Fragmentation of soil microbial community structure accelerates the degradation of shrub plantations in an arid desert ecosystem

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Abstract: Many large-scale ecological restoration projects (i.e., woody plant plantations) have showed the abrupt decrease in plant productivity in the late period. However, the degradation mechanisms of tree/shrub plantation remain unclear, especially in term of the belowground and aboveground relationships and the role of soil microorganisms. We measured the physiological, and morphological traits, and productivity dynamics of the shrub *Haloxylon ammodendron* together with soil physicochemical, enzyme activity properties and soil microbial communities across a 40-year shrub-land plantation chronosequence. Moreover, we examined the relative importance of shrub plantation age, edaphic conditions, and microbial community (i.e., functional composition, diversity, and structure of microbial community) on plant performance. We found that the soil of artificial *Haloxylon ammodendron* forest began to become salinization and desiccation, which lead to sharp decrease in the relative abundance of key decomposer and nutrient maker after 30 years shrub plantation. Meanwhile, the decreases in nutrient availability lead to competition between dominant species. The competition broke soil microbial network and the microbial functional system, with its significant negative effects on plant leaf

photosynthetic and productivity. Bacterial community structure had a direct effect on plant productivity, while fungal community structure had indirect effects through leaf physiology. Soil microbial co-occurrence networks become less stable due to decrease in dominant taxa with soil and salinization, and those changes in microbial community structure are strongly linked with soil functioning and plant productivity after long-term shrub plantation. Our results highlight the role of soil microbial community structure in degradation of shrub planted ecosystems.

Key words: Artificial forest degradation; Bacterial and Fungal community; Microbial co-occurrence networks; Nutrient deficiency; Leaf photosynthetic degradation; Plant productivity

INTRODUCTION

Dryland degradation and restoration are a daunting challenge globally. Drylands cover about 41% of the Earth's land surface and support a population of over 2 billion people, 90% of which live in developing countries (D′Odorico et al., 2013). However, over the past century, an increasing demand for food and fiber from the rapidly growing human population has led to extensive conversion of many of the dryland regions into intensively managed agricultural lands (Su *et al.,* 2020; add a few more refs). Consequently, many dryland regions experience rapid loss of natural vegetation and severe ecosystem degradation with reduced provision of ecosystem services (Millennium Ecosystem Assessment, 2005). To restore ecosystem services,

tree or shrub plantation has been widely adopted since the late 1960s (Piao et al., 2020; Bryan et al., 2018). However, many of these large-scale ecological restoration projects showed an abrupt decline in gross primary production in late stage of succession, especially in arid regions (Zastrow 2019; Feng et al., 2016). Elucidating the mechanisms underlying vegetation degradation with an integrative perspective of whole-system processes is critical for restoring dryland ecosystem functions efficiently.

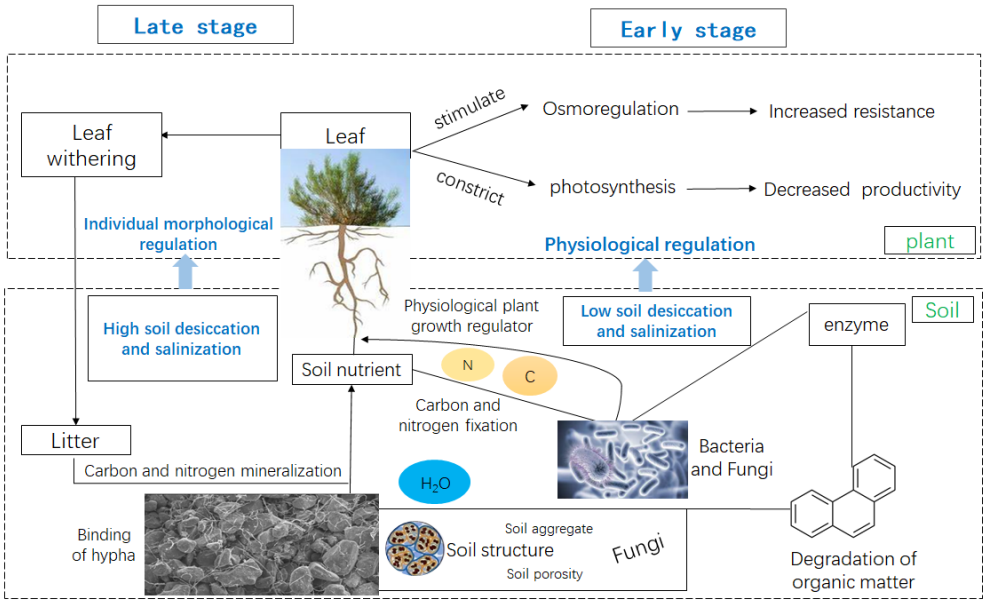

Figure 1 Conceptual diagrams show that the 'interactions' of soil and plant after long-term shrub plantation.

Belowground processes regulated by soil microbiomes play key roles in degradation. The interactions of belowground processes with aboveground plant communities are complex, involving processes governed by plant physiology and soil microbial community and their interactions, especially key soil processes such as

decomposition and nutrient mineralization. While the late-stage degradation of tree or shrub plantations has been often thought to result from soil moisture depletion and soil salinity (Wang & D'Odorico, 2019; Feng et al., 2016; Jackson et al., 2005), the roles of microbial activities are largely unexplored. Soil microorganisms are essential to soil function, particularly in organic matter decomposition and nutrient cycling, and therefore in regulating plant productivity and community dynamics, both positive and negative (Qiu et al., 2021; Harris, 2009). Most of soil microbes depends on a symbiotic relationship and form symbiotic structures with the roots of woody plants and drive the nutrient cycle in forest ecosystems. These microbes provide essential nutrients from soil or through N fixation and enhance plant tolerance to abiotic and biotic stresses. For instance, plant growth promote bacteria has unique traits, such as dormancy and osmoregulation as well as a weaker expression of genes regulating nutrient cycling. They are also capable of increasing the soluble sugars content and chlorophyll content in the leaves, which enable drought stress tolerance in plants (Chen et al., 2017). In addition, soil microbial communities could also affect plant growth or productivity indirectly by stabilizing soil structure. For instance, fungal hyphae ramify through soil, enmeshing and binding soil particles; bacteria produce gums and mucilages that act as adhesives (Harris, 2009). However, the tremendous diversity and complexity of soil microbiomes point to a grand question of how microbial community composition regulates these processes in influencing degradation.

Relating microbial community composition to degradation remains elusive.

However, sometimes the magnitude and direction of the effects of soil microbial community are highly variable, probably determined by the unique function of co-occurred species and may also vary in different environmental contexts or different growth stages. While Pregitzer et al. (2010) have shown plant local adaptation to soils that differed in microbial community, very few studies have examined how the complexity of microbial communities structure influences above-ground productivity (**Hol et al., 2010**). It is less understood about what indicators of soil microbial community composition, diversity, structure (i.e., networks), or functions (i.e., enzyme activity) could be the leading indicator of microbial communities in linking or interacting with aboveground plant communities. Microbial biodiversity has been thought and found to promote ecosystem functions. However, other studies also suggest that soil microbial structure and networks play more essential roles than biodiversity (Morriën et al., 2017; de Vries et al., 2018). A better understanding of these factors and their relative roles is thus essential to improve our ability to understand the soil microbial community role and its interaction with the above-ground components (Yao et al., 2018; Behie and Bidochka 2014). Ansering this question is essential for building the scientific basis for restoration. with implications on microbial management strategies in restoration projects (Farrell et al., 2020). Addressing this knowledge gap would directly inform which characters of belowground microbial communities could be better used as early warning signal of ecosystem degradation (Berdugo et al., 2020).

Addressing this challenge with a chronosequence holds multiple advantages.

446 A space-for-time design can help us evaluate the role of soil microbial community,
447 plant physiological traits, and soil environmental variables on the degradation of the
448 long-term shrub plantation in a desert ecosystem. The widely distributed desert
449 ecosystems in the arid regions of northwestern China offers a unique platform to
450 building such a chronosequence. Establishing native shrub *Haloxylon ammodendron*
451 has been widely implemented to restore desertified land across the region. For
452 instance, the Ant Forest initiative was launched and has planted almost 100 million
453 *Haloxylon ammodendron* to revitalize the most arid regions of China (refs). The
454 changes of metabolic substances of *Haloxylon ammodendron* during dehydration
455 showed that continuous drought promoted the accumulation of osmoregulation
456 substances in plant leaves, but severe drought caused irrecoverable damage to leaf
457 structure. Soil microbes are major drivers of dryland vegetation dynamics, structure,
458 and functioning, yet we lack an integrated understanding of the factors controlling
459 their magnitude and variability at the long-term scale. There, we set up a long-term
460 (40-year) restoration (planted) chronosequence of *Haloxylon ammodendron*
461 (*H.ammodendron*) in the fringe of the Badain Jaran Desert, Northeastern China.

462 With this long-term restoration chronosequence, we addressed the overarching
463 question of how microbial community contributes to degradation. Specifically, we
464 answered three questions: (i) what are the degradation characteristics in physiology
465 and productivity? (ii) How does microbial community change with shrub restoration
466 age, and which indicator (i.e., composition, diversity, structure) in microbial
467 community play the leading role in the vegetation degradation process, and (iii) what

468 are the direct and indirect effects of the key indicator and their relative significance in
469 shrub degradation?
470
471
472 **MATERIALS AND METHODS**
473 **Study Site**
474 This study was conducted in a sand-dune area (39° 21' N, 100° 21' E, elevation
475 1367 m) in the southern fringes of the Badain Jaran Desert in China's arid regions.
476 The climate in this region is temperate, arid and continental, receiving mean annual
477 precipitation of 117 mm, most of which occurs during June through September. The
478 potential evaporation is 2390 mm $year^{-1}$. The mean annual temperature is 7.6°C,
479 ranging from a minimum of – 27.0°C in January to a maximum of 39.1°C in July. The
480 average annual wind velocity is 3.2 m s^{-1}; Gales, with a wind velocity of > 17 m s^{-1},
481 occur for approximately 15 days each year. The soils are sandy, loose in texture, and
482 particularly susceptible to wind erosion. The landscape was originally a desert steppe.
483 However, in recent decades the area has degraded into mobile dunes mostly due to
484 prolonged heavy grazing by livestock with the rapidly increased human population in
485 the middle of last century. To prevent desertification and promote ecosystem
486 recovery, *H.ammodendron* seedlings have been planted with a high-density 2m × 2 m
487 on mobile dunes since 5-, 10-, 20-, 30- and 40-years ago, and subsequently a series of
488 shrub plantations has gradually established without irrigation. However, the planted *H.*
489 *ammodendron* degenerated after 40 years (Figure S1). The individual height, crown

and the ratio of green leaves sharply decreased and its belowground and aboveground biomass both decreased significantly (Wang et al., 2015). Such a long-term plantation offers a good opportunity to explore the subtle interactions between above- and below-ground components in the fragile ecosystem.

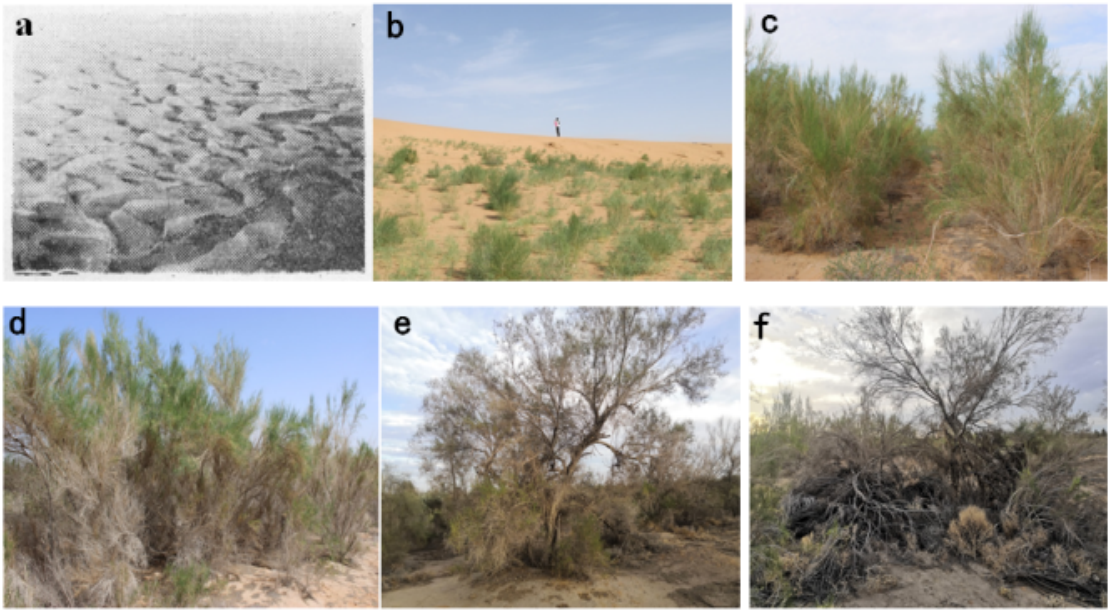

Figure 1. The degradation processes of *Haloxylon ammodedron* along 40-year plantation. a: mobile dunes in 1972; b: 5 years c: 10 years; d: 20 years; e: 30 years; and f: 40 years.

Vegetation and soil investigation

Space-for-time substitutions have been widely used to infer long-term temporal trends in vegetation and microbial succession. In the end of July and early August of 2018, a nested experimental design was used in which three typical sites (each with an area of 300 × 500 m) for every plantation age, separated by at least 200 m, were selected at random in the study area. At each of the three sites, three replicates of shrub quadrats (25 × 25 m), at least 50 m apart, were randomly selected.

In the shrub quadrats, morphological traits of ten *H.ammodendron* including canopy width, diameter of ground stem and height were recorded, and above-ground plant biomass of the *H.ammodendron* including leaves, branches, and stems was collected by clipping, oven-dried at 80°C for 48 h, and weighed. Meanwhile, their alive roots, branches and leaves were also collected. The roots of *H.ammodendron* for different plantation ages was mainly collected by digging the soil, extracting in layers near the stem of the plant, with a depth of 10 cm in each layer, and extracting twice to get 20 cm. After sampling, the healthy capillary roots were sieved out of the soil and measured with a vernier caliper. The green and yellow leaves and capillary roots are evenly stored in a foam incubator covered with dry ice for laboratory determination of physiological indicators of the leaves (i.e., three organic osmotic regulators: free proline, soluble protein and soluble sugar; and chlorophyll) and roots (root activity).

For six plantation ages of 0-, 5-, 10-, 20-, 30- and 40-years, three replicate sites were selected for vegetation survey and three 1-m-wide and 20-m-long transects were set up in each site to collect soil samples beneath the shrub canopy. Along each transect, five independent sampling plants were randomly selected to collect soil samples. To decrease spatial heterogeneity, the soil samples were collected from eight sampling points, and then mixed to two soil examples at the distance 0-10cm and 10-20cm from the sampling plant. A total of 72 bulk soil samples, were collected from the depth of 0-10cm and 10-20cm, and each plantation age consisted of six soil samples. After picking out the leaf litter, large particles and roots, each soil sample was thoroughly homogenized and divided into two subsamples: one was stored at 4°C

528 for soil physical-chemical factors and soil enzyme activity within two weeks, and the
529 other was stored at – 70°C until DNA extractions. Sieved samples were transferred to
530 the Biomarker Technologies Corporation, Beijing, China for DNA extraction
531 following a Standard Operating Procedure, where after the DNA extracts were
532 distributed to the various co-workers for further analyses (qPCR, and Miseq
533 sequencing, see **Appendix A, Materials and Methods** for details on sequencing).

534 **Soil physical-chemical analyses**

535 The soil water content at 0-10 cm and 10-20cm was gravimetrically measured
536 by oven-drying the fresh soil samples at 105°C until a constant weight. Soil particle
537 size distribution was measured by pipette method. Soil pH was determined by
538 potentiometric methods using a soil suspension with a soil: water ratio of 1:2.5 (w/v).
539 Electrolytic conductivity (EC) was measured in a soil suspension with a ratio of 1:5
540 (w/v) using an EC meter. Soil nutrient content was measured by using standard soil
541 testing methods: soil organic matter (SOM) was measured by potassium dichromate
542 volumetric method (external heating method); total nitrogen (TN) was measured by
543 the Kjeldahl procedure (UDK140 Automatic Steam Distilling Unit, Automatic
544 Titroline 96, Italy; ISSCAS, 1978); and total phosphorus (TP) was determined using
545 sulfuric acid-perchloric acid-molybdenum antimony colorimetric method. Soil
546 enzyme activity, β-glucosidase, urease and alkaline phosphatase (ALP), were
547 measured as described by Liu et al. (2019).

548 **Statistical analyses**

549 One-way analysis of variance (ANOVA) was used to test for significant
550 differences in soil physical, chemical and biological parameters among different-aged
551 sites with post hoc Duncan tests (P = 0.05). Spearman correlation analyses were
552 performed to test the relationships between the aggregate environmental factors and
553 microbial community structure by using SPSS Statistics software (IBM Corporation,
554 NY, USA). The redundancy analysis (RDA, CANOCO4.5) was used to evaluate
555 relationships between relative abundance of bacteria and fungi at genus level to soil
556 moisture, pH, salinity and nutrients.

557 **Microbial community diversity analysis**: alpha and beta diversity were used
558 to assess bacterial and fungal diversity for each age. Alpha diversity was defined as
559 the average OTU richness within a plantation age, which was determined by the
560 number of observed OTUs, Chao1 richness, ACE, Shannon's, and Simpson's
561 diversity using QIIME software. Beta diversity was defined as the average
562 Bray-Curtis dissimilarity values among samples within the different plantation age
563 sites, and visualized via nonmetric multidimensional scaling (NMDS).

564 **Network analysis:** Networks of each age were constructed using the relative
565 abundance of OTUs for six replicates (total 36 samples). Bacteria or fungi OTUs that
566 had sum reads >0.1% were selected for the network analysis. Corrections between
567 OTUs were examined by Spearman rank correlation test. Significantly correlated
568 genra ($r > 0.8$, $p < 0.05$) were used for the next network diagram construction. The

569 network properties were obtained using the igraph package (Csardi & Nepusz, 2006).
570 The network structure properties of the soil microbial community, network size (node
571 number) and complexity (edge number), connectedness (e.g., network density,
572 average shortest path length and network diameter), modularity (e.g., modularity,
573 number of community and average clustering coefficient), cohesion (the proportion of
574 positive and negative relationships) and stability (i.e., network size, complexity,
575 connectedness, modularity and cohesion) were used to assess soil bacterial and fungal
576 structures (Qiu et al., 2021). The network with higher stability (e.g., bigger size, more
577 complexity, connectedness, modularity, and positive cohesion) has a more stable
578 structure and stronger ability to resist environment stresses (Newman, 2006).

579 **Structural equation model (SEM) analysis**: We used SEM to identify the
580 direct and indirect effects of age, soil (SOM, TN, TP, silt and clay content, pH,
581 salinity and moisture), soil microbial community composition, structure (nodes,
582 edges, average clustering coefficient, number of communities, network diameter,
583 network density, average shortest path length, negative edges), and function (soil
584 β-glucosidase, urease and alkaline phosphatase), plant physiological traits, such as
585 photosynthetic organic matter (chlorophyll: chlorophyll a, b and total chlorophyll),
586 osmotic regulators (soluble sugar, soluble protein content and free proline content)
587 and root activity as drivers of the plant aboveground productivity. Based on the
588 hypothesized soil-plant-microbe mechanisms and available data, three steps were
589 involved in the SEM construction procedures. First, we screened for a set of indicators
590 of plantation age, soil properties and microbial community characteristics (i.e.,

591 composition, structure, function) effects on plant physiological traits and plant
592 productivity. Pearson correlations were used to select the indicators that exhibited
593 significant correlations with plantation age, soil properties, microbial community
594 composition, structure, function, plant physiological traits and plant productivity. The
595 soil property variables include the pH, salinity, and moisture. Microbial community
596 composition variables included the dominant genes, such as *Lectera* in fungal
597 community and *Sphingomonas* in bacterial community. Microbial community
598 function variables included soil enzyme activities, such as urease and alkaline
599 phosphatase. Microbial community structure variables included the node, edge,
600 average clustering coefficient (ACC) and negative relationships, which is an indicator
601 of bacterial and fungal community structure on plant physiological traits and
602 productivity. Plant physiological trait variables included soluble protein and sugars in
603 both old and young leaves. All selected variables were transformed to natural
604 logarithm values before the SEM analysis to mitigate departures from normality and
605 linearity. Second, the variables are generally correlated within each category of soil
606 properties, soil microbial community and plant physiology. To reduce collinearity
607 among predictor variables, we used principal component analyses (PCAs) to create
608 multivariate functional indexes for each category with multiple variables. For each
609 category of variables, the first principal component (PC1), which could explain
610 68-87 % of the total variance, was subsequently used in the SEM models. Then, three
611 separate SEM models of bacterial, fungal and total microbial community were
612 conducted. Third, we tested the goodness of fit of our models. To do so, we used the

chi-square test (χ^2, the model has a good fit when $0 \leq \chi^2 \leq 2$ and $0.05 < P \leq 1.00$) and the RMSEA; the model has a good fit ($0 \leq RMSEA \leq 0.05$ and $0.10 < P \leq 1.00$) (Chen et al., 2018). Finally, we confirmed the fit of the model using the Bollen-Stine bootstrap test. Our model showed a solid goodness of fit and, therefore, a satistactory fit to our data. The three SEM models were conducted with the software AMOS 20 (IBM SPSS Inc).

RESULTS

Degeneration in *H.ammodendron* morphological and physiological traits along 40 years plantation

The planted shrub *H. ammodendron* degenerated after 30–40 years. The stem biomass began to sharply decrease after 40 years (Figure 1a). The leaf and branch biomass of *H.ammodendron* increased during 5-20 years, but sharply decreased after 30 years (Figure 1b, c). Meanwhile, the ratio of yellow leaves also increased after 30 years (Figure 1e), suggesting the photosynthetic capacity of *H.ammodendron* began to decreased.

The physiology of root and leaf degenerated after 30 years. The root activity in 0-10 cm and 10-20cm decreased after 30 years (Figure 1d). Meanwhile, the osmotic adjustment substances (i.e., soluble protein and soluble sugar) in yellow leaves also decreased after 30 years (Figure 1 j, k, l), which suggest the failure of drought physiological regulation. The malondialdehyde and osmotic adjustment substances (i.e., soluble protein, soluble sugar and free proline) were mainly concentrated in yellow leaves (Figure 1f, j, k, l), while chlorophyll a, b and total chlorophyll were mainly in green leaves (Figure 1g, h, i), suggesting the photosynthetic rate of yellow leaves were much lower than green leaves. The decrease in osmotic adjustment substances and green leaves suggest the degeneration of drought physiological regulation.

Corresponding changes in edaphic properties were observed along 40 years *H. ammodendron* plantation (Figure 2). Soil electrical conductivity (EC), silt

and clay contents and soil nutrients (soil organic matter, total nitrogen and total phosphorus) significantly increased along the plantation age, and reached the highest level at year 40 (Figure 2a, b, c, d and e). Soil pH increased from 20 years to 30 years, while water content significantly decreased from year 30 (Figure 2f, g). Consistent with the pattern of soil water content, some soil enzyme activities (β-glucosidase at 10-20cm, and alkaline phosphatase at 0-10cm) also began to decrease after 30 years (Figure 2j).

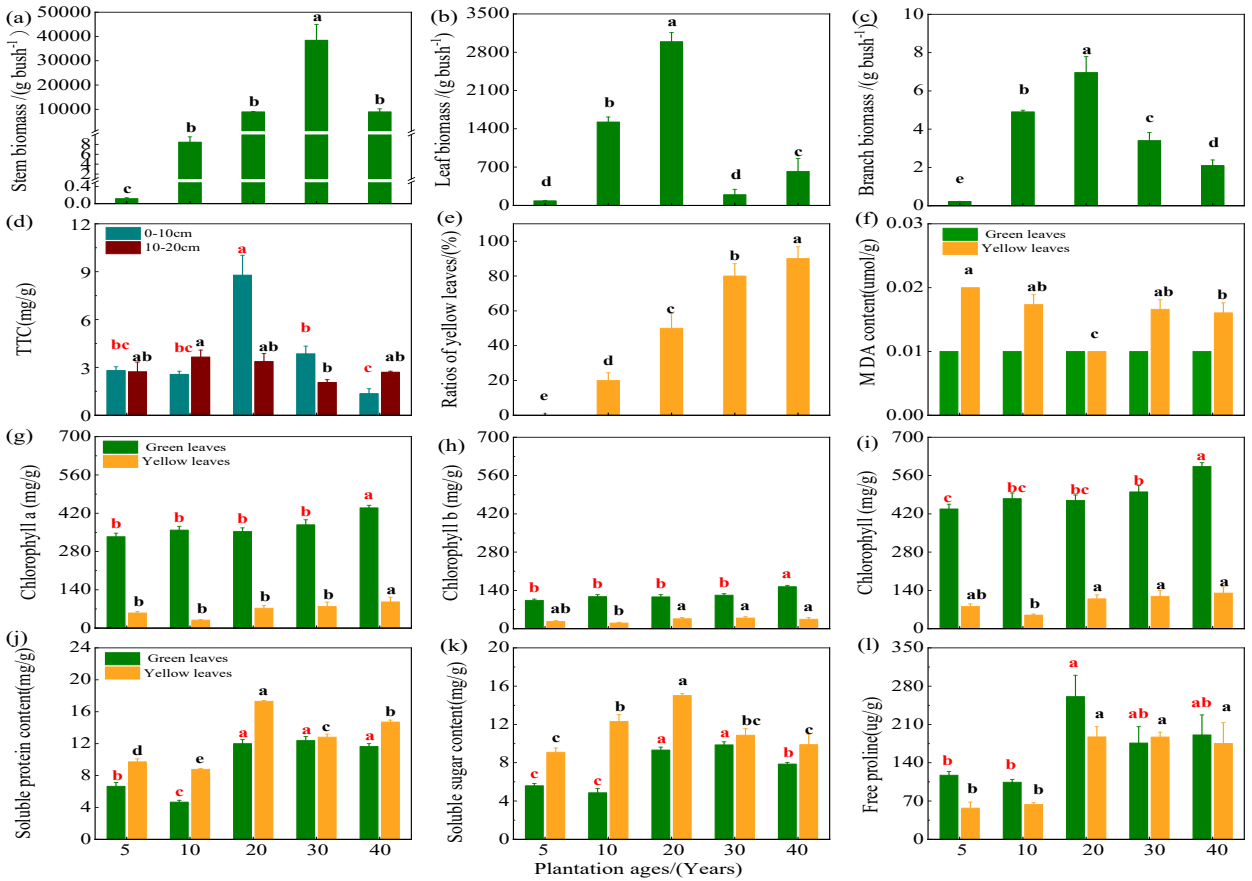

Figure 1 Changes in *H.ammodendron* biomass and physiology across different plantation ages. Changes in the biomass of stem **(a)**, leaf **(b)** and branch **(c)**, root activities **(d)**, ratio of yellow leaves **(e)**, leaf physiology in green and yellow leaves, including malondialdehyde (MDA) **(f)**, leaf chlorophyll a **(g)**, chlorophyll b **(h)** and total content **(i)**, and osmotic adjustment substances soluble protein **(j)**, soluble sugar **(k)** and free

652 proline **(l)**. Different lowercase letters above the bars show significant differences between different ages according to one-way ANOVA with

653 Duncan′s multiple range tests ($P<0.05$).

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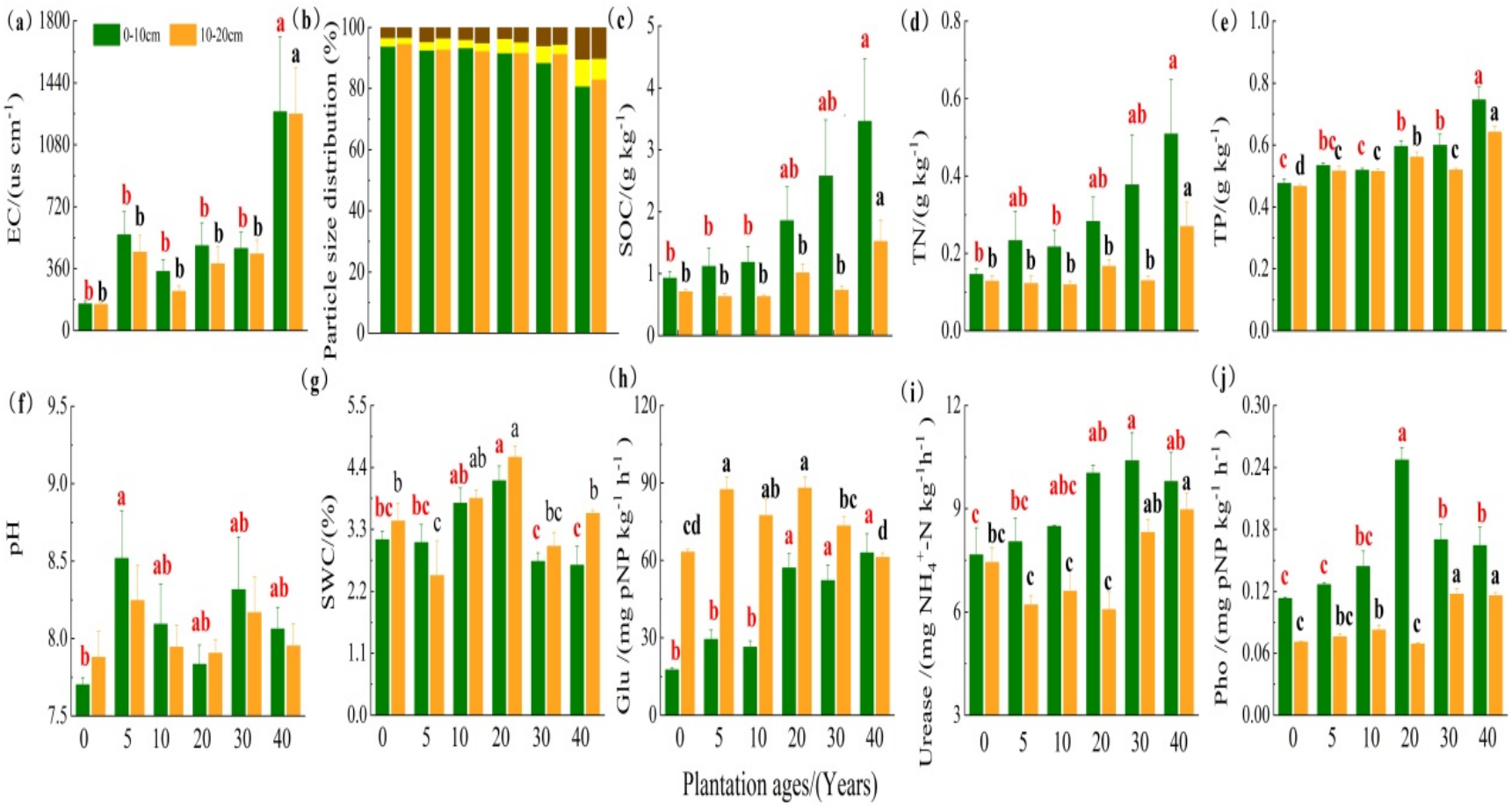

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656 **Figure 2 Changes in soil physic-chemical properties with plantation age.** Changes in soil EC (a), texture (b), SOC (c), TN (d), TP (e), pH(f),

657 Soil Water Content (SWC) (g), and enzyme activities β-glucosidase (h), urease (i) and alkaline phosphatase (j) in 0-10 cm and 10-20 cm.

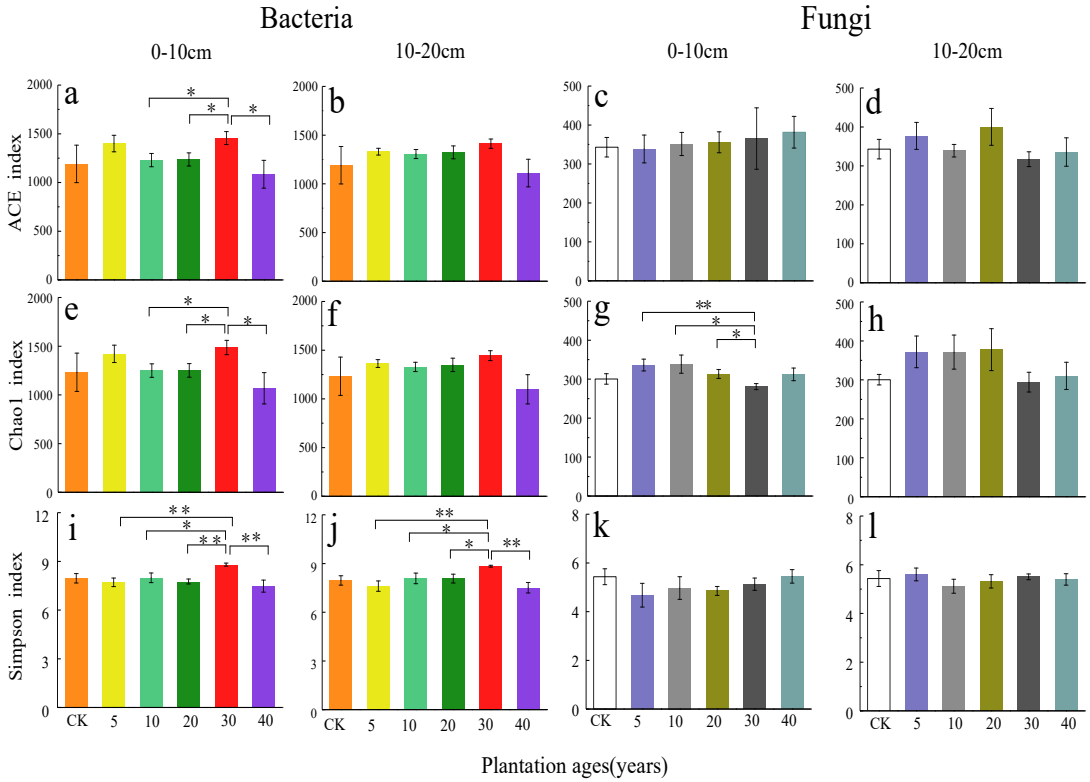
Changes in taxonomicl compositions of bacterial and fungal communities

Bacterial communities mainly consisted of Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, Gemmatimonadetes, Chloroflexi, Firmicutes and Cyanobacteria at 0-10cm (Figure 3a) and 10-20cm (Figure 3d). The relative abundances of dominant taxa Proteobacteria, Bacteroidetes and Cyanobacteria decreased after 30 years (Figure 3a, d). At the **class** level, the relative abundances of Alphaproteobacteria, Bacteroidia, and Longimicrobia decreased sharply after 30 years (Figure 3b, e). At the **genus** level, the relative abundances of Sphingomonas, Arthobacter and Pontibacter decreased after 30 years (Figure 3c, f). Similar trends were observed at both 0-10cm and 10-20cm (Figure 3).

For fungal community, Ascomycota and Basidiomycota were the dominant taxa at the **phyla** level, but the relative abundance of Ascomycota decreased during 20-40 years (Figure 4a, d). At the **class** level, the dominant taxa Sordariomycetes decreased sharply from 20-40 years, while Gammaproteobacteria increased significantly during 30-40 years (Figure 4e). At the genus level, *Aspergillus* was the dominant fungal genera during the early plantation stages (5-10 years), but *Lectera* become the dominant genera during20-40 years (Figure 4f). Similar trend was also observed at 0-10cm and 10-20cm for fungi (Figure 4).

Changes in alpha and beta diversity of soil bacterial and fungal communities

The alpha diversity of bacterial community at 0-10 cm showed hump-shaped patterns along the successional gradient, and the ACE, Chao 1 richness and Simpson diversity index at 30 years were significantly higher than other ages (Figure 6a, b, c). However, most of the alpha diversity index of fungi community did not show significant changes (Figure 6c, d, h, k, l). Only the value of Chao 1 decreased from 5 years to 30 years (Figure 3g).



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685 **Figure 6 Changes in ACE (a, b, c, d), Chao1 (e, f, g, h) and Simpson (i, j, k, l)**

686 **index of bacterial (a, b, e, f, i, j)and fungal (c, d, g, h, k, l) community in 0-10cm**

687 **(a, e, i, c, g, k) and 10-20 cm (b, f, j, d, h, l) across different successional stages of**

688 ***Haloxylon ammodendron* plantation (n = 6)**. Asterisk (*) indicates a significant

689 difference between different ages (P<0.05 from paired t tests)(*P <0.05; **P <0.01)

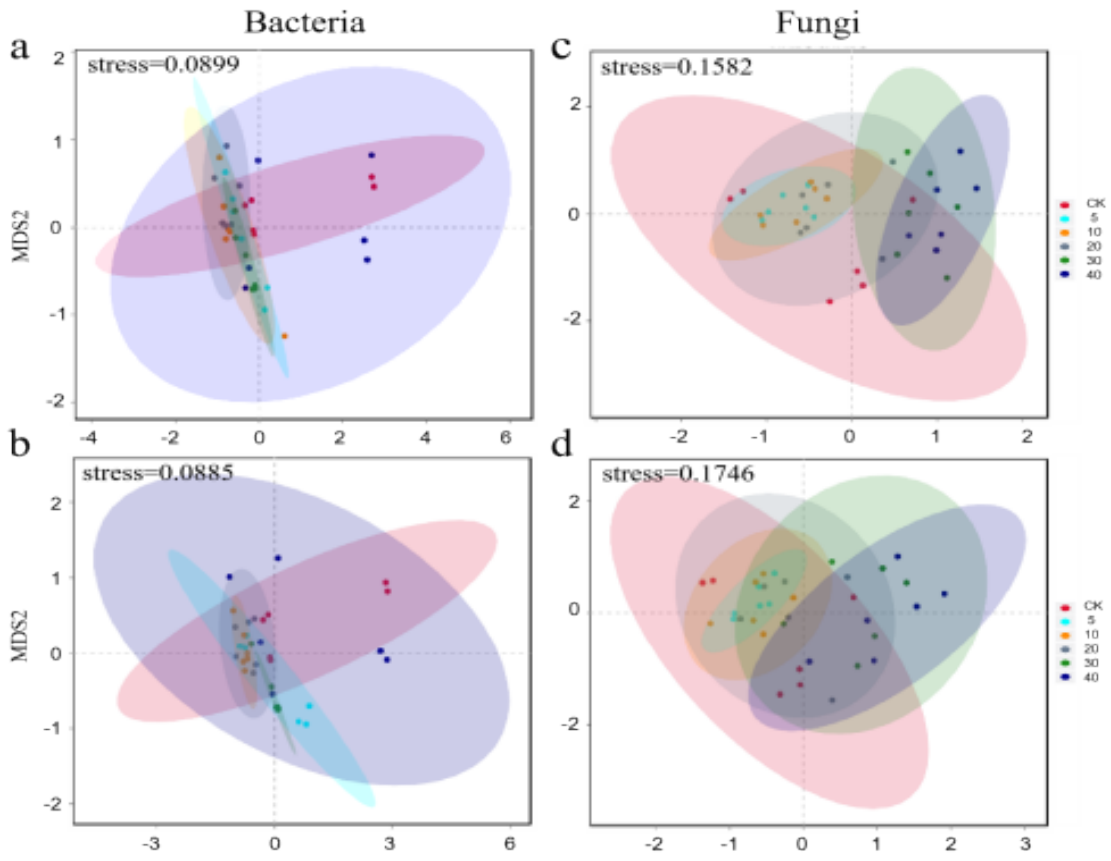

Figure 7 Non-metric multidimensional scaling (NMDS) analysis of bacterial and fungi community in the soil depths of 0–10 cm (a, c) and 10–20 cm (b, d) based on Bray–Curtis values of detected functional genes. Differences in beta-diversity among the bacteria in 0-10 (a) and 10-20cm (b) were estimated based on a Binary-Jaccard distance matrix of all soil samples.

Non-metric multidimensional scaling (NMDS) analysis revealed that the soil bacterial community of different plantation ages did not show distinct clusters in the ordination space. The fungal community showed differences between early plantation stages (5-10 years) and late stages (20-40 years) (Figure 7). What were the differences? Eloborate further how different they were.

Changes in bacterial and fungal community structures

The nodes of bacterial community networks decreased during year 10-20, and then increased during 30-40 (Figure 5c, d). Meanwhile, the edges also showed similar pattern, decreasing during year 10-20 and increasing during year 30-40. Notably, the bacterial networks were basically dominated by positive links, but the negative links sharply increased from year 30.

The nodes and edges of fungal community also decreased during year 30-40 (Figure 5k, l). Notably, the networks were basically dominated by positive links, while the negative links increased in the unique networks (Figure 5 d, e, k, l and Table 1). For example, the bacterial network of 20 year was identified as unique with decreased nodes and increased negative links (blue links). Those results collectively indicated that network structures were not preserved since 10-20 years.

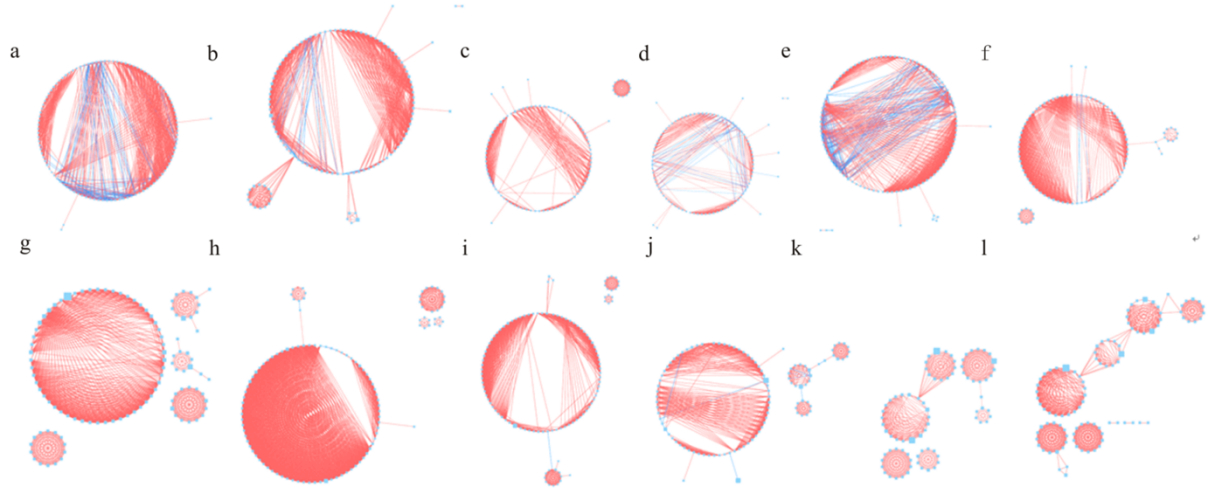

Figure 5. Succession of soil microbial co-occurrence networks across six plantation ages. a, b, c, d, e, f represent the networks of bacterial community of 0-, 5-, 10-, 20-, 30- and 40-year; g, h, i, j, k, l represent the networks of fungal community of 0-, 5-, 10-, 20-, 30- and 40-year. Large modules were shown in circular layout for the 12 networks. Red links indicate positive correlations between nodes. Blue links indicate negative correlations between nodes. If two modules linked in the

721 network, they are considered as module pairs.

722 Table 1 Topological properties of the network of co-occurrence of microbial communities along different plantation ages

		Bacteria						Fungi					
	Ages	**0**	**5**	**10**	**20**	**30**	**40**	**0**	**5**	**10**	**20**	**30**	**40**
Empirical network	nodes	107	110	95	90 ↓	101	95	106	112	101	103	81 ↓	98
	edges	823	716	464	378 ↓	793	727	842	1552	758	542	477 ↓	522
	Modularity	0.631	0.662	0.749	0.684↓	0.574	0.591	0.698	0.685	0.683	0.745	0.794	0.796
	NC	4	6	6	8	6	5	6	6	7	7	6	9
	Nd	7	9	11	10	9	12	4	9	10	8	5	13
	ND	0.145	0.119	0.104	0.094	0.157	0.163	0.151	0.250	0.116	0.103	0.147	0.110
	ASPL	3.204	3.837	4.086	3.776	3.032	4.129	2.201	2.797	3.694	3.740	2.419	5.020
	ACC	0.712	0.742	0.714	0.656	0.714	0.798	0.884	0.908	0.813	0.764	0.936	0.825
	PE (%)	89	96	97	89	84	99	100	99	99	96	100	100
	NE(%)	11	4	3	11 ↑	16 ↑	1	0	1	1	4	0	0
Random network	ASPLr	1.945 ± 0.005	2.067 ± 0.006	2.224±0.007	2.328 ± 0.008	1.913±0.006	1.905±0.005	1.924 ± 0.005	1.751 ± 0.001	2.077±0.005	2.202±0.006	2.003±0.007	2.168±0.006
	ACCr	0.145 ± 0.005	0.120 ± 0.006	0.104±0.008	0.095 ± 0.008	0.157±0.005	0.163±0.006	0.152 ± 0.005	0.250 ± 0.003	0.116±0.006	0.103±0.008	0.147±0.009	0.110±0.006

723 Abbreviations: NC, Number of communities; Nd, Network diameter; ND Network Density; ASPL, average shortest path length; ACC, average clustering coefficient; PE, Positive edges; NE, Negative edges. Subscript r indicates the

724 properties of the Erdos-Renyi random network.

725

726 **3.3 Associations between plantation age, edaphic, microbial community features**
727 **(composition, structure, and function) and shrub degradation**

728 The SEMs explained a large portion (71% to 82%) of the variation in the a
729 plant productivity along the gradient of plantation ages, indicating that it could
730 provide a strong and persuasive association between the plant productivity and
731 introduced explanatory variables which was explained mainly by soil
732 physicochemical variables and bacterial and fungal community structures which were
733 mainly represented by co-occurrence network. Among them, bacterial community
734 structure had the higher negative effects on plant productivity (86.9%) (Figure 8).

735 When the bacterial community was included in the SEM, we found that
736 bacterial structure was the most important driver of plant productivity, and directly
737 and negatively associated with the productivity. Plantation age had both direct and
738 indirect effects on plant productivity, with the positive direct effects and indirect
739 negative effects mediated by bacterial composition and structure. Soil EC had a
740 significant negative effect on plant productivity mainly through the indirect effects
741 mediated by structure (Figure 8a, d).

742 Fungal community structure also played a negative role in plant productivity
743 mainly through indirect effects mediated by leaf physiology, which declined with
744 increasing average clustering coefficient (ACC). Soil had a significant negative effect
745 on plant productivity through the direct effects and indirect effects mediated by fungal
746 community structure and leaf physiology (Figure 8b, e).

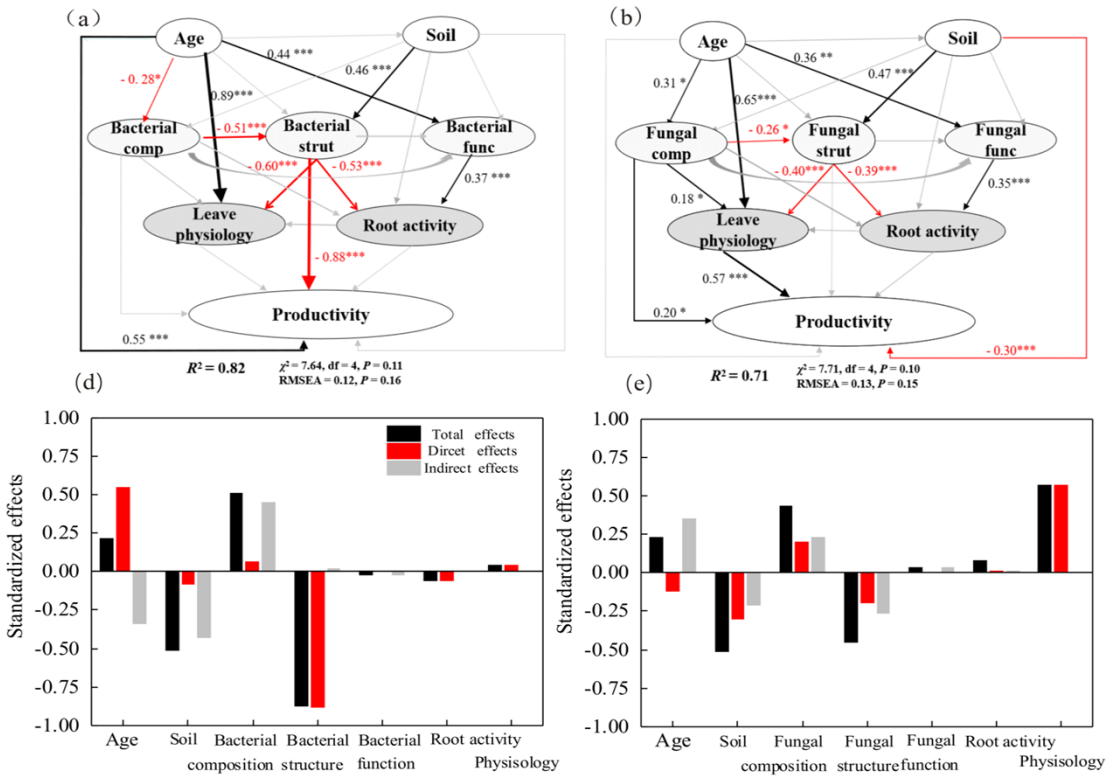

Figure 8 Structural equation models showing the direct and indirect effects of abiotic and biotic drivers on the productivity of planted *Haloxylon ammodendron* (Appendix B: Supplementary detailed results). **Above panel** involve in the direct and indirect effects of bacterial **(a)**, fungal **(b)** and the single-headed arrows indicate the hypothesized direction of causation. Solid black lines represent positive, linear associations, while red lines indicate negative, linear associations. The width of the arrows is proportional to the strength of the relationship. Ellipses represent the first component from the principal component analysis, conducted for the plantation age, soil physiochemical factors, soil microbial community composition, structure, and function, root activity and leaf physiology. **Below panel** involve in the standardized effects of bacterial **(d)**, fungal **(e)** from SEM on the productivity.

DISCUSSION

Degradation mechanism in planted *H.ammodendron*

In this study, we found that with the increased plantation age, the artificial shrub ecosystems have experienced soil desiccation and salinization, which influenced both the above-ground plant growth and the microbial community compositions and functions in soil during the late stages of 30-40 years. In arid desert ecosystems, native shrub species have evolved various physiological strategies to cope with drought stress, such as osmoregulation, dormancy and extracellular enzyme synthesis. In order to survive under lower water matric potentials, these shrubs accumulate solutes (osmolytes) to retain cell turgor. However, osmolyte accumulation could be too energetically expensive under intense soil desiccation conditions, and thus many desert shrubs may persist in a dehydrated state. In this study we found that the osmotic adjustment substance and chlorophyll content in *Haloxylon ammodendron* leaves significantly decreased from 30 to 40 years, and the morphological adjustments of *Haloxylon ammodendron* occurred to lower transpiration water consumption through reducing the biomass of leaf, branches and stems. These indicate that the nutrient deficiency in plant leaves is the main reason for the degradation of *Haloxylon ammodendron.* Not plant itself is exclusively responsible for degradation.

Changes in compositions and diversity of soil bacterial and fungal communities are not the best predictor

In arid desert ecosystems, soil autotrophs are the first to establish; then heterotrophic organisms arrived with the increased organic matter, and there is a switch in dominance from autotrophs to heterotrophic organisms as ecosystems mature. In this study, we found that there is a sharp decrease in the relative abundance of autotrophs (e.g., Proteobacteria and Cyanobacteria) as more-complex organic material enters the soil matrix in these systems and physical perturbations decrease after 20-30 years. Meanwhile, we also found that the relative abundance of most

776 abundant phylum Proteobacteria decreased during middle and late stages,
777 while Chloroflexi increased. Proteobacteria belong to copiotrophic microbes, and can
778 grow rapidly in soils with sufficient labile substrates (Zeng et al., 2017). Typically,
779 copiotrophic microbes are related to r-strategy, while oligotrophic microbes (e.g.,
780 Chloroflexi) are closely related to K- strategy (Zhou et al., 2017). The division
781 of microbial nutrition strategies could help to understand our results. The increase of
782 easily decomposable organic matter (such as glucose, root exudates) during early
783 plantation stage can stimulate the rapid increase of r-strategy bacteria, which in turn
784 caused the excitation effect to accelerate the decomposition of soil organic
785 matter (Morrissey et al., 2017). Moreover, the relative abundance of Chloroflexi,
786 typical k-strategy bacteria, has increased significantly, which further indicate that the
787 bacterial community transitioned from r-to k-strategy along the plantation age.

788 In this study, we also found that Ascomycetes (Ericoid mycorrhizal fungi) was the
789 dominant phylum, and decreased sharply during middle and late stages. Previous
790 studies have found that Ascomycetes (e.g., *Penicillium* and *Aspergillus*) are typically
791 associated with nutrient poor soils. A distinguishing feature of these Ascomycetes is
792 that they play important roles in decomposing complex organic matter, and also can
793 produce beneficial substances such as penicillin. Thus the relative abundance of
794 Ascomycetes may lead to short of nutrient to the plant (Yan et al., 2020).

795 Previous studies have shown that dynamic changes in microbial community
796 composition were caused by a variety of environmental factors and the cycling of
797 matter and nutrient (Qiao et al., 2019). At the middle plantation stage, the rapid
798 increase in clay and silt was the most predominant environmental factor that drove the
799 accumulation of soil nutrients and salts, leading to the huge changes in microbial
800 community composition (Figure S2). Additionally, the microbial community was
801 found to be significantly affected by biotic drivers (e.g., interspecific competition) and
802 other environmental factors besides soil nutrients and salts (e.g., moisture, pH). For
803 example, the competitive exclusion between fungi *Aspergillus* and *Lectera* was very
804 important in the assembly of soil microbial communities (Table S1).
805

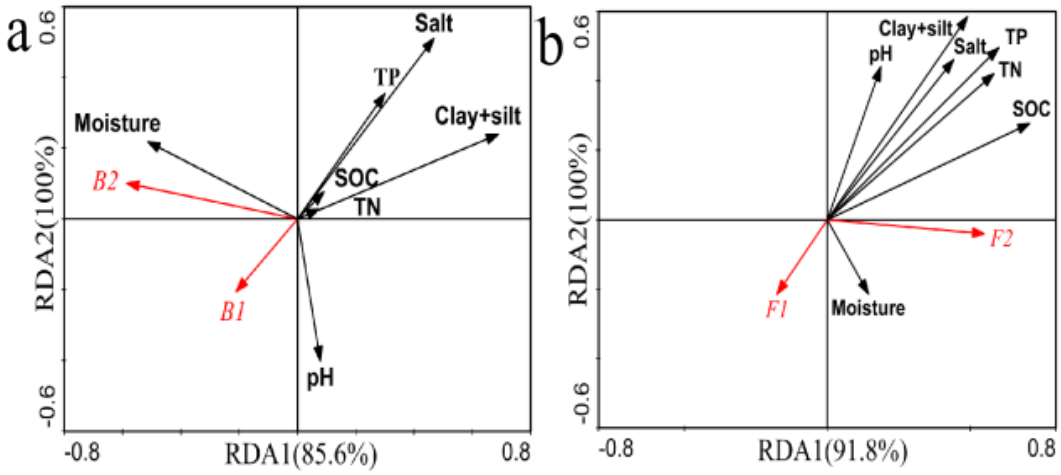

Figure S2 Redundancy analysis (RDA) plots showing the relationships between changed dominant bacterial (a) and fungal (b) taxa and soil physicochemical properties. Response variables (red arrows) are related to soil physicochemical properties (black arrows). The strength of their impact was directly proportional to the length of the arrow lines. B1, Proteobacteria_Sphingomonadaceae_Sphingomonas, B2, Proteobacteria_ Sphingomonadaceae_ unidentified; F1, Ascomycota_Aspergillaceae_ Aspergillus ; F2, Ascomycota_Plectosphaerellaceae_ Lectera

Table S1 Correlation relationship of dominant fungi in the genus level

Depths (cm)	Genus	Genus	weight	Relationship
0-10	*Lectera*	*Aspergillus*	0.3748	negative
	Lectera	*Tulostoma*	0.3819	negative
	Lectera	*Penicillium*	0.4069	negative
	Lectera	*Thielavia*	0.4371	negative
	Aspergillus	*Neocamarosporium*	0.3717	negative
	Aspergillus	*Tulostoma*	0.5854	positive
	Aspergillus	*Penicillium*	0.4577	positive
	Aspergillus	*Thielavia*	0.3557	positive
10-20	*Lectera*	*Thielavia*	0.509	negative
	Aspergillus	*Tulostoma*	0.5329	positive
	Aspergillus	*Subramaniula*	0.3599	positive
	Aspergillus	*Thielavia*	0.4589	positive
	Aspergillus	*Lectera*	0.4791	negative

Fragmentation in soil microbial community structures is a better proxy

This study found that long-term shrub plantation can significantly alter soil microbial community structures, and both of the bacterial and fungal microbial community structure had fragmented since middle stages (20-30 years), characterized by less complexity with more negative relationships. The reduced complexity and stability of microbial community structure was associated with shifts in microbial community compositions. Microbes in desert soils are often constrained due to carbon and moisture limitation, and are therefore dominated by photoautotrophs80. For instance, cyanobacteria carry out fixation of carbon and nitrogen, and are often the major primary producers where these elements form. As soil becomes drier, there is less water in soil pores, resulting in disconnected resource islands; subsequently, less SOC is decomposed. It has been proposed that microbial communities from nutrient-rich environment may form a more complex co-occurrence network, and more complex networks provide more functional redundancy and have greater community stability and resistance to environmental stresses and perturbation (Mougi and Kondoh, 2012). In this study we found a significant decrease in key decomposers during middle stages, such as Proteobacteria_Sphingomonadaceae_Sphingomonas and Ascomycota_Aspergillaceae_ Aspergillus, due to increases in soil nutrients and salts (Figure S6). These dominate taxa have the strong decomposition ability and enzyme activities, and their abundance decrease could reduce the nutrient pool. Moreover, reduced soil moisture also decreases soil nutrient availability directly by decreasing nutrient diffusion rates and indirectly by decreasing nutrient release from decomposition of soil organic matter due to constrained microbial activity. Moreover, the sharply declined nutrient availability in the soil along the successional gradient may further enhance the necessity of stronger competition (i.e., negative relationships) between functional groups of soil microbial community, which decrease the diversity in the community structure and multifunction.

Soil microbial communities are facilitators of planted shrub degradation. We found that the complexity of bacterial and fungal co-occurrence

852 networks abruptly decreased from middle stage (i.e., 10-20 years), which was earlier
853 than plant degradation at late stage (40 years). These results provide direct evidence
854 that the changes in microbial community "precede" the above-ground vegetation. As
855 such, dynamics or degradation of belowground soil microbial communities could be
856 the early warning signal to inform the aboveground or ecosystem degradation. We
857 interpret that the changes of vegetation are very slow processes especially for desert
858 ecosystems (Ransijn et al. 2015), but microbial community have the ability to evolve
859 on short ecological relevant timescales due to the relatively short generation times
860 (Lau and Lennon. 2011). Our results are in contrast to other studies which found the
861 preceding changes of aboveground vegetation with soil microbial communities as the
862 followers in restoration projects (Holtkamp et al., 2008; Harris, 2003). These past
863 these studies emphasized plant-fungi relationships (Behie et al., 2014;Semchenko et al.,
864 2018). However, in this study, the bacterial community showed higher richness and
865 thus may played a more important role in changes of vegetation than fungal
866 community. In addition, soil bacteria are able to metabolize a wider range of
867 compounds, and can provide available nutrients for plants (Zhong et al., 2018).
868 Therefore, compared with function of soil fungi, changes in bacterial community may
869 be the main reason for its preceding role of the changes in plant productivity in our
870 study.

871 Soil microbes usually play active positive roles in plant growth. These microbes
872 could improve the soil structure and improves the soil nutrients through its own
873 activities, promoting the development of plant roots and enhancing plant nutrition
874 absorption. In addition, plant could conduct physiological regulation to increase plant
875 resistance and promote plant growth under low stress environment (Figure 9). This
876 study highlighted the direct and indirect role of bacterial and fungal community
877 structure in governing the degradation process of planted shrubs. Although soil
878 moisture and pH played statistically significant roles in controlling the dynamics of
879 the plant productivity as revealed by structural equation models, the measured soil
880 variables were able to explain only minor portions of the plant productivity variations.

881 The co-occurrence networks with more negative edges affect the plant physiology and
882 productivity through affecting their important functions in soil nutrient availability
883 (Coban et al., 2022; Morriën et al., 2017; Delgado-Baquerizo et al., 2016). Firstly,
884 bacterial networks with more negative edges are likely to be associated with a less
885 functional system that could decompose and immobilize soil nutrients from the
886 organic to inorganic. Once the bacterial community structure break, these nutrients
887 will recirculate less efficiently within the plant-microbe system. The fragmentation of
888 fungal networks has a more indirectly role in regulating plant productivity by
889 affecting soil structure and soil/hydrological conditions. Because fungal hyphae can
890 enmesh and link mineral particles, which could help transport more soluble nutrients
891 from the surrounding soil matrix to plant roots (Morriën et al., 2017).

892

893 **An integrative mechanistic framework of degradation**

894 At last, we propose a conceptual framework (Figure 10): long-term shrub
895 plantation cause soil salinization and desiccation during late plantation ages, which
896 limited the migration of nutrients, reduces soil oxygen content, and often leads to
897 sharp reduction in beneficial microbes (e.g., autotrophic bacteria and ericoid
898 mycorrhizal fungi). The consequent decreased autotrophic bacteria could lead to a
899 nutrient limited environment, posing a potential risk of nutrient availability. Moreover,
900 the sharply declined nutrient availability in the soil along the successional gradient
901 may further enhance the necessity of stronger competition (i.e., negative relationships)
902 between dominant microbial groups. The shift in dominant species could lead to the
903 decrease in basic microbial community functions. For instance, in arid sand dunes
904 ecosystem, plant productivity is often limited by N availability, and the natural N
905 input into the biosphere is mostly provided by biological N fixation by bacteria
906 (Vitousek et al., 2002). Nitrogen fixing organisms or diazotrophs can exist in a
907 symbiotic relationship with their partners, which form symbiotic structures (Mus et al.,
908 2016). However, the fragmentation of bacterial community structure could destroy the
909 nutrient supply from bacterial community, which could directly lead to a decrease in

leaf photosynthetic degradation.

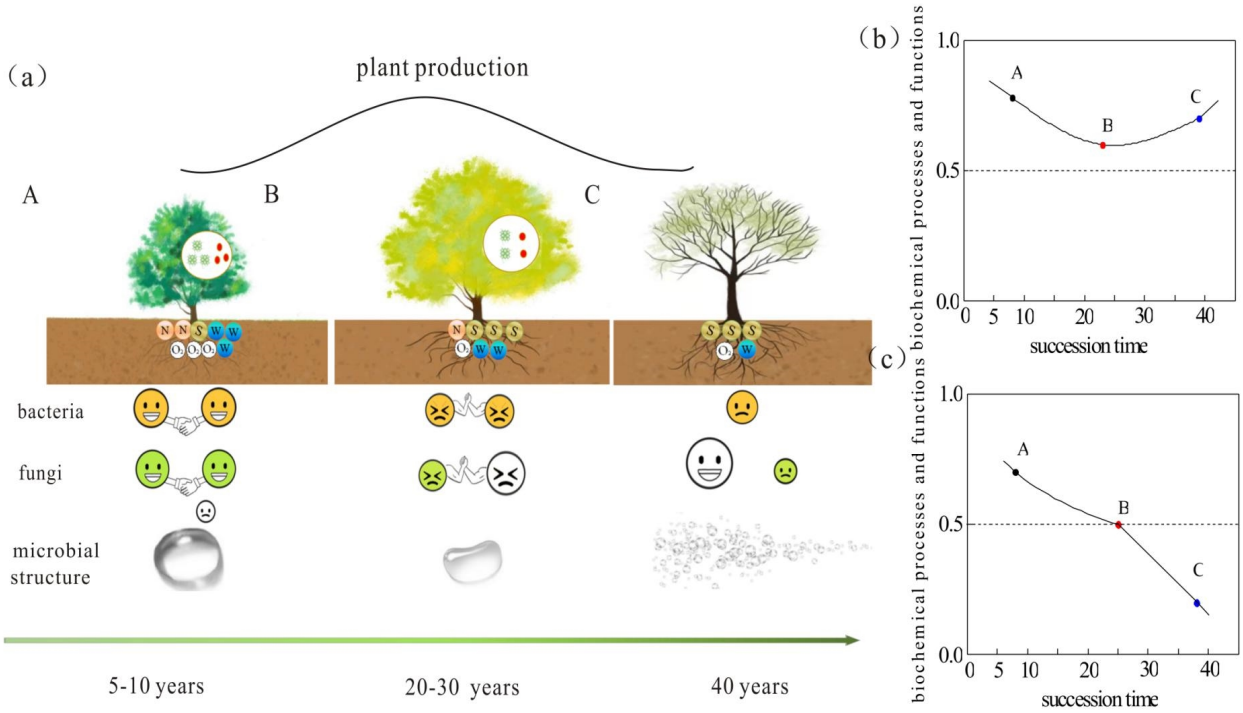

Figure 10 Conceptual diagrams (a) show that the changes in relationships among different microbial species and microbial community structure which directly lead to the changes in plant growth and productivity of different plantation ages with different soil conditions. In 5-10 years (stage A), the positive associations (positive correlations between nodes) could represent mostly cooperative behaviours such as syntrophic interactions and mutualistic interactions. By contrast, in 20-30 years (stage B), negative associations (negative correlations between nodes) could reflect mainly competition for limiting resources as well as distinctive environmental niches. After 40 years (stage C), the microbial community structure remained at a fragmented and less diversity state. Conceptual diagrams (b) show that the microbial community structure and function decreased from stage A to B, which did not break through the threshold. Thus, it could return to its original state with benign ecosystem functions when a perturbation or stress was released; (c) show that the microbial community structure and function decreased beyond a critical threshold. Thus, the microbial communities move toward the alternative state of degraded condition. At that point, the degraded state would be difficult to revert back to its initial state. Plant

928 physiology (= chlorophyll; = osmotic adjustment substances); Soil (= soil
929 water; = soil salts; = oxygen; = soil available nitrogen); A represents
930 early stage, B represents middle stage, C late stage.
931
932 **Conclusions**
933 Do you need a section to summarize? I suggesting doing so instead of your current
934 abrupt ending.

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Supporting Information Appendix

Appendix A: Soil DNA extraction, qPCR, and Miseq sequencing

Total bacterial and fungal DNA were extracted from samples using the Power Soil DNA Isolation Kit (MO BIO Laboratories) according to the manufacturer's protocol. DNA quality and quantity were assessed by the ratios of 260 nm/280 nm and 260 nm/230 nm. Then DNA was stored at -80°C until further processing. The V3-V4 region of the bacterial 16S rRNA gene and the ITS-ITS1 region of the fungal 18S rRNA gene were amplified with the common primer pair (Forward primer, 5'- ACTCCTACGGGAGGCAGCA-3'; reverse primer, 5'-GGACTACHVGGGTWTCTAAT-3' and fungal: Forward primer, 5'-CTTGGTCATTTAGAGGAAGTAA-3'; reverse primer, 5'-GCTGCGTTCTTCATCGATGC-3') combined with adapter sequences and barcode sequences. PCR amplification was performed in a total volume of 50 µl, which contained 10 µl Bµffer, 0.2 µl Q5 High-Fidelity DNA Polymerase, 10 µl High GC Enhancer, 1 µl dNTP, 10µM of each primer and 60 ng genome DNA. Thermal cycling conditions were as follows: an initial denaturation at 95 °C for 5 min, followed by 15 cycles at 95 °C for 1 min, 50 °C for 1 min and 72 °C for 1 min, with a final extension at 72 °C for 7 min. The PCR products from the first step PCR were purified through VAHTSTM DNA Clean Beads. A second round PCR was then performed in a 40µl reaction which contained 20 µl 2×Phµsion HF MM, 8 µl ddH_2O, 10µM of each primer and 10µl PCR products from the first step. Thermal cycling conditions were as follows: an initial denaturation at 98 °C for 30s, followed by 10 cycles at 98 °C for 10s, 65 °C for 30s min and 72 °C for 30s, with a final extension at 72 °C for 5 min. Finally, all PCR products were quantified by Quant-iT™ dsDNA HS Reagent and pooled together. High-throughput sequencing analysis of bacterial and fungial rRNA genes was performed on the purified, pooled sample using the Illumina Hiseq 2500 platform (2×250 paired ends) at Biomarker Technologies Corporation, Beijing, China. Sequencing analysis spliced the original data (FLASH, version 1.2.11), filtered the spliced sequence (Trimmomatic, version 0.33), and removed the chimera (UCHIME, version 8.1) to obtain a high-quality Tag sequence. Use USEARCH, version 10.0 to cluster the sequences at the level of 97% similarity, and filter OTU

963 with 0.005% of all sequences sequenced as a threshold. Based on the results of OTU analysis, the
964 classification database of 16S: Silva (http://www.arb-silva.de/) for bacteria and ITS: Unite for
965 fungi (Release 8.0, https://unite.ut.ee/) OTU performs species annotation and taxonomic analysis.
966 Unidentified sequences and non-microbial sequences were classified as unidentified. The phyla
967 and genera with>1% abundance were graphed, while phyla and genera whose abundance was less
968 than 1% were grouped as others.
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Figure 3 Relative abundance of dominant bacteria at Phylum (a, d), Class (b, e) and Genus level (c, f) in 0-10 cm (a, b, c) and 10-20 cm (c, d, e) across different successional stages of *Haloxylon ammodendron* plantation (n = 6).

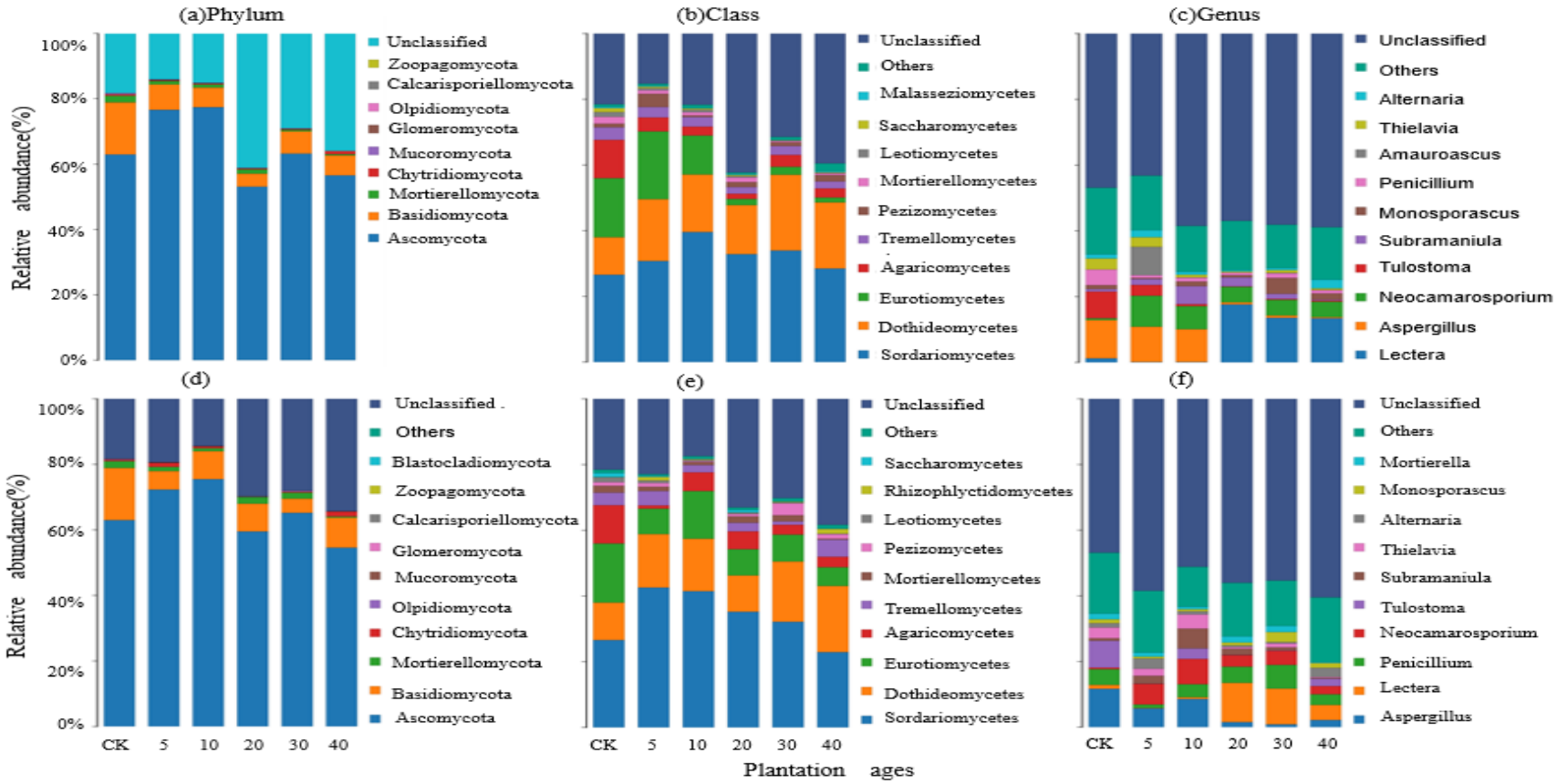

Figure 4 Relative abundance of dominant fungi at Phylum (a, d), Class (b, e) and Genus level (c, f) in 0-10 cm (a, b, c) and 10-20 cm (c, d, e) across different successional stages of *Haloxylon ammodendron* plantation (n = 6).