Forest Fragmentation Slows the Decomposition of Coarse Woody Debris in a Subtropical Forest

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Abstract

Forest fragmentation is increasing rapidly around the world, and edge effects caused by fragmented forests can influence ecosystem functions and ecological processes, including coarse woody debris (CWD) decomposition. Understanding the influencing mechanisms of edge effect on CWD decomposition is needed to assess the effects of forest fragmentation on C cycling and storage. We measured rates of mass loss of CWD of *Cinnamomum camphora* and *Pinus taiwanensis* over two years at two distances (0-5m *vs*. 60m) from a forest edge at two altitudes (215 and 1400 m a.s.l.), in a subtropical forest. In addition, we determined the microbial community of each CWD and the soil beneath via phospholipid fatty acids (PLFAs). Mass loss of CWD 60 m from the forest edge was > 15 % greater than that at the edge (0-5m). Mass loss was positively correlated with the abundance of microbial community and moisture content of the decaying CWD. Distance from edge explained 17.4% of the total variation of the microbial abundance in CWD. The results indicated that the reduced abundance of microbial communities and moisture content at forest edges reduced rates of decomposition of CWD. Long-term experiments with more tree species and more forest types are needed to assess the edge effect's generality.

1. Introduction

Forests around the world store a large amount of carbon (C) in soils, dead and living above-ground biomass (including coarse woody debris: CWD), which is regarded as a significant C sink (Pan et al., 2011). Understanding the factors that influence rates of C cycling processes in forests (including CWD decomposition) is necessary to quantify the role of global forests in the global C cycle (Pan et al., 2011; Intergovernmental Panel on Climate Change, 2014; Tang et al., 2018). Forest fragmentation due to natural and anthropogenic disturbances is a global phenomenon, affecting forest ecosystem functioning (Numata et al., 2010; FAO, 2010; Haddad et al., 2015; Barlow et al., 2016). Globally, nearly 20 % of all forest area is situated within 100 m of a forest edge (Haddad et al., 2015). Forest edges have distinct microclimates from forest interiors, including lower soil moisture, lower humidity, increased light availability, and increased wind and rain impacts (Laurance and Yensen, 1991; Didham & Ewers, 2012; Albiero-Júnior et al., 2020). These altered microclimatic conditions at forest edges can alter the decay rates of CWD. In a temperate forest in the United Kingdom, blocks of wood from European beech (*Fagus sylvatica*) placed at the forest edge lost mass at about half the rate of blocks placed 100 m within the forest (Crockatt & Bebber, 2015). The slower mass loss was attributed to the lower humidity and moisture content of the decaying wood at the forest edge (Crockatt & Bebber, 2015). In contrast, in a temperate forest in USA, Forrester et al. (2012) reported higher respiration rates from CWD in canopy gaps than under intact canopy.

Alterations in microclimatic conditions near forest edges may also influence soil microbial community composition. Previous studies have shown that the abundance of fungi strongly increased in response to changes in microclimate conditions due to edge effects (Boddy et al., 1989; Boddy, 2001; Castaño et al., 2018; van der Linde et al., 2018; Boeraeve et al., 2019). The fungal communities in soil and wood interact during all CWD decay phases (Mäkipää et al., 2017; Purahong et al., 2019; Wu et al., 2020, 2021), so changes in soil microbial communities due to edge effects could also alter fungal community dynamics within decomposing CWD. Reduced moisture availability at forest edges can affect the growth and activity of saprotrophic fungi (Crockatt & Bebber, 2015; Snäll & Jonsson, 2001) and mycorrhizal fungi (Boeraeve et al., 2019). In addition, the abundance of white rot species, such as *Xeromphalina campanella*, *Rigidoporus* sp. and *Skeletocutis odora*, is positively correlated with moisture content (Fukasawa et al., 2015, 2018).

Here, we compare rates of decomposition and microbial communities in CWD in the interior and edges of a subtropical forest ecosystem. We measured two-year mass loss of CWD of *Pinus taiwanensis* Hayata and *Cinnamomum camphora* (Linn.) Presl at the forest edge and 60 m into the forest and characterized the microbial community in the decaying CWD. The experiment was conducted at sites at two elevations (215m and 1400m a.s.l.). Specifically, we asked: (1) do CWD mass loss rates differ between forest edge and forest interior positions? (2), do microbial communities in decaying CWD differ between forest edge and interior positions? and (3) how do characteristics of the microbial community relate to environmental conditions in the two environments? Based on studies from temperate forests, we hypothesize that CWD decomposition rates will be lower at the forest edge than in the forest interior and that the differences will be related to changes in microbial communities and moisture.

2. Materials And Methods

2.1. Study area

This field research was conducted in a mixed coniferous-broad-leaved forest (CBF) at Lushan Mountain in Jiangxi Province, China (29°31'~29°41' N, 115°51'~116°07' E). The area is characterized as a subtropical monsoon climate with four distinct seasons. Mean annual precipitation and temperature range from 1308 to 2068 mm, and from 17.1 to 11.6 °C, respectively (Wu et al., 2019b). According to the FAO soil texture classification, soil types in Lushan change from ferric alisols at low elevations to haplic alisols at high ones (Liu & Wang, 2010; Wu et al., 2018b). Mixed coniferous–broad-leaved forests are dominated by several *Platycarya strobilacea* and *Acer davidii* species, and some deciduous woodland species and shrubs (Liu & Wang, 2010).

2.2. Sampling design

In December 2015, study sites were established in a mixed coniferous-broad-leaved forest at two altitudes (215m and 1400m). The sites at the two altitudes had similar aspect, slope steepness and position, stand age, and understory vegetation. Characteristics of the soils at the two sites are provided in Appendix 1. At each site, three plots were established within 0-5 m (Plot one: 2 m, Plot two: 3 m, Plots three: 2.5 m) of the forest edge, and another three plots were established 60 m (Plot one: 60 m, Plot two: 59.5 m, Plots threee: 59 m) inside the forest. The two tree species selected for CWD were *Pinus taiwanensis* Hayata and *Cinnamomum camphora* (Linn.) Presl. Fresh logs about 15 cm in central diameter were selected and cut into segments about 150 cm long (Table 1). Two CWD segments of each tree species were placed flush on the ground 30 cm from one another and 35 cm from the boundary of each plot. Therefore, a total of 48 CWD segments (2 altitudes × 2 edge distances × 3 plots × 2 CWD species × 2 segments) were tested.

2.3. Wood physicochemical properties analysis

A 2-cm-thick disk of each CWD was collected from a randomly selected place on each of the 48 logs at the beginning of the experiment and after 3, 6, 9, 12, 15, 18, 21, and 24 months. Disks were sealed in a plastic bag to preserve their moisture content before being transferred to the laboratory (Wu et al., 2018a, 2019a). The disk samples were collected more than 80 cm from the mid of wood. Each CWD sample was weighed and then oven-dried at 70°C and re-weighed, and their moisture content was calculated using equation (1).

$$M_{CWD} = \frac{W_w - W_d}{W_d} \qquad (1)$$

Where M_{CWD} (%) was the moisture content of each CWD during each measurement, W_w (g) was the wet wood weight, and W_d (g) was the dry weight.

The density of each CWD was calculated using equation (2): First, the weights of the disks of the CWD were measured (m, g), and the disks were placed in a container with a specific amount of water and wood disks in the container (V_1, ml), the initial volume of water (V_2, ml) and the density of each CWD sample (p, g/cm^3) was calculated.

$$\rho = m/(v_1 - v_2) \qquad (2)$$

Mass loss from each CWD was calculated using equation (3).

$$ML_{CWD} = \frac{M_i - M_t}{M_i} \qquad (3)$$

where ML_{CWD} (%) was the mass loss of each CWD sample during each measurement, M_i (g) was the initial dry mass, and M_t (g) was the wood mass after 3, 6, 9, 12, 15, 18, 21 or 24 months.

CWD temperature was measured at approximately 2 cm depth using a hand-held long-stem thermometer (Model SK-250WP, Sato Keiryoki Mfg. Co. Ltd, Tokyo, Japan). Concentrations of C and N in each CWD sample were determined using a TOC analyzer (Vario TOC, Elementar, German), and concentrations of lignin and cellulose were determined using the ADF-sulphuric method (Rowland et al., 1994) and the Kjeldahl method (K-370, Buchi Scientific Instruments, Switzerland). Soil available N (sum of the ammonium nitrogen, nitrate nitrogen, amino acid and readily hydrolyzed proteins nitrogen) was measured through the oxidation hydrolyzed into ammonia nitrogen, then absorbed by the boric acid solution and determined by sulfuric acid and titration (Liu, 1996). Soil available P was extracted using HCl-NH_4F solution and determined by Molybdenum-Antimony Anti colorimetric assay (Liu, 1996). Relative to *P. taiwanensis, C. camphora* CWD had higher initial concentrations of carbon and lignin, and lower cellulose (Appendix 1). Soil organic matter, N, hydrolyzed N and available P significantly differed between the two sites (Appendix 2).

2.4. Phospholipid fatty acid (PLFA) analyses

Microbial biomass and the relative index of bacterial to fungal biomass were estimated by PLFA analysis (Bossio & Scow, 1998; Olsson et al., 1999). CWD samples and mineral soil (0-5 cm) under each CWD segment were collected every three months during the study period and stored at -20°C for PLFA analysis. Concentrations of each PLFA were calculated relative to the 19:0 internal standard concentration. Total microbial biomass summed by each individual PLFAs (ng g^{-1} dry wood material). Microbial groups of bacteria (B), fungi (F), Gram-negative bacteria (G^-), Gram-positive bacteria (G^+), actinomycetes (ACT), and arbuscular mycorrhizal fungi (AMF) were biomarkers by the characteristic fatty acids (Appendix 3) (Olsson et al., 1999).

2.5. Data analysis

The effects of month, distance from the edge, and their interactions on temperature, moisture content, and mass loss of CWD were determined by repeated measures ANOVA for each species. We used three-way ANOVA to test the distance from edge, tree species, and altitude gradient on mass loss and microbial community changes. Due to significant interactions among altitude, edge distance, and species, all comparisons among altitude, edge distance or tree species were performed using one-way ANOVA of Dunnett's post-hoc. The microbial communities in the soil (0-5 cm), under each CWD and in the CWD itself were compared by simple correlation analysis, and differences in the PLFA signatures of the microbial community under CWD or soil among different treatments (tree species, altitude gradient or edge distance) were tested by redundancy analysis (RDA). All data were analysed using SPSS 20.0 (SPSS Inc., Chicago, USA). Differences were considered significant at $p < 0.05$.

3. Results

3.1. Distance from edge effects

During the two-year experimental period, the mean mass loss of *P. taiwanensis* and *C. camphora* 60 m away from the forest edge was significantly greater than that at the forest edge at both sites (Table 2 and Fig. 1). The moisture content of the CWD segments was also greater 60 m from the forest edge than at the edge throughout the two-year period (Fig. 2). There was a significant positive correlation between CWD's mass loss and moisture content for each altitude, edge distance, and tree species (Table 3).

3.2. Microbial community composition

Concentrations of total PLFA, total fungi, total bacteria, G^+ bacteria, G^- bacteria, soil fungi, and AMF in the soil beneath CWD of both tree species were all higher 60m from the forest edge than at the forest edge (Fig. 3). Concentrations of total PLFA, total bacteria, total fungi, G^+ bacteria, G^- bacteria, fungi, and AMF in the CWD of both tree species were also higher 60 m from the forest edge than at the edge (Fig. 4). The concentrations of fungal components (total fungi, fungi, and AMF) in the CWD were generally higher than that of bacteria components (total bacteria, G^+ bacteria, and G^- bacteria) (Fig. 4).

3.3. Relationship between soil and CWD microbial communities

Correlations between microbial communities in CWD and soil (Table 4) were generally positive in plots 60 m from the forest edge. There were some negative correlations between CWD fungi and soil fungi at the forest edge (Table 4).

3.4. Effects of edge distance and tree species on CWD microbial community

Distance to the forest edge had a larger influence on the CWD microbial community than did tree species or altitude (Table 5). Distance to edge explained 17.4% of the total variation, while tree species and altitude explained 3.1% and 10.9%, respectively (Table 5).

4. Discussion

Consistent with our hypothesis, mass loss of CWD within this studied subtropical forest was > 15 % greater than that at the edge, at both altitudes, which is lower to the 23 % greater mass loss of woodblocks placed 100 m into the forest than at the edge in a temperate forest (Crockatt & Bebber, 2015). The CWD at the forest edge had lower moisture content throughout the study, which is consistent with our hypothesis. Similarly, Crockatt and Bebber (2015) reported that the moisture content of the woodblocks increased with distance from the edge.

The higher moisture content of soil and wood in the forest interior probably facilitated the detection and colonization of CWD by microbes, which are largely soil-dwelling (Mäkipää et al., 2017; Fukasawa et al., 2018; Law et al., 2019). Malmivaara-Lämsä *et al*. (2008) found that fungal biomass was about 30 % higher 20 m inside the forest when compared to the edge, due to the higher humus moisture content inside the forest. In our study, CWD of both tree species in the forest interior had greater total PLFA, total bacteria, total fungi, G^+ bacteria, G^- bacteria, fungi, and AMF compared to CWD at the forest edge. Other studies have reported increased activity of both wood- and litter-decomposing saprotrophic fungi with distance from the forest edge (Snäll & Jonsson, 2001; Riutta et al., 2012; Crockatt & Bebber, 2015; Fukasawa et al., 2015, 2018; Ruwanza, 2019). Previous studies also reported that the abundance of mycorrhizal fungi was greater within forests than at edges (Malmivaara-Lämsä et al., 2008; Kjøller et al., 2012; Erlandson et al., 2016; Boeraeve et al., 2019). The abundance and diversity of various soil fauna groups may also be reduced near forest edges (Goosem, 2000; Laurance et al., 2002; Lehtinen et al., 2003; Watson et al., 2004; Laurance, 2004; Pfeifer et al., 2017).

Microorganisms community play a critical role in the process of wood decomposition (Harmon et al., 1986). The results observed in this study could be directly explained by the variation and changes of microbial decomposers communities in different edge distance. With the significantly larger and higher concentrations of wood fungal, bacterial and total PLFAs, the decomposition of CC and PT was faster in 60 m from the forest edge than at the edge. In addition, this study found that edge distance (17.4%) played a more important role than tree species (3.1%) and altitude gradient (10.9%) in determining the variation of microbial decomposers community of CWD itself (Table 5). Therefore, those results indicated that the degree and the existence of edge effects depended on the variation and characteristics of microbial community.

The fungal communities inhabited in wood and soil could interact and link at all the decay stage and process of CWD, which showed critical role in the decomposing of CWD (Purahong et al., 2019; Mäkipää et al., 2017). Therefore, CWD decomposition of different species could be determined by the significant relationship between soil and CWD microbial decomposers community observed in each edge distance and tree species combination (Fukasawa et al., 2018; Mäkipää et al., 2017; Wu et al., 2019b). Specifically, our study showed a negative relationship of fungi component between soil and CWD itself for CC and PT in forest edge, but positive correlations in 60 m from the forest edge (Table 4), which could be an reason for the results of the decompose of PT and CC was faster in 60 m from the forest edge than that in forest edge. Therefore, this study suggested that fungi played a significantly important role in determining the decomposition rate of CWD for the two species (Fig. 3), thus determining the variation of edge effects of CWD decomposition in subtropical forest. Previous studies also found that the abundance and community composition of variation faunal groups could be altered by the changes in forest edge effects (Goosem, 2000; Laurance et al., 2002; Lehtinen et al., 2003; Watson et al., 2004; Laurance, 2004; Pfeifer et al., 2017).

Malmivaara-Lämsä *et al*. (2008) found an increase in arbuscular mycorrhizal (AMF) and total fungal biomass by about 30% from the edge to 20 m inside the forest, which was directly explained by an increase in humus moisture, which result supported our study. In addition, the decrease of moisture content at the forest edge has been found to influence the decomposition rates of both wood- and litter-decomposing fungi (Riutta et al., 2012; Crockatt & Bebber, 2015; Ruwanza, 2019) and moisture content is known to influence the composition of ectomycorrhizal fungi (EcMF) community (Erland & Taylor, 2002; Erlandson et al., 2016). Similarly, decreased moisture availability at forest edges can be expected to affect the frequency of and decomposition by saprotrophic fungi (Crockatt & Bebber, 2015; Snäll & Jonsson, 2001), community composition of mutualistic fungi (Shi et al., 2002), mycorrhizal communities (Boeraeve et al., 2019) and interactions between different fungal groups (Kilpeläinen et al., 2017). In this study, the M_{CWD} of the two different tree species in 60 m from the forest edge was higher than in forest edge in each altitude gradient (Fig. 2). Meanwhile, Kjøller *et al.* (2012) found that the number of EcMF root tips, mycelial production and species richness were increased with increasing distance from the forest edge. Therefore, those results could partly explain the higher ML_{CWD} in 60 m from the forest edge than that in forest edge.

This study investigated CWD decomposition during a two-year experimental period, a relatively short time span considering the turnover time of wood. Long-term research is needed to determine decay rates and the proportion of the CWD mass that is converted into more persistent organic-matter pools over a longer study period. Our sampling method-collecting a 2-cm-thick disk from the end part of each CWD segment-would have increased exposure of the segment to fungal invasion. This would overestimate actual rates of decomposition but should be more realistic than the common practice of using woodblocks or tongue depressors.

5. Conclusion

Coarse woody debris of two tree species (*Cinnamomum camphora* and *Pinus taiwanensis)* placed at the edge of a subtropical forest decomposed slower than that placed 60 m within the forest. Rates of decay positively correlated with abundance of microorganisms in the CWD and the CWD moisture content. Distance from edge (17.4%) was more important than tree species (3.1%) and altitude gradient (10.9%) in determining microbial abundance in CWD. Our results indicate that the lower moisture content at forest edges reduce microbial activity and CWD decomposition rates. Given the increasing rate of forest fragmentation worldwide, higher rates of CWD decomposition at forest edges need to be incorporated into global C models.

Declarations

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Author Contributions

All authors contributed to the study at various phases. Specifically, C.S.W., C.J.S., B.Y.L., Z.J.Z., H.K.W., Y.Z., and Y.Q.L. were responsible for study design, data collection and analysis, and writing the early drafts of this research. C.S.W., and Y.Q.L. substantially contributed to interpreting and revising the manuscript.

Conflicts of Interest

The authors declare no conflict of interest.

References

Albiero-Júnior, A., Venegas-González, A., Rodríguez-Catón, M., Oliveira, J. M., Longhi-Santos, T., Galvão, F., Temponi, L.G., Botosso, P.C., 2020. Edge Effects Modify the Growth Dynamics and Climate Sensitivity of Araucaria angustifolia Trees. Tree-Ring Research 76, 11-26.

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees A.C., Nally R.M., Thomson, J.R., Ferraz, S.B., Louzada, J., Oliveira, V.H.F., Parry, L., Solar, R.R.C., Vieira, I.C.G., Aragão, L., Begotti, R.A., Braga, R.F., Cardoso, T.M., de Oliveira, R.C., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S.V., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 53, 144-147.

Boddy, L., 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 2001, 43-56.

Boddy, L., Owens, E.M., Chapela, I.H., 1989. Small scale variation in decay rate within logs one year after felling: effect of fungal community structure and moisture content. FEMS Microbiology Letters 62, 173-184.

Boeraeve, M., Honnay, O., Jacquemyn, H., 2019. Forest edge effects on the mycorrhizal communities of the dual-mycorrhizal tree species *Alnus glutinosa* (L.) Gaertn. Science of the Total Environment 666, 703-712.

Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microbial Ecology 35, 265-278.

Castaño, C., Lindahl, B.D., Alday, J.G., Hagenbo, A., de Aragón, J., Parladé, J., Pera, J., Bonet, J.A., 2018. Soil microclimate changes affect soil fungal communities in a Mediterranean pine forest. New Phytologist 220, 1211–1221.

Crockatt, M.E., Bebber, D.P., 2015. Edge effects on moisture reduce wood decomposition rate in a temperate forest. Global Change Biology 21, 698-707.

Didham, R.K., Ewers, R.M., 2012. Predicting the impacts of edge effects in fragmented habitats: Laurance and Yensen's core area model revisited. Biological Conservation 155, 104-110.

Erland, S., Taylor, A.F.S., 2002. Diversity of ecto-mycorrhizal fungal communities in relation to the abiotic environment. In: van der Heijden, M.G.A., Sanders, I.R. (Eds.), Mycorrhizal Ecology. Springer, Berlin, Heidelberg, pp. 163-200.

Erlandson, S.R., Savage, J.A., Cavender-Bares, J.M., Peay, K.G., 2016. Soil moisture and chemistry influence diversity of ectomycorrhizal fungal communities associating with willow along an hydrologic gradient. FEMS Microbiology Ecology 92, fiv148.

FAO., 2010. Global Forest Resources Assessment 2010. Food and Agriculture Organization of the United Nations, Rome.

Forrester, J.A., Mladenoff, D.J., Gower, S.T., Stoffel, J.L., 2012. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. Forest Ecology and Management, 265, 124-132.

Frostegård, Å., Bååth, E., 1996. The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. Biology and Fertility of Soils 22, 59-65.

Frostegård, A., Tunlid, A., Bååth, E., 2011. Use and misuse of PLFA measurements in soils. Soil Biology and Biochemistry, 43, 1621-1625.

Fukasawa, Y., Hyodo, F., Kawakami, S.I., 2018. Foraging association between myxomycetes and fungal communities on coarse woody debris. Soil Biology and Biochemistry 121, 95-102.

Fukasawa, Y., Matsuoka, S., 2015. Communities of wood-inhabiting fungi in dead pine logs along a geographical gradient in Japan. Fungal Ecology 18, 75-82.

Goosem, M., 2000. Effects of tropical rainforest roads on small mammals: edge changes in community composition. Wildlife Research 27, 151-163.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nichoils, A.O., Orrock, J.L., Song, D.X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1, e1500052.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15, 133-302.

Intergovernmental Panel on Climate Change., 2014: Climate Change 2014: Synthesis Report, in: Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, IPCC Geneva, Switzerland, 151 pp.

Kilpeläinen, J., Barbero-López, A., Vestberg, M., Heiskanen, J., Lehto, T., 2017. Does severe soil drought have after-effects on arbuscular and ectomycorrhizal root colonization and plant nutrition? Plant and Soil 418, 377-386.

Kjøller, R., Nilsson, L.O., Hansen, K., Schmidt, I.K., Vesterdal, L., Gundersen, P., 2012. Dramatic changes in ectomycorrhizal community composition, root tip abundance and mycelial production along a stand-scale nitrogen deposition gradient. New phytologist 194, 278-286.

Laurance, W.F., 2004. Forest-climate interactions in fragmented tropical landscapes. Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 359, 345-352.

Laurance, W.F., Lovejoy, T.E., Vasconselos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16, 605-618.

Laurance, W.F., Yensen, E., 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation 55, 77-92.

Law, S., Eggleton, P., Griffiths, H., Ashton, L., Parr, C., 2019. Suspended dead wood decomposes slowly in the tropics, with microbial decay greater than termite decay. Ecosystems 22, 1176-1188.

Lehtinen, R.M., Ramanamanjato, J., Raveloarison, J.G., 2003. Edge effects and extinction proneness in a herpetofauna from Madagascar. Biodiversity Conservation 12, 1357-1370.

Liu GS (1996). Soil physical and chemical analysis and description of cross-section. China Standard Press, Beijing. (In Chinese with English Abstract)

Liu, X.Z., Wang, L., 2010. Scientific survey and study of biodiversity on the Lushan Nature Reserve in Jiangxi province. Science Press, Beijing. (In Chinese with English Abstract)

Mäkipää, R., Rajala, T., Schigel, D., Rinne, K. T., Pennanen, T., Abrego, N., Ovaskainen, O., 2017. Interactions between soil-and dead wood-inhabiting fungal communities during the decay of Norway spruce logs. The ISME Journal 11, 1964-1974.

Malmivaara-Lämsä, M., Hamberg, L., Haapamäki, E., Liski, J., Kotze, D.J., Lehvävirta, S., Fritze, H., 2008. Edge effects and trampling in boreal urban forest fragments – impacts on the soil microbial community. Soil Biol. Biochem. 40, 1612–1621.

Numata, I., Cochrane, M.A., Roberts, D.A., Soares, J.V., Souza, C.M., Sales, M.H., 2010. Biomass collapse and carbon emissions from forest fragmentation in the Brazilian Amazon. Journal of Geophysical Research: Biogeosciences 115, G03027.

Olsson, P.A., Jakobsen, I., Thingstrup, I., Bååth, E., 1999. Estimation of the biomass of arbuscular mycorrhizal fungi in a linseed field. Soil Biology and Biochemistry 31, 1879-1887.

Pan, Y.D., Birdsey, R.A., Fang, J.Y., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S.L., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988-993.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodriguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F., Morante-Filho, J.C., Olivier, P., Peter, S.L., Pidgeon, A., Ribeiro, D.B., Scherber, C., Schneider-Maunoury, L., Struebig, M., Urbina-Cardona, N., Watling, J.I., Willig, M.R., Wood, E.M., Ewers, R.M., 2017. Creation of forest edges has a global impact on forest vertebrates. Nature 551, 187-191.

Purahong, W., Kahl, T., Krüger, D., Buscot, F., Hoppe, B., 2019. Home-Field Advantage in Wood Decomposition Is Mainly Mediated by Fungal Community Shifts at "Home" Versus "Away". Microbial Ecology 78, 725-736.

Riutta, T., Slade, E.M., Bebber, D.P., Taylor, M., Malhi, Y., Riordan, P., Macdonald, D.W., Morecroft, M.D., 2012. Experimental evidence for the interacting effects of forest edge, moisture and soil macrofauna on leaf litter decomposition. Soil Biology and Biochemistry, 49, 124-131.

Rowland, A.P., Roberts, J.D., 1994. Lignin and cellulose fractionation in decomposition studies using acid-detergent fibre methods. Communications in Soil Science and Plant Analysis 25, 269-277.

Ruwanza, S., 2019. The Edge Effect on Plant Diversity and Soil Properties in Abandoned Fields Targeted for Ecological Restoration. Sustainability 11, 140.

Shi, L., Guttenberger, M., Kottke, I., Hampp, R., 2002. The effect of drought on mycorrhizas of beech (*Fagus sylvatica* L.): changes in community structure, and the content of carbohydrates and nitrogen storage bodies of the fungi. Mycorrhiza 12, 303-311.

Snäll, T., Jonsson, B.G., 2001. Edge effects on six polyporous fungi used as old-growth indicators in Swedish boreal forest. Ecology Bulletins 255-262.

Tang, X.L., Zhao, X., Bai, Y.F., Tang, Z.Y., Wang, W.T., Zhao, Y.C., Wan, H.W., Xie, Z.Q., Shi, X.Z., Wu, B.F., Wang, G.X., Yan, J.H., Ma, K.P., Du, S., Li, S.G., Han, S.J., Ma, Y.X., Hu, H.F., He, N.P., Yang, Y.H., Han, W.X., He, H.L., Yu, G.R., Fang, J.Y., Zhou, G.Y., 2018. Carbon pools in China's terrestrial ecosystems: New estimates based on an intensive field survey. Proceedings of the National Academy of Sciences of the United States of America 115, 4021-4026.

van der Linde, S., Suz, L.M., Orme, C.D.L., Cox, F., Andreae, H., Asi, E., Atkinson, B., Benham, S., Carroll, C., Cools, N., De Vos, B., Dietrich, H.-P., Eichhorn, J., Gehrmann, J., Grebenc, T., Gweon, H.S., Hansen, K., Jacob, F., Kristöfel, F., Lech, P., Manninger, M., Martin, J., Meesenburg, H., Merilä, P., Nicolas, M., Pavlenda, P., Rautio, P., Schaub, M., Schröck, H.-W., Seidling, W., Šrámek, V., Thimonier, A., Thomsen, I.M., Titeux, H., Vanguelova, E., Verstraeten, A., Vesterdal, L., Waldner, P., Wijk, S., Zhang, Y., Žlindra, D., Bidartondo, M.I., 2018. Environment and host as large-scale controls of ectomycorrhizal fungi. Nature 558, 243-248.

Watson, J.E.M., Whitacker, R.J., Dawson, T.P., 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Biological Conservation 120, 311-327.

Wu, C.S., Mo, Q.F., Wang, H.K., Zhang, Z.J., Huang, G.X., Ye, Q., Zou, Q., Kong, F.Q., Liu, Y.Q., Wang, G.G., 2018b. Moso bamboo (*Phyllostachys edulis* (Carriere) J. Houzeau) invasion affects soil phosphorus dynamics in adjacent coniferous forests in subtropical China. Annals of Forest Science 75, 24.

Wu, C.S., Ulyshen, M., Shu, C.J., Zhang, Z.J., Zhang, Y., Liu, Y.Q., Wang, G.G., 2021. Stronger effects of termites than microbes on wood decomposition in a subtropical forest. Forest Ecology and Management 493, 119263.

Wu, C.S., Wang, H.K., Mo, Q.F., Zhang, Z.J., Huang, G.X., Kong, F.Q., Liu, Y.Q., Wang, G.G., 2019a. Effects of elevated UV-B radiation and N deposition on the decomposition of coarse woody debris. Science of the Total Environment 663, 170-176.

Wu, C.S., Zhang, Z.J., Shu, C.J., Mo, Q.F., Wang, H.K., Kong, F.Q., Wang, G.G., Liu, Y.Q., 2020. The response of coarse woody debris decomposition and microbial community to nutrient additions in a subtropical forest. Forest Ecology and Management 460, 117799.

Wu, C.S., Zhang, Z.J., Wang, H.K., Huang, G.X., Shu, C.J., Kong, F.Q., Zhang, Y., Wang, G.G., Liu, Y.Q., 2019b. Home-field advantage of CWD decomposition in subtropical forests varied by field sites. Forest Ecology and Management 444, 127-137.

Wu, C.S., Zhang, Z.J., Wang, H.K., Li, C., Mo, Q.F., Liu, Y.Q., 2018a. Photodegradation accelerates coarse woody debris decomposition in subtropical Chinese forests. Forest Ecology and Management 409, 225-232.

Zak, D.R., Ringelberg, D.B., Pregitzer, K.S., Randlett, D.L., White, D.C., Curtis, P.S., 1996. Soil microbial communities beneath *populus grandidentata* grown under elevated atmospheric CO_2. Ecological Applications 6, 257-262.

Zelles, L., 1999. Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biology and Fertility of Soils 29, 111-129.

Tables

Table 1. Initial diameter, length and density (mean ± SE, n=6) of the log segments of the two tree species at each altitude (215m and 1400m) and forest edge distance (edge and 60m from the forest edge). Note: experiment material was all of similar decay stage.

Tree species	Altitude	Edge distance	Average diameter (cm)	Average length (cm)	Average density (g/cm^3)
Pinus taiwanensis	215m	edge	16.21±2.07	147.35±4.26	0.405±0.04
		60m	15.87±1.94	150.06±3.88	0.411±0.03
	1400m	edge	15.66±2.11	147.56±4.16	0.403±0.04
		60m	16.19±1.96	150.33±3.94	0.406±0.05
Cinnamomum camphora	215m	edge	15.36±2.56	149.55±4.42	0.434±0.05
		60m	15.62±1.99	150.32±3.88	0.452±0.03
	1400m	edge	15.77±2.24	147.33±4.28	0.442±0.03
		60m	15.76±1.99	151.12±3.54	0.452±0.06

Table 2. Two-year average mass loss, temperature and moisture content of CWD (mean ± SE, n=6) of the two studied species at the two altitudes (215m and 1400m) and forest edge distances (edge and 60m from the forest edge) in Lushan Mountain, China. Different uppercase letters indicate significant differences between edge distances for the same species (e.g., *Pinus taiwanensis* or *Cinnamomum camphora*) at $p < 0.05$) and altitude. Different lowercase letters indicate significant differences among the two species for the same edge distance and altitude ($p < 0.05$). Different lowercase letters in brackets indicate significant differences between altitudes for the same edge distance and tree species ($p < 0.05$).

Tree species	Altitude	Edge distance	Mass loss (%)	Temperature (°C)	Moisture content (%)
Pinus taiwanensis	215m	edge	23.3±3.8 ^{Ba} (a)	16.71±1.32 ^{Aa} (a)	74.16±6.34 $^{Ba\ (a)}$
		60m	27.7±3.7 ^{Ab} (a)	16.01±1.11 ^{Aa} (a)	79.26±6.47 $^{Aa\ (a)}$
	1400m	edge	15.5±3.6 $^{Ba\ (c)}$	11.57±1.46 $^{Aa\ (c)}$	69.74±6.54 $^{Ba\ (b)}$
		60m	20.1±3.4 ^{Ab} (c)	10.74±1.53 $^{Aa\ (c)}$	75.36±6.25 $^{Aa\ (b)}$
Cinnamomum camphora	215m	edge	29.6±4.1 ^{Ba} (a)	17.48±1.27 $^{Aa\ (a)}$	73.60±6.13 $^{Ba\ (a)}$
		60m	34.0±4.5 ^{Aa} (a)	16.33±1.63 $^{Aa\ (a)}$	79.03±7.22 $^{Aa\ (a)}$
	1400m	edge	22.0±3.1 $^{Ba\ (c)}$	12.20±1.38 $^{Aa\ (c)}$	71.21±6.31 $^{Ba\ (b)}$
		60m	26.6±3.5 ^{Aa} (c)	11.04±1.75 $^{Aa\ (c)}$	76.16±6.44 $^{Aa\ (b)}$

Table 3. Correlations of mass loss with moisture content and temperature of CWD by altitude, forest edge distance, and tree species. *ns* not significant, * *p*0.05, ** *p*0.01, *** *p*0.001.

Tree species	Fixed effects	215m		1400m	
		edge	60m	edge	60m
Pinus taiwanensis	Mass loss × Moisture content	0.644**	0.689**	0.705**	0.731**
	Mass loss × Temperature	0.035 ^{ns}	0.058 ^{ns}	0.093 ^{ns}	0.051 ^{ns}
Cinnamomum camphora	Mass loss × Moisture content	0.672**	0.693**	0.711**	0.749**
	Mass loss × Temperature	0.078 ^{ns}	0.051 ^{ns}	0.064 ^{ns}	0.076 ^{ns}

Table 4. Correlation between the composition of different phospholipid fatty acid (PLFA) (ng g^{-1} dry mass) signatures of CWD and soil for each altitude, forest-edge distance, and tree-species combination. Total, total PLFA concentrations; B, bacterial PLFAs; F, fungal PLFAs; F/B, the fungal to bacterial ratio; G^{+}, Gram-positive bacteria; G^{-}, Gram-negative bacteria; G^{+}/G^{-}, ratio of Gram-positive to Gram-negative bacteria; AMF, arbuscular mycorrhizal fungi. *ns* not significant, * *p*0.05, ** *p*0.01, *** *p*0.001.

Fixed effects	Altitude	Edge distance	AMF	Fungi	Total Fungi	G^{+}	G^{-}	Total B	Total
Pinus taiwanensis × Soil	215m	edge	0.643*	-0.611*	-0.678*	0.822*	0.662*	0.704**	0.771**
		60m	0.801**	0.778**	0.791**	0.767**	0.683*	0.778**	0.804**
	1400m	edge	0.654*	-0.647*	-0.674*	0.789**	0.771*	0.782**	0.801**
		60m	0.812**	0.785**	0.799**	0.801**	0.788*	0.784**	0.797**
Cinnamomum camphora ×Soil	215m	edge	0.634*	-0.645*	-0.635*	0.811**	0.642*	0.661*	0.788**
		60m	0.803**	0.777**	0.781**	0.781**	0.650*	0.789**	0.804**
	1400m	edge	0.639*	-0.627*	-0.647*	0.789**	0.629*	0.796**	0.792**
		60m	0.811**	0.784**	0.796**	0.801**	0.640*	0.769**	0.781**

Table 5. Effects of tree species, altitude, and forest-edge distance on the selected phospholipid fatty acid (PLFAs) signatures of CWD tested with redundancy analysis (RDA).

Explanatory variable	Explained variance %	Contribution %	Pseudo-F	*P* ($<$ 0.05)
Tree species	3.1	9.5	3.8	0.036
Altitude	**10.9**	37.2	18.8	0.002
Forest edge distance	**17.4**	45.5	20.6	0.001

Figures

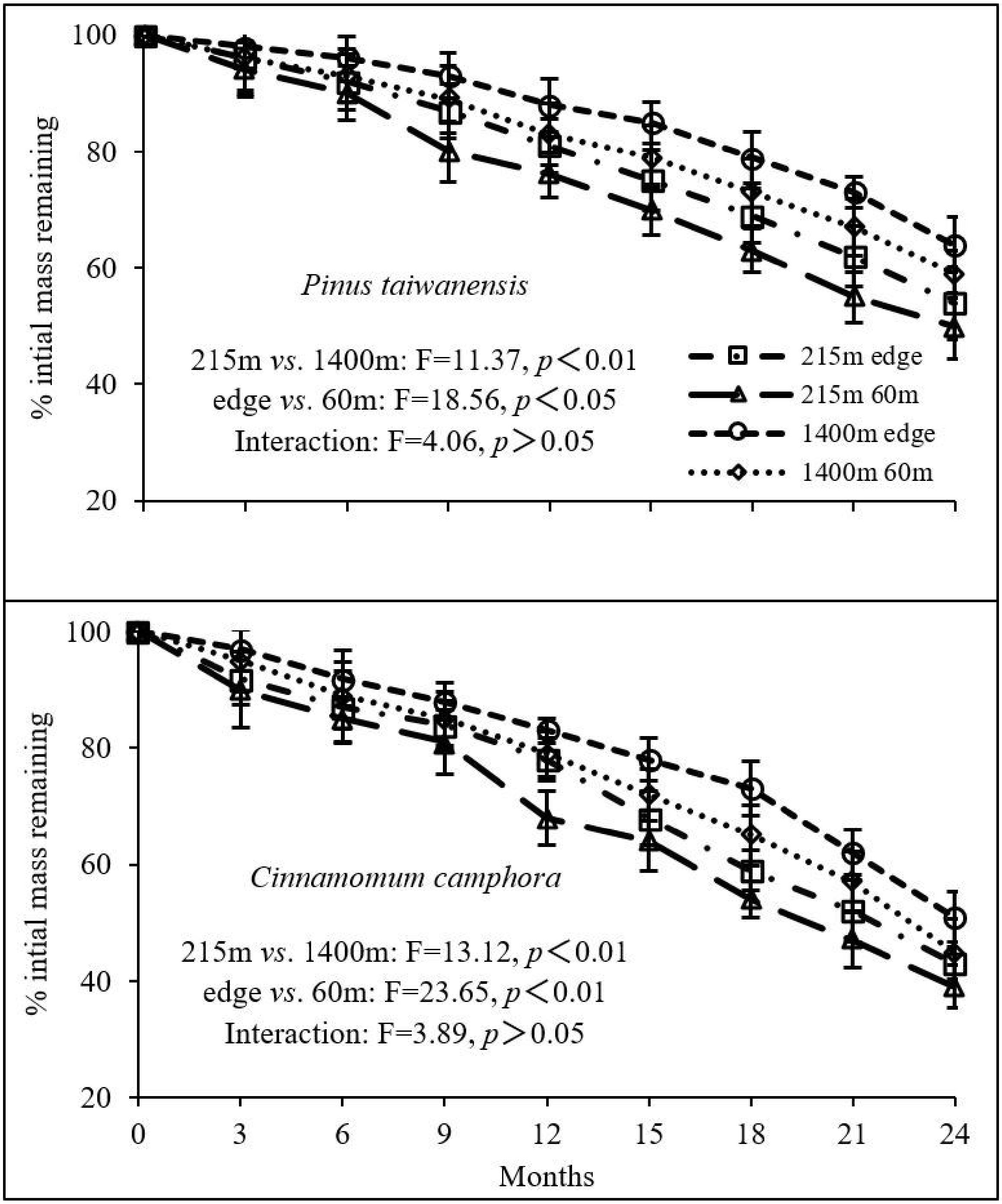

Figure 1

Patterns of mass loss of two tree species of CWD (fresh wood) at each altitude (215m and 1400m) and forest-edge distance (edge and 60m from the forest edge) during 24 months of decomposition in Lushan Mountain of subtropical China.

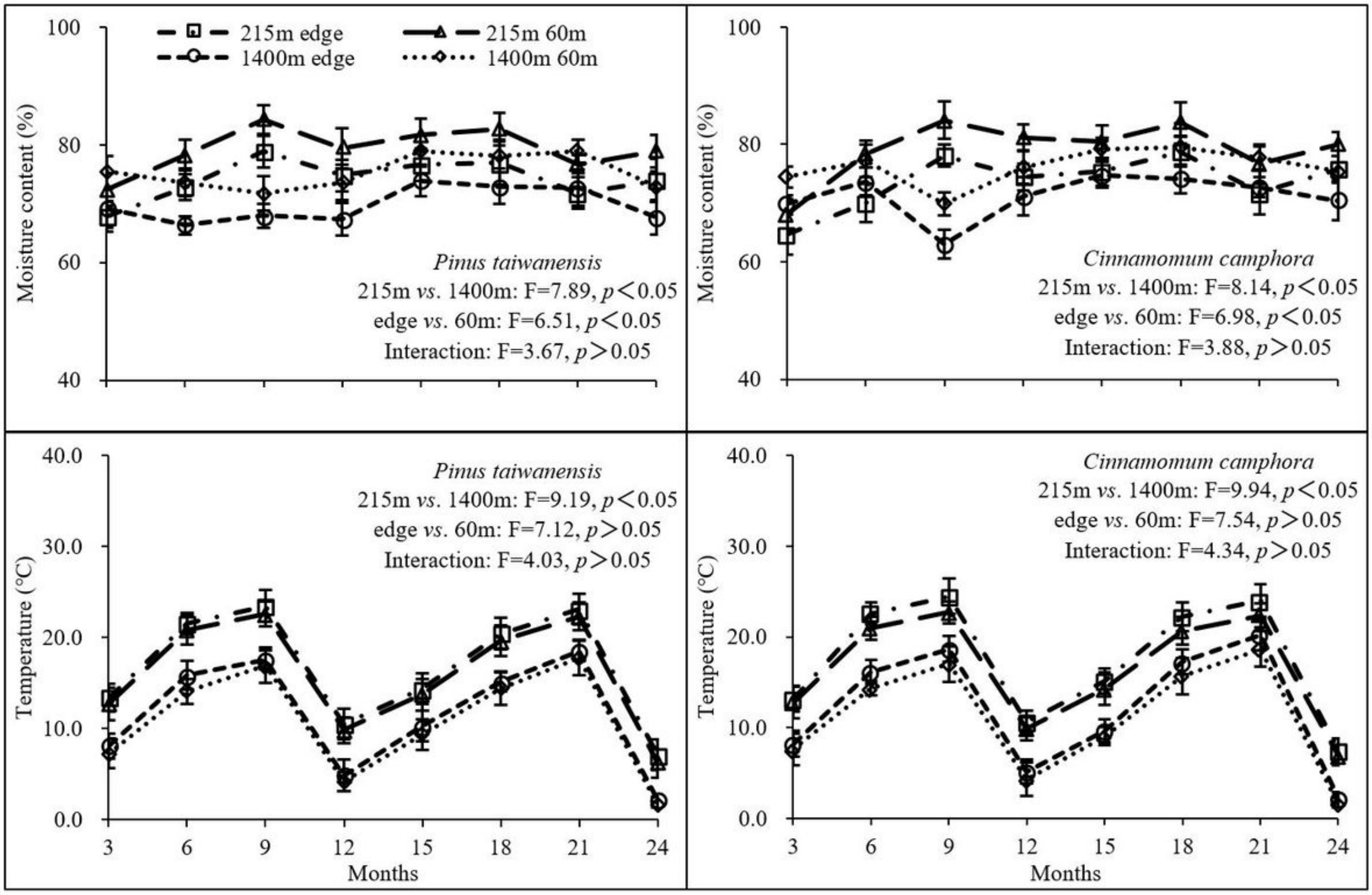

Figure 2

Temperature and moisture content of CWD of the two tree species at each altitude (215m and 1400m) and forest-edge distance (edge and 60m from the forest edge) during the 24-month incubation.

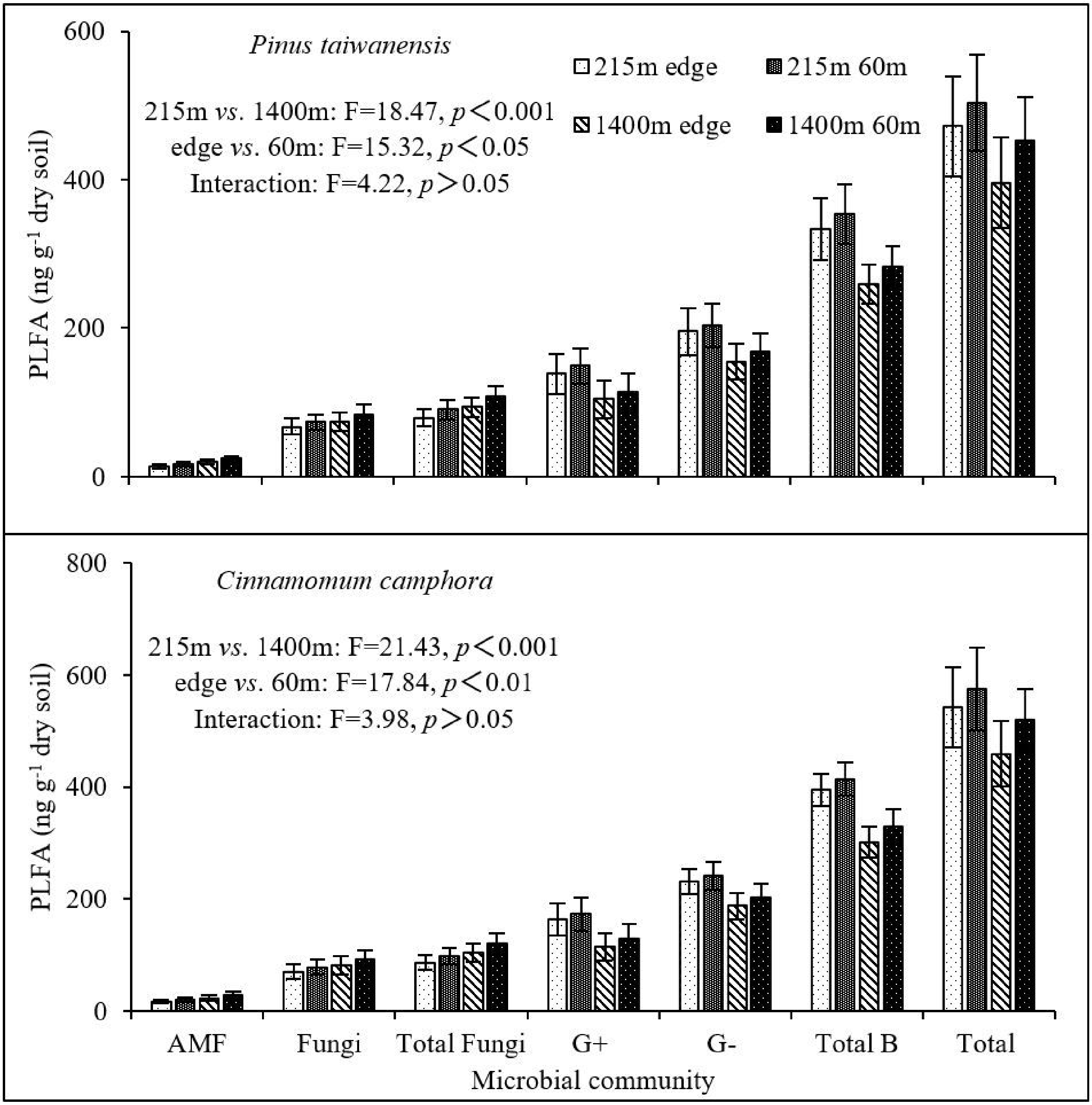

Figure 3

Soil phospholipid fatty acid (PLFA) (mean ± SE; ng g-1 dry soil) signatures (0-5cm) under CWD of the two tree species at each forest-edge distance (edge and 60m from the forest edge) and altitude (215m and 1400m) in Lushan Mountain of subtropical China. Total, total PLFA concentrations; B, bacterial PLFAs; F, fungal PLFAs; F/B, fungal to bacterial ratio; G+, Gram-positive bacteria; G-, Gram-negative bacteria; G+/G-, ratio of Gram-positive to Gram-negative bacteria; AMF, arbuscular mycorrhizal fungi.

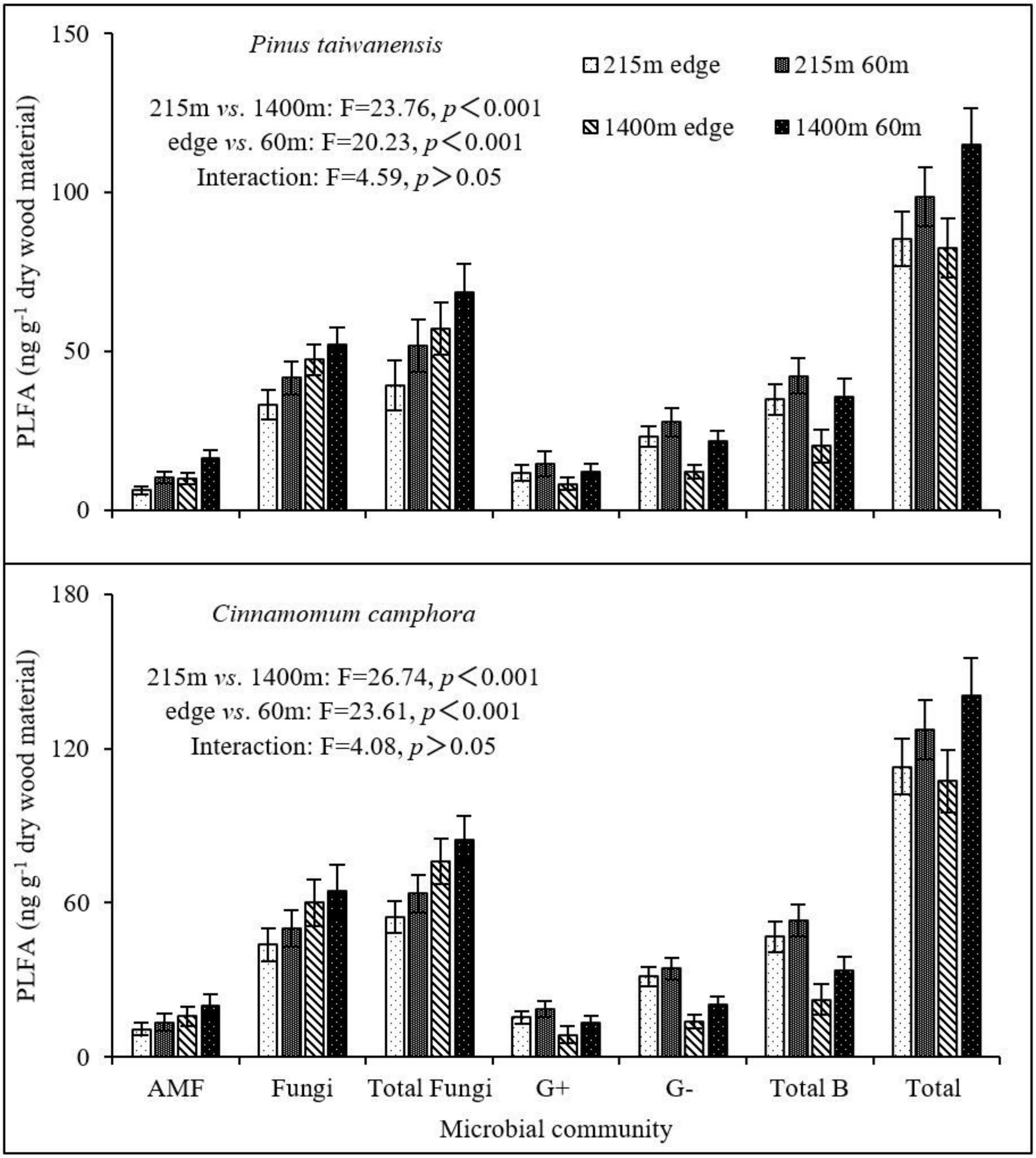

Figure 4

Phospholipid fatty acid (PLFA) (mean ± SE; ng g-1 dry wood material) signatures of the CWD of the two tree species at each forest-edge distance (edge and 60m from the forest edge) and altitude (215m and 1400m) in Lushan Mountain of subtropical China. Total, total PLFA concentrations; B, bacterial PLFAs; F, fungal PLFAs; F/B, the fungal to bacterial ratio; G+, Gram-positive bacteria; G-, Gram-negative bacteria; G+/G-, ratio of Gram-positive to Gram-negative bacteria; AMF, arbuscular mycorrhizal fungi.