

A meta-analysis of soil salinization effects on nitrogen pools, cycles and fluxes in coastal ecosystems

MINGHUA ZHOU¹, KLAUS BUTTERBACH-BAHL^{2,3}, HARRY VEREECKEN¹ and NICOLAS BRÜGGEMANN¹

¹Institute of Bio- and Geosciences-Agrosphere (IBG-3), Forschungszentrum Jülich GmbH, Jülich 52428, Germany, ²Institute of Meteorology and Climate Research – Atmospheric Environmental Research (IMK-IFU), Karlsruhe Institute of Technology, Garmisch-Partenkirchen 82467, Germany, ³International Livestock Research Institute (ILRI), Old Naivasha Road, Nairobi 00100, Kenya

Abstract

Salinity intrusion caused by land subsidence resulting from increasing groundwater abstraction, decreasing river sediment loads and increasing sea level because of climate change has caused widespread soil salinization in coastal ecosystems. Soil salinization may greatly alter nitrogen (N) cycling in coastal ecosystems. However, a comprehensive understanding of the effects of soil salinization on ecosystem N pools, cycling processes and fluxes is not available for coastal ecosystems. Therefore, we compiled data from 551 observations from 21 peer-reviewed papers and conducted a meta-analysis of experimental soil salinization effects on 19 variables related to N pools, cycling processes and fluxes in coastal ecosystems. Our results showed that the effects of soil salinization varied across different ecosystem types and salinity levels. Soil salinization increased plant N content (18%), soil NH_4^+ (12%) and soil total N (210%), although it decreased soil NO_3^- (2%) and soil microbial biomass N (74%). Increasing soil salinity stimulated soil N_2O fluxes as well as hydrological NH_4^+ and NO_2^- fluxes more than threefold, although it decreased the hydrological dissolved organic nitrogen (DON) flux (59%). Soil salinization also increased the net N mineralization by 70%, although salinization effects were not observed on the net nitrification, denitrification and dissimilatory nitrate reduction to ammonium in this meta-analysis. Overall, this meta-analysis improves our understanding of the responses of ecosystem N cycling to soil salinization, identifies knowledge gaps and highlights the urgent need for studies on the effects of soil salinization on coastal agro-ecosystem and microbial N immobilization. Additional increases in knowledge are critical for designing sustainable adaptation measures to the predicted intrusion of salinity intrusion so that the productivity of coastal agro-ecosystems can be maintained or improved and the N losses and pollution of the natural environment can be minimized.

Keywords: coastal ecosystem, denitrification, dissimilatory nitrate reduction to ammonium (DNRA), nitrogen cycle, salinity intrusion, sea-level rise, soil salinization

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Introduction

Sea-level rise (SLR), increased groundwater abstraction and decreased sediment loads by embanked rivers cause saltwater intrusions in coastal regions (Milly *et al.*, 2005; Van Dijk *et al.*, 2009; IPCC 2013; Rasmussen *et al.*, 2013), which drive widespread soil salinization in coastal ecosystems (Werner *et al.*, 2013; Chandrajith *et al.*, 2014). Agro-ecosystems in coastal regions feed over 40% of the world's population (Burke *et al.*, 2000). However, these systems are currently threatened by soil salinization, which is further aggravated by salinity intrusion because of climate change (Smajgl *et al.*, 2015). Particular concerns include the salinization effects on nitrogen (N) cycling

in coastal ecosystems (Herbert, 1999; Herbert *et al.*, 2015) because N is an essential nutrient for crop production and natural ecosystem functioning as well as affecting environmental quality from regional to global scales because of gaseous and hydrological N losses from ecosystems. Soil salinization can mediate ecosystem N cycling through direct impacts on microorganisms and their communities and functions (Santoro, 2010; Bernhard *et al.*, 2015) as well as through alterations of abiotic factors (e.g., soil cation and anion compositions) in coastal ecosystems (Marton *et al.*, 2012; Ardon *et al.*, 2013; Teixeira *et al.*, 2013). Therefore, soil salinity is likely a key regulator of plant and soil N pools, cycling processes and fluxes in coastal ecosystems, although one has to assume that the underlying regulatory mechanisms are complex.

Correspondence: Minghua Zhou, tel. +49 246161 9429, fax +49 246161 2518, e-mail: m.zhou@fz-juelich.de

Increases in soil salinity may decrease net photosynthesis and induce physiological stress on plant growth (Hester *et al.*, 2001), thereby resulting in decreases in plant biomass productivity in coastal ecosystems (e.g., Erickson *et al.*, 2007; Sutter *et al.*, 2014). In the Chesapeake Bay (USA), the plant biomass production was significantly decreased because of the inhibition of plant carbon assimilation at high salinity levels in a tidal freshwater wetland (Sutter *et al.*, 2014), although in the same study, the salt marsh plant biomass remained unchanged with increasing salinity, which was likely because the dominant species (e.g., *Spartina*) is more salt tolerant (Hester *et al.*, 2001). Soil salinization tended to enhance plant tissue N in a freshwater wetland (e.g., Erickson *et al.*, 2007) because plants can conserve nitrogen more effectively under salt stress, thereby resulting in a relative increase in plant N (Neubauer *et al.*, 2000). Comparable observations were also reported by Sutter *et al.* (2014) for a freshwater wetland where increasing soil salinity significantly increased plant tissue N, although such an effect was not found for a salt marsh. However, across different coastal ecosystems, the salinization effects on plant biomass and plant tissue N are inconsistent (Matamala & Drake, 1999; Erickson *et al.*, 2007; Sutter *et al.*, 2014).

Several experiments have shown that soil salinity is a key regulating factor of N mineralization in coastal ecosystems (Fang *et al.*, 2005; Noe *et al.*, 2013; Brouns *et al.*, 2014). Noe *et al.* (2013) found that N mineralization in a tidal freshwater forested wetland was stimulated by increasing salinity from 0.1 to 3.5 parts per thousand (ppt), which was likely because of plant stress, accelerated senescence and related additional plant biomass input to the soil. However, soil N mineralization as a biologically mediated process was inhibited by increasing soil salinity because microbial activity tends to be reduced at higher salinities (e.g., Pathak & Rao, 1998; Rath & Rousk, 2015). A review of soil salinization effects on N mineralization in coastal wetlands also suggests that N mineralization processes in coastal wetlands may be greatly impacted by soil salinization, although the underlying mechanisms are complex and depend on the ecosystem type and the soil's physical, chemical and biological properties (Bai *et al.*, 2012).

Nitrification that transforms NH_4^+ to nitrate (NO_3^-) via microbial processes can also be affected by salinization (Joye & Hollibaugh, 1995; Osborne *et al.*, 2015). Increasing soil salinity not only constrains the physiological fitness of nitrifiers but also affects the availability of soil oxygen, thereby resulting in a decrease in nitrification rates in coastal freshwater ecosystems (Joye & Hollibaugh, 1995; Rysgaard *et al.*, 1999; Giblin *et al.*, 2010). However, Magalhaes *et al.* (2005) found that nitrification rates were stimulated when the soil salinity

increased from 0 to 15 ppt in the Douro River Estuary of Portugal, which suggested that nitrifying bacteria in this estuary were salt tolerant. These conflicting findings indicate that the salinization effects on nitrification may vary across different coastal ecosystems.

Similar to nitrification, soil salinization has been shown to have contrasting effects on microbial denitrification through its differential effects on the physiology of soil microbes in various coastal ecosystems (Seitzinger *et al.*, 1991; Fear *et al.*, 2005; Giblin *et al.*, 2010; Bruesewitz *et al.*, 2013). For example, decreases in denitrification rates with increases in soil salinity were observed in the Parker River Estuary, Massachusetts, USA, which was explained by the inhibitory effect of soil salinization on the nitrification process and the reduced availability of nitrate as substrate for denitrification (Giblin *et al.*, 2010). However, Fear *et al.* (2005) found that increases in salinity (2–24 ppt) did not significantly stimulate or inhibit denitrification rates in the Neuse River Estuary of North Carolina (USA), which was likely because of the simultaneous change in other regulating parameters of denitrification, such as soil available oxygen and organic carbon (Rath & Rousk, 2015).

The relative importance of the dissimilatory nitrate reduction to ammonium (DNRA) for NO_3^- reduction has become increasingly evident in numerous coastal ecosystems (Dong *et al.*, 2011; Giblin *et al.*, 2013; Yang *et al.*, 2015), although it is not been well understood. Compared with denitrification, the DNRA transforms NO_3^- to NH_4^+ ; hence, N can be retained if the DNRA outcompetes denitrification for NO_3^- (Tobias *et al.*, 2001). The balance of the two processes is regulated by various environmental factors, such as salinity level as well as NO_3^- and organic C availability (Brunet & Garciagil, 1996; Giblin *et al.*, 2010; Dong *et al.*, 2011; Algar & Vallino, 2014). Increasing salinity has been found to favor the DNRA (e.g., Osborne *et al.*, 2015), and various reduced sulfur compounds (H_2S , FeS , $\text{S}_2\text{O}_3^{2-}$) have been shown to serve as electron donors for the DNRA in coastal ecosystems (Brunet & Garciagil, 1996). Previous studies have also demonstrated that the DNRA is favored over denitrification with high organic C availability (Gardner & McCarthy, 2009), although it may also be shifted to denitrification with increased in soil salinity (e.g., Giblin *et al.*, 2013). Thus, the balance of the DNRA and denitrification responds differently to soil salinity depending on the ecosystem and is tightly related to other environmental factors (e.g., NO_3^- and organic C availability).

The microbial N cycling processes drive and regulate the exchange of N compounds (e.g., N_2O , NO_3^- and NH_4^+) across the atmosphere–soil–hydrosphere interfaces in coastal ecosystems, which contribute to

regional and global N pollution (Teixeira *et al.*, 2013; Cornwell *et al.*, 2014; Bernhard *et al.*, 2015). Soil salinization, therefore, could directly affect gaseous and hydrological N losses from coastal ecosystems through alterations in soil microbial communities and their biochemical activities. Furthermore, soil salinity could also change other soil environmental parameters, such as soil available oxygen (Noe *et al.*, 2013), or ionic strength (Weston *et al.*, 2010). These changes might drive increased N losses from coastal ecosystems along hydrological and atmospheric pathways. Nevertheless, general patterns on how gaseous and hydrological N losses respond to soil salinization in coastal ecosystems have not yet been identified.

The inconsistent findings from different studies emphasize the need to synthesize available results to reveal a general trend of soil salinization effects on ecosystem N pools, cycling processes and fluxes in coastal ecosystems. Therefore, we conducted a meta-analysis to examine the responses of ecosystem N pools (soil total nitrogen, NH_4^+ , NO_3^- and microbial N pools, plant productivity and canopy N concentration), microbial N cycles (N mineralization, nitrification, denitrification, DNRA and Anammox) and gaseous and hydrological N fluxes (N_2O emission and hydrological NH_4^+ , NO_3^- , NO_2^- and DON fluxes) to salinization in coastal ecosystems.

Materials and methods

Data compilation

We searched for peer-reviewed journal articles published before May 2015 and listed in the ISI Web of Science. The search terms were 'nitrogen' and 'seawater intrusion'; 'nitrogen' and 'sea level rise'; 'nitrogen' and 'salinity' and 'coastal ecosystems'; and 'nitrogen' and 'salinity' and 'delta'. In total, 938 publications were found. The following criteria were applied to select appropriate studies: (i) only studies including no salinization (control) and salinization (treatment) experimental plots were selected; (ii) at least one of the selected variables was measured; (iii) only control and salinization treatment data were used for multifactorial studies and the interacting effects were excluded; and (iv) means and sample sizes had to be reported. We screened the publications in accordance with the above criteria, and 21 papers that reported the responses of N cycling processes to soil salinization in coastal ecosystems were selected from the 938 peer-reviewed publications (Table 1). These publications summarized 551 observations, and the compiled database included 19 variables related to ecosystem N pools [soil total nitrogen, NH_4^+ , NO_3^- and microbial biomass N, plant tissue N (a percentage of dry biomass) as well as plant below- and above-ground biomass], N cycling processes (N mineralization, nitrification, denitrification, DNRA and Anammox) and N

fluxes (N_2O emission and hydrological NH_4^+ , NO_3^- , NO_2^- and DON fluxes) (Appendix S1).

Because most studies reported more than one salinity level, one salinity level was defined as one treatment in this meta-analysis and all comparisons were recorded as independent observations. For this meta-analysis, we specifically selected studies with high-quality data (e.g., replicated randomized experiments, direct comparison of different, well-defined salinity levels with no salinity), justifying the consideration of the different salinity levels as independent treatments. For each study, we extracted information on the experimental location, ecosystem type, experimental method as well as the response variables. Data were extracted by GETDATA GRAPH DIGITIZER software (version 2.26; <http://www.getdata-graph-digitizer.com/download.php>) if the data were reported as figures in the original publication. We calculated the standard deviation from the sample size and standard error if not reported. Soil salinity data were also collected, and the salinity value was transformed to the unit of parts per thousand (ppt) if not already reported accordingly. Each study was grouped into one of the four ecosystems: freshwater wetland [e.g., freshwater forested wetland, river estuary, rice paddy (only one study with two observations)], salt marsh, grassland and vegetation-free system (i.e., bare soil). We also grouped the collected data into three soil salinization categories in accordance with the recommendation of the FAO (FAO, 1985): <6 ppt (slightly saline), 6–12 ppt (medium saline) and >12 ppt (highly saline).

Statistical analyses

For the responses of the ecosystem N pools, cycles and fluxes to soil salinization, we used the natural logarithm of the response ratio (RR) as a metric of the effect size in the present meta-analysis. For a given variable, RR was calculated as the ratio of its value in the salinization group (\bar{X}_t) to that in the control group (\bar{X}_c) (Douxchamps *et al.*, 2011) (Eqn 1). The logarithm of RR was calculated (Hedges *et al.*, 1999) to indicate the effects of soil salinization as follows:

$$\ln \text{RR} = \ln \left(\frac{\bar{X}_t}{\bar{X}_c} \right) \quad (1)$$

A value of zero for $\ln \text{RR}$ indicates that the salinization treatment had no effect. The variance of $\ln \text{RR}$ (v) for each study was calculated using the inverse of the pooled variance (Eqn 2; Hedges *et al.*, 1999):

$$v = (s_t^2/n_t\bar{X}_t^2) + (s_c^2/n_c\bar{X}_c^2) \quad (2)$$

where s_t and s_c are the standard deviations for all comparisons in the treatment and control groups, respectively, and n_t and n_c are the sample sizes for the treatment and control groups, respectively. For each study, the weighting factor w was calculated as the inverse of the pooled variance ($1/v$). When multiple observations were extracted from the same study, we adjusted the weights by the total number of observations (n) per site. The final weight (w') in this meta-analysis was calculated according to Eqn (3):

$$w' = w/n \quad (3)$$

The weighted effect size $\ln RR'$ and mean effect size $\overline{\ln RR'}$ for all observations were calculated using Eqns (4) and (5):

$$\ln RR' = w' \times \ln RR \quad (4)$$

$$\overline{\ln RR'} = \sum_i \ln RR' / \sum_i w' \quad (5)$$

where $\ln RR'_i$ and w'_i are the $\ln RR'$ and w' of the i th observation, respectively.

Bootstrapping procedures within the METAWIN 2.1 software (Arizona State University, Tempe, AZ, USA) were used to generate 95% confidence intervals for the weighted effect sizes using 4999 iterations (Rosenberg *et al.*, 2000). The soil salinization effects were considered significant if the 95% confidence intervals did not overlap with zero. The potential effects of publication bias were excluded by conducting a Kendall's tau rank correlation and fail-safe number tests within METAWIN 2.1 (Rosenberg *et al.*, 2000). We conducted a categorical randomized-effects model meta-analysis to compare the responses among ecosystem types and soil salinity gradients using a framework similar to an ANOVA, and the between-group heterogeneity was assessed using randomization procedures based on 4999 replications (Adams *et al.*, 1997). We also applied a continuous randomized-effects model meta-analysis to test the relationships between the variables' effect size ($\ln RR'$) and soil salinity levels across various coastal ecosystems. The statistical results for the total heterogeneity of the effect size among studies (Q_T), the differences among the group cumulative effect sizes (Q_M), the residual error (Q_E), and the slope and the probability value of the regression were reported.

Results

Increasing soil salinity significantly increased the plant N content by 17.6% across all coastal ecosystems, although it did not significantly affect the plant above- or belowground biomass (Fig. 1). However, if the salinization effects were analyzed separately for freshwater and salt marsh ecosystems, a significant increase in plant N could only be demonstrated for salt marsh ecosystems (95% CI of effect size: 0.027–0.202) (Fig. 2). Furthermore, plant N was significantly enhanced with increasing salinity under highly saline conditions but not under slightly saline conditions (Fig. 3).

We also found that soil salinization significantly increased the total soil nitrogen (TN) (209.9%) and soil NH_4^+ (11.7%) and decreased the soil microbial N (–73.8%). However, the soil NO_3^- was not significantly affected by salinization (Fig. 1). With regard to the ecosystem categories, the soil salinization effects did not change the soil total N and NH_4^+ in the grassland and nonvegetated ecosystems, whereas it did have a significantly positive effect on both the soil total N and NH_4^+ in freshwater wetlands (Fig. 2). However, we

found evidence that the soil total N and NH_4^+ responses to salinization were dependent on the salinity level (Fig. 3). Although there were no general patterns in the salinization effect on soil NO_3^- concentrations (Fig. 1), the responses were significantly negatively affected by salinity in the freshwater wetlands (Fig. 2) primarily under slightly saline conditions (Fig. 3).

On average, increasing the soil salinity significantly stimulated the net N mineralization (hereafter referred to as N mineralization) and anaerobic ammonium oxidation (Anammox) but did not change the biological N_2 fixation, net nitrification (hereafter referred to as nitrification), denitrification and the DNRA (Fig. 1). It should be noted that soil salinization increased the ratio of the DNRA to net denitrification (hereafter referred to as denitrification) by 82.5% (Fig. 1). A comparison of the different ecosystem types indicated that N mineralization was only stimulated by increasing soil salinity for freshwater wetlands and not for salt marsh and grassland ecosystems (Fig. 2). Potential denitrification was inhibited by increases in the soil salinity in the vegetation-free and salt marsh ecosystems, although it was not significantly affected in the freshwater wetlands and grasslands. The soil N mineralization was significantly stimulated by medium and high salinity, whereas nitrification was only significantly positively affected by slightly saline conditions (Fig. 3).

Increasing soil salinity significantly stimulated soil N_2O fluxes (Fig. 1), although the effect sizes varied across the various coastal ecosystems (Fig. 2). Soil N_2O fluxes were significantly stimulated by increasing salinity in the freshwater wetlands, whereas they were significantly inhibited by increasing soil salinity in the salt marshes. Increasing soil salinity also significantly enhanced hydrological NH_4^+ and NO_2^- fluxes and significantly decreased DON fluxes, although they did not induce changes in NO_3^- fluxes (Fig. 1).

Discussion

Plant biomass and plant N

Our meta-analysis indicated that soil salinization significantly increased plant N content and did not change the plant above- and belowground biomass (Fig. 1). Although soil salinity has been shown to induce physiological stress on plant growth and decrease plant biomass in most ecosystems (Hester *et al.*, 2001), the lack of change in plant biomass under soil salinization in the present meta-analysis might have been caused by shifts in the plant species community composition (Crain *et al.*, 2004; Sutter *et al.*, 2014). The plant biomass of salt marshes was reported to be unaffected (Erickson *et al.*, 2007) or even significantly enhanced (Sutter *et al.*,

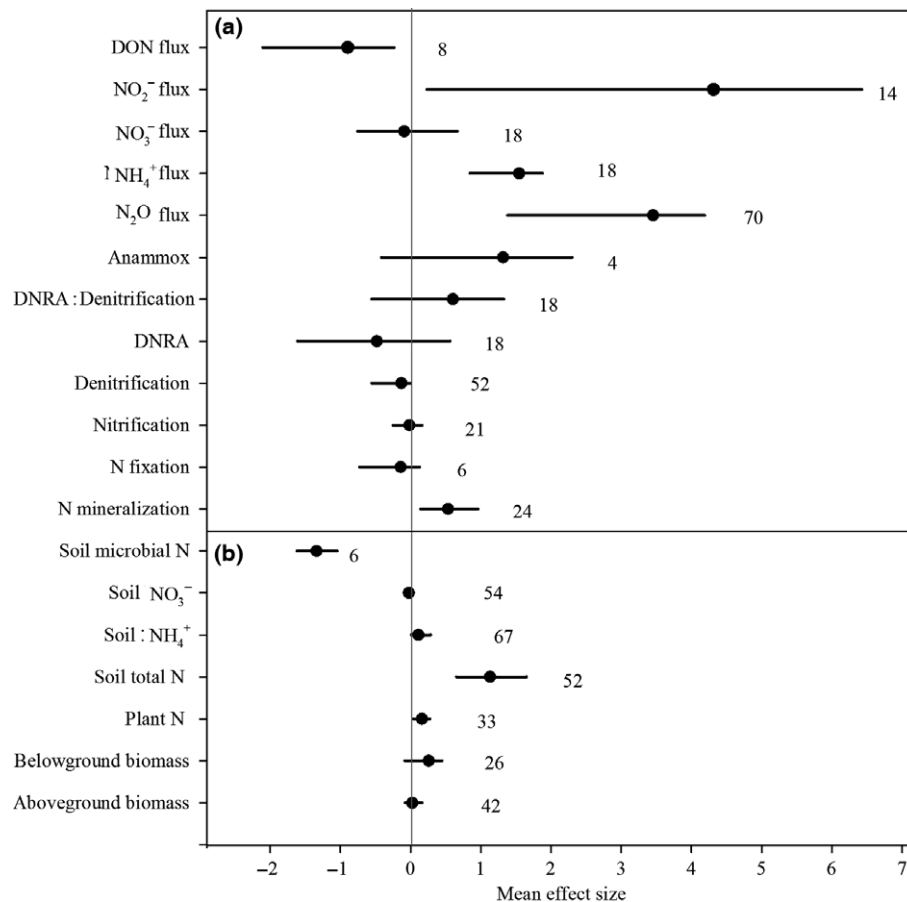


Fig. 1 The mean effect sizes of salinization on nineteen variables related to ecosystem N fluxes (a) and pools (b) in coastal ecosystems. The variables of nitrification and N mineralization refer to net nitrification and net N mineralization for all figures and tables throughout the manuscript, due to the unavailability of gross nitrification and gross N mineralization data in this meta-analysis. Error bars represent 95% bootstrapped confidence intervals (CIs). The number of observations for each variable is shown next to the error bars. The gray dashed line was drawn at mean effect size of zero. The effect of salinization was considered significant if the 95% CI of the effect size did not overlap zero.

2014) with increasing soil salinity in the Chesapeake Bay of USA. Therefore, salt-tolerant salt marsh plants, such as *Spartina*, may replace other less salt-tolerant species, such as *P. hemitomon* (e.g., Hester *et al.*, 2001). However, for most freshwater wetlands, soil salinization has been found to suppress plant growth and decrease plant biomass through declines in net plant CO₂ assimilation (Munns, 2002; Sutter *et al.*, 2014).

Compared with its effects on plant biomass, soil salinization significantly increased the plant N concentrations (Fig. 1). Different mechanisms could be responsible for this phenomenon:

- 1 the demonstrated increase in soil total N and soil NH₄⁺ which allows plants to more easily acquire N from soils (Fig. 1).
- 2 plant physiological responses. For example, some studies have found that freshwater wetland plants

tend to conserve nitrogen more efficiently under soil salinization and show decreases in CO₂ assimilation and increases in photorespiration (e.g., Sutter *et al.*, 2014). Moreover, root exudation seems to be increased by salinization (Neubauer *et al.*, 2013). These two factors together have been hypothesized to result in higher plant N content. Notably, this plant physiological response, that is, enhanced carbon respiration and decreased CO₂ assimilation, to salinity intrusion is a positive feedback to global climate change because increasing temperatures will indirectly result in increased salinization of coastal ecosystems through sea-level rises.

- 3 change in plant species composition due to salinity. In addition to a physiological explanation for increased plant N concentrations, Ryan & Boyer (2012) argue that the response of total ecosystem

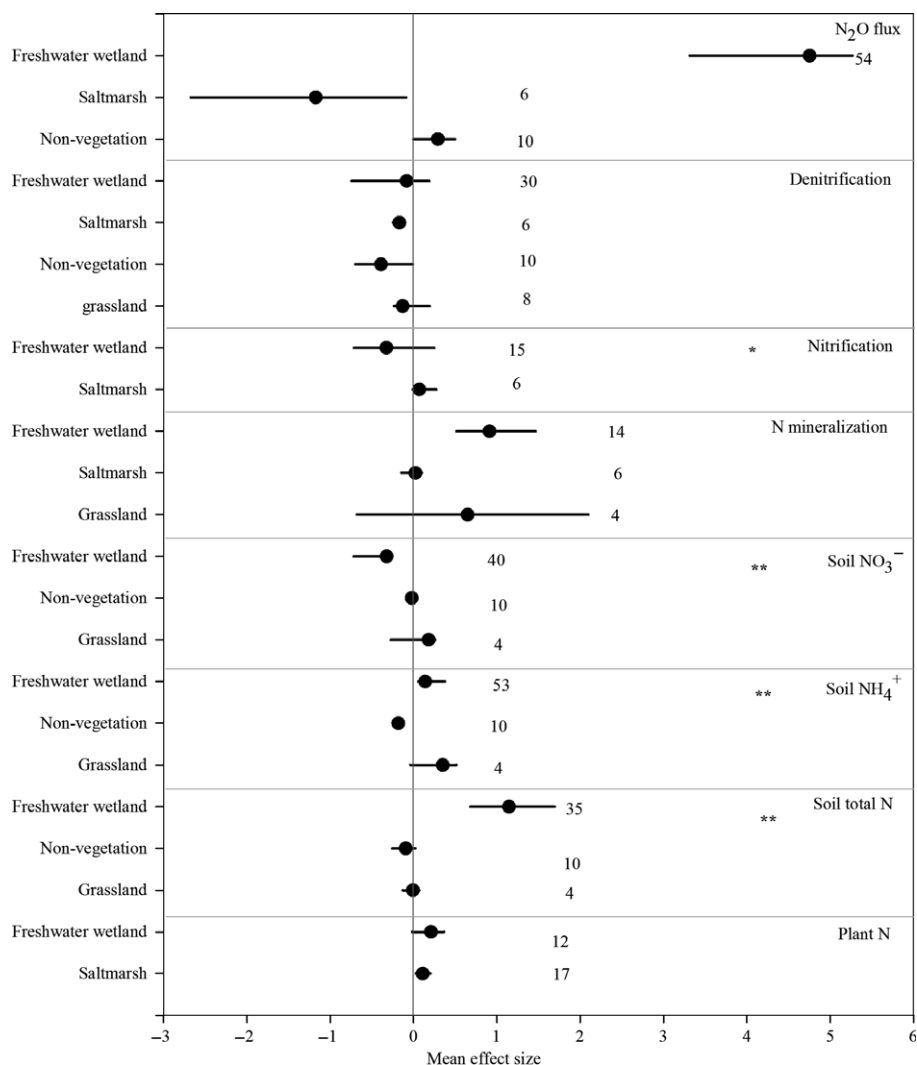


Fig. 2 The mean effect sizes of salinization on plant N, soil total nitrogen, soil NH_4^+ , soil NO_3^- , N mineralization, nitrification, denitrification and N_2O flux in coastal ecosystems. The variables are categorized into different groups depending on the ecosystem type. An unmentioned ecosystem type for a given variable indicates that there was no information available for this ecosystem. Error bars represent 95% bootstrapped confidence intervals (CIs). The number of observations for each variable is shown next to the error bars. The gray dashed line was drawn at mean effect size of zero. The effect of salinization was considered significant if the 95% CI of the effect size did not overlap zero. Asterisks indicate significant differences in salinization effects between the subcategories ($*P < 0.05$; $**P < 0.01$).

plant N concentrations to salinization could also be related to changes in the plant community composition toward more salt-tolerant plant species. For example, plant N was significantly enhanced with increasing salinity in a salt marsh in the San Francisco Bay (USA), which was likely because of the increased abundance of *Spartina* (salt-tolerant species) in the salt marsh system (Ryan & Boyer, 2012).

However, as indicated in our meta-analysis (Fig. 4), targeted studies that use salinity gradient approaches to test the effects of salinization on the plant N content

of coastal ecosystems are rare, and this knowledge gap directly pertains to the variability in the responses of plant N content and biomass under salinity intrusions in coastal ecosystems.

Soil N

Elevated salinity significantly increased the soil total N and NH_4^+ , decreased the microbial biomass nitrogen (MBN) and did not change the soil NO_3^- across the various coastal ecosystems (Fig. 1). The increased soil

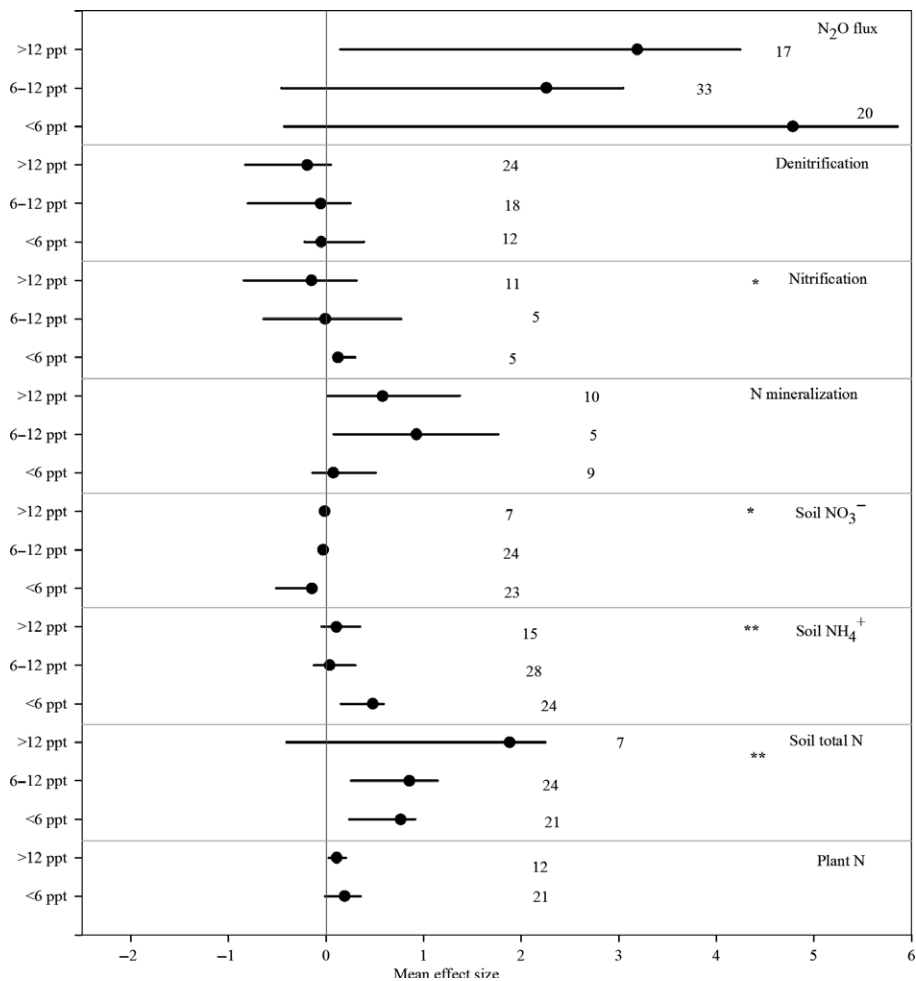


Fig. 3 The mean effect sizes of salinization on plant N, soil total nitrogen, soil NH₄⁺, soil NO₃⁻, N mineralization, nitrification, denitrification and N₂O flux categorized by different gradients of salinity stress, that is, low to moderate salinity (<6 ppt), moderate to high salinity (6–12 ppt) and high salinity (>12 ppt) in the coastal ecosystems. Error bars represent 95% bootstrapped confidence intervals (CIs). The number of observations for each variable is shown next to the error bars. The gray dashed line was drawn at mean effect size of zero. The effect of salinization was considered significant if the 95% CI of the effect size did not overlap zero. Asterisks indicate significant differences in salinization effects between the subcategories (**P* < 0.05; ***P* < 0.01).

total N could be related to the increased plant litter N input to the soil organic matter pool because soil salinization tends to enhance plant N content and results in increased plant litter input to soils because of the increased senescence of aboveground plant biomass following salt accumulation in leaves and other plant parts (Person & Ruess, 2003; Dausse *et al.*, 2012). The increased soil NH₄⁺ might be explained by the observed stimulation of the net N mineralization (Fig. 1). In addition, the increase in soil NH₄⁺ concentrations might also be explained by decreased plant NH₄⁺ uptake and/or microbial NH₄⁺ immobilization with increasing salinity. However, reports on the effects of salinization effects on these parameters in coastal ecosystems are not available (Fig. 4). The indicated

knowledge gaps also constrain our understanding of why soil salinization decreased soil microbial biomass nitrogen (MBN) across studies (Fig. 1). We hypothesize that the decrease in soil MBN is likely related to the effect of osmotic stress at high salinity on the abundance and community composition of soil microorganisms.

N mineralization

Our meta-analysis showed that soil salinization on average increased N mineralization by 70.6% (*P* < 0.05, Fig. 1), which may be explained by the stimulated plant litter N input from dead and stressed plants because of salinization, which was discussed in

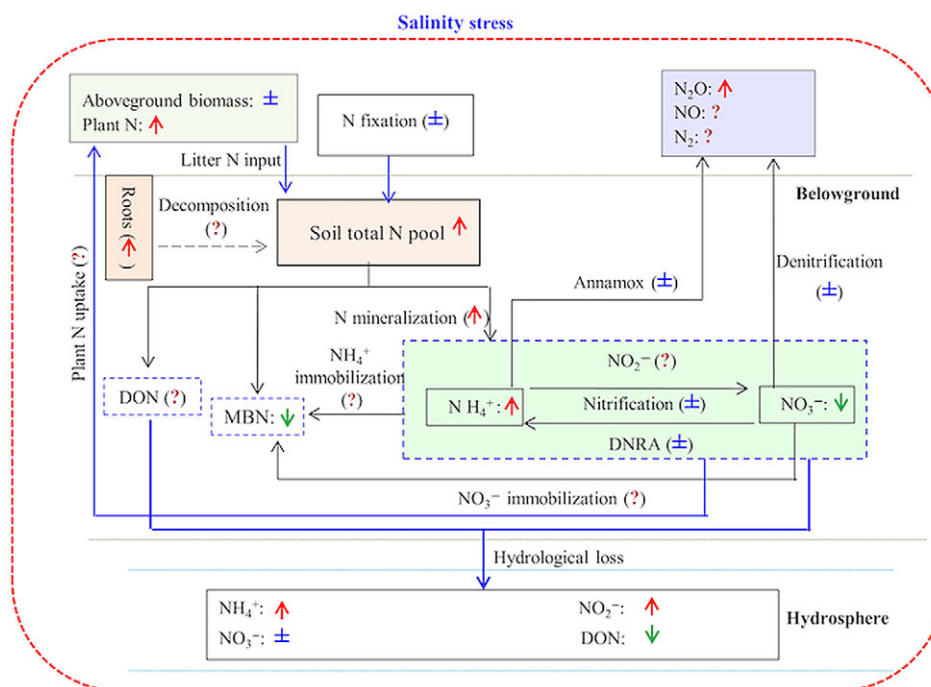


Fig. 4 A conceptual framework describing the responses of plant productivity, soil N pools, soil N cycling processes, and gaseous and hydrological N fluxes to salinity stress in the coastal ecosystems. Red upward arrows refer to increases by increasing salinization, green downward arrows refer to decreases by increasing salinization, blue '±' symbols refer to inconsistent responses to salinization, and pink '?' symbols indicate that there are currently no available studies.

the above sections. The increased input of detritus with greater N content can stimulate soil N mineralization rates, which likely occurs through priming effects (Kuzyakov *et al.*, 2000; Antheunisse *et al.*, 2007; Noe *et al.*, 2013). Studies have found that soil salinization enhances the relative abundance and activity of the specific microbial functional groups responsible for N mineralization (Muhammad *et al.*, 2006; Wong *et al.*, 2008), which could be another mechanism underlying the stimulation of net N mineralization found in this meta-analysis. The decrease in soil microbial biomass N observed in our meta-analysis (Fig. 1) suggests that microbial N immobilization is inhibited by increasing salinity in coastal ecosystems. Some studies found the increase in net N mineralization was along with the decrease in soil microbial biomass N likely due to the inhibited microbial N immobilization (e.g., Shaw & Harte, 2001; Kooijman *et al.*, 2009). Thus, the inhibited microbial N immobilization could be one cause of increased net N mineralization by soil salinization in coastal ecosystems.

Although the response of plant N to salinization in coastal ecosystems was revealed by the present meta-analysis, plant N uptake was found to be generally decreased by salinization in most inland crop systems (e.g., Van Hoorn *et al.*, 2001). Therefore, we assumed

that the reduction in microbial N immobilization and plant N uptake may also be responsible for the increased net N mineralization by salinization in coastal ecosystems.

Overall, our meta-analysis showed a significant salinization effect on net N mineralization, and the magnitude of the salinization effect was ecosystem dependent. The soil salinization effects on net N mineralization were significant in the freshwater wetlands, although they were not significant in salt marshes (Fig. 2). As discussed above, this phenomenon may be caused by the decrease in plant N assimilation because of the lower salt tolerance of plant species in freshwater wetlands compared with those in salt marshes. This finding can also explain the relatively larger effect size of N mineralization observed at higher salinity across different coastal ecosystems (Fig. 3).

Nitrification and Anammox

Although the general effect of salinization on nitrification was not significant across the different coastal systems (Figs. 1 and 2), soil salinization still significantly increased nitrification rates under slightly saline conditions (Fig. 3). Culture experiments showed that estuarine isolates of nitrifiers exhibited optimum

Table 1 Geographic location, ecosystem type, experimental method and variable number of studies used in this meta-analysis. ‘–’ means no available information

Study number	Reference	Country	Geographic location	Ecosystem types	Experimental method	Number of variables
1	Antheunisse <i>et al.</i> , (2007)	Netherlands	51°47'N, 4°13'E; 51°44'N, 4°21'E	Grassland	Mesocosm experiment	6
2	Ardon <i>et al.</i> , (2013)	United States	35°54'N, 76°09'W	Freshwater wetland	Field and microcosm experiments	3
3	Brouns <i>et al.</i> , (2014)	Netherlands	52°08'N, 4°50'E; 52°52'N, 5°48'E; 52°08'N, 4°48'E; 52°59'N, 6°24'E	Peat meadow	Laboratory experiment	2
4	Dausse <i>et al.</i> , (2012)	United Kingdom	–	Salt marsh	Field experiment	6
5	Dong <i>et al.</i> , (2011)	Thailand; Indonesia; Fiji	13°24'N, 99°59'E; 13°23'N, 100°00'E; 6°01'S, 106°37'E; 6°00'S, 106°38'E; 6°00'S, 106°38'E; 6°00'S, 106°38'E; 18°06'S, 178°32'E; 18°07'S, 178°31'E; 18°08'S, 178°30'E	Estuary	Field and laboratory experiments	3
6	Fear <i>et al.</i> , (2005)	United States	–	Estuary	Laboratory experiment	2
7	Gao <i>et al.</i> , (2014)	China	37°35', –38°12'N, 118°33', –119°20'E	Freshwater wetland	Laboratory experiment	2
8	Koop-Jakobsen & Giblin, (2009)	United States	–	Estuary	Laboratory experiment	2
9	Marton <i>et al.</i> , (2012)	United States	31°21'N, 81°32'W; 31°59'N, 81°17'W; 30°57'N, 81°53'W	Freshwater forested wetland	Laboratory experiment	1
10	Nielsen <i>et al.</i> , (2009)	Germany	–	Estuary	Field and laboratory experiment	3
11	Noe <i>et al.</i> , (2013)	United States	–	Freshwater forested wetland	Field and laboratory experiment	8
12	Osborne <i>et al.</i> , (2015)	United States	–	Freshwater wetland	Field, microcosm and laboratory experiments	1
13	Person & Ruess, (2003)	United States	–	Salt marsh	Field and laboratory experiment	1
14	Qin <i>et al.</i> , (2015)	China	–	Salt marsh	Laboratory experiment	3
15	Reddy & Crohn, (2014)	United States	33°35'N, 116°06'W	Nonvegetation	Laboratory experiment	5
16	Singh <i>et al.</i> , (2002)	India	–	Rice	Field experiment	3
17	Sutter <i>et al.</i> , (2015)	United States	–	Freshwater wetland	Field experiment	3
18	Sutter <i>et al.</i> , (2014)	United States	–	Freshwater wetland	Field experiment	3
19	Teixeira <i>et al.</i> , (2013)	Portugal	41°32'N, 8°47'W; 41°20'N, 8°44'W	Estuary	Laboratory experiment	1
20	Thomas & Christian, (2001)	United States	41°21'N, 70°23'W; 37°54'N, 75°36'W; 31°19'N, 81°18'W	Salt marsh	Field experiment	3
21	Zhang <i>et al.</i> , (2013)	China	37°35', –38°12'N, 118°33', –119°20'E	Estuary	Field experiment	4

nitrification rates at salinity levels of 5–10 ppt (Jones & Hood, 1980). Therefore, as observed in our meta-analysis (Figs 1–3), nitrification can be expected to

increase if soil salinity is within the optimum of 5–10 ppt and inhibited if soil salinity exceeds the optimum salinity range. It is noteworthy that nitrification rates

Table 2 Relationships between the effect size of experimental salinization on nitrogen (N) pools, cycles and fluxes with salinity levels across various coastal ecosystems. Statistical results were reported as total heterogeneity in effect sizes among studies (Q_T), the difference among groups cumulative effect sizes (Q_M) and the residual error (Q_E) from continuous randomized-effects model meta-analysis. The relationship is significant if $P < 0.05$

	Q_T	Q_M	Q_E	Slope	P value
N pools					
Plant N	20.2846	3.3143	16.9703	0.0072	0.94614
Soil total N	87.0357	0.0044	87.0313	0.0008	0.00124
Soil NH_4^+	298.8553	39.3227	259.5326	0.0229	0.0000
Soil NO_3^-	50.8337	0.8515	49.9822	-0.0044	0.91547
N cycles					
N mineralization	18.2022	0.2224	17.9799	0.0098	0.37619
Nitrification	16.0101	1.0596	14.9506	-0.0200	0.31276
Denitrification	43.4929	6.8344	36.6585	-0.0405	0.01235
N fluxes					
N_2O flux	40.1332	0.0987	40.0345	0.0194	0.97734
NH_4^+ flux	13.8164	5.2932	8.5232	0.0540	0.68005
NO_3^- flux	22.2664	0.0328	22.2336	0.0110	0.17469
NO_2^- flux	6.8399	1.2840	5.5560	0.1492	0.91021

are highly dependent on soil oxygen and NH_4^+ availability, which may also be altered by salinization in coastal ecosystems (Rysgaard *et al.*, 1999; Noe *et al.*, 2013). For example, increasing salinity can reduce the oxygen available to nitrifying bacteria to oxidize ammonium to nitrate, which was observed in a Danish estuarine ecosystem (Rysgaard *et al.*, 1999). Our meta-analysis highlights the gap in knowledge on the response of nitrification to soil salinization, which impedes our ability to predict the effect of salinity intrusions on nitrification and nitrogen cycling and the losses in coastal ecosystems under future climatic conditions.

Our meta-analysis also revealed that soil salinization on average stimulated Anammox more than twofold (Fig. 1) because Anammox bacteria in general are highly tolerant to salt stress (Xiao & Roberts, 2010). A recent review also revealed that Anammox could be stimulated by increasing salinity below 15.0 ppt, although it may be inhibited at higher salinity (Jin *et al.*, 2012), which may explain our observations that Anammox was enhanced when the salinity was between 3 and 15 ppt. Furthermore, it should be noted that the effect size of Anammox was governed by the salinity level as well as the salt type. Dapena-Mora *et al.* (2007) reported that Anammox was not inhibited at salinity levels below 8.8 ppt but was significantly inhibited at salinity levels of 7.0 ppt if the salt composition was shifted from NaCl to KCl and/or Na_2SO_4 . Although previous studies typically focused on the response of Anammox to salinity during wastewater treatment, few studies have been conducted in coastal ecosystems

(Schmid *et al.*, 2007; Jin *et al.*, 2012) despite the universal finding of Anammox in anoxic marine environments (Xiao & Roberts, 2010). This knowledge gap limits our ability to quantitatively predict the response of Anammox to salinity intrusions in coastal ecosystems.

Denitrification and dissimilatory nitrate reduction to ammonium (DNRA)

Overall, soil salinization consistently decreases denitrification across coastal ecosystems, although its effect is not statistically significant (Figs 1–3). Denitrification occurs preferentially under anoxic conditions and is the primary N cycling process for N removal in coastal ecosystems (Dong *et al.*, 2011). The identified positive correlation between salinity levels and salinization effect size on denitrification rates in our meta-analysis (Table 2) indicates that soil salinity is a key regulating factor of microbial denitrification in coastal ecosystems, although denitrification is also controlled by temperature, oxygen, dissolved organic C and nitrate availability (e.g., Butterbach-Bahl *et al.*, 2013). Soil salinity natural gradients and laboratory manipulation experiments have shown that elevated salinity primarily results in sulfide toxicity to denitrifiers and changes in microbial composition (Santoro *et al.*, 2006; Santoro, 2010), which decreases denitrification rates (Dong *et al.*, 2011; Marton *et al.*, 2012). Moreover, soil salinization may also indirectly affect denitrification by shifting soil redox conditions and changing the availability

of C and N substrates (Noe *et al.*, 2013; Morrissey *et al.*, 2014; Osborne *et al.*, 2015). For instance, decreases in nitrification rates by increases in soil salinity resulted in a lower availability of soil NO_3^- as a substrate for denitrification (Fig. 1; Noe *et al.*, 2013). Decreases in the release of dissolved organic carbon (DOC) under soil salinization could also constrain denitrification through a reduction of organic C availability (Rath & Rousk, 2015). Furthermore, a decrease in soil respiration by soil salinization (Wong *et al.*, 2008) could reduce soil oxygen consumption and inhibit denitrification as a result of alterations in the aeration status of the soil.

Soil salinization on average decreased the DNRA by 38.2%, although this effect was not significant (Fig. 1). Under anoxic soil conditions, the DNRA can consume 5–40% of the total nitrate pool (Osborne *et al.*, 2015), although most of the N can be retained in coastal ecosystems (e.g., as reviewed by Giblin *et al.*, 2013). The soil aeration status, NO_3^- and organic C availability as well as the soil pH have been identified as the regulating factors of DNRA in most ecosystems (e.g., as reviewed by Rutting *et al.*, 2011). Therefore, the decreased DNRA by soil salinization, as found in our meta-analysis, can be explained by either the direct inhibition of the related microbial DNRA activity or indirectly by the decreased availability of soil NO_3^- because of inhibited nitrification (Jin *et al.*, 2012). However, the DNRA was positively correlated with soil salinity in the freshwater wetlands of Massachusetts (USA) because of the interaction of soil salinity and nitrate availability (Giblin *et al.*, 2010). Thus, the mechanism underlying the DNRA response to soil salinity appears to be complex because the effect of soil salinity is often coupled with other factors that regulate the DNRA. However, the number of observations reported in the literature is limited.

Although increased soil salinity inhibited denitrification and the DNRA, soil salinization favored the DNRA relative to denitrification across coastal ecosystems ($P < 0.05$; Fig. 1). Similarly, several studies reported that increasing soil salinity tended to favor the DNRA over denitrification, which was likely because of an increase in sulfate reduction (e.g., Brunet & Garciagil, 1996; Giblin *et al.*, 2010). In addition to an increase in sulfide concentrations, elevated soil salinity favors anoxic conditions, which likely induce denitrification in coastal ecosystems. Therefore, it is unclear whether increasing salinity triggers a switch of denitrification to DNRA. Nevertheless, previous studies have demonstrated that the balance between denitrification and DNRA, which are two processes that compete for nitrate, is also dependent on various other factors, such as the soil

redox status, temperature, soil C and N availability (Dong *et al.*, 2011; Giblin *et al.*, 2013; Osborne *et al.*, 2015). For instance, Dong *et al.* (2011) reported the relative importance of the DNRA and showed that denitrification was dependent on both the availability of organic C and nitrate in the soil and temperatures in a tropical estuary. At high soil temperatures and low organic C and nitrate concentrations, the DNRA was the dominant nitrate reduction process relative to denitrification. It is noteworthy that NO_3^- can be retained in the soil rather than lost to the atmosphere as N_2O if the DNRA outcompetes denitrification for soil nitrate (Tobias *et al.*, 2001). Overall, the response of the ratio of DNRA to denitrification to soil salinity in coastal ecosystems is not clarified in the current literature.

N loss

On average, increasing soil salinity significantly stimulated soil N_2O emissions (Fig. 1), although the magnitude of the response varied across different ecosystems and salinity levels (Fig. 2; Fig. 3). Soil N_2O can be produced by several biotic processes, such as microbial nitrification and denitrification (as reviewed by Butterbach-Bahl *et al.*, 2013), and abiotic processes, such as the chemical reactions of nitrite and hydroxylamine (as reviewed by Heil *et al.*, 2016), that are regulated by various environmental factors. There are several possible explanations for the increase in soil N_2O emissions with increasing soil salinity. First, higher soil salinity can directly inhibit the last step of the denitrification chain of specific denitrifiers, including the reduction of N_2O to N_2 , which is likely because osmotic stress induced by salinization can suppress the denitrifiers responsible for reducing N_2O to N_2 (Reddy & Crohn, 2014). Similarly, Marton *et al.* (2012) found that soil N_2O emissions positively responded to elevated salinity in a tidal freshwater wetland of the Satilla River delta in southern Georgia (USA) because the enzyme N_2O reductase was inhibited at higher salinity levels, which resulted in greater N_2O emissions. Second, increasing soil salinity can stimulate sulfate reductions, thereby leading to elevated H_2S concentrations that can effectively inhibit N_2O reductase (Sorensen *et al.*, 1980). However, previous studies often used the ratio of N_2 to N_2O as an indicator of the N_2O reduction activity of denitrifying communities because a direct quantification in the field was not possible (e.g., Sorensen *et al.*, 1980). A major unknown variable in this context is the response of N_2O reductase activity to soil salinity levels as well as salt species. Third, increasing salinity levels can reduce microbial activity and limit the availability of labile

organic carbon (e.g., reviewed by Rath & Rousk, 2015). Thus, soil salinization can indirectly inhibit N_2O reduction, and several studies have demonstrated that the addition of labile C tends to stimulate the reduction of N_2O to N_2 via denitrification (Sanchez-Martin *et al.*, 2008; Senbayram *et al.*, 2012). However, Wang *et al.* (2009) found that in a freshwater wetland of the Yangtze River Estuary in China, high soil salinity inhibited nitrification and decreased nitrate production, which could lead to a reduction in denitrification and soil N_2O emissions. A fourth possibility could be that because of the stronger inhibition of nitrite oxidizers relative to ammonia oxidizers by salinity, the associated nitrite accumulation (e.g., Zhao *et al.*, 2014) could lead to a higher abiotic (chemical) formation of N_2O in the soil, such as through the reaction of nitrite with hydroxylamine, another reactive nitrification intermediate (see Heil *et al.*, 2016, for a more detailed introduction into the various chemical reactions in soil leading to N_2O formation).

Increasing soil salinity significantly increased the hydrological NH_4^+ and NO_2^- fluxes and decreased the DON fluxes but did not significantly change the NO_3^- fluxes (Fig. 1). Consistent with our meta-analysis, increases in NH_4^+ fluxes at elevated salinity have also been observed in several studies (Dausse *et al.*, 2012; Ardon *et al.*, 2013; Noe *et al.*, 2013). The soil salinization effects on hydrological NH_4^+ fluxes exhibited the same pattern as the net N mineralization (Fig. 1), suggesting that increased net N mineralization is a likely cause of the increased hydrological NH_4^+ fluxes with increasing salinity. The increased hydrological NH_4^+ fluxes caused by increasing soil salinity may also be explained through a promotion of the displacement of NH_4^+ adsorbed to cation exchange sites because of the intrusion of salt cations in coastal ecosystem (e.g., Weston *et al.*, 2010). Nevertheless, positive salinization effects on net N mineralization may include an increased release of NH_4^+ from organic N compounds, which could also explain the decrease in DON fluxes found in the meta-analysis (Ardon *et al.*, 2013).

As revealed by a recent review (Dendooven *et al.*, 2010), the increase in NO_2^- fluxes with increasing soil salinity observed in our meta-analysis is likely caused by the inhibitory effects of salinization on the oxidation of NO_2^- to NO_3^- (i.e., second step of nitrification) because nitrite oxidizers react more sensitively to salt stress compared with ammonia oxidizers, which results in a mismatch of NO_2^- production and consumption in favor of production.

Overall, our analysis indicates that the improved N status (e.g., increased soil total N) is due that salinization tends to stimulate the N cycling processes which conserves reactive nitrogen in the system, for

example, reduced nitrification, stimulation of dissimilatory nitrate reduction to ammonium or reduced denitrification, although these stimulation effects are not statistically significant (Fig. 1). However, there are still major knowledge gaps as the magnitude of N_2 emissions was hardly assessed and effects of salinization on nitrate leaching and/or NH_3 volatilization were hardly explored. That means, in contrast to other terrestrial ecosystems, a direct positive link between ecosystem N status and environmental N losses cannot be drawn in coastal ecosystems on the basis of available knowledge. Therefore, it is so far not clear whether the positive salinization effect on ecosystem N status is directly resulting in increase in N losses.

Limitations and perspective

As mentioned above, in addition to the soil salinity level, other factors have also been shown to control the responses of N pools, cycling process and fluxes under soil salinization in coastal ecosystems, and these factors include the salt ion species and the relative abundance and community of plant species (e.g., Osborne *et al.*, 2015; Yang *et al.*, 2015). Unfortunately, the interactions of these factors with salinity level could not be revealed in our meta-analysis because of insufficient data, which may constrain our conclusions to some extent. Nevertheless, using the available information, we formulated a conceptual framework that highlights the current knowledge gaps on the response of ecosystem N pools, cycles and fluxes to soil salinization in coastal ecosystems (Fig. 4). However, the changes in the soil gross N turnover processes and rates in coastal ecosystems under increasing salinity intrusions resulting from sea-level rise are not well understood because the salinization effects on microbial N transformation (e.g., ammonification, nitrification, denitrification and DNRA) and N immobilization have not been simultaneously quantified. Moreover, the role of plant–microbe interactions in mediating the responses of ecosystem N pools, cycling processes and fluxes to salinity intrusions in coastal ecosystem is still unclear despite their importance in most ecosystems (Robertson & Vitousek, 2009).

Although nitrogen is an indispensable nutrient for agricultural production, agriculture largely contributes to N pollution through the insufficient management of N loss processes. Salinization significantly affects crop productivity and N cycling in agricultural soil, which has been primarily demonstrated for inland arable land (Funakawa *et al.*, 2000; Dendooven *et al.*, 2010), which accounts for approximately 10% of the

global arable land (Szabolcs, 1989). Among the available salinization effects on inland agro-ecosystems, most studies have focused on crop productivities, and only limited attention has been paid to N cycling and losses (e.g., Funakawa *et al.*, 2000). Moreover, to the best of our knowledge, all of the available studies in coastal regions have focused on natural and/or seminatural ecosystems. Thus, it remains unclear whether our current understanding of ecosystem N cycling and flux responses to soil salinization for these ecosystems (i.e., inland agro-ecosystems and natural/seminatural coastal ecosystems) can be extrapolated to coastal agro-ecosystems, which are also major food production areas worldwide because of the formation of soils on fertile sediments and the high availability of water (Atapattu & Molden, 2006). Thus, further research is needed on the responses of ecosystem N cycling and fluxes in coastal agro-ecosystems to soil salinization because such knowledge is critical for implementing sustainable agricultural production while minimizing N pollution.

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References

- Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling tests for meta-analysis of ecological data. *Ecology*, **78**, 1277–1283.
- Algar CK, Vallino JJ (2014) Predicting microbial nitrate reduction pathways in coastal sediments. *Aquatic Microbial Ecology*, **71**, 223–238.
- Antheunisse AM, Loeb R, Miletto M, Lamers LPM, Laanbroek HJ, Verhoeven JTA (2007) Response of nitrogen dynamics in semi-natural and agricultural grassland soils to experimental variation in tide and salinity. *Plant and Soil*, **292**, 45–61.
- Ardon M, Morse JL, Colman BP, Bernhardt ES (2013) Drought-induced saltwater incursion leads to increased wetland nitrogen export. *Global Change Biology*, **19**, 2976–2985.
- Atapattu S, Molden D (2006) Achieving food and environmental security: better river basin management for healthy coastal zones. *Environment and Livelihoods in Tropical Coastal Zones*, **22**, 293–301.
- Bai J, Gao H, Xiao R, Wang J, Huang C (2012) A review of soil nitrogen mineralization as affected by water and salt in coastal wetlands: issues and methods. *Clean-Soil Air Water*, **40**, 1099–1105.
- Bernhard AE, Dwyer C, Idrizi A, Bender G, Zwicker R (2015) Long-term impacts of disturbance on nitrogen-cycling bacteria in a New England salt marsh. *Frontiers in Microbiology*, **6**, 46.
- Brouns K, Verhoeven JTA, Hefting MM (2014) The effects of salinization on aerobic and anaerobic decomposition and mineralization in peat meadows: the roles of peat type and land use. *Journal of Environmental Management*, **143**, 44–53.
- Bruesewitz DA, Gardner WS, Mooney RF, Pollard L, Buskey EJ (2013) Estuarine ecosystem function response to flood and drought in a shallow, semiarid estuary: Nitrogen cycling and ecosystem metabolism. *Limnology and Oceanography*, **58**, 2293–2309.
- Brunet RC, Garcigal LJ (1996) Sulfide-induced dissimilatory nitrate reduction to ammonia in anaerobic freshwater sediments. *FEMS Microbiology Ecology*, **21**, 131–138.
- Burke L, Kura Y, Kassem K, Revenga C, Spalding M, McAllister D (2000) Pilot analysis of global ecosystems: Coastal ecosystems. Available at: <http://www.wri.org/publication/pilot-analysis-global-ecosystems-coastal-ecosystems>. (accessed 15 January 2016).
- Butterbach-Bahl K, Baggs EM, Dannenmann M, Kiese R, Zechmeister-Boltenstern S (2013) Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philosophical Transactions of the Royal Society B-Biological Sciences*, **368**, 20130122.
- Chandrajith R, Chaturangani D, Abeykoon S, JaC B, Van Geldern R, Edirisinghe E, Dissanayake CB (2014) Quantification of groundwater-seawater interaction in a coastal sandy aquifer system: a study from Panama, Sri Lanka. *Environmental Earth Sciences*, **72**, 867–877.
- Cornwell JC, Glibert PM, Owens MS (2014) Nutrient fluxes from sediments in the San Francisco Bay Delta. *Estuaries and Coasts*, **37**, 1120–1133.
- Crain CM, Silliman BR, Bertness SL, Bertness MD (2004) Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology*, **85**, 2539–2549.
- Dapena-Mora A, Fernandez I, Campos J, Mosquera-Corral A, Mendez R, Jetten M (2007) Evaluation of activity and inhibition effects on Anammox process by batch tests based on the nitrogen gas production. *Enzyme and Microbial Technology*, **40**, 859–865.
- Dausse A, Garbutt A, Norman L, Papadimitriou S, Jones LM, Robins PE, Thomas DN (2012) Biogeochemical functioning of grazed estuarine tidal marshes along a salinity gradient. *Estuarine Coastal and Shelf Science*, **100**, 83–92.
- Dendooven L, Alcantara-Hernandez RJ, Valenzuela-Encinas C, Luna-Guido M, Perez-Guevara F, Marsch R (2010) Dynamics of carbon and nitrogen in an extreme alkaline saline soil: a review. *Soil Biology and Biochemistry*, **42**, 865–877.
- Dong LF, Sobey MN, Smith CJ *et al.* (2011) Dissimilatory reduction of nitrate to ammonium, not denitrification or Anammox, dominates benthic nitrate reduction in tropical estuaries. *Limnology and Oceanography*, **56**, 279–291.
- Douchamps S, Frossard E, Bernasconi SM, Van Der Hoek R, Schmidt A, Rao IM, Oberson A (2011) Nitrogen recoveries from organic amendments in crop and soil assessed by isotope techniques under tropical field conditions. *Plant and Soil*, **341**, 179–192.
- Erickson JE, Megonigal JP, Peresta G, Drake BG (2007) Salinity and sea level mediate elevated CO₂ effects on C₃-C₄ plant interactions and tissue nitrogen in a Chesapeake Bay tidal wetland. *Global Change Biology*, **13**, 202–215.
- Fang HL, Liu GH, Kearney M (2005) Georelational analysis of soil type, soil salt content, landform, and land use in the Yellow River Delta, China. *Environmental Management*, **35**, 72–83.
- FAO (1985) Salty Soils. In: *Irrigation Water Management*, 1985. Food and Agriculture Organization of the United Nations, Via delle Terme di Caracalla, Rome, Italy. Available at: <http://www.fao.org/docrep/r4082e/r4082e08.htm#7.2.2>. (accessed 20 April 2016).
- Fear JM, Thompson SP, Gallo TE, Paerl HW (2005) Denitrification rates measured along a salinity gradient in the eutrophic Neuse River Estuary, North Carolina, USA. *Estuaries*, **28**, 608–619.
- Funakawa S, Suzuki R, Karbozova E, Kosaki T, Ishida N (2000) Salt-affected soils under rice-based irrigation agriculture in southern Kazakhstan. *Geoderma*, **97**, 61–85.
- Gao HF, Bai JH, He XH, Zhao QQ, Lu QQ, Wang JJ (2014) High temperature and salinity enhance soil nitrogen mineralization in a tidal freshwater marsh. *PLoS ONE*, **9**, e95011.
- Gardner WS, Mccarthy MJ (2009) Nitrogen dynamics at the sediment-water interface in shallow, sub-tropical Florida Bay: why denitrification efficiency may decrease with increased eutrophication. *Biogeochemistry*, **95**, 185–198.
- Giblin AE, Weston NB, Banta GT, Tucker J, Hopkinson CS (2010) The effects of salinity on nitrogen losses from an oligohaline estuarine sediment. *Estuaries and Coasts*, **33**, 1054–1068.
- Giblin AE, Tobias CR, Song B, Weston N, Banta GT, Rivera-Monroy VH (2013) The importance of dissimilatory nitrate reduction to ammonium (DNRA) in the nitrogen cycle of coastal ecosystems. *Oceanography*, **26**, 124–131.
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- Heil J, Vereecken H, Brüggemann N (2016) A review of chemical reactions of nitrification intermediates and their role in nitrogen cycling and nitrogen trace gas formation in soil. *European Journal of Soil Science*, **67**, 23–39.
- Herbert RA (1999) Nitrogen cycling in coastal marine ecosystems. *FEMS Microbiology Reviews*, **23**, 563–590.

- Herbert ER, Boon P, Burgin AJ *et al.* (2015) A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. *Ecosphere*, **6**, 1–43.
- Hester MW, Mendelsohn IA, Mckee KL (2001) Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora*: morphological and physiological constraints. *Environmental and Experimental Botany*, **46**, 277–297.
- IPCC (2013) Introduction. In: *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM), pp. 119–158. Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Jin RC, Yang GF, Yu JJ, Zheng P (2012) The inhibition of the Anammox process: a review. *Chemical Engineering Journal*, **197**, 67–79.
- Jones RD, Hood MA (1980) Effects of temperature, pH, salinity, and inorganic nitrogen on the rate of ammonium oxidation by nitrifiers isolated from wetland environments. *Microbial Ecology*, **6**, 339–347.
- Joye SB, Hollibaugh JT (1995) Influence of sulfide inhibition of nitrification on nitrogen generation in sediments. *Science*, **270**, 623–625.
- Kooijman AM, Van Mourik JM, Schilder MLM (2009) The relationship between N mineralization or microbial biomass N with micromorphological properties in beech forest soils with different texture and pH. *Biology and Fertility of Soils*, **45**, 449–459.
- Koop-Jakobsen K, Giblin AE (2009) Anammox in tidal marsh sediments: the role of salinity, nitrogen loading, and marsh vegetation. *Estuaries and Coasts*, **32**, 238–245.
- Kuzyakov Y, Friedel JK, Stahr K (2000) Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry*, **32**, 1485–1498.
- Magalhaes CM, Joye SB, Moreira RM, Wiebe WJ, Bordalo AA (2005) Effect of salinity and inorganic nitrogen concentrations on nitrification and denitrification rates in intertidal sediments and rocky biofilms of the Douro River estuary, Portugal. *Water Research*, **39**, 1783–1794.
- Marton JM, Herbert ER, Craft CB (2012) Effects of salinity on denitrification and greenhouse gas production from laboratory-incubated tidal forest soils. *Wetlands*, **32**, 347–357.
- Matamala R, Drake BG (1999) The influence of atmospheric CO₂ enrichment on plant-soil nitrogen interactions in a wetland plant community on the Chesapeake Bay. *Plant and Soil*, **210**, 93–101.
- Milly PCD, Dunne KA, Vecchia AV (2005) Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, **438**, 347–350.
- Morrissey EM, Gillespie JL, Morina JC, Franklin RB (2014) Salinity affects microbial activity and soil organic matter content in tidal wetlands. *Global Change Biology*, **20**, 1351–1362.
- Muhammad S, Muller T, Joergensen RG (2006) Decomposition of pea and maize straw in Pakistani soils along a gradient in salinity. *Biology and Fertility of Soils*, **43**, 93–101.
- Munns R (2002) Comparative physiology of salt and water stress. *Plant Cell and Environment*, **25**, 239–250.
- Neubauer SC, Miller WD, Anderson IC (2000) Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study. *Marine Ecology Progress Series*, **199**, 13–30.
- Neubauer SC, Franklin RB, Berrier DJ (2013) Saltwater intrusion into tidal freshwater marshes alters the biogeochemical processing of organic carbon. *Biogeosciences*, **10**, 8171–8183.
- Nielsen M, Gieseke A, De Beer D, Revsbech NP (2009) Nitrate, nitrite, and nitrous oxide transformations in sediments along a salinity gradient in the Weser Estuary. *Aquatic Microbial Ecology*, **55**, 39–52.
- Noe GB, Krauss KW, Lockaby BG, Conner WH, Hupp CR (2013) The effect of increasing salinity and forest mortality on soil nitrogen and phosphorus mineralization in tidal freshwater forested wetlands. *Biogeochemistry*, **114**, 225–244.
- Osborne RI, Bernot MJ, Findlay SEG (2015) Changes in nitrogen cycling processes along a salinity gradient in tidal wetlands of the Hudson River, New York, USA. *Wetlands*, **35**, 323–334.
- Pathak H, Rao DLN (1998) Carbon and nitrogen mineralization from added organic matter in saline and alkali soils. *Soil Biology and Biochemistry*, **30**, 695–702.
- Person BT, Ruess RW (2003) Stability of a subarctic salt marsh: plant community resistance to tidal inundation. *Ecoscience*, **10**, 351–360.
- Qin DH, Gao M, Wu XQ, Du XY, Bi XL (2015) Seasonal changes in soil TN and SOC in a seawall-reclaimed marsh in the Yellow River Delta, China. *Journal of Coastal Conservation*, **19**, 79–84.
- Rasmussen P, Sonnenborg TO, Gonciar G, Hinsby K (2013) Assessing impacts of climate change, sea level rise, and drainage canals on saltwater intrusion to coastal aquifer. *Hydrology and Earth System Sciences*, **17**, 421–443.
- Rath KM, Rousk J (2015) Salt effects on the soil microbial decomposer community and their role in organic carbon cycling: a review. *Soil Biology and Biochemistry*, **81**, 108–123.
- Reddy N, Crohn DM (2014) Effects of soil salinity and carbon availability from organic amendments on nitrous oxide emissions. *Geoderma*, **235**, 363–371.
- Robertson GP, Vitousek PM (2009) Nitrogen in agriculture: balancing the cost of an essential resource. *Annual Review of Environment and Resources*, **34**, 97–125.
- Rosenberg MS, Adams DC, Gurevitch J (2000) *MetaWin: Statistical Software for Meta-Analysis*. Sinauer Associates, Sunderland, MA, USA.
- Rutting T, Boeckx P, Muller C, Klemmedtsson L (2011) Assessment of the importance of dissimilatory nitrate reduction to ammonium for the terrestrial nitrogen cycle. *Biogeosciences*, **8**, 1779–1791.
- Ryan AB, Boyer KE (2012) Nitrogen further promotes a dominant salt marsh plant in an increasingly saline environment. *Journal of Plant Ecology*, **5**, 429–441.
- Rysgaard S, Thastum P, Dalsgaard T, Christensen PB, Sloth NP (1999) Effects of salinity on NH₄⁺ adsorption capacity, nitrification, and denitrification in Danish estuarine sediments. *Estuaries*, **22**, 21–30.
- Sanchez-Martin L, Valjejo A, Dick J, Skiba UM (2008) The influence of soluble carbon and fertilizer nitrogen on nitric oxide and nitrous oxide emissions from two contrasting agricultural soils. *Soil Biology and Biochemistry*, **40**, 142–151.
- Santoro AE (2010) Microbial nitrogen cycling at the saltwater-freshwater interface. *Hydrogeology Journal*, **18**, 187–202.
- Santoro AE, Boehm AB, Francis CA (2006) Denitrifier community composition along a nitrate and salinity gradient in a coastal aquifer. *Applied and Environmental Microbiology*, **72**, 2102–2109.
- Schmid MC, Risgaard-Petersen N, Van De Vossenberg J *et al.* (2007) Anaerobic ammonium-oxidizing bacteria in marine environments: widespread occurrence but low diversity. *Environmental Microbiology*, **9**, 1476–1484.
- Seitzinger SP, Gardner WS, Spratt AK (1991) The effect of salinity on ammonium sorption in aquatic sediments—implications for benthic nutrient recycling. *Estuaries*, **14**, 167–174.
- Senbayram M, Chen R, Budai A, Bakken L, Dittter K (2012) N₂O emission and the N₂O/(N₂O + N₂) product ratio of denitrification as controlled by available carbon substrates and nitrate concentrations. *Agriculture, Ecosystems and Environment*, **147**, 4–12.
- Shaw MR, Harte J (2001) Response of nitrogen cycling to simulated climate change: differential responses along a subalpine ecotone. *Global Change Biology*, **7**, 193–210.
- Singh M, Bhattacharya AK, Nair TVR, Singh AK (2002) Nitrogen loss through subsurface drainage effluent in coastal rice field from India. *Agricultural Water Management*, **52**, 249–260.
- Smajgl A, Toan TQ, Nhan DK *et al.* (2015) Responding to rising sea levels in the Mekong Delta. *Nature Climate Change*, **5**, 167–174.
- Sorensen J, Tiedje JM, Firestone RB (1980) Inhibition by sulfide of nitric and nitrous-oxide reduction by denitrifying pseudomonas fluorescens. *Applied and Environmental Microbiology*, **39**, 105–108.
- Sutter LA, Perry JE, Chambers RM (2014) Tidal freshwater marsh plant responses to low level salinity increases. *Wetlands*, **34**, 167–175.
- Sutter LA, Chambers RM, Perry JE (2015) Seawater intrusion mediates species transition in low salinity, tidal marsh vegetation. *Aquatic Botany*, **122**, 32–39.
- Szabolcs I (1989) *Salt-Affected Soils*. CRC Press, Inc, Boca Raton, FL.
- Teixeira C, Magalhaes C, Joye SB, Bordalo AA (2013) The role of salinity in shaping dissolved inorganic nitrogen and N₂O dynamics in estuarine sediment-water interface. *Marine Pollution Bulletin*, **66**, 225–229.
- Thomas CR, Christian RR (2001) Comparison of nitrogen cycling in salt marsh zones related to sea-level rise. *Marine Ecology Progress Series*, **221**, 1–16.
- Tobias CR, Anderson IC, Canuel EA, Macko SA (2001) Nitrogen cycling through a fringing marsh-aquifer ecotone. *Marine Ecology Progress Series*, **210**, 25–39.
- Van Dijk D, Koenders M, Rebel K, Schaap M, Wassen M (2009) State of the art of the impact of climate change on environmental quality in The Netherlands. A framework for adaptation. Report Knowledge for Climate KfC 006/09, 56 pp.
- Van Hoorn JW, Katerji N, Hamdy A, Mastrorilli M (2001) Effect of salinity on yield and nitrogen uptake of four grain legumes and on biological nitrogen contribution from the soil. *Agricultural Water Management*, **51**, 87–98.
- Wang DQ, Chen ZL, Sun WW, Hu BB, Xu SY (2009) Methane and nitrous oxide concentration and emission flux of Yangtze Delta plain river net. *Science in China Series B-Chemistry*, **52**, 652–661.

- Werner AD, Bakker M, Post VEA *et al.* (2013) Seawater intrusion processes, investigation and management: recent advances and future challenges. *Advances in Water Resources*, **51**, 3–26.
- Weston NB, Giblin AE, Banta GT, Hopkinson CS, Tucker J (2010) The effects of varying salinity on ammonium exchange in estuarine sediments of the Parker River, Massachusetts. *Estuaries and Coasts*, **33**, 985–1003.
- Wong VNL, Dalal RC, Greene RSB (2008) Salinity and sodicity effects on respiration and microbial biomass of soil. *Biology and Fertility of Soils*, **44**, 943–953.
- Xiao YY, Roberts DJ (2010) A review of anaerobic treatment of saline wastewater. *Environmental Technology*, **31**, 1025–1043.
- Yang WH, Traut BH, Silver WL (2015) Microbially mediated nitrogen retention and loss in a salt marsh soil. *Ecosphere*, **6**, 7.
- Zhang LH, Song LP, Zhang LW, Shao HB, Chen XB, Yan K (2013) Seasonal dynamics in nitrous oxide emissions under different types of vegetation in saline-alkaline soils of the Yellow River Delta, China and implications for eco-restoring coastal wetland. *Ecological Engineering*, **61**, 82–89.

- Zhao W, Wang YY, Lin XM, Zhou D, Pan ML, Yang J (2014) Identification of the salinity effect on N₂O production pathway during nitrification: using stepwise inhibition and ¹⁵N isotope labeling methods. *Chemical Engineering Journal*, **253**, 418–426.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Calculation of the effect size of soil salinization on each variable related to coastal ecosystem N pool, cycling and flux.