

Response of soil fungal community in winter wheat to warming and fertilization regimes

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1 **Response of soil fungal community in winter wheat to**
2 **warming and fertilization regimes**

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7 **Abstract**

8 **Abstract:** Understanding soil fungal diversity under global warming is significant
9 for the assessment of climate change impacts on soil health and soil nutrient
10 transformation. The interaction effect of warmer temperatures and fertilization
11 regimes on fungal communities in the soils of winter wheat fields is unclear. Two-year
12 potting experiments were conducted under nighttime warming and different
13 fertilization regimes. The two-year continuous temperature increase significantly
14 decreased the soil's pH. Warming and fertilization did not significantly change the
15 dominant fungal phyla in the soil. However, it significantly increased the soil fungal
16 richness and diversity compared with no warming and no fertilization. Warming
17 increased richness and diversity by 4.15% and 4.24%, respectively, and fertilization
18 increased richness and diversity by 14.15% and 4.27%, respectively. Furthermore,
19 warming significantly increased the relative abundance of *Fusarium*, which is the
20 causal agent of winter wheat root rot, from 1.75% to 3.62%. However,
21 fertilization reduced the relative abundance of *Fusarium*, especially under the
22 combined application of organic and inorganic fertilizers, suggesting that organic
23 manure addition could impair soil fungal pathogens under future warming. The
24 structural equation model demonstrated that the influence of soil temperature on
25 fungal diversity was direct and mediated through soil carbon nitrogen ratios. Soil

26 temperature and soil organic matter directly affected soil fungal diversity and were the
27 most significant parameters influencing fungal diversity.

28 **Keywords:** nighttime warming; fertilization regimes; soil fungal; community
29 diversity

30 **Introduction**

31 In the past few decades, with climate change, continuous global warming has led
32 to rising global temperatures (Ye et al. 2020), which are expected to increase by 1.5°C
33 or more in the next 20 years. Global warming is highly variable, and asymmetric
34 diurnal warming is one of the main features (Yan et al. 2017; Li et al. 2020).
35 Asymmetric diurnal warming shows that the rate of global warming at night is higher
36 than that in the daytime (Richard et al. 2017; Rossi et al. 2017). Fertilization is an
37 important management measure in agricultural production that affects the physical
38 and chemical properties of soil, thus affecting the quality and sustainable utilization of
39 soil (Francioli et al. 2016; Zhang et al. 2015). The phenomenon of unreasonable
40 fertilizer application structure in agricultural production is widespread, especially the
41 emphasis on chemical fertilizers and neglect of organic fertilizers, the emphasis on
42 nitrogen fertilizers and light phosphorus and potassium fertilizers, etc (Huang et al.
43 2020). In the long run, this may not only have caused a series of problems such as soil
44 caking, soil acidification and soil nutrient imbalance (Guo and Wang. 2021), but also
45 have altered soil microbial community composition and diversity (Campbell et al.
46 2010; Gu et al. 2019).

47 Fungi are critical microorganisms in soil ecosystems that play a fundamental

48 ecological role as decomposers, symbionts or pathogens for plants and animals (Miao
49 et al. 2016; Tedersoo et al. 2014), such as the formation and decomposition of soil
50 organic matter, the recycling and utilization of nutrients, and the maintenance and
51 improvement of soil fertility (Chen et al. 2019; Fraç et al. 2018). For example, there
52 are symbiotic fungi that can form symbiotic relationships with crops. In addition,
53 organic matter in the soil is decomposed by nutrient fungi which in turn release
54 carbon into the soil. Fungi are also affected by temperature (Mateos-Rivera et al.
55 2016), pH (Liu et al. 2015), moisture (Watson et al. 2017), and soil nutrients (Pan et al.
56 2020). To date, some studies have been conducted to test the composition of fungal
57 communities affected by warming and different fertilization regimes. Previous studies
58 on the effects of warming on soil microbial community structure have yielded many
59 different conclusions. Fungal community structure is altered by changes in
60 temperature (Mucha et al. 2018). A small increase in temperature promotes respiration
61 in the roots of the crop and will promote crop growth (Song et al. 2018), which in turn
62 will affect the percentage of fungi in the microbial community (Classen et al. 2015;
63 Mucha et al. 2018). A short-term (15 months) soil warming experiment revealed that
64 warming (elevated 1 and 2°C) did not markedly alter the overall soil fungal
65 community structures and α -diversity on the Tibetan Plateau (Xiong et al. 2014).
66 However, other studies have shown that prolonged and sustained warming can cause
67 fungal species and populations to decline. (DeAngelis et al. 2015; Liang et al. 2015).
68 Most studies have shown that different fertilization treatments lead to changes in
69 microbial community structure. The results of Wang et al. (2018) showed that the

70 effects of increased nitrogen fertilization on fungal diversity in forest and
71 desert/shrubland ecosystems were inconsistent with the findings in farmland
72 ecosystems. Fungal diversity in forest and desert/shrubland ecosystems decreased
73 with increasing N application; fungal diversity in farmland decreased with increasing
74 N application. Soil microbial community diversity significantly increased by organic
75 fertilizer application (Gu et al. 2019). Application of phosphorus fertilizer to the soil
76 significantly reduced the abundance of fungal communities in alpine meadows
77 thereby altering the fungal community structure (He et al. 2016). These research
78 results show that the response of soil fungal communities respond to nighttime
79 warming and fertilization application is complex.

80 To date, most studies on the effects of climate warming on soil fungal
81 communities have been conducted in forest, alpine, and grassland soils (Zhang et al.
82 2014; Kim et al. 2015; Solly et al. 2017; Cao et al. 2020), and the main method of
83 fertilization has been nitrogen fertilizer, which limits our ability to understand the
84 structure of soil fungal communities in farmland ecosystems change pattern of soil
85 fungal communities in farmland ecosystems. A stable fungal community composition
86 plays an important role in the soil biochemical cycle, maintaining plant health and
87 stabilizing ecosystems (Sun et al. 2017). Thus, investigating soil fungal communities
88 is important. In this study, the objectives were to :1) identify how the soil physical and
89 chemical properties shift in response to nighttime warming and different fertilization
90 regimes; 2) exploring the changing patterns of soil fungal communities affected by
91 nighttime warming and different fertilization measures; and 3) exploring the main

92 factors that influence the structure of fungal communities. This experiment aims to
93 provide a theoretical basis for scientific fertilization practices and sustainable
94 agricultural development.

95 **Materials and Methods**

96 **2.1 Site description**

97 The winter wheat pot experimental field was located at the Baima Experimental
98 Station of Nanjing Agricultural University in Nanjing, Jiangsu Province (31°37'N,
99 119°09'E), from October 2019 to June 2021. The climate of the site is humid
100 subtropical monsoon, with an average annual rainfall of 1147 mm. The annual
101 average temperature is 16.0°C, and the maximum and minimum temperatures are 41.6°C
102 and -14.8°C respectively. The physical and chemical properties of the soil before
103 planting are shown in Table 1.

104 **2.2 Experimental design and soil sampling**

105 The winter wheat variety used in this experiment was Yangmai 16, and sixteen
106 treatments were replicated four times for a total of 64 pots. (1) Two different soils
107 were used, one from Xuchang city (XC, alkaline soil with high nutrient content) and
108 another from Baima town (BM, acidic soil with low nutrient content). (2) Two
109 temperature treatments were designed, a nighttime warming (NW, warming time was
110 18:00-06:00) and an ambient (AMB) treatment. The heating source was an electric
111 heating tube with infrared radiation. During the whole growth period of wheat, the
112 height was continuously adjusted to keep the distance between the heating device and
113 the crop canopy at 1.5 m (Fig 1). Empty stands without heating pipes were erected in

114 the control area to offset the possible shading effects. The soil temperature increased
115 by approximately 1 °C. (3) Four types of fertilizer application measures are set(CK:
116 with no fertilizer added), application of mineral nitrogen fertilizers (N: 225 kg N
117 ha⁻¹yr⁻¹), application of mineral nitrogen, phosphorus and potassium fertilizers (NPK:
118 225 kg N ha⁻¹yr⁻¹, 170 kg P₂O₅ ha⁻¹yr⁻¹ and 170 kg K₂O ha⁻¹yr⁻¹), NPK combined
119 with organic fertilizer (M) (NPKM: 225 kg N ha⁻¹yr⁻¹, 170 kg P₂O₅ ha⁻¹yr⁻¹, 170 kg
120 K₂O ha⁻¹yr⁻¹ and 12.5 g M per pot). The nitrogen fertilizer was urea, which was
121 applied twice at a basal dressing to topdressing ratio of 1:1. Additional fertilizer
122 before the wheat pulling stage. Phosphorus and potassium fertilizers were calcium
123 superphosphate and potassium chloride, respectively, and organic fertilizer was
124 organic compound fertilizer, in which the ratio of N:P:K content was 3:1:2, which
125 were all applied before sowing. The size of the plastic bucket used in this experiment
126 was 27 cm in diameter and 24 cm in height. A total of 7.5 kg of soil was packed into
127 each pot. In each pot, 12 wheat seeds were evenly sown, setting seedlings to 8 plants
128 at the wheat trefoil stage.

129 **2.3 Sample collection and physicochemical analysis**

130 Soil samples at a depth of 0-20 cm were collected on April 6th and May 23rd,
131 2021, respectively. One portion of the soil samples was sieved (2 mm) to remove the
132 plant materials, and roots and stored in a 4°C refrigerator for soil physicochemical
133 property analysis, and others were stored at -70°C for DNA extraction and analysis of
134 sequencing data.

135 A temperature recorder (ZDR-41, Hangzhou Zeda Instrument Co., Ltd.,

136 HuangZhou, China) was used to automatically monitor the 5 cm underground soil of
137 winter wheat in the whole growing period. The recorder automatically recorded and
138 saved the temperature data every 30 minutes. The pH was measured using a pH meter,
139 at a soil: water ratio of 1:5. Soil moisture content was determined by drying the soil at
140 105 °C for 12 h. Ammonium nitrogen was determined by the indophenol blue
141 colorimetric method, and nitrate nitrogen was analysed via ultraviolet
142 spectrophotometry. Soil total nitrogen (TN) was determined by the Kjeldahl method.
143 Soil organic matter (SOM) was measured by the external heating method with
144 potassium dichromate (K₂Cr₂O₇). Available phosphorus (AP) was determined by
145 sodium bicarbonate–ultraviolet spectrophotometry. Soil available potassium (AK) was
146 measured using flame atomic absorption spectrophotometry.

147 **2.4 DNA extraction and analysis of sequencing data**

148 According to the manufacturer's protocols, total DNA of soil microorganisms
149 was extracted from 0.5 g soil of each subsample with a PowerSoil kit (MoBio
150 Laboratories Carlsbad, CA, USA). PCR amplification of the V3-V4 hypervariable
151 region fragment of the 18S rRNA gene was performed using ITS1 (ITS1 5'
152 -CTTGGTCATTTAGAGGAAGTAA-3') and ITS2 (ITS2 5'
153 -GCTGCGTTCTTCATCGATGC-3') as sequencing primers to purify the DNA
154 sequence (Yu et al., 2019). The thermocycling conditions were as follows:
155 predenaturation at 95 °C for 2 min, denaturation at 95 °C for 30 s, annealing at 55 °C
156 for 30 s, extension at 72 °C for 30 s, 25 cycles, and extension at 72°C for 5 min. Each
157 sample had 3 replicates. The PCR products of the same sample were mixed and

158 detected by 2% agarose gel electrophoresis. The PCR products were cut and
159 recovered by using the AxiPrepDNA gel recovery kit (AXYGEN Company) and
160 eluted by Tris HCl and 2% agarose electrophoresis. With reference to the preliminary
161 quantitative results of electrophoresis, the PCR products were detected and quantified
162 with the QuantiFluor™-ST blue fluorescence quantitative system (Promega), and the
163 corresponding proportions were mixed according to the sequencing quantity
164 requirements of each sample. The fungi were sequenced on the Illumina MiSeqPE250
165 platform of Shanghai Meiji Biomedical Technology Co., Ltd.

166 **2.5 Statistical Analysis**

167 Process all sequencing data on the Majorbio Cloud Platform
168 (<http://www.majorbio.com>, accessed on 3 May 2020). Mothur software (version
169 1.31.2, <http://www.mothur.org/>) was used to analyse the α diversity index of fungi
170 (including Shannon, Simpson, Chao1 and ACE) (Schoch et al. 2012). A bubble map
171 (correlation) between soil properties and fungal alpha diversity was constructed using
172 the “corrplot” package in R software. Two-way analysis of variance (ANOVA) was
173 applied to evaluate the effects of nighttime warming, different fertilization treatments,
174 and their interaction on the diversity of soil fungi. The data presented in this paper are
175 the average of three repetitions. The underlying data were analyzed using SPSS
176 software, version 16.

177 **Results**

178 **3.1 Soil physicochemical properties**

179 Tables 2 and 3 show the changes in soil physicochemical properties as a result of

180 nighttime warming and different fertilization practices. Among these two soils, the
181 NW and fertilization treatments had lower pH values than the CK treatment regardless
182 of the fertilizer regime, and the effect of warming was more obvious ($P < 0.01$). In XC
183 soil, the soil AK ($P < 0.01$) and AP contents considerably decreased in the NW
184 treatment, while fertilizer application eased this downwards trend to a certain extent,
185 especially in NPKM-treated soils. The contents of three different forms of nitrogen
186 showed different response trends under NW and different fertilization regimes. NW
187 increased the content of soil $\text{NH}_4^+\text{-N}$ and TN but decreased the content of $\text{NO}_3^-\text{-N}$.
188 Fertilizer addition resulted in a significant increase in soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and TN
189 ($P < 0.01$) compared with the CK group. In BM soil, the change trend of soil nutrients
190 was roughly the same as that in XC soil. Compared with CK, NW led to higher soil
191 $\text{NH}_4^+\text{-N}$ and TN, which increased TN by 32.3% on average and reduced the contents
192 of soil AK, AP and $\text{NO}_3^-\text{-N}$. NW had no significant effect on SOM content in soil.
193 Fertilization increased the contents of soil $\text{NO}_3^-\text{-N}$, $\text{NH}_4^+\text{-N}$ and TN, which showed
194 $\text{NPKM} > \text{NPK} > \text{N} > \text{CK}$ treatment as a whole.

195 Variance analysis showed that NW had a significant impact on other
196 environmental factors except AP. All environmental factors were significantly
197 affected by fertilization. Nighttime warming and fertilization had an interactive effect
198 on soil TN, AP and AK.

199 The variance analysis showed that NW had a significant impact on all
200 environmental factors except soil organic matter. Fertilization had a significant impact
201 on all environmental factors. NW and fertilization had an interactive effect on soil TN,

202 $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, AP and AK.

203 **3.2 Soil fungal community composition**

204 Warming and fertilization did not significantly change the dominant phylum of
205 soil fungi (Figs. 3,4). *Ascomycota* dominated across treatments, with relative
206 abundances ranging from 34.84% to 67.48%, followed by *Mortierellomycota*
207 (12.66% – 33.81%), *Basidiomycota* (1.92% – 13.65%) and *Opisthokonta* (0.2% –
208 18.26%). However, the relative abundances changed. The highest abundance in both
209 soils was in the phylum *Ascomycota*. Overall, NW increased the relative abundance of
210 *Ascomycota* but decreased that of *Basidiomycota* under the same fertilization
211 application level in the two soils. However, under the treatment of nitrogen fertilizer
212 alone, NW reduced the abundance of *Ascomycetes* and increased the abundance of
213 *Basidiomycetes*.

214 At the genus level (Figs. 5,6), among these two soils, night-time warming
215 decreased the relative abundance of *Mortierella* but increased it in fertilized
216 treatments in both soils as a whole. Nighttime warming also increased the relative
217 abundance of *Fusarium*. Compared with CK, fertilization reduced the relative
218 abundance of *Fusarium* in BM soil, especially under the NPKM treatment.

219 **3.3 Analysis of igh-Quality sequences**

220 In XC soil, the alpha diversity index results of the fungal community showed that
221 NW generally increased the Ace (797.4) and Chao (803.6) indices by an average of
222 2.13% and 1.54%, respectively. Different fertilization regimes had the same effect on
223 richness, and the influence trend was NPKM>N>NPK>CK under the two temperature

224 treatments. Among them, the increase effect of NPKM treatment was the most
225 obvious, which increased the Ace index by 19.2% and 23.6% and the Chao index by
226 23.3% and 24.3%, respectively. Nighttime warming and fertilization also significantly
227 changed the richness of fungi in BM soil (Table 5). NW increased the Ace (537.1)
228 and Chao (534.1) indices of BM soil by an average of 10.0% and 5.81%, respectively.
229 The Ace index and Chao index of the CK treatment were obviously lower than those
230 of all fertilization treatments, which was consistent with the results of the XC soil.
231 Additionally, the Shannon index of the NW treatment was significantly higher than
232 that of the AMB treatment, while the Simpson index was lower than that of the AMB
233 treatment in the two soils. These results indicate that NW increased the diversity of
234 soil fungal communities.

235 The variance analysis showed that fertilization had a significant effect on the
236 richness and Simpson index of soil fungi in XC soil. NW had a significant effect on
237 the diversity index but had a slight effect on the richness, and the interaction between
238 temperature and fertilization had little effect on the richness of soil fungi.
239 Temperature, fertilization, and the interaction between temperature and fertilization
240 had a significant impact on the richness and Simpson index of soil fungi in BM soil,
241 especially fertilization, which had the greatest impact on richness.

242 **3.4 Correlation analysis between soil fungal community diversity and** 243 **environmental factors**

244 For the XC soil (Fig. 7), there was a positive correlation among ST, AK, AP,
245 $\text{NH}_4^+\text{-N}$, SOM and soil fungal community diversity, while SM (soil moisture) and pH
246 were negatively correlated with it. Soil AP and SOM had the greatest influence on the
247 richness of soil fungal communities in winter wheat ($P>0.01$). For the BM soil (Fig.

248 8), ST, SM, pH and AK were the key factors affecting the change in soil fungal alpha
249 diversity in BM. ST, AK, AP, SOM and soil fungal alpha diversity were positively
250 correlated. At the same time, soil pH and SM were negatively correlated with soil
251 fungal alpha diversity in both soils, which indicated that decreasing soil moisture and
252 soil pH properly can increase the diversity and richness of soil fungi.

253 **3.5 The effects of soil physical and chemical properties on fungal diversity**

254 To further explore the direct and indirect effects of night-time warming and
255 fertilization on soil fungal communities, we synthesized the experimental data of XC
256 and BM soils and used AMOS software to build a structural equation model to verify
257 our hypothesis. Soil temperature ($\beta=0.368$, standardized coefficient) can directly
258 affect the diversity of soil fungal communities (Fig. 9), and it can also indirectly affect
259 fungal communities by affecting SM, pH, SOM and the soil carbon-nitrogen ratio
260 (C/N). Among them, the correlations between soil temperature and soil moisture
261 ($\beta=-0.589$, standardized coefficient) and C/N ($\beta=-0.229$, standardized coefficient)
262 were the strongest. The ST and SOM ($\beta=0.078$, standardized coefficient) reached a
263 significant level with the diversity of oil fungal communities.

264 **Discussion**

265 **4.1 Effects of night-time warming and different fertilization regimes on soil** 266 **physicochemical factors**

267 Our research showed that night-time warming reduced soil pH to a certain extent,
268 which was similar to the results of Guo et al (2021). Organic fertilizer application
269 reduced the pH value of alkaline soil while alleviating the decrease in pH in acidic
270 soil, which was consistent with the research results of Wei et al (2017). This
271 discrepancy may be attributed to the application of organic fertilizer increasing the

272 content of soil organic carbon, and organic carbon is an acid-base buffer that can
273 neutralize the acidity and alkalinity of soil and make the soil tend to be neutral (Wang
274 et al. 2016). Studies have shown that warming promotes the wheat root activity, which
275 is beneficial to the nitrogen uptake from soil (Purakayastha et al. 2019). In this study,
276 the $\text{NH}_4^+\text{-N}$ content of the soil after warming treatment was significantly higher than
277 that of CK, which may be because the temperature rise in a certain range enhanced the
278 nitrogen conversion and ammonification, and facilitated the conversion of amino
279 acids to $\text{NH}_4^+\text{-N}$ (Guo et al. 2015). However, in alkaline soil, $\text{NH}_4^+\text{-N}$ in the surface
280 layer was easily volatilized in the form of NH_3 molecules (Beier et al. 2004; Xu et al.
281 2021), and we observed that the $\text{NH}_4^+\text{-N}$ content in XC soil was slightly lower than
282 that in BM soil. Fertilization could increase the concentration of available nitrogen in
283 soil. In this study, different forms of nitrogen contents increased to different degrees
284 under the fertilization treatment. It was found that AP, AK and SOM levels in the soil
285 were increased to varying degrees by the application of organic fertilizers. (Bei et al.
286 2018; Lu et al. 2021). The results of this study are similar to its.

287 **4.2 Effects of nighttime warming and different fertilization regimes on soil fungal** 288 **community**

289 In this study, *Ascomycota*, *Mortierellomycota*, *Basidiomycota*, and
290 *Olpidiomycota* were the dominant fungal phyla in the two different soil types,
291 accounting for more than 80% of the total fungal phyla. Similar results have been
292 observed in other studies (Pan et al. 2020; Yao et al. 2021; Wang et al. 2022). This
293 result showed that the strong adaptations of these species to the wheat soil
294 environment. *Ascomycota* grow rapidly and are capable of breaking down substances

295 in the soil that are difficult to break down, such as lignin and keratin. It is the main
296 driver of nutrient cycling and energy flow (Beimforde et al. 2014). It is also the main
297 decomposer in agricultural soils (Ma et al. 2013), and the addition of organic fertilizer
298 is beneficial to its growth (Wang et al. 2018). Overall, NW increased the relative
299 abundance of *Ascomycota* in the two soils. However, under the treatment of nitrogen
300 fertilizer alone, NW reduced the abundance of *Ascomycota*. *Fusarium* is a fungal
301 pathogen that causes great harm to the roots of crops such as wheat and corn
302 (Fernandez et al. 2005; Liu et al. 2015; Tagele et al. 2019). In this experiment, the
303 abundance of *Fusarium* increased under the night-time warming treatment, but in the
304 combination treatment of organic fertilizer and inorganic fertilizer, its abundance was
305 lower than that of the control and chemical fertilizer treatments, which indicated that
306 the organic fertilizer application could reduce the risk of diseases caused by *Fusarium*
307 in winter wheat. This conclusion was also obtained by Wen et al (2020).

308 Our study showed that fungal community compositions were significantly
309 altered after night-time warming and different fertilizer applications. However, it was
310 found that short-term warming treatments in alpine peatlands did not result in
311 significant changes in the α diversity of fungal communities. (Wang et al. 2022).
312 DeAngelis et al (DeAngelis et al. 2015) demonstrated that long-term experimental
313 warming often leads to a decrease in soil fungal abundance. Wen et al (2020) found
314 that organic fertilizer significantly changed the α diversity of soil fungi, while
315 chemical fertilizer did not. Xiang et al (2020) reported that the abundance and
316 diversity of fungi increased with the application of organic fertilizer and NPK, and

317 long-term fertilization led to great changes in the composition of fungal communities.
318 In this experiment, our results showed that both warming and fertilization could
319 increase the diversity and richness index of soil fungal communities in the two soils,
320 in which temperature was the predominant factor influencing the diversity of soil
321 fungi, and the richness was mainly related to fertilization. The differences may be
322 caused by a variety of factors, such as differences in temperature increase range, soil
323 types, research methods and research duration (Leon-Sanchez et al. 2018).

324 **4.3 Environmental factors affecting soil fungal community structure under** 325 **nighttime warming and fertilization.**

326 Pearson correlation analysis found that ST, AK, SOM and AP had significant
327 relationships with the composition of the XC and BM fungal communities. Soil
328 organic carbon and AK, and AP contents have ever been reported as important factors
329 influencing the fungal community (Cai et al. 2021). Ma et al (2018) also found that
330 organic matter was an important factor in the change in fungal community
331 composition. It may be that most fungi are heterotrophs and their growth is dependent
332 on external carbon sources, so unstable organic matter has profound influences on
333 their abundance (Broeckling et al. 2008). By analyzing the structural equation model
334 we found that increased soil temperature affects organic matter and carbon to nitrogen
335 ratios, which indirectly leads to changes in soil fungal community structure. The SEM
336 further explained that the soil organic matter addition significantly increased the
337 diversity of soil fungal communities. Liu et al (Liu et al. 2022) also showed that there
338 was an obvious positive correlation between organic matter and the diversity of soil
339 fungi in the effects of warming on wheat soil fungi experiments. Proper increases in

340 soil temperature and soil environments rich in organic matter may be beneficial to
341 improve the diversity of fungal communities.

342 **Conclusions**

343 Two years of night-time warming and different fertilization regimes had a
344 significant impact on soil physicochemical properties, soil fungal species composition,
345 richness and diversity in winter wheat. Both night-time warming and fertilization,
346 especially the addition of organic fertilizer, significantly increased the richness and
347 diversity of soil fungal communities compared to CK. The SEM further revealed that
348 ST and SOM play an important role in shaping the structure of fungal communities.
349 Furthermore, the addition of organic fertilizer can reduce the relative abundance of
350 *Fusarium*. Thus, the incidence of winter wheat root rot may be reduced.

351 **Credit authorship contribution statement**

352 **Ning Han:** Writing – original draft, Formal analysis, Writing – review & editing. **Chaoran**
353 **Yang:** Formal analysis. **Mengting Liu:** Visualization. **Xinyu Pei:** Formal analysis. **Ruilin Mao:**
354 **Supervision. Changqing Chen:** Conceptualization, Methodology, Software.

355 **Declaration of Competing Interest**

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

358 **Data availability**

359 Data will be made available on request.

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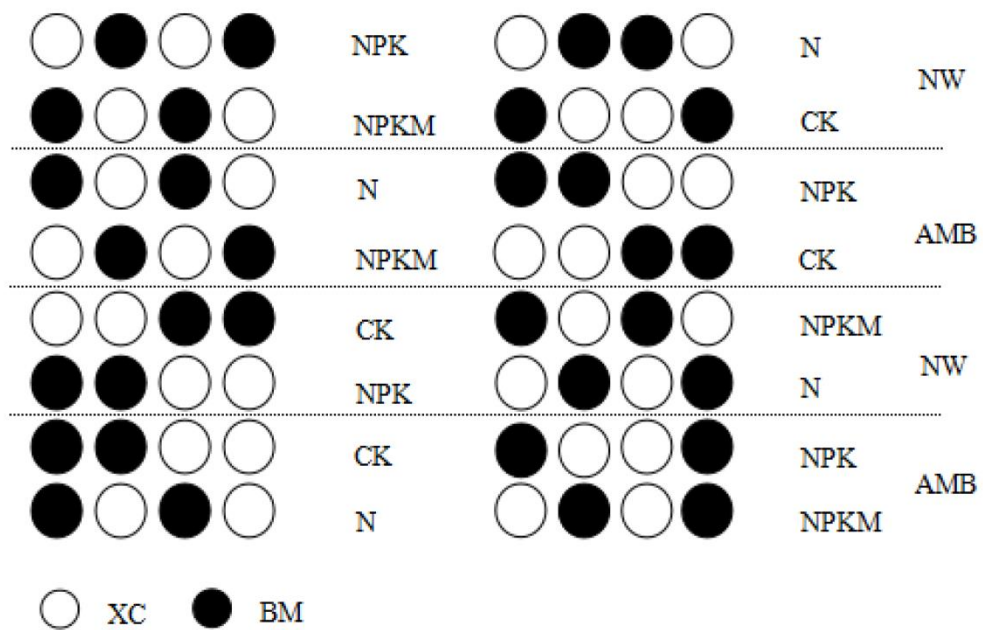
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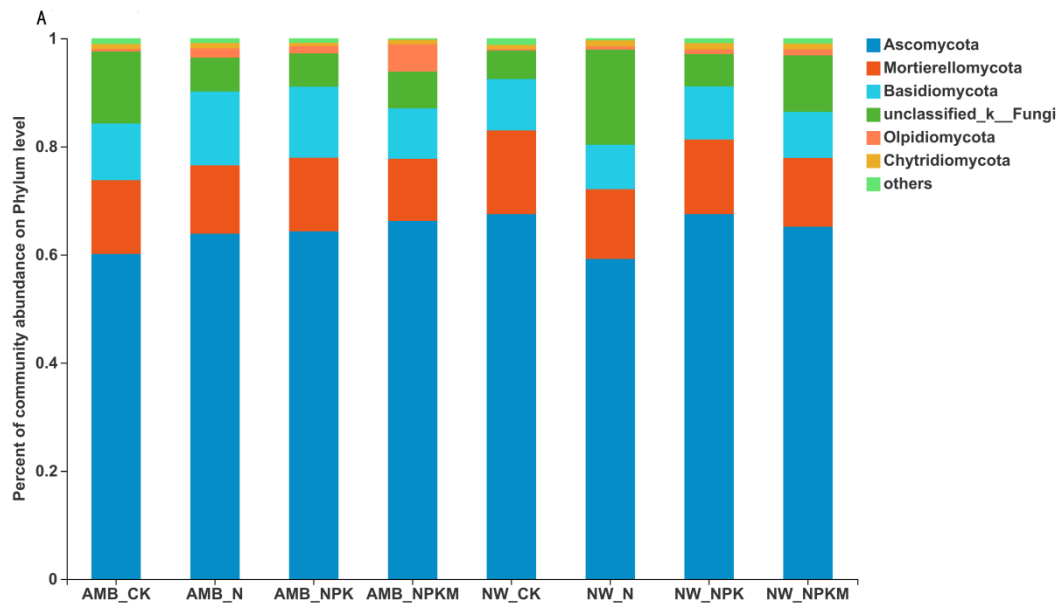
548 Fig. 1 System structure of Free Air Temperature Increased (FATI) in winter wheat field.



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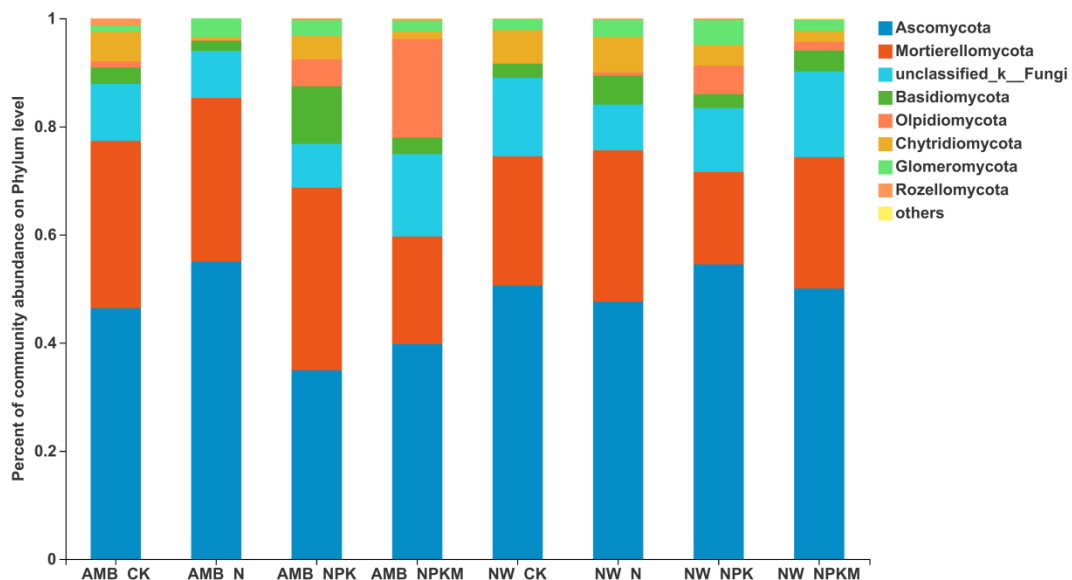
550 Fig. 2 Experimental plot layout. XC (the soil from Xuchang city); BM (the soil from Baima town); AMB:
551 ambient; NW: nighttime warming; CK: control; N: application of mineral N fertilizers; NPK: application of

552 mineral N, P and K fertilizers; NPKM: manure fertilizer and NPK plus manure.



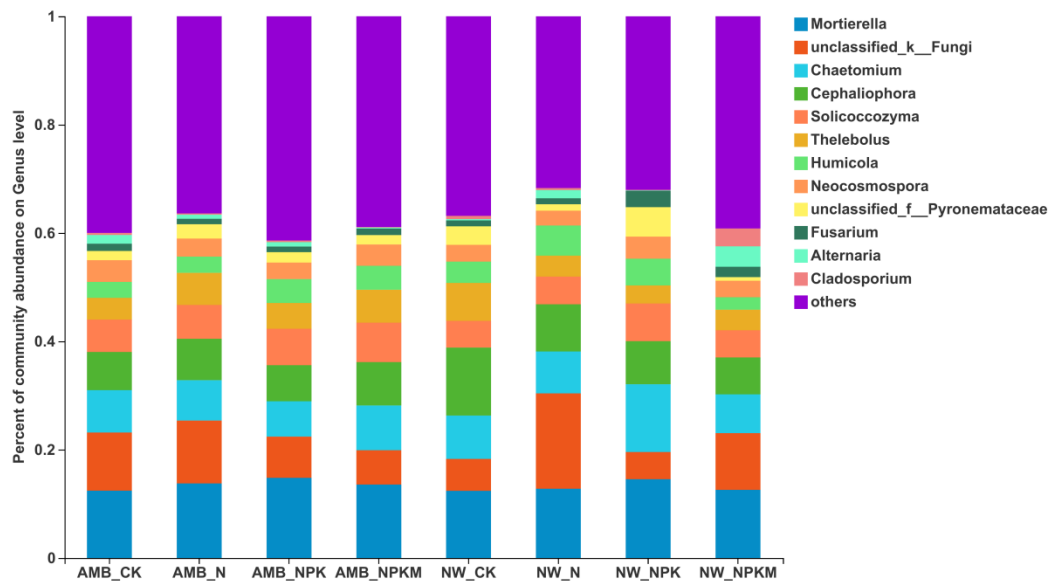
553

554 Fig. 3 Effects of night-time warming and different fertilization regimes on the community structure of soil
 555 fungi at the phylum level of XC. AMB: ambient, NW: nighttime warming, Percent of community
 556 abundance < 1% are classified as “Others”, the same below. AMB: ambient; NW: nighttime warming; CK:
 557 control; N: application of mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM:
 558 manure fertilizer and NPK plus manure.

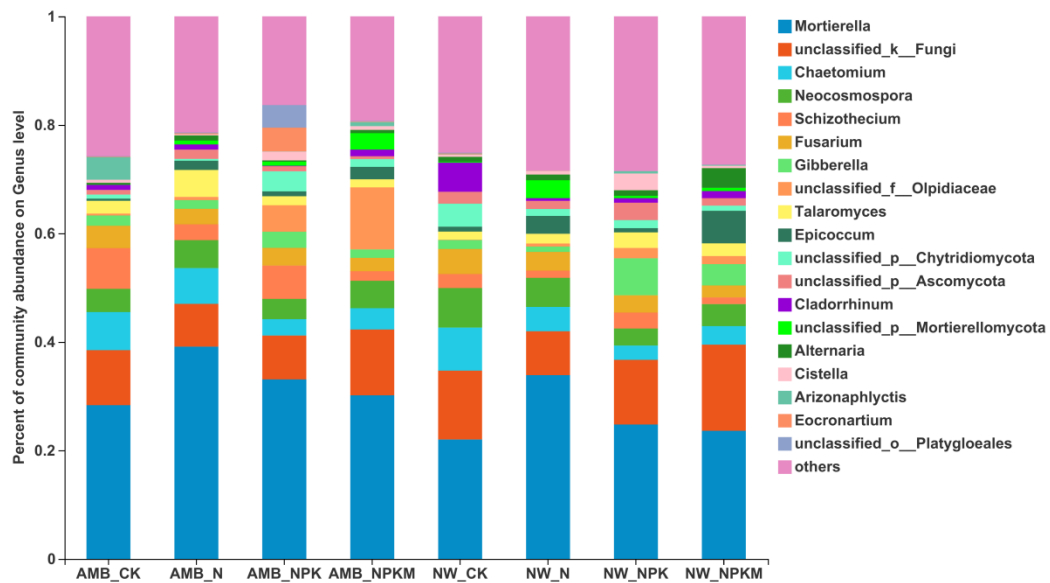


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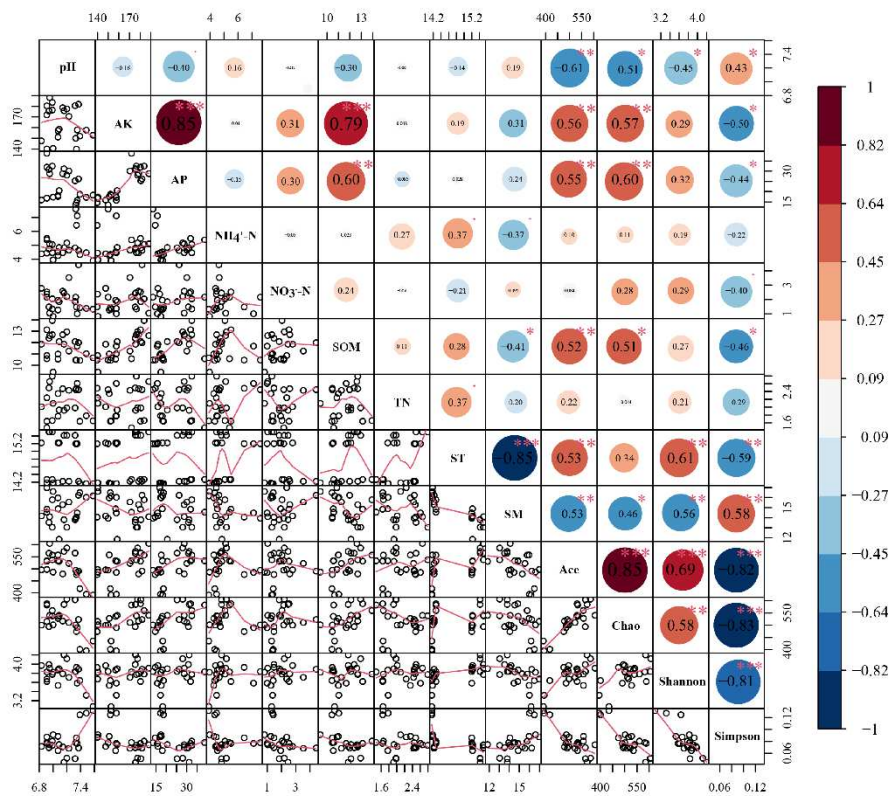
560 Fig. 4 Effects of night-time warming and different fertilization regimes on the community structure of soil
 561 fungi at the phylum level of BM. AMB: ambient; NW: nighttime warming; CK: control; N: application of
 562 mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM: manure fertilizer and
 563 NPK plus manure.



564
 565 **Fig. 5 Effects of night-time warming and different fertilization measures on the community structure of soil**
 566 **fungi at the genus level of XC. AMB: ambient; NW: nighttime warming; CK: control; N: application of**
 567 **mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM: manure fertilizer and**
 568 **NPK plus manure.**

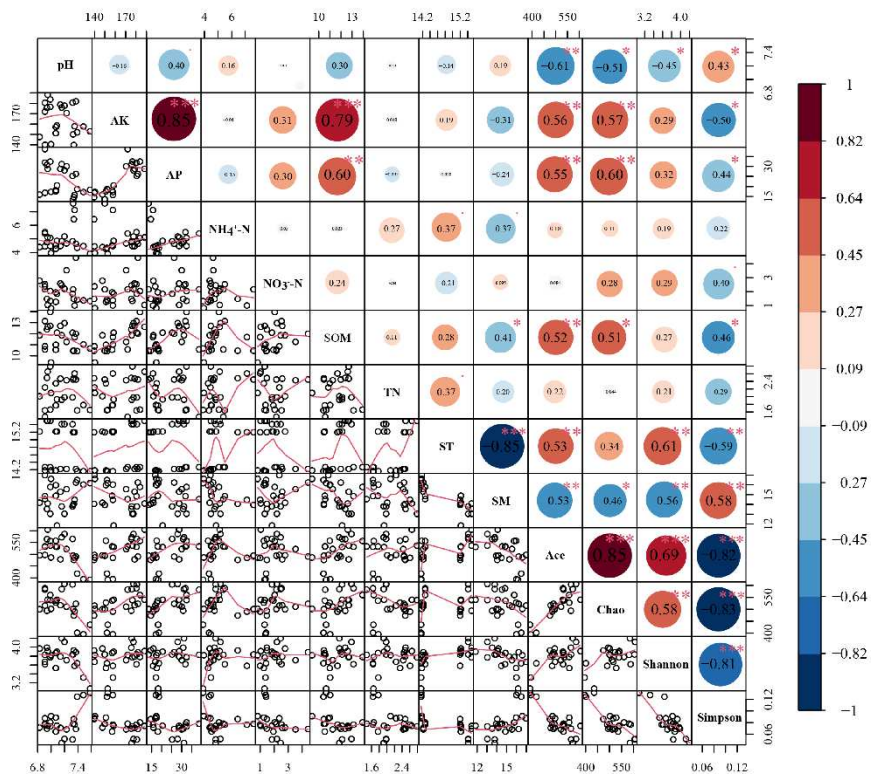


569
 570 **Fig. 6 Effects of night-time warming and different fertilization measures on the community structure of soil**
 571 **fungi at the genus level of BM. AMB: ambient; NW: nighttime warming; CK: control; N: application of**
 572 **mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM: manure fertilizer and**
 573 **NPK plus manure.**



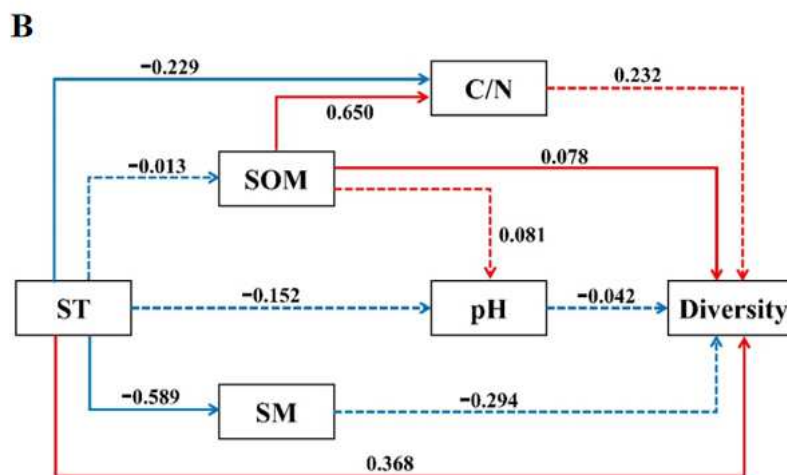
574

575 **Fig. 7** Pearson correlation analysis showing the relationships between environmental factors and soil fungal
 576 community alpha diversity of XC. pH: soil acidity, AK: available potassium, AP: available phosphorus,
 577 NH₄⁺-N: ammonium nitrogen, NO₃⁻-N: nitrate nitrogen, SOM: organic matter, TN: total nitrogen, ST: soil
 578 temperature, SM: soil moisture, the same as below.



579

580 Fig. 8 Pearson correlation analysis showing the relationships between environmental factors and soil fungal
 581 community alpha diversity of BM. pH: soil acidity, AK: available potassium, AP: available phosphorus,
 582 NH₄⁺-N: ammonium nitrogen, NO₃⁻-N: nitrate nitrogen, SOM: organic matter, TN: total nitrogen, ST: soil
 583 temperature, SM: soil moisture, the same as below.



$P=0.748$; $CMIN=1.22$; $GFI=0.992$; $AIC=37.22$; $RMSEA=0.000$

584

585 Fig. 9 Structural equation models as predictors of soil fungal diversity.

586 Solid red arrows represent positive paths ($P<0.05$), solid blue arrows represent negative paths ($P<0.05$) and
 587 dotted grey arrows represent nonsignificant paths ($P>0.05$). The estimated value of the path coefficient
 588 represents the size of the impact scale. ST: soil temperature; SM: soil moisture; pH: soil acidity; SOM: soil
 589 organic matter; C/N: soil carbon nitrogen ratio.

590

591 Table 1 Basic physical and chemical properties of tested soil

Soil	pH	SOM g·kg ⁻¹	TN g·kg ⁻¹	AP mg·kg ⁻¹	AK mg·kg ⁻¹
XC	7.40	18.79	3.90	41.81	191.92
BM	6.63	10.70	2.62	23.98	146.24

592 XC(the soil from Xuchang city); BM(the soil from Baima town); pH: soil acidity; SOM: organic matter;

593 TN: total nitrogen; AP: available phosphorus AK: available potassium.

594 Table 2. Effects of night-time warming and different fertilization regimes on soil properties of XC

Temperature	Fertilization	pH	AK mg·kg ⁻¹	AP mg·kg ⁻¹	NH ₄ ⁺ -N mg·kg ⁻¹	NO ₃ ⁻ -N mg·kg ⁻¹	TN g·kg ⁻¹	SOM g·kg ⁻¹
AMB	CK	7.95±0.08a	182.13±2.56c	30.29±0.87c	2.92±0.19b	14.93±0.30c	3.47±0.05c	18.64±0.22a
	N	7.90±0.06a	183.11±4.49c	33.15±1.60c	3.16±0.10b	16.86±0.17b	3.63±0.01b	19.18±0.84a
	NPK	7.94±0.08a	217.38±0.00b	40.46±1.93b	3.51±0.08a	17.25±0.53b	3.89±0.07a	19.17±1.23a

	NPKM	7.85±0.06a	229.14±5.09a	45.13±0.23a	3.61±0.09a	18.15±0.11a	3.84±0.05a	19.99±0.50a
	CK	7.72±0.04a	171.36±4.49c	31.62±1.66c	3.06±0.04d	14.20±0.69c	3.69±0.08c	17.77±0.14b
NW	N	7.68±0.01ab	180.17±4.82bc	31.77±1.04c	3.37±0.07c	15.74±0.85b	3.77±0.04b	17.92±0.31b
	NPK	7.69±0.06ab	186.05±4.49b	37.22±1.86b	3.64±0.04b	16.71±0.16ab	3.78±0.09b	18.20±0.32b
	NPKM	7.60±0.06b	203.68±3.39a	48.36±1.11a	3.89±0.04a	17.39±0.23a	4.22±0.03a	18.68±0.41a
Analysis of	T	89.285**	109.354**	0.001	21.260**	16.984**	52.585**	18.323**
variance	F	3.598*	118.718**	156.288**	68.885**	50.750**	83.448**	3.370*
	T×F	0.126	15.020**	6.207**	0.741	0.393	23.216**	0.176

595 *Numbers with different letters are significantly different at $p < 0.05$ (LSD). Mean \pm standard error
596 of the mean (SEM) ($n = 5$). The last three lines indicate the significance of the influence of the two
597 factors and their interactions; T: warming effect; F: fertilization effect; T \times F: interaction effect
598 between the temperature and fertilization; AMB: ambient; NW: nighttime warming; CK: control;
599 N: application of mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM:
600 manure fertilizer and NPK plus manure. AK: available potassium; AP: available phosphorus;
601 $\text{NH}_4^+\text{-N}$: ammonium nitrogen; $\text{NO}_3^-\text{-N}$: nitrate nitrogen; TN: total nitrogen; SOM: organic matter.
602 (the same below)

603 **Table 3. Effects of night-time warming and different fertilization regimes on soil properties of BM**

Temperature	Fertilization	pH	AK $\text{mg}\cdot\text{kg}^{-1}$	AP $\text{mg}\cdot\text{kg}^{-1}$	$\text{NH}_4^+\text{-N}$ $\text{mg}\cdot\text{kg}^{-1}$	$\text{NO}_3^-\text{-N}$ $\text{mg}\cdot\text{kg}^{-1}$	TN $\text{g}\cdot\text{kg}^{-1}$	SOM $\text{g}\cdot\text{kg}^{-1}$
AMB	CK	6.87±0.01a	129.05±4.92c	10.61±0.48c	3.41±0.07b	12.15±0.33b	1.51±0.03c	9.61±0.35b
	N	6.82±0.03ab	131.42±3.37c	26.00±0.55b	3.42±0.10b	13.56±0.43a	1.66±0.06b	10.15±0.51ab
	NPK	6.81±0.02b	142.96±11.50b	26.77±1.02b	3.46±0.01b	13.10±0.28a	1.72±0.10b	10.53±0.40a
NW	NPKM	6.85±0.03ab	164.51±3.59a	30.49±2.22a	3.61±0.10a	13.37±0.52a	1.85±0.06a	10.29±0.22ab
	CK	6.83±0.05a	116.86±4.02b	14.04±0.98c	3.36±0.04c	11.06±0.17c	2.28±0.10c	9.72±0.28a
	N	6.74±0.02b	128.28±3.74a	20.91±0.88b	3.39±0.06c	11.55±0.32b	2.32±0.09c	9.92±0.17a

604 **Table 4. Alpha diversity index table of soil fungi of XC**

Temperature	Fertilization	Ace	Chao	Shannon	Simpson
AMB	CK	728.08±41.10b	722.31±43.07b	4.14±0.01a	0.0399±0.0031a
	N	774.87±14.45b	781.67±18.16b	4.18±0.18a	0.0354±0.0008b
	NPK	752.42±18.58b	770.96±30.17b	4.21±0.14a	0.0325±0.0007b
	NPKM	867.64±23.13a	890.56±42.51a	4.27±0.12a	0.0282±0.0005c
NW	CK	722.50±31.30c	715.38±25.02c	4.22±0.04b	0.0327±0.0003a
	N	811.13±25.17b	827.26±12.64b	4.30±0.00a	0.0306±0.0019a
	NPK	762.63±9.16bc	782.51±18.84b	4.36±0.08a	0.0286±0.0035a
Analysis of variance	NPKM	893.20±29.94a	889.34±35.24a	4.33±0.03a	0.0289±0.0009a
	T	2.435	0.944	6.904*	23.238**
	F	39.475**	31.901**	2.032	17.986**
	T×F	0.735	0.871	0.262	4.246*

605 T: temperature, F: fertilization, * and ** indicate significant differences at the 0.05 and 0.01 levels,
606 respectively, the same as below. AMB: ambient; NW: nighttime warming; CK: control; N:

607 application of mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM:
 608 manure fertilizer and NPK plus manure.

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610 **Table 5. Alpha diversity index table of soil fungi of BM**

Temperature	Fertilization	Ace	Chao	Shannon	Simpson
AMB	CK	400.85±14.83b	410.52±21.90c	3.35±0.29b	0.1279±0.0036a
	N	513.94±38.19a	515.07±13.36b	3.68±0.15ab	0.0888±0.0019b
	NPK	497.55±22.80a	516.77±6.12b	3.80±0.09a	0.0693±0.0015d
	NPKM	540.66±14.43a	576.87±14.91a	3.74±0.11a	0.0783±0.0017c
NW	CK	485.03±9.09b	488.21±13.61b	3.78±0.18a	0.0801±0.0053a
	N	519.79±20.98b	525.54±21.77b	3.91±0.05a	0.0701±0.0054b
	NPK	574.75±10.52a	598.52±11.65a	4.05±0.19a	0.0491±0.0038c
Analysis of variance	NPKM	568.94±34.15a	524.28±26.32b	3.89±0.11a	0.0724±0.0026b
	T	25.796**	16.264**	16.052**	318.936**
	F	25.938**	46.273**	5.061*	204.428**
	T×F	3.89*	19.151**	0.824	46.028**

611 T: temperature, F: fertilization, * and ** indicate significant differences at the 0.05 and 0.01 levels,
 612 respectively, the same as below. AMB: ambient; NW: nighttime warming; CK: control; N:
 613 application of mineral N fertilizers; NPK: application of mineral N, P and K fertilizers; NPKM:
 614 manure fertilizer and NPK plus manure.

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