

1 **Changes in fungal communities across a forest disturbance gradient**

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19 Running Head: Forest disturbance affect soil fungal communities

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22

23 **Abstract**

24 Deforestation has a substantial impact on above ground biodiversity, but the response of
25 below ground soil fungi remains poorly understood. In a tropical montane rainforest in
26 southwestern China, plots were established along a forest degradation gradient ranging from
27 mature and regenerated forests to open land to examine the impacts of forest degradation and
28 deforestation on ecosystem diversity and function. Here, we evaluate the changes in below
29 ground fungal diversity and community composition using a metabarcoding approach. Soil
30 saprotrophic fungal richness declined with increasing forest disturbance. For example,
31 *Penicillium* spp. (Phosphorus (P) solubilizing fungi) dominated in mature forest, but were
32 less abundant in regenerating forest and showed the lowest abundance in open land sites.
33 Conversely, the abundance of facultative pathogenic fungi increased along the disturbance
34 gradient. The decline in soil saprophytic fungi may be a direct result of forest disturbance or
35 it may be associated with increased availability of soil phosphorus indirectly through an
36 increase in soil pH. The increase in abundance of facultative pathogenic fungi may be related
37 to reduce competition with saprotrophic fungi, changes in microclimate or increased spore
38 rain. These results demonstrate a loss of dominant P solubilizing saprotrophic fungi along the
39 disturbance gradient, indicated a change from soil P limitation in mature tropical forest to soil
40 C limitation in deforested sites. The increased prevalence of pathogenic fungi may inhibit
41 plant succession following deforestation. Overall, this research demonstrates that soil fungi
42 can be used as a sensitive indicator for soil health to evaluate the consequences of forest
43 disturbance.

44

45 **Importance**

46 The soil fungal functional group changes in response to forest disturbance indicated a close
47 interaction between the above-ground plant community and the below-ground soil biological
48 community. Soil saprotrophic fungi declined in relative abundance with increasing forest
49 disturbance. At the same time, the relative abundance of facultative pathogenic fungi
50 increased. The loss of saprotrophic fungal richness and abundance may have been a direct
51 result of forest disturbance or an indirect result of changes in soil pH and soil P. Furthermore,
52 the dominant P solubilizing saprotrophic fungi was replaced by diverse facultative pathogenic
53 fungi, which have weaker C decomposition ability. These changes potentially indicate a shift
54 from soil phosphate limitation to carbon limitation following deforestation. This study
55 suggests that changes in fungal functional group composition can be used as an indicator of
56 the effects of forest disturbance on soil carbon and nutrients.

57

58 **Key words**

59 illumina sequencing, forest disturbance, fungal functional groups, tropical forest, P extraction,
60 soil health.

61

62 **Introduction**

63 Habitat disturbance and land use intensification are the principle drivers of global
64 biodiversity loss in terrestrial ecosystems (1). Degradation of natural forest induces serious
65 damage to the soil, such as negative changes in particle aggregation, erosion and nutrient
66 leaching, and the loss of several organisms below ground that provide important ecosystem
67 functions (2, 3). Recently, the response of soil microbial communities to forest disturbance
68 have been widely discussed and attracted increased attention (4).

69 Soil fungal communities are key components involved in soil biogeochemical cycling.
70 They are affected by changes in plant community composition and in turn affect plant growth
71 (5). According to their different functions, soil fungi can be separated into saprotrophic,
72 symbiotic and pathogenic fungi. Soil organic matter and plant litter are predominantly
73 decomposed by saprotrophic fungi, and consequently these fungi provide significant soil
74 carbon resources to support plant growth in most forest ecosystems (6). Plant growth in
75 tropical forests is commonly limited by P availability (7, 8). Therefore, some fungal groups
76 can promote plant growth by increasing availability of this nutrient. For example, arbuscular
77 mycorrhizal fungi (AMF) in tropical and subtropical forests can help their host tree absorb P
78 from soil (9). Some rhizosphere fungi produce organic acids to solubilize phosphates,
79 including *Penicillium* and *Aspergillus* spp, thereby promoting plant growth in tropical forests.
80 Pathogenic fungi typical have negative plant-fungi interactions, which inhibit plant growth
81 and change the plant community composition and diversity (10). Understanding the changes
82 in the abundance of these functional groups under forest disturbance is important for
83 understanding the stability and resilience of the ecosystem.

84 Forest disturbance changes vegetation characteristics (e.g., plant biomass, species
85 composition and canopy structure) and thus exerts substantial impacts on soil properties (e.g.,
86 soil C, elemental stoichiometry and pH) (11, 12). Such changes can affect soil fungal

87 attributes. A global meta-analysis found that forest degradation reduces soil C and N content,
88 increases soil pH and increases C decomposition rates. The study also found a decrease in
89 soil fungal biomass in disturbed sites, but increased species diversity (13). Consistent with
90 previous studies, they further point out that the changes in soil pH were significantly
91 correlated with changes in soil fungal community composition (14). Besides loss of host
92 species, forest disturbance can also cause the direct loss of mycorrhizal fungi and rhizosphere
93 fungi (15). However, the relative strength of these factors in determining fungal community
94 composition in tropical systems is not well understood. Accurate predictions of the impacts of
95 forest disturbance depend on identifying edaphic factors associated with significant shifts in
96 fungal communities.

97 The effects of canopy opening on understory environments can be particularly
98 pronounced in tropical and subtropical forests, due to the increase in light, precipitation and
99 also temperature. Previous studies indicate that limited canopy opening can increase spatial
100 variance in soil nutrients and carbon, and C decomposition rates may be higher under canopy
101 gaps (16). In addition, canopy openings can enable colonization by new plant species and
102 fungal spores (17). The scale of a canopy opening is an important factor in driving these
103 environmental changes. Small canopy openings have been found to benefit forest
104 development in some studies (18). Several studies of soil fungi have concentrated on newly
105 created or drastically disturbed forest habitats, such as post flooding, fire or logging, and
106 focus on changes in tree species composition or soil properties (19, 20). However, it is rare
107 for studies to investigate how soil fungi respond to long-term forest disturbances associated
108 with canopy opening. Knowledge on how soil fungi respond to the canopy opening may help
109 us to understand the effects of changes in above-ground vegetation on below-ground
110 biological processes.

111 In a tropical monsoon rainforest in southwest China, we set up a series of sampling plots

112 across a forest disturbance gradient (Fig S1). In this forest, the disturbance was caused by
113 shifting cultivation and the expansion of traditional tea plantations. Our previous studies
114 investigated changes in tree and liana community composition (21), litter inputs and litter
115 decomposition (22), insect diversity and composition (23) and soil and leaf litter mesofauna
116 community composition (22) across the disturbance gradient. We found significant changes
117 in above-ground (plant and micro-climate) and below-ground environments (soil), Belecourt
118 e al 2016 together with a significant decline in rates of litter decomposition along the
119 disturbance gradient (24). However, inferences concerning soil biochemical cycling were
120 hard to predict, although we expect changes in the fungal composition particularly as a
121 consequence of drastically lower C inputs in deforested sites. The current study expands on
122 our previous work by using Illumina-sequencing to examine fungal diversity and community
123 composition along the forest disturbance gradient, and identified the factors driving fungal
124 community change. We had three aims in this study: (1) We examined whether forest
125 disturbance triggers taxonomical or functional changes in the soil fungi community. It has
126 been shown that highly degraded sites are nutrient limited. Hence, we hypothesized that soil
127 fungi will decline in their diversity and change composition along the disturbance gradient; (2)
128 We evaluated the effects of biotic (i.e., plant) and abiotic (i.e., soil properties and
129 microclimate) factors on the diversity and composition of associated fungal groups. We
130 hypothesized that biotic factors contribute to most of the variation in fungal characteristics
131 than abiotic factors due to the close linkage between above- and below-ground communities;
132 (3) We aimed to explore the potential role of soil fungi as indicator of soil heath under forest
133 disturbance.

134

135

136 **Results**

137 **Soil fungal diversity different with forest disturbance**

138 Forest disturbance significantly reduced saprotrophic fungal richness, while facultative
139 fungal richness increased along the disturbance gradient. As a result the highest total fungal
140 richness occurred in deforested open land sites (Fig. 1). Saprotrophic fungal species richness
141 decline by 20% along the disturbance gradient from mature forest to deforested sites. With
142 the reduced abundance of saprotrophic fungi, there was a substantial increase in the
143 proportion of facultative fungi, most of which harbored pathogenetic ability (Fig. 1 and Fig.
144 S2). Total fungi species richness was most strongly associated with soil P concentration ($P =$
145 0.017 ; $P_{\text{adj}} = 0.051$) (Table 2). Structural equation modeling also suggested that forest
146 disturbance has a direct negative effect on changes of soil saprotrophic fungi (Estimate (β) = -
147 0.61 , $P < 0.01$) (Fig. 2). Soil saprotrophic fungal abundance was strongly negatively
148 correlated with soil P concentration ($\beta = -0.66$, $P < 0.01$) and positively correlated with soil C
149 concentration ($\beta = 0.37$, $P < 0.01$) (Fig. 2). Soil P was indirectly affected by forest
150 disturbance through changes in soil pH (Fig. 2). In total, environmental factors explained 41%
151 of the variance in the abundance of saprotrophic fungi (Fig. 2). These results suggested that
152 edaphic variables rather than plant community properties were the best predictors of fungal
153 richness under forest disturbance.

154 **Fungal taxonomic and functional composition changed with forest disturbances**

155 Fungal communities in deforested sites were significantly different from those in forest
156 sites (mature and regenerating forests) in both wet and dry seasons (Fig. 3). A procrustes
157 analysis revealed that the composition of fungal communities was significantly correlated
158 among wet and dry season, but the overall dissimilarity among communities increased from
159 wet to dry season (Fig. 3). PERMANOVA analysis indicated that forest disturbance ($R^2 =$
160 0.07 ; $P < 0.00$) and seasonal change ($R^2 = 0.03$; $P < 0.00$) both had significant effects on soil

161 fungal community composition. NMDS vectors analysis revealed that total fungal community
162 composition was affected by soil pH ($R^2 = 0.35$; $P < 0.00$), Mn concentration ($R^2 = 0.34$; $P <$
163 0.00), Fe concentration ($R^2 = 0.19$; $P = 0.01$), Ca concentration ($R^2 = 0.13$; $P = 0.02$), soil
164 C:N ($R^2 = 0.16$; $P = 0.01$) and soil P concentration ($R^2 = 0.13$; $P = 0.03$) (Table S2).

165 Forest disturbance reduced the relative abundance of total saprotrophic fungi, but
166 increased those fungi with pathotrophic ability within saprotrophic fungi (Fig. 4a). Strictly
167 saprotrophic fungi have an important role in decomposition and dominated in forest sites (Fig.
168 S2). For example, *Penicillium*, a saprotrophic fungi, dominated in mature forest, was less
169 abundant in regenerating forest, and least abundant in open land, regardless of the season (Fig.
170 S3). In contrast, weakly saprotrophic fungi increased in abundance in disturbed forest sites
171 (Fig. S2). For example, *Cryptococcus*, a common soil saprophytic yeast with a weak
172 pathotrophic ability, was more abundant in regenerating forest than in mature forest (Fig. S3).
173 Finally, the percentage of pathotrophic fungi within the saprotrophic fungi was two times
174 higher in open land sites than in forests (Fig. 4b). *Fusarium* is a common plant pathogenic
175 fungal group and was abundant in open land samples, but rare in regenerating and mature
176 forests (Fig. S3). *Didymella*, another fungal plant pathogen, was more abundant in mature
177 forest and open land than in regenerating forest in the wet season, but in the dry season it was
178 only abundant in open land (Fig. S3).

179

180 **DISCUSSION**

181 **Forest disturbance changes above- and below-ground biodiversity**

182 In our study site, tree species richness was found to decline in response to forest
183 disturbance, along with associated changes in community composition and structure (25).
184 Large trees were removed in the forest in order to open the canopy for understory planting
185 with tea (26). In contrast, understory vegetation (e.g., shrub and grass) increased their

186 diversity due to the increased availability of light (27). Therefore, at least in regenerating
187 forest, the total plant diversity actually increased and provided more diverse habitat and
188 substrates for soil fungal community, especially for the symbiotrophic fungi and saprotrophic
189 opportunities (28). Saprotrophs comprised 40% of the total fungal species richness, while
190 mycorrhizal fungi made up less than 10%. Such fungal community composition can be
191 explained by differences between bulk soil and rhizosphere soil. AMF dominate in monsoon
192 tropical forest, but are mainly concentrated in rhizosphere soil. Therefore, the effects of forest
193 disturbance on the bulk soil fungal community are mainly reflected in changes in
194 saprotrophic fungi.

195 **Decline in dominant saprotrophic fungi with increasing forest disturbance**

196 Dominant saprotrophic fungi declined in diversity and abundance with increasing forest
197 disturbance and these changes were apparently driven by changes in soil properties rather
198 than changes in vegetation (such as plant diversity). Soil pH was significantly higher in open
199 land sites, as compared to mature or regenerating forest sites. However, soil pH may not
200 directly affect fungal community structure (14, 29, 30). Rather, changes in plant community
201 and soil pH contributed to the differentiation of local soil P concentrations, which were
202 significantly correlated with saprotrophic and pathogenic fungi abundance. The soil microbial
203 P extractor, *Penicillium*, dominated fungal communities in forests (31). It is commonly
204 known that soil P is a limiting factor in many tropical forests (32). Plant root exudates,
205 mycorrhizal fungi and soil saprotrophic P extractor fungi can increase the P availability to
206 plants in tropical forests (33). Soil pH in tropical forests is typically low (about 4-5), and
207 raising soil pH (5-6) can increase the release of P and its availability to plants and other biota
208 (34). The relative abundance of soil P extractor fungi declined from mature forest to
209 regenerating forest to open land, suggesting an increase in P availability along the disturbance
210 gradient (35). As well as soil pH and soil P concentration, soil fungal composition and

211 richness were also correlated with soil Fe and Mn concentration, which are important cations
212 affecting microbial enzyme activities in litter and soil organic matter decomposition (36). The
213 reduced species richness of saprotrophic fungi might further indicate a decrease in litter
214 decomposition capacity in disturbed sites, supporting our previous report of declining
215 decomposition rates along the disturbance gradient in this forest (22). Together with higher
216 soil P availability but lower decomposition rates, soil C availability declined along the
217 disturbance gradient and may be a new limiting factor for soil microbial decomposition (37).

218 Increased canopy opening caused by forest disturbance can lead to higher variation in
219 microclimate patterns for precipitation, temperature and light (38, 39). Fluctuations in
220 microclimate are significant in monsoon tropical areas. However, the canopy can buffer the
221 influence of changes, providing a more stable environment with lower light and precipitation
222 availability (40). In a previous study at our study site, we found that the soil temperature and
223 moisture were significantly higher in open land sites than in primary (mature) and
224 regenerating forests, especially during the dry season (21, 22) (Table 1). As expected in this
225 seasonal tropical ecosystem, the change from wet to dry periods exerted a strong influence on
226 the structure of fungal communities (41, 42). For example, the dominant fungal genus,
227 *Penicillium*, was represented in both seasons but with much higher relative abundance in the
228 dry season (Fig. S3). We speculate that high soil moisture in the wet season may limit the
229 growth of some fungi, including *Penicillium*, by increasing the abundance of anaerobic
230 microsites (41, 43). Furthermore, seasonal variation in the fungal community composition
231 was substantially more in open land as compared to forest sites, which may result from the
232 buffering effects of canopy cover (44, 45). In addition, the seasonal changes affected the
233 saprotrophic fungi more than other groups. In tropical forests, saprotrophic fungi most live in
234 the litter layer (46). The litter and surface soil layers are most prone to variation in above-
235 ground microclimatic conditions, such as prolonged dryness during the dry season.

236 Nevertheless, in this study, seasonal sampling may not have captured all the important
237 ambient environmental change; for example, large moisture pulses, soil moisture changes and
238 other environmental factors that occur within seasons.

239 **Deforestation contributes to increase facultatively pathogenic fungi**

240 Facultative pathogenic fungi were found to make up large proportion of soil fungal
241 community in disturbed sites, especially in deforested sites. We did not find significant
242 effects of any specific single environmental factors correlated with these changes. The
243 changes of these facultative pathogenic fungi might suggest a complex interaction between
244 soil and plants. For example, increased understory vegetation increased the heterogeneity of
245 litter and root composition, which may provide diverse ecological niches for pathogenic fungi.
246 Additionally, increased light may induce saprotrophic fungi to express parthenogenesis (47).
247 Besides changes in microclimate, canopy opening can also afford opportunities for free
248 fungal spores in the air to be deposited on the soil (48). The air above the tropical forest
249 canopy is full of fungal spores, especially of plant pathogenic fungi (49). These airborne
250 fungal spores could be deposited to soil in canopy gaps (50). Further analysis on the co-
251 occurrence of fungal species among habitats (Fig. S4) suggested that more unique species
252 appeared in deforested sites, especially in the wet season. Furthermore, we found a higher
253 abundance of pathogenic fungi in open land sites, and most of these species belong to wind
254 transported species. Pathogens and other symbiotic fungi that infect above-ground plant parts
255 commonly disperse as airborne spores (51). For example, *Cryptococcus* and *Didymella* have
256 been reported as saprophytic pathogens and have been transported worldwide by wind (52,
257 53). Studies have also found that high light levels trigger pathogenicity of these fungi while
258 low light favor endosymbiotic development, which constrains recruitment of endophyte-
259 infested seedlings to the shaded understory through limiting survival of seedlings in direct
260 sunlight (52, 54, 55). Hence, canopy opening may not only introduce new pathogenic fungi,

261 but also induced their parthenogenesis.

262 **Soil fungi can be used as an indicator of soil heath in forest disturbances**

263 Previous studies on forest disturbance have mainly discussed changes in vegetation
264 (especially the loss of functional plant species, such as N fixing trees) or soil properties (soil
265 C and N) (56–58). However, it is often difficult to detect the changes in soil nutrient status.
266 Hence, scientists have been trying to use soil microbial functional groups to detect soil
267 nutrient limitation, because the soil microbial community is much more sensitive to soil
268 nutrient limitation than plants (59, 60). Our results indicated a close correlation between
269 changes in soil P with dominant soil fungal species, and suggest that dominant soil fungal
270 groups can be used as bio-markers to predict the condition of limiting soil nutrients (61). The
271 increase in pathogenic fungi may have a negative impact on the rate of forest succession (62).
272 Additionally, soil fungal community composition changed seasonally, and these changes
273 were more significant in deforested areas than in forests (63, 64). These results support the
274 notion that changes in the composition and diversity of soil fungi not only indicate changes in
275 the soil environment, but also contribute to the effects of forest disturbance on ecosystem
276 function.

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278

279 MATERIALS AND METHODS

280 **Forest disturbance history.** Our research was conducted in Mengsong, Xishuangbanna,
281 SW China (UTM/WGS84: 47Q 656355 E, 2377646 N, 1100–1900 m asl). The climate is
282 strongly seasonal with 80% of the rainfall occurring over six months from May to October.
283 Annual mean precipitation varies from 1600 to 1800 mm (65). Forest in the area has been
284 classified as seasonal tropical montane rain forest, which grades into seasonal evergreen
285 broad-leaved forest on hill slopes and ridges (66). The rain forest contains many floristic
286 elements in common with rain forests throughout Asia, although Dipterocarps are absent. The
287 evergreen broadleaf forest is floristically similar to more seasonal forests to the north, with
288 many species of Fagaceae and Lauraceae in the canopy.

289 The primary forests here have a density canopy covering, but the canopy structure has
290 often been changed due to long-term farming activities. The local farmers in this area
291 commonly cut down trees in the forest to increase light availability to understory tea
292 plantations. These openings may extend through time to complete deforestation. In these
293 plantations human activities, including fertilization and frequent harvesting, cause serious
294 disturbance to the environment (67). In the past farmers also practiced slash-and-burn
295 agriculture but a logging ban in the 1980s stopped this activity. So nowadays the landscape
296 has patches of forest at various stages of regrowth, as well as mature forests.

297 **Plot design and sample collection.** During 2010 to 2013, 28 sampling plots were
298 established using a stratified random approach that resulted in 10 mature forest plots, 12
299 regenerating forest plots and 6 open habitat plots interspersed across the landscape (22) (Fig.
300 S1). Samples from each sub-plot were pooled together into one sample to represent this plot.
301 Soil samples were collected in June 2012 (wet season) and February 2013 (dry season),
302 immediately after litter fall and during the period of the highest expected microbial activity.
303 Fresh litter and twigs were removed from the surface and soil cores of 10 cm depth were

304 taken in the A layer by gently pounding metal rings into the ground. The samples were
305 transported to the laboratory in sterile plastic bags on ice and stored overnight at 4°C.
306 Approximately 20 g of moist subsample were stored at -20°C for subsequent analysis. The
307 soil characteristics and plant properties were investigated by previous authors (22).

308 **PCR amplification.** DNA was extracted from 0.5 g of soil per sample using the Soil DNA
309 Isolation Kit (MoBio, Carlsbad, CA, USA) according to the manufacturer's protocols. PCR
310 was performed using forward primers (ITS1) and degenerate reverse primer ITS2aR (68).
311 The PCR cocktail comprised 0.6 µl DNA, 0.5 µl each of the primers (20 µ M), 5µl 5× HOT
312 MOLPol Blend Master Mix (Molegene, Germany) and 13.4 µl double-distilled water. PCR
313 was carried out in four replicates in the following thermocycling conditions: an initial 15 min
314 at 95°C, followed by 30 cycles of 95°C for 30 s, 55°C for 30s, 72 °C for 1 min, and a final
315 cycle of 10 min at 72°C. PCR products were pooled and their relative quantity was estimated
316 by running 2µl DNA on 1% agarose gel for 15 min. DNA samples yielding no visible band or
317 a strong band were re-amplified using 35 and 25 cycles instead. We also used negative (for
318 DNA extraction and PCR) and positive controls throughout the experiment. Amplicons were
319 purified by use of Qubit 2.0 Fluorometer (Invitrogen), and the Qubit dsDNA HS Assay Kit
320 (Invitrogen). Purified amplicons were subjected to normalization of quantity by use of
321 SequalPrep Normalization Plate Kit (Invitrogen, Carlsbad, CA, USA) following the
322 manufacturer's instructions. Sequencing was carried out on an Illumina MiSeq sequencer at
323 the Research and Testing Laboratory Inc., U.S.A. Although all sequencing runs in this study
324 were paired-end, only the forward reads were analyzed for the purposes of this study.

325 **Microbial community analysis.** Pyrosequencing resulted in 1174278 reads with a
326 median length of 512 base pairs (bp). Raw Illumina fastq files were de-multiplexed, quality-
327 filtered, and taxonomic analyzed using QIIME (v. 1.4.0-dev) workflow using IPython
328 Notebook (69). The data analysis consisted of demultiplexing and quality filtering, OTU

329 picking and diversity analyses stages. In the first stage, reads were filtered using settings
330 described in manual, as modulated by the parameters (p), (q), (r), and (n) described in (22). In
331 the second stage, OTUs were assigned using the QIIME UCLUST13 wrapper, with a
332 threshold of 97% pairwise nucleotide sequence identity (97% ID), and the cluster centroid for
333 each OTU was chosen as the OTU representative sequence (70). During the taxonomic
334 analysis stage, OTU representative sequences were then classified taxonomically using non-
335 default reference database from UNITE databases (71), filtered at 97% ID, using a 0.80
336 confidence threshold for taxonomic assignment. Furthermore, we assigned each fungal genus,
337 family or order to functional categories using the FUNGuild website (72). If different
338 lifestyles were present in specific genera, we chose the dominant group (> 75% of species
339 assigned to a specific category) or considered its ecology unknown (< 75%) levels (Table S1).

340 **Statistical analyses.** All the datasets were rarefy to 1000 per sample, using the function
341 '*rarefy*' in R package 'vegan'(73), to reduce differences in sequencing depth. We chose to
342 analyze richness and community composition in groups that were represented by at least 450
343 OTUs (fungi, Ascomycota, Basidiomycota, saprotrophic fungi, mycorrhizal fungi and
344 pathogenic fungi). For richness analyses of soil fungi, we counted the OTU richness using the
345 function '*diversity*' in R package 'vegan', and standardized the OTU richness using the
346 function '*scale*' in R package 'vegan'(73).

347 Concentrations of soil nutrients and vegetation measurements were logarithm or
348 square-root transformed prior to analyses to improve the distribution of residuals and reduce
349 non-linearity. To disentangle the effects of edaphic and floristic variables on residual richness
350 of soil fungi, individual variables were subjected to multiple regression model selection based
351 on the corrected Akaike Information Criterion (AIC). The components of best models were
352 forward-selected to determine their adjusted coefficients of determination as implemented in
353 the 'vegan' package in R (73). The effects of forest disturbance and season change on fungal

354 species richness data were statistically evaluated by one-way ANOVA (assumptions were
355 tested by Levene's test for homogeneity of variances and Chi-square test for normality).
356 When groups were significantly different, ANOVAs were followed with Tukey's HSD test.
357 When P values ≤ 0.05 , examined values were considered to be significantly different.
358 Bonferroni correction was used to adjust the P value in multiple comparisons.

359 We used Structural Equation Models (SEM) using Amos ver.22 (SPSS, Chicago, IL,
360 USA) to determine the direct and indirect paths between forest disturbance, environmental
361 predictors and richness of mycorrhizal fungi and saprotrophic fungi. Based on the results of
362 best variable indicators selection, we chose to include soil variables (soil pH and P
363 concentration), plant diversity (Shannon diversity index) and saprotrophic groups into model
364 construction. We tested all direct and indirect relations among exogenous and endogenous
365 variables. Then the fit of models was maximized based on both chi-square test and root mean
366 square error of approximation and Comparative Fit Index. Bootstrapping is preferred to the
367 classical maximum likelihood estimation in these cases because in bootstrapping probability
368 assessments are not based on the assumption that the data match a particular theoretical
369 distribution. There is no single universally accepted test of overall goodness of fit for SEM,
370 applicable in all situations regardless of sample size or data distribution. Here we used the χ^2
371 test (χ^2 ; the model has a good fit when χ^2 is low ($\sim \leq 2$) and P is high (traditionally ≥ 0.05))
372 and the root MSE of approximation (RMSEA; the model has a good fit when RMSEA is low
373 ($\sim \leq 0.05$) and P is high (traditionally > 0.05)). In addition, and because some variables were
374 not normal distributed, we confirmed the fit of the model using the Bollen-Stine bootstrap
375 test (the model has a good fit when the P value is high (traditionally > 0.10) (74).

376 Fungal community composition was analyzed using Global Nonmetric
377 Multidimensional Scaling (GNMDS). The effects of forest disturbance and seasonal change
378 were analyzed using multivariate analysis of variance (PERMANOVA) with the '*adonis*'

379 function in package ‘vegan’. The effects of edaphic and floristic variables on community
380 composition of soil organisms were determined based on either “Bray-Curtis” dissimilarity
381 after abundances were “Hellinger transformed”, and excluding OTUs that occurred in a
382 single sample. We used the function ‘*envfit*’ to fit environmental variables while plotting the
383 non-metric multidimensional scaling (NMDS) ordination with ‘*metaMDS*’ result (75). To test
384 the correlation in community composition among soil fungi in wet and dry season, we
385 calculated the bidirectional Procrustes correlation coefficient using the ‘*procrustes*’ function
386 with 5000 permutations as implemented in the ‘vegan’ package. All statistical analyses were
387 carried out with the R software v3.0.2 (76).

388 **Accession number(s).** The raw sequencing reads were submitted to the NCBI Sequence
389 Read Archive (SRA) under the Project no. PRJNA412774, available at
390 <http://www.ncbi.nlm.nih.gov/sra/>, accessions no. from SRR6125802 to SRR6125608.

391

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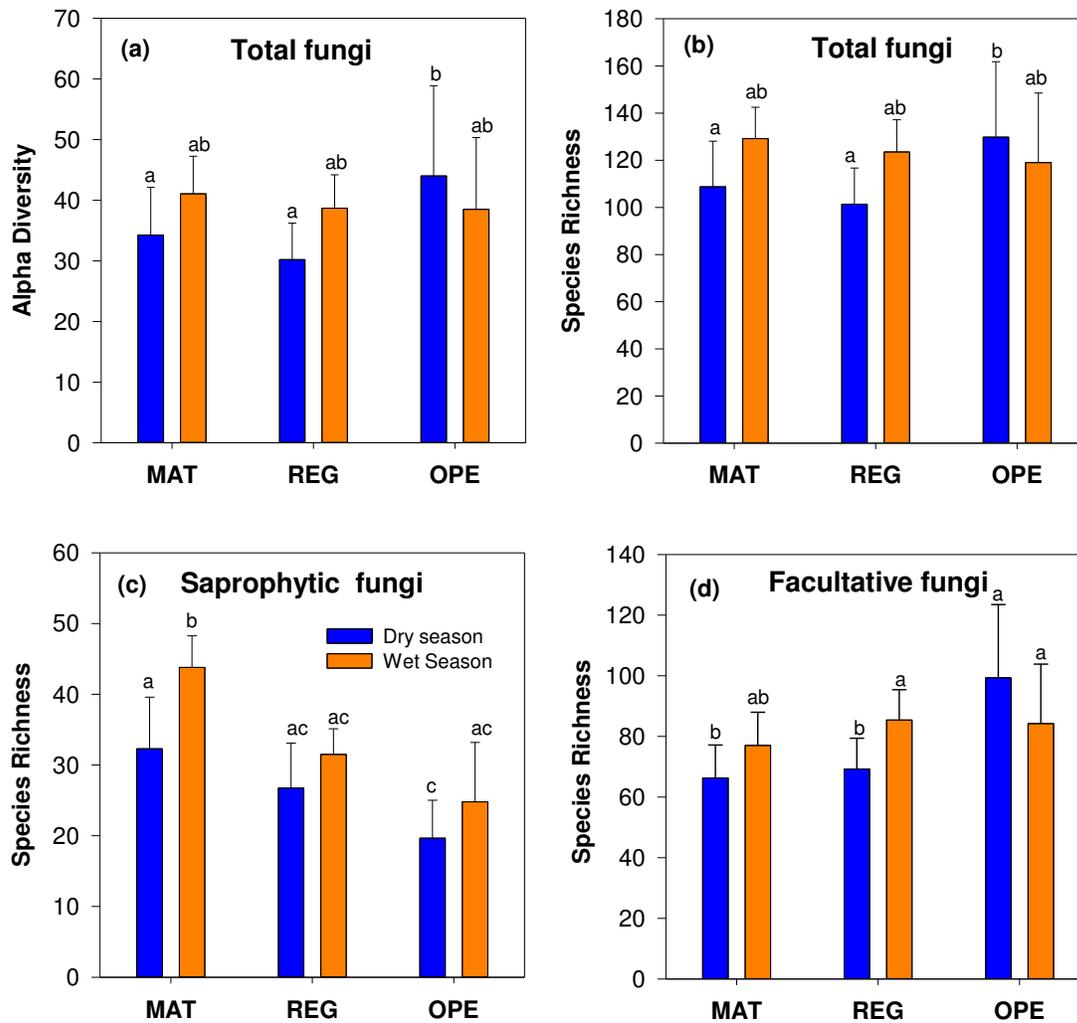


FIG 1 The total fungal diversity (a and b) and dominant functional group (c and d) response to different land cover types after forest disturbance. Saprophytic fungi were the dominant fungal group in these land cover types. Facultative fungi include several fungal groups that have multi-trophic modes, such as Pathotroph-Saprotroph, Pathotroph-Saprotroph-Symbiotroph and Pathotroph-Symbiotroph (for details refer to supplements Fig S2). MAT = mature forest, REG = regenerating forest, OPE = open land. Within each panel, different letters indicate a significant difference.

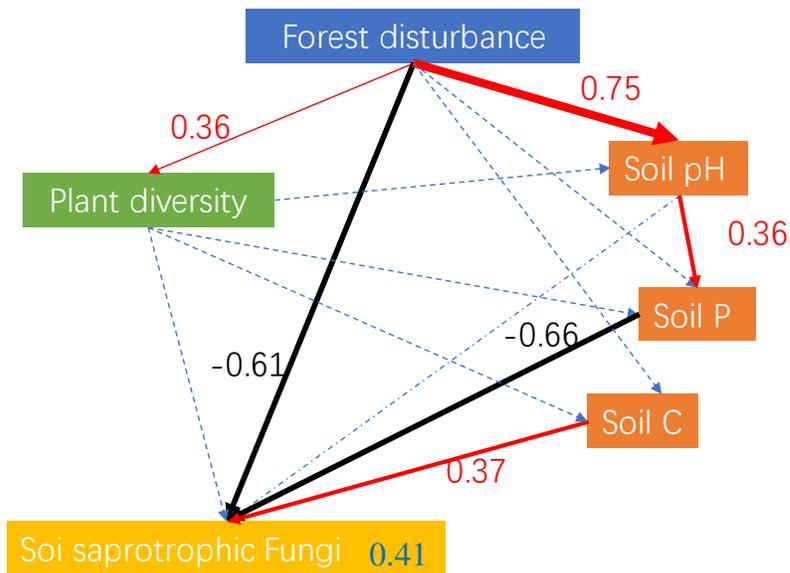


FIG 2 Structural equation model demonstrating the direct and indirect effects of forest disturbance, edaphic and floristic variables on species richness of saprotrophic fungi. The model explained 41% of the variance in abundance of saprotrophic fungi among samples. Red and black arrows indicate positive and negative relationships, respectively. The width of arrows is proportional to the strength of path coefficients. Numbers above arrows indicate standardized path coefficients. Dashed blue lines indicate tested hypotheses that were not significant.

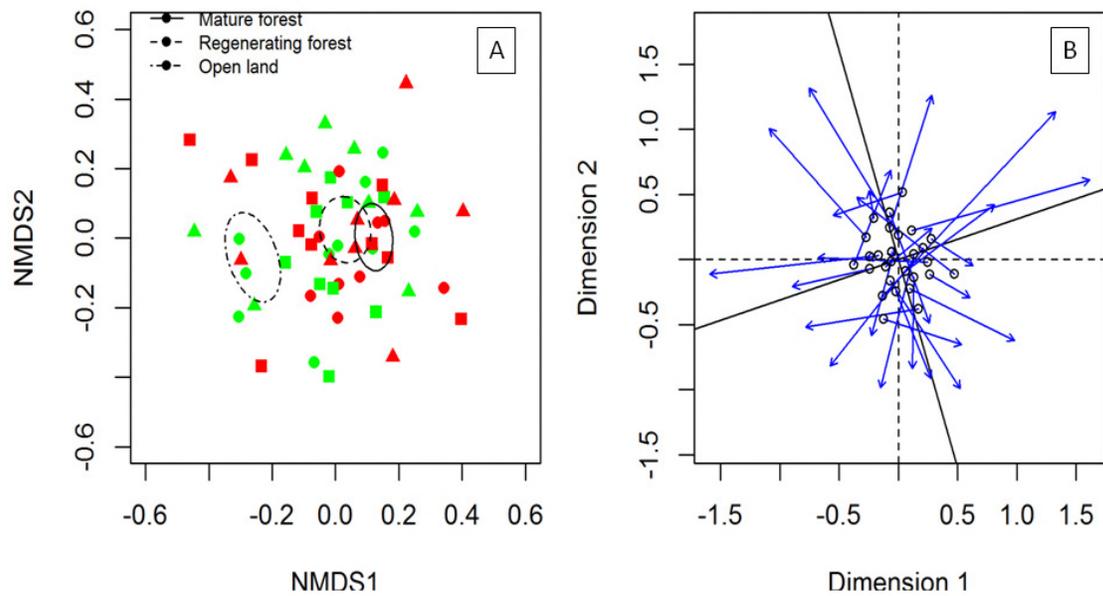


FIG 3 (A) Non-metric multidimensional scaling (NMDS) plot of the fungal community composition (relative abundance data were Hellinger transformed) in three land cover types along a forest disturbance gradient. The ellipses represent the group mean standard error. Red indicates dry season composition and green wet season composition. Circles = mature forest; Triangles = regenerating forest; squares = open land (deforested). (B) Procrustes analysis of seasonal change (from wet season to dry season) of soil fungal community composition based on the NMDS plot. There was a highly significant correlation between the wet season community composition and dry season community composition across sites ($R^2 = 0.41$, $P = 0.01$). However, as indicated by the increased spread of the points (most arrows point away from centre), the fungal communities were more dissimilar in dry season than that in wet season.

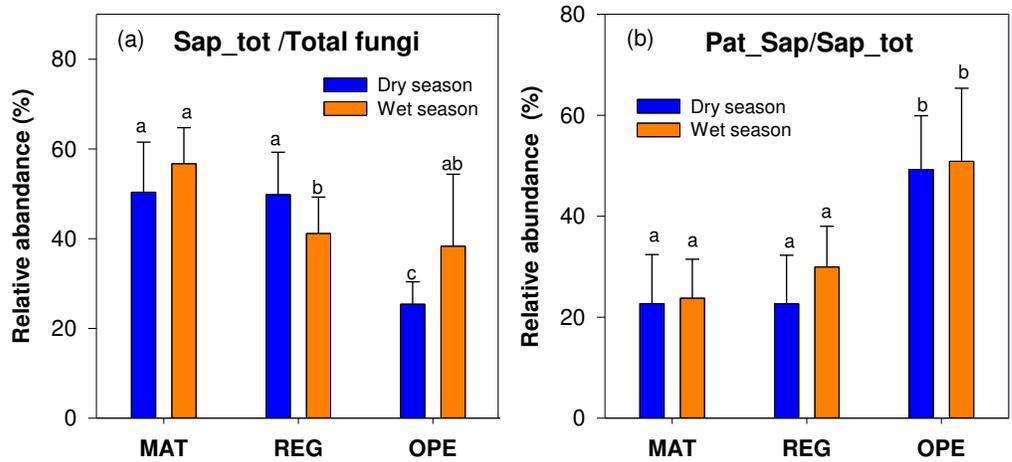


FIG 4 (a) The relative abundance of saprotrophic fungi with respect to total fungi and (b) the relative abundance of pathogenic saprotrophic fungi (Pathotroph-Saprotroph) within saprotrophic fungi among habitats along a forest disturbance gradient. Sap = Saprotroph, Pat_Sap = Pathotroph-Saprotroph. MAT = mature forest, REG = regenerating forest, OPE = open land. Within each panel, different letters indicate a significant difference.

Table 1. Mean (SD) daily maximum air temperature (Temp.), soil water content (Soil water), relative humidity (RH) and median photosynthetically active radiation (PAR) for 3 months in the middle of the wet (June–August) season in 2012 and dry (February–April) season in 2013. Data were recorded in the understory at three sites along a forest-disturbance gradient representing MAT = mature forest, REG = regenerating forest and OPE = open land. For PAR, readings 1 hr either side of the solar noon were used.

Season		Temp (°C)	Soil water (m ³ m ⁻³)	RH (%)	PAR (μE)
Wet	MAT	20.6 ^a (1.5)	0.12 (0.04)	98.0 (2.1)	9.8 ^a (4.5)
	REG	21.5 ^a (1.7)	0.29 (0.01)	98.5 (1.7)	31.1 ^a (14.1)
	OPE	23.0 ^b (3.0)	0.22 (0.05)	96.7 (2.7)	668.2 ^b (498.5)
Dry	MAT	22.3 ^a (2.4)	0.04 (0.05)	64.6 (15.6)	20.4 ^a (12.7)
	REG	25.6 ^a (3.0)	0.05 (0.02)	72.2 (16.1)	20.5 ^a (6.2)
	OPE	29.2 ^b (3.0)	0.06 (0.04)	66.6 (14.7)	1419.0 ^b (391.2)

Table 2 Best regression models fungal richness for total fungi and waprotophic fungi. NA:

Not Available"

	Total fungi				Saprotrophic fungi			
	Estimate	SE	<i>P</i>	<i>P</i> _{adj}	Estimate	SE	<i>P</i>	<i>P</i> _{adj}
Soil total P	-4.191e ⁻⁰¹	1.698e ⁻⁰¹	0.017	0.051	-3.684e ⁻⁰¹	1.229e ⁻⁰¹	0.004	0.012
Tree diversity			NA	NA	-3.408e ⁻⁰¹	1.229e ⁻⁰¹	0.008	0.023
Soil Fe	3.049e ⁻⁰¹	1.698e ⁻⁰¹	0.078	0.235			NA	NA