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Effects of ant colonies on molecular characteristics of dissolved organic matter in peatland soils, Northeast China

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ABSTRACT

Increasing water discharge has resulted in rising dissolved organic matter (DOM) in draining peatlands. However, how contents and spectral characteristics of DOM changed by increasing terrestrial ants in peatland with water level decreasing, were not well revealed. In the present work, chemical and molecular composition of DOM in ant and nearby soils were characterized using UV–Visible absorption and fluorescence excitation-emission matrix (EEM) combined with parallel factor analysis (PARAFAC). Results indicated that four fluorescence components were identified, of which endogenetic fluorophores accounted for a higher proportion (79.21 ± 0.06%) of the total variability of all four. DOM from ant mound soils had lower aromaticity, humification degree, and smaller molecular size than those from control soil. The influence of microorganisms on the content and structure of DOM was crucial in the ant mound soil, whereas the effect from soil physicochemical properties was apparently more pronounced in the control soil. The study demonstrated that the endogenetic and microbial substances were closely related to the compositional variability of DOM in ant and control soils of peatlands.

1. Introduction

Peatlands are carbon-rich ecosystems that cover just 3% of the land surface but store one-third of the world's soil carbon (Jenkinson et al., 1991). Preservation of soil organic matter (SOM) from decomposition depends on the waterlogged and anaerobic soil conditions in peatlands (Blodau et al., 2004; Fletcher et al., 2004). To date, large areas of peatland have been drained for agriculture worldwide (Page and Baird, 2016), which strongly altered hydrological regimes of peatland and transformed peatlands into greenhouse gas sources from carbon sinks (Adji et al., 2014; Turetsky et al., 2011). Drainage changes not only soil physical and chemical properties (Heller et al., 2015; Tiemeyer et al., 2007), but also alters soil fauna biomes (Laiho et al., 2001; Wei et al., 2018). For instance, colonies of soil dwelling ants into peatlands have been observed in peatlands when surface water table is decreasing (Punttila et al., 2016). Ant colony establishment generates a broad spectrum of ecological effects, from altering soil texture at the fine scale to having effects on the carbon cycle at the regional scale through changes to hydrological processes and plant communities (Cammeraat et al., 2002; Farji-Brener, 2010; Folgarait, 1998; Sousa-Souto et al., 2012; Wu et al., 2010).

Previous investigations have mainly focused on elemental, plant and microbial change before and after ant colony establishment, there are very few studies on molecular changes of dissolved organic matter (DOM), which should be paid more attention (Filser et al., 2016). As the most bioavailable fraction of SOM, DOM is sensitive to bioturbation, and highly involved in a series of critical environmental and ecological processes. Consequently, DOM exerts a large impact upon the biogeochemical cycling of soil carbon and nitrogen (Cleveland et al., 2007; Kalbitz et al., 2000). Chromophoric dissolved organic matter (CDOM) is that fraction of DOM capable of absorbing ultraviolet (UV) light and the visible spectra (Zhu et al., 2018), and this UV–Visible absorption has been widely applied for characterizing the components, sources, and dynamic processes of DOM (Stedmon et al., 2003). Specifically, the UV–Vis absorbance ratio and spectral slope can be used to infer the molecular weight and aromaticity of DOM, as well as its humification degree and even origin (Li and Jin, 2017). Further, DOM also contains numerous unsaturated aliphatic chains and aromatic structures, all of which have fluorescence effects (Baker, 2002). Accordingly, fluorescence excitation-emission matrix combined with parallel factor analysis

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(EEM-PARAFAC) has become a popular tool for probing the fluorescence characteristics of DOM and exploring its environmental behavior in various terrestrial ecosystems (Mangalgiri et al., 2017; Stedmon and Bro, 2008).

Ants (e.g., *Lasius flavus*), as important social macrofauna, influence the soil organic carbon (SOC) cycling process, directly or indirectly, by burrowing channels underground or building nests (Cammeraat and Risch, 2008; Folgarait, 1998; H. Wu et al., 2013). A wide variety of studied have been performed to evaluate impacts of ant colonies on soil carbon cycle, but yield some controversial debates. Significant SOM contents were observed in soils from ant nests compared with the nearby soils (Cammeraat et al., 2002; Sousa-Souto et al., 2012; Wagner et al., 2004). However, nest-mound soil of *Lasius flavus* exhibited lower contents of SOM and DOM than the control soils (Bierbass et al., 2015). It appeared that disparate impacts of ant bioturbation on soil properties depend on ant species, habits, colony time, and ecosystems. But, there is little disagreement that ant nest soils support more microbial biomass and soil biota diversity (Debruyn and Conacher, 1990; Wagner et al., 1997). In view of drastic changes in soil conditions caused by mound-building, it is certain that molecular of SOM or DOM would be greatly altered, however, this issue remains unclear. Zhang et al. (2018) reported that molecular components of SOM varied remarkably between ant mounds and the nearby soils, of which the most obvious change was the exhausting of lignin components and hugely increasing nitrogen-containing moieties of SOM in the ant mound soils compared with the nearby soils. Yet, there has been little consensus on the influences of ant colonization on molecular components of DOM, which has hindered us from better understanding the interactions between ecological engineers and carbon cycle.

Climate change, drainage and conversion to arable farmlands currently have exacted a toll on peatlands, and caused widespread drying of peatlands (Mitsch et al., 2013). It was predicted that climate change may boost ant progressively colonizing higher latitudes and altitudes in the North Hemisphere (Bertelsmeier et al., 2015), where peatlands mainly distribute and the currently too cold climatic conditions are expected to become more suitable for ant inhabitant (Bertelsmeier et al., 2013; Hellmann et al., 2008; Walther et al., 2009). Currently, in-depth research on identifying the source and molecular structure characteristics of DOM after ant colony establishment in this study area is still scarce. Characterizing DOM's chemical and molecular composition after ant colony establishment can thus provide essential information for obtaining a complete picture of local carbon and nutrient cycles, and a better understanding of the environmental role of organic carbon in ecosystem systems.

In this study, we compared different DOM molecular features between ant mounds and surrounding soils in the Jinchuan peatland, which is experiencing decline of surface water table due to nearby anthropogenic reclamation and significant warming during the past several decades (Shi, 2019; Wang et al., 2016; Wang et al., 2017). We found drying in the Jinchuan peatlands resulted in pervasive ant colony establishment in the field survey. It is hypothesized that ant colonies alter soil chemistry and molecular features of DOM. Here, we address three questions in this study: (1) Does ant colony establishment alter soil texture in *Lasius flavus* ant mound soils relative to surrounding soils? (2) Does ant colony establishment alter molecular features of DOM? (3) How does ant colony establishment along with variation of soil properties and microbial communities affect soil DOM cycle?

2. Materials and methods

2.1. Study site and sampling

The study was conducted in the Jinchuan Peatland (42°20′56″N, 126°22′51″E) in Jilin Province, China. This peatland developed from a quaternary crater lake and is elliptical in coverage with an elevation of 613–619 m and an area of 110.8 hm^2. The mean annual temperature is 4.1 °C and the mean annual precipitation is approximately 704.2 mm. The dominant vegetation of the study site is a mix of *Carex schmidtii*, *Etulao valifolia*, *Phragmites australis* and *Thelypteris palustris* (Qin, 2020; Zhang et al., 2016).

Lasius flavus is the predominant ant species in the Jinchuan peatland, and they build ant mounds densely with an approximate diameter of 30–60 cm and about 20 cm height. In October 2020, six ant mounds inhabited by *Lasius flavus*, having a height of 15 cm and 30–50 cm in diameter were selected for soil sampling. The surrounding soil was randomly collected at least 3 m from the edge of each *Lasius flavus* mound to avoid potential effects from ant nesting activity (Fig. 1). Undisturbed samples of 0–10 cm, 10–20 cm, 20–30 cm depth were collected from the center of ant mounds and from the nearby soils. The 10–20 cm depth was labeled as the ant-active layer because most ants lived within this depth. The 0–10 cm depth was the topsoil layer where plant roots concentrated. The 20–25 cm depth was the subsoil layer without ant activities, where there was persistent water both in ant mounds and in the control soils. Soil samples were freeze-dried, passed through a 2-mm sieve and stored at 4 °C in pre-numbered amber glass bottles before chemical analyses.

2.2. Chemical analysis

Soil organic carbon (SOC) and total nitrogen (TN) contents were analyzed by dry combustion on an elemental analyzer (Elementar Analysensysteme GmbH, Langenselbold, Germany). Dissolved organic matter (DOM) was extracted by deionized water at the rate of 1:10 (w/v) and determined by a total carbon analyzer (TOC-2000, Gangdong, China). Soil water contents (SWC) were determined by oven soil to constant weight at 105 °C for 8 h. Soil pH was measured by mixing soil with deionized water at a ratio of 1:5 (w/v).

2.3. Characterizing DOM by UV–Vis and fluorescence spectrum

The UV–Vis spectrum and fluorescence spectrum were employed to characterize molecular features of DOM. Before conducting the UV measurements, as recommended, DOM contents were diluted to no more than 10 $mg \cdot L^{-1}$ with deionized water, to obtain an absorbance >0.05 and to minimize influences from the inner filtering (Huang et al., 2018). Absorption spectra were recorded from 200 nm to 800 nm and Milli-Q water was used as the blank. The scanning speed was set to 1 nm using a UV–Vis spectrophotometer (UV-6100MPC, Yuanxi Corp, Shanghai, China) equipped with a 1-cm quartz cuvette. DOM indices, ratios of absorbance ratios at different bands including SR($S_{275-295}$/$S_{350-400}$), $SUVA_{254}$, $SUVA_{260}$, A_{250}/A_{365}, and A_{253}/A_{203},were applied to characterize source, structure, and composition of DOM. Detailed information can be found in Supplementary Table S1.

DOM fluorescence was measured on a Hitachi Fluorescence spectrophotometer (F-4700, Hitachi, Tokyo, Japan). Three-dimensional scans were performed at 5 nm excitation steps from 250 to 450 nm, reading emissions at 2 nm steps from 300 to 600 nm, generating excitation-emission matrices (EEMs) for each sample. The spectrophotometer was automatically calibrated according to the Raman signal of the instrument and standardized in quinine sulfate units. Both Raman scattering and Rayleigh scattering were eliminated by subtracting the blank water samples and via manual zeroing (Hernández-Sánchez et al., 2017; Osburn et al., 2012). Four fluorescence indices were used to judge the source and humification degree of DOM. The fluorescence index (FI), as the ratio of excitation wavelength (Ex) at 370 nm and emission wavelength (Em) at 470 and 520 nm, is used to differentiate DOM sources (Cory and Mcknight, 2005). The humidification index (HIX) refers to the ratio of integral values of Em at 435–480 and 300–345 nm when Ex is 254 nm. It reflects the humification process of DOM (Zsolnay et al., 1999). The biological index (BIX) is the ratio of fluorescence intensity of Em at 380 and 430 nm when Ex is 310 nm, it can be used to characterize the autogenic property of DOM (Birdwell and Engel, 2010).

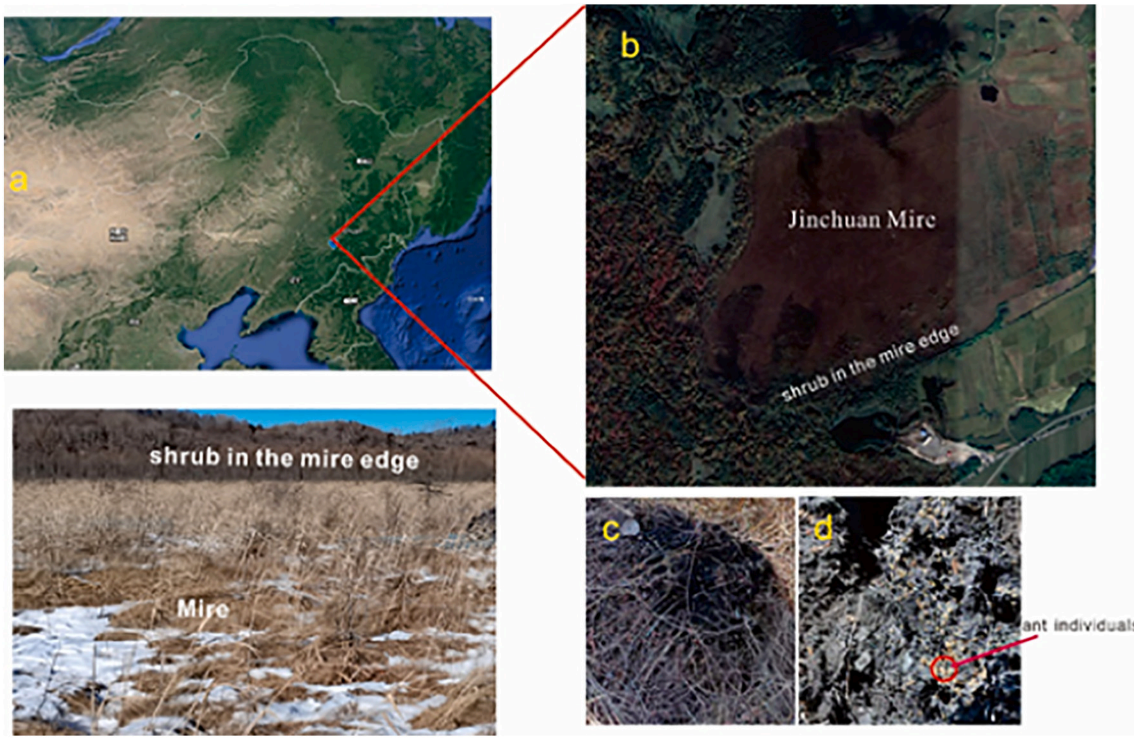

Fig. 1. Location of study area and representative ant colonies.

The freshness index (β:α) is the ratio of the maximum fluorescence intensity between the emission wavelength Em at 380 nm and the range 420–435 nm when the excitation wavelength Ex = 310 nm. It is considered as the proportion of fresh organic matter in DOC (Wilson and Xenopoulos, 2009).

2.4. Phospholipid fatty acids (PLFAs) assay

PLFA extraction was performed according to the method reported by Rajendran et al. (1992), and was determined by gas chromatography with a flame ionization detector (Agilent-6980N, Agilent Technologies, Palo Alto, America). The PLFA markers used for taxonomic microbial groups were bacteria (Bc: gram-positive bacteria (G+), gram-negative bacteria (G−), or general bacteria (B)), fungi (F), and actinomycetes (Ac). The identification, quantification, and nomenclature of PLFAs were in accordance with the method proposed by MacNaughton et al. (1999). The PLFAs, namely 12:0, 14:0, 15:0, 16:0 DMA, 17:0, 18:0, 20:0, 22:0, 23:0, and 24:0, were used as indicators of general bacteria (Willers et al., 2015), while 18:2 w6c, 18:1 w9c, and 18:3 w6c were used as indicators of fungi (Frostegård and Bååth, 1996), with 16:0 10-methyl, 17:1 w7c 10-methyl, 17:0 10-methyl, 18:1 w7c 10-methyl, and 18:0 10-methyl used as indicators of actinomycetes (Rathore et al., 2017). PLFAs specific for G- included 10:0 3OH, 16:1 w9c, 16:1 w7c, 17:1 w8c, 17:0 cyclo w7c, 18:1 w5c, 18:1 w6c, 18:1 w7c, 18:1 w8c and 19:0 cyclo w7c, 20:1 w9c, and 21:1 w3c and 22:1 w8c (Si et al., 2017; Yao et al., 2018).With respect to G+, 13:0 anteiso, 14:0 iso, 15:1 iso w6c, 15:1 iso w9c, 15:0 iso, 15:0 anteiso, 16:0 iso, 17:0 iso, 17:0 anteiso, and 18:0 iso were the biomarkers (Yao et al., 2018).

2.5. Statistical analyses

The 3D fluorescence spectra and parallel factor analysis (PARAFAC) modeling simulation were analyzed by Matlab software (version 2016b) (Shafiquzzaman et al., 2014). Differences of physicochemical property, PLFA concentration, and spectral indices between ant mounds and control soils were evaluated by one-way analysis of variance (ANOVA), respectively. Significant differences between means were established by Duncan's multiple comparison tests at $p < 0.05$ level. All data were checked to be normally distributed by Shapiro-Wilk test before the ANOVA. These were performed by the statistical package SPSS 22.0. The figures of box plots and principal components analysis (PCA) were drawn by Origin 9.0. Pearson correlation analysis was applied to investigate relationships among the spectral indexes, fluorescence components of DOM, and physicochemical properties in ant mounds and control soils. Thermal map of correlations were constructed using the 'corrplot' package in R 3.6.3. Structure equation model (SEM) was established to reveal direct and indirect effects of ant colony establishment on DOM contents and humification using the "Lavaan" package in R 3.6.3 (Jorgensen and Jak, 2020).

3. Results

3.1. Comparison of physicochemical properties between ant mounds and control soils

Ant mounds building had greatly altered soil properties. On the whole, ant mounds had significantly higher DOM contents, from 1.41 g kg^{-1} to 13.13 g kg^{-1} with an average of 4.63 g kg^{-1}, than those in the control soils, from 1.1 g kg^{-1} to 6.92 g kg^{-1} with an average of 2.45 g kg^{-1} ($F = 18.506$, $p < 0.001$). SOC, SWC and C/N in ant soils were significantly lower than those from the control soils (for SOC: $F = 25.584$, $p < 0.001$; for SWC: $F = 53.490$, $p < 0.001$; for C/N: $F = 63.336$, $p < 0.001$). The average TN content in ant soils was 20.56 g kg^{-1}, significantly higher but by a small margin than those of the controls soils ($F = 12.025$, $p = 0.001$). The pH values did not differ significantly between ant mounds and the control soils ($F = 0.559$, $p = 0.458$).

It appeared that differences of soil properties between ant mounds and the control soils depended on if the sample layers were inhabited by ants (Table 1). Ant-active layers showed disparate properties with other layers of ant mounds, characterized by higher DOM and TN (for DOM: $F = 5.781$, $p = 0.008$; for TN: $F = 3.486$, $p = 0.045$) and lower SWC, SOC and C/N (for SWC: $F = 19.028$, $p < 0.001$; for SOC: $F = 4.538$, $p = 0.020$;

Table 1
Comparison of soil physicochemical properties between ant mound and control soils in the Jinchuan peatland.

Soil layers	Site	SWC (%)	pH	DOC (g/kg)	SOC (g/kg)	DOC/SOC (%)	TN (g/kg)	C/N
Topsoil	Ant mound	$55.20 \pm 3.42^{a,\dagger}$	5.80 ± 0.21^{c}	4.43 ± 1.21^{c}	263.16 ± 21.82^{a}	1.74 ± 0.006^{ab}	20.34 ± 0.98^{b}	12.93 ± 0.77^{b}
	Control	70.77 ± 1.78^{c}	5.47 ± 0.15^{c}	3.85 ± 1.69^{c}	308.59 ± 36.35^{b}	1.25 ± 0.006^{b}	20.38 ± 0.91^{b}	15.12 ± 1.47^{ab}
Ant-active layer	Ant mound	63.42 ± 4.91^{b}	5.49 ± 0.27^{b}	5.64 ± 2.69^{cd}	265.02 ± 22.49^{a}	2.18 ± 0.012^{a}	20.79 ± 1.24^{b}	12.74 ± 0.64^{ab}
	Control	70.62 ± 1.66^{c}	5.56 ± 0.07^{d}	1.96 ± 0.71^{a}	306.90 ± 44.34^{b}	0.68 ± 0.004^{a}	18.96 ± 1.45^{c}	16.19 ± 2.10^{bc}
Subsoil	Ant mound	67.94 ± 2.67^{c}	5.51 ± 0.25^{bc}	2.24 ± 0.77^{b}	286.50 ± 40.14^{a}	0.78 ± 0.002^{b}	20.31 ± 1.63^{b}	14.05 ± 1.06^{d}
	Control	70.04 ± 2.71^{c}	5.60 ± 0.03^{a}	1.57 ± 0.53^{ab}	330.83 ± 20.60^{b}	0.47 ± 0.001^{a}	19.08 ± 0.85^{bc}	17.36 ± 1.11^{c}

Values within a column followed by the same letter are not significantly different at $p < 0.05$ (by Duncan's test). SWC, soil water content; DOC, dissolved organic carbon; SOC, soil organic carbon; TN, total nitrogen.
† Values in the table are mean ± standard deviation.

for C/N: $F = 6.332$, $p = 0.006$). The DOC/SOC ratio of the ant mounds soil always exceeded that of the control soil, and it reached the highest value in the ant-active layer ($F = 22.139$; $p < 0.001$).

3.2. Variation of soil microbial community with ant colonies establishment

The microbial community's abundance in the ant mounds and control soil was analyzed using PLFAs (Fig. 2). Total microbial abundance (TPLFAs) showed a distinct difference between ant mounds (640.00 ± 25.56 nmol g^{-1}) and the control soil (450.18 ± 39.14 nmol g^{-1}) ($F = 16.489$, $p < 0.001$). The mean value of gram-negative bacteria (G−) (192.95 nmol g^{-1}) in ant mound soils was the highest, followed by general bacteria (B) (158.01 nmol g^{-1}), and the lowest mean value in the actinomycetes (Ac) (67.86 nmol g^{-1}). Importantly, the gram-positive bacteria (G+), gram-negative bacteria (G−), fungi (F) and Ac were all significantly more abundant in ant mound soils than those in control soil (G+: $F = 11.886$, $p = 0.001$; G−: $F = 14.549$, $p < 0.001$; F: $F = 6.588$, $p = 0.013$; Ac: $F = 19.921$, $p < 0.001$).

3.3. PARAFAC components of DOM in ant mounds and control soils

Representative EEM components of the ant mounds and control soils are shown in Fig. 3. Four and two components were extracted from the EEM dataset in the ant mounds and control soil OM using PARAFAC analysis, respectively. Concerning the ant mounds soil samples, two

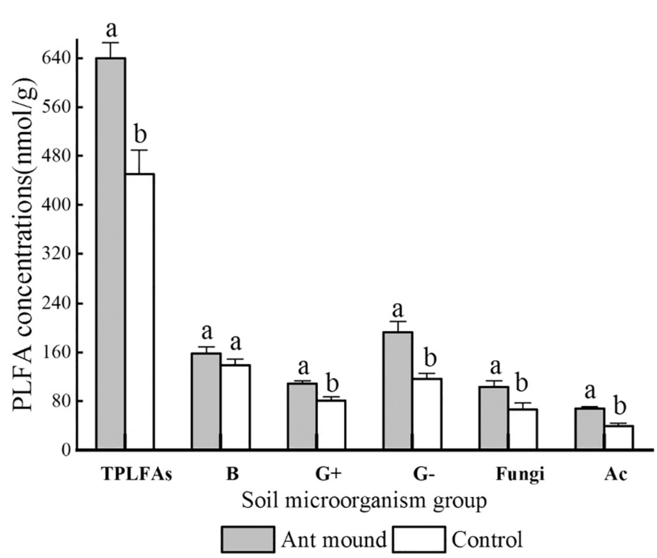

Fig. 2. PLFA biomass of soil microorganisms in the ant mounds and control soils.
TPLFAs: total microbial abundance; B: general bacteria; G+: gram-positive bacteria; G−: gram-negative bacteria; F:fungi; Ac: actinomycetes.
Different letters above a pair of bars indicate significant differences at the $p < 0.05$ level (Duncan's multiple comparison tests) between the two soil types.

humic-like substances (C1 and C2) and two protein-like substances (C3 and C4) were distinguishable (Fig. 3a). The quantitative comparison versus those previously reported in the literature is shown in Supplementary Table S2. The spectra of C1 had two clear excitation wavelengths (at 240 nm and 310 nm) with a single maximum emission wavelength (420 nm), and was categorized as microbial humic-like fluorophores, potentially produced by endogenetic substances (Mesfioui et al., 2015). The component C2 (Ex/Em = 270,360/466) was assigned to the terrestrially derived humic-like (peak D) fluorophores (He and Hur, 2015; Li et al., 2017). It was chiefly produced by the decomposition of terrestrial plants and animals (Zsolnay et al., 1999). C3 (Ex/Em = 225,280/336) was typically classified as a tryptophan-like (Peak T) component (Ohno and Bro, 2006), and the component C4(Ex/Em = 220,270/300) mainly included a tyrosine-like (peak B) fluorophores (Li et al., 2017). Both C3 and C4 were presumably derived from autochthonous microorganisms. As for the control soil OM (Fig. 3b), the C1 (Ex/Em = 256/434) belonged to UV fulvic-like (peak A) fluorescence, which represented an external source input (He and Hur, 2015). The two corresponding fluorescence peaks of the C2 (Ex/Em = 220,280/306) were fluorescence peak B (tyrosines) and peak T (tryptophans), both representing the metabolites of microorganisms (Chen et al., 2003; Wang et al., 2020). In the ant mound soil's DOM, the autogenic protein components C4 and C3 displayed the highest loadings, followed by C1 (fulvic acid), and the exogenous humic-like fluorescence C2 had the lowest loadings (Fig. 4a). The loadings of C2 (i.e., tyrosine and tryptophan) in the control soil surpassed those of C1 (fulvic acid) (Fig. 4c).

In our study, the maximum fluorescence intensity (F_{max}) of each component was used to represent its relative intensity. The respective contribution rates of these fluorescence components in each soil layer of DOM in ant mounds and controls were manifested in Fig. 4b, d. The average contribution rate of F_{C1}, F_{C2}, and F_{C3+C4} in ant mounds were 27.18 (±0.07) %, 20.79 (±0.06) %, and 52.03 (±0.12) %, respectively. Evidently, the percentage of microbial humic-like C1 (F_{C1}) was higher than terrestrial humic-like C2 (F_{C2}). Endogenetic fluorescence ($F_{C1+FC3+FC4}$) in the ant mound soil accounted for 79.21% of F_{Ctot}, and the contribution rate of which in the ant-active layer was 80.45 (±0.07) % on average. These proportion were significantly higher than those (51.53 (±0.1)%; 54.59 (±0.10%)) of the control soil. Furthermore, with greater soil depth, the proportion of endogenetic components in ant mound soils gradually increased whereas its proportion of ectogenic components decreased.

3.4. Characteristics of the fluorescence spectrum and UV–Vis absorbance parameters

Spectral indexes (FI, HIX, BIX, and β:α) are feasible ways of inferring the sources and humification degree of DOM (Fig. 5, Supplementary Table S3). In this study, FI values of ant soils was significantly higher than that of control soil ($F = 4.950$; $p = 0.03$). Most FI values of ant soils, about 73.3% of the total, exceed 1.9 and the ant-active layers had the highest FI values. The BIX ranged from 0.57 to 1.13 in ant mound soils, and BIX values of ant-active layer were significantly higher than those of control soil ($F = 4.414$; $p = 0.04$). Notably, the BIX values lower than 0.7

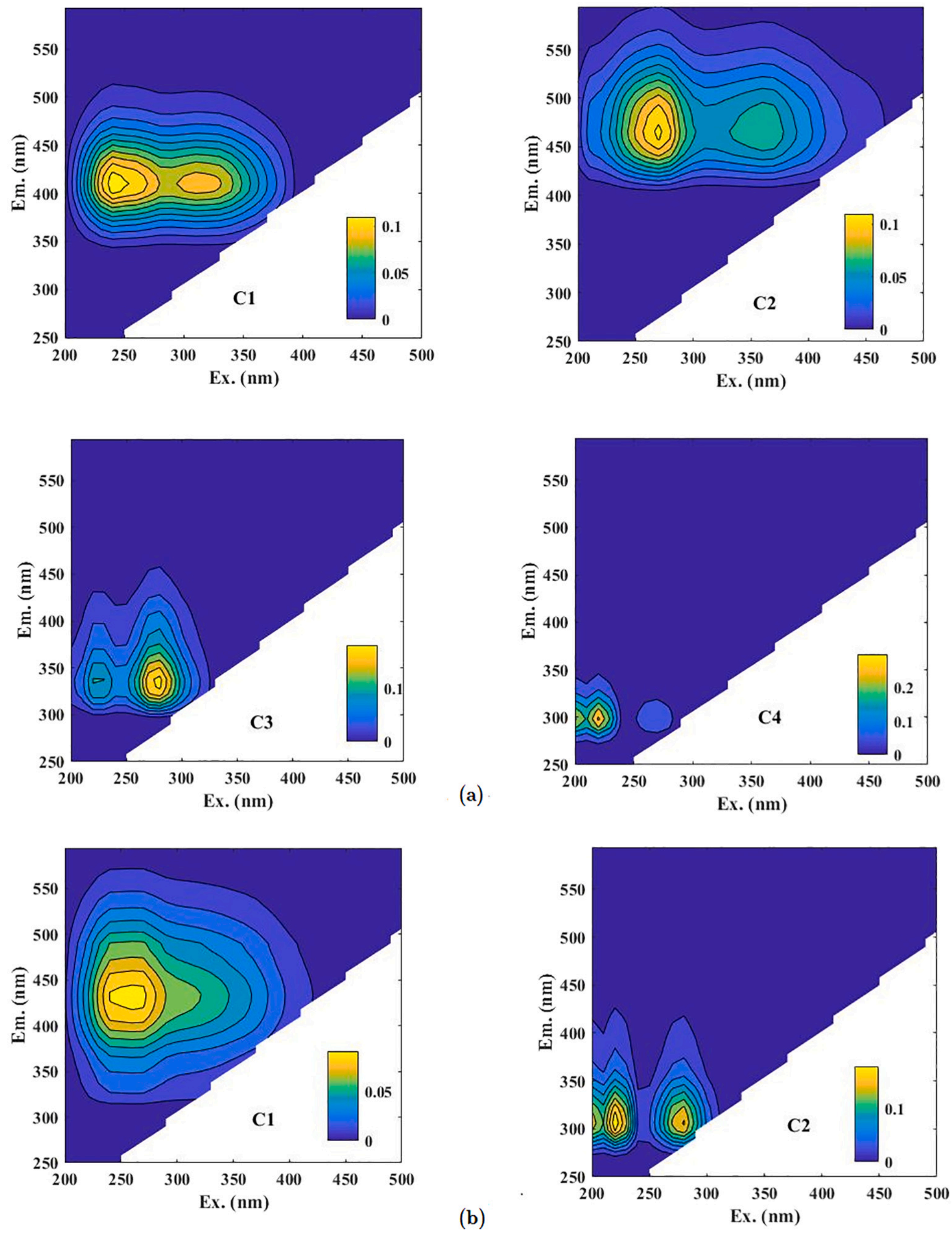

Fig. 3. Contour plots of EEM-PARAFAC components of DOM in ant mound soils (a) and control soils (b) of Jinchuan peatland. The color indicates the degree of fluorescence intensity under the excitation (Ex) and emission (Em) wavelengths.

always appeared in the topsoil. The mean HIX values were 2.64 and 1.98 in ant mounds and the control soils, respectively, and they differed significantly ($F = 9.034$; $p < 0.004$). On the whole, β:α values showed little variation with depth, either in ant mounds or in control soils.

The spectral indexes of DOM UV–Vis absorbance are shown in Fig. 6 and Supplementary Table S3. The ant soils had significantly higher SR values than those of control soils ($F = 7.306$; $p = 0.009$). The average $SUVA_{254}$ in the ant-active layer was 1.36 L mg C^{-1} m^{-1}, less than that in control soil (1.57 ± 0.52 L mg C^{-1} m^{-1}). The mean $SUVA_{254}$ of the ant-active soil layer was also lower than that of topsoils (2.00 ± 0.87 L mg C^{-1} m^{-1}) and subsoils (1.92 ± 0.67 L mg C^{-1} m^{-1}). Ant mounds had indistinctive higher $SUVA_{260}$ values than control soil ($F = 1.869$; $p = 0.177$). The A_{250}/A_{365} values of these two soil types were both greater than 3.5, and the ant soils had higher values. The ratio of A_{253}/A_{203} presented significant variations between ant mounds and control soils ($F = 5.441$, $p = 0.023$), and they were significantly higher in the ant-active layers of ant mounds ($F = 3.543$, $p = 0.043$).

3.5. Correlation analysis

DOM significantly related to SOC and C/N in the ant mound soil, while negatively related to pH in the control soil ($r = -0.369$; $p = 0.045$) (Fig. 7). The significant positive correlation was observed between C1 and C2, and likewise between C3 and C4 ($r = 0.873$, $p < 0.01$; $r = 0.48$, $p < 0.01$). There were significant negative correlations between DOM and $SUVA_{254}$ or $SUVA_{260}$ in the ant mound soils ($SUVA_{254}$: $r = -0.362$, $p = 0.05$; $SUVA_{260}$: $r = -0.422$, $p = 0.02$). The FI indices linearly related to DOM component. The best goodness-of-fit was for fulvic acid and FI ($r = 0.35$, $p < 0.01$). Furthermore, fulvic acid contained more carbonyl and hydroxyl groups, and its relative molecular mass was also small. HIX was significantly and negatively related with autochthonous components in both ant mound soils and control soils (ant mounds: $r = -0.644$, $p <$

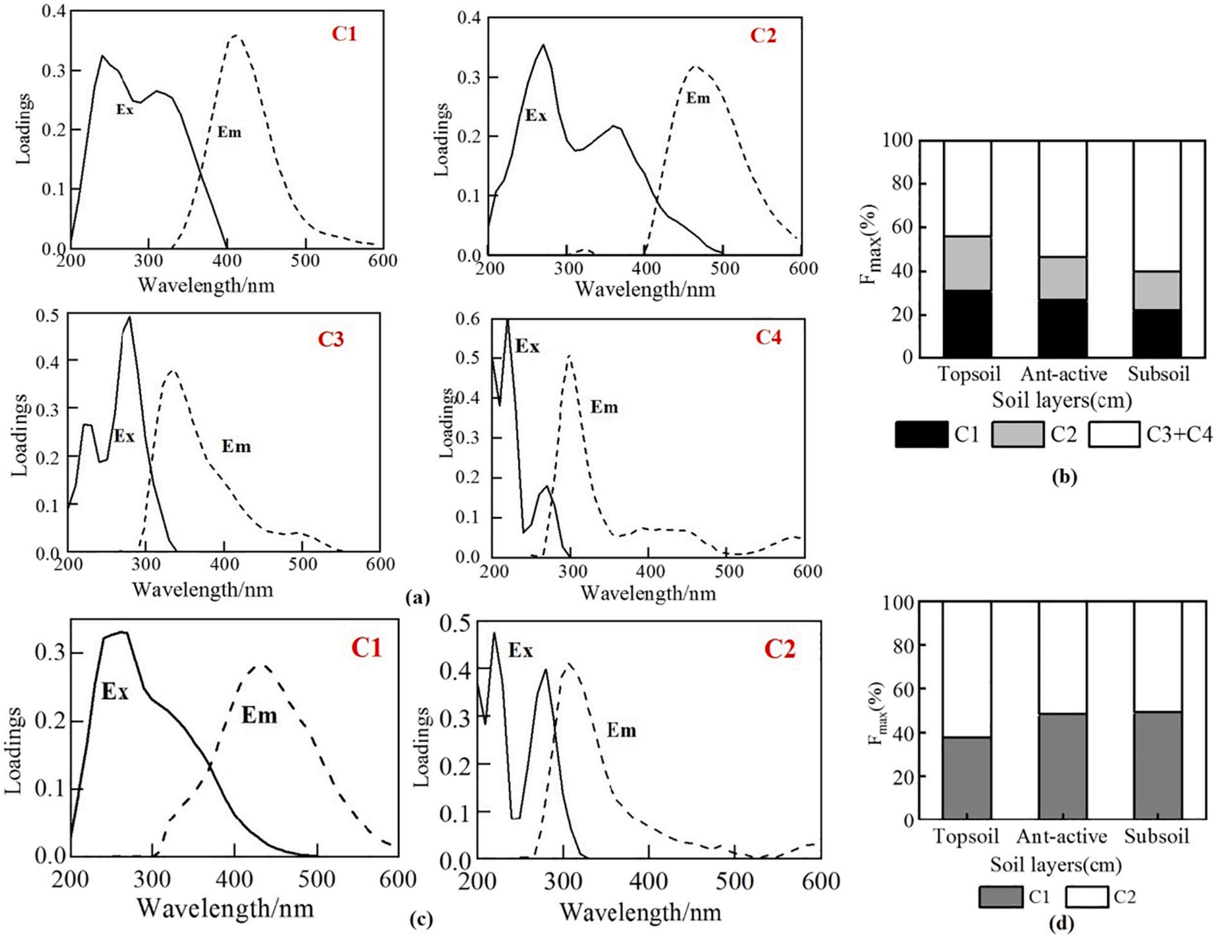

Fig. 4. Spectral loadings of identified PARAFAC components and percentage of maximum fluorescence intensity (F_{max}) of ant mound soil (a, b) and control soil (c, d).

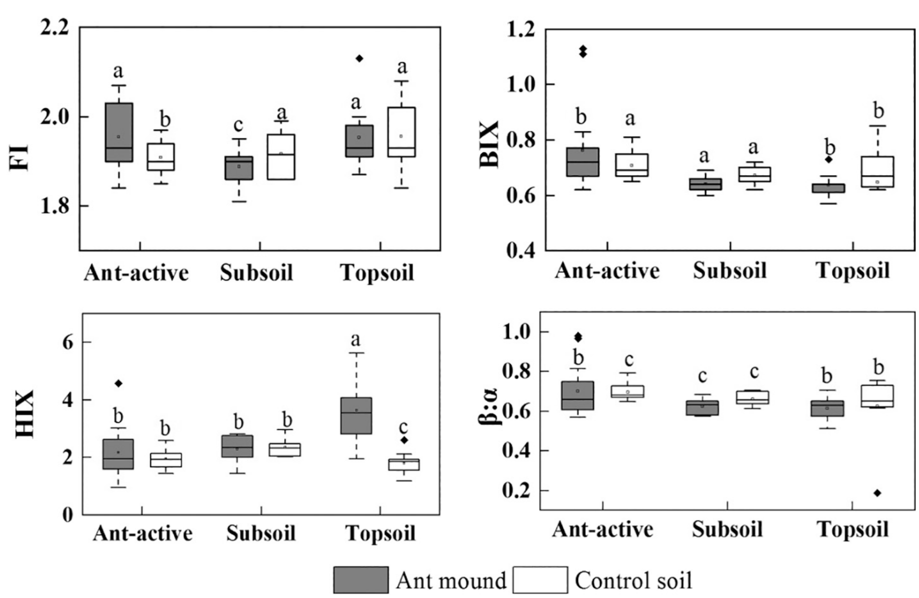

Fig. 5. Variation of fluorometric ratios in the ant mound and control soil types. FI: Fluorescence index; BIX: Biological index; HIX: Humification index; β: α: Freshness index.
Different letters represent significant differences between ant mound and control soil at the $p < 0.05$ level (Duncan's multiple comparison tests).

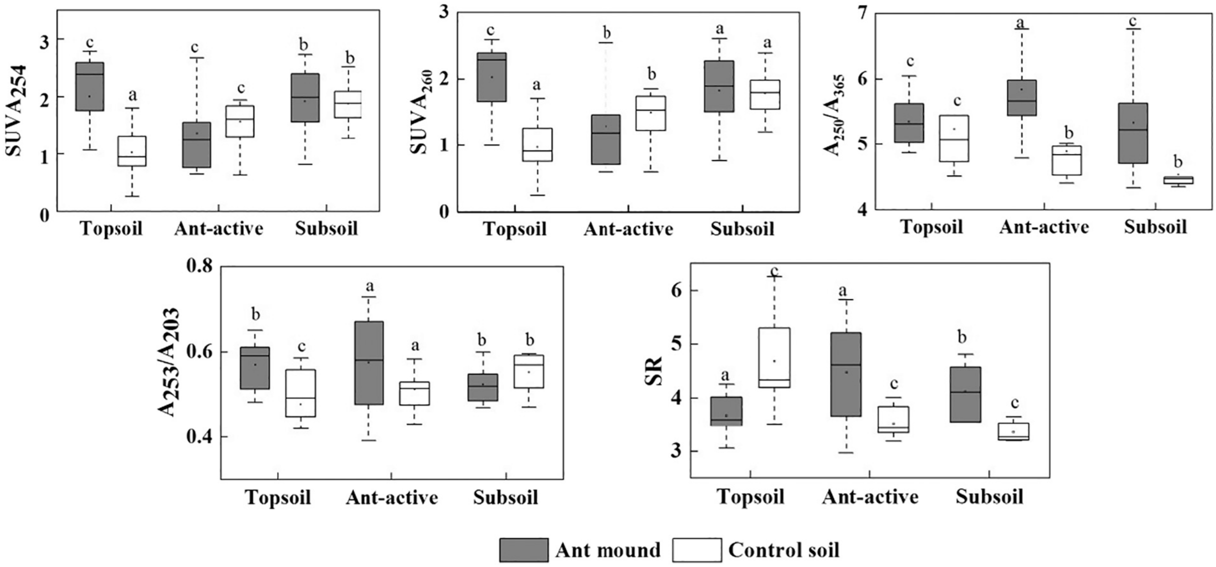

Fig. 6. Variation of UV–Vis spectral indexes in the ant mound and control soil types. The lowercase letters indicate significantly different groups. Different letters represent significant differences between ant mound and control soil at the p < 0.05 level (Duncan's multiple comparison tests).

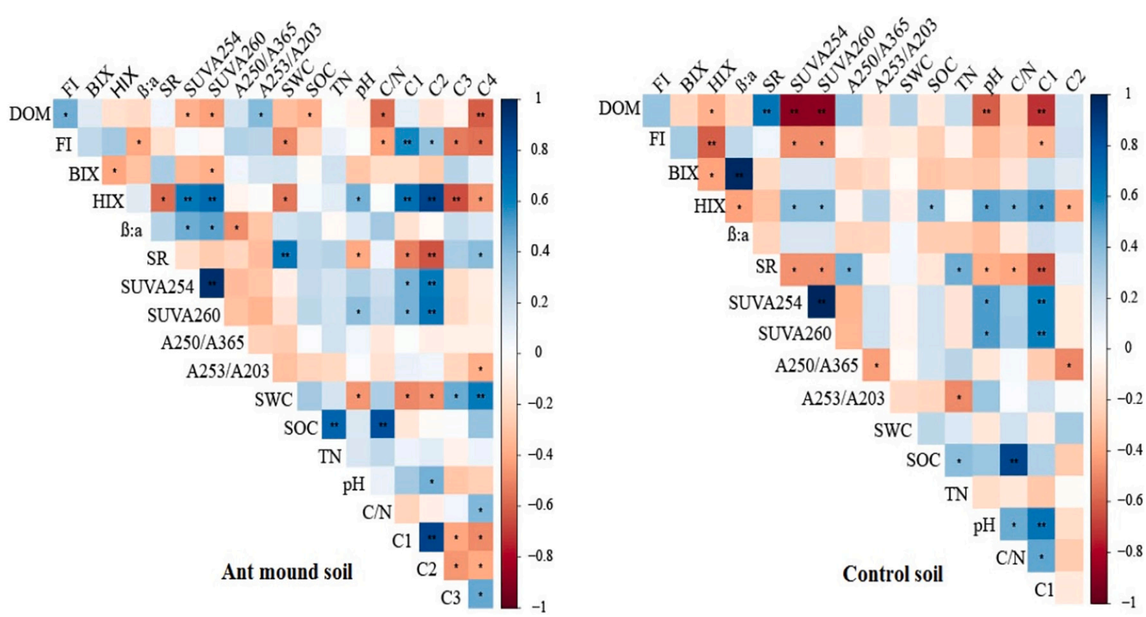

Fig. 7. Thermal map of correlations (Pearson's correlation analysis) among the spectral indexes, fluorescence components, and physicochemical properties of DOM in the ant mound and control soil types of a peatland.
* Significant at the 0.05 probability level.
**Significant at the 0.01 probability level.

0.01; control soils: $r = -0.369$, $p = 0.045$).

3.6. Multivariate analysis

Principal components analysis (PCA) was applied to investigate potential relations between DOM and environmental factors (Fig. 8). The principal component analysis (PCA) results indicated that two principal components were identified and explained 63.2% of the total variance. The first principal component (PC1, 50.1% of total variance) separated soil physicochemical properties from microbial communities. All PLFAs and microbial species had positive loadings on PC1. The second principal component (PC2, 13.1% of total variance) separated DOM compounds indicative of DOM humification processes from fresh DOM input.

Considering complex interactions among various environmental factors, the SEM model was employed to reveal mechanism affecting DOM and its humification with ant colony establishment (Fig. 9). It was clear that ant colony had significantly negative effects on soil nutrients supply ($p < 0.01$) and regulating microorganisms indirectly ($p < 0.05$). Soil nutrients promoted microbe effectively, to a significant level. Soil nutrients also showed positive effects whereas microbe presented negative effects on the humification level of DOM.

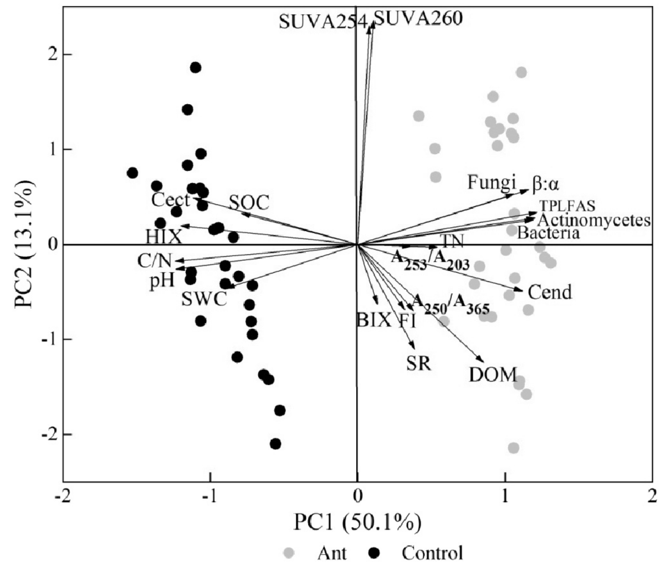

Fig. 8. Principal component analysis (PCA) of the sources of DOM in ant mound soil and control soil of a peatland. Cend denotes the endogenous fluorescence components while Cect represents the ectogenic fluorescence components.

4. Discussion

4.1. Molecular characteristics and stability of DOM

Our present work presented distinct changes of soil physicochemical properties stemming from the excavation activities by ants during mounds construction, toward to neutral soil pH and augmented nutrient content (Frouz et al., 2003). Notably, lower C/N ratios in ant mounds indicated faster SOM decomposition rate, which was similar to those reported in Domisch et al. (2008). SWC and DOM showed similar variation trend in the vertical direction of ant mounds, and this might because of the frequent alternation of wetting and drying in ant mounds. This microenvironment was conducive to SOM dissolution and the dispersion of aggregates, and thereby promoted DOM content. Zi et al. (2016) also found that the amount of SOC leached out was higher than that in other moisture environments, thereby increasing the DOM content in the waterlogged *Spartina* Wetland of Jiaozhou Bay.

The spectroscopic indices of BIX showed great variations in the range of 0.57–1.13 in ant mound soils, implying that DOM in the ant mound soil was not only derived from microbial activities (especially in the ant-active layer), but also from plant litter degradation and root exudates (especially in the topsoil) (McKnight et al., 2001; Weishaar et al., 2003). In ant mound soils, the average HIX of ant-active layer was lower than that of topsoil and subsoil, manifesting that DOM of the ant-active layer was more bioavailable and easily utilized by microorganisms. DOM of topsoils in ant mounds was characterized by high $SUVA_{254}$, HIX and low BIX, which commonly were proxy of high aromaticity and humification degree that stems from plant-derived DOM inputs (Fellman et al., 2010). The values of $SUVA_{254}$ in the topsoil and subsoil of anthill was higher than those in control soil. This is likely due to plant-derived DOM, particularly aromatic-enriched components, which were still preserved after the biodegradation processes in topsoil (Wieder et al., 2008). The DOM in the ant-active layer of ant mounds, with FI > 1.9 and SR > 1, was autochthonous, and its humification degree was weak (HIX < 4). Furthermore, the ant-active layer had the highest β:α value. These results demonstrated that recently generated endogenesis was a crucial factor affecting DOM after ant colony establishment (Lu et al., 2015).

High A_{250}/A_{365} and SR values were indicative of low-molecular-weight DOM contributions from microbial sources. There were more DOM components with high molecular weights (mainly humic acid) in the control soil, implying more terrestrial input of DOM substances. High positive relationships between SR and fluorescence intensity of the endogenetic component supported that the protein-like components had more pronounced effect on molecular weight of DOM than that of humic-like components in ant mounds (Fig. 7). Compared with control soils, ant colony establishment accelerates autochthonous complex macromolecular DOM degradation into low-molecular-weight fractions that consist of few aromatic compounds or those with a conjugated, unsaturated double-bond structure (Murphy et al., 2011). Notably, A_{253}/A_{203} values of the ant-active layer were higher than those of the topsoil and subsoil. A probable explanation was that the establishment of ant colonies decreased the amount of aliphatic chains in the substituent of benzene ring compounds, whereas increased the carbonyl, carboxyl, ester, and other substituent, this hypothesis was also verified by appearance of more aromatic functional groups, carbohydrates, and polysaccharides in ant mounds (Weishaar et al., 2003).

Fluorescence spectral analysis differentiated DOM into terrestrial and biological sources (Miller and McKnight, 2010). The humus-like

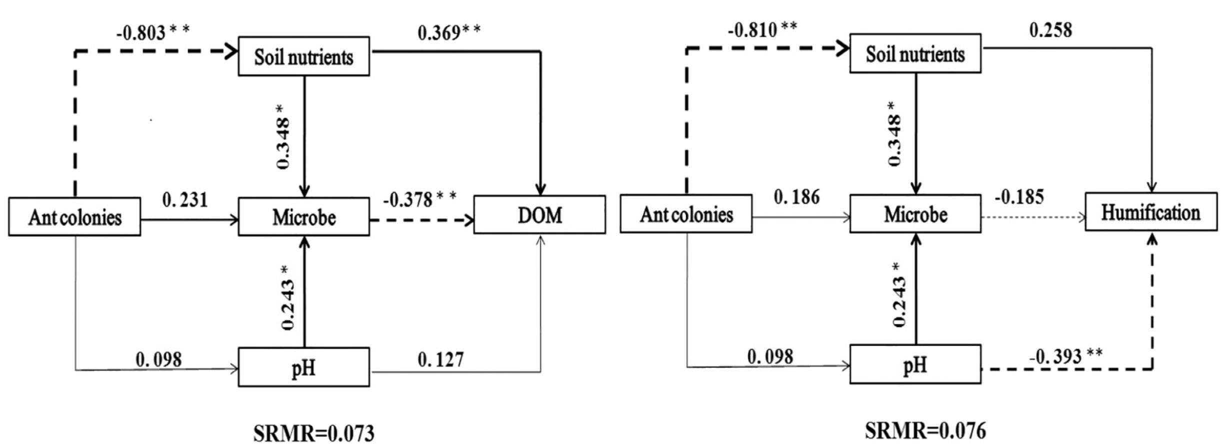

Fig. 9. SEM models showed effects of ant colonies on DOM contents and the humification degree.
*Significant at the 0.05 probability level; **Significant at the 0.01 probability level.
Numbers on the line were path coefficients. Line widths represent the relative values of path coefficients. Dashed or solid lines showed the negative or positive effects, respectively. There were five latent variables in the SEM model. The Ant invasion block were categorical variables assigned to 0 (control soils) and 1 (ant mounds). The Soil Nutrients including SOC, TN, SWC and C/N. The Microbe block included microorganisms with all PLFA biomarkers. The pH was soil pH. The DOM block was soil DOM content, and the Humification was reflected by $SUVA_{254}$. Fitness of the model was tested using the SARM parameters, and it was acceptable when SARM was lower than 0.08.

components proxy DOM from terrestrial sources, which were from decay of plant and animal residues. The protein-like components are composed of endogenous metabolites decomposed by microorganisms. In ant mound soils, apparently positive correlation indicated that the two humus-like and protein-like components may have the same source or trend in change, respectively. In contrast, two fluorescence components of control soil had different sources. There was positive correlation between $SUVA_{254}$ and $SUVA_{260}$ (Fig. 7), suggesting that humification degree of DOM depended on hydrophobic components. The hydrophobicity of organic matter and its impediment to water is currently one of the accepted mechanisms for the stability of SOC (Liu et al., 2007). Aromaticity and hydrophobicity of DOM were weaker in ant mounds than in control soils, implying the easier utilization of DOM in ant mounds. In addition, proportions of hydrophobic components to total DOM of ant mounds were lower than those of control soils (Fig. 6), which was, at least partly, responsible for lower SOC and higher DOM contents in ant mounds.

4.2. How did ant colony in combination with microorganisms' variation affect DOM and its spectral features?

Ant colony altered structures of microbial community greatly, thereby not only affecting DOM utilization, but also changing DOM yields and molecular features. The interactions of ant with microbe were vital to soil C dynamics (Six et al., 2002). Ant mounds, maintaining suitable humidity with high temperature and abundance of nutrients, could breed microbial abundance to a far greater magnitude than in the surrounding soil (Wagner et al., 2015). The microbial communities showed a striking difference between ant mounds and the control soils, with higher total PLFA contents and more species in the former. Ant colony establishment tended to increase microbial abundance that could stimulate protein-like substance yields. Meanwhile, stronger litter degradation also resulted in more intense fluorescence signal of the humic-like in topsoils of ant mounds than that in control soils (Fig. 4b).

Based on the sign and the contribution of measured parameters, the first principal component (PC1, 50.1% of total variance) can be interpreted as separating soil physicochemical properties from microbial communities. PC2 could be interpreted as a factor associated with humic-like aromatic compounds and condensed polyaromatic structures (Shafiquzzaman et al., 2014). Indeed, the $SUVA_{254}$ had the highest positive loadings on PC2. It was clear that all ant mound soils located in the positive scores on the PC1 axis, which indicated impacts of microorganisms on DOC content and molecular features in ant mounds were more important than those of control soils (Shafiquzzaman et al., 2014). In contrast, all control soils were in the negative regions of PC1 axis, showing that DOM of control soils mainly affected by soil physicochemical conditions. In summary, DOM properties were primarily derived from autochthonous sources but not from allochthonous sources in ant mounds.

Based on the result of SEM, we speculated that DOM mainly originated from organic matter mineralization after ant colony establishment, while microorganisms served as carbon consumer but not provider in ant mounds. This was confirmed by more CO_2 emission from ant mounds than from the nearby soils in our previous work (H. Wu et al., 2013; H.T. Wu et al., 2013). Weakening DOM humification mainly stemmed from variation of pH but not microbes. The higher value of pH in the ant mound was mainly ascribed to decreasing SWC caused by undergoing climate warming here (Frouz et al., 2008), and future climate change was predicted to introduce more ant colonies, consequently decreased humification degree of DOM.

5. Conclusion

In this study, molecular features of DOM were investigated and compared based on UV–Vis spectral analysis and 3D EEM-PARAFAC between ant mounds and control soils in a peatland. Three key conclusions can be derived from the findings of this work. Firstly, this study has shown great differences in DOM chemical fractions between ant mounds and control soils. The protein-like fluorescence reflecting endogenetic source contribution to DOM holded a paramount position in ant mound soils. The second major finding was that DOM of ant mound soils was abundant with fulvic-like substances. Compared with control soil, the DOM of ant soils was characterized by lower molecular weight, aromaticity, humification, and molecular condensation degree. The third significant finding to emerge from this study was that the properties of DOM in ant mound soils were primarily affected by the autochthonous sources. Compared with control soils, variations of soil nutrients and microbial communities play more important roles in regulating DOM content and humification degree in ant mound soils. On the whole, the study contributes to our understanding of the environmental role of ant colonies in local organic carbon cycle. Future work should take into account how ant colony establishment affects soil C dynamics by regulating DOM at large spatial scales, and roles of ant-microorganism interactions should be well documented.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2021.104298.

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