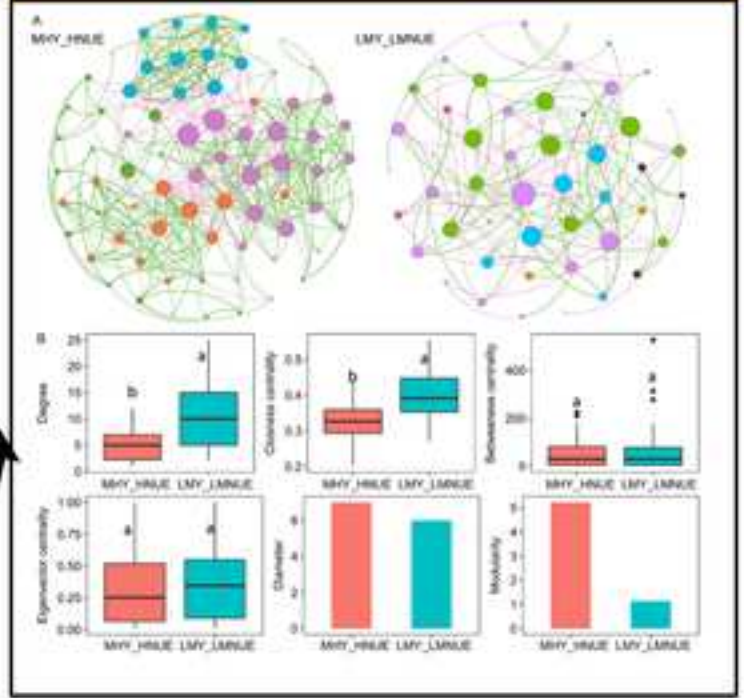
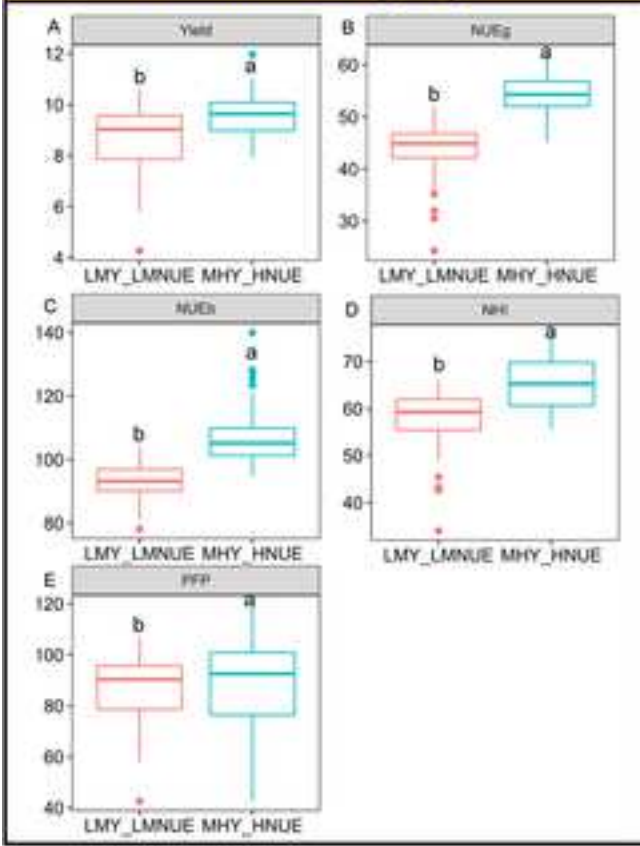


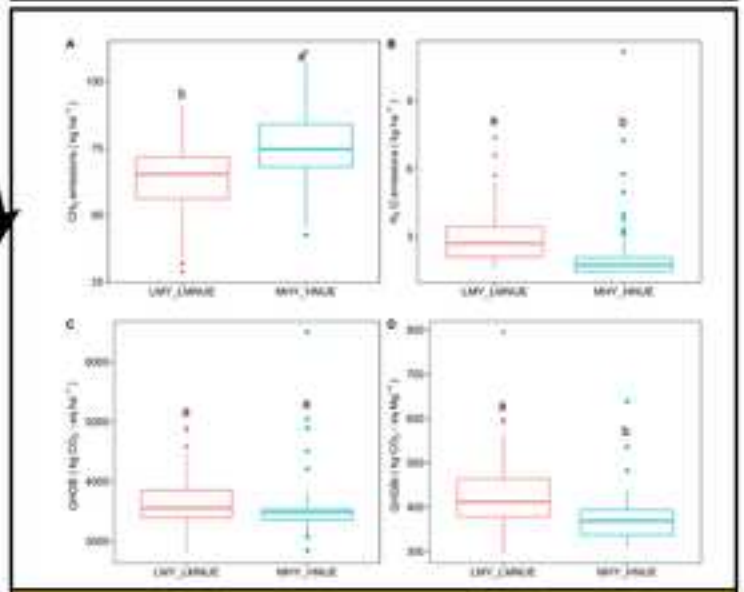
The stability of co-occurrence network



Differences in yield and NUE between the groups



Environmental effects



Highlights:

- Limited knowledge on yield, NUE, and GHG emissions in new rice genotypes with reduced N application
- Genotypes showed significant yield and NUE variations, with 47 classified as MHY_HNUE (moderate-high yield, high NUE)
- N uptake at heading and N concentrations in straw and grain driven the relationship between yield and NUE
- Increase in pre-anthesis temperature consistently lowered yield and NUE
- MHY_HNUE genotypes exhibited 12.8% lower yield-scaled greenhouse gas balance

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58 **Abstract**

59 Significant advancements have been made in understanding the genetic regulation of
60 nitrogen use efficiency (NUE) and identifying crucial NUE genes in rice. However, the
61 development of rice genotypes that simultaneously exhibit high yield and NUE has
62 lagged behind these theoretical advancements. The grain yield, NUE, and greenhouse
63 gas (GHG) emissions of newly-bred rice genotypes under reduced nitrogen application
64 remain largely unknown. To address this knowledge gap, field experiments were
65 conducted, involving 80 *indica* (14 to 19 rice genotypes each year in Wuxue, Hubei)
66 and 12 *japonica* (8 to 12 rice genotypes each year in Yangzhou, Jiangsu). Yield, NUE,
67 agronomy, and soil parameters were assessed, and climate data were recorded. The
68 experiments aimed to assess genotypic variations in yield and NUE among these
69 genotypes and to investigate the eco-physiological basis and environmental impacts
70 of coordinating high yield and high NUE. The results showed significant variations in
71 yield and NUE among the genotypes, with 47 genotypes classified as moderate-high
72 yield with high NUE (MHY_HNUE). These genotypes demonstrated the higher yields
73 and NUE levels, with 9.6 t ha⁻¹, 54.4 kg kg⁻¹, 108.1 kg kg⁻¹, and 64% for yield, NUE for
74 grain and biomass production, and N harvest index, respectively. Nitrogen uptake and
75 tissue concentration were key drivers of the relationship between yield and NUE,
76 particularly N uptake at heading and N concentrations in both straw and grain at
77 maturity. Increase in pre-anthesis temperature consistently lowered yield and NUE.
78 Genotypes within the MHY_HNUE group exhibited higher methane emissions but
79 lower nitrous oxide emissions compared to those in the low to middle yield and NUE
80 group, resulting in a 12.8% reduction in the yield-scaled greenhouse gas balance. In
81 conclusion, prioritizing crop breeding efforts on yield and resource use efficiency, as
82 well as developing genotypes resilient to high temperatures with lower GHGs, can
83 mitigate planetary warming.

84 **KEYWORDS:** rice yield; nitrogen use efficiency; greenhouse gas emissions; high
85 temperature; newly-bred rice genotypes

87 **1. Introduction**

88 Nitrogen (N) is a vital component for life and is required for the survival of all organisms
89 (Harrison et al., 2009; Christie et al., 2020). Rice, as one of the staple crops that play a
90 crucial role in global food security (Peng et al., 2004; Zhu et al., 2018), has seen a
91 substantial increase in yield through the application of N fertilizer. However, the
92 excessive use of N fertilizer exacerbates environmental problems, including soil
93 acidification, air pollution, ozone depletion, global warming and water eutrophication
94 (Galloway et al., 2008; Van Grinsven et al., 2013; X. Chen et al., 2014; Cui et al., 2014).
95 The challenge of feeding a rapidly growing global population sustainably, equitably,
96 and in a climate-resilient manner without degrading natural resources requires
97 innovative approaches that balance yield improvement and environmental protection
98 (Alexandratos and Bruinsma., 2012; Harrison et al., 2021).

99 Expanding cropping areas can lead to increased food production, but it may come at a
100 cost to other commodities or environmental conservation (Harrison et al., 2021). On
101 the other hand, intensifying land use can also increase food supply (Peng et al., 2009;
102 Wang and Peng., 2017), but it must be done in a sustainable manner (Muleke et al.,
103 2022). Over the past 60 years, rice production in China has doubled due to the
104 development of semidwarf and hybrid rice genotypes (Peng et al., 2009; Wang and
105 Peng., 2017), with potential yield benefits of up to 50% from genotypes with semi-
106 dwarfism and heterosis (Yuan, 2017). The recent emergence of contemporary
107 genotypes with larger sinks, such as greater panicle size, fewer tillers, higher grain
108 filling, and greater grain weight has led to higher yields (Yang and Zhang, 2010a,
109 2010b). However, the adoption of practices that enable higher yields, such as excessive
110 N fertilizer use, often overlooks the potential environmental consequences of surplus
111 or unused nitrogen (Christie et al., 2020).

112 Numerous studies have shown that N use efficiency (NUE) tends to decrease with

113 increasing N fertilizer application (Huang et al., 2019; Peng et al., 2010; Zhang et al.,
114 2013), although the magnitude and nature of N losses to environment depend on the
115 timing, rate, type, and method of N application (Smith et al., 2021). To mitigate
116 potential effects of excessive N application on social, economic, human and
117 environmental capital (Shahpari et al., 2021), a wide range of research has been
118 conducted since the end of 20th century (Fan et al., 2016; Xu et al., 2012; Zhang, 2007).
119 Compared with *status quo* farmers' practices, reduced N application through real-time
120 N management and site-specific N management has shown increased yield and NUE
121 simultaneously across a number of rice production sites (Cassman et al., 1996; Peng
122 et al., 2006, 2010). At the same time, evaluation of rice genotypic variation in NUE has
123 also been conducted and significant differences have been reported for both *indica*
124 and *japonica* genotypes in different parts of the world, although NUE has never been
125 set as a breeding target in rice breeding (Broadbent et al., 1987; Hamaoka et al., 2013;
126 Koutroubas and Ntanos, 2003; Wu et al., 2016).

127 NUE can be separated into component indexes, including N uptake, transportation and
128 utilization (Peng et al., 2006). NUE for grain production (NUE_g, kg grain yield over total
129 N uptake) and partial factor productivity of applied N (PFP, kg grain per kg N applied)
130 are often applied in genotypic comparisons. Recently, our understanding of genetic
131 regulation in N uptake, assimilation, signaling, and utilization has been greatly
132 increased, and strategies for improving crop NUE have also been proposed (Xu and
133 Takahashi, 2020; Yu et al., 2022). In rice, *indica* and *japonica* exhibit differential nitrate-
134 absorption activity, with *indica* genotypes having higher values (Hu et al., 2015). Field
135 evaluation using near-isogenic and transgenic lines demonstrated that the *japonica*
136 variety carrying the *NRT1.1B-indica* allele had higher yield and NUE compared with the
137 wildtype (Hu et al., 2015). Sun et al. (2014) reported that *DEP1* regulated panicle size
138 and NUE simultaneously, and therefore could coordinate high yield and high NUE in
139 rice. Liu et al. (2021) found that introgression of the *OsTCP19* allele associated with a
140 high tillering response to nitrogen in modern rice genotypes boosts grain yield and
141 NUE under low or moderate levels of N application. Despite these breakthroughs in

142 theoretical studies of rice NUE, breeding rice genotypes for coordinated high yield and
143 high NUE is still at the preliminary stage.

144 Management and genotype combinations that are contextualized to particular
145 environments can advance yield and NUE of rice (Ibrahim et al, 2019); notwithstanding
146 that such systems should account for potential changes in climate warming or
147 variability (B. Wang et al., 2020; Wang et al., 2018; W. Wang et al., 2020). Extreme
148 weather events in which are potentially damaging to global agricultural production are
149 increasingly common in many regions of the world (Harrison, 2021). In 2022, ambient
150 temperatures above 38 °C lasted for over two weeks at booting and heading stages in
151 main rice growing areas of China. Rice plants are highly sensitive to changes in climate
152 conditions (Ziska and Bunce, 2007; Ziska et al., 2018). Global warming during different
153 rice growing stages tends to decrease N uptake with an increase in the tissues' N
154 content (Xiong et al., 2017; Wang et al., 2018). Elevated temperature decreased N
155 recovery efficiency, N agronomic efficiency, and N physiological efficiency in early rice
156 due to a reduction in grain yield caused by extreme temperatures, while warming
157 increased plant N uptake and NUE in late rice as no heat stress existed (Wang et al.,
158 2020; Zhang et al., 2022). Zhang et al. (2022) found that a previously unidentified allele
159 of the nitrate transporter gene *OsNRT2.3* was required to maintain high yield and high
160 NUE in rice under high temperatures. In addition, the heterogeneity of minimum and
161 maximum temperature on rice yield might confer different NUE by affecting N uptake
162 and biomass accumulation (Peng et al., 2004).

163 Developing green super rice (GSR) was proposed in 2007, and one aspect of the project
164 was to improve N use efficiency while maintaining a high yield potential (Zhang, 2007).
165 To date, a number of new genotypes have been released, but there is still not a good
166 understanding of the relationship between yield and NUE in rice and its eco-
167 physiological basis. Moreover, it has been found that high-yielding rice genotypes
168 show significantly decreased CH₄ emissions, especially under continuous flooding
169 (Jiang et al., 2017,2019). In double cropping systems, N₂O emissions were consistently

170 and negatively correlated with N agronomy efficiency (NAE), but no clear relationship
171 between CH₄ emissions and NAE was observed under optimal N management (Yu et
172 al., 2021). To date, it is unclear whether improvement in NUE of different rice
173 genotypes could affect GHG emissions. Therefore, this study aimed to understand the
174 eco-physiological mechanisms relating to the interplay between yield and NUE and the
175 potential environmental benefits of increased cropping with high NUE genotypes.
176 Nearly one hundred rice genotypes, including 80 *indica* rice genotypes were planted
177 during 2014-2018 in Hubei province and 12 *japonica* rice genotypes during 2017-2019
178 in Jiangsu province, both key rice production zones in. The objectives were to: (1)
179 determine the genotypic variations in yield and NUE among these newly-bred rice
180 genotypes, (2) examine the eco-physiological mechanisms underlying high yield and
181 high NUE, and (3) verify whether high yield and high NUE genotypes exhibited
182 significantly decreased GHG emissions.

183 **2. Methods and materials**

184 **2.1 Experiment sites**

185 In this study, Hubei and Jiangsu provinces were selected as representative areas for
186 single-season *indica* and *japonica* rice (Fig. 1). The growing area and rice production in
187 these provinces are 21% and 24% of the total amount in China's single-season rice
188 growing system, respectively. The average solar radiation of Yangzhou experiment sites
189 was higher than that of Wuxue, but the temperature and precipitation indices in
190 Yangzhou were relatively lower than that in Wuxue during the rice growing (Fig.1 and
191 Supplementary Table S1). The soils of Wuxue were clay loam with a pH of 4.6-5.6,
192 organic matter (OM) of 26.7-33.5 g kg⁻¹, total N (TN) of 1.83-3.01 g kg⁻¹, available P
193 (OP) of 4.91-33.5 mg kg⁻¹ and available K (AK) of 105.8-176.6 mg kg⁻¹ (Supplementary
194 Table S2). Soils in Yangzhou were of sandy loam texture with pH of 6.0, OM of 25.5 g
195 kg⁻¹, TN of 1.52 g kg⁻¹, OP of 34.7 mg kg⁻¹, and AK of 87.9 mg kg⁻¹ on average across
196 the experiment years.

197 **2.2 Plant materials and experiment design**

198 From 2014 to 2018, 14-19 newly released rice genotypes were selected each year as
199 research subjects in Wuxue, Hubei province. Most genotypes were hybrid *indica* rice,
200 and only ten rice genotypes were inbred rice (Chunliangyouyuehesimiao,
201 Huanghuazhan, Huangguanghuazhan1hao, Huangsilizhan, Lvjian1, Lvjian8,
202 Wushansimiao, Xiushui134, Yungeng29, Zhongzu14). Among these ten inbred rice
203 genotypes, Lvjian1, Lvjian8, Xiushui134 and Yungeng29 were *japonica* rice. At the
204 Yangzhou experiment site, 8-12 *japonica* rice genotypes were selected each year to
205 evaluate their differences in yield and NUE from 2017 to 2019. Details of the selected
206 rice genotypes were listed in the Supplementary Excel File.

207 The experiments in Wuxue and Yangzhou were arranged in a completely randomized
208 block design with four or three replications, respectively. The seedlings were raised in
209 a seedbed with a sowing date of May 23~26 and 28~29 in Wuxue and Yangzhou,
210 respectively. After 25 days, seedlings were transplanted on June 17~20 and 22~23,
211 respectively, with two seedlings per hill. The fertilizers were manually incorporated 1
212 day before transplanting for basal application (40 kg P ha⁻¹ calcium superphosphate
213 and 50 kg K ha⁻¹ potassium chloride). Additional K was topdressed at panicle initiation
214 stage at a rate of 50 kg ha⁻¹ during the experimental period. N application of the
215 farmer's practice is usually excessive, 180 kg ha⁻¹ in Wuxue and 270 kg ha⁻¹ in Yangzhou
216 on average, respectively. To evaluate the performance of the yield and NUE under
217 reduced N conditions, 100 kg ha⁻¹ N fertilizer in Wuxue and 180 kg ha⁻¹ N fertilizer in
218 Yangzhou were adopted. The ratio of N (urea) application at basal, topdressings at mid-
219 tillering, and panicle initiation to spikelet differentiation stage were 4:3:3. Pests and
220 diseases were controlled using insecticides and fungicides.

221 **2.3 Crop measurements**

222 The phenology of the rice developmental stage at heading (HD) and physiological
223 maturity (PM) were recorded. Twelve hills of rice plants were sampled from each plot.
224 Plant height and stem numbers were recorded. The plant samples were separated into

225 leaf, stem, and panicle. The green leaf area was measured using a leaf area meter (LI-
226 3100, LI-COR, Lincoln, NE, USA) and was expressed as the leaf area index (LAI). The
227 specific leaf weight (SLW) was defined as the ratio of the leaf dry weight to the leaf
228 area. The dry weight (DW) of different parts of a plant was determined after oven
229 drying at 80°C to a constant weight.

230 At PM stage, the panicles were hand-threshed, and the filled spikelets were separated
231 from unfilled spikelets after submerging them in tap water. The empty spikelets were
232 separated from the half-filled spikelets through winnowing. Three 30-g subsamples of
233 filled spikelets, three 2-g subsamples of empty spikelets, and the total number of half-
234 filled spikelets were obtained to quantify the number of spikelets per m². The dry
235 weights of rachis, filled, half-filled, and unfilled spikelets were determined after oven
236 drying at 80°C to constant weight. The spikelets per panicle and grain filling percentage
237 were calculated. In addition, the grain yield was determined from a 5 m² area in each
238 subplot and was adjusted to a standard moisture content of 0.14 g H₂O g⁻¹ fresh weight.
239 The tissue N concentration of each component at HD and PM was determined using
240 an Elemental analyzer (Elementar Vario MAX CNS/CN, Elementar Trading Co., Ltd,
241 Germany). The plant N accumulation at HD and PM was calculated as the sum of N in
242 each of the organs. The N use efficiency for grain production (NUE_g) was calculated as
243 the grain yield per unit plant N accumulation. The N use efficiency in biomass
244 production (NUE_b) was determined as the ratio of biomass production to plant N
245 accumulation. The N harvest index (NHI) was calculated as the percentage of
246 accumulated N in grain to plant N accumulation. The partial factor productivity of
247 applied N (PFP) is commonly expressed as yield per unit N input (Peng et al., 2006,
248 2010).

249 **2.4 Environmental effects estimation**

250 Estimation of the nitrous oxide (N₂O) emissions was based on the empirical equations
251 from the IPCC's Good Practice Guidance 2006 methodology (Eggleston et al., 2006),
252 which has been widely applied (Aliyu et al., 2019; X. Yu et al., 2021; Yuan et al., 2021).

253 The direct emissions of N₂O from agricultural fields were quantified utilizing a
254 correlation established between N surplus and N₂O emissions (Zou et al., 2010). N
255 surplus was determined as the difference between the aboveground N uptake of the
256 crop, including both inorganic and organic sources, and the rate of N application (Van
257 Groenigen et al., 2010). The total emissions of N₂O were computed as the aggregation
258 of direct and indirect N₂O emissions, with the latter being approximated to constitute
259 20% of the direct emissions (IPCC 2019). The detailed equation for estimation of N₂O
260 is as follows:

$$261 \quad \text{N}_2\text{O emission (kg N}_2\text{O-N ha}^{-1}\text{)} = 1.435 + 0.081 \times e^{0.0443 \times \text{N-surplus}}$$

262 The CH₄MOD model was used to simulate CH₄ emissions of rice genotypes. This daily
263 step-based, semi-empirical model can simulate CH₄ production and emissions in paddy
264 fields under various conditions and agricultural practices (Huang, 2004; Huang et al.,
265 1998) and is recommended by the IPCC (Eggleston et al., 2006). The model includes
266 two sub-models: one for simulating the production of methanogenic substrates from
267 root exudation and organic matter, and another for simulating CH₄ production and
268 emissions through rice plants and bubbles. It has been extensively validated and used
269 worldwide, with minimal input data required (Bogner et al., 2000; Jiang et al., 2023).
270 The main input parameters for the CH₄MOD model include daily air temperature, soil
271 sand percentage, phenology of rice, organic matter addition, rice grain yield, and water
272 management patterns, which were recorded during experiment periods. As we did not
273 know which emission types of these rice genotypes, sensitivity analysis was employed
274 to address the uncertainty and refine the simulation of CH₄ emissions. In this process,
275 we adopted a step size of 0.01, ranging from 0.5 to 1.5 of the variety index. The average
276 simulated values were then used as representative CH₄ emissions for the specific rice
277 genotype.

278 GHG emissions, including CH₄ and N₂O were expressed as the greenhouse gas balance
279 (GHGB, kg CO₂-eq ha⁻¹), which was calculated as follows:

280
$$\text{GHGB} = \text{N}_2\text{O} \times 298 + \text{CH}_4 \times 25$$

281 Where 298 and 25 were the global warming potential (GWP) coefficients for N₂O and
282 CH₄ from a period of 100 years, respectively (IPCC, 2007). Yield-scaled greenhouse gas
283 balance (GHGBi; kg CO₂-eq Mg⁻¹) was calculated as follows:

284
$$\text{GHGBi} = \frac{\text{GHGB}}{\text{Grain yield}}$$

285 **2.5 Statistical Analysis**

286 K-means clustering was initially used to clarify the rice genotypes into six groups using
287 the package factoextra (version 1.0.7). Furthermore, to understand the relationship
288 between yield and the NUE of the rice populations at a coarse level, the yield, NUE_g,
289 NUE_b, NHI, and PFP were employed as proxies to construct a hierarchical cluster
290 heatmap using the package pheatmap with default settings (version 1.0.12). The
291 columns were annotated by group number (1–6), categorized by K-means clustering
292 and the subgroups based on the variated trend of the yield and NUE among groups.

293 Co-linearity among independent variables will influence the stability of the final results
294 in regression models. Because strong collinearity occurred among particular growth
295 properties, N properties, and environmental factors (weather and soil properties), we
296 used cluster analysis to assess the collinearity or redundancy of environmental
297 variables by the varclus procedure in the Hmisc R package before further analyses
298 (version 4.6.0). In addition, principal component analysis (PCA) was conducted for
299 each of the four type variables using the FactoMineR and factoextra R packages
300 (version 1.0.7). The important variables with low collinearity were selected by setting
301 the threshold of pearson R² at 0.6 and according to loading values on the PCA
302 dimensions.

303 After the variable selection procedure, we used the varpart function in vegan package
304 (version 2.5.7) to estimate the proportion of variation of yield and NUE that was
305 explained uniquely by the effect of growth properties, N properties and environmental
306 factors (climate and soil properties). Non-metric multidimensional scaling (NMDS)

307 using Bray-Curtis dissimilarity of Yield, NUE, and biotic or abiotic variables were
308 performed with the vegan package. The Mantel test (Rossi, 1996) was carried out using
309 the “mantel_test” function in the LinkET R package (version 0.0.3.6) to evaluate
310 relationships among Yield, NUE, and the selected biotic and abiotic variables.
311 Similarities or dissimilarities in yield and NUE were calculated by the Euclidean
312 distance via the “vegdist” function in the vegan R package, and other biotic and abiotic
313 variables distance were also calculated by the Euclidean distance based on the matrix
314 of the measured variable.

315 Co-occurrence networks were constructed for different classifications of yield and NUE
316 groups by pearson correlations using the “corr.test” function in the psych R package
317 (version 2.1.9). A correlation was considered statistically robust between two items
318 with pearson's correlation coefficient (ρ) > 0.6 and the p -value <0.05 (Xu et al., 2021).
319 The network analysis was conducted with psych package and visualized in Gephi 0.9.2
320 based on the Fruchterman-Reingold algorithm (Bastian et al., 2009). The network
321 parameters were extracted, including nodes, edges, degree, eigenvector centrality,
322 complexity (linkage density; degree/node), diameter, transitivity, and modularity.

323 All data were analyzed with R software (<http://www.r-project.org/>, version 4.1.2). For
324 statistical analysis, the data were first tested for normality using Kolmogorov-Smirnov
325 method, and then were subjected to ANOVA for multiple sets of data for pairwise
326 comparisons. A backward stepwise regression linear model was constructed to
327 investigate the effects of biotic and abiotic variables on yield and NUE indices among
328 the rice genotypes across year and experiment sites. Histograms, boxplots, and forest
329 figures were generated using the package ggplot2 (version 3.3.6).

330 **3. Results**

331 **3.1 Yield, NUE, and biotic variables**

332 The mean values of the yield and its components for these rice genotypes were as
333 follows: 9.1 t ha⁻¹ for yield, 224 for panicles per unit area, 200.4 for spikelets per panicle,

334 43.9×10^3 for spikelets per unit area, 81.3% for grain filling percentage, and 24.9 mg
335 for individual grain weight, with the coefficient of variation (CV%) ranging from 10.7 to
336 20.5% (Supplementary Table S3). The parameters for NUE varied from the lowest value
337 of 49.0 kg kg^{-1} for NUE_g to the highest value of 100.3 kg kg^{-1} for NUE_b , while the
338 coefficient of variation (CV%) of partial factor productivity (PFP) was the highest
339 among the indicators, exceeding 20.0%. At the HD stage, the average plant height was
340 128.5 cm, the number of stems per unit area (SN) was 254.2, the aboveground biomass
341 (TDW) was 11.3 t ha^{-1} , the leaf area index (LAI) was $7.0 \text{ m}^2 \text{ m}^{-2}$, the specific leaf weight
342 (SLW) was 44.2 mg cm^{-2} , and the crop growth rate (CGR) was $18.3 \text{ g m}^{-2} \text{ d}^{-1}$, the
343 coefficient of variation (CV%) for all of these parameters was between 10.7% and
344 16.9%. At the PM stage, the plant height and CGR decreased compared to the values
345 observed at the HD stage, but the TDW increased significantly. The coefficient of
346 variation (CV%) for these parameters was around 10.0% and did not exceed 13.0%. At
347 the HD stage, the N concentration was higher in the leaf tissues, followed by the
348 panicle and stem organs. However, at the PM stage, the N concentration in these
349 organs was lower compared to that at the HD stage. The CV% for N concentration
350 indicators was mostly above 13.0%, although the CV% for N concentration in filled
351 grains was 8.7%. The average N uptake at the HD and PM stages was 159.2 and 181.5
352 kg ha^{-1} , respectively, with a relatively larger CV% for N uptake at the HD stage.
353 Histograms showed that the parameters had a partially skewed distribution
354 (Supplementary Fig. S1). To further analyze the datasets, the scaled method was used
355 to adjust the dataset to a normal distribution. After this adjustment, the values of the
356 Kolmogorov-Smirnov test range were mostly larger than 0.05, except for PFP, HD.SLW,
357 HD.CGR, and HD.LeafN (Supplementary Table S3).

358 **3.2 Yield and NUE variation among groups**

359 Using K-means clustering, we categorized genotypes into six groups (Fig. 2 and
360 Supplementary Fig. S2). The average yield of genotypes in group 1 was the highest at
361 10 t ha^{-1} , followed by genotypes in groups 5, 3, and 6, which had median yield levels.

362 The yield of genotypes in group 4 was the lowest. The NUE_g of genotypes in groups 1
363 and 6 was the largest, followed by genotypes in groups 3, 5, and 2. NUE_g of group 4
364 was the lowest of all groups. The variation pattern of NUE_b and NHI between groups
365 was similar to the variation in NUE_g . PFP was calculated from yield values divided by
366 the N application rate. Therefore, the varied characteristics were in line with the
367 variation of the yield among groups, except that the value of genotypes in group 6 was
368 the lowest, attributable to its N level.

369 After analyzing the variation pattern in yield and NUE indices among groups, we
370 divided them into two distinct categories based on their change gradient. Groups 1, 3,
371 and 6 were classified as having a middle to high yield and NUE level (MHY_HNUE),
372 while groups 2, 4, and 5 were categorized as having a low to middle yield and NUE level
373 (LMY_LMNUE) (Fig. 3). The MHY_HNUE group had significantly higher yield and NUE
374 indices than the LMY_LMNUE group. Details of the clarified groups of the rice
375 genotypes were shown in Supplementary Fig. S3. The hierarchical cluster results
376 agreed with the K-means cluster findings, which enhanced the robustness of the
377 classification results. The linear correlation analysis revealed a strong and positive
378 association between yield and NUE_g , NUE_b , NHI, and PFP for the LMY_LMNUE group.
379 In contrast, for the MHY_HNUE group, only a significant correlation was observed
380 between PFP and yield (Fig. 4).

381 **3.3 Co-occurrence network and its stability**

382 Yield and NUE co-occurrence networks were constructed based on Pearson
383 correlations among rice genotypes of different groups to investigate rice genotypes'
384 interconnections along the gradient of variation in Yield and NUE (Fig. 5A). We found
385 that node connectedness (degree), and centrality (closeness, eigenvector, and
386 betweenness) network nodes, increased significantly by 110.9%, 21.9%, 7.1%, and
387 12.8%, respectively, in the LMY_LMNUE group, compared to MHY_HNUE group (Fig.
388 5B). Increases in these properties for nodes suggested lower network stability. This
389 was confirmed by the changes observed in the properties characterizing the overall

390 network structure of the LMY_LMNUE and MHY_HNUE groups, which displayed a 14.3%
391 decrease in diameter and a 78.1% decrease in modularity with LMY_LMNUE (Fig. 5B).

392 **3.4 Relationship of yield and NUE similarities over different variables properties.**

393 To ensure that the effects of multicollinearity were avoided, a pearson correlation
394 cluster was utilized to preselect the parameters for analysis. As shown in
395 Supplementary Fig. S4 and S5, the selected parameters included yield components
396 such as panicles per unit area, grain filling percentage, grain weight, and spikelets per
397 panicle, growth properties such as LAI, CGR, SLW at the HD stage, and CGR, TDW, and
398 plant height at the PM stage, N properties such as N concentration of organs at the HD
399 stage, stem N, leaf N, and filled grain N, as well as N uptake at the PM stage.
400 Additionally, climate properties such as minimum and maximum temperature, solar
401 radiation, and precipitation during pre- and post-heading stages were considered, as
402 well as soil properties such as OP, AK, pH, and TN. The results of non-metric
403 multidimensional scaling showed that the selected parameters could effectively
404 classify the groups of MHY_HNUE and LMY_LMNUE (Supplementary Fig. S6).
405 Correlation analysis indicated that yield was linearly and positively related to the grain
406 filling percentage in the LMY_LMNUE category, and was further significantly and
407 positively influenced by spikelets per panicle in the MHY_HNUE category or the
408 combined group (Supplementary Fig. S7).

409 To better understand the drivers of these relationships between yield, NUE, and biotic
410 and abiotic factors distance, we conducted a Mantel test (Fig. 6). Our results revealed
411 that specific growth properties (with the exception of HD.SN), N properties, climate
412 elements, and soil elements were responsible for the significant changes in the
413 relationships between yield and NUE similarities over biotic and abiotic factors
414 distance. Furthermore, PCA was used to character the individual parameter effect (Fig.
415 7). The results showed that growth parameters significantly loaded on the PCA1 and
416 PCA2 axes, explaining 37.7% and 26.4% of the variation in the changes of yield and
417 NUE, respectively. N properties on PCA1 and PCA2 explained 41.6% and 23.0% of the

418 changing pattern of yield and NUE, with most parameters significantly loaded on PCA1.
419 With respect to climate variables, most loaded considerably on PCA1, while the
420 minimum and maximum temperature during pre-heading stage loaded on PCA2. Soil
421 elements significantly loaded on PCA1, while OP loaded on the PCA2 axis, with PCA1
422 and PCA2 explaining 56.7% and 24.5% of the variation, respectively.

423 **3.5 Biotic and abiotic factors between groups of MHY_HNUE and LMY_LMNUE**

424 ANOVA tests between the newly classified groups of MHY_HNUE showed that the
425 grain filling percentage and grain weight of yield components were significantly higher
426 than the LMY_LMNUE (Table S4). The CGR at the HD stage and TDW at the PM stage
427 were relatively higher in MHY_HNUE, compared to LMY_LMNUE, but the plant height
428 was lower. The N concentration of organs in MHY_HNUE at both the HD and PM stages
429 consistently showed lower values than those in LMY_LMNUE. Significant differences
430 were also observed between the two groups in the minimum and maximum
431 temperatures during pre- and post-heading stages, with MHY_HNUE exhibiting lower
432 values than LMY_LMNUE. Lastly, it was found that soil properties such as TN and AK
433 were lower in MHY_HNUE than in LMY_LMNUE, while pH was higher.

434 **3.6 Effects of biotic and abiotic factors on yield and NUE**

435 The variance partition analysis revealed that the N properties indices accounted for
436 16% of the variation in both yield and NUE, whereas growth properties, climate, and
437 soil elements collectively explained a similar proportion of about 2% each
438 (Supplementary Fig. S8). Backward stepwise-regression models, including all the
439 growth, N, climate, and soil predictors, explained 69.8%, 89.2%, 99.1%, 83.4%, and
440 92.3% (adjusted R^2) of the total variances observed in yield, NUE_g , NUE_b , NHI, and PFP,
441 respectively (Fig. 8). For yield, panicle N concentration at HD stage, N uptake at PM
442 stage, the minimum temperature at the post-heading stage, and OP and TN had
443 positive effects on yield formation, but N concentration of organs at PM stage and
444 maximum temperature at the pre-heading stage, and AK had adverse impacts on yield
445 variation. Regarding NUE_g , plant height at the PM stage, and N concentration of stem

446 at the HD stage, the maximum temperature at the post-heading stage and OP had
447 positive effects, N concentration and N uptake of organs, and the minimum
448 temperature at the post-heading stage had adverse effects. Our observations revealed
449 that several factors negatively impacted NUE_b , including SLW at HD, N uptake at PM,
450 the minimum temperature during pre- and post-heading stages, and AK. Conversely,
451 N concentration of organs at HD and PM (except for the N concentration of the stem
452 and leaf at PM stage), TDW, plant height at PM, and maximum temperature during
453 pre-heading had positive and significant contributions to the formation of NUE_b . In
454 terms of NHI, SLW at HD, N concentration of the stem and leaf at PM, maximum
455 temperature at the pre-heading stage, and solar radiation at the PM stage had
456 negative effects. However, N concentration of the panicle and stem, N uptake,
457 maximum temperature at the post-heading stage, pH, and organic phosphorus (OP)
458 positively affected NHI. The factors affecting PFP were similar to those included in the
459 yield regression model. The effects of the concentration of organs at HD and PM stages,
460 maximum temperature at the pre-heading stage, and N uptake were compatible with
461 their impact on rice yield. Additionally, we observed that maximum temperature at
462 post-heading stage had positive effects on PFP, which was opposite to the effects of
463 minimum temperature.

464 **3.7 Environmental effects**

465 To address the uncertainty regarding the emission types of the rice genotypes, we
466 conducted a sensitivity analysis to refine the simulation of CH_4 emissions.
467 Supplementary Fig. S9 illustrates that the mean values of simulated CH_4 emissions
468 were higher for individual rice genotypes in the MHY_HNUE group than those in the
469 LMY_LMNUE group. Consequently, we observed a significant increase in the simulated
470 CH_4 emissions of the MHY_HNUE group. However, the N_2O emissions in the
471 MHY_HNUE group showed a remarkable decrease relative to those in the
472 LMY_LMNUE group (Fig. 9). As a result, there were no noticeable differences in the
473 greenhouse gas balance (GHGB) between the two groups. Nevertheless, the yield-

474 scaled greenhouse gas balance (GHGBi) decreased significantly in the MHY_HNUE
475 group compared to that in the LMY_LMNUE group.

476 **4. Discussion**

477 **4.1 Stability of the coordination of yield and NUE**

478 In this study, we examined 80 *indica* and 12 *japonica* rice genotypes, including the
479 most recent and advanced bred rice genotypes released from 2006 to 2019. The
480 comprehensive results of our study showed that the yield ranged from 4.2 to 12.0 t ha⁻¹,
481 the most useful NUE indices of NUE_g, NUE_b, NHI, and PFP ranged from 24.3 to 62.0
482 kg kg⁻¹, 78.1 to 148.7 kg kg⁻¹, 34.1 to 75.8%, and 39.9 to 119.7 kg kg⁻¹, respectively
483 (Supplementary Fig. S1). K-means and hierarchical clustering corroborated the
484 disparities in yield and NUE, as group 4 was characterized by reduced yield and NUE,
485 while group 1 demonstrated the highest yield and NUE in general under a reduced N
486 rate (Fig. 2). The results of the study revealed a transparent gradient from low yield
487 and NUE to moderate or relatively higher yield and NUE, which was confirmed in two
488 additional groups. Notably, the rice genotypes of MHY_HNUE exhibited a higher
489 capacity for both yield and NUE compared to the LMY_LMNUE groups (Fig. 3).
490 Furthermore, the MHY_HNUE genotypes demonstrated greater stability compared to
491 the LMY_LMNUE groups, as evidenced by a decrease in the degree and centrality co-
492 currency network, coupled with an increase in the diameter and modularity. Prior
493 studies indicated that increased node connectivity (Fan et al., 2018), centrality (Jordán,
494 2009), and complexity (May, 2019) were associated with reduced network stability.
495 These network analyses originate from graph theory (Pavlopoulos et al., 2011) or social
496 network analysis (Otte and Rousseau, 2002) and have previously been utilized to
497 explore the stability of microbial networks in response to disturbances (de Vries et al.,
498 2018; Xiao et al., 2018). To the best of our knowledge, this was the first instance where
499 network analysis was applied to evaluate the stability of the coordination of yield and
500 NUE. The findings of this study suggested that specific rice genotypes held promise as

501 sources for further increases in both yield and NUE in China. However, variation in yield
502 and NUE was often determined by the interplay between genotype and N rate (Nehe
503 et al., 2018; Wang et al., 2021a; Zhang et al., 2013). In the current rice breeding
504 programs, rice genotypes are usually developed in environments where N is abundant,
505 providing limited information on the performance of the rice genotypes when N supply
506 is restricted. Therefore, we recommend that breeders carry out at least two N levels
507 (moderate and reduced N rate) to reduce the uncertainty of the performance of rice
508 genotypes under low N levels.

509 **4.2 Effects of growth and N properties on yield and NUE**

510 The results of the study revealed that growth and N properties played a significant role
511 in the variations of yield and NUE (Figs. 6, 7). Individually, growth properties only
512 explained 2% of the coordination of yield and NUE, whereas N properties contributed
513 significantly, explaining 16% of the variation (Supplementary Fig. S8). The stepwise
514 regression analysis confirmed these findings, indicating that growth indicators such as
515 dry matter, plant height, and CGR at PM stage, as well as SLW at HD stage, primarily
516 influenced the formation of NUE_g , NUE_b and NHI formation but did not have significant
517 effects on the yield and PFP variation. This suggested that to achieve high yield and
518 NUE characteristics, focus should be placed primarily on the N properties. Yield
519 formation depends on the accumulation and translocation of dry matter to the panicle
520 tissues (Huang et al., 2019; Yang and Zhang, 2010b). Previous linear regression results
521 recommended increasing leaf net photosynthesis rate while reducing respiration rate
522 to achieve higher dry matter accumulation (Li et al., 2009; Wang et al., 2018). However,
523 a higher dry matter phenotype only resulted in a higher NUE_b and did not significantly
524 increase yield, likely due to limitations in the flux of carbohydrates from source to sink
525 organs (Yang and Zhang, 2010a, 2010b). The study also observed a significant positive
526 contribution of N uptake to yield at the PM stage, while high N concentration in organs
527 had a negative effect on yield formation. Thus, while high yield is partly related to dry
528 matter accumulation, it is also dependent on the translocation and distribution of N.

529 Previous studies demonstrated that the yield advantage of ordinary hybrid rice over
530 inbred rice was mainly due to higher aboveground dry matter, while for super hybrid
531 rice, higher grain yield was attributed to both high harvest index and aboveground dry
532 matter at 90 kg ha⁻¹ N rate (Huang et al., 2018). In this study, while a few super hybrid
533 rice genotypes were used and classified into 1 or 3 groups, for most rice genotypes,
534 biomass accumulation was still the primary driver for the improvement of yield and
535 NUE.

536 The effects of N concentration in tissues at HD and PM stages were controversial to
537 the yield and NUE (NUE_g, NHI, and PFP) simulation. Previous studies primarily focused
538 on the N concentration at the PM stage while ignoring the effects of N concentration
539 at the HD stage. For instance, Huang et al. (2018) and Wu et al. (2016) recommended
540 reducing the N concentration in leaf, stem, and grain tissues at maturity to improve
541 NUE_g, particularly for stem N. We concur with these recommendations if the focus is
542 solely on yield-related NUE indices. However, when considering biomass-based NUE,
543 we found that a higher tissue N concentration should be targeted, particularly at the
544 HD stage. This indicated that the N concentration at HD stage may have a significant
545 influence on yield and NUE. Nehe et al. (2018) investigated 28 wheat genotypes and
546 found that N uptake at anthesis was crucial for higher yield and NUE, as it maintained
547 green leaves, reduced the N translocation rate, and ultimately lowered N
548 concentration in grains while increasing yield. In this study, we found that N uptake at
549 PM was primarily derived from the HD stage rather than the period between HD and
550 PM stages, suggesting that higher N concentration and N uptake at HD should be
551 targeted to increase yield and NUE simultaneously.

552 **4.3 Effects of climate and soil properties on yield and NUE**

553 Climate variables, such as solar radiation and temperature, can influence rice yield and
554 NUE (Peng et al., 2004; Wang et al., 2021b). Many studies have investigated the
555 asymmetric effects of temperature on rice yield production (Peng et al., 2004; Shi et
556 al., 2016; Wang et al., 2016; W. Wang et al., 2020). Generally, increasing temperature

557 at high latitudes can increase yield, but at low latitudes, it can decrease rice production
558 (Wang et al., 2016; H. Zhang et al., 2019). Our study demonstrated that the maximum
559 temperature at the pre-heading stage negatively affected yield, while the minimum
560 temperature at the post-heading stage positively regulated it. These results partly
561 agreed with previous findings, which also addressed the crucial and positive effects of
562 the maximum temperature at the post-heading stage on rice yield (Welch et al., 2010).
563 While the positive impact of radiation use efficiency on rice yield has been recognized
564 (Wang et al., 2016), we did not observe a significant influence of solar radiation on the
565 yield. The absence of a clear observation can be attributed to the challenge of
566 discerning the independent effects of weather variables, as they often lack
567 independence (Deng et al., 2015). Temperature indices, especially the minimum
568 temperature at pre- and post-heading stages, negatively affected NUE_g , NUE_b , and PFP.
569 A plausible explanation for this phenomenon could be the effects of temperature on
570 N uptake. Prior research suggested that elevated temperatures increase N uptake by
571 increasing leaf evaporation rates (Chen et al., 2014; Wang et al., 2018). Higher
572 temperatures also increased the capacity for adaptation, which can enhance nutrient
573 uptake to meet or alleviate the adverse effects of an increased minimum temperature
574 that does not exceed natural threshold values (Shi et al., 2017). The maximum
575 temperature at the post-heading stage contributed to higher NUE_g , NHI, and PFP. The
576 physiological mechanism underlying these results remained unclear. An increase in
577 maximum temperature at the post-heading stage can avoid the potential influence of
578 low temperature on yield formation, particularly for grain filling quality (Arshad et al.,
579 2017).

580 Total soil N has been shown to have a positive effect on rice yield, but it can also
581 decrease NUE when the soil has ample N supply. The N concentration in plant tissues
582 tends to increase with higher levels of indigenous N in the soil, which may lead to
583 decreased NUE despite increased yield (Yin et al., 2021). Total soil N has a positive
584 effect on rice yield, but it can also decrease NUE when the soil has ample N supply.
585 The N concentration in plant tissues tends to increase with higher levels of indigenous

586 N in the soil, which may lead to decreased NUE despite increased yield (Duan et al.,
587 2014), highlighting the importance of phosphorus in achieving a balance between
588 yield and NUE. To achieve simultaneous increases in yield and NUE, adjusting the N
589 and phosphorus rates should be considered for long-term soil amelioration, rather
590 than focusing on short-term gains.

591 **4.4 Environment effects**

592 The results of our study indicated that rice genotypes with high yield and NUE tended
593 to increase CH₄ emissions but decrease N₂O emissions. These findings appeared to
594 contradict those reported by Jiang et al. (2017), which suggested that high-yielding
595 rice genotypes could reduce CH₄ emissions. The CH₄ formed in the soil is released into
596 the atmosphere through the rice plant. Up to 90% of the CH₄ emission was rice plant-
597 mediated through the well-developed intracellular air spaces (aerenchyma) in leaf
598 blades, leaf sheaths, culm, and roots (Lou et al., 2008; Schütz et al., 1989). Differences
599 in the amount and type of aerenchyma between genotypes may contribute to
600 variations in gas transport capabilities and CH₄ emissions. Furthermore, longer
601 growing periods for high-yielding and NUE rice genotypes may also increase CH₄
602 emissions during the growing season. However, no significant difference in CH₄
603 emissions between early and late-maturing rice genotypes was observed, as the
604 emission rates during the ripening stage were relatively low and had minimal effects
605 on the total CH₄ flux in late-maturing genotypes (Gutierrez et al., 2013). A meta-
606 analysis conducted by Chen et al. (2021) found that an increase in root biomass could
607 enhance CH₄ emissions. However, the improvement in CH₄ fluxes and cumulative CH₄
608 emissions were relatively stable at approximately 36.6% and 29.5%, respectively,
609 regardless of the increased percentage of root biomass (Chen et al., 2021). This finding
610 demonstrated that root biomass may had a limited effect on CH₄ emissions. Other
611 studies proposed that root exudates could increase the soil organic carbon content in
612 the rhizosphere, providing more carbon sources for methanogens, and hence leading
613 to higher methane emissions (Aulakh et al., 2001; Jia et al., 2006). High-yield and NUE

614 rice genotypes are generally associated with a larger root system (Zhang et al., 2018,
615 2021), which could contribute to increased CH₄ emissions.

616 Although N₂O emissions from paddy rice growing systems are generally lower than CH₄
617 emissions, N₂O has a larger global warming potential. A study by Cui et al. (2022)
618 estimated that the annual N₂O emissions per year in China's rice growing system have
619 decreased from 1980 to 2017, mainly due to the decreased N application rate (Cui et
620 al., 2022). Researchers have found a positive relationship between NUE and N₂O
621 emissions reduction under reduced N rates (Huang and Tang, 2010; K. Yu et al., 2021;
622 C. Zhang et al., 2019). Higher N uptake by roots could reduce the N residual in the soil,
623 decrease the N source for denitrifying microorganisms, and hence mitigate the
624 emission of N₂O. Rice root exudates could increase the soil carbon content and
625 improve the soil C/N ratio, affecting the N₂O emission rate. In our study, improvement
626 in NUE significantly reduced the GHGBi, mostly driven by the N₂O emission reduction.
627 The findings demonstrated that through NUE enhancement of rice genotypes, we can
628 further mitigate greenhouse gas emissions and the followed adverse effects under
629 reduced N rate.

630 **4.5 Limitations**

631 Our study demonstrated that an increase in N uptake at the HD stage and a decrease
632 in N concentration of leaf, stem, and grain at the PM stage were crucial for optimizing
633 the coordination of yield and NUE. An increase in N uptake during the HD stage can
634 provide sufficient nutrition for yield and biomass production, promoting stay-green
635 characteristics and sustained photosynthesis in the leaves. However, high N uptake
636 during HD may prolong the maturity of rice plants, which could increase the risk of
637 lodging. Additionally, reducing N concentration in the grain exacerbates hidden hunger
638 for nutrition caused by elevated CO₂ levels, which have been shown to decrease
639 protein content (Smith et al., 2018). While the increased temperature can partly
640 counteract or mitigate this trade-off, it can also result in yield losses, particularly in
641 regions where warming is predicted to occur during critical developmental periods

642 (Cai et al., 2016; Wang et al., 2018). In future climate conditions, minimum and
643 maximum temperatures are predicted to increase by approximately 2-5 °C under
644 middle or high emission scenarios (Wang et al., 2021b), which would exceed the
645 minimum temperature levels in our study and potentially decrease rice yield and
646 further reduce NUE. The effects of increased temperature require further evaluation
647 through additional field experiments to refine our findings. Nonetheless, our present
648 study, involving nearly 100 released rice genotypes, can help improve our
649 understanding of how to simultaneously increase yield and NUE in current
650 environmental conditions. We recommend that breeders consider temperature
651 tolerance characteristics when screening for yield and NUE performance in near future.
652 Although we used the CH4MOD and IPCC procedures to estimate the impact of rice
653 genotypes on greenhouse gas emissions, there were still uncertainties associated with
654 the equations. For instance, the characteristics of emission types of these rice
655 genotypes were unclear, therefore we were not clear what's the specific values of
656 variety index should be used. To address the uncertainty and refine the simulation of
657 CH₄ emissions, a sensitivity analysis was used with a 0.01 step size from 0.5 to 1.5 of
658 the variety index in the simulation process. However, further experimentation with the
659 selected rice genotypes in two groups is urgent to assess their effects on CH₄ and N₂O
660 emissions.

661 **5. Conclusion**

662 A comprehensive evaluation was conducted to assess the coordination of yield and
663 NUE in newly-released rice genotypes from 2006 to 2019 and to determine the
664 potential for reducing environmental impacts. Growth, nitrogen, climate, and soil
665 properties were analyzed to uncover the critical factors affecting yield and NUE. There
666 was uncertainty in selecting for higher yield and NUE in the current breeding system.
667 The results showed that only a portion of the rice genotypes was classified as having
668 moderate-high yield and high NUE, and these genotypes maintained stability in the

669 coordination of yield and NUE. N-associated characteristics played a crucial role in this
670 stability, particularly N uptake at the heading stage and N concentration in organs at
671 maturity. The paradox was that lower N or protein in grain resulting from higher NUE
672 could result in hidden famine for the countries or regions that relied on rice for the
673 bulk of calorie intake. In addition, climate change can be a complication in delivering
674 both high yield and NUE, as future temperatures could exceed the tolerance threshold
675 of rice. Therefore, future breeding efforts should not only focus on increasing crop
676 production and resource use efficiency but also prioritize resilience to climate change.
677 This study provides a preliminary evaluation of the potential benefits of reducing N₂O
678 emission and yield-scaled GHGB. More nuanced field experiments are needed to
679 address the uncertainty associated with these results.

680 **CRedit authorship contribution statement**

681 Jianchang Yang, Fei Wang, and Weilu Wang conceived the study; Shaobing Peng, Weilu
682 Wang, Kuanyu Zhu, and Dongling Ji compiled the data; Weilu Wang, Jianchang Yang,
683 and Fei Wang led the data assessment with the contributions of Longlong Xia, Bin
684 Wang, Lijun Liu, Junfei Gu, Hao Zhang, Ke Liu, and Linhan Ouyang; Fei Wang and Weilu
685 Wang interpreted the results with the contribution of Shaobing Peng, Irakli Loladze,
686 Matthew Tom Harrison, William J. Davies, Pete Smith, Longlong Xia, and Wen Zhang;
687 Fei Wang, Jianchang Yang, and Weilu Wang led manuscript writing with substantial
688 contributions of all authors.

689 **Declaration of competing interest**

690 The authors declare that they have no known competing financial interests or personal
691 relationships that could have appeared to influence the work reported in this paper.

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975 **Figure legends**

976 **Fig. 1** Maps of the experiment sites (Wuxue and Yangzhou) and weather conditions
977 during rice growing period.

978 **Fig. 2** Boxplot of the yield and NUE indices of the six groups based on the K-means
979 cluster analysis. A, yield; B, NUE_g ; C, NUE_b ; D, NHI; E, PFP. The different letter indicates
980 the statistical significance at 0.05 level. NUE_g , nitrogen use efficiency for grain
981 production; NUE_b , nitrogen use efficiency in biomass production; NHI, nitrogen harvest
982 index; PFP, partial factor productivity. The box boundaries indicate the 25th and 75th
983 percentiles; the black line within the box mark the median; and whiskers below and
984 above the box indicate the 10th and 90th percentiles, respectively.

985 **Fig. 3** Boxplot of the yield and NUE indices of the two groups LMY_LMNUE and
986 MHY_HNUE. A, yield; B, NUE_g ; C, NUE_b ; D, NHI; E, PFP. LMY_LMNUE represents the
987 low to moderate yield and nitrogen use efficiency group; MHY_HNUE represents
988 moderate to high yield and high nitrogen use efficiency group. Different letters indicate
989 statistical significance at the 0.05 level. NUE_g , nitrogen use efficiency for grain
990 production; NUE_b , nitrogen use efficiency in biomass production; NHI, nitrogen harvest
991 index; PFP, partial factor productivity. The box boundaries indicate the 25th and 75th
992 percentiles; the black line within the box mark the median; and whiskers below and
993 above the box indicate the 10th and 90th percentiles, respectively.

994 **Fig. 4** Linear regression of the yield and NUE. LMY_LMNUE represents low to moderate
995 yield and nitrogen use efficiency group; MHY_HNUE represents moderate to high yield
996 and high nitrogen use efficiency group. NUE_g , nitrogen use efficiency for grain
997 production; NUE_b , nitrogen use efficiency in biomass production; NHI, nitrogen harvest
998 index; PFP, partial factor productivity.

999 **Fig. 5** Co-occurrence network analysis. LMY_LMNUE represents low to moderate yield
1000 and nitrogen use efficiency group; MHY_HNUE represents moderate to high yield and
1001 high nitrogen use efficiency group. Different letters indicate the statistical significance
1002 at the 0.05 level.

1003 **Fig. 6** Correlations between growth, nitrogen, climate and soil factors and relationships
1004 between yield and NUE. Line width corresponds to the Mantel's r statistic, and line
1005 color denotes the statistical significance based on 999 permutations. Pairwise
1006 comparisons of independent factors are also shown, with a color gradient denoting
1007 Pearson's correlation coefficient, and these factors are synthesized into four groups
1008 based on attribute of data surveyed. Asterisks indicate the statistical significance ($***P$
1009 < 0.001 ; $** P < 0.01$; and $* P < 0.05$). The variables are described in Supplementary
1010 Table S4.

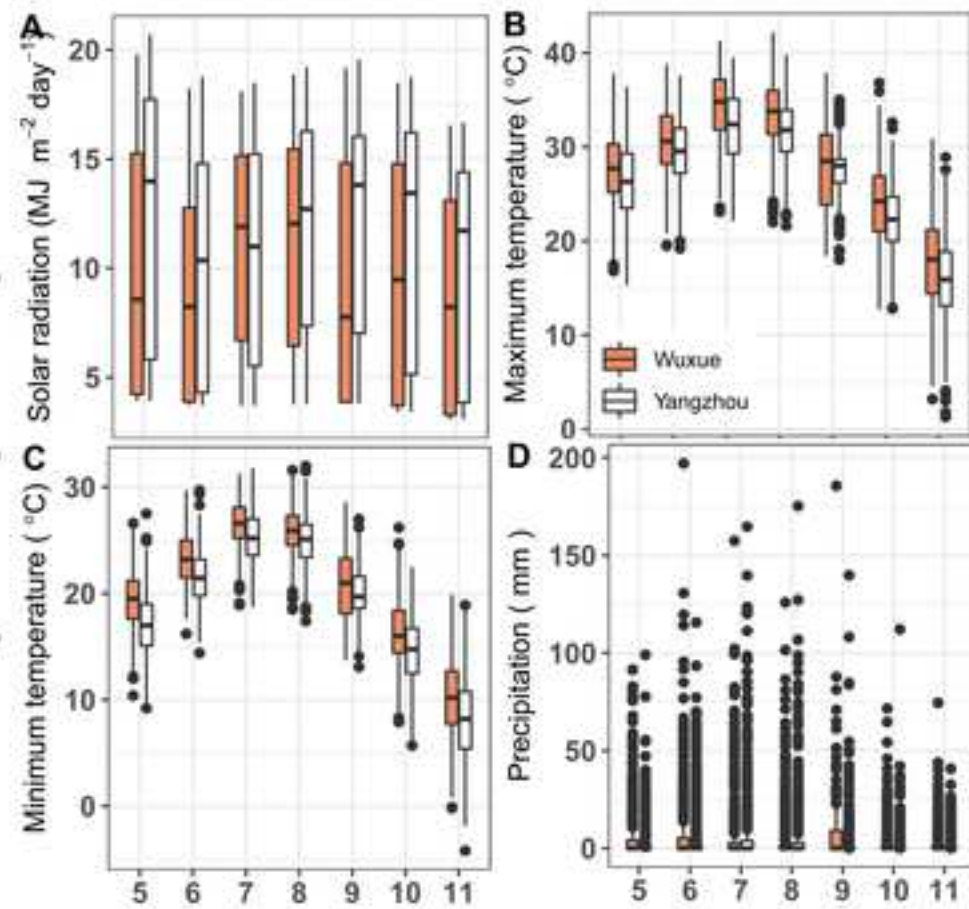
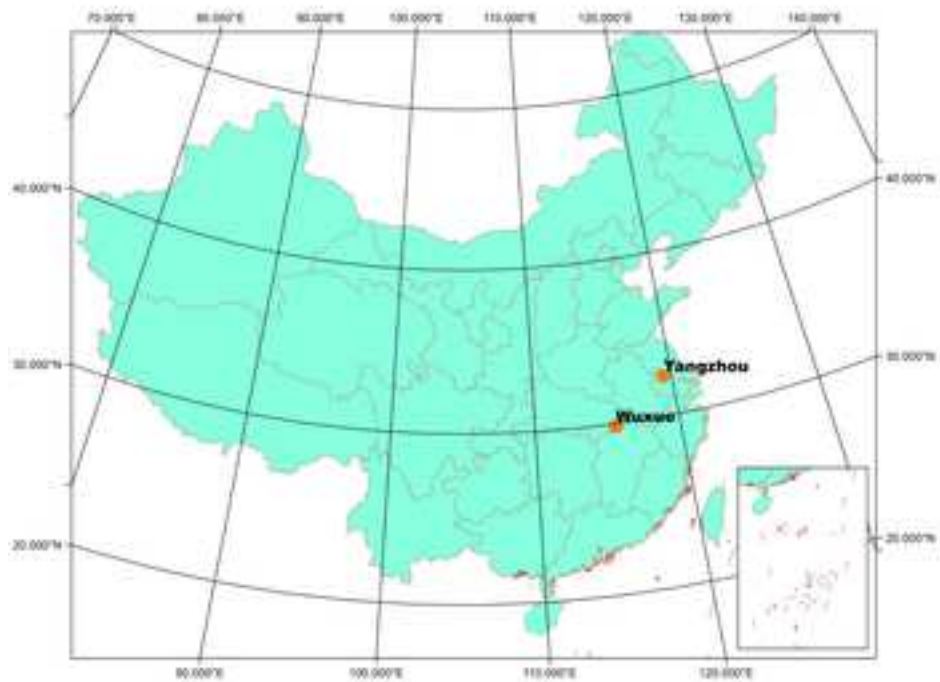
1011 **Fig. 7** Principal component analysis of (A) growth variables, (B) nitrogen-related
1012 variables, (C) climate variables, and (D) soil variables. Dim1 and Dim2 present the first
1013 and second principal components, respectively. The variables are described in
1014 Supplementary Table S4.

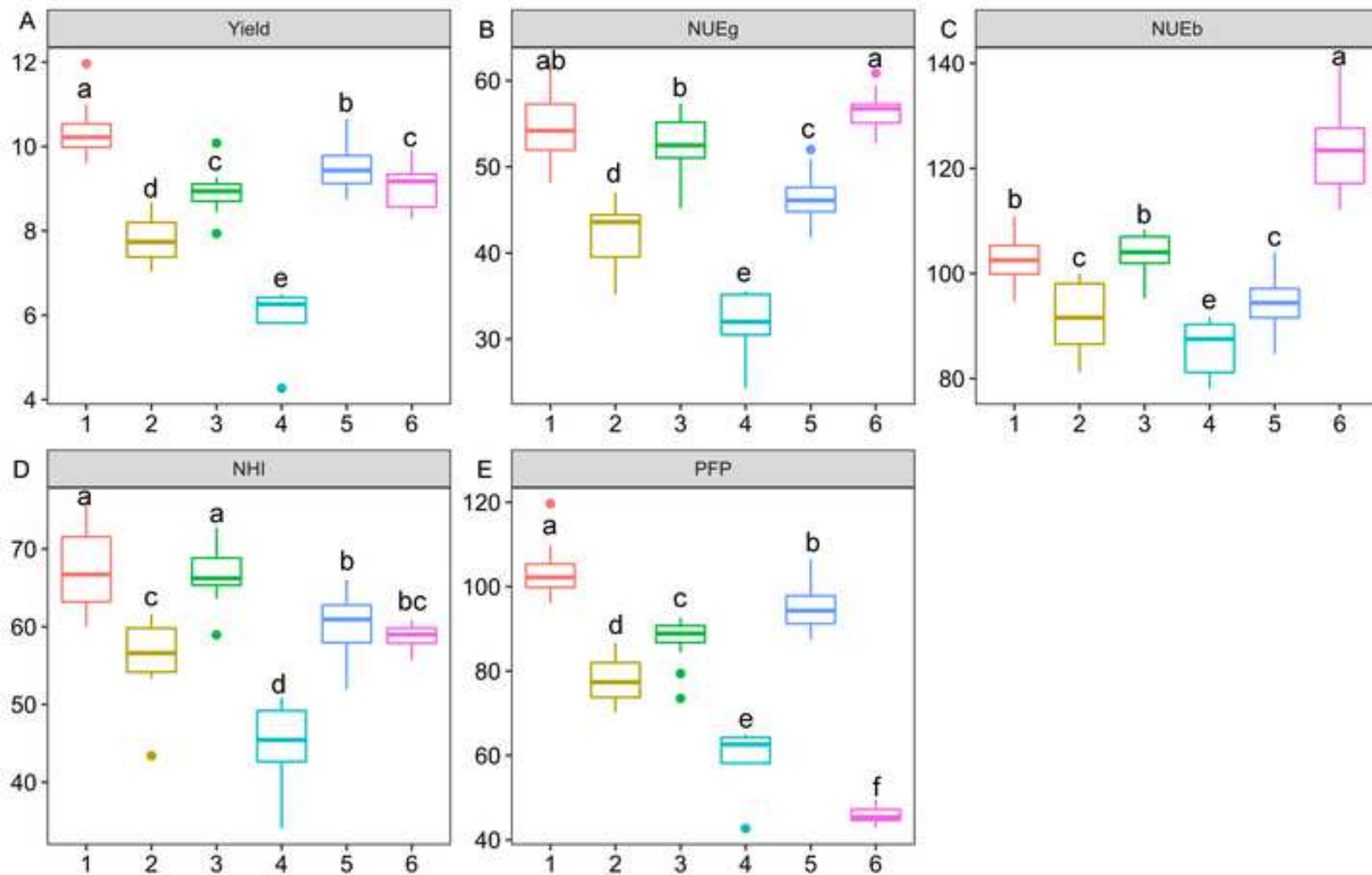
1015 **Fig. 8** Stepwise regression analysis. A, yield; B, NUE_g ; C, NUE_b ; D, NHI; E, PFP. Asterisks
1016 indicate the statistical significance ($*** P < 0.001$; $** P < 0.01$; and $* P < 0.05$). NUE_g ,
1017 nitrogen use efficiency for grain production; NUE_b , nitrogen use efficiency in biomass
1018 production; NHI, nitrogen harvest index; PFP, partial factor productivity. The variables
1019 are described in Supplementary Table S4.

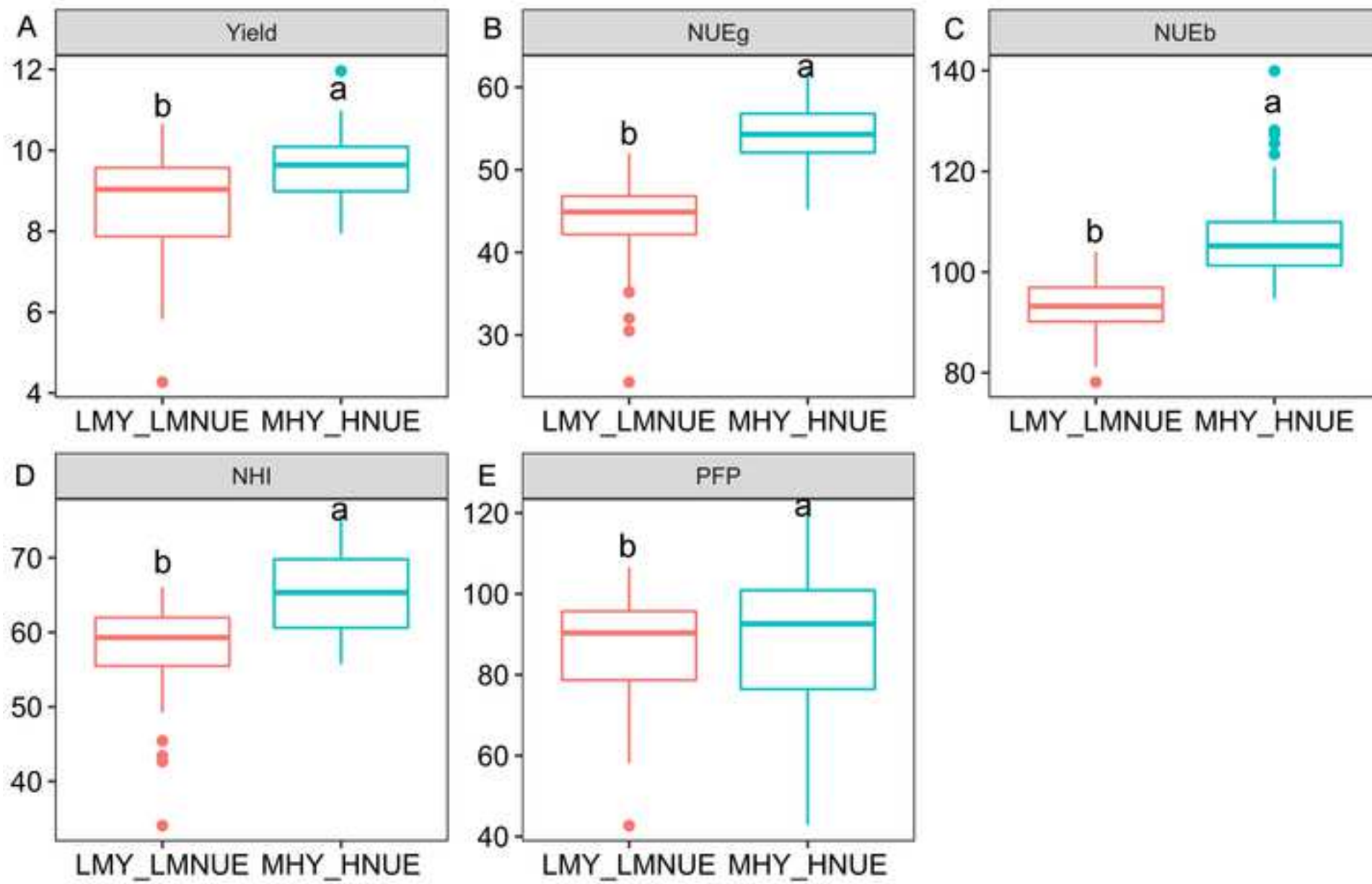
1020 **Fig. 9** Environmental effects of the rice cultivars of groups LMY_LMNUE and

1021 MHY_HNUE. A, CH₄ emissions; B, N₂O emissions; C, greenhouse gas balance (GHGB);
1022 D, scaled greenhouse gas balance (GHGBi). LMY_LMNUE represents the low to
1023 moderate yield and nitrogen use efficiency group; MHY_HNUE represents the
1024 moderate to high yield and high nitrogen use efficiency group. Different letters indicate
1025 statistical significance at the 0.05 level.

Figure 1







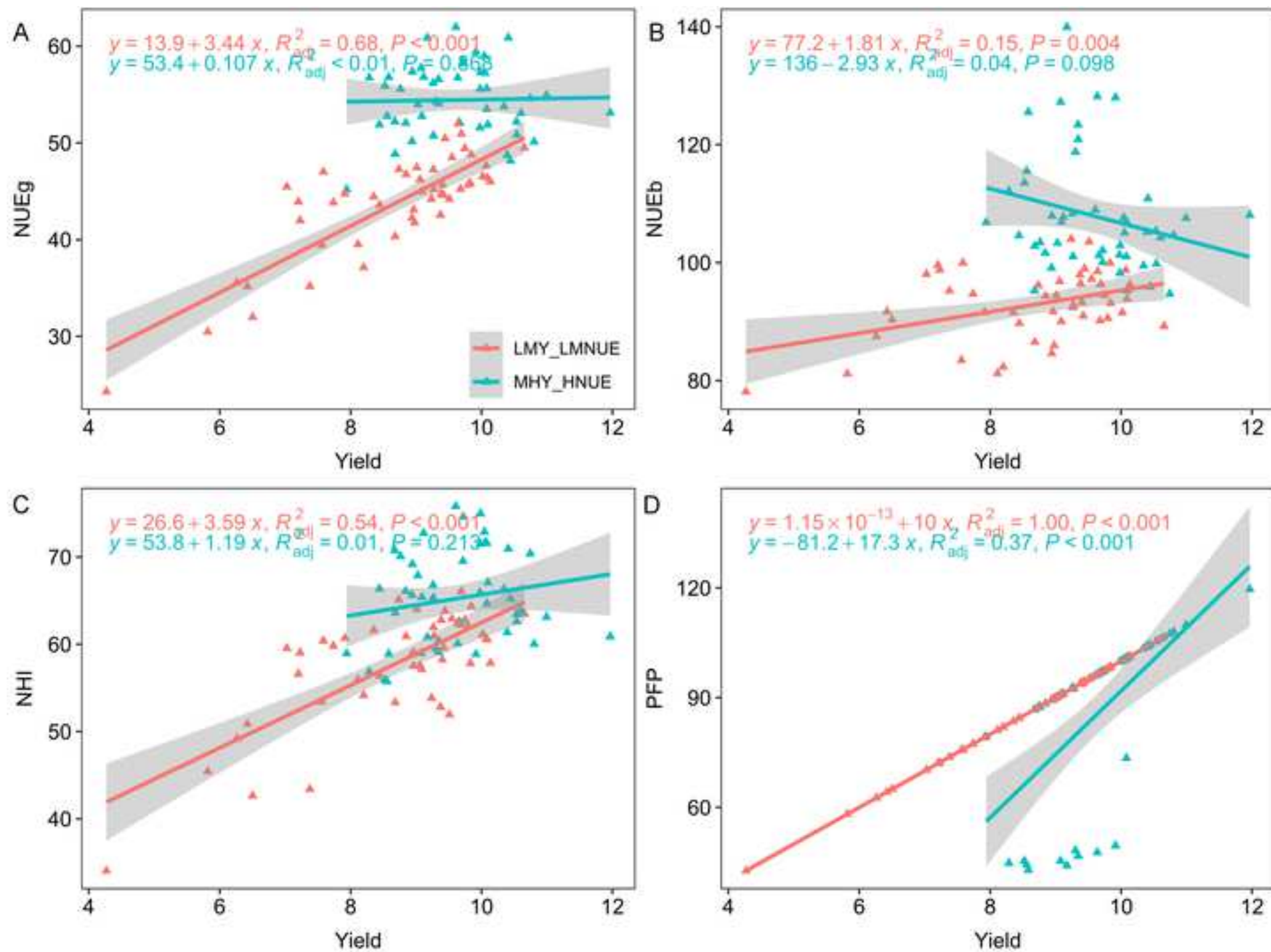


Figure 6

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