Enhanced soil quality after forest conversion to vegetable cropland and tea plantation has contrasting effects on soil microbial structure and functions

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32 **Abstract**

33 Land-use changes could potentially exert a strong influence on soil quality and
34 soil microbial communities. Moreover, microbial taxa are also important drivers of
35 soil ecological functions. However, the linkage between soil quality and soil microbial
36 communities is in need of deeper understanding. In this study, we examined the
37 effects of soil quality on microbial community structure and functions after forest
38 conversion to vegetable cropland and tea plantations. Soil quality index was
39 significantly increased after natural forest conversion to vegetable cropland and tea
40 plantations. Soil bacterial beta diversity significantly correlated to soil quality, but the
41 sensitivity of individual microbial groups varied in response to changes in soil quality.
42 Higher soil quality promoted bacterial diversity in vegetable cropland but decreased it
43 in tea plantations, which implied soil quality was a structural factor in bacterial
44 community composition but had contrasting effects for croplands versus plantations.
45 Agricultural management played a negative role in maintaining microbial interactions,
46 as identified by the network analysis, and furthermore the analysis revealed key
47 functions of the microbial communities. After land-use change, the abundance (e.g.,
48 level, intensity) of microbial N-cycling function increased in tea plantations but
49 decreased in vegetable cropland. The abundance of C-cycling function featured an
50 opposite trend. Higher level of N-fixation in tea plantations but the higher abundance
51 of N-oxidation in vegetable cropland was demonstrated. Higher abundance of
52 ammonia-oxidizing bacteria and ammonia-oxidizing archaea as identified by qPCR in
53 vegetable cropland corroborated the FAPROTAX function prediction. Therefore, the

54 key taxa of soil microbial communities and microbial functions were largely
55 dependent on changes in soil quality and determined responses to specific agricultural
56 management.

57 **Keywords:** land use change; soil quality; microbial diversity; co-occurrence network;
58 C and N cycling; agricultural management

59

60 **1. Introduction**

61 Land-use change is the most impactful factor on the surface cover and soil
62 quality of ecosystems (Foley et al., 2005). Moreover, land-use changes modify soil
63 microbial communities, which are important drivers for maintaining soil quality and
64 ecological functions (Jesus et al., 2009; Lehmann et al., 2020). The ecological
65 functions of soil microorganisms play indispensable roles in carbon (C) and nitrogen
66 (N) cycling and are closely related to plant productivity and sustainability. Thus,
67 microorganisms and related ecological functions impact the health of soils, plants and
68 animals (Fierer, 2017). This necessitates understanding the effects of modifications in
69 structure and functions of microbial communities resulting from land use change and
70 management (Fierer, 2017; Nemergut et al., 2013).

71 Soil quality represents the capacity of a soil to provide ecological services, and it
72 is an important index for revealing land sustainability and productivity (Doran, 1994).
73 Among various natural and anthropogenic factors, the type (mineral and organic) and
74 amount of fertilization play leading roles in maintaining or altering soil quality. For
75 example, during the conversion from natural broad-leaf forest to tea (*Camellia*

76 *sinensis* L.) plantations, mineral fertilization decreased organic carbon (SOC) stock
77 and hence negatively affected the soil quality (Fan and Han, 2018; Zhu et al., 2020).
78 Long-term N fertilization commonly induces soil acidification (Guo et al., 2010;
79 Kuzyakov et al., 2021, Geoderma). Changes in the aboveground vegetation cover
80 impact soil quality because of differences in plant physiological preferences for
81 certain nutrients as well as differing strategies for the belowground distribution of
82 photosynthesized C (e.g., C:N ratio) and quantity of litters (Leff et al., 2012; Pausch
83 and Kuzyakov, 2018; Sayer et al., 2011). Therefore, types of fertilization and
84 vegetation cover are the key parameters for determining the soil quality index.

85 Soil quality directly and indirectly influences soil microbial communities. For
86 example, soil pH is one of the most powerful drivers affecting microbial diversity.
87 Lower pH inhibits microbial multiplication and growth (Malik et al., 2018; Tripathi et
88 al., 2018; Zhalnina et al., 2015). N availability is another notable factor impacting the
89 diversity and structure of bacterial communities (Cederlund et al., 2014; Sul et al.,
90 2013; Wang et al., 2018). Many studies have focused on one or several specific
91 components (e.g., SOC, pH) of soil quality to address its effects on the diversity and
92 abundance of soil microbial taxa (Cederlund et al., 2014; Malik et al., 2018). However,
93 studying individual soil properties may not accurately represent the holistic soil
94 quality-related ecological functions of microorganisms (Guo et al., 2020). Soil quality
95 is a multifactorial index that characterizes the potential of a soil to sustain its
96 ecological services. Microbial communities, in turn, impact soil quality via nutrient
97 cycling. But changes in microbial structure and functions may occur faster than

noticeable changes in soil quality index (Bünemann et al., 2018). This is why soil quality and microbial diversity are closely correlated and interactive (Guo et al., 2020; Ji et al., 2020). However, microbial parameters are often not included in the commonly used soil quality index. In this study, we explored the links between soil quality and the complexity (diversity, structure, and functions) of microbial communities under land-use change from natural forests (unmanaged ecosystems) to vegetable cropland or tea plantation.

Tea (*Camellia sinensis* L.) is a perennial evergreen broad-leaf cash crop, and tea plantations in eastern China are typically established after conversion from forests. Tea plantations are currently covering 3.06 million ha in China alone and rapidly expanding in the world (Fan and Han, 2020). Tea plants are well adapted to grow in acidic soils ($\text{pH} < 5.5$) in contrast to other crops ($5.5 < \text{pH} < 8.9$) (Guo et al., 2010). Therefore, changes in diversity, structure and functions of soil microorganisms are expected with conversion from natural forest to tea plantations when compared to other crops such as vegetables.

We have analyzed microbial communities via pyrosequencing the soils of a natural broad-leaf forest, a vegetable cropland, and three tea plantations with high, medium, and low productivity (classified based on fertilization amounts and tea yields; see details in Materials and Methods). Our research questions are (i) how does soil quality respond to land-use change from forest to vegetable cropland and tea plantations? as well as (ii) does the structure and function of microbial communities depend on soil quality? The main goal was to explore linkages between soil quality

120 and microbial ecological functions for improving sustainable agriculture.

121

122 **2. Materials and Methods**

123 **2.1 Site description and soil collection**

124 The experimental fields were established at the Chinese Academy of Agricultural
125 Sciences Tea Research Institute, Hangzhou City, Zhejiang Province, Eastern China
126 (120°09'E, 30°14'N), a region with a subtropical humid monsoon climate. The mean
127 annual air temperature of the region is 17.0 °C, and the mean annual precipitation is
128 1533 mm (Fan and Han, 2020). The experimental fields included three land-use types:
129 (i) a broad-leaf evergreen forest; (ii) a household vegetable field; and (iii) tea
130 plantations (Table 1). The tea plantations were further divided in three groups based
131 on fertilization amount and yield as: high tea productivity (HP_tea), medium tea
132 productivity (MP_tea), and low tea productivity (Low_tea).

133 The soil at the experimental field is classified as Ultisols (US Taxonomy) which
134 has been developed on Anshan quartz free porphyry parental material (Han et al.,
135 2007). The vegetable field and tea gardens were transformed from forest
136 approximately 35 years ago. The vegetable field was covered by plants throughout
137 most of the year, and 1 t ha⁻¹ lime was applied after deforestation to raise the pH value.
138 In tea gardens, tea is harvested from mid-March to mid-April for the spring
139 production of Westlake *Longjing* green tea. Afterward, heavy pruning management is
140 applied to leave *in situ* as surface mulch. Field management including weeding and a
141 fertilization schedule were similar in tea plantations, though fertilization amounts

142 varied. The distance between the five experimental fields is less than 1 km. Detailed
143 information on types of vegetation and land-use management can be found in Table 1.

144 In each field, we set up three 20 m×20 m plots. Six soil samples were randomly
145 collected from each plot at a depth of 0–20 cm, using an auger to form a composite. In
146 total, 15 soil samples (5 land-use fields × 3 replicated plots) were collected. All soil
147 samples were sieved through 2 mm in the field, transferred to laboratory within an
148 hour and stored at -18 °C until analyses. A portion of the samples was air dried for
149 soil properties analyses.

150 **2.2 Soil physiochemical analyses**

151 Air-dry soil samples were used to measure pH, SOC, total N content,
152 exchangeable P and K. Moist soil samples from the field were used to determine
153 microbial biomass, water dissolved organic C (DOC), water dissolved nitrogen
154 (DON), NO₃⁻-N, and NH₄⁺-N. For details on measurement methods please refer to
155 (Fan et al., 2015; Fan and Han, 2020). In brief, a combined glass electrode (Orion
156 3-Star Benchtop pH Meter; Thermo Scientific Waltham, MA, USA) was used to
157 determine soil pH; soil total N and SOC content were determined by a Vario Max CN
158 Analyzer (Elementar Analysensysteme GmbH, Langenselbold, Germany); a C/TN
159 analyzer (multiN/C 2100; Analytikjena, Jena, Germany) were used to measure DOC
160 and DON; fumigation–potassium sulfate (K₂SO₄) extraction method used for MBC
161 and MBN determination where MBC and MBN were calculated from the difference
162 between the extracted organic C and N content of fumigated and un-fumigated soils
163 using a k_{ec} factor of 0.45 (Joergensen, 1996). Exchangeable P was extracted with 0.03

mol L⁻¹ ammonium fluoride and 0.025 mol L⁻¹ hydrochloric acid; available soil K was extracted with 1 mol L⁻¹ ammonium acetate; all extractions were done in a 1:10 soil-water ratio, and the oscillation was 30 min. The elements K and P were determined using inductively coupled plasma atomic emission spectroscopy (ICP-AES; JAC IRIS/AP, Thermo Jarrell Ash Corporation, Franklin, USA). NO₃⁻-N and NH₄⁺-N were extracted with 0.05 M CaCl₂ and measured using continuous flow injection colorimetry (Flow Access 12.0, Skalar, Dutch). The measured soil physiochemical properties are showed in Table S1.

2.3 Soil quality index

Soil quality index based on management assessment framework was determined according to (Shao et al., 2020) as follows: the principal component analysis (PCA) was performed to select the minimum data set (MDS) of properties (Table S1), which could best represent soil quality and are sensitive to land management (Nakajima et al., 2015). Significant principal components (PCs) (eigenvalues ≥ 1 , Table S2) were chosen to weigh properties, and a property was selected when its score value was above 10% of the highest indicator (Andrews and Carroll, 2001). Notably, the indicator with highest score value in PC was selected into the MDS when the above selected indicators were multicollinear ($p < 0.05$) based on the Pearson's correlation (Table S3). Thereafter, the selected indicators were transformed and normalized to a value between 0.1 and 1.0 using the standard score function method. Three standard scoring functions (i) “more is better” (ii) “less is better” and (iii) “optimum” were applied to standardize the MDS indicators. The weight of indicators in MDS based on

186 the communality of the PCA (Table S2) was calculated as the quotient of the
187 communality divided by the sum of the communality of indicators in the MDS (Shao
188 et al., 2020). Finally, soil quality index was calculated as follows (Doran, 1994):

$$Soil\ quality\ index = \sum_{i=1}^n W_i S_i$$

189 W_i is the weighing value, and S_i is the transformed score of the selected
190 indicators. The quality index commonly corresponds to a proxy showing capability of
191 a soil to produce higher yields. However, in the current study, we highlight that a
192 higher quality index did not represent a higher capacity of soil to sustain all plant
193 growth but intended for specific land uses (e.g., tea plantation).

194 **2.4 DNA extraction and pyrosequencing**

195 Genomic DNA was extracted from 0.5 g soil sample using the Mo Bio PowerSoil
196 DNA isolation kit (Carlsbad, CA, USA) according to the manufacturer protocol. The
197 DNA purity and concentration were determined using the NanoDrop ND 200
198 spectrophotometer (Thermo Scientific, USA). The V4-V5 variable region of the
199 bacterial 16S rRNA gene was amplified using the primers 515F
200 (5'-CCATCTCATCCCTGCGTGTCTCCGAC-3') and 907R
201 (5'-CCTATCCCCTGTGTGCCTTGGCAGTC-3'). All the polymerase chain reactions
202 (PCR) were performed with 1 µL purified DNA template (10 ng), 5 µL 10 × PCR
203 buffer, 2.25 mmol L⁻¹ MgCl₂, 0.8 mmol L⁻¹ deoxyribonucleotide triphosphate
204 (dNTP), 0.5 µmol L⁻¹ of each primer, 2.5 U Taq DNA polymerase, and sterile filtered
205 milli-Q water to a final volume of 50 µL. All reactions were carried out in a PTC-200
206 thermal cycler (MJ Research Co., New York, USA). PCR cycles included a 4 min

207 initial denaturation at 94 °C, followed by 30 cycles of denaturation at 94 °C for 1 min,
208 annealing at 53 °C for 30 s, extension at 72 °C for 1 min, and a 5-min final elongation
209 step at 72 °C. PCR products were quality-screened and purified using the Qiagen Gel
210 Extraction kit (Qiagen, Hilden, Germany).

211 The abundance of ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing
212 archaea (AOA) was determined by real-time quantitative polymerase chain reaction
213 (qPCR) using primers that amplify *amoA* genes.

214 **2.5 454 Pyrosequencing and sequencing data analysis**

215 Pyrosequencing was performed on a Roche Genome Sequencer FLX+ using
216 Titanium chemistry by Macrogen (Roche Applied Science, Mannheim, Germany).
217 Three standard flow-gram format (SFF) files were generated by 454 pyrosequences.
218 The SFF file was analyzed by the software package Mothur (version 1.33.2). The
219 work flow was similar with (Gui et al., 2021). Briefly, De-noising was conducted with
220 the AmpliconNoise, and UCHIME algorithms were used to reduce sequence errors
221 and remove chimeras. Remaining sequences were aligned with the SILVA-based
222 bacteria reference database. Sequences with 97% similarity were clustered into the
223 same Operational Taxonomic Units (OTUs) according to the UCLUST algorithm. For
224 each OTU, the Green Gene database was applied to annotate taxonomic information.

225 **2.6 Data analyses**

226 The least significant difference (LSD) test was used to determine differences in
227 soil physicochemical properties between the experimental fields. The within sample
228 alpha (α -) diversity of soil bacterial communities was calculated based on the OTU

229 table as observed OTU number, ACE (Abundance-based Coverage Estimator metric),
 230 Chao1, and Shannon diversity index. Principal Coordinate Analysis (PCoA) based on
 231 Bray-Curtis distance between samples were calculated as the beta (β) diversity of
 232 microbial communities (compositional dissimilarity between fields) using the *ampvis2*
 233 package in R (v4.0.3). Differential OTU abundance was performed using a
 234 generalized linear model with p value <0.01 in the BioConductor package *EdgeR*.

235 The co-occurrence patterns between bacterial OTUs were explored using
 236 network analysis, and the relative abundance of OTUs above 0.05% was selected.
 237 Pairwise Pearson correlations were calculated between the remaining OTUs. A valid
 238 co-occurrence was considered as a statistically robust correlation between taxa when
 239 the Pearson's correlation (r) was >0.6 and the p value was <0.01 . Each node indicated
 240 individual OTU, and each edge represented the pairwise correlations between nodes
 241 standing for a significant metabolic association in the network. Multiple topological
 242 properties (i.e., number of nodes and edges, average degree) were calculated and
 243 visualized using *igraph* package in R (v4.0.3). Functions were inferred using
 244 FAPROTAX (Louca et al., 2016), which is a conservative algorithm currently
 245 matching 80 functions against 7600 functional annotations of 4600 prokaryotic taxa.
 246 Significant difference ($p < 0.5$) of functions between fields was revealed by STAMP
 247 (Statistical Analysis of Taxonomic and Functional Profiles) (Parks et al., 2014), and
 248 the multiple test correction were used *Bonferroni* method.

249 **2.7 Data availability**

250 Sequencing data are available in the NCBI SRA data repository under project No.

251 PRJNA750877.

252

253 **3. Results**

254 **3.1 Soil quality index**

255 The PCA analysis showed that samples from forest, vegetable field, and tea
256 gardens distributed in different quadrants featured a higher degree of soil
257 heterogeneity after land use change and a strong difference between vegetable fields
258 and tea plantations (Fig. S1). Indeed, soil quality index was highest in vegetable
259 cropland with Chinese cabbage and radish (Table 1), followed by tea plantations and
260 forest (Fig. 1). Among tea plantations, soil quality index was highest for high tea
261 productivity (HP_tea). There was no significant difference between medium and low
262 tea productivity plots (MP_tea vs. LP_tea). Among the measured properties, soil pH,
263 DOC, NH_4^+ -N, NO_3^- -N and available P were the significant factors for the soil quality
264 (Table S2).

265 **3.2 Distribution of taxa and phylotypes across land-use types**

266 99.6% of sequences were classified into the phyla of bacteria, and the total OTU
267 number was 5662 defined by 97% sequence similarity. Three phyla including
268 Proteobacteria, Acidobacteria, and Actinobacteria were predominant (relative
269 abundance of each > 10%) (Fig. 2b). The most abundant phylum Proteobacteria, with
270 an average relative abundance of 35.2%, included the following classes:
271 Alphaproteobacteria (17.3%), Gammaproteobacteria (11.9%), Betaproteobacteria
272 (3.9%), and Deltaproteobacteria (2.2%). The relative abundance of Proteobacteria,

273 Bacteroidetes, and Nitrospira were positively correlated, but the abundance of
274 Acidobacteria, Chloroflexi, and Armatimonadetes were negatively correlated to the
275 soil quality index (Fig. 2a).

276 Using OTU counts from forest soil as a control and an adjusted *p* value cutoff of
277 0.01, there were 215 OTUs enriched and 252 OTUs depleted in samples of vegetable
278 cropland. Comparatively, the amount of enriched and depleted OTUs was much lower
279 in tea plantation than in vegetable cropland (Fig. 3a). The number of enriched and
280 depleted OTUs showed weak positive correlations with soil quality (Fig. S2).
281 Noteworthy, there were overlaps in enriched OTUs between soil samples of vegetable
282 field and tea gardens (89 out of the 215 OTUs enriched) (Fig. 3b). The enriched
283 OTUs mainly consisted of Proteobacteria and Acidobacteria (Fig. 3d). However, 248
284 out of 252 OTUs were depleted only in samples of vegetable cropland (Fig. 3c), and
285 Proteobacteria was the most depleted phylum (Fig. 3e). Therefore, land use change
286 from forest to tea plantation had less effect on microbial communities compared with
287 vegetable cropland.

288 **3.3 Correlations between bacterial diversity and soil quality index**

289 The α -diversity, which indicates the richness and diversity of microbial
290 communities, was generally highest in soils of vegetable cropland than in other soils
291 (Fig. 4a). Among tea plantations, α -diversity increased with decreasing amounts of
292 fertilization and tea yields. We found positive correlations between soil quality and
293 α -diversity after land use conversion from forest to vegetable field, but negative
294 correlations after land use change from forest to tea plantations were observed (Fig.

4b). Bacterial communities were tightly associated with respective ecosystems and land use types, explaining 74.8% of bacterial community variation (PCoA analysis, Fig. 4c). 64.7% of bacterial variation among fields was significantly related to the soil quality changes (Fig. 4d). Microbial diversity was strongly dependent on the soil quality: there were distinct effects of soil quality on microbial diversity between vegetable field and tea plantations because of different soil characteristics (Table S1). Soil pH and $\text{NH}_4^+\text{-N}$ were the most important variables for explaining diversity dissimilarity in bacterial communities (RDA analysis, Fig. S3; Mantel test, Fig. S4; Pearson correlation, Fig. S5).

3.4 Co-occurrence network analysis

The nodes in the network were assigned to eleven bacteria phyla (Fig. 5a, Fig. S6). Among these, six phyla (Acidobacteria, Proteobacteria, Actinobacteria, Verrucomicrobia, Bacteroidetes, and Firmicutes) were widely distributed, accounting for 84% of all nodes. Acidobacteria was the most abundant phyla in the network of forest soil, but Proteobacteria was dominant in vegetable field and tea plantations. The highest abundance of Nitrospira with nitrite-oxidizing bacteria responsible for nitrification was distributed in the bacterial networks of vegetable field (Fig. 5a).

Compared to forest, the number of edges was larger in a network of vegetable field but lower tea plantations (Fig. S7). The degree (the number of edges per node, which implies the interactions between microbial communities) decreased in both vegetable field and tea plantations (Fig. 5b). This indicates weaker response of soil bacterial taxa to field managements (e.g., fertilization) after land use conversion from

317 natural forest to vegetable cropland and tea plantations.

318 **3.5 Microbial functions related to C- and N-cycling**

319 Thirty-seven microbial functional categories out of 80 functions from
320 FAPROTAX (a functional annotations dataset) were assigned. Therein, 11 microbial
321 functions were clustered in C-cycling and 12 microbial functions were clustered in
322 N-cycling (Fig. 6a). Seven microbial functions of C-cycling and three microbial
323 functions of N-cycling were identified to differ significantly among fields (Fig. 6c,
324 STAMP analysis).

325 The abundance of microbial C-cycling functions increased after land use change
326 from forest to vegetable field, but decreased after land use change from forest to tea
327 plantations. The abundance of microbial N-cycling functions was significantly higher
328 in tea plantations than in vegetable field. Subsequently, we found that the abundance
329 of N-fixation (i.e., Nitrogen_fixation) was higher in tea plantations than in vegetable
330 field, but the abundance of N-oxidation (i.e., Nitrification,
331 Aerobic_ammonia_oxidation) was higher in vegetable field than in tea plantations
332 (Fig. 6c). Moreover, the relative abundance of ammonia-oxidizing bacteria (AOB)
333 and ammonia-oxidizing archaea (AOA) were significantly higher in soil samples of
334 vegetable field than in tea plantations (Fig. 6d), which corroborates the function
335 prediction by FAPROTAX. Significant correlations between soil quality index and
336 relative abundance of AOB and AOA were observed (Fig. S8), demonstrating the
337 contrasting effects of land use types on microbial functioning groups.

338

339 4. Discussion

340 Soil quality index significantly increased after natural forest conversion to
341 vegetable cropland and tea plantations (Fig. 1), directly addressing the first research
342 question. Land management-driven changes in soil quality index were higher in
343 vegetable cropland than tea plantations. Soil pH and $\text{NH}_4^+\text{-N}$, which were largely
344 affected by land use types, were the most important factors in driving bacterial
345 diversity dissimilarity and soil quality changes because pH strongly affects the
346 availability of soil nutrients and stability of soil aggregates (Slessarev et al., 2016);
347 moreover, pH can also directly influence the structure of microbial communities (Figs.
348 S3-5). For example, the abundance of Acidobacteria phyla (which are particularly
349 abundant in acidic soils) was significantly lower in vegetable cropland than the two
350 tea plantations (Fig. 2). NH_4^+ is the ready source of N for microorganisms, which
351 implies that soil microorganisms were most likely N-limited in tea plantations (see
352 below).

353 Microbial communities respond rapidly to changes in soil quality caused by land
354 use change and agricultural managements (Ji et al., 2020; Malik et al., 2018). The
355 significant and positive correlations between the bacterial community and the soil
356 quality index (Fig. 4d) demonstrates that soil quality is a responsible factor in
357 assembling the microbial community structure (Guo et al., 2020), which positively
358 supports our second research question. The linkages between soil quality and
359 dominant bacterial taxa were either positive (i.e., Proteobacteria, Bacteroidetes, and
360 Nitrospira) or negative (i.e., Acidobacteria, Chloroflexi, and Armatimonadetes) or

insignificant (Fig. 2a), which demonstrates that individual microbial taxa respond differently to soil quality changes. Positive correlation between soil quality and bacterial α -diversity after forest conversion to vegetable field and negative correlations following conversion to tea plantations (Fig. 4b) implies that soil quality as a structuring factor in bacterial community composition has contrasting effects in croplands and plantations. Higher soil quality promoted bacterial diversity in vegetable cropland but inhibited bacterial diversity in tea plantations. This is inconsistent with fungal diversity response to soil quality. Delgado Baquerizo et al. (2017) showed that soil fungal biodiversity was positively and strongly related to soil quality at the continental scale; however, Guo et al. (2020) illustrated that the linkage between soil quality and fungal biodiversity was weaker in agricultural ecosystems than in natural ecosystems. So, linkages between microbial community and soil quality were not only affected by the types of land-use but also by the intensity of land use managements (e.g., anthropogenic pressure) (Delgado Baquerizo et al., 2017).

The interactions (i.e., degree of network) of soil bacterial communities became weaker in response to field managements (e.g., fertilization) after land use conversion from natural forest to vegetable field and tea plantations (Fig. 5), which demonstrates that land use management plays a negative role in maintaining microbial interactions, since mineral and organic fertilizers provide large amounts of ready-to-use nutrients or easily decomposed substrates, which may reduce the mutualistic network of microorganisms (Berry and Widder, 2014).

383 Previous studies have shown that C and N availability can influence the structure
384 of soil bacterial communities (Cederlund et al., 2014; Sul et al., 2013; Wang et al.,
385 2018) because soil microorganisms are generally N limited or co-limited by C and N
386 sources (Chen et al., 2018; Wardle, 1992). Increasing microbial C-cycling in
387 vegetable field in contrast to tea plantation (Fig. 6b) indicates that microbial
388 functional groups developed directionally and deterministically due to the specific
389 land managements, which drives variations in soil quality under different land uses
390 and changes in microbial function groups. Higher abundance of N-fixation (i.e.,
391 Nitrogen_fixation) in tea plantations and higher abundance of N-oxidation (i.e.,
392 Nitrification, Aerobic_ammonia_oxidation) in vegetable cropland (Fig. 6c) suggests
393 contrasting N demand depends on the land-use type. Comparably, soil
394 microorganisms were more N-limited in tea plantations than that in vegetable field.
395 Higher abundance of ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing
396 archaea (AOA) in vegetable cropland soil measured by qPCR corroborated the
397 function prediction by FAPROTAX. Moreover, the significant correlation between
398 soil quality index versus the abundance of AOB and AOA (Fig. S8) demonstrates that
399 the key taxa of microbial communities were strongly dependent on soil quality.
400 Land-use changes drive changes in soil quality, depending on management, which
401 reshapes the microbial community. Changes in soil microbial communities in turn
402 control various soil biogeochemical cycles (Kuypers et al., 2018). Accordingly,
403 microbial parameters as sensitive factors in different land uses can be included in the
404 commonly used soil quality index.

405

406 **5. Conclusions**

407 We confirmed that the soil quality index was significantly increased after natural
408 forest conversion to agricultural land use (e.g., vegetable cropland, tea plantations).
409 The structure and functions of microbial communities were influenced by soil quality,
410 but individual microbial taxa respond differently to changes in soil quality. Microbial
411 function N cycling thrives in tea plantations, whereas C-cycling thrives in vegetable
412 croplands. Co-occurrence network analysis demonstrated agricultural management
413 played a negative role in maintaining microbial interactions. Consequently,
414 deciphering the relationships between microbial parameters-related soil quality and
415 ecosystem functions provides a new opportunity for improving sustainable
416 agriculture.

417

418 **Acknowledgements**

419 This research was supported by the National Key R&D Program of China
420 (2017YFE0107500). Heng Gui would like to thank the support from Yunnan
421 Fundamental Research Projects (grant NO. 2019FB063) and the National Natural
422 Science Foundation of China (NSFC Grant 32001296). Kazem Zamanian would like
423 to thank the Research Fund for International Young Scientists of National Natural
424 Science Foundation of China to K.Z. (Grant number: 42050410320). Funding for
425 study abroad program by the government of Shandong Province for financial support
426 for Dr. Hongcui Dai

427

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Figures and tables

Fig. 1 Soil quality index in forest, vegetable field, and tea plantations with high productivity (HP_tea), medium productivity (MP_tea), and low productivity (LP_tea). Lowercase letters represent significant differences at $p < 0.05$ between land uses by LSD.

Fig. 2 Relative abundance of top eleven phyla in forest, vegetable field, and tea plantations with high productivity (HP_tea), medium productivity (MP_tea), and low productivity (LP_tea). Lowercase letters represent significant differences at $p < 0.05$ between land uses by LSD.

Fig. 3 Enriched and depleted OTUs in vegetable field and tea plantations compared to forest. (a) Enrichment and depletion in fields as compared with forest. Each point represents an individual OTU, and the position along the x axis represents the abundance fold change compared with forest. (b) and (c) Shared numbers of differentially enriched and depleted OTUs between each field as compared with forest. (d) and (e) Number of depleted and enriched OTUs in each phyla.

Fig. 4 Microbial diversity in forest, vegetable field, and tea plantations with high productivity (HP_tea), medium productivity (MP_tea), and low productivity (LP_tea). (a) Within sample alpha diversity. Lowercase letters represent significant differences at $p < 0.05$ between land uses. (b) Pearson correlations between the soil quality index and bacterial alpha diversity. ** represents the correlation is significant at the 0.01 level, * represents the correlation is significant at the 0.05 level. (c) Beta diversity. (d) Relation Blue dotted lines represent the 95% confidence interval of regression analyses.

573

574 **Fig. 5** Characters of bacterial co-occurrence networks in forest, vegetable field, and
575 tea plantations with high productivity (HP_tea), medium productivity (MP_tea), and
576 low productivity (LP_tea). (a) The relative abundances and amounts of nodes
577 contributed into co-occurrence networks grouped by phyla. (b) The number of nodes,
578 edges, and degree in each network.

579

580 **Fig. 6** Abundance of ammonia oxidizing bacteria (AOB) and archaea (AOA) in forest,

581 vegetable field, and tea plantations with high productivity (HP_tea), medium

582 productivity (MP_tea), and low productivity (LP_tea). Box plots: upper and lower

583 bars represent maximum and minimum observations, respectively; top and bottom of

584 boxes represent third and first quartiles; thin horizontal solid lines in boxes represent

585 median values; stars represent mean values. Lowercase letters represent significant

586 differences at $p < 0.05$ between land uses.

587 Table 1 Land-use types and practices of the experimental fields. For tea plantations, HP, MP and LP mean high-, medium- and low productivity,
588 respectively.

Land use type		Land use practice					
		Soil temperature (□)	Soil water content (%)	Mineral fertilizers as urea and compound fertilizers (kg N ha ⁻¹ yr ⁻¹)	Organic fertilizers as farmyard manure and (biogas slurry in vegetable field, and rape see cake in tea plantations) (kg ha ⁻¹ yr ⁻¹)	Litter, residues or pruned trimmings (t ha ⁻¹ yr ⁻¹)	Tea yield (ha ⁻¹ yr ⁻¹)
Forest	<i>Schima crenata</i> Korthals, <i>Castanopsis sclerophylla</i> and <i>Cinnamomum camphora</i>	24.0	29.6	NA	NA	10	NA
Vegetable field	Chinese cabbage (<i>Brassica rapa chinensis</i>) and radish (<i>Raphanus sativus</i>)	26.1	15.6	300	10 000	4	NA
HP_tea	<i>Camellia sinensis</i> L. Longjing43	24.7	27.0	600	2 250	13.4	280
MP_tea	<i>Camellia sinensis</i> L. Longjing43	25.0	26.2	450	1 120	9.4	200
LP_tea	<i>Camellia sinensis</i> L. Longjing43	25.8	23.3	300	1 120	6.2	150

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