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RESEARCH ARTICLE

Shifts in soil ammonia-oxidizing community maintain the nitrogen stimulation of nitrification across climatic conditions

Yong Zhang[1,2] | Xiaoli Cheng[1] | Kees Jan van Groenigen[3] | Pablo García-Palacios[4,5] | Junji Cao[6] | Xunhua Zheng[6] | Yiqi Luo[7] | Bruce A. Hungate[8] | Cesar Terrer[9] | Klaus Butterbach-Bahl[10,11] | Jørgen Eivind Olesen[12,13,14] | Ji Chen[2,12]

[1]Key Laboratory of Soil Ecology and Health in Universities of Yunnan Province, School of Ecology and Environmental Science, Yunnan University, Kunming, China

[2]State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an, China

[3]Department of Geography, Faculty of Environment, Science and Economy, University of Exeter, Exeter, UK

[4]Instituto de Ciencias Agrarias, Consejo Superior de Investigaciones Científicas, Madrid, Spain

[5]Department of Plant and Microbial Biology, University of Zurich, Zurich, Switzerland

[6]Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, China

[7]School of Integrative Plant Science, Cornell University, New York, Ithaca, USA

[8]Department of Biological Sciences, Northern Arizona University, Arizona, Flagstaff, USA

[9]Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Massachusetts, Cambridge, USA

[10]Institute for Meteorology and Climate Research, Atmospheric Environmental Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany

[11]Center for Landscape Research in Sustainable Agricultural Futures, Land-CRAFT, Department of Agroecology, Aarhus University, Aarhus, Denmark

[12]Department of Agroecology, Aarhus University, Tjele, Denmark

[13]Aarhus University Centre for Circular Bioeconomy, Aarhus University, Tjele, Denmark

[14]iCLIMATE Interdisciplinary Centre for Climate Change, Aarhus University, Roskilde, Denmark

Correspondence

Xiaoli Cheng, Key Laboratory of Soil Ecology and Health in Universities of Yunnan Province, School of Ecology and Environmental Science, Yunnan University, Kunming, China.
Email: xlcheng@ynu.edu.cn

Ji Chen, State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences.
Email: ji.chen@agro.au.dk

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Abstract

Anthropogenic nitrogen (N) loading alters soil ammonia-oxidizing archaea (AOA) and bacteria (AOB) abundances, likely leading to substantial changes in soil nitrification. However, the factors and mechanisms determining the responses of soil AOA:AOB and nitrification to N loading are still unclear, making it difficult to predict future changes in soil nitrification. Herein, we synthesize 68 field studies around the world to evaluate the impacts of N loading on soil ammonia oxidizers and nitrification. Across a wide range of biotic and abiotic factors, climate is the most important driver of the responses of AOA:AOB to N loading. Climate does not directly affect the N-stimulation of nitrification, but does so via climate-related shifts in AOA:AOB. Specifically, climate modulates the responses of AOA:AOB to N loading by affecting soil pH, N-availability and moisture. AOB play a dominant role in affecting nitrification in dry climates, while the impacts from AOA can exceed AOB in humid climates. Together, these results suggest that climate-related shifts in soil ammonia-oxidizing community maintain the

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N-stimulation of nitrification, highlighting the importance of microbial community composition in mediating the responses of the soil N cycle to N loading.

KEYWORDS
ammonia oxidizers, climate change, microbial community structure, nitrification, nitrogen addition, soil properties

1 | INTRODUCTION

Humans add approximately threefold reactive nitrogen (N) into terrestrial ecosystems compared with natural sources, potentially increasing nitrification in soils (Bowles et al., 2018; Sutton et al., 2011). Nitrification is the key process controlling N losses, since it produces nitrate, which can be easily leached, or lost by denitrification as nitrous oxide and dinitrogen gas (Butterbach-Bahl et al., 2013). For example, the global rate of nitrous oxide emissions from N additions is estimated at about 7 Tg N year^{-1} (Tian et al., 2020). Nitrification is also affected by climatic conditions, such as temperature and precipitation (Bowles et al., 2018; Wang et al., 2014). However, the understanding of the responses of nitrification to enhanced N loading across climatic conditions is still incomplete.

Nitrification has long been considered to be initiated with the oxidation of ammonia to hydroxylamine by ammonia-oxidizing archaea (AOA) and bacteria (AOB) (Kuypers et al., 2018; Zhang et al., 2022). Nevertheless, AOA or AOB abundances have limited power to explain the responses of nitrification to N loading (Carey et al., 2016). Emerging studies suggest that the AOA:AOB ratio (an indicator of the structure of ammonia oxidizers) can be used to capture changes in nitrification (Aigle et al., 2020; Sims et al., 2012). However, the responses of soil AOA:AOB to N loading and the potential implications for nitrification remain unknown.

In addition to N loading characteristics (e.g., rate), soil factors may drive the responses of soil AOA:AOB to N loading, possibly altering nitrification. For instance, early studies report that the growth of ammonia oxidizers depends on soil factors including pH, N-availability and moisture. Prosser and Nicol (2012) show that AOA mostly are acidophilic and prefer to utilize slow-released ammonia from organic N mineralization, while AOB mainly are neutro-alkalinophilic and favored by high-levels ammonia from external N loadings. Liao et al. (2022) show that AOB are more negatively affected by increasing soil moisture than AOA. Previous meta-analyses indicate that N loading decreases soil pH, but this effect may vary with the factors like soil moisture and the N-source (Tian & Niu, 2015; Zhang et al., 2022). Therefore, the effects of N loading on AOA:AOB and nitrification may associate with soil factors, but global evidence is lacking.

Recent studies suggest that climatic conditions substantially alter microbial responses to N loading by affecting soil factors (Borer & Stevens, 2022; Greaver et al., 2016). For example, aridity index (the ratio of annual precipitation to annual potential evapotranspiration; lower aridity index indicates more dry climate, whereas higher aridity index indicates more humid climate) significantly affects soil factors including pH, N-availability and moisture, which often drive microbial abundance and composition (Delgado-Baquerizo et al., 2013; Seneviratne et al., 2010; Slessarev et al., 2016). However, whether and how climatic conditions influence the effects of N loading on soil AOA:AOB and nitrification, and whether climatic impacts on AOA:AOB exert effects on nitrification remain unclear. These knowledge gaps limit our ability to predict N-induced changes in nitrification across climatic conditions, likely leading to over- or under-estimation of N losses (Bowles et al., 2018; Tian et al., 2020).

To explore the relative influence of soil factors, climatic conditions and N loading characteristics on the responses of soil AOA:AOB and nitrification to N loading, we collected data on the effects of N loading on soil AOA:AOB and nitrification from 68 field studies worldwide (Figures S1 and S2). A broad range of potential predictors were also recorded, including climatic conditions, soil factors, N loading characteristics, etc. We then analyzed the data by using meta-forest analysis (Terrer et al., 2021), regression analysis, and structural equation modeling test (Moreno-Jiménez et al., 2019). This study was motivated by the following two fundamental questions: (1) what are the key drivers of the responses of AOA:AOB and nitrification to N loading; and (2) how do the responses of nitrification link with the responses of AOA:AOB?

2 | METHODS

2.1 | Literature search

To make our results comparable to other meta-analyses of N loading experiments, we focused only on potential nitrification as in earlier meta-analyses (Carey et al., 2016; Zhang et al., 2022). By using Web of Science (webofscience.com) and China National Knowledge Infrastructure (oversea.cnki.net), we searched the scientific literature evaluating the effects of N loading on soil ammonia oxidizers and/or potential nitrification. Relevant articles published before 2022 were retrieved using two sets of search terms: (i) one for ammonia oxidizers: ("nitrogen addition" OR "nitrogen amendment" OR "nitrogen enrichment" OR "nitrogen fertili*" OR "nitrogen deposition" OR "nitrogen load*") AND ("soil" AND "gene*" AND "*PCR") AND ("*amoA" OR "AOA" OR "AOB"); (ii) and a second for potential nitrification: ("nitrogen addition" OR "nitrogen amendment" OR "nitrogen enrichment" OR "nitrogen fertili*" OR "nitrogen deposition" OR "nitrogen load*") AND ("soil" AND "nitrification").

The articles were then selected according to the following criteria: (i) soils were sampled from surface layers (<20 cm) under field conditions; (ii) both archaeal and bacterial *amoA* abundances were quantified by qPCR, and/or potential nitrification was estimated from the rate of nitrate or nitrite production during 24 h incubation under optimal conditions (Zhang et al., 2022); (iii) ambient and N loading treatments were applied for at least 1 year; (iv) mean values, standard deviations and replicate numbers could be acquired directly or indirectly. Observations disturbed by other experimental factors (e.g., irrigation, warming, precipitation, CO_2 enrichment, nitrification inhibitors, etc.) were excluded (Horz et al., 2004). For multiyear experiments, data on the last measurements in the growing season were preferentially used (Zhang et al., 2022). A total of 68 eligible studies were identified (Figures S1 and S2), of which 56 reported on ammonia oxidizers, 43 reported on potential nitrification, and 31 covered both.

2.2 | Data extraction

2.2.1 | Response variables

Data were taken directly from tables and text, or extracted from figures using Grapher software (goldensoftware.com). We obtained the ratios of AOA:AOB by using reported archaeal and bacterial *amoA* abundances. To explore linkages between potential nitrification and AOA:AOB, we also gathered potential nitrification data if available. Within the 68 identified studies, there were 143 paired observations of AOA:AOB (Data S1), 98 observations of potential nitrification (Data S2), and 67 observations covering both (Data S3).

2.2.2 | Predictor variables

We documented potentially relevant environmental and experimental factors as predictor variables. (i) Location: latitude (°), elevation (m). (ii) Climate: aridity index, mean annual temperature (MAT, °C). (iii) Vegetation: aboveground biomass (AGB, g C m^{-2}), ecosystem type (cropland, grassland or forest). (iv) Soil: pH, the ratio of C to N (C:N), available P (AP, mg kg $soil^{-1}$), bulk density (BD, g soil cm^{-3}), clay (%), volumetric moisture (%), and N-mineralization rate (mg kg $soil^{-1}$ day^{-1}). (v) N loading characteristics: rate (g N m^{-2} $year^{-1}$), duration (year), form (urea, NH_4NO_3 or others), and amount of N application (g N m^{-2}). Because aridity index integrates the effects of rainfall and warming, it is generally considered as an integrator of climatic conditions (Garcia-Palacios et al., 2018). Based on aridity index, we grouped study sites to be located either in dry (aridity index <0.65) or humid (aridity index ≥0.65) climates. The cutoff of 0.65 was defined by the United Nations Convention to Combat Desertification (Dudley & Alexander, 2017). Almost 30% of environmental data were not reported in the primary studies (Data S1–S3). We obtained these from various online databases: extracting location data from Google Earth (earth.google.com), climate data from WorldClim (Fick & Hijmans, 2017) and CGIAR-CSI (Zomer et al., 2022), vegetation data from ORNL DAAC (Spawn et al., 2020), and soil data from SoilGrids250m (Hengl et al., 2017), SoMo.ml (Orth, 2021), the soil N database (Elrys et al., 2022), and the soil P database (Yang et al., 2013).

2.3 | Statistical analyses

2.3.1 | Effect sizes

We assessed the effect of N loading on each response variable by calculating the natural logarithmic response ratio (ln*R*) of the N loading treatment relative to the ambient treatment, where ln*R* was weighted by the inverse of its variance (Chen et al., 2018; Hedges et al., 1999). Response ratios of AOA:AOB and potential nitrification were marked as $\ln R_{(AOA:AOB)}$ and $\ln R_{(Nitrification)}$, respectively. The mean effect size ($\overline{\ln R}$) was estimated in a weighted mixed-effects model by using the R package *metafor* (Viechtbauer, 2010). Some studies contributed more than one paired observation, thus we considered "study" and "observation" as random factors. For the ease of interpretation, the mean effect size was transformed into percentage change, that is, $\left(e^{\overline{\ln R}} - 1\right) \times 100\%$. The mean effect of N loading is considered significant at $p < .05$.

2.3.2 | qPCR effectiveness and publication bias

The test of moderators in the R package *metafor* (Viechtbauer, 2010) was used to evaluate the impacts of primer selections and inhibition tests (Data S1) on response ratios of *amoA* abundances. The impact of methodological approaches is considered significant if $p < .05$ (Zhang et al., 2022). In addition, we assessed publication bias by two tests. Spearman's correlation test was used to test the correlation between individual effect sizes and the corresponding variances. Publication bias is considered absent if Spearman's correlation is non-significant (Nerlekar & Veldman, 2020). We also used Rosenberg's fail-safe number (*f*) analysis. The dataset is considered unbiased if *f* is larger than $5n+10$, where *n* is the number of observations (Rosenberg, 2005). We did not detect any impact of methodological approaches nor publication bias in our dataset (Tables S1 and S2).

2.3.3 | Variable importance

To identify the most important predictors of $\ln R_{(AOA:AOB)}$ and $\ln R_{(Nitrification)}$, we performed meta-forest analysis (Terrer et al., 2021). The meta-forest analysis is an adaptation of the random-forest algorithm for meta-analysis: weighted bootstrap sampling is used to ensure that more precise studies exert greater influence in the model-building stage. These weights are based on random-effects, so that studies with smaller sampling variance have a larger probability of being selected, but this advantage is diminished as the number of between-studies heterogeneity increases. Although selecting a random subset of the features at each candidate split in the meta-forest analysis can help avoid overfitting and multicollinearity, spatial autocorrelation is not accounted for in the meta-forest analysis due to computational limitations (Liang et al., 2022; van Lissa, 2020).

All potential predictors were included in the meta-forest model by using the R package *metaforest* (van Lissa, 2020). This model was run with 10,000 iterations, and was replicated 100 times by a recursive algorithm provided by the R package *metafor* (Viechtbauer, 2010). Predictors that reduced predictive performance (i.e., negative importance) were dropped, while predictors that improved predictive performance (i.e., positive importance) were maintained. Model parameters were further optimized by using the *train()* function from the R package *caret* (Kuhn, 2008). We calculated tenfold cross-validated R^2 values by using 75% of the dataset as training data and 25% for validation. The relative importance of each predictor was derived from the optimized model.

2.3.4 | Empirical relationships

Meta-forest analysis identified aridity index as the most important predictor of $\ln R_{(AOA:AOB)}$ and $\ln R_{(AOA:AOB)}$ as the best predictor of $\ln R_{(Nitrification)}$ (Figure 1). Regression analysis was used to assess the relationship between $\ln R_{(AOA:AOB)}$ and aridity index. The optimal regression model was selected by Bayesian information criterion (BIC; linear and quadratic models were considered). To further explore potential impacts of aridity index on nitrification, we assessed the relationships between $\ln R_{(Nitrification)}$ and $\ln R_{(AOA:AOB)}$, and between $\ln R_{(Nitrification)}$ and aridity index. The interaction between aridity index and $\ln R_{(AOA:AOB)}$ on $\ln R_{(Nitrification)}$ was tested by regression analysis.

2.3.5 | Structural equation modeling

Aridity index has been shown to substantially affect soil factors including pH, N-availability and moisture (Delgado-Baquerizo et al., 2013; Seneviratne et al., 2010; Slessarev et al., 2016), and these soil factors typically determine the niche of ammonia oxidizers (Liao et al., 2022; Prosser & Nicol, 2012). Based on this understanding, we built a structural equation modeling (Figure S3) to test the underlying mechanisms of aridity index in affecting $\ln R_{(AOA:AOB)}$. Soil N-availability was indicated by N-mineralization rate and N loading rate. We included a random effect based on the geographical distance, to remove confounding effects due to spatial autocorrelation (Moreno-Jiménez et al., 2019). The performance of structural equation modeling was evaluated by chi-squared test, which is considered convergent if $p > .05$. Structural equation modeling was conducted with the R package *piecewiseSEM* (Lefcheck, 2016).

2.3.6 | Climate change projections

To understand how future climate change may impact $\ln R_{(AOA:AOB)}$ and $\ln R_{(Nitrification)}$, we accessed global mean aridity index from 2000 to 2100 projected by the fifth Coupled Model Intercomparison Project (CMIP5) under the representative concentration pathways RCP4.5 and RCP8.5 (Huang et al., 2016). These projections of aridity index were used to simulate global mean $\ln R_{(AOA:AOB)}$ and $\ln R_{(Nitrification)}$ from 2000 to 2100 by scaling-up the observed relationships ($\ln R_{(AOA:AOB)}$ vs. aridity index, and $\ln R_{(Nitrification)}$ vs. aridity index). The *predict()* function from the R package *car* (Fox & Weisberg, 2019) was run to simulate the predicted values ($\widehat{\ln R}$) of $\ln R_{(AOA:AOB)}$ and $\ln R_{(Nitrification)}$ from 2000 to 2100. To ease interpretation, the predicted values were reported as percentage change, that is, $\left(e^{\widehat{\ln R}} - 1\right) \times 100\%$.

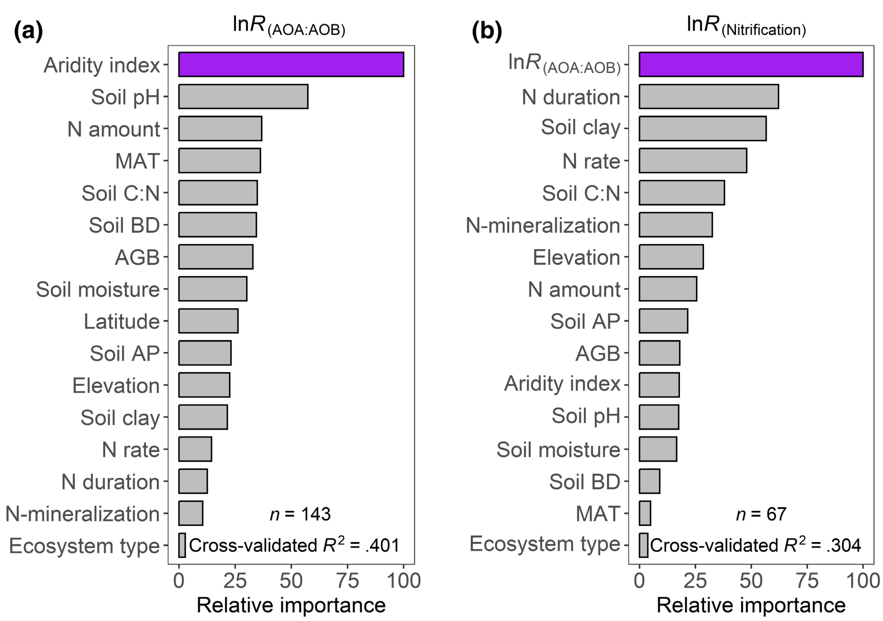

FIGURE 1 The most important predictors for the effects of N loading on AOA:AOB ($\ln R_{(AOA:AOB)}$) and potential nitrification ($\ln R_{(Nitrification)}$). (a) Relative importance of 17 predictors (N form was dropped due to negative importance) of $\ln R_{(AOA:AOB)}$ derived from meta-forest model. (b) Relative importance of 18 predictors (N form and latitude were dropped due to negative importance) of $\ln R_{(Nitrification)}$ derived from meta-forest model. AGB, aboveground biomass; AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; AP, available phosphorus; BD, bulk density; C:N, the ratio of carbon to nitrogen; MAT, mean annual temperature.

3 | RESULTS

Across a wide range of environmental and experimental factors, aridity index was the most important predictor of $\ln R_{(AOA:AOB)}$ (Figure 1a), where $\ln R_{(AOA:AOB)}$ increased with aridity index ($p<.001$; Figure 2a). The mean effect of N loading on AOA:AOB differed between dry (aridity index <0.65) and humid (aridity index ≥0.65) climates ($p<.001$). Specifically, N loading reduced AOA:AOB by 67% in dry climates ($p<.001$), while this effect was not significant in humid climates ($p=.165$).

Structural equation modeling test showed that aridity index modulated the responses of AOA:AOB to N loading by affecting soil pH, N-mineralization rate, and soil moisture (Figure 3). The responses of AOA and AOB abundances to N loading differed in their relationships to aridity index, soil pH, N-mineralization rate, soil moisture, and N loading rate (Figure S5). The responses of AOA abundance increased with aridity index and N-mineralization rate, while the responses of AOB abundance decreased with aridity index and soil moisture, and increased with soil pH and N loading rate ($p<.05$).

Furthermore, $\ln R_{(AOA:AOB)}$ was the best predictor of $\ln R_{(Nitrification)}$ (Figure 1b), in which $\ln R_{(Nitrification)}$ showed a U-shaped relationship with $\ln R_{(AOA:AOB)}$ ($p<.001$; Figure 2b). However, aridity index had no direct influence on $\ln R_{(Nitrification)}$ ($p=.469$; Figure 2c), with a similar N-stimulation of potential nitrification in both dry and humid climates ($p=.804$). Specifically, N loading increased potential nitrification by 63% and 57% in dry ($p<.001$) and humid climates ($p=.003$), respectively. There was a strong interactive effect between aridity index and $\ln R_{(AOA:AOB)}$ on $\ln R_{(Nitrification)}$ ($p<.001$; Figure S4). The negative relationship between $\ln R_{(Nitrification)}$ and $\ln R_{(AOA:AOB)}$ was clear in dry climates ($p=.023$), but no clear relationship was found in humid climates ($p=.742$; Figure 2d).

By scaling-up our results using climate change projections of aridity index, we estimated that the global mean effect of N loading on AOA:AOB will diminish by 5%–8% from 2000 to 2100 under RCP4.5 and RCP8.5 (Figure 4a), while the global mean responses of potential nitrification will be largely unaffected (Figure 4b).

4 | DISCUSSION

4.1 | Climate modulates the responses of ammonia oxidizers to N loading

Our results suggest that climate (indicated by aridity index; lower aridity index indicates more dry climate, whereas higher aridity index indicates more humid climate) primarily regulates the responses of soil AOA:AOB to N loading by affecting soil pH, N-availability and moisture (Figures 1a, 2a and 3). First, difference in soil pH between climates can induce selection pressures on AOA and AOB, thereby regulating the responses of AOA:AOB to N loading (Figure 3; Figure S5). Although N-induced changes in soil pH are not related to aridity index (Table S4), background soil pH (i.e., soil pH in ambient conditions) decreases

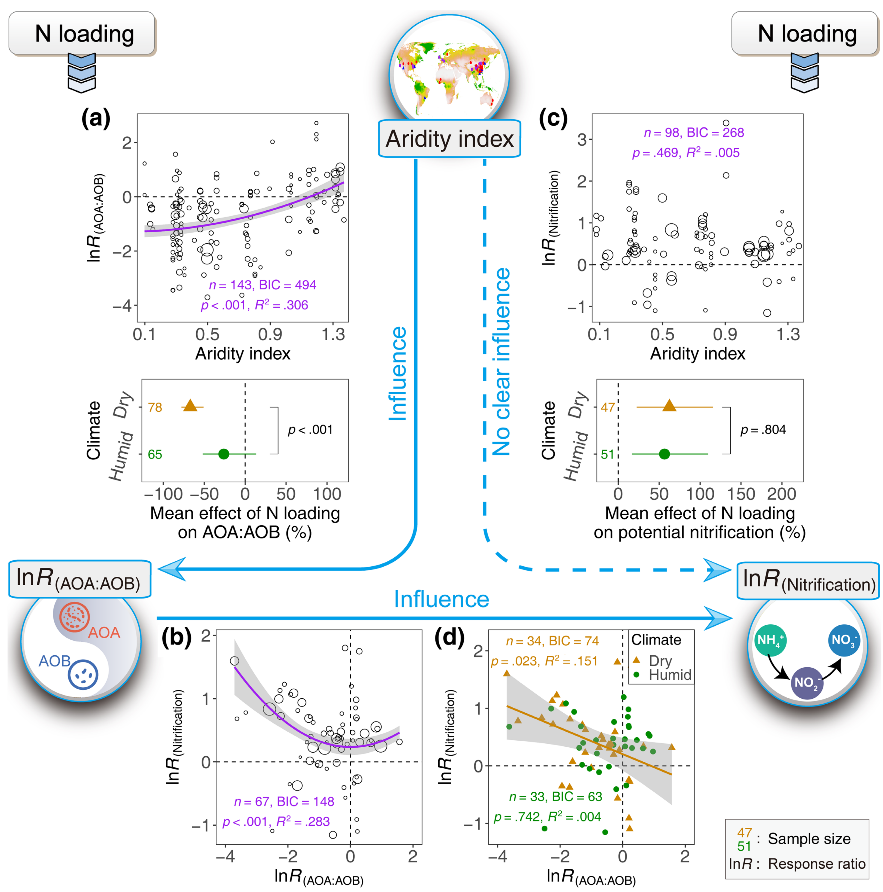

FIGURE 2 Climate indirectly modulates the effects of N loading on potential nitrification ($\ln R_{(Nitrification)}$) by affecting shifts in AOA:AOB ($\ln R_{(AOA:AOB)}$). (a) Relationship between $\ln R_{(AOA:AOB)}$ and aridity index. (b) Relationship between $\ln R_{(Nitrification)}$ and $\ln R_{(AOA:AOB)}$. (c) Relationship between $\ln R_{(Nitrification)}$ and aridity index. (d) Interaction between climate and $\ln R_{(AOA:AOB)}$ on $\ln R_{(Nitrification)}$. The sizes of empty dots are proportional to model weights. Difference between dry (aridity index <0.65) and humid (aridity index ≥0.65) climates was evaluated by Student's t-test. Error bars show 95% confidence intervals, and the corresponding numbers indicate sample sizes. Lower aridity index indicates more dry climate, whereas higher aridity index indicates more humid climate. AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria.

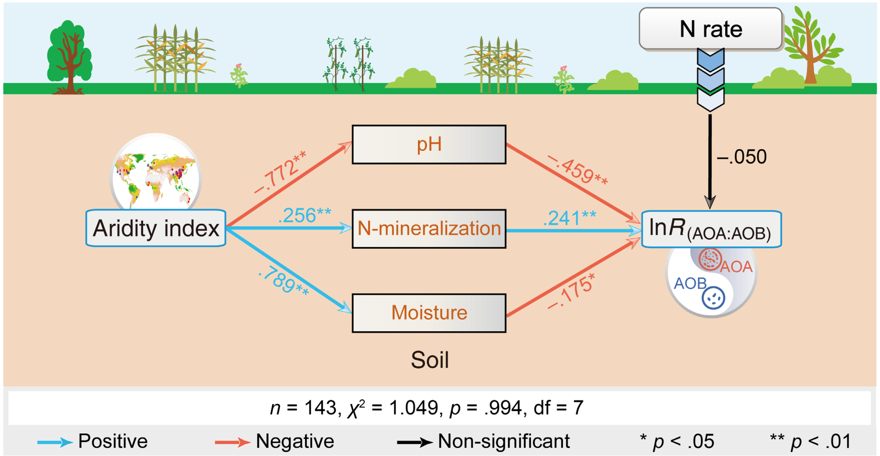

FIGURE 3 Structural equation modeling test of how aridity index affects the responses of AOA:AOB to N loading ($\ln R_{(AOA:AOB)}$). Nitrogen-mineralization rate and N loading rate can reflect soil N-availability. The numbers on arrows indicate standardized path coefficients of structural equation modeling. Lower aridity index indicates more dry climate, whereas higher aridity index indicates more humid climate. AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria.

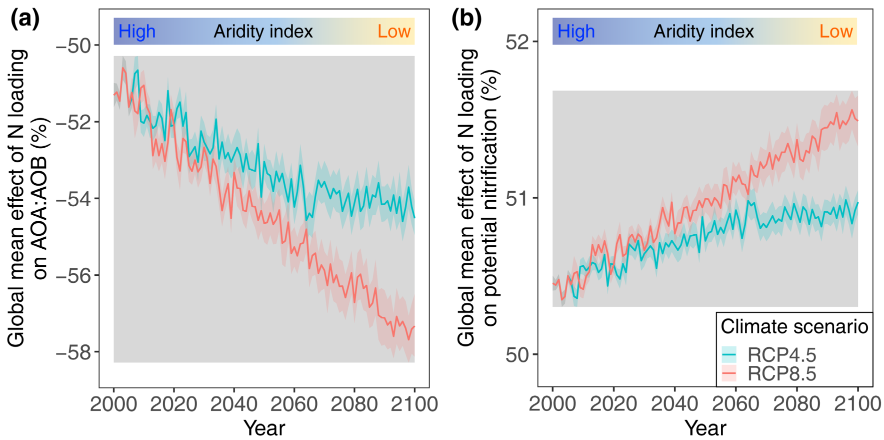

FIGURE 4 Potential changes in global mean effects of N loading on AOA:AOB and potential nitrification from 2000 to 2100 that are scaled-up from the observations. Temporal variations in global mean effects of N loading on (a) AOA:AOB and (b) potential nitrification from 2000 to 2100 under RCP4.5 and RCP8.5. Colored shading area indicates 95% confidence intervals, and gray shading area denotes the ranges of temporal variations. Lower aridity index indicates more dry climate, whereas higher aridity index indicates more humid climate. Notice difference in scales between panels. AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; RCP, representative concentration pathway.

with aridity index (Figure S5). Alkaline soils are more common in dry climates while acid soils are widely distributed in humid climates (Table S3). Alkaline soils generally favor AOB growth, whereas acid soils can better facilitate AOA growth (Prosser & Nicol, 2012). This explanation aligns with the positive correlation coefficient between the responses of AOB and soil pH, and the negative correlation coefficient between the responses of AOA and soil pH (Figure S5).

Second, climate to some extent affects soil N-availability, which in turn mediates the responses of AOA:AOB to N loading because of different N preferences between AOA and AOB (Figure 3; Figure S5). Nitrogen loading can stimulate soil N mineralization, and this effect increases with aridity index (Cheng et al., 2020). Soil N mineralization rate increases with aridity index (Figure S5), suggesting that organic-derived N is more abundant in humid climates than in dry climates (Table S3). AOA mostly prefer to utilize slow-released ammonia from organic N mineralization, while AOB are mainly favored by high-level ammonia from external N loadings (Prosser & Nicol, 2012). Consistent with those preferences, the responses of AOA increase with N mineralization rate, and the responses of AOB increase with N loading rate (Figure S5).

Third, the responses of AOA:AOB to N loading partly depend on soil moisture, where soil moisture is often coupled with climate (Figure 3; Figure S5). Nitrogen loading has no clear effect on soil moisture, and this effect is not affected by aridity index (Table S4). However, as aridity index increases, soil moisture rises accordingly (Figure S5). AOB often decrease with rising soil moisture, while AOA generally increase or remain unchanged (Liao et al., 2022; Yue et al., 2021). This interpretation is in line with the negative relationship between the responses of AOB and soil moisture, and the non-significant relationship between the responses of AOA and soil moisture (Figure S5).

4.2 | Shifts in ammonia oxidizers maintain the N-stimulation of nitrification

The U-shaped relationship between the responses of potential nitrification and the responses of AOA:AOB under N loading (Figure 2b) suggests that the responses of nitrification vary nonlinearly with the responses of AOA:AOB. This finding is consistent with studies showing that microbial function can shift with community structure across different climates (Chase et al., 2021; Crowther et al., 2019; Fernandez et al., 1999; Hoffmann & Sgro, 2011). On the other hand, N loading stimulates potential nitrification to a similar extent across different climates (Figure 2c), indicating that climate-related shifts in soil ammonia-oxidizing community maintain the N-stimulation of nitrification. Specifically, AOB play a dominant role in affecting nitrification in dry climates, while the impacts from AOA can exceed AOB in humid climates (Figure S6).

The structure–function relationship of soil ammonia-oxidizing community can be affected by environmental conditions (Zhang, Chen, et al., 2023). For example, we observe that climate alters the relationship between the responses of potential nitrification and the responses of AOA:AOB under N loading (Figure 2d). However, other factors (e.g., trait distributions within a community, species-species interactions, evolutionary dynamics, and community assembly processes) may also affect the structure–function relationship of ammonia oxidizers (Nemergut et al., 2014). These factors may interact with environmental conditions, adding uncertainty to future projections of nitrification. Therefore, further research is required to quantify these interactions.

4.3 | Implications and potential uncertainties

We quantified the relationships among ammonia-oxidizing community structure, function, and environmental conditions, thereby advancing the understanding of the responses of ammonia oxidizers and nitrification to N loading in three ways. (1) AOA:AOB is a better predictor of nitrification under N loading than either AOA or AOB abundances (Carey et al., 2016). (2) AOA:AOB exerts a significant influence on nitrification at the global scale, challenging the common assumption that microbial community structure controls function predominantly at the local scale (Schimel & Gulledge, 1998). (3) In addition to earlier identified key drivers (soil pH, N-availability and moisture) of ammonia oxidizers (Liao et al., 2022; Prosser & Nicol, 2012), we offer new insights in terms of climatic impacts of ammonia oxidizers.

Furthermore, we inferred a persistent N-stimulation of potential nitrification under future climate change scenarios despite clear shifts in AOA:AOB (Figure 4). However, key microbial traits (e.g., AOA:AOB and nitrification) are insufficiently considered in current ecosystem models, potentially leading to model uncertainties (Crowther et al., 2019; Hawkes & Keitt, 2015; Nevison et al., 2022). For example, without considering shifts in AOA:AOB, the CLASSIC model (Asaadi & Arora, 2021) simulates a large increase in N-stimulation of nitrification under climate change. This result contradicts the finding of our meta-analysis, which suggests a stable N-stimulation. Hence, incorporating shifts in AOA:AOB into microbial trait-based frameworks may help to simulate future changes in soil N cycling (Chen et al., 2023; Crowther et al., 2019).

A few potential limitations of our analyses should be noted. First, spatiotemporal variability may be underrepresented in our dataset. For example, there are unbalanced samples across climatic zones and different sampling years among studies. Covering underrepresented areas (especially tropical and polar zones) in future research projects will likely advance the understanding of microbial feedbacks to N loading. Second, missing data were imputed using some global databases, potentially introducing bias into our results. For instance, the ensemble models producing SoilGrids250m database explain 83% variation in observed soil pH (Hengl et al., 2017), and the unexplained 17% variation introduces some potential uncertainty into our results. Third, inherent model limitations may affect variable importance analysis and future projection. One example is that machine learning-based meta-forest analysis is data-hungry while our sample size is relatively small. Another example is that there are no observational data of the future period to validate the CMIP5 ensemble (Huang et al., 2016). Further development of global databases and mechanistic models may decrease these potential uncertainties. Fourth, although we revealed relationships among ammonia oxidizers, nitrification and climate under N loading, the acclimatization rates of different guilds to climate change are still unclear. This challenge can be addressed through manipulative experiments (Hoffmann & Sgro, 2011). Fifth, the use of DNA-based methods and potential rates may only provide limited information of ammonia oxidizers and nitrification (Zhang, Chen, et al., 2023). The development and wider application of new techniques is therefore critical, such as in-situ methods measuring N-cycling genes and rates.

In summary, our work indicates that climate-related shifts in soil ammonia-oxidizing community maintain the N-stimulation of nitrification, emphasizing the key role of climate in mediating the responses of ammonia oxidizers to N loading. Therefore, considering climate-related shifts of ammonia oxidizers in ecosystem models may improve predictions of soil N cycling under future climatic conditions.

AUTHOR CONTRIBUTIONS

Yong Zhang: Conceptualization; data curation; formal analysis; visualization; writing – original draft; writing – review and editing. **Xiaoli Cheng:** Conceptualization; data curation; formal analysis; funding acquisition; visualization; writing – original draft; writing – review and editing. **Kees Jan van Groenigen:** Funding acquisition; methodology; writing – review and editing. **Pablo García-Palacios:** Methodology; writing – review and editing. **Junji Cao:** Writing – review and editing. **Xunhua Zheng:** Writing – review and editing. **Yiqi Luo:** Methodology; writing – review and editing. **Bruce A. Hungate:** Methodology; writing – review and editing. **Cesar Terrer:** Methodology; writing – review and editing. **Klaus Butterbach-Bahl:** Methodology; writing – review and editing. **Jørgen Eivind Olesen:** Methodology; writing – review and editing. **Ji Chen:** Conceptualization; data curation; formal analysis; funding acquisition; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.20022878 (Zhang, Cheng, et al., 2023).

ORCID

Yong Zhang https://orcid.org/0000-0002-1181-032X
Xiaoli Cheng https://orcid.org/0000-0002-0346-675X
Kees Jan van Groenigen https://orcid.org/0000-0002-9165-3925
Pablo García-Palacios https://orcid.org/0000-0002-6367-4761
Junji Cao https://orcid.org/0000-0003-1000-7241
Xunhua Zheng https://orcid.org/0000-0002-4138-7470
Yiqi Luo https://orcid.org/0000-0002-4556-0218
Bruce A. Hungate https://orcid.org/0000-0002-7337-1887
Cesar Terrer https://orcid.org/0000-0002-5479-3486
Klaus Butterbach-Bahl https://orcid.org/0000-0001-9499-6598
Jørgen Eivind Olesen https://orcid.org/0000-0002-6639-1273
Ji Chen https://orcid.org/0000-0001-7026-6312

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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