparian detritivores and transported between terrestrial and stream systems (figure 1, PW2). At sub-lethal salt levels, terrestrial plants can incorporate ions from soil into their leaf vacuoles where enough storage can change live and abscised leaf tissue chemistry (*uptake* (*8*), figure 2) [126–128]. The majority of the limited research is on how soil Na content alters plant chemistry under controlled laboratory conditions, natural gradients from coastlines [129,130] or salted roads [71], and agriculture-related [131] research. These studies demonstrate that salinization can, in some cases, drastically increase plant tissue Na content, which is typically positively correlated with soil salt levels, and the magnitude of plant Na change is highly context- and species-specific (figure 2; electronic supplementary material, table S1 and citations therein). Despite the inextricable link between riparian and stream systems, relatively few studies have examined riparian salinization impacts on plant chemistry. The exceptions are studies of halophytes like *Tamarix* or riparian plants for phytoremediation of toxic soils [49,132]. However, plants exposed to low-level salt increases often have reduced photosynthesis and biomass, higher rates of senescent leaves and altered timing of leaf dropping [126,128]. Together, these changes in *litterfall (9)* quantity and deposition to aquatic systems may decrease aquatic detritivore diversity and production to alter stream 'brown webs' [62,133].

Salt-enriched leaves may alter microbial decomposers and detritivore activity in both riparian and stream systems through altered detrital quality (*litterfall (9)*). Salt is often limiting for inland terrestrial plant consumers (including detritivores) [31]. In particular, Na tends to limit heterotrophic metabolic function, but not plant function because most plants do not require Na for growth and reproduction [134,135]. Terrestrial heterotrophs concentrate Na 10–100 times more than plants and must constantly balance Na intake with loss [134,136]. Consequently, even small increases in Na can stimulate decomposition in inland or Na-limited environments [51,137,138]. By contrast, too much salt reduces plant photosynthesis that means fewer carbohydrates relative to leaf tissue biomass and earlier abscission. Thus, Na-enriched riparian leaves could stimulate or suppress *consumption (10)* by terrestrial microbial decomposers, especially fungi, detritivores and *decomposition (11)* to then change DOM and FPOM available for heterotrophic recycling (*consumption (14)*) and *leaching and transport (12)* to streams [73,127,133,139].

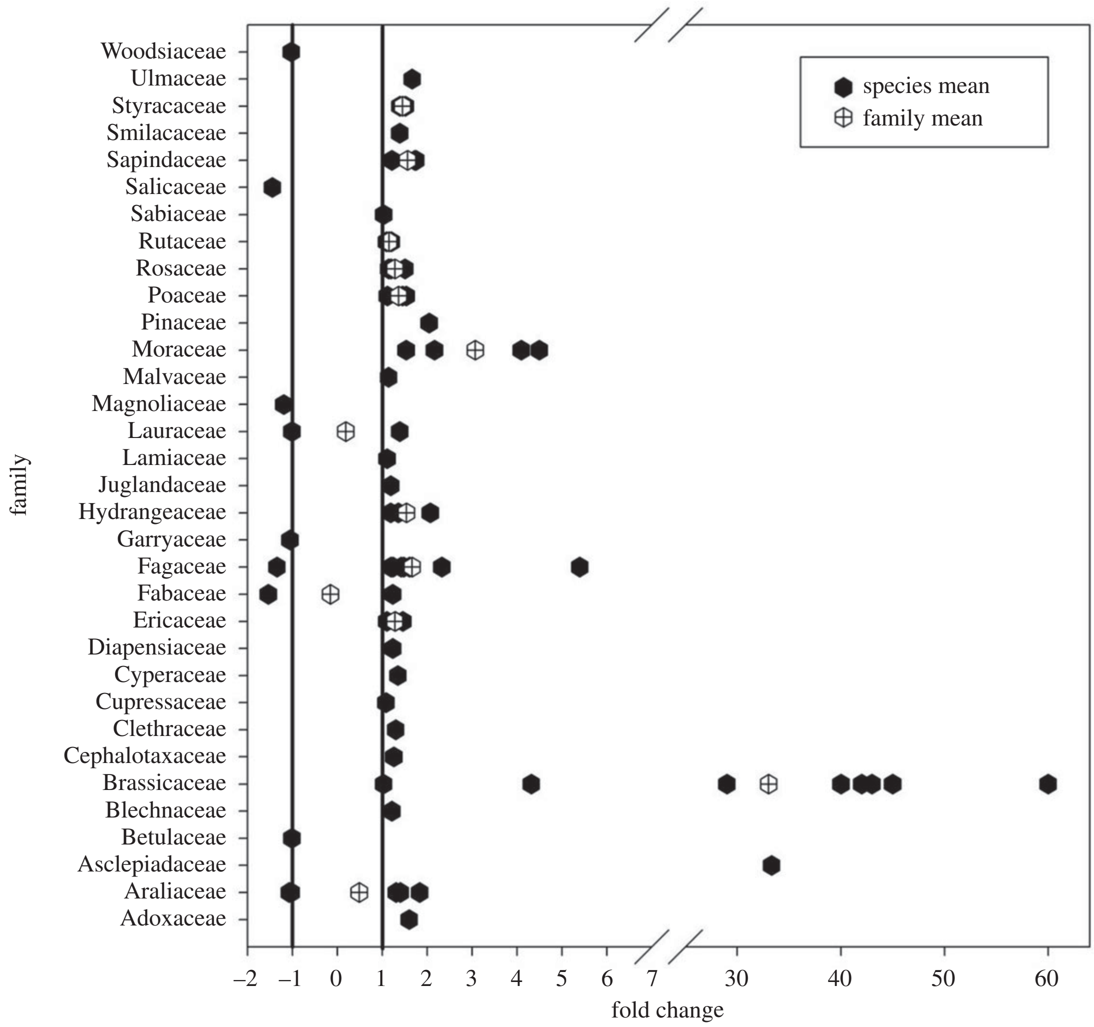

Figure 2. Mean fold change of Na leaf concentration for plant species (closed hexagons) and plant families (open-crossed hexagons). Fold change was calculated based on mean Na leaf concentrations from plants in salty (greater than 100 km from the coast or salted road or experimental salt addition treatments) divided by non-salty (less than 100 km or controls) plant Na leaf concentrations (reversed for negative values). Values of 1 indicate no change. Positive values indicate plants in saltier areas had increased Na leaf content relative to non-salty areas. Negative values indicate plants in saltier areas had decreased Na leaf content relative to non-salty areas. Family mean values between −1 and 1 indicate no consistent trend. Note scale on *x*-axis changes after the break. Data and sources are in the electronic supplementary material, table S1.

DOM includes all organic compounds passing through a 0.45 µm filter like carbohydrates, amino acids and humic substances and dissolved organic carbon (DOC) is a significant portion of DOM [140]. DOC can constitute up to 98% of total organic matter inputs in stream systems [141] with the majority derived from riparian soils and riparian detritus [142]. Inputs depend on land use and cover, where typically more forested streams, streams close to wetlands, or water treatment facilities have higher DOC than urban or agricultural streams [143,144]. Riparian-derived DOC has increased in freshwater systems in the northern hemisphere since the early 1990s where road salting is prevalent and increased DOC can negatively impact freshwater water quality by decreasing transparency, increasing acidity and transporting metals [145–147]. However, DOC can also provide a nutrient source for freshwater microbial decomposers and detritivores, with bacteria and fungi benefiting in particular [61,148]. Increased watershed salinization may be responsible, in part, for rising riverine DOC from organic matter leaching from watershed soils [73,139,149]. However, the mechanisms driving increased DOC remains poorly understood [140,150].

Salt-enriched leaves may enter stream systems through *litterfall (9)* and alter the aquatic microbial and macroinvertebrate detritivore community composition, production and decomposition rates. Terrestrial–aquatic altered connections and reciprocal flows from salt-enriched leaves and salt-enriched insects represent an overlooked pathway by which stream ecosystems may change from rising salts (*emergence (7)*). Probably, the natural co-occurrence of salty leaves (PW2) with low-level increases in stream salinization (PW1) will have synergistic interactions on algal growth, *death and colonization (3)* and microbial decomposers and detritivores through patterns of *consumption (4)*, *(6)* to change *decomposition (5)* and insect production that will alter reciprocal flows *(emergence (7))*.

(c) Pathway 3: salts can directly stimulate microbial decomposer and detritivore growth in riparian areas to alter riparian carbon cycling

Soil salts can be consumed by terrestrial microbial decomposers and detritivores (*consumption* ((*13*)) [33]. Increased salinization of riparian soils may alter the DOM and FPOM quantity and quality entering streams (figure 1, PW3). If salt additions stimulate microbial decomposer and detritivore activity leading to faster *decomposition (11)*, then riparian–stream detrital linkages are also probably altered from greater DOM and FPOM production, recycling (*consumption 14*) and *leaching* and *transport (12)*. Therefore, increased riparian–stream salinization could increase the quantity of organic matter transported to streams and may be responsible, in part, for rising DOC in freshwater ecosystems [133].

3. Future directions

We present three conceptual frameworks for further understanding the direct and indirect pathways by which salinization may change 'brown webs' (figure 1): subsidy–stress [74], reciprocal flows [67] and more broadly, riparian–stream connections [108]. Subsidy–stress responses were predicted for biotic pools in terrestrial and aquatic systems; yet, salt concentration thresholds for autotrophs and heterotrophs are currently unavailable. Subsidy–stress thresholds would provide predictive directional changes in detrital quality, quantity and decomposition and subsequent fluxes within and across ecosystem boundaries. The contribution of and controls on reciprocal energy and matter flowing from riparian to stream [151] and stream to riparian [152] areas has been documented in 'brown webs' under limited environmental context.

Even less is known about how contaminants will change the composition and magnitude of energy and nutrient flux across boundaries (e.g. [153–155]). Reciprocal flows occur among riparian–stream connections (upstream–downstream, surface–hyporheic–groundwater, riparian–stream–wetland) that connect the watershed with currencies measured as elemental and organism flux. Virtually nothing is known about how these watershed connections will change from salinization (be it sub-lethal or lethal), despite the global potential for shifts in riparian and stream autotroph composition and production and detrital processing. Interdisciplinary research teams will have to work at multiple spatial scales and across large geographical gradients of salt deposition, land use and climate to fully address how salinization is altering 'brown webs'. At the watershed scale, multiple interacting stressors are the norm [156,157], where riparian composition and nutrients from fertilizers are interacting with salts in soils and freshwater, and rising water temperatures and altered hydrology all act to change detrital processing. Initial unravelling of some of these interactions has already resulted in unexpected synergistic effects driven by detrital composition and salt concentrations and identity in riparian [49], stream [14] and wetland communities [158]. We provide here a framework to support future studies.

Data accessibility. Data are available as part of the electronic supplementary material.

Competing interests. We declare we have no competing interests.

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