Effects of climate and soil properties on regional differences in nitrogen use efficiency and reactive nitrogen losses in rice

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Abstract
Nitrogen (N) use efficiency worldwide varies greatly due to climate, agronomic, and soil factors. However, the information on individual effects of these factors on N use efficiency is crucial but has remained scanty. Given that climate cannot be regulated, understanding the relative importance of fertilizer and soil variations on regional differences in N use efficiency is critical. Here, we constructed a database of 302 studies from 1986 to 2020 in East and Northeast China to determine the effects of climate, soil properties, and fertilizer N (FN) rate on variations in N use efficiency (agronomic efficiency (AE), apparent recovery efficiency (RE), physiological efficiency (PE), N harvest index, partial factor productivity), N surplus, grain N content, and reactive N (Nr) losses (N2O emissions, NH3 volatilization, Nr leaching, and runoff). Rice yield was comparable between two regions under farmers’ N practices, yet the N input was considerably higher in East China. All indices of N use efficiency, except RE, are higher in Northeast China. Differences in AE were dominated by the ability of the plant to mobilize N (PE) rather than N uptake (RE), FN, or Nr loss. Soil properties and FN related to optimizable N management accounted for 29% (RE), 39% (PE), and 43% (Nr losses) of the variations, of which key factors as pH showed a negative effect while available N (AN) correlated positively to the N use efficiency. To realize high N use efficiency, pivotal effects of pH, AN, and FN on N use efficiency under certain climate zone should be considered.

1. Introduction
Nitrogen (N) is an essential nutrient for plant growth and development, with an optimal supply having fundamental effects on crop production (FAO 2018). However, the rapid increase in N fertilizer application worldwide has exceeded the crop N consumption, increasing environmental pollution with reactive N (Nr), causing global warming, eutrophication, and other ecological and social problems (Chen et al 2014, Hundey et al 2016). Therefore, enhancing crop N use efficiency with lower fertilizer N (FN) input and higher crop productivity has become an important challenge in sustainable agriculture (Masclaux-Daubresse et al 2010).

Rice is the main staple crop in Asia, occupying 12% of global arable land and feeding more than half of the world population (Muthayya et al 2014, FAO 2018). However, N fertilizer application during rice cultivation is irrationally high in China, accounting for 15.2% of the global fertilizer consumption (Heffer et al 2017). Due to the wide distribution of Chinese rice-growing regions from frigid to subtropical zones, apparent N recovery efficiency (RE) and physiological N efficiency (PE) vary widely from 30% to 46% and 33 to 49 kg kg−1, respectively (Che et al 2015).

Agronomic efficiency (AE), PE, and partial factor productivity (PFP) are routinely used to assess N use efficiency and are highly interrelated. As an important indicator of grain production and environmental
degradation, RE was recently proposed as an index of sustainable development goals by the UN General Assembly (Sustainable Development Solutions Network 2015). Global cereal RE was documented at 33% in 1999 (Raun and Johnson 1999). Although with the development of advanced techniques, cereal RE was estimated to increase by only 2% in 2015 (Omara et al 2019). Similarly, PFP and PE have also shown stagnation, or decrease, during the past two decades (Ciampitti and Vyn 2014, He et al 2020). Efforts have therefore been made to reduce the gap between current levels and the target N use efficiency for the dual goals of food safety and environmental sustainability (Hakeem et al 2011, Zhang et al 2015). In doing so, it is important to consider the differences in fertilizer performance under different soil and climate conditions, which can hinder improvements in N use efficiency (Xia et al 2017, Li et al 2018).

Currently, the relative contributions of soil and climate to the heterogeneity of N use efficiency and Nr losses under rice production remain unknown. When applied to fields, N fertilizer undergoes both physical and biochemical processes in the soil, which are highly sensitive to soil properties or climate changes (Brevik 2012). Meanwhile, the efficiency of rice to uptake fertilizer, indigenous soil N supply, and Nr losses varies with the management practice, cultivar (Omara et al 2019, Gao et al 2020), climate condition, and soil properties (Cassman et al 1998). The diverseness of AE under similar N management practices in different regions further suggests the salient effect of environmental factors on the performance of N use efficiency (Wang et al 2020). Soil with a high N buffering capacity promotes N fertilizer conservation, resulting in higher RE and lower Nr losses (Quan et al 2021). Given that climate change is rather unpredictable in certain rice-growing regions, understanding the contribution of soil properties and FN rate to regional variability in N use efficiency and Nr losses is crucial for the development of knowledge-based management practices.

East and Northeast China represent two major rice-growing regions, comprising 19% and 17% of the total rice cultivation area in China, respectively (Rural Social Economic Investigation Department of National Bureau of Statistics 2019). Rice production is comparable between two regions at 7–8 Mg ha$^{-1}$, while FN application varies greatly from 220 to 360 kg N ha$^{-1}$ and 135 to 225 kg N ha$^{-1}$, for East and Northeast China, respectively (Zhang et al 2018). Assuming that crop N requirements are similar at approximately equivalent rice yield, it implies contradicting patterns of N use efficiency between the two regions. We hypothesize that the different N use efficiencies between two regions might owe more to the soil properties and climatic factors. In this study, we carried out a meta-analysis based on a regional database compiled using 3394 observations from 302 articles based in East and Northeast China. Using these regions as a case study, the objectives of this study are to (a) compare the difference in N use efficiency response to FN between two regions; (b) unravel the major contributors behind the diverseness of N use efficiency and Nr losses; (c) propose effective ways for supporting site-specific FN management.

2. Materials and methods

2.1. Description of the rice-growing regions

Two representative rice-growing regions were selected (East and Northeast China) to compare differences in yield, Nr losses, and N use efficiency. Here East China mainly includes five provinces or municipalities (Jiangsu, Anhui, Zhejiang, Shanghai, and Shandong), and is located between 27°–38° N and 114°–123° E, with a subtropical monsoon climate (figure 1(a)). The rice-growing area comprises 19% of the total production area in China, and the major paddy soil type in this region is Stagnic Anthrosols or Stagnic Luvisols (International Union of Soil Sciences Working Group WRB 2014) with high variation in soil properties. Northeast China is one of the key rice-growing regions in China representing 17% of the national total across three provinces (Heilongjiang, Jilin, Liaoning) ranging between 38°–53° N and 118°–135° E, encompassing two climatic zones (figure 1(b)). The typical paddy soil types in Northeast China are Haplic Luvisols or Lithic Leptosols (International Union of Soil Sciences Working Group WRB 2014). The major rice cultivation systems in East China are rice-wheat and rice-rape rotations, with a rice-growing period from mid-April to early October, whereas the single-rice growing period in Northeast China is early May to late September. Farmers’ N application rate (FNR) was defined as 220–360 kg N ha$^{-1}$ in East China and 135–225 kg N ha$^{-1}$ in Northeast China, based on the survey results of Zhang et al (2018).

2.2. Data collection

A database of the two rice-growing regions was constructed based on peer-reviewed journal articles and master/PhD theses published from 1986 to January 2020. The publication databases included the Web of Science (Thomson Reuters, USA) and China National Knowledge Infrastructure, with the following search terms used as keywords: ‘China’ AND ‘rice’, ‘Leach$^*$ OR ‘Runoff’ OR ‘N$_2$O’ OR ‘NO$_2$’ OR ‘Nitrous oxide’ OR ‘Ammonia’ OR ‘NH$_3$’, ‘Reactive nitrogen’, ‘Nitrogen uptake’ OR ‘Nitrogen recovery’ OR ‘NUE’ OR ‘Nitrogen use efficiency’, ‘Yield’. Duplicates in the database were identified before selecting eligible data by the following criteria: (a) consisted of replicated field-based or undisturbed lysimeter experiments based on rice cultivation in East or Northeast China; (b) N input was in the form of chemical
fertilizer, without straw/organic manure/enhanced-efficiency fertilizer application; (c) at least one of the following indices was reported and monitored throughout the rice-growing season: yield, \( N_2O \) emissions, \( \text{Nr} \) leaching from the top 1 m of the soil profile, \( \text{Nr} \) runoff, \( \text{NH}_3 \) volatilization, crop N uptake, and apparent N RE.

The database included a total of 302 published experimental studies conducted in East and Northeast China, of which 194, 74, 112, 47, 55, and 112 comprised data on yield, \( \text{NH}_3 \), \( N_2O \), \( \text{Nr} \) runoff, \( \text{Nr} \) leaching, and apparent N RE, respectively (Figure 1). Several observations were derived from a single study site if multiple treatments or dependent variables were reported. In total, 236 and 71 of the studies were constructed in East and Northeast China, respectively, with five studies comprising observations in both regions. Units of the value obtained from articles were unitized into kg N ha\(^{-1}\) for inorganic N input and Nr losses, Mg ha\(^{-1}\) for yield production, kg kg\(^{-1}\) N for AE and PE, and % for RE and the N harvest index (NHI). Figure digitization was performed using Origin Pro (Version 2019b, USA) when data were presented as plots only.

Soil properties and climatic factors were also extracted for comparison and determination of their contributions to FN performance between the two regions (Figure S1 available online at stacks.iop.org/ERL/17/054039/mmedia). The information included the geographical location, climate data (mean seasonal temperature (MST), mean seasonal precipitation (MSP), mean seasonal sunshine hours (MSS), and mean seasonal humidity (MSH)), soil physical properties (clay content and bulk density), soil chemical properties (pH, soil organic carbon (SOC), total N (TN), total P, total K, available N (AN), available P, available K). Information on soil pH and clay fractions was obtained from the Harmonized World Soil Database (Nachtergaele et al 2012), while data on MST, MSP, MSS, and MSH were obtained from the China Meteorological Data Service Centre (http://data.cma.cn/en) using the geographical location of each study when corresponding soil or climate data was not reported. Rice cultivars were clustered into five groups to determine the effect of rice cultivars on N use efficiency in the two rice-growing regions (supplementary note 1).

2.3. Data analysis

Linear and nonlinear mix-effect models with the site as random effect accounting for between-study variability were established using the maximum likelihood method in the nlme package (Zuur et al 2009, Core Team R 2014). Models were created based on the peer-reviewed database for both regions as follows:

\[
\text{Yield} = \alpha_i + \beta_i N + \gamma_i N^2 \tag{1}
\]

\[
\text{Nr-} \text{NH}_3 = \delta_i + \varepsilon_i N \tag{2}
\]

\[
\text{Nr-} N_2O / \text{Leaching} / \text{Runoff} = \zeta_i \times e^{\delta N} \tag{3}
\]

where Yield represents rice grain yield (Mg ha\(^{-1}\)); \( N \) is the N fertilizer application rate (kg N ha\(^{-1}\)); \( \alpha_i, \beta_i, \gamma_i, \delta_i, \varepsilon_i, \zeta_i \) and \( \eta_i \) are corresponding parameters; and \( \text{Nr} \) is the Nr loss (kg N ha\(^{-1}\)).

Data on variables related to N use efficiency indices (PFP, AE, RE, PE, NHII; definitions for these indices are provided in supplementary note 2), and grain N content in response to N application rate were obtained using mix-effect models with site as a random effect as follows:

\[
\text{AE}/\text{Grain N content} = \alpha_i + \beta_i N \tag{4}
\]

\[
\text{RE}/\text{NHII}/\text{PE}/\text{PFP} = \gamma_i \times e^{\delta N} \tag{5}
\]

where NHII indicates the N harvest index. Marginal and conditional \( r^2 \) values were calculated to determine the variance explained by the fixed and random effects of each model (Nakagawa and Schielzeth 2013). The population prediction interval procedure in the MASS package was used to calculate confidence limits based on Bolker (2008).

Here we used N surplus as an indicator of risks for N loss or soil N depletion, under straw removed and straw return scenarios in two rice-cultivated regions (supplementary note 2).
Figure 2. Rice yield performance and N use efficiency in each rice growing region. (a) Responses of the partial factor productivity (PFP), agronomic efficiency (AE), and physiological efficiency (PE) performance to N rates in East China (red) and Northeast China (blue). Values in parentheses after the number of observations (n) represent the number of studies from which the findings originated, while values in parentheses after the $R^2$ represent the conditional $R^2$ indicating the proportion of total variance explained by the combination of fixed and random effects. $^\ast P < 0.01$ and $^\ast\ast P < 0.05$ indicate the significance of the regression. (b) Effects of farmers’ N practices on rice yield, PFP, RE, PE, and AE in each region. Vertical lines: minimum and maximum values; boxes: upper and lower quartiles; horizontal lines within boxes: median; dot within boxes: mean. Values in parentheses represent the number of observations. $^\ast P < 0.05$ represents significant differences between regions.

The multivariable relationships between the N use efficiencies and factors (climate, soil property, and FN) were examined using structural equation models (SEM). Mixed-effect SEM models were used to assess the multivariable relationship between Nr discharge pathways (NH$_3$, leaching, runoff, and N$_2$O) and factors (climate, soil property, and FN), with factors treated as fixed effects, and sites treated as random effects. The analysis processes are detailed in supplementary note 3.

3. Results

3.1. Performance variability of FN in rice of East and Northeast China

The quadratic functions fit well with the response of rice yield to FN in both regions (figure 2(a)). Although the highest yield was similar between the two regions, the corresponding N fertilizer rate was higher in East (249 kg N ha$^{-1}$) than in Northeast China (173 kg N ha$^{-1}$). Under FNR, Northeast China yielded more rice than East China (figure 2(b)), with 8.55 vs 7.91 Mg ha$^{-1}$, respectively. All variables related to N use efficiency decreased with increasing FN (figures 2(a) and S2(a)). The exponential response models fit well with both the PFP-FN and PE-FN, while the linear models fit with RE-FN, AE-FN, and NHI-FN, with all models showing a sharper decrease in Northeast compared to East China. Grain N content increased with increasing FN in both regions (figure S2(b)). Among the indices of N use efficiency under FNR, RE was surprisingly comparable between the two regions, ranging from 36% to 38% (figure 2(b) and table S1). In contrast, PFP, PE, and AE were significantly higher in Northeast than East China. A high discrepancy was found in PFP between the two regions (52.29 kg kg$^{-1}$ in Northeast China and 29.87 kg kg$^{-1}$ in East China). PE was 54.51 kg kg$^{-1}$ in Northeast China and 29.85 kg kg$^{-1}$ in East China. AE was 16.94 kg kg$^{-1}$ and 9.07 kg kg$^{-1}$ in Northeast and East China, respectively. Under FNR, NHI was also significantly greater in Northeast than in East China (figure S2(c)), while the grain N content was higher in East (13.88 g kg$^{-1}$) than in Northeast China (10.55 g kg$^{-1}$; figure S2(d)). Grain N uptake and straw N uptake were 23% and 44% higher in East than Northeast China, respectively (figures S2(e) and (f)).

N surplus under FNR was significantly higher in East China than that in Northeast China under both scenarios (figures S2(g) and (h)). N surplus was positive in East China irrespective of straw removal or return, but a potentially negative N surplus was observed in Northeast China under the straw removal scenario.

NH$_3$ volatilization had a positive linear association with FN, while N$_2$O emission and Nr leaching and runoff exhibited exponential increases in response to FN (figure 3(a)). NH$_3$ volatilization and N$_2$O emission were roughly double in East than Northeast China under FNR, while no difference was found in Nr leaching and runoff between the two regions (figure 3(b)). The total Nr losses in both regions responded exponentially to FN with greater losses in East China under FNR. East China had relatively greater emission factors (EFs) of total Nr losses than Northeast China (figure S3). Northeast China shows comparable values of NH$_3$ EF with Intergovernmental Panel on Climate Change (IPCC) Tier 1 guidelines, while EF in East China is
The fraction of Nr loss through leaching and runoff in both regions and the N$_2$O EF in Northeast China are considerably lower than the default value of IPCC.

3.2. Effects of climate and soil property related factors on N use efficiency and Nr losses

After selecting the key factors by SEM, four soil property factors, three climatic factors, and FN were most related to the variation of N use efficiency (figure 4). The SEM revealed a negative correlation between RE and MSP, MSS, and FN (figure 4(a)). The climate, soil properties, and FN accounted for 71%, 11%, and 18% of the explained variance in RE, respectively (figure 4(b)), of which pH accounted for 8%. PE was negatively affected by MST and FN, but positively affected by MSP, with the relative contributions of the climate, soil properties, and FN being 61%, 25%, and 14%, respectively, of which pH and soil AN explained 10% and 11% of the variation. AE was positively correlated with both PE (55% relative effect) and RE (36%), but negatively correlated with Nr losses (3%) and FN (6%).

Soil property factors including pH, AN, and FN had significant correlations with Nr losses, while climatic indices like MSP and MSS exhibited negative
effects, and MST showed a positive link (figure 4(a)). Soil property factors (TN, AN, and C:N), climatic factors (MST, MSP, MSS, MSH), and FN related to the variability in each Nr output (absolute value) accounted for 7%–38%, 26%–43%, and 19%–68% of the explained variance, respectively (figure 5). A lower AN exhibited higher potential for each Nr loss except NH$_3$ volatilization, yet the N rate related positively with all Nr losses. Whereas the C:N ratio showed a negative relationship with NH$_3$ volatilization, it correlated positively with Nr leaching. A higher MST tended to incur stronger Nr discharge, while MSS and MSH had a consistently negative effect on each of the Nr output pathways.

4. Discussion

4.1. Characteristics of N use efficiency and Nr losses in two regions

Our findings, showing that rice yields in Northeast China under FNR are comparable to those in East China but require less N input, are consistent with previous region-scale studies (Wu et al. 2015, Zhang et al. 2018) and the national statistical data, denoting a higher N use efficiency in Northeast China. Yet, the assumption that Northeast China has higher RE than East China itself may not accurately explain the discrepancy in N use efficiency between the two regions, considering the high variability of apparent RE in Northeast China (figure 2(a)). Similarly, previous studies show that RE was statistically insignificant between East and Northeast China (Zhang et al. 2008, Che et al. 2015). A more significant regional difference in N use efficiency was ascribed to the PE, showing roughly 80% higher in the Northeast than that in East China (figure 2(b)), in agreement with Che et al. (2015) and Xu et al. (2015). Moreover, higher crop N uptake per unit of N input in Northeast China denoted that crops relied more on soil internal N supply in this region compared with East China (Yan et al. 2022), which may be attributed to higher SOC in Northeast China (figure S1(d)).

It can be extrapolated that the differences in AE are caused by the ability to remobilize crop N (PE, which accounted for 55% of the relative effect on AE) rather than the ability to uptake N from the soil (RE, accounting for 36% of the relative effect) in two regions (figure 4(b)). Moreover, a comparable RE and relatively lower Nr losses in Northeast than East China implies its higher soil N buffering capability. A long-term field experiment conducted in Northeast China showed the potential of N accumulation in soil (Jia...
et al. 2017). PE was statistically higher in Northeast China, suggesting a higher ability of crops to transform N into economic yield (Dobermann 2005). We found significantly higher grain N content in East China compared to Northeast China, which could be correlated with PE differences. Swain et al. (2006) also confirmed a high contribution of grain N content on N use efficiency. A lower grain N content implied a lower N requirement under similar grain yield in Northeast China. Together, higher PE and lower grain N content in Northeast China than in East China could partly explain its lower N rate yet comparable rice yield.

4.2. Climatic factors, soil properties, and N rate dominate N use efficiency and Nr losses
N use efficiency is known to vary according to different climate and soil conditions, and in some cases, climatic effect outweighs the effect of soil fertility (Brant and Chen 2015). In our study, the relative contribution of climatic factors to N use efficiency is higher than that of soil properties. The effect of MSS on the productivity of rice is parabolic, with more sunshine hours at tillering benefitting increases in the productive panicle number (Zhong et al. 2013). A higher MST tended to increase the efficiency of N transfer within the crop (PE; Wang et al. 2015). Recent research also revealed the positive effect of temperature and precipitation on Nr loss pathways and sugarcane yield production (Thorburn et al. 2017, Li et al. 2020, Wu et al. 2021). In contrast, when the correlation between factors and the PFP gap was analyzed under a similar latitude scale in the Yangtze Delta region where climates are similar, the impact of climate was less than that of soil fertility (An et al. 2018). Overall, although climatic factors have predominant contributions to the variation of N use efficiency, they are rather unpredictable and uncontrollable in certain rice-cultivated regions, which implies the significance of soil properties and FN from the perspective of enhancing N use efficiency.

Soil fertility indices are also the major contributors to the diversity of N use efficiency, with pH and AN playing an indispensable role in the variation of RE, PE, and Nr losses (figure 4(b)). Previous studies unveiled that soil acidity may affect root physiological characteristics, while soil physical properties affect mineral N fixation and N-cycling processes (Scherer et al. 2014, Pinton et al. 2016, Sun et al. 2021). In addition, soil pH and AN were found to have a more pronounced effect on the ability to transform N acquired from fertilizer into rice yield (PE) compared to N recovery from soil N sources (RE, figure 4(b)). In accordance, Liu et al. (2010) revealed large variation in PE between experimental sites with soil pH ranging from 5.7 to 8.6, while Meena et al. (2016) reported a higher PE in alluvial soil (higher pH and AN) than in red soil. Since the proportion of FN losses was higher in East than Northeast China, the soil N buffering capacity also contributed to the differences in N use efficiency between two regions (figure 3). Soil with higher pH is a hotspot for gaseous N output (NH₃, N₂O, and N₂) under rice cultivation (Čuhel and Simek 2011, Abalos et al. 2014, Yang et al. 2020). Similarly, we revealed that soil pH and AN impacted N use efficiency by directly affecting soil Nr losses (figure 4). Taken together, soil property partly determined the characteristic of N use efficiency and Nr losses between East and Northeast China by changing the efficiency of transforming N acquired from fertilizer into rice yield, and influencing soil N buffering capacity.

As expected, FN is highly correlated with N use efficiency and Nr losses, contributing to 14%–18% of the variation in N use efficiency and 13% in Nr losses (figures 4 and 5), which is partly attributed to the ‘law of diminishing returns’ between N inputs and N yields (Quan et al. 2021). Regions with excessive N application like East China resulted in unproportionally high N surplus (figure S2(g)), causing diminishing effect on N use efficiency (figure S5) while increasing the potential of Nr losses (figure 5). In Northeast China, however, N surplus is considerably low due to low farmers’ N input and high rice yield, resulting in higher N use efficiency yet a potential for soil N deficit. Such effect of N rate on N use efficiency, in part, explained the lower N rate but higher N use efficiency in Northeast China, and implied the possibility of optimizing N rate in East China.

4.3. Perspective for N use efficiency improvement
Since N rate and soil properties contributed to 29%–39% of the relative effects (figure 4), the overuse of FN and the discordance between N management and soil properties should be considered in rice production. Chinese N consumption in rice accounts for 24.5% of global total fertilizer use by rice (Heffer et al. 2017), and a large portion of farmers adopt FN that exceeds the threshold, with roughly half of the counties in East China applying N rates higher than the optimum rate, while in Northeast China the proportion is about 25% (Zhang et al. 2018). It therefore requires the development of sustainable FN management (Ministry of Agriculture and Rural Affairs of the People’s Republic of China 2015). However, variability in the yield–N response in different regions (figure 2(a)) hinders the adoption of a uniform FN, since it overlooks the regional differences in crop N demands, thereby negatively impacting the crop productivity (Cui et al. 2013). Moreover, rather than partially maximizing crop production, a balance between economic return and social costs of Nr on the human health, the ecosystem, and the climate is also required (Zhang et al. 2018). Accordingly, a well-developed regional rice N application strategy that optimizes N input to maintain yield while minimizing Nr losses could ultimately further increase RE across China.

Knowledge-based N management is recommended in terms of synchronizing crop N demands with
N supply (Abalos et al 2014, Xia et al 2017). Therefore, the variation under different soil and climatic conditions should be considered. The pH and AN accounted for 9%–21% of the total variation in the N use efficiency (figure 4), which reveals the importance of considering various soil fertilities in optimizing N management strategies. A large proportion of field airborne N losses within Chinese paddy fields attributing to NH$_3$ (figure 3), N$_2$, and N$_2$O emissions are partly dominated by soil pH and AN (Cuhel and Simek 2011, Zhan et al 2021). Increasing the ammonium retention time and suppressing nitrification are therefore promising in terms of boosting N use efficiency in NH$_3$ and N$_2$O emission hotspots like East China (Xia et al 2017, Subbarao and Searchinger 2021). Higher N surplus results in lower RE and AE (figure S5), suggesting that a N surplus benchmark is beneficial in improving the N use efficiency (Zhang et al 2019). Yet, under low external N input, locations with high N use efficiency like Northeast China (figure S2(h)) and Africa are at risk of unsustainable farming that depletes soil intrinsic N stocks (Conant et al 2013, Man et al 2017). A similar scenario showed that an extremely low fertilization rate may lead to soil N mining and degraded soil health (EU Nitrogen Expert Panel 2015). Moreover, farmers are more inclined to return crop residues in East than Northeast China (Zhang et al 2017), implying the need for straw return in low N surplus regions to enhance soil fertility. A more rational method to achieve high N use efficiency is therefore required to reduce the risk of soil N stock degradation, e.g. organic agriculture and conservation tillage (Chinese Academy of Sciences 2021). An insignificant increase trend or stagnant in indices of N use efficiency (RE, PE, AE) under FNR in both regions from 1986 to 2020 (figure S6) is in accordance with the trend of global cereal RE (Omara et al 2019), echoing the importance of achieving target N use efficiency by soil property-specific knowledge-based N management and FN optimization.

4.4. Sources of uncertainty
We noticed, however, that uncertainty exists in the assessment of N use efficiency in our study. Firstly, rice cultivars may affect the differences in AE, PE, and RE between the two regions, but could not be quantified by SEM analysis, thus overlapping the contribution of key factors on N use efficiency. Yet, the effect of cultivar on N use efficiency is limited in that N use efficiency in the Northeast remains higher than in East China when the rice cultivar group are identical (figure S4). Secondly, when the experiment period was extended, the harvested N in unfertilized plot would decrease due to soil N stock degradation, resulting in overestimated apparent RE compared with the $^{15}$N tracer approach. Nevertheless, it may only impact the value of RE with a limited influence on the relative effect of factors. Thirdly, other climatic factors like solar radiation intensity and edaphic factors like enzyme activity may also affect the N use efficiency, which we did not take into consideration due to data limitation. Overall, further understanding of the constraints on regional N use efficiency would require a more precise and comprehensive dataset, which was beyond the scope of this study.

5. Conclusions
Based on a case study in two rice cultivated regions of China—East and Northeast China, here we present the discrepancy in regional N use efficiency and quantify the key factors contributing to the differences. Our results echo the importance of the plants ability to remobilize N on the regional difference in AE. We provided an evidence-based perspective that higher soil N retention capability and plant N transformation capability, rather than higher efficiency of N recovery in Northeast China promotes its high N use efficiency. Although climatic factors dominated the effects on the divergence of N use efficiency between two regions, the climate itself is rather unpredictable and uncontrollable in certain rice-growing regions. Among the key indicators, soil and N rate accounted for 29%–39% of the relative effects, with pH and AN playing major roles (11%–30%).

Improving N use efficiency during cereal production cannot be achieved unless both the differences in soil indigenous N supply and FN are considered. This requires policy incentives that support region-specific methods. Specifically, stakeholders should facilitate large-scale testing of the efficiency of different N-enhancing approaches in different crop varieties as well as different soils and agro-ecological zones.

Data availability statement
The datasets generated during the current study are available from the corresponding authors on reasonable request.

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Author contributions
Xiaoyuan Yan and Xu Zhao designed this project; Siyuan Cai contributed to data collection, and analysis; Siyuan Cai and Xu Zhao wrote the manuscript. All authors discussed the results and commented on the manuscript.

Conflict of interest
The authors declare no competing interests.

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