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MINI REVIEW

Cation responses to global changes alter ecological processes in ombrotrophic systems

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Abstract

1. Ombrotrophic bogs, which store large amounts of carbon as peat, receive all their mineral nutrition through deposition. This limited nutrient input means they are particularly sensitive to local and global changes that displace vital cations.
2. We review how acid deposition drives cation displacement (i.e. sodium, magnesium, potassium and calcium) in ombrotrophic bogs. We then synthesise the literature across scales of ecological organisation on the role of cation availability in shaping plant stoichiometry and function, community dynamics and ecosystem function.
3. Acid deposition from industrialisation drives declines in cation concentrations in peat, and although recovery is underway, cations remain depleted in acid-affected areas. Cation depletion could cause decreased *Sphagnum* spp. growth and decreased plant diversity. There is higher uncertainty in how cations contribute to ecosystem processes. Future trends will likely be dictated by climate change-driven increases in marine deposition, which will increase cation concentrations in maritime bogs and alter ecological processes across scales.
4. *Synthesis*. There is limited yet compelling evidence that cation availability is a key determinant of ecological processes across scales. We propose a research agenda to understand how past and future changes in cation availability may alter carbon cycling in bogs and explore potential management.

KEYWORDS
cation cycling, community, ombrotrophic systems, peat, *Sphagnum*, stoichiometry

1 | INTRODUCTION

All life requires a mixture of roughly 25 elements that perform different biochemical functions (da Silva & Williams, 2001; Sterner & Elser, 2002). The absence of any one of these elements can reduce organismal performance and alter ecosystem function (Kaspari, 2021; Kaspari & Powers, 2016). Each element has a specific geography, where its abundance is determined by geology, climate, deposition,

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biological fixation and other processes (Kaspari & Powers, 2016). These specific geographies overlap to create mosaics across ecosystems with multi-elemental surpluses and shortfalls (Kaspari, 2021; Kaspari & Powers, 2016). This raises questions about life on the extremities of these mosaics, where there is little available mineral nutrition for biological functioning (Verboom et al., 2017).

Ombrotrophic bogs are one such 'extreme' environment, where all their nutrition comes from deposition and recirculation because there is no access to the underlying geology and mineral soil (Bragazza et al., 2004; Wang & Moore, 2014). Water inundation and anoxia, combined with the low-nutrient content of bogs, restrict decomposition more than it limits production by autotrophs (Mander et al., 2025), which over thousands of years leads to massive amounts of stored carbon (Dargie et al., 2017; Yu, 2012). This makes bogs highly sensitive to nutrient and acid deposition. For instance, peatlands had higher decomposition rates and CO_2 release along a nitrogen (N) deposition gradient across Europe because N stimulated microbial enzyme activity (Bragazza et al., 2006). However, low levels of N can stimulate productivity (Turunen et al., 2004), while higher levels can shift vegetation communities away from peat-forming species (Evans et al., 2014), suggesting that effects depend on critical load thresholds. While anthropogenic deposition has been reduced in some regions, the legacy and continued deposition in peatlands across the world continue to alter biodiversity (Ritson & Lindsay, 2023) and biogeochemical cycling (Chen et al., 2020).

Since bogs begin with so little nutrition, imbalances driven by higher nitrogen, sulphate and other acidifying compounds will displace essential cations and likely play an outsized role in ecological processes (Sanger et al., 1996). For instance, the UK has been home to one of the largest 'unintentional experiments with terrestrial ecosystems' (Lee, 1998) caused by pollution from coal burning during the Industrial Revolution, with the Peak District National Park suffering the worst sulphur, nitrogen and heavy metal deposition. This caused the virtual disappearance of *Sphagnum* moss species, which form peat, and decreased plant biodiversity across much of the Peak District from the mid-19th century onwards, as sulphate loads increased and pH decreased on the peat (Ritson & Lindsay, 2023). This acidification has altered peatland biogeochemistry across much of the globe, leading to lowered dissolved organic carbon fluxes due to solubility controls (Evans et al., 2011, 2012; Monteith et al., 2007). Outside of peat systems, past work on cation displacement from acid is generally unequivocal. For instance, an N-deposition simulation experiment in Slovakian alpine grasslands with a 150 kg/ha/year addition gradient caused declines in soil calcium (Ca), magnesium (Mg), potassium (K) and molybdenum (Mn; Bowman et al., 2008). A meta-analysis found that Mg, K and Ca decline in both forests and grasslands with nitrogen deposition/fertilisation that acidifies the soil (Tian & Niu, 2015). Although the impact of acid deposition on the dissolved organic carbon balance of peatlands is understood, the ecological effects of leached Ca, Mg, Na (sodium) and K through acid deposition are less well studied.

Cation loss could alter the vegetation community and function of peatlands because they perform vital roles despite their relatively low abundance in tissues (Kaspari, 2021). To start, Ca is tied to oxygen production in the light-harvesting steps of photosynthesis, integral to cell wall structural integrity in plants, and essential for intercellular communication and osmoregulatory function of organisms (da Silva & Williams, 2001; Kaspari, 2021; White & Broadley, 2003). Magnesium is the centre of chlorophyll antennae, where electrons are ripped from water molecules in photosynthetic light reactions, essential in phosphate metabolism, and a cofactor for Rubisco in the carbon fixation steps of photosynthesis (da Silva & Williams, 2001; Skinner, 2005; Verbruggen & Hermans, 2013). Potassium, after N, is the next most abundant non-C, -H, -O element in photosynthetic tissues and is a key electrolyte for osmoregulation in all of life (da Silva & Williams, 2001; Sardans & Peñuelas, 2015). Sodium is an 'uncoupled' nutrient (Lynn et al., 2023) crucial to the osmoregulation, muscular and neural function of animals (and potentially fungi; Scharnagl et al., 2017) but is actively expelled by most plant species (da Silva & Williams, 2001; Kaspari, 2020), suggesting Na bolsters animal populations while stressing most plant species. Despite their crucial role in maintaining organismal growth and homeostasis, cations and micronutrients, generally, have received much less attention than C, N and P in past ecological research (Kaspari, 2021).

Here, we review the literature on how cations shape the biodiversity and ecosystem functioning (i.e. primarily carbon cycling) of ombrotrophic peatlands. We argue that cation availability may have a disproportionate influence in ombrotrophic systems because their acidity, high cation exchange capacity (CEC) of the keystone *Sphagnum* spp., hydrological disconnection from the bedrock and reliance on deposition leave ombrotrophic systems on the extreme low end of cation availability in terrestrial systems. This could make cation availability a potent constraint on physiological processes (e.g. photosynthesis and microbial respiration) that scale up to alter community patterns and ecosystem processes. We review the evidence for this general hypothesis from the literature and highlight how past, present and future global changes alter the cation profile of these important systems (Figure 1). We propose novel research directions that will fill key research gaps around cation limitation in peatlands.

2 | PEAT, ACID DEPOSITION AND CATIONS

Cation dynamics in peat are highly dependent on binding affinities and their leaching kinetics. *Sphagnum* peats have high CEE and bind divalent cations (e.g. Mg^{2+} and Ca^{2+}) more strongly than monovalent cations (e.g. K^+ and Na^+; Brehm, 1968; Clymo, 1963). This translates to the divalent cations leaching at a higher rate in response to acidification compared with monovalent cations because they occupy more of the exchange sites (Evans et al., 2008).

Cation concentration characteristics are not completely distinct between peatlands categorised as bogs or fens. They differ in that ombrotrophic systems (bogs) receive all their cations as wet and dry deposition, while fens also receive cations from

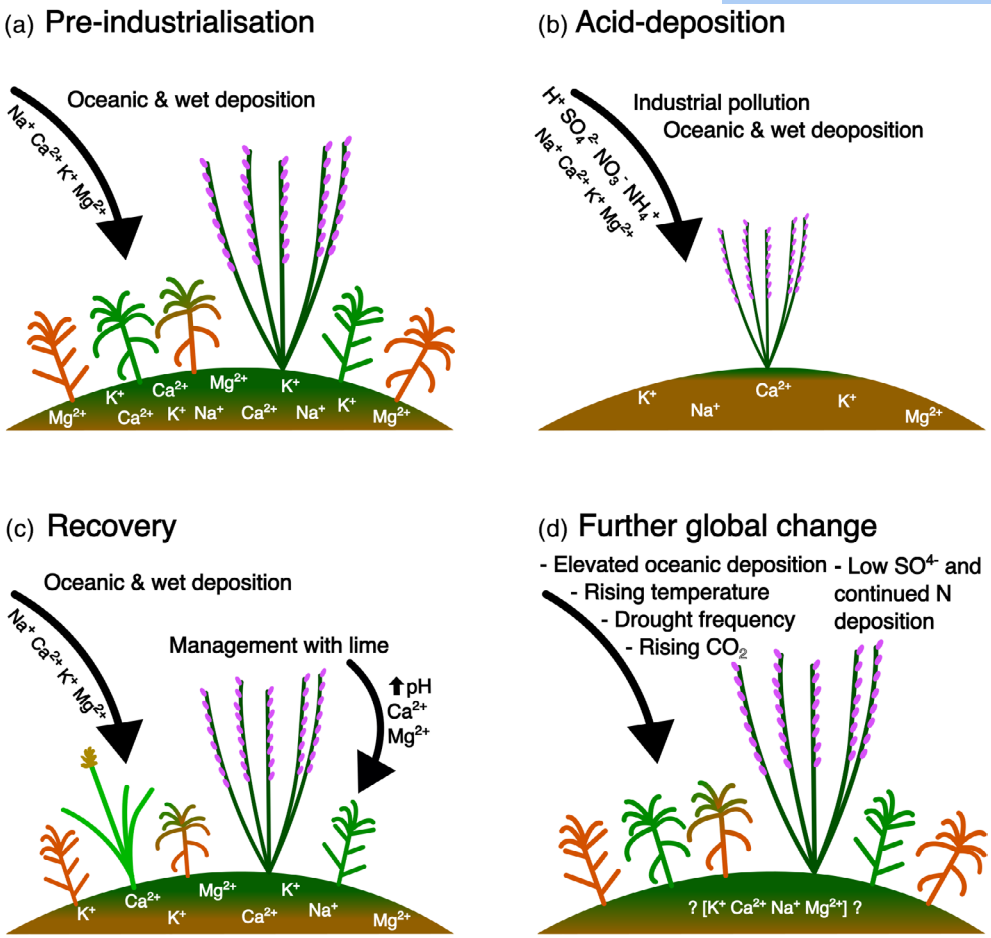

FIGURE 1 Past, present and future of ombrotrophic bog diversity and ecosystem function with cation fluctuations: (a) is a 'pristine' bog before industrialisation receiving cations through deposition that replenishes cation concentrations in the peat, which likely maintains healthy peat production (i.e. greener than brown), a diverse community of *Sphagnum* spp. (represented by different shapes and colours) and healthy Ericaceous shrubs; (b) shows how acid deposition from industrial pollution leads to cation leaching that causes reduced or the cessation of peat production (i.e. browner), the elimination of *Sphagnum* spp. (pictured) in the extreme or at least lower *Sphagnum* spp. diversity and growth, and reduced shrub size or, in the extreme, the complete loss of vascular plants; (c) represents cation recovery as cation deposition and liming management (mainly $CaCO_3$ that often contains small amounts of Mg^{2+}) balances out past effects of acid deposition, leading to cation accumulation in the peat, restoration of peat production, more *Sphagnum* diversity and growth, more herbaceous species diversity (e.g. graminoids) and shrub recovery; and finally, (d) highlights the unknown indirect effects that further global changes will have on how cation availability contributes to the processes described in this review, beyond the more studied effects of these global changes. Peat cation concentrations are figurative and do not represent hypothesised stoichiometric ratios that vary from system to system.

weathering via groundwater or riverine transport. This leads to some overlap in cation concentrations observed in peat systems, depending on the amount of deposition received and the local geology, with 'poor fens' bridging between fens and true ombrotrophic bogs. For example, in their review of cation concentrations in ombrotrophic systems in the northern hemisphere, Bourbonniere (2009) found that Ca concentrations in pore waters and peatland pools varied from 0.06 to 9.8 mg/L in bogs, 0.1 to 16 mg/L in poor fens and 1.4 to 428 mg/L in rich fens, whereas Mg varied between 0.04 and 2.8 mg/L in bogs, 0.16 and 4.6 mg/L in poor fens and 0.27 and 125 mg/L in rich fens.

Beyond differences in mineral weathering from bogs to fens, the main source of cations is deposition, particularly in maritime regions where sea spray deposition leads to a higher Mg/Ca ratio and pH closer to the sea (Sjörs & Gunnarsson, 2002). This gradient can be large, where Na and Mg concentrations in an oceanic bog were triple those of a continental site in Canada (Shotyk et al., 1990), and Na, Ca and Mg levels were elevated in oceanic bogs compared with their continental counterparts in Scandinavia (Damman, 1978). Higher Na and Mg in surface waters of oceanic sites correspond to higher concentrations in *Sphagnum* mosses (Maimer et al., 1992). Comparing sites at the extreme ends of the maritime versus continental continuum, Gorham and Cragg (1960) found that peat pools on the Falkland Islands with high marine deposition had two orders of magnitude higher cation concentrations when compared to continental bogs in the Sudeten Mountains in Poland.

Peat cations have dramatically decreased during the post-industrial period in acid deposition-affected areas (Sanger et al., 1996; Skiba et al., 1989). This consequently lowers P and Mg leaf concentrations in vegetation from acid-affected peats (Sanger

et al., 1996). Areas with lower acid deposition, such as Siberia and northern Finland, comparatively have Ca and Mg concentrations that are roughly constant down the peat profile (Kaila & Kivekäs, 1956; Stepanova et al., 2015). However, these studies have typically looked at cation concentrations at low-depth resolutions across full cores, rather than focusing on more recent processes in the last ~150 years when leaching occurred at acid-affected sites. For instance, the Holcroft Moss raised bog in the UK (Figure 2) has a section between 50 and 150 mm depth with lower Mg concentration, counter to findings in Scandinavia, which showed minimal differences between the peat surface concentration and the 0–200 mm depth (Damman, 1978). This suggests higher Mg leaching during this period, though movement within the peat may also contribute to this effect.

Acid deposition has recently decreased with more regulation and reduction in coal-burning sulphate pollution from the 1970s onwards. Soils are recovering from acidification, albeit slowly (Figure 1; e.g. Akselsson et al., 2013), with reversals in pH and leaching during drought-induced acidification (Tipping et al., 2003). This has reduced cation leaching from peat systems. For example, a long-term UK water monitoring network around the Etherow river, which largely drains an ombrotrophic blanket bog in the Peak District National Park, shows Ca^{2+} and Mg^{2+} concentrations have approximately halved since the 1980s (Monteith et al., 2022). This suggests that acid deposition cessation has led to the recovery of peat's CEE. A recovery to pre-industrial cation concentrations in the upper peats and plant matter may be underway, yet we know little about how this recovery relates to the community assembly and biogeochemical processes of the system. This is particularly pertinent as some restoration practices involve adding calcium hydroxide (i.e. liming) to raise the pH of the system to speed acidification recovery (Andersen et al., 2017; Worrall et al., 2011). More recently, some studies have explored the potential of amendments such as iron and calcium sulphate to suppress methane emissions from rewetted peatlands (e.g. Jeewani et al., 2025). These restoration practices deliberately favour fast-growing graminoids to stabilise eroding bare peat. Whether bryophytes can thrive in these landscapes once the chemistry has been altered is still unclear (Ritson & Lindsay, 2023). In addition to the intended calcium addition, the calcium hydroxide often contains magnesium hydroxide impurity (Stimson et al., 2017), which could accelerate the recovery of Mg to pre-industrial concentrations, or beyond, creating another 'unintended experiment' in these landscapes.

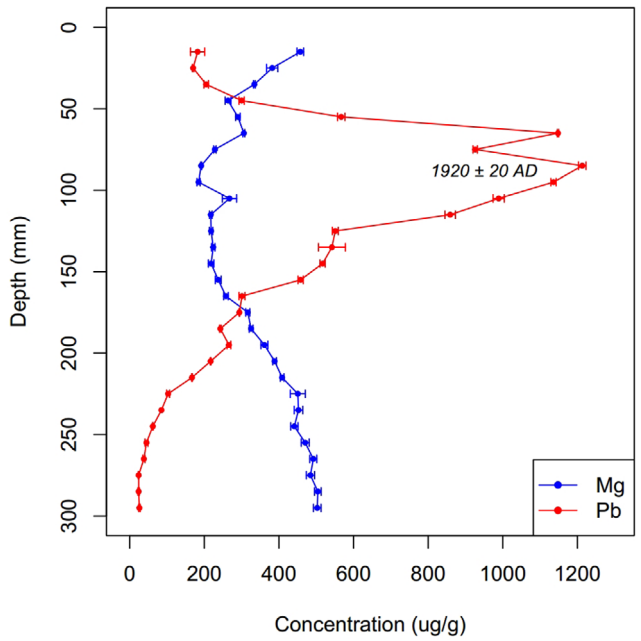

FIGURE 2 Variation in Mg concentration measured via inductively coupled plasma optical emission spectroscopy with peat depth at Holcroft Moss, UK collected in 2015 and reanalysed from Ryan and Fletcher (2025). The core has a highly leached section between 50 and 150 mm depth, corresponding to the peak of the Industrial Revolution, as evidenced by elevated Pb concentration from coal combustion and industrial activity. The age of the Pb maximum in the Holcroft Moss peat stratigraphy is constrained by combined AMS ^{14}C dating and spheroidal carbonaceous particle counts (Garcés-Pastor et al., 2023). Values at 10 mm depth are still 24% lower than the pre-industrial period.

3 | ECOLOGICAL RESPONSES OF BOGS TO CATION SHORTFALLS ACROSS SCALES

Here, we describe the evidence that cation loss from bogs may have large ecological effects across organisational scales, from tissue chemistry and individual performance to community dynamics and ecosystem function. Figure 3 illustrates the relationships between these organisational scales and highlights the knowledge gaps in how changes at one organisational level cascade to the next (e.g. community change alters ecosystem function).

3.1 | Stoichiometry, individual performance and cation in bogs

The ratio between the constitutive elements that make up organisms (i.e. stoichiometry) can yield insights into what elemental shortfalls are limiting growth and performance (Sterner & Elser, 2002). Past work in bogs, as in other systems (Kaspari, 2021), has focused on N and P stoichiometry, yet there is compelling evidence that other elements alter organismal performance. For instance, the stoichiometric response of *Sphagnum* spp. to N, PK and NPK fertilisation treatments from a bog in Ottawa, Canada, found that the moss is chronically K-limited, even with K addition (Wang et al., 2016). Further evidence supports this finding, where *Sphagnum* N:P:K stoichiometry from 24 ombrotrophic bogs across Vermont and Massachusetts, USA, suggested P was the most likely limiting nutrient, but K concentrations in capitula were low enough to limit growth (Gotelli et al., 2008). Cation concentrations in the tissues of 13 different *Sphagnum* species in a Finnish bog varied greatly (in C.V.—Mg 21.6%, Ca 26.6%, K 31.1% and Na 43.4%), suggesting requirements or uptake of these

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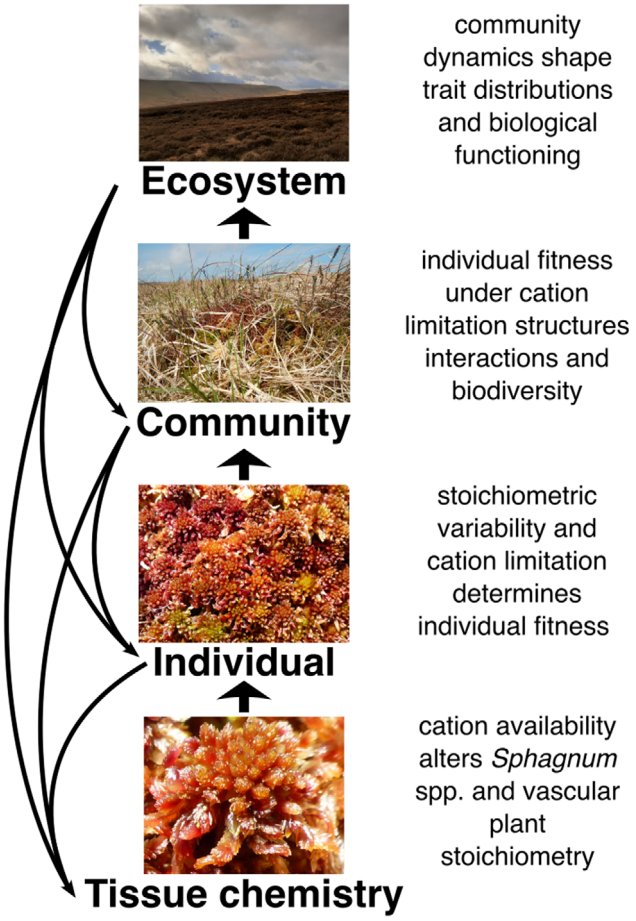

FIGURE 3 Cation availability shapes ecological processes across hierarchical scales. Note that there are feedbacks within these systems. For instance, nutrient deposition or leaching at the ecosystem level feeds back to determine the tissue chemistry of an individual, which can alter their fitness and restructure competitive dynamics between *Sphagnum* spp. and vascular plants. Photo credits—Jonathan P. Ritson.

micronutrients are species specific (Aulio, 1980), meaning responses to acidification and recovery could also be species specific, altering community composition. Interestingly, growing different *Sphagnum* spp. in high $CaCl_2$ concentrations leads to sharp increases in tissue Ca concentrations coupled with decreases in Mg, suggesting the two cations compete with one another in tissues with little effect on performance measured as K leakage (Koks et al., 2022). Together, these analyses suggest that *Sphagnum* is often K and potentially Mg-limited, with further evidence that N deposition intensifies this limitation while leaching Ca and Mg (Bragazza et al., 2004).

There is limited but supportive experimental evidence that *Sphagnum* spp. fitness is limited by cation availability. For instance, K and P addition coupled with ammonia and nitrate, reflecting N-deposition, in Scottish peat bogs, increased *Sphagnum* spp. branch growth and photosynthetic material length by roughly 25% over N-deposition treatments alone (Carfrae et al., 2007). Unfortunately, the coupled addition of P and K in this experiment limits the conclusions we can draw on the relative importance of either nutrient. Given that K is an electrolyte that regulates cellular osmotic potential (Sardans & Peñuelas, 2015) and requires energy-consuming active transport across membranes (da Silva & Williams, 2001), abundant K may reduce the costs to plants for nutrient translocation, water retention and growth (Kaspari & Welti, 2023). But much more work is needed to disentangle variation among *Sphagnum* spp. growth responses to K in addition to the other individual cation elements.

3.2 | Cations and vegetation diversity

Vegetation communities in ombrotrophic systems vary based on water availability, light, pH and nutrient availability, including cation concentrations (Andrus, 1986). Generally, higher cation availability is associated with higher vegetation diversity. This fits with plant life-history strategy theory (Grime, 1973, 2006), in which community diversity is constrained in extremely low-nutrient environments by the limited species pool adapted to such extreme stress. This occurs across bog to fen gradients (Tahvanainen, 2004), where increasing geological mineral availability causes the cation availability gradient, and relative distance to a coast, where sites further away from the coast receive less ocean-derived Mg and Na (Glaser, 1992; Kleinebecker et al., 2010; Neiland, 1971). These differences can be stark, with Kleinebecker et al. (2010) noting that oceanic blanket bogs in Patagonia were dominated by cushion-forming vascular plants, including *Donatia fascicularis* and *Astelia pumila*, whereas *Sphagnum magellanicum* dominated with decreasing maritime influence. This may be due to the competitive strategy of *Sphagnum*, wherein it acidifies its environment to facilitate cation uptake such that many higher plants cannot tolerate the low pH and cation availability (van Breeman, 1995). Where marine deposition increases Ca and Mg availability, this competitive strategy may begin to fail.

Cation availability is often correlated with other environmental factors (e.g. pH), making it difficult to isolate the effects of cation availability alone on vegetation assembly in ombrotrophic systems. For example, a report measuring *Sphagnum* spp. cover at 36 blanket bog sites across the UK found that *Sphagnum* spp. cover increased with Mg concentrations in the peat. However, as Mg covaries with historic deposition chemistry, the authors downplayed this finding and emphasised that *Sphagnum* loss was likely caused by high sulphate deposition (Carroll et al., 2009). While acidification is indeed likely the dominant factor, Mg limitation is also a potential cause in declining *Sphagnum* success, given its roles in photosynthesis and phosphate metabolism (da Silva & Williams, 2001).

Aspects of bog communities other than richness likely vary with cation availability but are seldom studied. A peatland fertilisation study using K and Mg showed an increase in the fen species *Schoenus nigricans* growth rates, where K availability appeared to limit its growth (Boatman, 1962). Similarly, natural oceanic-to-continental bog gradients show elevated Na, Ca and Mg concentrations in *Sphagnum* growing in oceanic sites, yet it is unclear whether this leads to any changes in productivity (Damman, 1978). There is also little understanding of how declining cation

concentrations alter stress tolerance, like drought, which may be dependent on K (Sardans & Peñuelas, 2015) and Mg (Santos et al., 2023) availability.

3.3 | Cation influence over ecosystem processes

There is little work describing the role of cations in ombrotrophic bog ecosystem function, yet there are hints that cations may be crucial in regulating the carbon cycle. Potassium, in particular, emerges as a key micronutrient governing ecosystem processes. For instance, multiple studies have found that K increases the biomass production of bog species (Boatman, 1962; Hoosbeek et al., 2002), which suggests that restoring K availability in bogs may enhance their production and carbon storage rates, depending on K effects on decomposition. The productivity responses of bogs to K availability suggest that K effects on individual growth (described above for *Sphagnum* spp.) scale up to ecosystems. There is some evidence that higher Na in peat increases decomposition rates from a *Sphagnum* spp. litter bag decomposition experiment along microtopographic gradients in a Finnish bog (Mäkilä et al., 2018), which aligns with the hypothesis that fungi, bacteria and invertebrate mesofauna of the decomposer community are Na-limited (Kaspari, 2020; Scharnagl et al., 2017). However, other work suggests that CEE, base saturation and the concentrations of Ca, Mg, K and Na were unrelated to the decompositional stage in three bogs from Alberta, Canada (Rippy & Nelson, 2007).

Ombrotrophic bogs undergo frequent inundation that creates anoxic environments primed for methane production (Mander et al., 2025), a potent greenhouse gas. The cellular physiology of methanogenic microbes suggests that higher available Na will increase methane production (Jarrell & Kalmokoff, 1988). Indeed, an incubation study using *Sphagnum*-dominated peat from boreal Canada found that methane production doubled with NaCl addition (Basiliko & Yavitt, 2001). Additionally, methane production increased with the sum availability of cations (i.e. K, Na, Mg, Ca) in incubations from a Scottish raised bog subjected to different metal amendments used to release bound cations from exchange sites (i.e. added Mg^{2+}, Al^{3+} and Pb^{2+}; Gogo & Pearce, 2009). This is compelling evidence that cation availability plays a key role in bog methane production.

Different cations have unique cycling patterns, often based on binding affinity (Clymo, 1963), in bogs and may be sensitive to global change. Some cations (Mg and K) in Canadian bogs appear to be recycled in the vegetation at a higher rate than N and Ca because C:Mg and C:K increase with bog core depth up to ~100 cm and accumulate at lower depths, while C:N and C:Ca sharply decrease with core depth (Wang et al., 2015). *Sphagnum* spp. litter decomposition experiments in Italian bogs found that K leaches rapidly from decomposing tissues, highlighting the high leachability of K, given its relatively low binding affinity, while other cations were not measured (Bragazza et al., 2007). In a Welsh bog dominated by *Sphagnum* and *Juncus*, higher β-glucosidase activity was associated with increased carbon cycling under inundation, but under drought, higher β-glucosidase activity increased mineralisation of Mg and Ca (Freeman et al., 1997). Whether these newly available cations are reincorporated into the vegetation or lost from the system is an open question. Together, the evidence suggests that K is important for ecosystem function in bogs, but given Mg, Na and Ca have seldom been explored experimentally, it is difficult to draw conclusions without more work.

4 | FUTURE TRAJECTORIES FOR CATIONS IN PEAT

Evidence from our own coring (Figure 2) and decreased cation flux out of ombrotrophic bogs into streams and rivers (Monteith et al., 2022) suggests that areas affected by acid deposition are recovering to pre-industrial levels. This may be accelerated for some elements (i.e. Ca and Mg) by restoration efforts (Stimson et al., 2017). Further changes may be brought about by climate change (Figure 1). In Europe and eastern North America, marine deposition rates are strongly controlled by the North Atlantic Oscillation (NAO), which affects storm frequency and severity. Future warming could increase the variability in the NAO (Goodkin et al., 2008), meaning marine deposition could be elevated and reach further inland, altering soil biogeochemistry (Evans, 2005). This could expand the higher diversity maritime bogs inland as deposition increases, potentially at the expense of *Sphagnum* mosses. As bog vegetation diversity relates to the interaction of marine deposition and latitude (Glaser, 1992), regional-scale modelling is needed to understand the potential effects.

Past forecasts of future carbon fluxes in peatlands focused on temperature, photosynthetically active radiation and water table/soil moisture (e.g. Gallego-Sala et al., 2018). More recent peatland forecasts incorporate nutrient limitation and suggest that reduced precipitation will lower N mineralisation rates and consequently reduce net primary production, turning peatlands into net C sources (Zhao et al., 2022). However, our review suggests there may be direct effects of cation availability on biogeochemical cycling in bogs (e.g. K limitation of productivity), as well as indirect effects through changes in vegetation composition, but this requires more evidence. Current forecast models, such as the one described in Zhao et al. (2022), incorporate variation in vegetation communities and their related decomposition and nutrient mineralisation rates, suggesting the forecast could incorporate information on cation availability with appropriate data. This is especially promising as recent forecasts suggest that the incorporation of multi-element limitation improves predictions of terrestrial carbon balance (Yang et al., 2023). Therefore, we need to understand how elevated cation concentrations may alter C fluxes and vegetation composition in peatlands.

While we expect altered deposition patterns to be the main driver of future cation availability in bogs, other global changes will interactively shape the direction and magnitude of how cations shape

ecological processes. However, there is little experimental work to draw conclusions from, making this an important area for future research. The work that has been done suggests that global change effects on cation dynamics may be system- and nutrient-dependent. For instance, elevated CO_2 can cause declines in *Sphagnum* spp. litter K content (Hoosbeek et al., 2002). Curtinrich et al. (2022) found that warming accelerated iron redox cycling, which led to greater carbon release. Given that iron is a vital micronutrient for catalysis and other cellular functions (da Silva & Williams, 2001), this response could have wider implications for the ecology and biogeochemistry of peatlands.

5 | FUTURE RESEARCH DIRECTIONS

We offer a prioritised list of the key knowledge gaps on how past changes have affected cations in ombrotrophic systems and their consequences for their responses to future global change. We prioritised the list by (a) clarifying the basic role of cations in ombrotrophic systems; then (b) how we can predict and manage cation availability and its effects under global change. Given the outsized role ombrotrophic peatlands play in carbon budgets, knowledge of the effects of cation supply on key processes could help constrain projections of carbon sequestration under future climate and deposition chemistries.

1. *Do single cations and/or co-limitation shape ecological processes in bogs?* There are few investigations into the ecological function of individual cations in bogs. Many of the experiments described here do not perform individual cation additions, but add them in combination with other nutrients (e.g. Carfrae et al., 2007; Larmola et al., 2013; Moore et al., 2019). This both limits an experiment's ability to assess 'Liebig's Law' like single nutrient limitation and co-limitation, where multiple resources simultaneously affect processes like growth (Kaspari & Powers, 2016; Sperfeld et al., 2016). The first step is investigating the role of these cations when added in isolation and, better yet, more work on the role of co-limitation in bog species, communities and ecosystem function.
2. *What is the impact of cation depletion on ecosystem function in bogs? And what will current cation recovery mean for productivity, decomposition and resilience?* As reviewed above, there is some evidence that K can increase production (Hoosbeek et al., 2002) and that Na will increase decomposition (Mäkilä et al., 2018), but Mg, Na and Ca have rarely been investigated for their potential influence on ecosystem function. The paucity of studies likely reflects the general underrepresentation of micronutrients in ecological research (Kaspari, 2021). The combined evidence that cations, in particular K and Mg, increase bog species growth and alter plant community dynamics suggests that these effects will scale up to alter ecosystem function as cation concentrations recover in bogs (Figure 3). The dosing of Ca and Mg in UK peatland restoration offers a way of studying at least some of these effects at a landscape scale. Disentangling the direct effect of acid deposition versus the secondary effect of cation leaching represents a difficult barrier to understanding the causes of degradation in peatland systems observed since the Industrial Revolution.
3. *How will future increases in storminess under climate change alter the vegetation composition and ecosystem function of bogs? How far will this effect extend inland and how does this interact with changes in temperature and precipitation?* Modelling work will likely be needed to understand the potentially interacting effects on productivity, decomposition and vegetation assembly, with the potential to include these elements in global peatland carbon models. This question highlights the geographic specificity of cation and nutrient limitation, where multiple abiotic and biotic processes (e.g. distance to coasts, precipitation, geology and N-fixation) create geographic mosaics of nutrient availability (Kaspari & Powers, 2016). We would expect cation limitation to be most common in inland bogs far from oceanic deposition. These processes are likely even more complicated in fens, where underlying geology plays a part in controlling cation availability. This may be critical to understand future carbon sequestration rates, given the evidence we highlight that maritime bogs are less likely to be dominated by *Sphagnum*, the keystone genus responsible for peat formation.
4. *How do cation limitation and recovery alter microbial community dynamics and functioning?* We have focused this review on vegetation responses to cation limitation, but microbial functioning in bogs is important for carbon cycling (Ritson et al., 2021) and likely cation-limited. Given the evidence above that processes like methanogenesis are Na-limited (Basiliko & Yavitt, 2001) and that Na deposition will increase with climate change-driven storminess (Soares et al., 2016), bogs could increase methane production and become a carbon source in the future.
5. *Is global change causing nutrient dilution in bogs?* While acid deposition is the most likely driver of cation loss from bogs, other global changes such as rising atmospheric CO_2 can cause declines in the relative cation density of plant tissues by enhancing biomass growth without commensurate nutrient uptake—a phenomenon known as nutrient dilution (Kaspari & Welti, 2024; Lynn et al., 2025). There is compelling evidence that these global changes are driving nutrient dilution for N across the globe (Mason et al., 2022), but there is less evidence for elements outside of N (e.g. Welti et al., 2020) and even less for bogs. Past work in ombrotrophic bogs found experimentally elevated (e)CO_2 increased the C:N of *Sphagnum* spp. (Hoorens et al., 2003) and the first 30 cm of the peat profile (Ofiti et al., 2022), suggesting nutrient dilution for N. Hoosbeek et al. (2002) found that *Sphagnum* spp. K% in litter declined in response to eCO_2, providing a key example of non-N nutrient dilution in bogs. This experimental evidence for nutrient dilution in ombrotrophic bogs is supported by Figure 2, where Mg levels have not recovered to pre-industrial levels after acid deposition decline, suggesting that post-industrial peat may exhibit nutrient dilution. However, nutrient dilution requires testing against alternative hypotheses (e.g. climate change-driven changes in

precipitation altering leaching rates). Future work should sample at depth for cation and carbon concentrations across wider environmental contexts to disentangle the effects of historical deposition from other global changes on peat cation concentrations.

6 | CONCLUSION

Micronutrients have often been overlooked in ecology, despite their critical role in cellular functioning and organismal homeostasis. This is particularly true for cations in ombrotrophic bogs, where a legacy of acid deposition and complete reliance on deposition for mineral nutrition can create extreme cation limitation. Our review suggests that cation limitation alters *Sphagnum* stoichiometry and reduces its growth, which could alter competition and environmental filters that determine diversity, and thereby change the traits of the biota performing ecosystem functions (Figure 3). Yet, we lack the data to draw firm conclusions around these mechanisms. Our proposed research agenda would contribute towards filling the knowledge gaps around cation biogeochemical cycling and its consequences in bogs.

AUTHOR CONTRIBUTIONS

Joshua S. Lynn and Jonathan P. Ritson contributed equally, conceived of the review and led the writing with contributions from all authors. Benjamin Bell conducted the initial literature search and screening. Peter Ryan and William Fletcher performed the reanalysis of previously published core data.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

This review does not contain original data. However, the data for Figure 2 have been deposited on Figshare at Ryan and Fletcher (2025) with DOI: https://doi.org/10.48420/30648092.

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