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Tibetan meadow degradation alters resource exchange currency, network complexity, and biomass allocation tradeoff of arbuscular mycorrhizal symbiosis

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Summary

The response of arbuscular mycorrhizal (AM) symbiosis to environmental fluctuations involves complex interactions between host plants and fungal partners, between different AM fungal members, and between AM fungal vegetative or reproductive structures; yet a systematic understanding of these responses to meadow degradation remains relatively unknown, particularly in Tibetan meadow. Here, we approached this knowledge gap by labeling dual isotopes of air $^{13}CO_2$ and soil $^{15}NH_4Cl$, computing ecological network of AM fungal community, and quantifying AM fungal biomass allocation among reproductive spore, and vegetative intra- and extra-radical hyphae. We found that the exchange currency of photosynthate and nitrogen between plants and AM fungi was increased with increasing severity of meadow degradation, indicating greater dependence of host plant on this symbiosis for resource acquisition. Besides, using 18S rRNA amplicon sequencing, we found that AM fungal co-occurrence networks were complexified by meadow degradation, supporting the stress gradient hypothesis. Meadow degradation also increased AM fungal biomass allocation toward traits associated with resource acquisition (intra- and extra-radical hyphae) at the expense of reproductive spores. Our findings suggest that an integrated consideration of resource exchange, ecological networks and biomass allocation may be important for the restoration of degraded ecosystems.

Keywords: arbuscular mycorrhizal fungi, resource exchange currency, network, biomass allocation, Tibetan alpine meadow, degradation

Introduction

The Anthropocene has witnessed significant degradation of grasslands, along with declines in biodiversity and ecosystem services (Gibbs & Salmon, 2015; Bardgett *et al.*, 2021; Bai & Cotrufo, 2022). Alpine meadows are especially sensitive to degradation caused by anthropogenic activities and climate change due to the short growing seasons and often slow growth strategies of many of the local biota (Dong *et al.*, 2020; Breidenbach *et al.*, 2022). The Tibetan Plateau, the largest high-altitude meadow system in the world, plays an essential role in water storage for local ecology and human populations (Bai & Cotrufo, 2022; Zhu *et al.*, 2023). However, as a result of overgrazing, exotic species invasion, and climate change-induced warming and drought, approximately 90% of the Tibetan Plateau is considered degraded (Harris, 2010). These degraded alpine meadows are characterized by a reduction in plant cover, nitrogen (N) availability, soil erosion, and substantial nutrient losses (Breidenbach *et al.*, 2022; Li *et al.*, 2022), potentially further exacerbating the sensitivity of these systems to future disturbance.

To cope with these environmental perturbations like those in this meadow system, plants often enlist microbial partners (de Vries *et al.*, 2020; Coban *et al.*, 2022). In particular, root-associated mutualists known as arbuscular mycorrhizal (AM) fungi can play an outsized role in the stability and functioning of grassland systems (Smith & Read, 2008; Davison *et al.*, 2015; Vetrovsky *et al.*, 2023). These fungi can increase plant access to limiting soil nutrients (Hodge *et al.*, 2010) and water (Kakouridis *et al.*, 2022). The response and functioning of arbuscular mycorrhiza to grassland degradation may involve the interaction between the host plant and AM fungal partner, the interaction between different AM fungal taxa, and the biomass allocation among AM fungal vegetative and reproductive structures. Thus, a thorough understanding of the response and function of AM symbiosis to grassland degradation is important for the sustainability of the Tibetan Plateau.

The stability of plant-AM fungal symbiosis depends on cooperation of both partners, where the fungus provides the plant with access to limiting nutrients, while

the plant supplies the fungal partner with photosynthate (Kiers *et al.*, 2011). Biological market theory posits that the reciprocal regulation of these "goods" between the host plant and AM fungi is essential for the maintenance and prosperity of AM symbiosis (Selosse & Rousset, 2011; Bennett & Groten, 2022; Martin & van der Heijden, 2024). For example, fostered by dual-labeling of carbon (C) and N isotopes, several previous studies have found that the currency in exchanging plant-derived C for AM fungi-derived N was variable with the identity of AM fungal taxa (Arguello *et al.*, 2016), soil nutrient availability (Liu *et al.*, 2021), plant development stage (Tome *et al.*, 2015), and atmospheric CO_2 concentrations (Tome *et al.*, 2015; Zhang *et al.*, 2015; Charters *et al.*, 2020) (Table S1). The degradation of grassland is often coupled with a reduction in N availability and an increase in harsh environmental conditions, due to heavy soil erosion and substantial nutrient losses (Breidenbach *et al.*, 2022; Li *et al.*, 2022). In the context of our system, plants in degraded alpine meadows must cope with declines in N availability, which may shift "market" exchange rates for plant-fungal partners. Thereby, we hypothesize H_1 that the currency in exchanging plant C for AM fungal N will be higher in the degraded meadow than in the non-degraded meadow.

In addition to the reciprocal regulation between plant and AM fungi, the response of AM symbiosis to meadow degradation may also involve the interaction with different members of the AM fungal community, which may be depicted by the complexity of co-occurrence network. Our hypothesis in this area is guided by the stress gradient hypothesis (Brooker *et al.*, 2007; Hammarlund & Harcombe, 2019), which posits that positive associations should increase in frequency under stress. Several recent studies found that the positive associations of fungal and bacterial communities were increased by stress caused by drought, degradation, and elevation/water availability (Che *et al.*, 2019; Hernandez *et al.*, 2021; Gao *et al.*, 2022). However, to our knowledge, how the associations among AM fungal taxa response to meadow degradation remains unknown. Here, guided by the stress gradient hypothesis and considering the increase of resource scarcity and environmental harshness in degraded meadow, we hypothesize that H_2, the complexity of co-

occurrence network increases in degraded meadow compared to non-degraded meadow.

The functioning of arbuscular mycorrhiza is eventually defined by the biomass allocation among three typical morphological structures, i.e., intraradical hyphae (arbuscule, vesicles and coils), extraradical hyphae, and asexual spores (Choi *et al.*, 2018; Chaudhary *et al.*, 2022). Extraradical hyphae are responsible for accessing critical inorganic nutrients from the soil matrix, intraradical hyphae (e.g. arbuscules) form the interface for the exchange of these inorganic nutrients and plant photosynthates, and dormant asexual spores are important propagules for AM fungal colonization and dispersal that represent an important survival strategy under adverse environmental conditions (Chagnon *et al.*, 2012; Chaudhary *et al.*, 2022) (Table S2). A recent study in wheat field found that the ratio of AM fungal extraradical hyphal density (ERHD) to intraradical colonization rate (IRCR) was decreased significantly with N fertilization (Babalola *et al.*, 2022). However, few studies have investigated how meadow degradation may impact AM fungal biomass allocation to growth versus reproduction (Tian *et al.*, 2009; Mao *et al.*, 2019). Under resource limitation, trait tradeoffs theories for microbes suggest that traits associated with stress tolerance and resource acquisition would be upregulated (Malik *et al.*, 2020; Wang *et al.*, 2023). For example, AM fungi would be more likely to invest in traits associated with resource acquisition such as (intra- and extra-radical) hyphal growth to improve C for nutrient exchange with host plants, this would come at the cost of fungal spore production. Besides, in adapting to the stressed degraded meadow, dormant AM fungal spores may germinate to active (intra- and extra-radical) hyphae to improve the nutrient condition of the host, as a result depleting the soil spore pool. Therefore, we hypothesize H_3, that degradation increases AM fungal biomass allocation to vegetative hyphae at the expense of reproductive spore.

Here, we test these three hypotheses along a meadow degradation gradient in the Tibetan Plateau (Fig. S1), by blending ^{13}C and ^{15}N isotope labeling, 18S rRNA gene amplicon sequencing, and morphological examination. Our H_1 (degradation increases

at the community level

the currency in exchanging plant C for AM fungal N) was supported by the finding that the ratio of ^{13}C: ^{15}N increased from non-degraded, through moderately degraded, to severely degraded meadow. The H_2 (degradation increases network complexity) was supported by the finding that the complexity of the AM fungal co-occurrence network increased from non-degraded, through moderately degraded, to severely degraded meadow. The H_3 (degradation increases AM investment in nutrient acquisition at the cost of reproduction) was supported as that meadow degradation significantly decreased AM fungal reproductive spore density (SD), but increased vegetative intra- and extra-radical hyphal density.

Results and discussion

Before hypotheses testing, we measured vegetation and soil variables in the non-degraded, moderately degraded and severely degraded meadows (Fig. S1). The results showed that plant aboveground biomass, plant belowground biomass, plant species richness, plant coverage and soil available phosphorus (AP), ammonium-nitrogen (NH_4^+-N), nitrate-nitrogen (NO_3^--N), soil organic carbon (SOC), total nitrogen (TN), easily extractable glomalin-related soil protein (EE-GRSP) and total glomalin-related soil protein (T-GRSP) were all decreased by meadow degradation (Fig. S2-3).

AM fungal community characterization: AM fungal community was characterized from root and soil samples collected from the same non-degraded, moderately degraded and severely degraded meadows using 18S rRNA metabarcoding amplicon sequencing. Our analysis detected 115 AM fungal operational taxonomical units (OTUs) dominated by *Glomus*, *Claroideoglomus* and *Rhizophagus* (Fig. 1a; Fig. S4-6). Principal coordinate (PCo) analysis detected significant associations of AM fungal community composition with compartment (root v.s. soil), degradation stage (non-, moderately, or severely), and their interaction (Fig. 1b). The effects of compartment and meadow degradation on AM fungal community is complemented with the detection of 16 AM fungal OTUs significantly biased in the three meadow degradation stages and two compartments (Fig. 1c-d; Fig. S7). Furthermore, the Bray-Curtis dissimilarity of AM

fungal community between root and soil was increased significantly by meadow degradation (Fig. 1e), suggesting increases of niche differentiation between root and soil AM fungal community. Meanwhile, meadow degradation caused the dispersion in beta diversity of AM fungal community in root but not in soil (Fig. 1f).

Testing H_1: Meadow degradation increases the currency in exchanging plant-derived C for AM fungi-derived N

To test our H_1 that meadow degradation increases the currency in exchanging plant C for AM fungal N, we performed a greenhouse experiment of meadow plants growing on soil collected from the non-degraded, moderately degraded and severely degraded meadow (Fig. S1). The system was dual labeled with $^{13}CO_2$ (air chamber) and $^{15}NH_4Cl$ (in-growth bottle) 94 days after the seedling was planted (Fig. 2a-b), and harvested three days later. We measured the concentration of ^{15}N in each individual plant and the concentration of ^{13}C in AM fungal biomass, via phospholipid fatty acid (PLFA) analysis (Olsson *et al.*, 1995). The currency of resource exchange is depicted by the ratio of AM fungal ^{13}C: plant ^{15}N (C: N).

We found that the concentration of ^{13}C detected in AM fungal hyphae was significantly lower in non-degraded meadow as compared to the moderately and severely degraded meadows (Fig. 2c), whereas the concentration of ^{15}N detected in plants was not significantly affected by meadow degradation (Fig. 2d). As a result, the resource exchange currency as depicted by the ratio of ^{13}C: ^{15}N was significantly higher in the moderately and severely degraded meadows, as compared to that in the non-degraded meadow (Fig. 2e).

Our dual isotopes label-based research supports H_1, as degradation increased the currency in the exchange of plant photosynthate and AM fungal absorbed N (Fig. 2). The detected increase in C: N currency exchange is not due to the reduction of resource availability in the severely degraded meadow, as the same substrate was used in our greenhouse-based dual isotope research. Because our system was inoculated with AM fungal community derived from soil of different degradation

levels, our finding suggests that the variation in AM fungal community structure might be responsible for the increase in the currency of C: N exchange with increasing intensity of meadow degradation.

Our study built on previous studies that used a single AM fungal species, by using an AM fungal community to investigate the currency of resource exchange between plants and AM fungi. For example, a previous study suggested that the currency in the exchange between plant C and AM fungal N can vary with the identities of plant and AM fungi (*Funneliformis mosseae* or *Rhizophagus intraradices*) that are involved in the formation of common mycorrhizal networks in a compartmentalized pot system in a greenhouse (Walder *et al.*, 2012). Furthermore, a positive correlation between a plant photosynthetic rate and the hyphal N absorption capacity of two AM fungal species (*F. mosseae* and *R. intraradices*) has been implied in a compartmented pot system (Tome *et al.*, 2015). To our knowledge, we are the first to show that the currency in exchanging C and N between plant and AM fungi is increased by inoculation of AM fungal community from the soil with increasing intensity of degradation. Our finding suggests a greater dependence of host plant on AM symbiosis for resource acquisition in degraded meadow, and this conditioned might be harnessed for the resistance, resilience, and restoration of Tibetan meadow.

Testing H_2: Meadow degradation increases network complexity

Our H_2 was tested by computing the pairwise Spearman correlations among AM fungal OTUs in each meadow degradation level. The distribution density curve of all-correlations (both significant and non-significant) showed that the proportion of positive correlations was significantly higher in the severely and moderately degraded meadows, as compared to the non-degraded meadow (Fig. S8-9). We found support for the stress gradient hypothesis because meadow degradation increased the relative frequency of positive correlations among AM fungal taxa (Fig. S8-9).

Our co-occurrence network analysis showed that meadow degradation increased the complexity of the AM fungal network from non-degraded meadow, through

moderately to severely degraded meadow, as evidenced by the doubling of edge number, connectivity, average degree and average clustering coefficient, and increasing dominance of *Glomus* taxa (Fig. 3d-h). Specifically, the number of significant positive correlations doubled in the severe degraded meadow as compared to the non-degraded meadow (Fig. 3). Note, in our system, the number of positive associations was highest in resource poor (low in N and phosphorus availability), severely degraded meadow; however, a recent study found that positive associations were highest in grassland receiving the highest amount of N input (Wu *et al.*, 2022). Due to the huge difference in experiment design (degradation v.s. N addition), ecosystem type (alpine meadow v.s. temperate grassland), and sampling types (root + soil v.s. soil only) and the complex function that AM fungi perform with respect to resource absorption, how the AM fungal community might respond to environmental changes remains to be investigated. Our finding suggests more cooperation among AM fungal taxa in degraded meadow, which may be essential for resource scavenge and stress resistance in degraded meadow.

Testing H_3: Meadow degradation increases AM fungal biomass allocation to hyphae at the expense of spore.

To test our H_3, we measured root AM fungal IRCR and soil ERHD and SD, and calculated the ratios between IRCR: ERHD, IRCR: SD, and ERHD: SD. Our analysis supports the H_3, as degradation increased AM fungal biomass allocation to hyphae at the expense of spore (Fig. 4). Specifically, in the severely degraded meadow as compared to the non-degraded meadow, AM fungal ERHD and IRCR roughly doubled, whereas AM fungal soil SD roughly halved (Fig. 4b, c). As a result, with a stable ERHD: IRCR ratio, both the SD: ERHD and SD: IRCR dropped with increasing degradation level (Fig. 4d-f). Our findings in Tibetan meadow are partially supported by a previous study in Inner Mongolia grassland. Tian *et al* found grazing-induced degradation decreased AM fungal SD and increased or decreased IRCR depending on the identity of the plant species (Tian *et al.*, 2009). In addition, another study along a transect from Tibetan

meadow to steppe found that topsoil removal-induced degradation decreased ERHD and SD but increased IRCR (Mao *et al.*, 2019). However, neither study captured the signal of AM fungal biomass allocation, because the SD: IRCR, SD: ERHD and ERHD: IRCR ratios were not calculated. Together, our current work and certain previous studies confirm that habitat degradation induces changes in AM fungal biomass allocation, though the precise patterns of changes may differ with ecosystem and degradation type. Our finding showed that meadow degradation increased AM fungal biomass allocation to hyphae at the expense of spore, indicating that restoration of degraded meadow might be accelerated by exogenous additions of AM fungal spores.

Conclusion

We detected a systematic response of AM symbiosis to meadow degradation, by showing an increase in the exchange currency between plant C and AM fungal N, an increase in the complexity of AM fungal co-occurrence network and an increase in AM biomass allocation toward hyphae at the expense of spores. Our ability to detect this systematic response largely relies on blending techniques of dual isotope labeling, 18S rRNA gene amplicon sequencing, and morphological examination. Our finding is important because Tibetan meadow is one of the most fragile yet essential ecosystems on the planet, and we found that AM symbiosis is more than only responsive and may be essential to the restoration of meadow degradation.

Materials and Methods

Our research site was located at the Naqu Ecological and Environmental Observation and Research Station (31°16'N, 92°06'E, 4500 m above sea level, mean annual temperature of -2.1 °C, mean annual precipitation of 406 mm), a distribution center of *Kobresia pygmaea*, the iconic plant species of the Tibetan alpine meadow ecosystem (Li *et al.*, 2016). Our research used 18 total plots of non-degraded (6 plots), moderately degraded (6 plots), and severely degraded (6 plots) meadows previously established by Li *et al.* (2016) (Fig. S1). Briefly, six replication plots, each 5 m × 5 m, and at least 20

m away from each other were randomly selected for each degradation level. The non-degraded meadow was intact turf with >90% canopy coverage dominated by *Kobresia pygmaea*; the moderately degraded meadow was patched turf with ~40% coverage by *Kobresia pygmaea* accompanied with crusts of Cryptogams; the severely degraded meadow was deserialized turf dominated by forbs (e.g. *Lancea tibetica*) (Fig. S1). In July 2018, a vegetation survey and sampling of roots and soil were performed in each plot. Plant community coverage, species identity, richness and composition were measured using point-intercept sampling with a 50 cm × 50 cm square frame. Subsequently, plant aboveground biomass was collected by clipping each plant at the soil surface, and plant belowground biomass was collected from two soil cores (diameter 5 cm, depth 20 cm), both of which were then dried at 60 °C for 48 hours.

At each quadrat, five soil cores were collected randomly and mixed into one sample. Soil samples were sifted through a 2-mm mesh sieve, the recovered roots were washed with distilled water. The root and soil samples were immediately packed in an ice box and transported to the laboratory. Root samples and soil subsamples were stored at -20 °C for DNA extraction and measurements of AM fungal IRCR and ERHD. Fresh soil subsamples were used to measure soil AP, NH_4^+-N, NO_3^--N, pH and for the mycorrhizal inoculation experiment. The other portion of each soil sample was air-dried to measure SOC, TN, TP, AM fungal SD, EE-GRSP and T-GRSP. Five dominant and companion plant individuals were selected randomly from each quadrat and pooled as one sample to store at -20 °C for DNA extraction. In total, 72 samples were collected (three degradation stages × four types of samples (soil + mixed root + dominant plant + companion plant) × six replicates).

Soil AP and TP were extracted with $NaHCO_3$ and $KClO_4$-H_2SO_4 respectively, and then quantified with the Mo-Sb colorimetric method (Bray & Kurtz, 1945; Bowman, 1988). Soil NH_4^+-N was measured by the indophenol blue method (Dorich & Nelson, 1983), and NO_3^--N was measured with a UV spectrophotometer at wavelengths 270 nm and 210 nm (Norman *et al.*, 1985). Soil TN was determined by the Kjeldahl method (Davidson *et al.*, 1970). SOC was estimated by the potassium dichromate titrimetric

method (Sims & Haby, 1971). Soil pH was measured in a 1:2.5 (w/v) soil-to-water suspension with a pH meter. EE-GRSP and T-GRSP were determined by the procedures reported by Wright and Upadhyaya (1996).

AM fungal spores were extracted from 50.0 g of air-dried soil by wet sieving (bottom 38 µm mesh) and the sucrose centrifugation method (Brundrett *et al.*, 1994). The extraradical hyphae were extracted from 5.0 g of frozen soil using a membrane filter, stained with Trypan blue and examined using the grid line intersection method under ×200 magnification by observing 25 random fields of view (Brundrett *et al.*, 1994). The plant roots were washed carefully and cut into 1-cm fragments, treated with 10% KOH at 90 °C for 30 min, and acidified in 2% HCl at room temperature for 10 min, followed by staining with 0.05% Trypan blue at 90 °C for 10 min. Finally, 100 dyed root segments were randomly selected and measured for AM fungal colonization by the grid line intersection method under ×200 magnification (Mcgonigle *et al.*, 1990).

The DNA was extracted from 0.1 g fine roots and 0.5 g soil using the Powerplant and Powersoil DNA Isolation Kits (MoBio Laboratories, USA), respectively. To amplify the 18S rRNA gene, a two-step polymerase chain reaction (PCR) was performed using the NS31/AML2 primer pair (Lumini *et al.*, 2010) and AMDGR/AMV4.5NF (with 12-base barcode sequences) primer pair (Sato *et al.*, 2005; Van Geel *et al.*, 2014), using the PCR conditions described by Dong et al. (2021). The PCR products were purified with an agarose gel DNA purification kit (AP-GX-250G; Axygen, United States) and quantified using a NanoDrop 8000 (NanoDrop Technologies, Wilmington, DE, USA), then pooled together with the same molar amount (100 ng) from each sample and sequenced on the Illumina MiSeq PE250 platform at Chengdu Institute of Biology, Chinese Academy of Sciences, China. The sequences obtained in this study were submitted to the GenBank database (PRJNA1060898).

The raw sequence was subjected to quality control using Quantitative Insights Into Microbial Ecology (QIIME v1.7.0), and the obtained high-quality sequences were imported into USEARCH v11.0 for dereplication, and chimeras were detected and removed (Caporaso *et al.*, 2010; Edgar, 2013). All non-chimeric sequences were

clustered into OTUs at a 97% similarity level. The representative sequences of OTUs were uploaded to the National Center for Biotechnology Information (NCBI) and the MarrjAM database (Opik *et al.*, 2010) for taxonomic identification. The phylogenetic tree of AM fungal OTUs was constructed according to Neighbor-Joining by using MEGA 7.0 software (Kumar *et al.*, 2008).

The greenhouse microcosm experiment, consisting of dominant and companion plants with and without mycorrhizal inoculum was performed at the Lhasa agroecological experiment station (29°40'N, 91°20'E, 3688 m above sea level) in July 2019. Each pot (height: 45 cm, diameter: 32 cm) was filled with 2.0 kg of substrate mixed with soil collected from nearby meadows and river sand (1:1, V/V), and steam-autoclaved twice (1 day interval, 121 °C for 2 hours). Fresh soil collected from the aforementioned meadow plots were used as mycorrhizal inoculums (40 g per pot), which was added into the center of the autoclaved substrate soil in each pot. In addition, 40 g of corresponding sterilized soil inoculum was added to create the non-mycorrhizal treatment (NM, 4 replications). To correct for the differences in communities of other non-AM fungi soil microbe, a soil microbial wash treatment was applied to each NM pot, and it was prepared according to Jiang *et al.* (2018). We blended 40 g of living-soil inoculum in 200 ml water, passed it through a 38 μm sieve, and added the soil filtrate to each NM pot.

For transplantation of dominant and companion plants, three individuals of either dominant or companion plant were collected at an early growth stage with the same height from the corresponding degradation plots. Prior to transplantation, the roots were washed and sterilized with 75% alcohol for 10 min. The main root of each plant was retained, and the fine roots were cut off to eliminate the influence of indigenous microorganisms. The three individuals of dominant or companion plant were transplanted into pot separately, and 10 days later, the seedlings were thinned to one individual per pot. A total of 48 pots (three degradation stages × two plant species × two inoculation types × four replicates) were grown in the greenhouse (day 25 ˚C, night 17 ˚C), watered every 2 days, and the location of pots was randomly

372 switched every week.

373 The in-growth bottles (8 cm high, 3 cm diameter, connected with a 10 cm syringe
374 for $^{15}NH_4Cl$ injection) containing sterilized substrate were buried to a depth of 5-15 cm
375 in soil and 5 cm away from the plants. The bottle mouth was covered by 30 μm mesh
376 (allowing the hyphae to pass through, but not roots). We put the in-growth bottles
377 with inclining at 45° to prevent leakage of $^{15}NH_4Cl$ labeling solution (Fig. 2a, b). We
378 dissolved 2 mg of $^{15}NH_4Cl$ in deionized water (i.e., 99 atom% ^{15}N, applied 1 mL of 2
379 mg/mL) with a nitrification inhibitor (3,4-dimethyl pyrazole phosphate) that inhibits
380 the transformation of NH_4^+-N to NO_3^--N (Zerulla *et al.*, 2001). The ^{15}N isotope labeling
381 was performed in the AM treatment, and the same corresponding amount of $^{14}NH_4Cl$
382 was in the NM treatment.

383 The target plant was covered with a $^{13}CO_2$ pulse-labeling chamber (30 cm high,
384 12 cm diameter) with a 5 mm pinhole at the top (Fig. 2a, b). We applied pulse labeling,
385 i.e., 20 ml of $^{13}CO_2$ (99 atom% ^{13}C) through the pinhole every 2 hours 3 times, and
386 sealed the pinhole immediately after each labeling. At midday, the AM inoculated
387 plants were labeled with $^{13}CO_2$ for 6 hours. Correspondingly, the non-mycorrhizal
388 plants were placed in the open air. The plants and in-growth bottles were destructively
389 harvested 3 days after isotope labeling (Koegel et al., 2013).

390 After 14 weeks, all individual plants were harvested to determine the ^{15}N
391 concentration of the plant, and the ^{13}C concentration of AM fungal hypha. Plants were
392 dried and ground into powder, and the ^{15}N concentration was determined using a
393 Delta V Advantage isotope ratio mass spectrometer and an EA-HT element analyzer
394 (Thermo Fisher Technology Company, USA). Soil PLFA extraction and ^{13}C-PLFA analysis
395 from in-growth bottles were carried out according to Zhang's method (Zhang *et al.*,
396 2019).

397 The concentrations of plant ^{15}N and AM fungal ^{13}C were calculated as follows:

398 Plant ^{15}N or AM fungal ^{13}C = T% ×(atom% AM –atom% NM) × 100/(99-atom% NM)

399 Where atom% AM is the atom percentage excess ^{15}N of plant or PLFA 16:1ω5c-
400 ^{13}C of AM fungal hyphae in AM inoculated treatments, atom% NM is the mean atom

percentage excess ^{15}N of plant or PLFA 16:1ω5c-^{13}C of AM fungal hyphae from four randomly chosen NM treatments, and T% is the total N concentration of plant or C concentration of AM fungal hyphae in AM inoculated treatments.

Statistical analysis

To estimate the effects of degradation and plant species on the currency in exchanging plant C for AM fungal N, the concentration of AM fungal ^{13}C and plant ^{15}N, and the ratio of ^{13}C: ^{15}N were analyzed by linear mixed-effect models using the lmer function in the lme4 package (Bates *et al.*, 2015), in which degradation was treated as a fixed factor, and plant species as a random factor.

All statistical analyses were conducted using R v.4.1.3 (R Development Core Team, 2018). First, the normality and homoscedasticity of the data were determined by using the Shapiro and Bartlett tests. When the data of soil properties, plant community characteristics, isotope concentration, AM fungal community variables, and morphological structure traits satisfied the assumption of homogeneity of variance, all significant differences of these data were tested by analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) at $P < 0.05$. If the data did not satisfy the homogeneity assumption, a nonparametric Kruskal–Wallis test was carried out by using the kruskal.test function in R.

To examine how correlations between AM fungal taxa change along a degradation gradient, we conducted a co-occurrence network analysis using the igraph package (Csárdi G *et al.*, 2024). The Spearman's correlation (Rho) coefficient between the pairwise OTUs was inferred by the psych package with a threshold of FDR-adjusted $P < 0.05$ and $r > |0.6|$ (Revelle, 2023). To visualize the variations in AM fungal community composition, the AM fungal Bray–Curtis dissimilarity was subjected to PCo analysis using the pcoa command in the ape package (Paradis *et al.*, 2004). The distance matrices of the AM fungal community (Hellinger transformed) were calculated by Bray–Curtis dissimilarity using the vegdist command in the vegan package (Clarke *et al.*, 2006). Permutational analysis of variance (PERM ANOVA) was carried out to assess the effect of compartment (root v.s. soil), degradation stage, and the interaction

between them on Bray–Curtis dissimilarities using the adonis command in vegan package (Oksanen J *et al.*, 2022).

To explore the distribution of root and soil AM fungal taxa recovered from the non- degraded, moderately degraded and severely degraded meadow root and soil samples, we plotted ternary diagrams using the ggtern package (Hamilton & Ferry, 2018). In addition, we conducted indicator species analysis of AM fungal OTUs for each degradation using the indval function in the labdsv package with the indicator values (indval) and $P < 0.05$ (Roberts, 2023). To test the homogeneity of the AM fungal community in root and soil along a degradation gradient, the beta-dispersion of AM fungal communities was explored with the betadisper function in the vegan package (Oksanen J *et al.*, 2022).

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Competing interests

None declared.

Author contributions

QD, BJ and YL conceived and designed the study. QD and SR conducted field, greenhouse and laboratory work. QD performed the statistical analyses. QD wrote the manuscript and CG gave critical revisions.

Data availability

Raw sequencing data have been deposited in the NCBI Sequence Read Archive under accession no. PRJNA1060898.

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658 **Figure Legends**

659

660 **Fig. 1 Meadow degradation promotes niche differentiation between root and soil**
661 **arbuscular mycorrhizal (AM) fungal communities. a** Bar graph showing the relative
662 abundance of AM fungal operational taxonomic units (OTUs) in root and soil along a
663 degradation gradient. **b** Principal coordinate (PCo) analysis of AM fungal community
664 Bray–Curtis dissimilarity with permutational analysis of variance (PERM ANOVA)
665 showing significant association of AM fungal community composition with
666 compartment, degradation stage, and their interaction. **c-d** Ternary plot
667 demonstrating the distribution of **c** root and **d** soil AM fungal indicator taxa detected
668 from the non-, moderately and severely degraded meadows. **c** Note we detected
669 biases for seven taxa of *Acaulospora* (1), *Claroideoglomus* (5), and *Rhizophagus* (1)
670 toward non-degraded meadow, and four taxa of *Glomus* toward moderately or
671 severely degraded meadows in root. **d** Five *Glomus* taxa exhibited significant bias
672 toward non-, moderately, or severely degraded meadows in soil. **e** Pairwise
673 dissimilarity between root and soil AM fungal community significantly increased from
674 non-, through moderately to severely degraded meadow. The P value above the
675 horizontal lines marked treatments in comparison, and the significance of difference
676 was tested by the Wilcoxon signed-rank test. **f** Beta-dispersion analysis showing that
677 the dissimilarity of AM fungal community was significantly higher in root than in soil
678 under moderately and severely degraded meadows, but not under non-degraded
679 meadow, as detected by the paired T-test at $P < 0.05$.

680

Fig. 2 Meadow degradation increased the currency in exchanging carbon (C) for nitrogen (N) between plants and arbuscular mycorrhizal (AM) fungi. a The schematic diagram of the in-growth bottles and $^{13}CO_2$ pulse-labeling chamber used in the isotope labeling experiment. The in-growth bottles (8 cm high, 3 cm diameter, connected with a 10 cm syringe for $^{15}NH_4Cl$ injection) containing sterilized substrate were buried to a depth of 5-15 cm in soil and 5 cm away from the plants. The bottle mouth was covered by 30 μm mesh (allowing the hyphae to pass through, but not roots). We put the in-growth bottles with inclining at 45° to prevent leakage of $^{15}NH_4Cl$ labeling solution. The $^{13}CO_2$ pulse-labeling chamber (30 cm high, 12 cm diameter) with a 5 mm pinhole at the top covered the target plant for labeling $^{13}CO_2$. **b** Photo of experimental instrument and plant. **c-d** The result of mixed-effect models showed that **c** the concentration of ^{13}C detected in AM fungal hyphae was significantly lower in non-degraded meadow as compared to the moderately and severely degraded meadows, whereas **d** the concentration of ^{15}N detected in plants was not significantly affected by meadow degradation. **e** The resource exchange currency as depicted by the ratio of ^{13}C: ^{15}N was significantly higher in the moderately and severely degraded meadows, as compared to that in the non-degraded meadow. The P value above the horizontal lines marked treatments in comparison, and the significance of difference was tested by linear mixed-effect models with the degradation as a fixed factor and plant identity as a random factor.

Fig. 3 Meadow degradation increased the co-occurrence network complexity of the arbuscular mycorrhizal (AM) fungal community. a-c The co-occurrence network of AM fungal community in **a** non-degraded, **b** moderately degraded, and **c** severely degraded meadows showed an increase in complexity with the increase of degradation severity. Node colors in the co-occurrence network indicated the genera of AM fungal taxa, and the edge colors represent positive (pink) and negative (blue) associations. **d** The increase in the dominance of *Glomus* taxa to network complexity with increasing meadow degradation level, as evidenced by the more than doubled degree of *Glomus* taxa in the network of severely degraded meadow as compared to that in the non-degraded meadow. **e-h** An increase in network complexity by meadow degradation is evidenced by the doubling of **e** edge number, **f** connectance, **g** average degree and **h** average clustering coefficient.

Fig. 4 Meadow degradation increased arbuscular mycorrhizal (AM) fungal biomass allocation to hyphae at the expense of spore. a-c Analysis of variance (ANOVA) showed that meadow degradation significantly **a** decreased AM fungal spore density (SD, per gram of dry soil), **b** increased extraradical hyphal density (ERHD, per gram of dry soil), and **c** increased intraradical colonization rate (IRCR, per 100 root fragments). **d-f** Meadow degradation significantly **d** decreased the SD: ERHD ratio, **e** decreased the SD: IRCR ratio, but **f** did not significantly influence the ERHD: IRCR ratio. Different letters above the boxes indicated significant differences at $P < 0.05$ among the non-, moderately and severely degraded meadows according to Tukey's honestly significant difference or Kruskal–Wallis test. **g** A schematic diagram of the response of AM fungal SD**,** ERHD and IRCR to meadow degradation. Note our findings suggest that meadow degradation increased AM fungal biomass allocation to both the intra- and extra-radical hyphae at the expense of spore.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Photographs of non-degraded, moderately degraded, and severely degraded meadows in a Tibetan meadow.

Fig. S2 The characteristics of plant community for non-degraded, moderately degraded and severely degraded meadows in the field.

Fig. S3 The properties of soil for non-degraded, moderately degraded and severely degraded meadows in the field.

Fig. S4 Rarefaction curve of AM fungal OTUs in root and soil along a degradation gradient.

Fig. S5 Phylogenetic tree of representative sequences of AM fungal OTUs obtained in this study.

Fig. S6 Pie chart of the relative abundance of AM fungal OTUs and sequencing reads.

Fig. S7 Ternary plot of root and soil AM fungal indicator taxa detected from the non-, moderately and severely degraded meadows.

Fig. S8 Frequency distributions of all correlations between AM fungal taxa as assessed by Spearman's Rho.

Fig. S9 Correlations between AM fungal taxa in non-degraded, moderately degraded and severely degraded meadows.

Table S1 List of studies investigating the currency in exchanging C for nutrients (N; P) between plant and AM fungi by isotope labeling technology.

Table S2 List of studies investigating the changes of AM fungal biomass allocation.

Fig.1

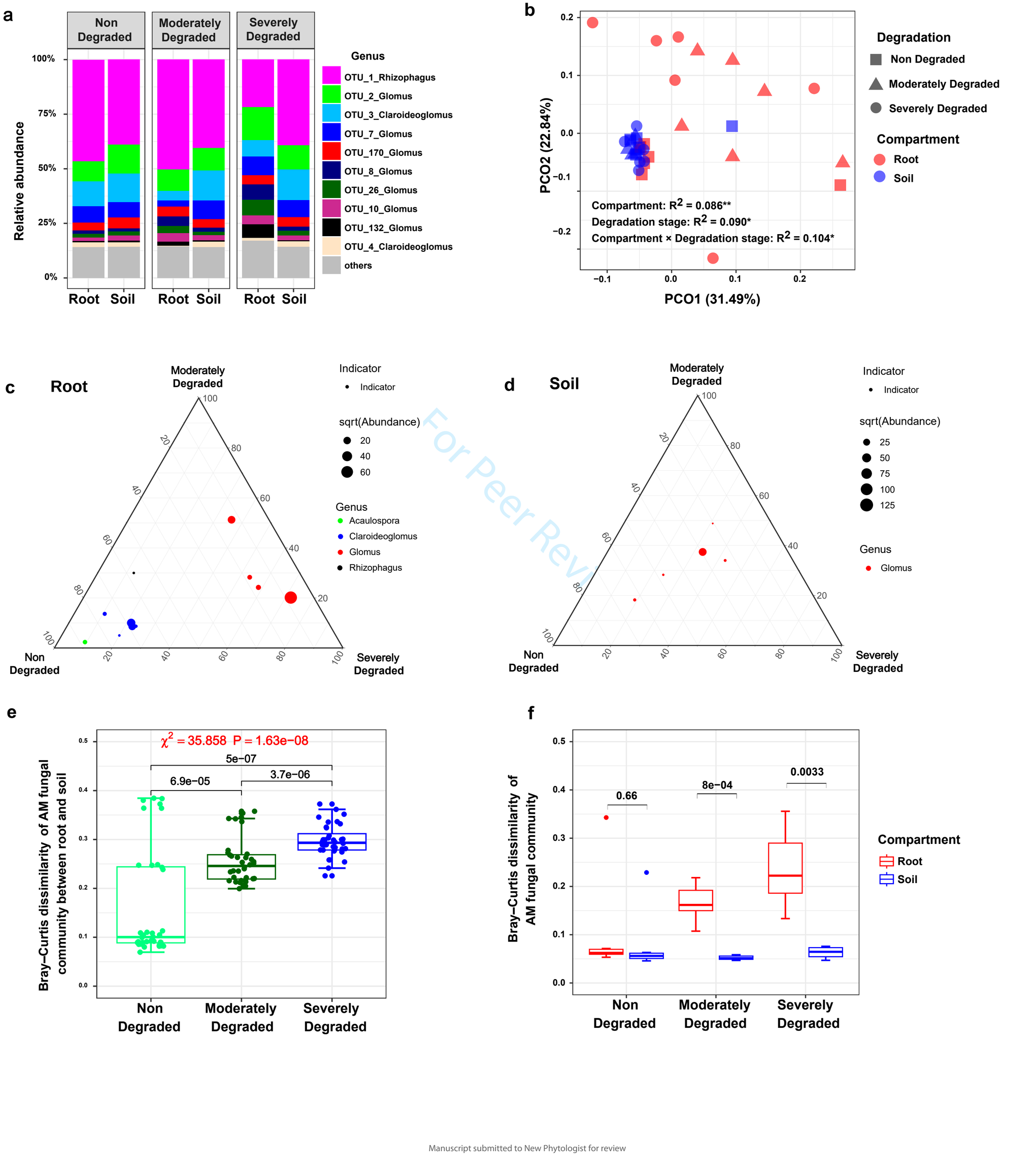


Fig.2

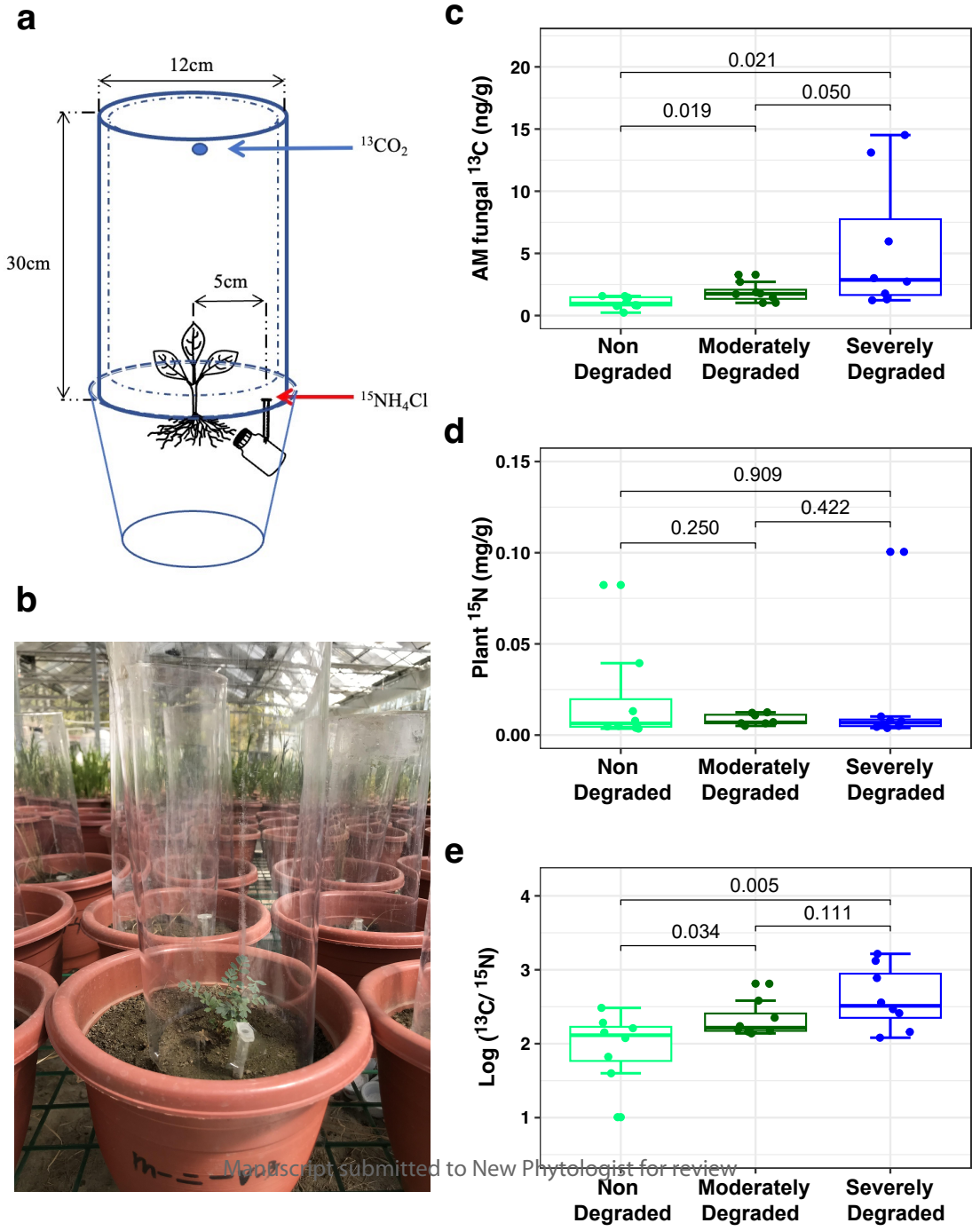
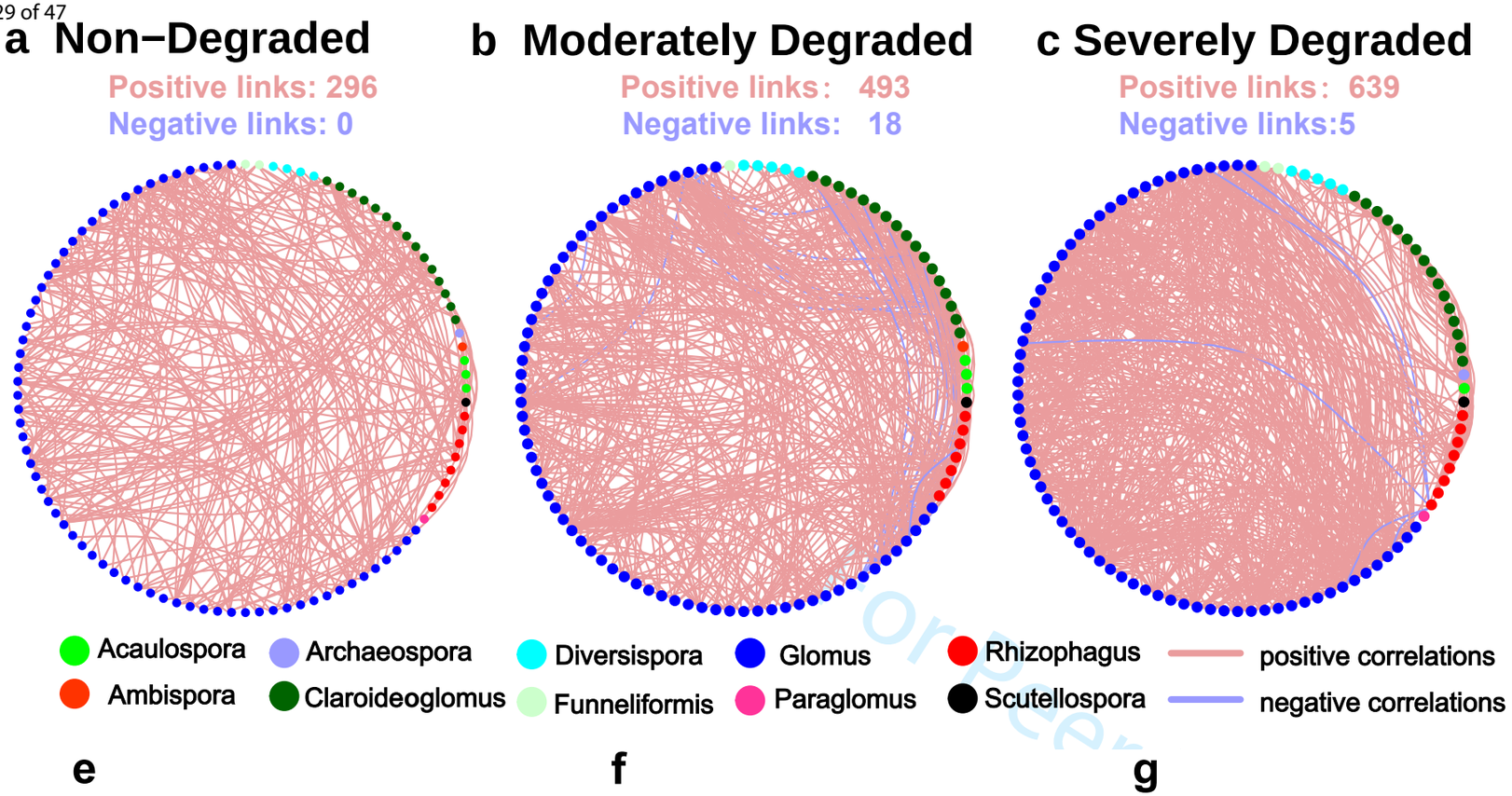
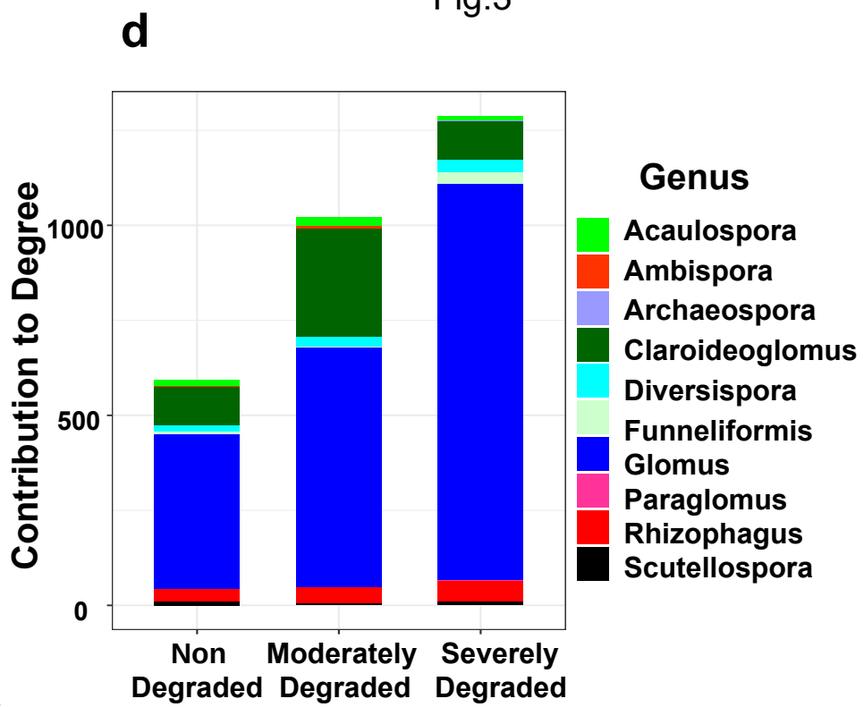
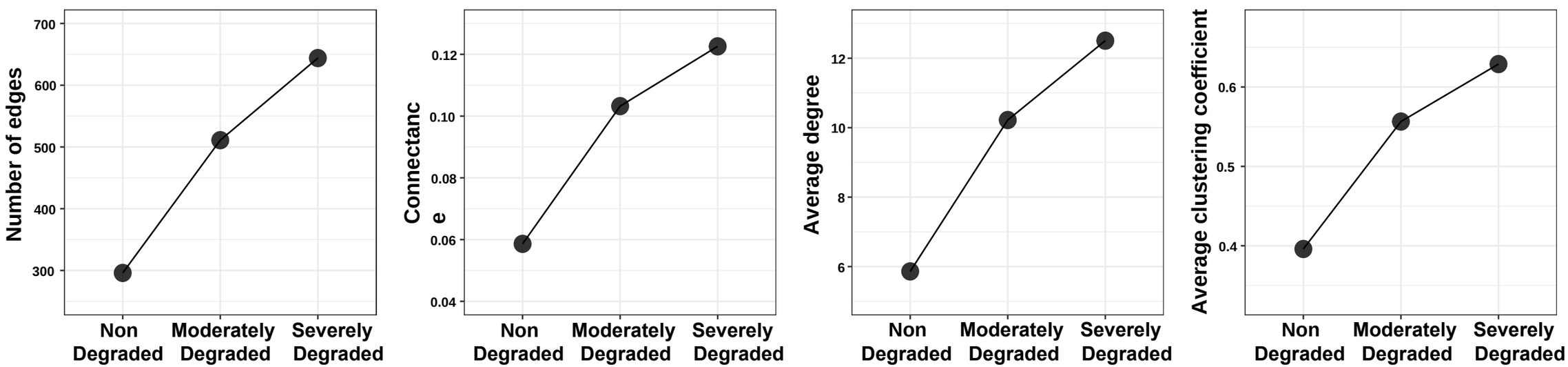
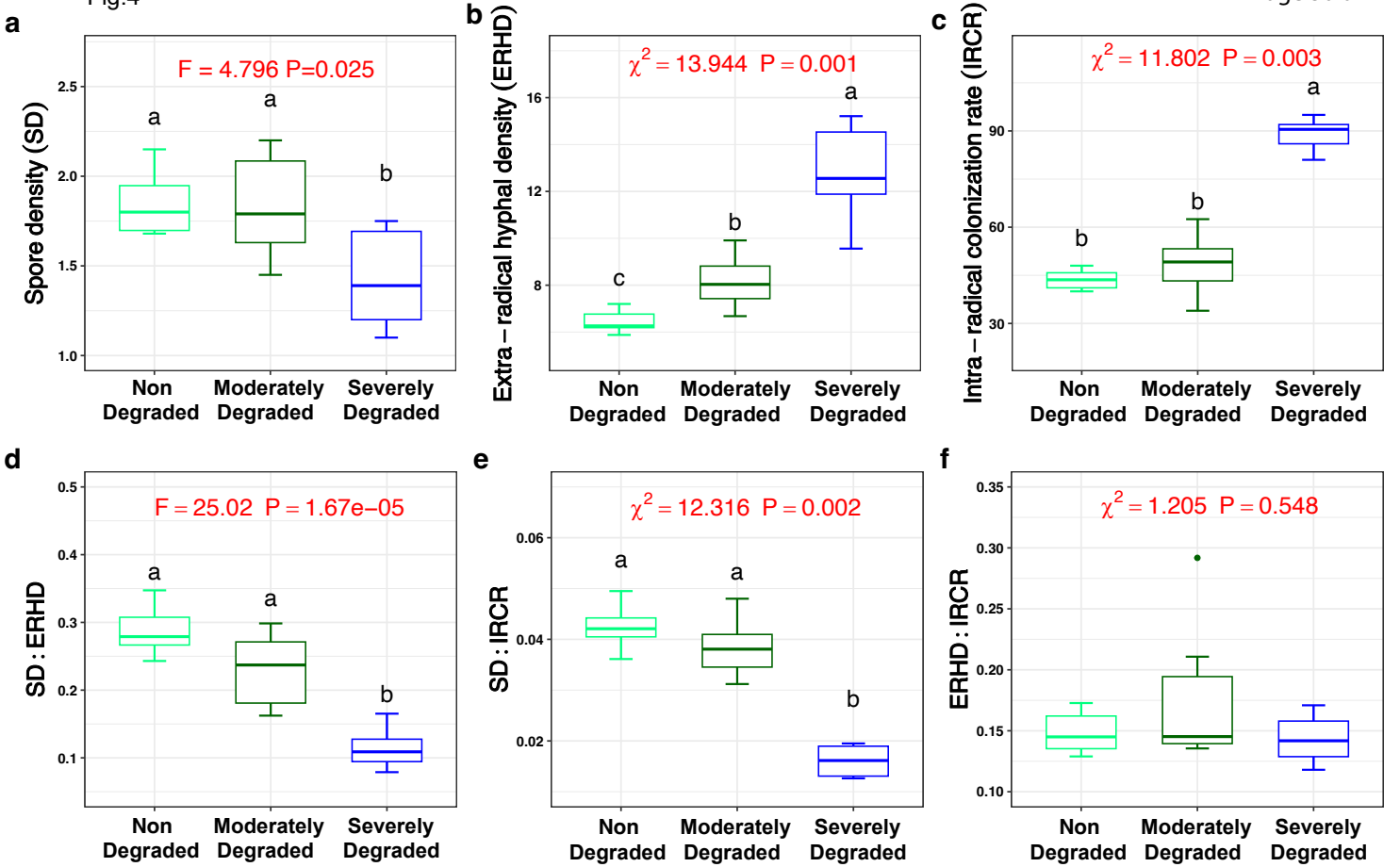


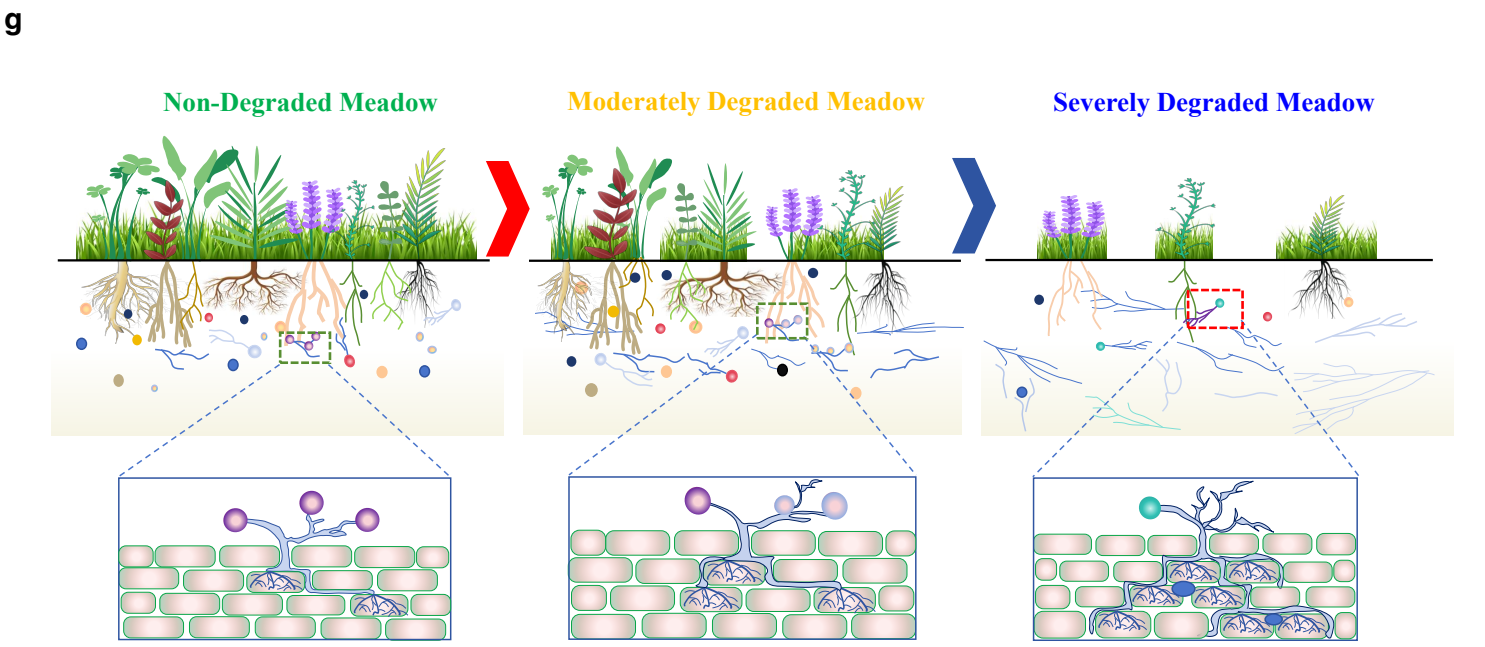
Fig.3


a Non−Degraded
Positive links: 296
Negative links: 0
b Moderately Degraded
Positive links: 493
Negative links: 18
c Severely Degraded
Positive links: 639
Negative links:5
Acaulospora
Ambispora
Archaeospora
Claroideoglomus
Diversispora
Funneliformis
Glomus
Paraglomus
Rhizophagus
Scutellospora
positive correlations
negative correlations


d
Contribution to Degree
1000
500
0
Non Degraded
Moderately Degraded
Severely Degraded
Genus
Acaulospora
Ambispora
Archaeospora
Claroideoglomus
Diversispora
Funneliformis
Glomus
Paraglomus
Rhizophagus
Scutellospora


e
Number of edges
700
600
500
400
300
f
Connectance
0.12
0.10
0.08
0.06
0.04
g
Average degree
12
10
8
6
h
Average clustering coefficient
0.6
0.5
0.4
Non Degraded
Moderately Degraded
Severely Degraded


a
Spore density (SD)
F = 4.796 P=0.025
a
a
b
Non Degraded
Moderately Degraded
Severely Degraded
b
Extra – radical hyphal density (ERHD)
χ2 = 13.944 P = 0.001
c
b
a
c
Intra – radical colonization rate (IRCR)
χ2 = 11.802 P = 0.003
b
b
a
d
SD : ERHD
F = 25.02 P = 1.67e–05
e
SD : IRCR
χ2 = 12.316 P = 0.002
f
ERHD : IRCR
χ2 = 1.205 P = 0.548


g
Non-Degraded Meadow
Moderately Degraded Meadow
Severely Degraded Meadow

Article title:

Tibetan meadow degradation alters resource exchange currency, network complexity, and biomass allocation tradeoff of arbuscular mycorrhizal symbiosis

Qiang Dong[1,2], Shi-Jie Ren[2], Claire Elizabeth Willing[3], Catharine Allyssa Adams[4,5], Yao-Ming Li[2], Bao-Ming Ji[2]*, Cheng Gao[1,6]*

The following Supporting Information is available for this article:

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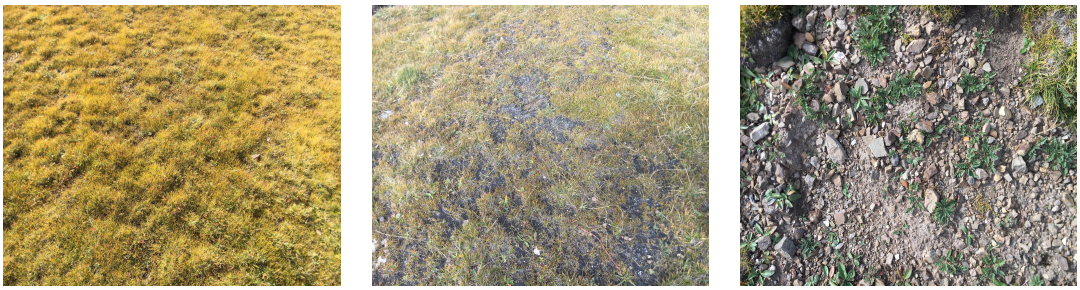


Fig. S1 Photographs of non-degraded, moderately degraded, and severely degraded meadows in a Tibetan meadow.

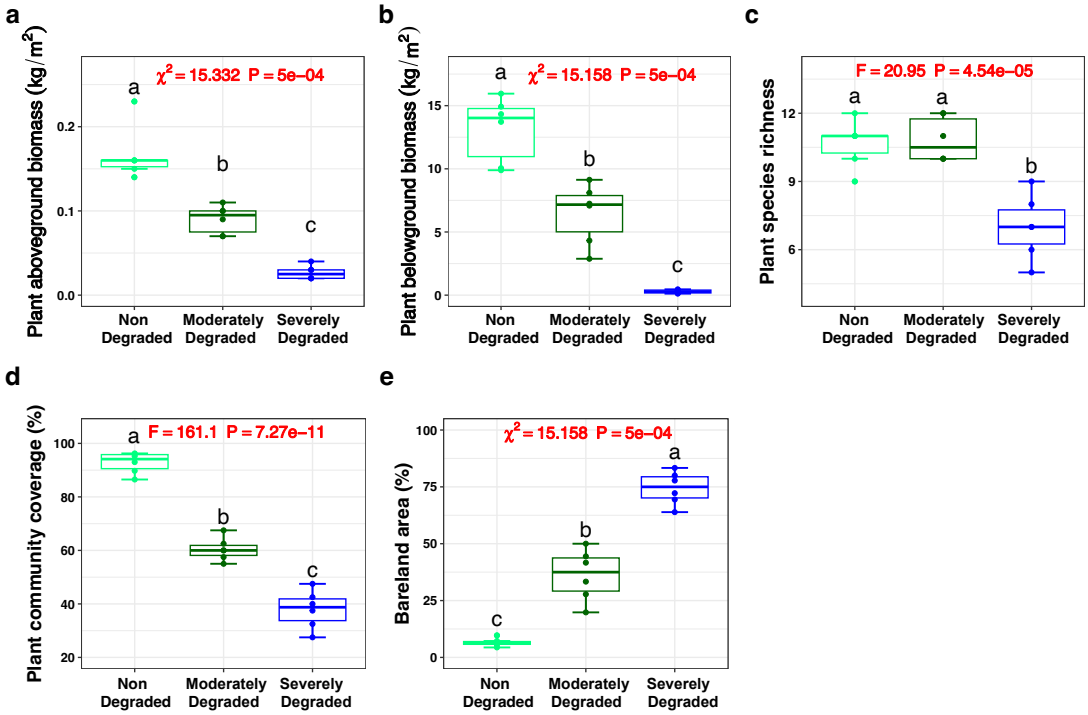


Fig. S2 The characteristics of plant community for non-degraded, moderately degraded and severely degraded meadows in the field (mean ± SD, n = 6). The result of analysis of variance (ANOVA) and Kruskal–Wallis test showed that meadow degradation significantly decreased plant aboveground biomass, belowground biomass, species richness and community coverage, thereby increased bareland area. Different letters above the boxes indicated significant differences at $P < 0.05$ among the non-, moderately and severely degraded meadows according to Tukey's honestly significant difference or Kruskal–Wallis test.

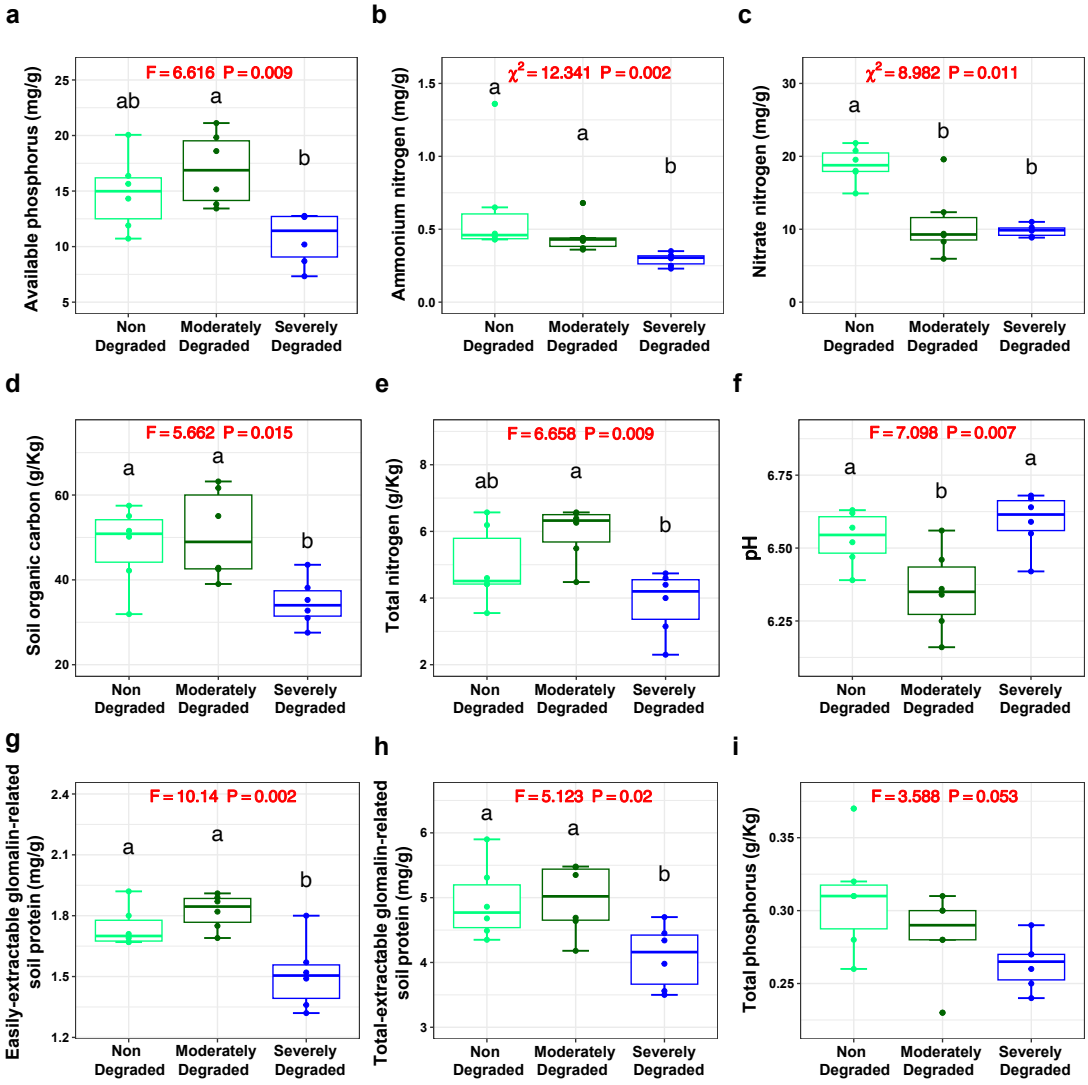
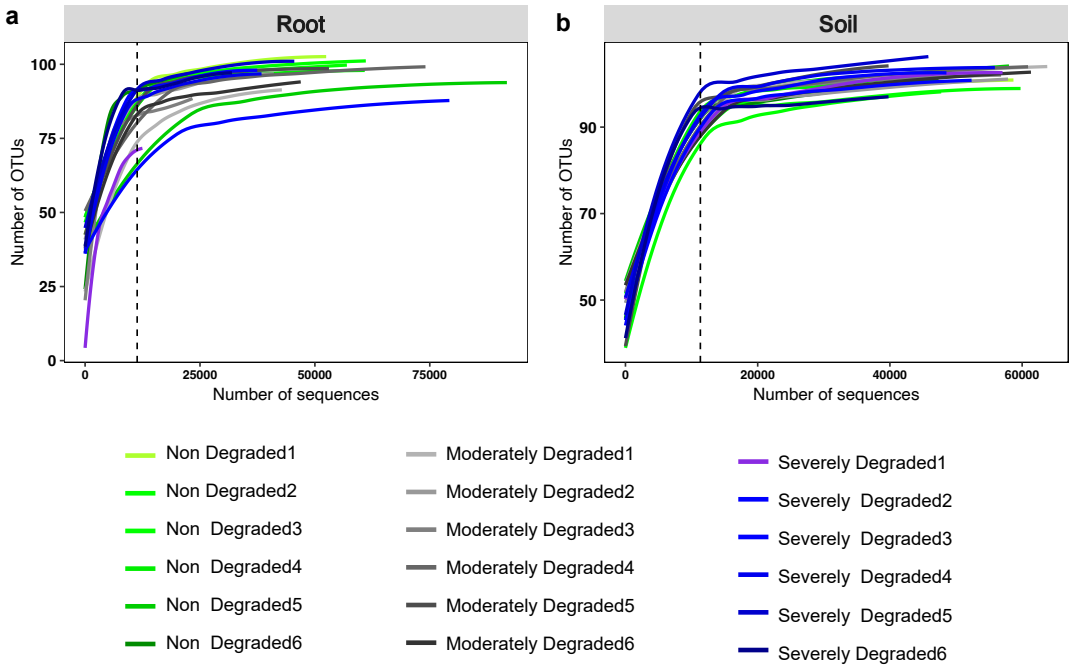


Fig. S3 The properties of soil for non-degraded, moderately degraded and severely degraded meadows in the field (mean ± SD, n = 6). The result of analysis of variance (ANOVA) and Kruskal–Wallis test showed that meadow degradation significantly affected soil available phosphorus (AP), ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), soil organic carbon (SOC), total nitrogen (TN), pH, easily-extractable glomalin-related soil protein (EE-GRSP) and total-extractable glomalin related soil protein (T-GRSP), but not total phosphorus (TP). Different letters above the boxes indicated significant differences at $P < 0.05$ among non-, moderately and severely degraded meadows according to Tukey's honestly significant difference or Kruskal–Wallis test.



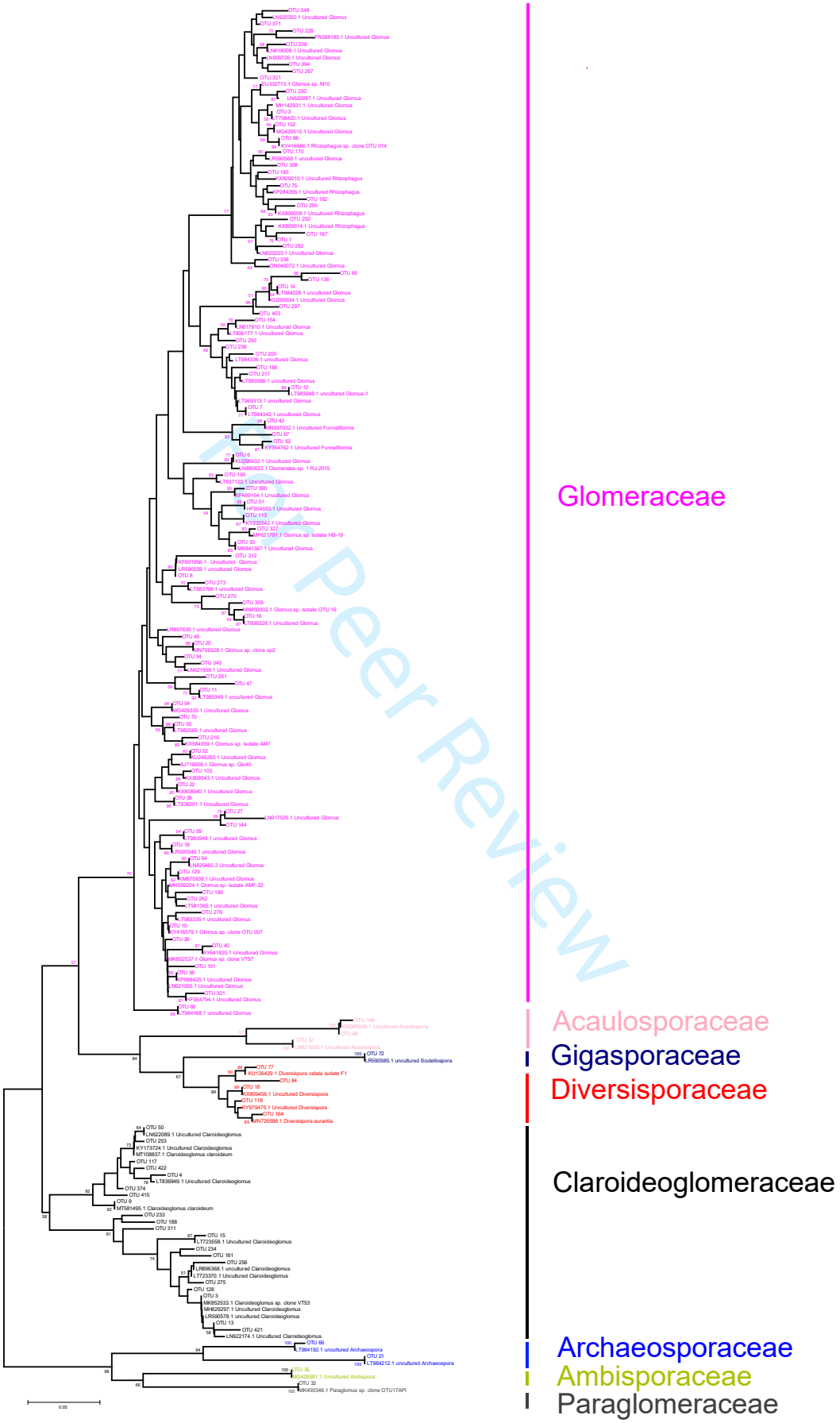
57

58 **Fig. S4** Rarefaction curve of arbuscular mycorrhizal (AM) fungal operational taxonomic

59 units (OTUs) in **a** root, **b** soil along a degradation gradient. The number of observed

60 OTUs was compared across samples when samples were rarefied at 11,329 sequences.

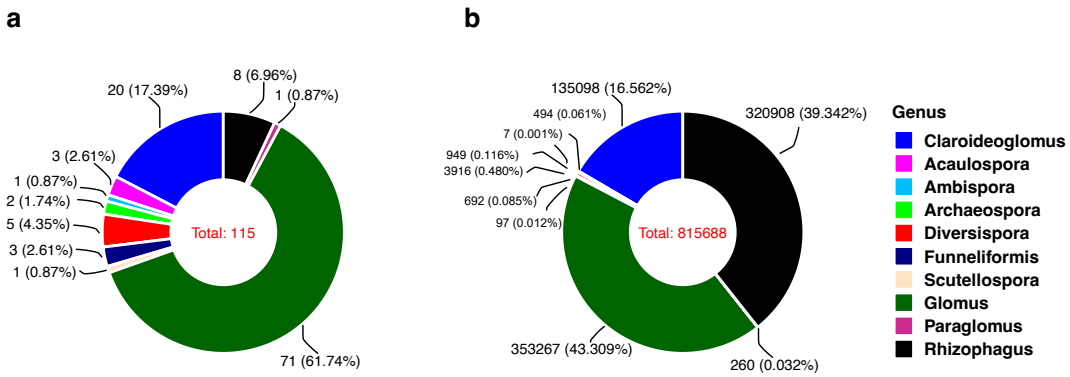
61


Glomeraceae
Acaulosporaceae
Gigasporaceae
Diversisporaceae
Claroideoglomeraceae
Archaeosporaceae
Ambisporaceae
Paraglomeraceae

62

6

Fig. S5 Phylogenetic tree of representative sequences of arbuscular mycorrhizal (AM) fungal operational taxonomic units (OTUs) obtained in this study with referenced sequences from the National Center for Biotechnology Information (NCBI) and MarrjAM database (http://maarjam.botany.ut.ee).



68

69 **Fig. S6** The pie graphs showed that the relative abundance of detected arbuscular

70 mycorrhizal (AM) fungal genera **a** operational taxonomic units (OTUs) and **b**

71 sequencing reads dominated by *Glomus*, *Claroideoglomus* and *Rhizophagus*.

72

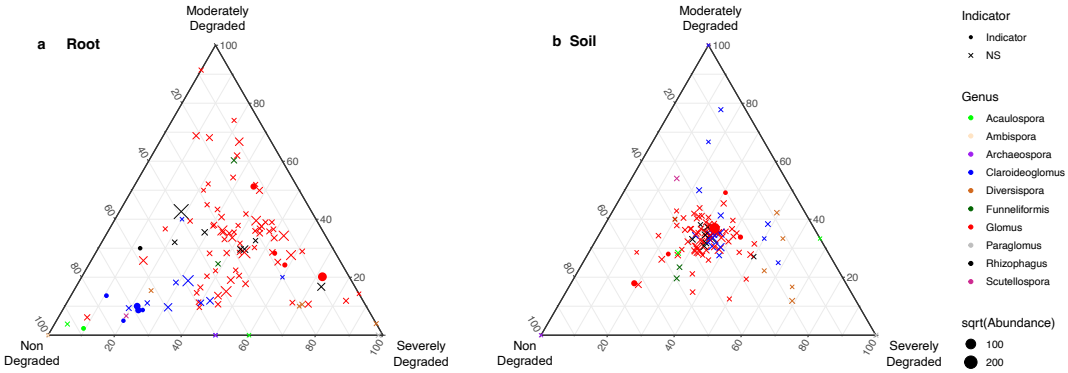


Fig. S7 Ternary plot demonstrating the distribution of **c** root and **d** soil AM fungal indicator taxa detected from the non-, moderately and severely degraded meadows. **a** Note we detected biases for seven taxa of *Acaulospora* (1), *Claroideoglomus* (5), and *Rhizophagus* (1) toward non-degraded meadow, and four taxa of *Glomus* toward moderately or severely degraded meadows in root. **b** Five *Glomus* taxa exhibited significant bias toward non-, moderately, or severely degraded meadows in soil. Note ternary plots showed the distribution of both significant and non-significant (NS) AM fungal taxa detected from the non-, moderately and severely degraded meadows.

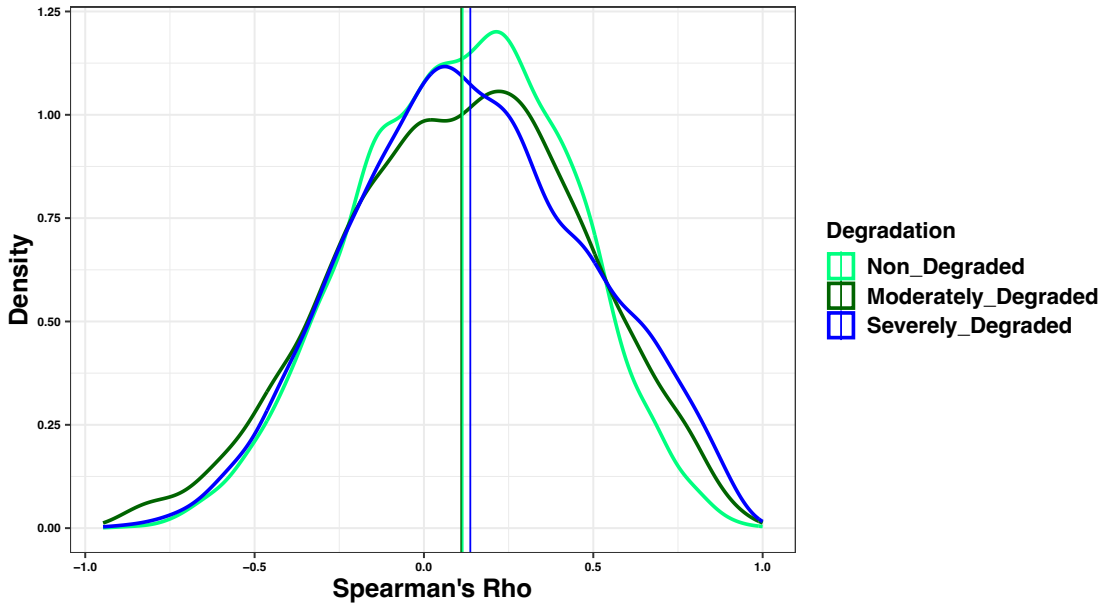


Fig. S8 Frequency distributions of all correlations between arbuscular mycorrhizal (AM) fungal taxa as assessed by Spearman's Rho. Meadow degradation increased the proportion of correlations between AM fungal taxa.

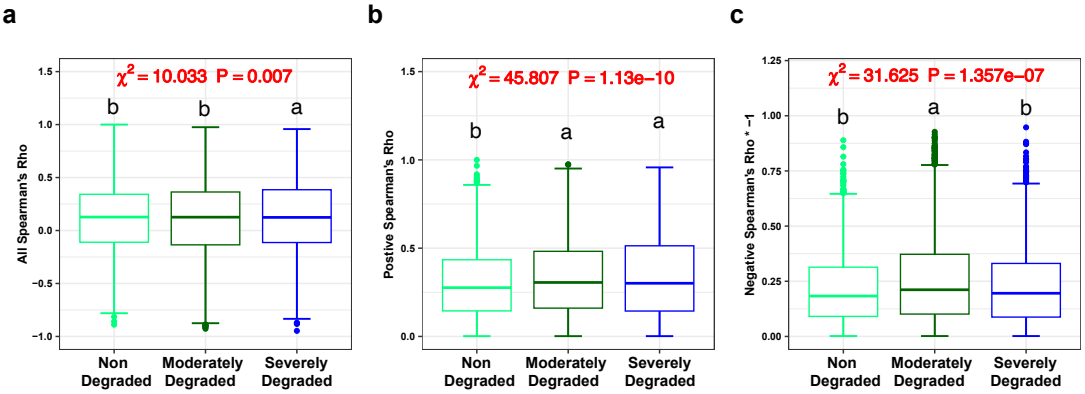


Fig. S9 Correlations between arbuscular mycorrhizal (AM) fungal taxa in non-degraded, moderately degraded and severely degraded meadows. **a-c** The result of Kruskal–Wallis test showed that meadow degradation significantly affected the all- correlation, positive correlation and negative correlation. **c** The positive correlation was significantly higher in the severely and moderately degraded meadows, as compared to the non-degraded meadow.

Table S1 List of studies investigating the currency in exchanging carbon (C) for nutrients (nitrogen, N; phosphorus, P) between plant and arbuscular mycorrhizal (AM) fungi by isotope labeling technology.

Study	Ecosystem	Treatment	Exchange type	Change in currency	Conclusion
(Arguello *et al.*, 2016)	split-root system, greenhouse	AM fungal species identity and combination	Plant ^{14}C ~ AM fungal ^{33}P	*/*	Plants received more ^{33}P from less cooperative AM fungi in the presence of another AM fungal species
(Ji & Bever, 2016)	Split-root system, greenhouse	Phosphorus/ AM fungal species	Plant ^{14}C ~ AM fungal ^{32}P, and ^{33}P	NS/*	Host plant preferentially allocated more C to the roots associated with the fungus delivering higher P per unit plant C
(Zheng *et al.*, 2015)	split-root system	light/ AM fungal species	Plant ^{14}C ~ AM fungal ^{33}P	ND/ ND	Plant preferential allocation towards the most beneficial mycorrhizal mutualist depends upon aboveground resources
(Williams *et al.*, 2017)	compartmented pot system	Nitrogen/ phosphorus	Plant ^{13}C ~ AM fungal ^{33}P	+/-	An alteration in the terms of P–C exchange under N fertilization regardless of soil P status
(Tome *et al.*, 2015)	compartmented pot system	Harvest time	Plant ^{13}C ~ AM fungal ^{15}N	+	The N uptake was linearly correlated with the ^{13}C fixed by the plants
(Gavito *et al.*, 2005)	Two compartment Petri dishes	Temperature / AM fungal species	root compartment D-glucose ^{13}C ~ hyphal ^{33}P	ND/ ND	Root C uptake and translocation in the fungus were reduced by low temperatures. Uptake and translocation of ^{33}P by fungal hyphae were similar between 10 and 25°C.
(Hodge & Fitter, 2010)	compartmented pot system	Microcosm units/ AM fungal species/time	^{15}N / ^{13}C - labeled organic patch	ND/ ND/ ND	Substantial N acquisition by AM fungi from organic material
(Kiers *et al.*, 2011)	Triple-plate experiments	Phosphate supply/Sucrose supply/ AM fungal species	Root ^{14}C ~ hyphae ^{33}P	ND/ ND/ *Glomus intraradices* > *Glomus aggregatum*	Host allocated more C (^{13}C) to more cooperative AM fungi than less cooperative AM fungal species

(Walder *et al.*, 2012)	compartmented pot system	Plant culture system/ AM fungal species	Root ^{13}C ~ hyphae ^{15}N / ^{33}P	Sorghum (C4) > Flax (C3)/ Sorghum: *Glomus intraradices* < *Glomus mosseae* Flax: *Glomus intraradices* > *Glomus mosseae*	Sorghum (C4) invested more C in the AM fungi than flax (C3), but received less N and P from the AM fungi than did flax.
(Liu *et al.*, 2021b)	compartmented pot system	Plant culture system/ Nitrogen	hyphae ^{15}N / ^{13}C	ND	
(Liu *et al.*, 2021a)	compartmented pot system	Plant culture system/ phosphorus	hyphae ^{15}N / ^{13}C	ND	
(Charters *et al.*, 2020)	compartmented pot system	elevated CO_2/ aphid herbivory	Plant ^{14}C ~ AM fungal ^{33}P	ND	Insect herbivory drove asymmetry in C for nutrient exchange between symbionts
(Nuccio *et al.*, 2013)	compartmented pot system	AM fungus was permitted or excluded	^{13}C- and ^{15}N labeled root litter	ND	AM fungus significantly modifies the soil bacterial community and N cycling during litter decomposition
(Grabmaier *et al.*, 2014)	Greenhouse pots	Earthworms/ AM fungi	earthworms were dual-labeled with ^{15}N and ^{13}C	ND/ND	
(Xu *et al.*, 2018)	compartmented pot system	Phosphorus/ without or with AM fungi	Maize leaves dual-labeled with ^{15}N:^{13}C	ND/ND	The host can acquire more nutrients through the AM from organic matter when soil P availability was low
(Zhang *et al.*, 2015)	glass growth chambers	ambient and low atmospheric CO_2 /AM fungi	Plant ^{13}C ~ hyphae ^{15}N	ND/ND	Plant C limitation does not reduce N transfer from AM fungi to *Plantago lanceolata*
(Thirkell, Tom J. *et al.*, 2020)	compartmented pot system	ambient and elevated atmospheric CO_2/ two barley cultivars	Plant ^{14}C ~ hyphae ^{15}N+^{33}P	ND/ND	

(Thirkell, T. J. *et al.*, 2020)	compartmented pot system	ambient and elevated atmospheric CO_2/three wheat cultivars	Plant ^{14}C ~ hyphae ^{15}N+^{33}P	ND/ND	C for nutrient exchange between AM fungi and wheat varies according to cultivar and changes in atmospheric C dioxide concentration
(Hoysted *et al.*, 2023)	in vitro monoxenic experimental system	intact fungi, trenched fungi and with no fungi present	Plant ^{14}C ~ hyphae ^{15}N+^{33}P	ND	Clover gained both ^{15}N and ^{33}P tracers directly from fungus in exchange for plant-fixed C in the absence of other micro-organisms
(Bever *et al.*, 2009)	split-root system,	AM fungal species identity and combination	Plant ^{14}C	ND	Host plants allocated more C toward the fungus that better promoted plant growth
(Hodge *et al.*, 2001)	compartmented pot system	without or with AM fungi	organic material with ^{13}C and ^{15}N	ND	AM fungus accelerates decomposition and acquires N directly from organic material

98 *, significant affect; +, significant increase; −, significantly decrease; NS, not significant;

99 ND, not done.

100

Table S2 List of studies investigating the changes of arbuscular mycorrhizal (AM) fungal biomass allocation.

Study	Ecosystem	Treatment	SD: ERH	ERH: IRCR	SD: IRCR	Note
(Babalola *et al.*, 2022)	wheat field	Nitrogen / Water / Time	ND / ND / ND	* / * / *	ND / ND / ND	
(Johnson *et al.*, 2003)	Grassland	Nitrogen/site/season	ND / ND / ND	ND / ND / ND	ND / ND / ND	N enrichment impacts mycorrhizal allocation across a wide range of grassland ecosystems
(Weber *et al.*, 2019)	multi-factorial field experiment	global change drivers	ND	ND	ND	Glomeraceae, Claroideoglomeraceae and Paraglomeraceae as a rhizophilic guild that allocates more AM biomass to roots than soil, and the Gigasporaceae and Diversisporaceae as an edaphophilic guild that allocates more AM biomass to soil than roots
(Hart & Reader, 2002)	Conetainers culture	21 AM fungi isolates/ harvest dates/ four host plants	ND / ND / ND	ND / ND / ND	ND / ND / ND	The colonizing strategies of AM fungi differ considerably and that this variation is taxonomically based at the family level
(Mao *et al.*, 2019)	the Qinghai-Tibet highway from Xidatan to Amdo	Distance from highway	ND	ND	ND	The root length AM colonization in disturbed habitat was about twice that in undisturbed habitat, while inverse patterns were observed for the extraradical hyphal length density and spore density in soils

*, significant affect; NS, not significant; ND, not done.

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