Effect of mulching on soil properties, microbial diversity and activities, and crop yield

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Abstract

Aims - Plastic films are used to mulch soils to control weeds, especially in organic farming. Their application leaves persistent plastic fragments in soils, with poorly understood environmental and health consequences. Plant fiber textiles (bio-canvas) are promising alternatives since they are more persistent than straw mulching and are entirely biodegradable. Hemp fibers are particularly interesting materials due to their renowned resistance, allelopathic and trophic properties for soil life. However, their effects on soil microbiota and yield remain unclear.

Methods - In a greenhouse experiment, we assessed the effect of soil mulching (bare soil control, plastic mulch, hemp straw mulching, hemp-canvas) on lettuce growth, soil climatic conditions, enzymatic activities and microbial communities (bacteria and fungi). Our experiment allowed to distinguish effects associated to mulching, being i) the homogeneity of soil covering (plastic mulch and hemp canvas) or not (control, hemp mulch), ii) the biodegradability (hemp mulch, hemp canvas) or not (control, plastic mulch), and iii) their interaction.

Results - An interaction occurred between cover homogeneity and biodegradability when using the hemp canvas, leading to higher soil relative water content, stable soil temperature, higher laccase and arylamidase activities, and different soil microbial community structures and fungal diversity, with comparable lettuce yields to that obtained with plastic mulch. Plastic cover induced higher soil temperatures, lower enzymatic activities, and different soil microbial community structures.

Conclusions - We conclude that hemp canvas secures lettuce yields, but through different mechanisms compared to plastic mulch, notably *via* a biostimulating effect on soil microbial diversity and functioning.

Introduction

The control of weeds in agricultural fields is a recurring issue in modern farming (Bagavathiannan et al. 2019). Weeds are competing with crops for resources and may host pests and phytopathogens of crops, leading to important yield losses (Chikowo et al. 2009). Chemical herbicides are applied worldwide to control broadleaf weeds in crops (Cooper and Dobson, 2007). While efficient, cheap and easy to apply for farmers (Pimentel et al. 1992), their use caused the emergence of weed resistance (Richeter et al. 2002) and the contamination of arable soils (Silva et al. 2019) and connected environmental resources (Riedo et al. 2021). Due to health and environmental concerns, there is a public demand for herbicide use reduction (Mogensen and Spliid 1995; Margni et al. 2002), thus calling for the development of environmentally-safe alternatives to control weeds. Mulching, consisting in covering a soil, is an efficient solution to retain soil humidity and prevent weed germination and growth by creating a physical barrier limiting the evaporation and restricting access to light. Hence, the main desired feature of a mulch is its capacity to homogeneously cover soil while avoiding negative environmental impacts, e.g. through degradability.

Amongst materials used, plastic mulch has become popular (Steinmetz et al. 2016), especially in vegetable farms (Beriot et al. 2021) and organic farming (Bond and Grundy, 2001). Amongst known advantages besides efficient weed control, plastic film is: i) affordable for farmers (Mugalla et al. 1996), ii) robust toward weathering thus enabling growth of perennial crops (Hablot et al. 2014), iii) involved in pest damage reduction in specific cases (Mac-Kenzie and Ducan 2001 ; Notingham and Kuhar 2016), iv) accelerating plant maturation, harvest, yields, and sometimes quality (Ricotta and Masiunas 1991; Lament 1993; Laugale et al. 2015; Zhang et al. 2017), v) increase water retention while reducing evaporation, thus improving water use efficiency for the crops when irrigation is applied below the mulch (Li and Xiao 1992; Wang et al. 2009; Zhang et al. 2017), and vi) increasing superficial soil temperature due to low albedo and air fluxes (Liu et al. 2010). Hence, most advantages of plastic mulch for agriculture are linked to a physical barrier effect instigated by the fact that it fully covers the soil homogeneously. Plastic mulching also has disadvantages such as: i) accelerated organic matter turnover and depletion in crop soils (Lee et al. 2018) which may impact greenhouse gases emissions (Nan et al. 2016; Zhao et al. 2022), ii) sorption and releasing of agrochemicals (Nerín et al. 1996) in addition to additives contained in plastic itself (Wang et al. 2019), iii) water repelling, causing increased runoff and accelerated soil erosion in some cropping systems (Rice et al. 2004), iv) costs associated to their removal, resulting in no net labor savings for farmers (Schonbeck 1999; Berger et al. 2013; Steinmetz et al. 2016), v) their disposal through incineration, generating toxic greenhouse gas (Van Ruijven & Van Vuuren, 2009), vi) the consequences of their direct incorporation into crop soils when not removed by farmers, and the uncertain biodegradability of bio-sourced plastics (Bandopadhyay et al. 2018), vii) their accumulation in crop soils (Zhou et al. 2019) and transfer to connected water compartments (Derraik, 2002), viii) their fragmentation in micro/nano-plastics and accumulation, spreading and effects in trophic levels (Beriot et al. 2021; Steinmetz et al. 2016; Bradney et al. 2019, Iqbal et al. 2020), ix) their potential risk for human health (Lehner et al. 2019) and x) their degradation recalcitrance and forecasted long-term environmental persistence (Barnes et al. 2009). Plastic mulch was also associated with contrasted effects on crop soil microbial diversity and activity (Shen et al. 2016; Wang et al. 2016), with potentially important consequences yet to be discovered considering the crucial role of microbes in crop soil functioning (Wall et al. 2012). The European trend is currently toward a global reduction of all “single-use” plastic-based products (European Parliament, 2019), hence calling for soil mulching alternatives in agriculture.

Bio-sourced mulching is a promising solution for sustainable agriculture. In particular, bio-canvas generated from rigid plant fibers by hydro-bounding (weaving by high-pressure water jets without additives) provide solid, homogeneous and degradable canvas which can advantageously replace plastic mulch to control weeds development (Tan et al. 2016). Amongst available plant materials, hemp (*Cannabis sativa* L.) is of prime interest (Schluttenhofer and Yuan, 2017) due to i) its eco-friendly and sustainable cropping properties (e.g. weed control in crop rotations; Montford and Small 1999; Poisa and Adamovics, 2010), ii) the resistance and durability of its high quality fibers (Schluttenhofer & Yuan, 2017) enabling the manufacturing of homogeneous canvas that fully cover the soil, and iii) its beneficial properties when composted and integrated in soils (Dresbøll and Magid 2005). Studies have suggested allelopathic effects of hemp fibers on soil microbes (Pudelko et al. 2014; Agnieszka et al. 2016) through the release of secondary metabolites (e.g. nonintoxicating phytocannabinoids, terpenes, and phenolic compounds, see Schluttenhofer & Yuan, 2017). While the exact mechanisms are not fully understood, trophic and ecotoxicological effects associated with the biodegradation of hemp on in-soil living organisms (Radwan et al. 2009; Nissen et al. 2010; Frassinetti et al. 2018; Scott et al. 2018) and their activity (Van der Werf et al. 1995; Winston et al. 2014; Aubin et al. 2015; Ahmad et al. 2016) is often reported. We hypothesized that hemp canvas will act as a homogeneous physical barrier restricting weeds access to light and changing to soil properties, but also will act on the soil microbiota through the release of secondary metabolites and carbon during its biodegradation. Therefore, the hemp canvas may modify abiotic and biotic soil properties, with potential subsequent effects on the development and productivity of arable crops.

We estimated the relative importance of soil mulch homogeneity and biodegradability on plant growth, soil abiotic properties and soil microbiota. We used soil mesocosms cropped with lettuces under greenhouse conditions with i) no mulching (bare soil control), ii) plastic mulch (as the current reference agricultural practice), iii) hemp straw mulch (same density as for the canvas) or iv) hemp canvas made of woven fibers. We assumed here that i) the plastic mulch and hemp canvas will have a physical effect due to their homogeneity and full covering of soil, likely on soil water content and temperature, ii) the hemp straw mulching and canvas will in addition have a nutrient and/or allelopathic effect on soil living-organisms due to the biodegradability of hemp and, iii) the hemp canvas will allow to test the potential interaction between cover homogeneity and biodegradability. The effects of soil mulching were assessed on plant growth parameters, soil temperature, soil moisture, soil microbial community compositions (bacteria and fungi) and enzymatic activities.

Materials And Methods

i. Soil and experimental unit preparation

A sandy crop soil from an organic vegetable farm (Table S1) was sampled (May 2019, Auxonne, France, 47°11'08.1"N 5°24'05.9"E) and brought to the 4PMI greenhouse platform (Plant Phenotyping Platform for Plant-Microbe Interaction, INRAE BFC Centre Dijon). The soil was dried (room temperature), sieved (2mm), and stored in a sealed box. Twenty mesocosms (17x27x37cm) containing 17 kg of dry soil were set (Fig. S1). Containers are pierced and placed on individual trays to allow sub-irrigation and drainage. The soil was rewetted to 80% of the relative water content (RWC). Four soil mulching (treatments) were applied with five mesocosm (biological replicates): i) no mulching (bare soil control); ii) plastic mulch (30µm, ~ 29 g/m², CELLOPLAST SA, Val-du-Maine, France); iii) hemp mulch with free fibers partially covering the soil surface, iv) hemp canvas fully covering the soil surface. Hemp fibers and canvas were applied at the same density (hemp density: 400g/m^{2,} Geochanvre F SA, Lézinnes, France, https://www.geochanvre.fr/). Mesocosms were randomly set on three tables in a greenhouse compartment for two weeks to stabilize. Four young lettuce seedlings (*Lactuca sativa* var. Isadora, Provence Plant SA, Tarascon, France) were transplanted in each corner of all mesocosm, by cutting the mulch if necessary (Fig. S1). Lettuces were grown four weeks (16h day light, 18°C nighttime, 22°C daytime). Watering was applied from the top everyday by generous mist-spraying above lettuces, and from the bottom once a week by sub-irrigation to reset to 80% RWC. Containers were randomized every week.

ii. Soil physical parameters

During the growth period, one mesocosm of each treatment was equipped with a probe buried ~ 10cm in the soil (SD12, CAMPBELL SCIENTIFIC L.T.D, Vincennes, France) to monitor the relative humidity and temperature (Fig. S1). Probes were connected to a custom portable data acquisition device to record data, which were extracted and analyzed with the Rgui software (R Core Team 2021). The humidity was expressed as percentage of the soil relative water content (RWC), and shown as the overall mean calculated based on the averaged records obtained every hour for each mulch treatment. For the soil temperature, since similar trends where observed between all mulch treatments for day and night temperatures, data are shown as the overall mean calculated based on the average day and average night records of each day.

iii. Lettuce yield

At harvest, lettuce shoots were collected and weighted (fresh weight of shoots) and dried (50°C, 48h). Roots were extracted, washed thoroughly and dried (50°C, 48h) to obtain the dry weight. Dry shoot weight was divided by the dry root weight to obtain the shoot-root ratio.

iv. Soil DNA extraction, amplicon preparation, sequencing and bioinformatics

At harvest, 50g of homogeneous bulk soil free from roots were sampled and stored at -20°C. Soil metagenomic DNA was extracted from 250 mg (DNeasy PowerSoil-htp 96 well DNA isolation kit, Qiagen, France). Bacterial and fungal diversity were obtained by sequencing the V3-V4 hypervariable regions of the bacterial 16S rRNA gene (small subunit of the prokaryotic ribosomal operon, Baker et al. 2003, Herlemann et al. 2011) and ITS2 region (Internal Transcribed Spacer 2 in the ribosomal operon of fungi, Ihrmark et al. 2012; White et al. 1990) via Illumina Miseq 2 x 250 bp paired-end analysis. We analyzed both the 16S rRNA and ITS2 sequences using an OTU pipeline, as previously described (Jacquiod et al. 2022). Note that despite the minor presence of Archaeal and Protozoan taxa in the 16S rRNA gene and ITS amplicon profiles, we refer to bacterial and fungal communities for simplicity reasons in the text. The list and description of sequenced samples is provided Table S2. Raw sequences were submitted to the SRA public repository (Sequence Read Archive, acceptance on-going).

v. Soil enzymatic activities

At harvest time, 500 g of homogeneous fresh soil material free from lettuce roots was sampled in the middle of each mesocosms, placed in sealed plastic bags and shipped to the Biochem-Env Platform (Versailles, France). An ISO standardized procedure was applied (ISO20130, 2018; Cheviron et al. 2022), including an estimation of the total water content of each soil sample in order to calculated enzymatic activities based on dry soil weight. The following activities were measured: xylanase, cellulase, βglucosidase for the C-cycle; phosphatase, alkaline phosphatase, phosphodiesterase for the P-cycle; arylamidase for the N-cycle; arylsulfatase for the S-cycle. Laccase activity was measured to estimate the recalcitrant organic matter degradation with an adapted protocol (Eichlerová et al. 2012). Soil respiration was used as a proxy for the global metabolic activity and monitored with MicroResp™ method (Campbell et al, 2003).

vi. Univariate statistical analysis

The effect of mulch homogeneity, biodegradability and their potential interaction were tested on all recorded variables with the two-factor model "~homogeneity*biodegradability" with the following attributes for the four treatments: Bare soil control (homogeneous effect = No; biodegradation effect = No); ii) Plastic mulch (homogeneous effect = Yes; biodegradation effect = No); iii) Hemp straw mulching (homogeneous effect = No; biodegradation effect = Yes); iv) Hemp canvas (homogeneous effect = Yes; biodegradation effect = Yes). Statistical analyses were performed with the Rgui software (R Core Team 2021). Normality was verified using the Shapiro test and the variance homogeneity Bartlett test. If normality was kept, significance was inferred from ANOVA under Tukey's Honest Significant Detection post-hoc test (HSD, package *agricolae*, de Mendiburu 2019). If normality was rejected, significance was inferred from the non-parametric Scheirer-Ray-Hare test under the Dunn post-hoc test, allowing to test interactions between two factors and estimate variability partition (Sokal & Rohlf, 1995). Data is expressed as averaged values with standard error of the mean (± SEM).

vii. Multivariate analysis of the soil microbiota

Microbiota diversity coverage was assessed with rarefactions curves (Fig. S2). Samples were normalized by random resampling (n = 17.000 for 16S rRNA gene, n = 31.000 for ITS2), as recommended (Schöler et al. 2017). Alpha diversity indices were calculated with the '*vegan'* R package (Dixon et al. 2003), using the following indices: observed richness (S), estimated Chao-1 richness, estimated ACE richness (Abundance Coverage Estimator), the Simpson reciprocal index (1/D, D = Dominance), the Shannon index (H) and the Equitability (H/ln(S)). Community beta diversity was estimated with the Bray-Curtis dissimilarity index with a PERMANOVA and distance-based redundancy analysis (db-RDA, Bray-Curtis dissimilarity ~ homogeneity*biodegradability, 10.000 group permutations, '*adonis*' and '*capscale*' functions, '*vegan*' package, Dixon et al. 2003). Discriminant OTUs whose abundance was changed by mulch homogeneity, biodegradability, and the interaction were identified from the raw unrarefied data with a Likelihood F-test under negative binomial distributions and generalized linear models (nbGLM, LFT, FDR-adjusted $P < 0.01$, Fold-Change > 2), as recommended (MacMurdies and Holmes 2014; Scholer et al. 2017). We tested the congruence between the microbial community structure and the collection of all variables measure in the study (climatic, lettuce growth, enzymatic variables) *via* a the sparse partial least square discriminant analysis (sPLS-DA) implemented in the '*mixOmics*' package (function '*block.splsda'*, Rohart et al. 2017). Two independent sPLS-DA models were generated, one for bacteria and the other for fungi.

Results

i. Soil temperature and moisture

The daily soil RWC (Fig. 1A) was the lowest with plastic mulch, and the highest with the hemp canvas. The bare soil and the soil covered with hemp mulch were intermediate. Significantly higher RWC were recorded for biodegradable mulch compared to others (w/o: 53.31 ± 0.49%, w: 56.51 ± 0.45%, variance = 26.30%, $P < 1.00E-7$, Table S3). A significant homogeneity*biodegradability interaction was detected (variance = 41.75%, $P < 1.00E-7$, Table S3), as the presence of homogeneous mulching had converse consequences depending on biodegradability: the hemp canvas had a higher soil RWC than the bare soil, whereas the plastic mulch was lower. A trend was detected for the homogeneous mulching effect on RWC, slightly higher when absent (w/o: 55.29 ± 0.53%, w: 54.54 ± 0.40%, variance = 2.10%, $P = 0.05$, Table S3), and mainly driven by the plastic mulch.

The daily soil temperature (T°C, Fig. 1B) was the lowest in bare soil, and the highest with plastic mulch (+ 1.04°C compared to the control). The hemp-based treatments were intermediate. A "homogeneity*biodegradability" interaction was detected (variance = 23.91%, $P = 7.88E-3$, Table S3), as mulch homogeneity did not change the temperature for biodegradable mulch, while significantly increasing temperature with plastic mulch. A trend was detected for the homogeneous mulching effect on soil temperature (w/o: 22.26 ± 0.16%, w: 22.73 ± 0.17%, variance = 14.65%, $P = 0.04$, Table S3), in favor of higher soil temperature when mulching was homogeneous. Biodegradability did not impact temperature ($P = 0.53$, Table S3).

ii. Lettuce yields

Lettuces fresh shoot, dry shoot and dry root weight were significantly higher with plastic mulch than with the hemp mulch, while intermediate for the bare soil and with hemp canvas (Fig. 2, A-C). Lettuces fresh and dry shoot weight were not statistically different between the hemp canvas and the plastic mulch. The shoot-root ratio was not affected (Fig. 2, D). A trend was detected for mulch biodegradability (variance = 14.65%, $P = 0.04$, Table 1), impacting fresh shoot weight by 70.90g (w/o: 306 ± 27.18g, w: 235.10 ± 28.76g), dry shoot weight by 7.8g (w/o: 36.00 ± 2.50g, w: 28.00 ± 2.82g), and dry root weight by 2.72g (w/o: 14.34 ± 1.04g, w: 11.62 ± 1.04g), mostly due to the difference between hemp mulch and plastic mulch, while no difference was observed between the control and the hemp canvas (Fig. 2). A strong effect of mulch homogeneity was detected (variance = 47.11%, $P = 2.00E-3$, Table 1) with higher yields whit homogeneous mulching than without, impacting fresh shoot weight by 125.10g (w/o: 333.10 ± 18.82g, w: 208.00 ± 24.93g), dry shoot weight by 11.8g (w/o: 26.20 ± 2.67g, w: 38 ± 1.64g), and dry root weight by 4.87g (w/o: 10.55 ± 0.76g, w: 15.42 ± 0.82g). No interaction was detected ($P = 0.92$, Table 1). Detailed analysis of lettuce traits is presented in Table S3.

Table 1

PERMANOVA results from the different datasets. The table shows respectively the PERMANOVA results from the lettuce traits (Euclidean distance), the bacterial (16S) and fungal (ITS) alpha diversity (Euclidean distance), beta diversity (Bray-Curtis dissimilarity), and soil enzymatic activities (Euclidean distance). The same model was tested for all datasets (dataset ~ cover homogeneity*cover biodegradability, 10.000 free permutations).

Dataset	**Factors**	**df**	**SOS**	**F**	**Var. (%)**	***P***	**Signif.**
Plant traits	Homogeneity	1	80453	20.0373	47.11	2.00E-3	**
	Biodegradability	1	26028	6.4824	15.24	2.60E-2	*
	Interaction	1	69	0.0173	37.61	0.92	-
	Residuals	16	64243	0.37614	-	-	
Bacterial alpha diversity	Homogeneity	1	94056	1.08	5.03	0.32	-
	Biodegradability	1	48217	0.56	2.58	0.52	-
	Interaction	1	340043	3.92	18.19	4.99E-2	*
	Residuals	16	1387356	0.74	-	-	-
Fungal alpha diversity	Homogeneity	1	483722	7.08	18.15	1.17E-2	*
	Biodegradability	1	1014806	14.85	38.07	7.99E-4	***
	Interaction	1	73587	1.08	2.76	0.32	-
	Residuals	16	1093591	0.41	-	-	-
Bacterial beta diversity	Homogeneity	1	0.1	1.51	7.04	2.91E-2	*
	Biodegradability	1	0.12	1.84	8.6	1.10E-3	**
	Interaction	1	0.13	2.05	9.56	1.00E-4	***
	Residuals	16	1.05	-	74.8	-	-
Fungal beta diversity	Homogeneity	1	0.12	1.24	6.09	4.80E-2	*
	Biodegradability	1	0.15	1.55	7.59	3.00E-4	***
	Interaction	1	0.15	1.57	7.7	2.00E-4	***

Dataset	Factors	df	SOS	F	Var. (%)	*P*	Signif.
	Residuals	16	1.52	-	78.62	-	-
Soil enzymatic profil	Homogeneity	1	113.54	9.67	30.47	9.99E-5	***
	Biodegradability	1	17.86	1.52	4.79	0.21	-
	Interaction	1	53.37	4.54	14.32	1.81E-2	*
	Residuals	16	187.91	0.5	-	-	-

iii. Soil bacterial community: Alpha diversity

Bacterial alpha diversity indices were analyses together by PERMANOVA (Table 1) and were presented separately (Fig. 3, panels A to F). A trend was detected in favor of an interaction between mulch homogeneity and biodegradability (variance = 18.19%, $P = 0.049$). Homogeneity ($P = 0.32$) and biodegradability ($P = 0.52$) had no effect. The bacterial Shannon index was significantly higher with plastic mulch than in bare soil, and intermediate in with hemp canvas or mulch (Fig. 3, E). Higher Shannon and Equitability where observed when a homogeneous mulch was applied (Fig. 3, E-F). A “homogeneity*biodegradability” interaction was detected for the estimated bacterial richness (ACE, Fig. 3, C). The detailed analysis of indices is provided in Table S3.

iv. Soil fungal community: Alpha diversity

Fungal alpha diversity indices were analyses together by PERMANOVA (Table 1) and were presented separately (Fig. 3, panels G to L). A significant effect of mulch homogeneity (variance = 18.15%, $P = 0.01$) and biodegradability (variance = 38.07%, $P = 7.99\text{E-}4$) were detected. The interaction had no effect ($P = 0.32$). Except the Simpson Reciprocal, all indices were significantly lower with hemp canvas compared to plastic mulch and also the bare soil (except the Equitability), while the hemp mulch remained intermediate (Fig. 3, G, H, I, K, L). Mulch homogeneity was significant for the observed richness, Chao-1 and ACE, with higher diversity without homogeneous mulching ($P < 0.05$, Fig. 3). Except the Simpson Reciprocal, a biodegradability effect was detected for all indices, with a decreased richness and evenness with hemp-based mulching compared to the others (Fig. 3, G, H, I, K, L). The interaction had no effect. The detailed analysis of indices is provided in Table S3.

v. Soil bacterial community analysis: Beta diversity

The constrained beta diversity model of the soil bacterial community structure was significant (variance = 25.20%, $P < 9.9\text{E-}4$, Fig. 4). Bacterial communities of bare soil were separated from other treatments (CAP1 = 12.61%), concomitantly to lower abundance of Acidobacteria and higher Actinobacteria, Firmicutes and Cyanobacteria. Soil bacterial communities with hemp canvas segregated from with plastic or hemp mulch (CAP2 = 6.83%), concomitantly to a higher abundance of Proteobacteria. Mulch homogeneity was significant (variance = 7.04%, $P = 0.03$), affecting 22 discriminant bacterial OTUs (Table S4). Most (20/22) were significantly decreased with homogeneous mulch, belonging to Proteobacteria (unclassified Erwinia: 21-folds, *Acinetobacter lwoffii*: 56-folds, unclassified Cystobacter: 23-folds), Firmicutes, Bacteroidetes (unclassified Flavobacteriaceae: 30-folds), Cyanobacteria (*Acutodesmus obliquus*: 47-folds). The remaining two were increased with homogeneous mulch: an Actinobacteria (unclassified Acidimicrobiales: 4-folds) and a Verrucomicrobia (unclassified Prosthecobacter: 9-folds). Mulch biodegradability was also significant (variance = 8.60%, $P = 1.10E-3$), affecting 33 discriminant bacterial OTUs (Table S5). Most (25/33) were significantly increased by mulch biodegradability, belonging to Proteobacteria like Enterobacteriaceae (unclassified Erwinia: 40-folds, unclassified Enterobacteriaceae: up to 34-folds, *Escherichia coli*: 4-folds), Xanthomonadaceae (*Luteimonas mephitis*: 3-folds), Sphingomonadaceae, Oxalobacteraceae, Pseudomonadaceae, Moraxellaceae (*Acinetobacter lwoffii*: 9-folds, an unclassified Acinetobacter: 72-folds), a Firmicutes (Unclassified Exiguobacterium: 10-folds) and a Verrucomicrobia (unclassified Prosthecobacter: 23-folds). The remaining height were decreased by mulch biodegradability, including Cyanobacteria (*Acutodesmus obliquus*: 29 folds), Proteobacteria (an unclassified Cystobacter: 12-folds and *Corallococcus exiguus*: 3-folds), an Actinobacteria (Unclassified Micromonosporaceae: 3-folds), a Firmicutes (Unclassified Bacillus: 4-folds). The interaction was also significant (variance = 9.56%, $P = 1.00E-4$, Table 1), affecting the abundance of 141 discriminant bacterial OTUs (Fig. S3), mostly Actinobacteria and Firmicutes OTUs whose abundance was higher in the bare soil compared to the other treatments. A Proteobacterial-driven cluster showed reinforced abundance with hemp canvas compared to the other treatments (left red box, Fig. S3). Another cluster driven by Actinobacteria was significantly enriched in the bare soil and had maintained abundances with hemp canvas, unlike with the plastic and hemp mulches (right red box, Fig. S3). The SPLs-DA revealing a strong correlation between the soil bacterial community structure and the soil and plant growth parameters ($R^2 = 0.71$, $P = 9.9E-14$, Fig. S4).

vi. Soil fungal community analysis: Beta diversity

The constrained beta diversity model of the soil fungal community structure was significant (variance = 21.38%, $P < 9.9E-4$, Fig. 4). Soil fungal communities with hemp canvas segregated from the other treatments (CAP1 = 9.48%), concomitantly to a reduction in Ascomycota and an increase in unclassified fungi abundances (Fig. 4). The second axis differentiated soil communities of the bare soil to that of the hemp mulch (CAP2 = 7.01%). Mulch homogeneity was significant (variance = 6.09%, $P = 4.80E-2$), affecting 17 discriminant ITS OTUs (Table S4). Half (8/16) were decreased by mulch homogeneity, mostly unclassified Ciliophora (up to 17-folds) and Chromista (up to 50-folds), an Ascomycota (*Penicillium kongii*: up to 64-folds) and an Olpidiomycota (*Olpidium brassicae*: 17-folds). The other half was increased by mulch homogeneity, mostly from Ascomycota (three unclassified Sordariomycetes: up to 69-folds, an unclassified Rhytismataceae: 22-folds, *Stachybotrys chartarum*: 7-folds, *Septoria cretae*: 4-folds) and Chytridiomycota. Mulching biodegradability was also significant (variance = 7.59%, $P = 3.00E-4$), affecting 17 discriminant ITS OTUs (Table S5). Most (12/17) were increased by mulch biodegradability, mostly Ascomycota (unclassified Sordariomycetes: up to 28-folds, *Phialophora* *cyclaminis*: 10-folds, *Stachybotrys chartarum*: up to 16-folds, *Penicillium kongii*: 15-folds) and Ciliophora (up to 14-folds). The remaining five were decreased by mulch biodegradability, mostly Ascomycota (unclassified Cladophialophora: 30-folds, *Septoria create*: 4-folds) and a Basidiomycota (unclassified Kondoa: 32-folds). The interaction was also significant (variance = 7.70%, $P = 2.00E-4$, Table 1), affecting 41 discriminant ITS OTUs (Fig. S5), mostly Ascomycota OTUs whose abundances were enriched in some treatments. OTUs specifically enriched by the hemp canvas were belonging to unclassified Sordariomycetes and *Stachybotrys chartarum* (red square, Fig. S5). The SPLs-DA also revealed a strong correlation between fungal community structure and the soil and plant growth parameters ($R^2 = 0.74$, $P < 2.20E-16$, Fig. S4).

vii. Soil enzymatic activities

No differences in soil respiration were observed (Fig. S6). The soil enzymatic activities involved in the carbon cycle (Fig. 5, panels A-D), the nitrogen cycle (panel E), the sulfur cycle (panel F) and the phosphate cycle (panels G) were affected by mulching. The xylanase and cellulase activities were significantly lowered with plastic mulch than in other treatments (Fig. 5, A-B). The laccase activity was significantly different in all treatments, ranking from higher to lower activity: hemp canvas > plastic mulch > bare soil > hemp mulch (Fig. 5, C). The βglucosidase activity was significantly lower with the hemp canvas and plastic mulch compared to the bare soil; the hemp mulch level being intermediate (Fig. 5, D). The arylamidase activity was significantly lower with plastic mulch compared to the bare soil and hemp canvas; the hemp mulch level being intermediate (Fig. 5, E). The arylsulfatase activity was significantly lower with plastic mulch compared to the bare soil and hemp mulch; the hemp canvas level being intermediate (Fig. 5, F). The alkaline phosphatase activity was significantly lower with plastic mulch compared to hemp canvas; the bare soil and hemp mulch were intermediate (Fig. 5, G). No differences were observed for the phosphatase and the phosphodiesterase activities (Fig. 5, H-I). The detailed analysis of enzymatic activities is presented in Table S3.

The PERMANOVA revealed a significant effect of mulch homogeneity (variance = 30.47%, $P < 9.99E-5$, Table 1),) and a significant interaction (variance = 14.32%, $P = 0.02$), but no effect of mulch biodegradability ($P = 0.21$). Mulch homogeneity affected several enzymatic activities, mostly due to the difference between plastic mulch and hemp canvas (Fig. 5, B, F). The highest laccase activities and lowest βglucosidase activities were observed with homogeneous mulching (Fig. 5, C, D). Similarly, mulch biodegradability affected several enzymatic activities, mostly due to the difference between plastic mulch and hemp canvas (Fig. 5, B, E, G, H). Significant interactions were detected: soil with plastic mulch had significantly lower xylanase, cellulase, laccase, arylamidase and alkaline phosphatase activities than those with hemp canvas (Fig. 5, A, B, E, F, G). The interaction detected for the laccase activity showed a converse trend, as mulch homogeneity led to a significant increase for the hemp canvas compared to the plastic mulch (Fig. 5, C).

Discussion

We aimed to describe the effects of plant-based canvas on lettuce growth, soil temperature and humidity, enzymatic activities and the soil microbial community structure. Our results show that the mulching treatment has significant consequences for crop yield and for soil abiotic and biotic properties. We interpreted our results by considering two main properties: (i) mulch homogeneity, which ensures a good weed control, (ii) mulch biodegradability, which prevents negative environmental impacts while feeding soil organisms. We also looked for potential interactions resulting from these two properties.

i. Effects of homogeneous covers

Mulch homogeneity was the most influential factor tested in this study. Several effects were weakly significant ($0.04 < P < 0.05$), such as the slightly changes in soil climatic parameters. While this may be explained by a physical barrier effect trapping heat that radiates from soil (Liu et al. 2010) and increasing water run-off (Rice et al. 2004), the difference between the plastic mulch and hemp canvas also played a role (see discussion section iii.). Still, mulch homogeneity was clearly beneficial for the lettuce weight, with the equally highest yields achieved with the hemp canvas and plastic mulch. The higher temperature with homogeneous mulch may explain this result. Soil temperature is known to accelerate plant growth (Wilcox and Pfeiffer 1990) and is an important climatic variable for lettuce growth (Salomez and Hofman 2007; Gruda 2008). However, it is likely that different mechanisms are at play between plastic mulch and hemp canvas (see discussion section iii.).

Mulch homogeneity had important consequences on the soil enzymatic profile, with marked effects were detected on activities related to the carbon-cycle. The βglucosidase activity (which targets labile carbon sources) was decreased, while the laccase activity (which targets recalcitrant sources) was boosted by mulch homogeneity. Temperature may explain this trend, as it is a strong predictor of the microbial activities in soils (Pietikäinen et al. 2005). Here, the higher temperature with homogeneous mulching may have enhanced microbial activity toward more accessible carbon sources. The decrease in βglucosidase activity may be due to the exhaustion of accessible soil nutrients at harvest, hence the increase of the laccase activity, denoting a shift toward recalcitrant substrates by the microbial community. Since the soil respiration was stable across treatments, this indicates that the soil activity was maintained despite these changes, concurring with the idea that the soil functioning was shifted/restructured by mulching. This functional shift due to mulch homogeneity was reflected by small, but significant changes in the soil microbial diversities and community structures. Amongst the taxa negatively impacted by mulch homogeneity, some show consistent trends, like the autotrophic Cyanobacteria *Acutodesmus obliquus* which likely decreased due to the lack of light. On the other hand, important taxa involved in C-cycling were increased by mulch homogeneity, like members from Sordariomycetes (Su et al. 2020), and *Stachybotrys chartarum* involved in recalcitrant matter decomposition *via* its laccase activity (Mander et al. 2006). Agronomically important microbial species were also affected by mulch homogeneity, like the phytopathogens *Septoria cretae* (Quaedvlieg et al. 2013) and *Olpidium brassicae* (Lot et al. 2002), as well as the pesticide removing species *Acinetobacter lwoffii* (Tao et al. 2019). To summarize, mulch homogeneity resulted in higher lettuce yields and significant changes in soil microbial diversity and activities related to the C-cycle, both likely mediated by the concomitant increase in soil temperature.

ii. Effect of mulch biodegradability

Mulch biodegradability was the second most influential factor. Mulch biodegradability had a positive effect on soil RWC and a negative effect on soil temperature, likely due to (i) a water retention effect of the hemp fibers, as reported with plant residues mulching in other systems (Tuure et al. 2021; Wang et al. 2021) and (ii) a better transfer of water from the surface to the soil due to the permeability of hemp, by opposition with plastic impermeability and the dry top soil crust observed with the bare soil. These two soil climatic parameters are known to influence each other (Al-Kayssi et al. 1990, Qiao et al. 2019): having in mind that the heat capacity of water is higher than that of air, the increase in RWC may contribute to lower soil temperature. This might explain the weak negative effect of mulch biodegradability on lettuce yields, especially with hemp mulch. The lower lettuce yields with hemp mulch may be a consequence of timing in organic matter degradation timing and N immobilization in the microbial compartment (Chen et al. 2014). A transitory disequilibrium in the C/N ratio may have occurred when hemp carbon was incorporated to the soil, as this may have favored microbial growth and nitrogen uptake at the detriment of lettuces. This is supported by the mulch biodegradability effect detected for several soil enzymatic activities across the carbon, nitrogen and phosphate cycles, being significantly higher for the cellulase, arylamidase, alkaline phosphatase and phosphatase under hemp-based mulch treatments. Finally, a negative allelopathic effect of hemp on lettuce cannot be excluded, although hemp residues are known to have beneficial effects on the yield of some crops (e.g. barley, Zou et al. 2015).

Mulch biodegradability had marked effects on soil microbial communities. Contrasted effects on microbial alpha diversity were detected, as important modification occurred for fungi while no effects were observed for bacteria. This may denote a preferential allelopathic/trophic effect of hemp on fungal diversity. In terms of community structure, mulch biodegradability clearly affected both fungal and bacterial profiles, with three-times more OTUs being enriched (37) than reduced (13) when mulching with hemp was applied. A wide diversity of bacterial OTUs where stimulated within Proteobacteria, especially from families renowned to host species involved in nutrient cycling and that are associated to beneficial effects on plants like Oxalobacteraceae (Janthinobacterium: Yin et al. 2021, Massilia: Xiao et al. 2022), Sphingomonadaceae (Kaistobacter: Ji et al. 2021), Xanthomonadaceae (*Luteimonas mephitis* and Thermomonas: Lee et al. 2022, Xie et al. 2022, Lysobacter: Xiao et al. 2022). Some of them are known for their pivotal roles in lignin decomposition in soils (Geobacter: Merino et al. 2021; Prosthecobacter: Zhu et al. 2020). Agronomically important taxa were also increased, like the pathogens from Erwinia whose abundance in soil is related to C/N ratio (Xie et al. 2022), Azoarcus members potentially involved in soil pesticide degradation (Lian et al. 2022), and Exiguobacterium members which are potential plastic degraders (Maroof et al. 2022). On the other hand, some bacterial taxa were reduced by hemp-based covers, such as members from Cystobacter, the predatory bacteria members from Corallococcus (Livingstone et al. 2018), and Cyanobacteria members.

As stated above, hemp decreased soil fungal richness and evenness, suggesting a selection effect toward specific fungal taxa. Discriminant OTUs revealed 12 taxa that were stimulated by hemp, including again unclassified Sordariomycetes and *Stachybotrys chartarum* which are involved in organic matter decomposition (Mander et al. 2006, Su et al. 2020), and also unclassified protozoans from Ciliphora. Protozoans may be stimulated by soil organic matter addition under anaerobic conditions (e.g. during soil biosolarization, Randall et al. 2020). The higher soil moisture with biodegradable mulch may induce partially anoxic conditions favoring protozoans. Biodegradable mulch also influenced the abundance of phytopathogens via the decrease of *Septoria cretae* (Quaedvlieg et al. 2013) and the increase in *Phialophora cyclaminis* (Williams, 1991), but also the decrease in members from the Basidiomycota yeast Kondoa, which were shown to be associated with increased crop yields (Stefan et al. 2021).

iii. Combined effects of mulch homogeneity and biodegradability

The interaction between mulch homogeneity and biodegradability mostly affected soil climatic variables, microbial community structures and enzymatic activities. This included soil water, as seen with the significantly diverging RWC levels between plastic mulch and hemp canvas compared to the two others modalities without mulch homogeneity. This highlights the advantage of weaving hemp fibers into a canvas, improving soil moisture. The low soil RWC with plastic mulch may be due to impermeability which has increased water runoff on the sides of the mesocosm and reduced soil RWC at the level of the probe. While soil temperature was stabilized amongst hemp treatments, the plastic mulch significantly increased it relative to the bare soil. While higher temperature was likely responsible for better lettuce growth, it likely also increased transpiration rates, which may explain the negative correlation between temperature and RWC. The higher temperature under plastic mulch could also be due to the low albedo of the black film and the insulating effect, both trapping calories in the soil. Still, the differences in soil functioning instigated by plastic mulch compared to the hemp canvas had similar end result in terms of lettuce yields.

The interaction notable effects on the soil microbiota, with very distinct bacterial and fungal assemblages observed with the hemp canvas compared to the others. This featured fungal OTUs belonging to Ascomycota with renowned activity toward the decomposition of organic matter the Sordariomycetes (Su et al. 2020), *Stachybotrys chartarum* (Mander et al. 2006), and also an Orbiliaceae, known for its nematode trapping and feeding habits (Li et al. 2006). We found two clusters of soil bacterial OTUs with remarkable abundance signatures associated to the hemp canvas. The first one is driven by Proteobacteria members, poorly noticed in the bare soil and at an intermediate level with the plastic and hemp mulches, but showing enhanced abundances with the hemp canvas. This cluster features taxa involved in soil nutrient cycling and plant beneficial effects, as Shpingomonadaceae, Xanthomondaceae, Caulobacteraceae and Sphingomonadaceae (see section ii.). The second cluster is driven by Actinobacteria members from Nocardiaceae, showing an important decrease with plastic and hemp mulch compared to the bare soil, but with maintained abundances with the hemp canvas. Soil Nocardiceae microbes are involved in organic matter decomposition (Jacquiod et al. 2013) and bioremediation (Pathom-Aree et al. 2021). This supports mulching with a homogeneous canvas made of weaved biodegradable hemp fibers instigates a possible biostimulation of the soil microbial community, respectively *via* the stimulation and the maintain of two specific sets of microbial taxa compared to their basal level in the bare soil. This steering of specific microbial groups concurs with important functional changes observed.

The soil enzymatic profile was altered by the interaction. This was often due to the lower levels recorded for the plastic mulch compared to the other treatments. This was observed for the xylanase and cellulase activities (C-cycle), both targeting intermediately complex carbon sources, and also the arylamidase (N-cycle), arylsulfatase (S-cycle) and alkaline phosphatase (P-cycle). This suggests that a nutrient depletion occurred with plastic mulch, likely due to the higher soil temperature and microbial activity, which may have provided the nutrients to sustain the better lettuce growth. The soil activity profile with the hemp canvas was often similar to that of the bare soil and the hemp mulch, with increases for the laccase and the arylamidase activities. This has to be discussed in light of the possible biostimulation of microbes induced by the hemp canvas, featuring key microbial members involved in nutrient cycling. Hence, our results also indicate that soil mulching with hemp canvas changes the soil activity and functioning. This could be due to the conjunction of effects on climatic variable (stable soil temperature and higher water level) and the carbon source (biodegradation of hemp) acting synergistically, and leading to similar lettuce yields to that of plastic mulch. Mulching with hemp canvas seems a good alternative to plastic mulch, especially towards the biostimulation effect detected on the microbial abundances and activities. The increase in tested enzymatic activities should not lead to a decrease in soil organic matter content, since respiration rates remain stable. Finally, even if lettuces grown with hemp canvas did not perfectly yield the exact same shoot biomass than with plastic mulch, a possibility could be to dye plant fiber-based canvas with dark pigments to reduce their albedo, capture more heat and increase soil temperature to improve the yields.

Abbreviations

RNA (Ribo Nucleic Acid); ITS (Internal Transcribed Spacer); ANOVA (Analysis of Variance); PERMANOVA (Permutational Analysis of Variance); OTU (Operational Taxonomic Unit).

Declarations

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Figures

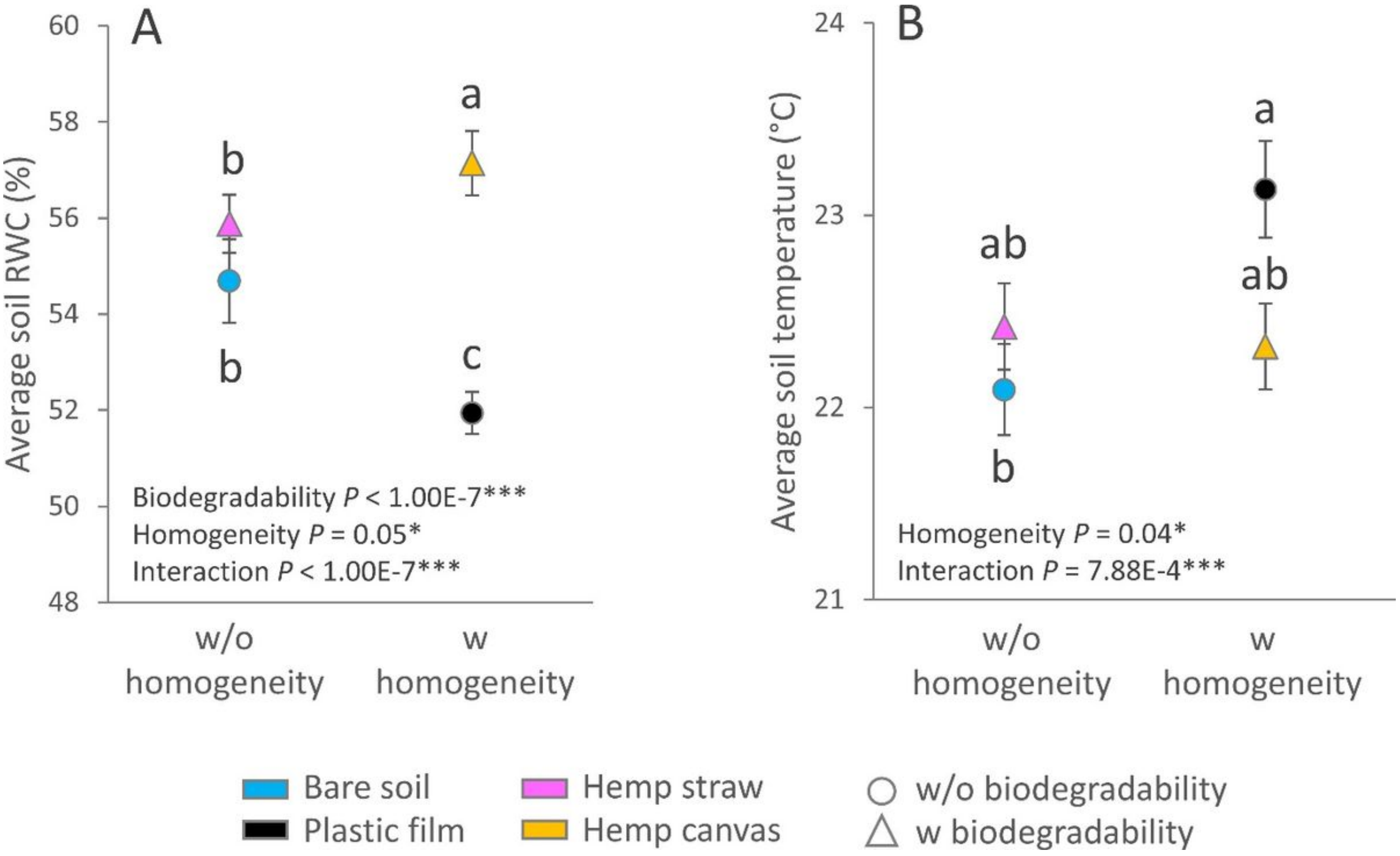

Figure 1

Soil relative water content (RWC) and temperature recorded during the experiment. (A) Average soil RWC and (B) average soil temperature recorded by the probe in the soil mesocosm of each treatment. For the soil RWC, values were calculated based on the averaged records obtained every hour (Mean ± SEM, n = 852). For the soil temperature, values were calculated based on the average day and average night records of each day (Mean ± SEM, n = 84). Statistical analysis were done using the Sheierer-Ray-Hare test, followed by post-hoc multiple testing with false discovery rate p-value adjustment (FDR, p < 0.05).* for *P*< 0.05 ; ** for *P* < 0.01 and *** for *P* < 0.001.

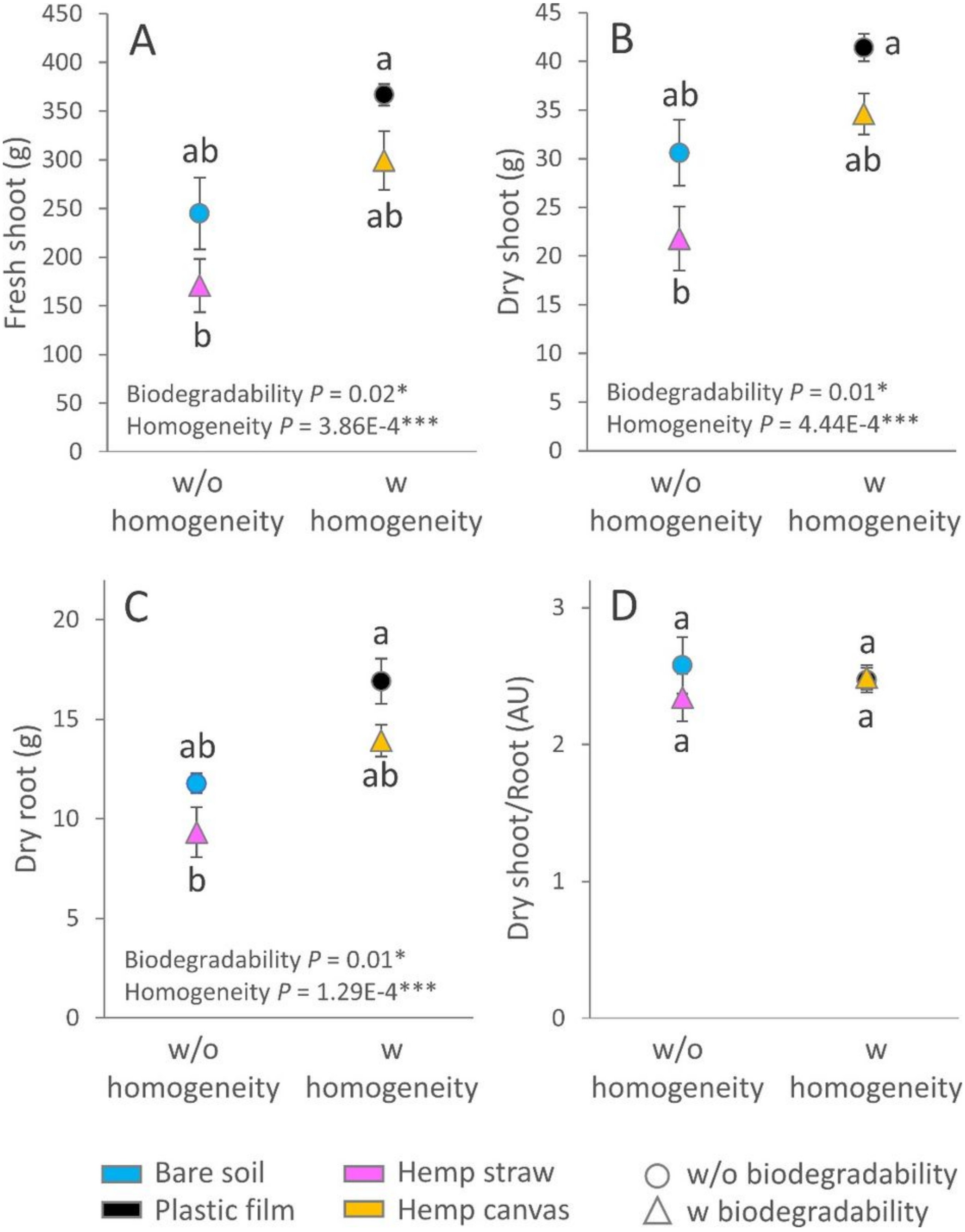

Figure 2

Lettuce growth parameters recorded under each soil cover modality at harvest. (A) The fresh shoot biomass, (B) the dry shoot biomass, (C) the dry root biomass, (D) the shoot-to-root ratio. Mean ± SEM, n = 5. Based on data normality, the significance of homogeneity and biodegradability of the covers was tested either via ANOVA (* for $P< 0.05$; ** for $P < 0.01$; *** for $P < 0.001$).

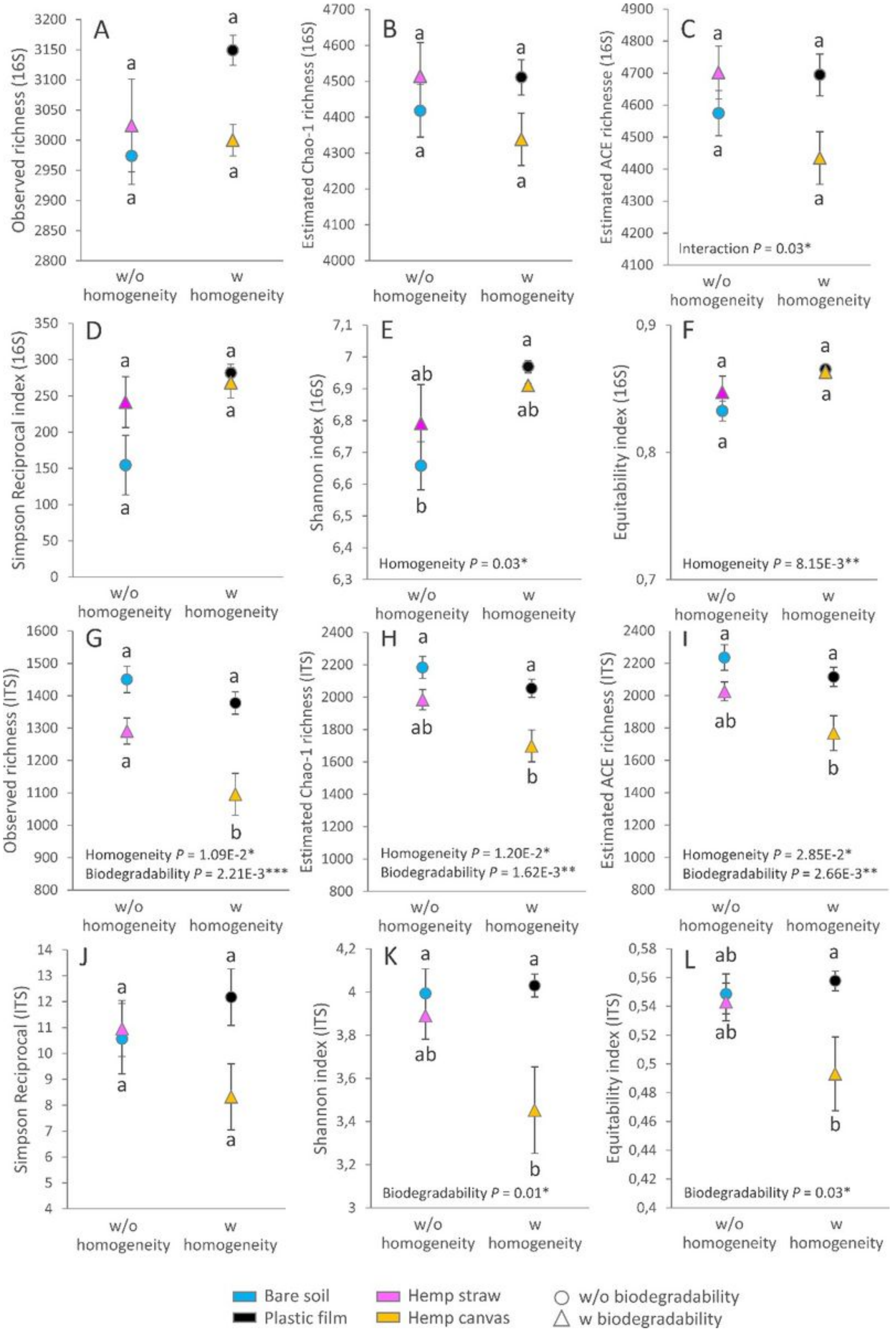

Figure 3

Alpha-diversity analysis of the soil bacterial and fungal communities. Panels A-F are showing diversity indices of the bacterial community (16S), and G-L those of the fungal community. Mean ± SEM, n = 5. Based on data normality, the significance of homogeneity and biodegradability of covers was tested either via ANOVA or Kruskal-Wallis ($P < 0.05$),followed by post-hoc multiple testing with false discovery rate p-value adjustment (FDR, $p < 0.05$). * for $P < 0.05$; ** for $P < 0.01$ and *** for $P < 0.001$.

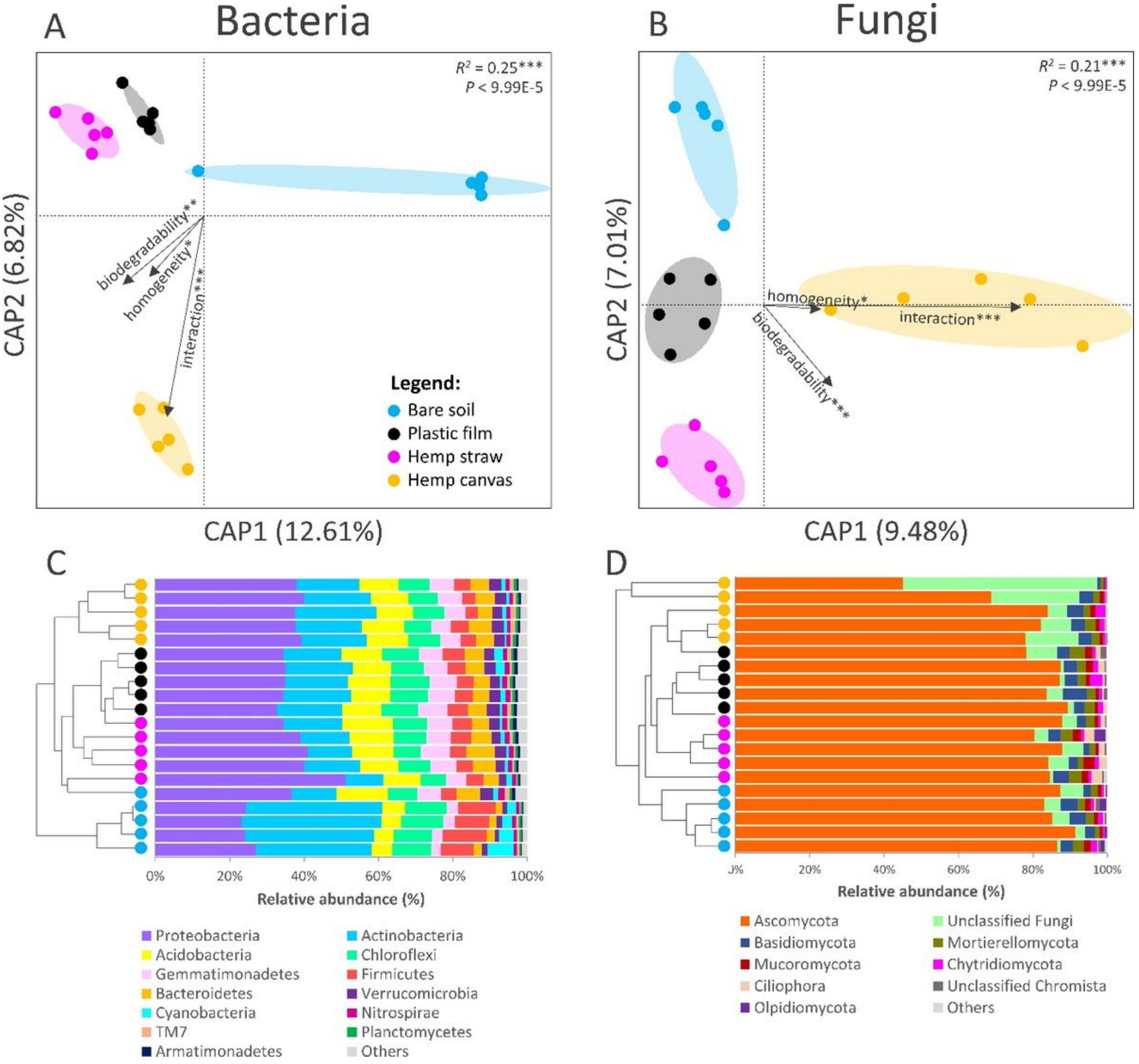

Figure 4

Bacterial and fungal soil community structures and compositions. (A) Bacterial and (B) fungal community structures estimated by distance-based redundancy analysis (db-RDA) based on the type of soil cover applied (community ~ cover homogeneity*cover biodegradability, Bray-Curtis dissimilarity). The relevance of the constrained models was tested using 10.000 free permutations. Relative abundance of (C) bacterial and (D) fungal phyla, and their grouping according to taxonomy.

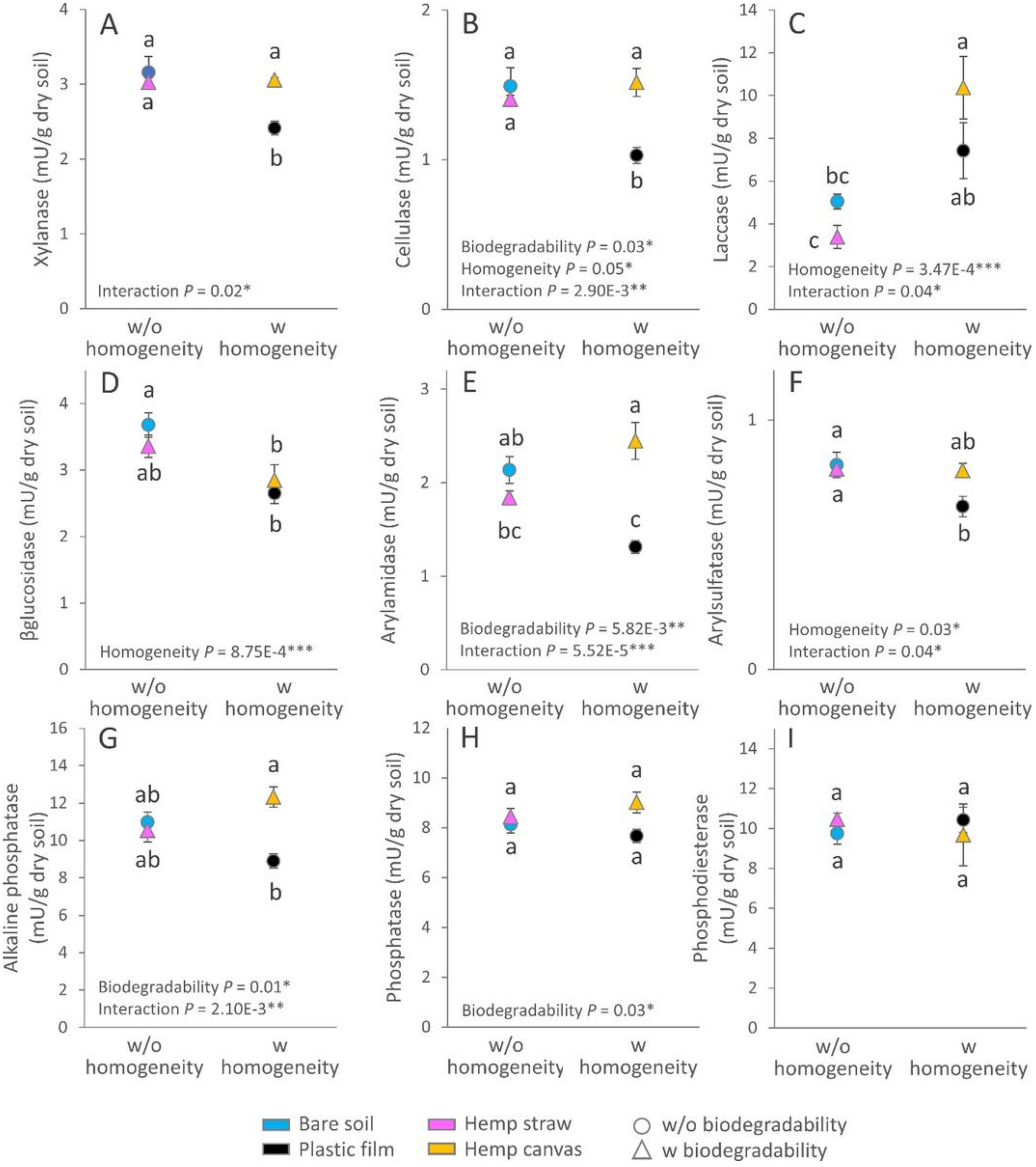

Figure 5

Soil parameters measured under the cover modalities at harvest. Figure shows the activities of (A) xylanase, (B) cellulase, (C) laccase, (D) βglucosidase, (E) arylamidase, (F) arylsulfatase, (G) alkaline phosphatase, (H) phosphatase, (I) phosphodiesterase. Enzymatic activities were all performed at standardized temperature and soil humidity. Mean ± SEM, n = 5. Based on data normality, the significance of homogeneity and biodegradability of the covers was tested either via ANOVA or the

Sheirer-Ray-Hare test ($P < 0.05$), followed by post-hoc multiple testing with false discovery rate p-value adjustment (FDR, $p < 0.05$). * for $P < 0.05$; ** for $P < 0.01$ and *** for $P < 0.001$.

Supplementary Files

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