

## REPORT

# Do wood-boring beetles influence the flammability of deadwood?

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### Abstract

Global warming increases the risk of wildfire and insect outbreaks, potentially reducing the carbon storage function of coarse woody debris (CWD). There is an increasing focus on the interactive effects of wildfire and insect infestation on forest carbon, but the impact of wood-boring beetle tunnels via their effect on the flammability of deadwood remains unexplored. We hypothesized that the presence of beetle holes, at natural densities, can affect its flammability positively through increased surface area and enhanced oxygen availability in the wood. To test this, wood-boring beetle holes were mimicked experimentally in decaying logs of two coniferous species, and flammability variables of these treated logs were compared. We found that wood-boring beetles partly increased the flammability of CWD of both species (via promoting deadwood smoldering combustion) when their holes were parallel with the airflow. Even when accounting for the influences of wood density and cracks, these radial holes continued to have a notable impact on deadwood flammability. While these holes did not make the wildfire more intense, they significantly increased carbon loss during combustion. This suggests that wood-boring beetles will enhance carbon release from deadwood into the atmosphere during wildfire.

### KEYWORDS

beetle tunnels, carbon stock, coarse woody debris, coniferous, fire experiments, flammability, gymnosperm, wildfire, wood traits

## INTRODUCTION

Forests absorb large amounts of CO<sub>2</sub> including that from anthropogenic emissions, thereby acting as important carbon (C) sinks (Canadell & Raupach, 2008; Luysaert et al., 2018). Deadwood, particularly coarse woody debris (CWD; diameter >5 cm), plays a key role in this process as its large annual input and low decomposition rate make it a significantly large contributor to the terrestrial

carbon pool (Cornwell et al., 2009; Wijas et al., 2024; Zuo et al., 2018). Thus, for understanding global carbon cycling under climate change, it is critical to study CWD turnover (Brovkin et al., 2012; Cornwell et al., 2009). However, the carbon sink function of forest including CWD is under threat under the ongoing climate change. Global warming and associated higher frequency and severity of drought periods (IPCC, 2021; Lindner et al., 2010) increase the risk of wildfires (Jain et al., 2022;

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Seidl et al., 2017) and insect outbreaks (Logan et al., 2003; Robbins et al., 2022; Weed et al., 2013). Both processes can transform forests from a carbon sink to a net carbon source (Kurz, Dymond, et al., 2008; Kurz, Stinson, et al., 2008).

Much research has been done on the relationship between carbon storage and wildfires (Hurteau et al., 2008; Hurteau & North, 2009) or insect outbreaks (Arora et al., 2016; Kurz, Dymond, et al., 2008), and the interaction between the two is also becoming a popular research topic (Seidl et al., 2017). However, most research has focused on bark beetles (Anderegg et al., 2015; Hlásny et al., 2021; Sommerfeld et al., 2021). Bark beetles are well known to invade and feed on the phloem of weakened living trees or new deadwood, and bore tunnels in the young bark tissues to lay their eggs. The galleries that their larvae subsequently excavate in the resource-rich phloem seem not to affect the flammability of trees (Harvey et al., 2013). In contrast, no fire-related research has focused on wood-boring beetles that invade standing or downed deadwood. For instance, long-horned beetles (Cerambycidae) and cardinal beetles (Pyrochroidae) bore deep tunnels into the wood (i.e., xylem). These beetle holes can influence deadwood flammability via increased surface area-to-volume ratio, which in turn can accelerate fuel drying and oxygen flow during combustion (Cornelissen et al., 2017; Rothermel, 1972). How the presence of beetle tunnels affects the flammability of wood has not been studied before.

Based on our recent observations in Dutch forests and tree plantations (Appendix S1: Figure S1), once dead and decaying, coarse wood tends to be colonized by longhorn beetles (Cerambycidae) or cardinal beetles (Pyrochroidae), which bore deep radial or longitudinal holes into the wood. We hypothesized that the presence of beetle holes in deadwood, at natural densities, can affect its flammability positively through increased surface area and enhanced oxygen availability in the wood. To test this, two types of wood-boring beetle holes were simulated experimentally: radial and longitudinal holes. Through this experimental approach, we aimed to answer this fundamental question of whether and how the flammability of deadwood is affected by wood-boring beetle tunnels, thereby controlling for any confounding environmental factors.

## MATERIALS AND METHODS

### Study species and beetle hole simulation

Logs of two coniferous species important in NW European forests or forestry plantations (Cornelissen et al., 2012), i.e., *Abies grandis* (D. Don) Lindl. and *Picea abies* (L.) H. Karst. (both are hosts for wood-boring beetles), were

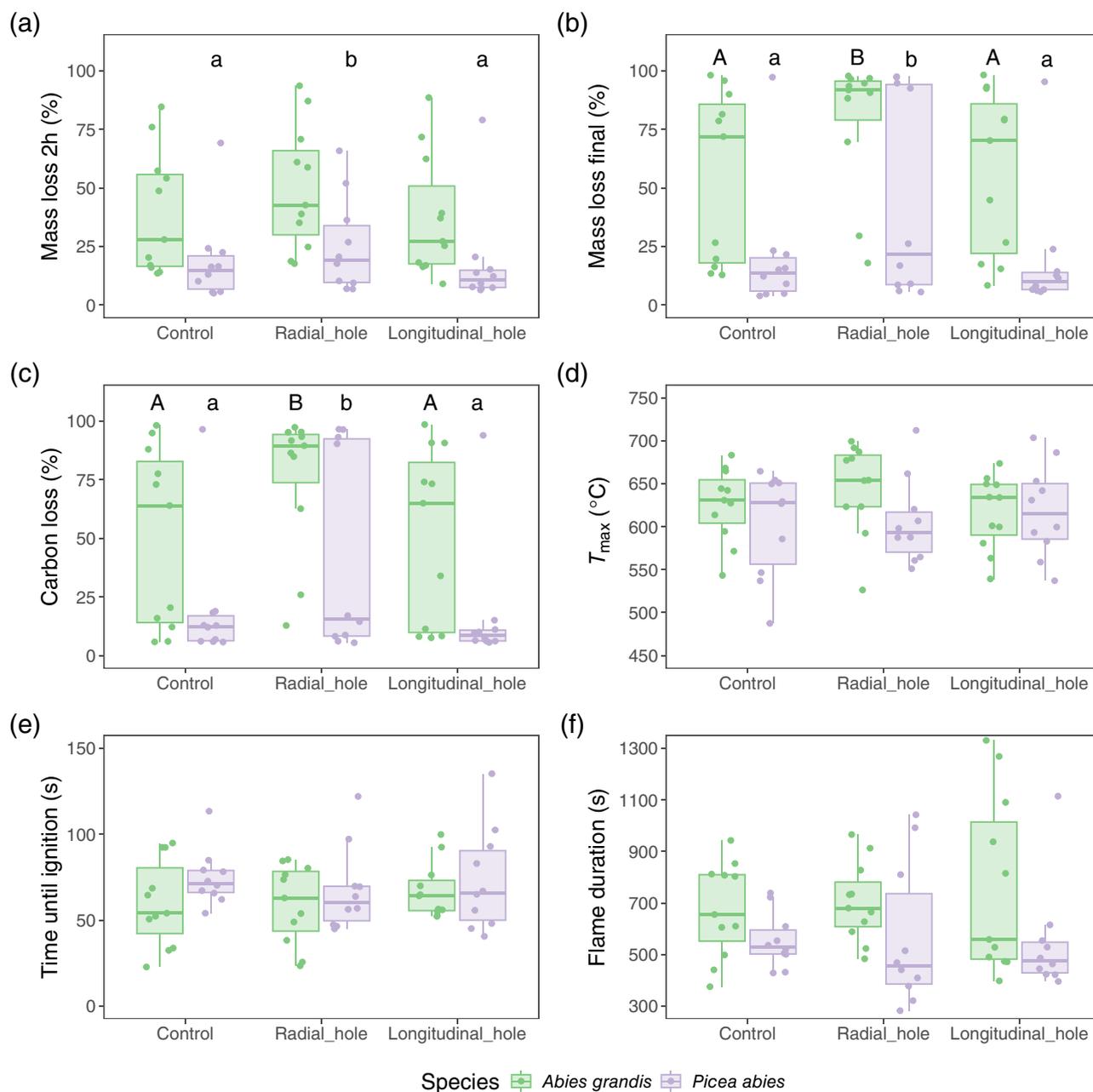
collected on October 23, 2020, at Arboretum Oostereng near Wageningen, the Netherlands. Logs were cut into 20 cm samples (Appendix S1: Figure S2a) as detailed in Appendix S1: Section S1. After air-drying, samples were selected for the treatments (details in Appendix S1: Section S2). Treatments were applied to *A. grandis* samples on December 2020 and to *P. abies* samples on June 2021. Treatments were as follows: (1) mimicking radial beetle holes (see Appendix S1: Figure S2b), (2) mimicking longitudinal beetle holes (see Appendix S1: Figure S2c), and (3) a control without holes added. In our blocked design, three 20 cm samples of the three respective treatments from the same log formed one block. Longer logs with six or more samples contained two blocks and at most six samples were selected from the same log. In total, 33 samples were selected from nine logs of *A. grandis* and 30 samples from 10 logs of *P. abies*.

### Flammability and wood trait measurements

The experimental burns were conducted in the Fire Laboratory of Amsterdam for Research in Ecology located at Vrije Universiteit Amsterdam. Samples were burned in a block order with one or two blocks a day, and the blocks of each treatment originating from the same log were burned on the same day, in random order. Fuel flammability can be categorized into four components: ignitability (ease of plant ignition), combustibility (the intensity or speed at which a fire burns), sustainability (how long the fuel burns), and consumability (proportion of biomass combusted; Anderson, 1970). Correspondingly, six flammability parameters were measured: (1) time until ignition (TUI; in seconds), (2) flame duration (FD; in seconds), (3) mean maximum temperature ( $T_{\max}$ ; in degrees Celsius), (4) percentage mass loss after 2 h ( $ML_{2h}$ ; in percentage), (5) the final percentage mass loss ( $ML_{\text{final}}$ ; in percentage), and (6) carbon loss ( $C_{\text{loss}}$ ; in percentage). For details, see Appendix S1: Section S3. Wood density (in grams per cubic centimeter) was measured from the subsample. Crack volume ( $V_{\text{crack}}$ ; in cubic centimeters) was calculated as the total volume of cracks on each sample.  $V_{\text{crack}}$  and volume of treatment holes were added up as total missing volume ( $V_{\text{total}}$ ; in cubic centimeters); for details, see Appendix S1: Section S4.

### Data analysis

To test the effects of the treatments on flammability parameters of each species, we applied linear mixed models to fit the flammability parameters with beetle



**FIGURE 1** Boxplot showing the distribution of flammability parameters of two gymnosperm species under three experimental treatments. Dots are raw data. Mass loss 2 h represents percentage mass loss after 2 h (in percentage), mass loss final represents final percentage mass loss (in percentage), and  $T_{max}$  represents mean maximum temperature (in degrees Celsius). Different uppercase letters indicate significantly different effects of treatments on *Abies grandis*, and lowercase letters on *Picea abies*, as revealed by linear mixed model results (see Appendix S1: Table S2), followed by a post hoc test ( $p < 0.05$ ; see Appendix S1: Table S3). The absence of lowercase and uppercase letters denotes no significant influences.

hole treatments, with block (log ID) as the random effect, as flammability tests were conducted following a block order, and all samples in each block were from the same “mother log” sharing similar initial characteristics (e.g., diameter, density, moisture content, and chemical concentration). Meanwhile,  $V_{crack}$  was added as covariate

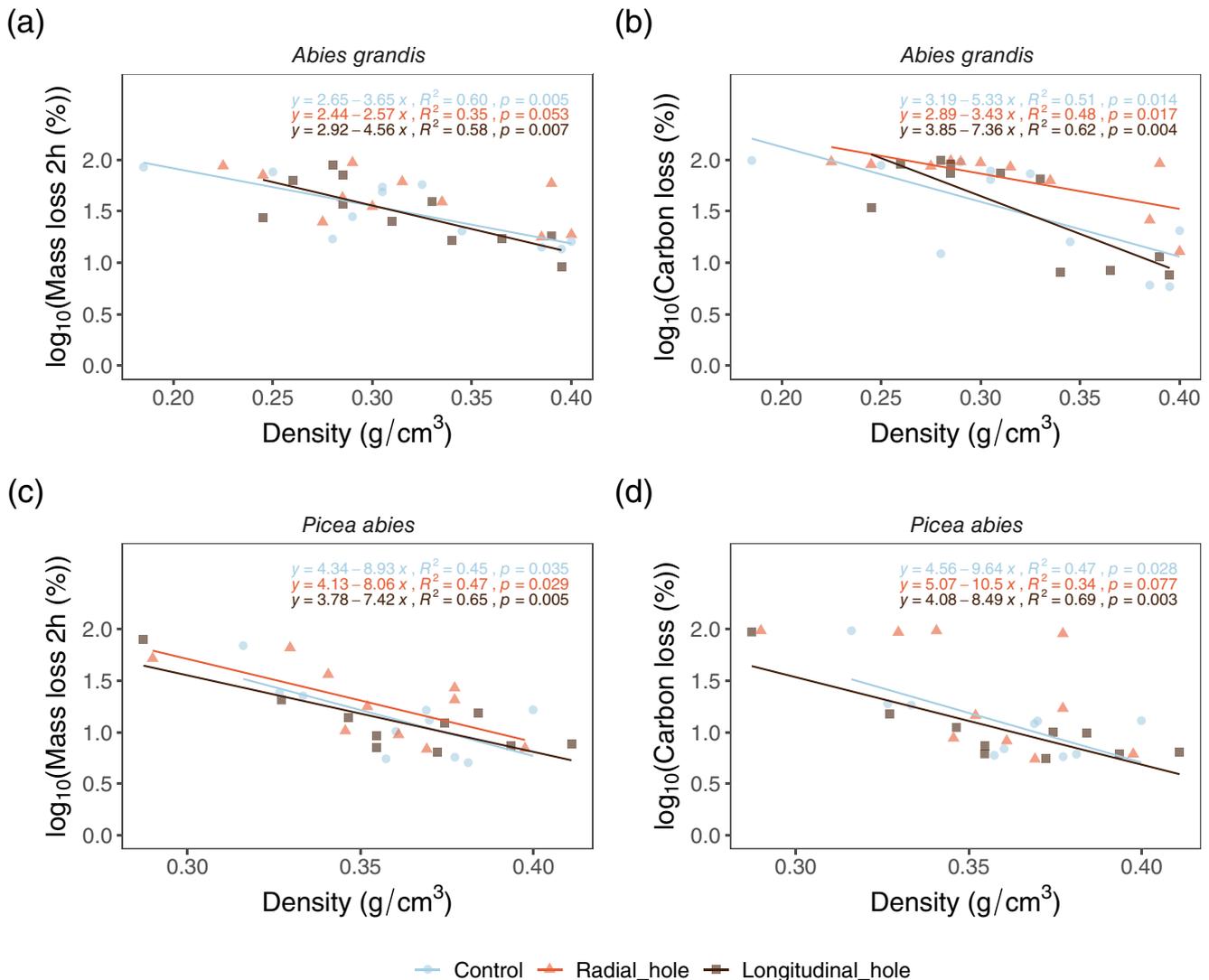
due to its potential effect as a confounding factor. Models were fitted with R package lmerTest (Kuznetsova et al., 2017) and tested by the Kenward–Roger’s method (Kenward & Roger, 1997). When a significant treatment effect was found, a post hoc test was used to determine pairwise differences between treatments. All models were

tested for normality and homogeneity of residual variance by visual inspection of residual and probability plots. All flammability parameters were  $\log_{10}$ -transformed to better fit the assumption of the models. Linear regression was used to check the correlation between wood density with flammability parameters, wood density with  $V_{\text{crack}}$ , and  $V_{\text{total}}$  with flammability parameters. All data were processed in R 4.2.2 (R Core Team, 2022).

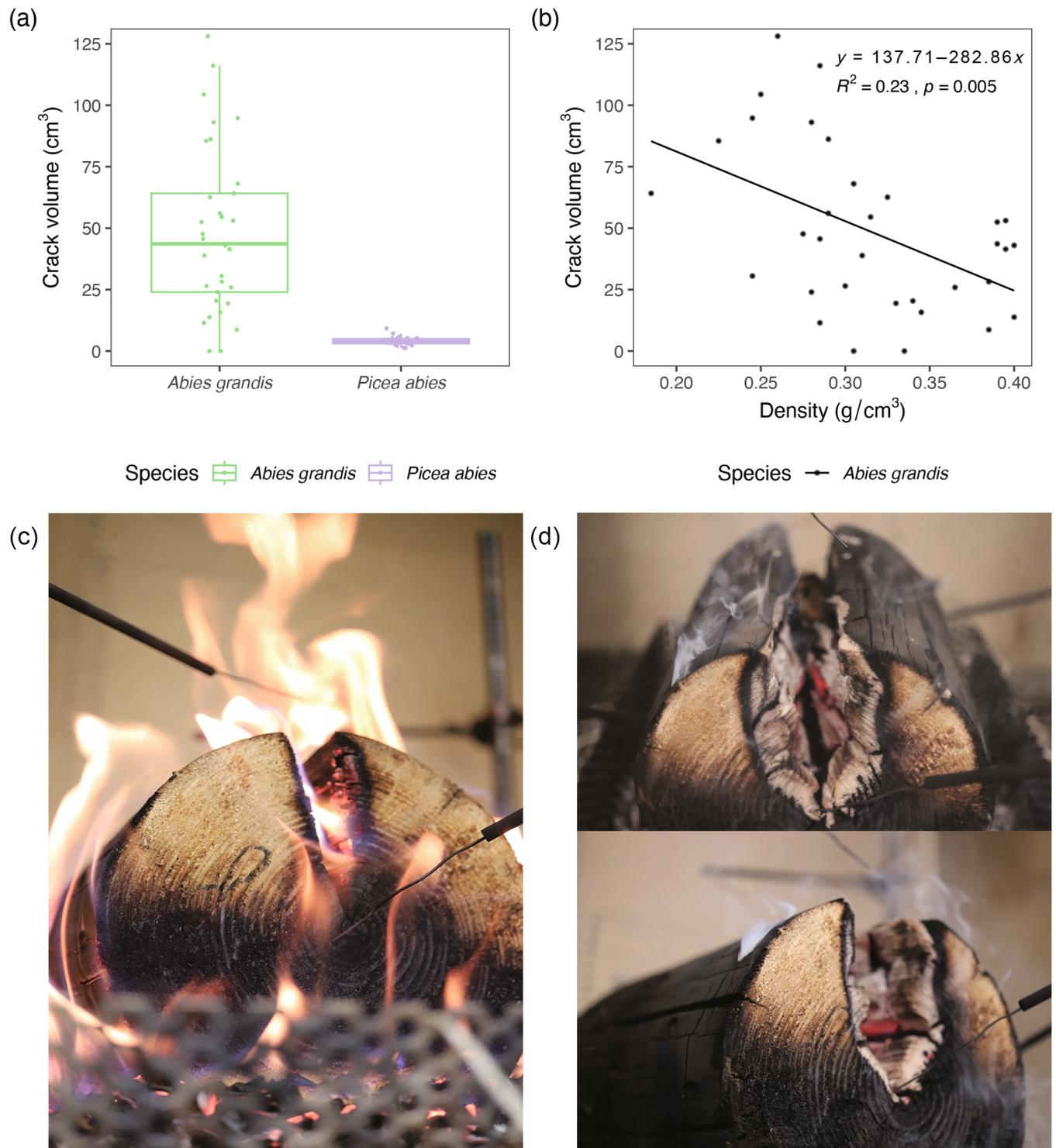
## RESULTS

The radial hole treatment (compared with control and with the longitudinal treatment) significantly increased  $ML_{2h}$  of *P. abies*, and  $ML_{\text{final}}$  and  $C_{\text{loss}}$  of both species,

and this response was not influenced by  $V_{\text{crack}}$  (Figure 1; Appendix S1: Tables S2 and S3). This lack of confounding effect of  $V_{\text{crack}}$  may be because the samples in each treatment came from the same logs and probably broadly shared the same pattern of crack formation, which is related to wood traits. Based on the significant treatment effects on  $ML_{2h}$ ,  $ML_{\text{final}}$ , and  $C_{\text{loss}}$ , we did a follow-up analysis to check the relationships of wood density with these parameters. Wood density had a negative correlation with all three flammability parameters (Figure 2; Appendix S1: Figure S5). These correlations were mostly significant except for those of density with  $ML_{2h}$  of *A. grandis* (Figure 2a), density with  $ML_{\text{final}}$  of *P. abies* (Appendix S1: Figure S5b), and density with  $C_{\text{loss}}$  of *P. abies* (Figure 2d) under the radial hole treatment. Wood cracked mostly in *A. grandis* logs (Figure 3a). We



**FIGURE 2** Relationships between wood density and two flammability parameters of *Abies grandis* and *Picea abies*. Mass loss 2 h represents percentage mass loss after 2 h (in percentage). Data were grouped by treatment (shown in different colors).  $R^2$  and  $p$  values are given. Only significant linear relations are shown with regression lines (see Appendix S1: Table S4).

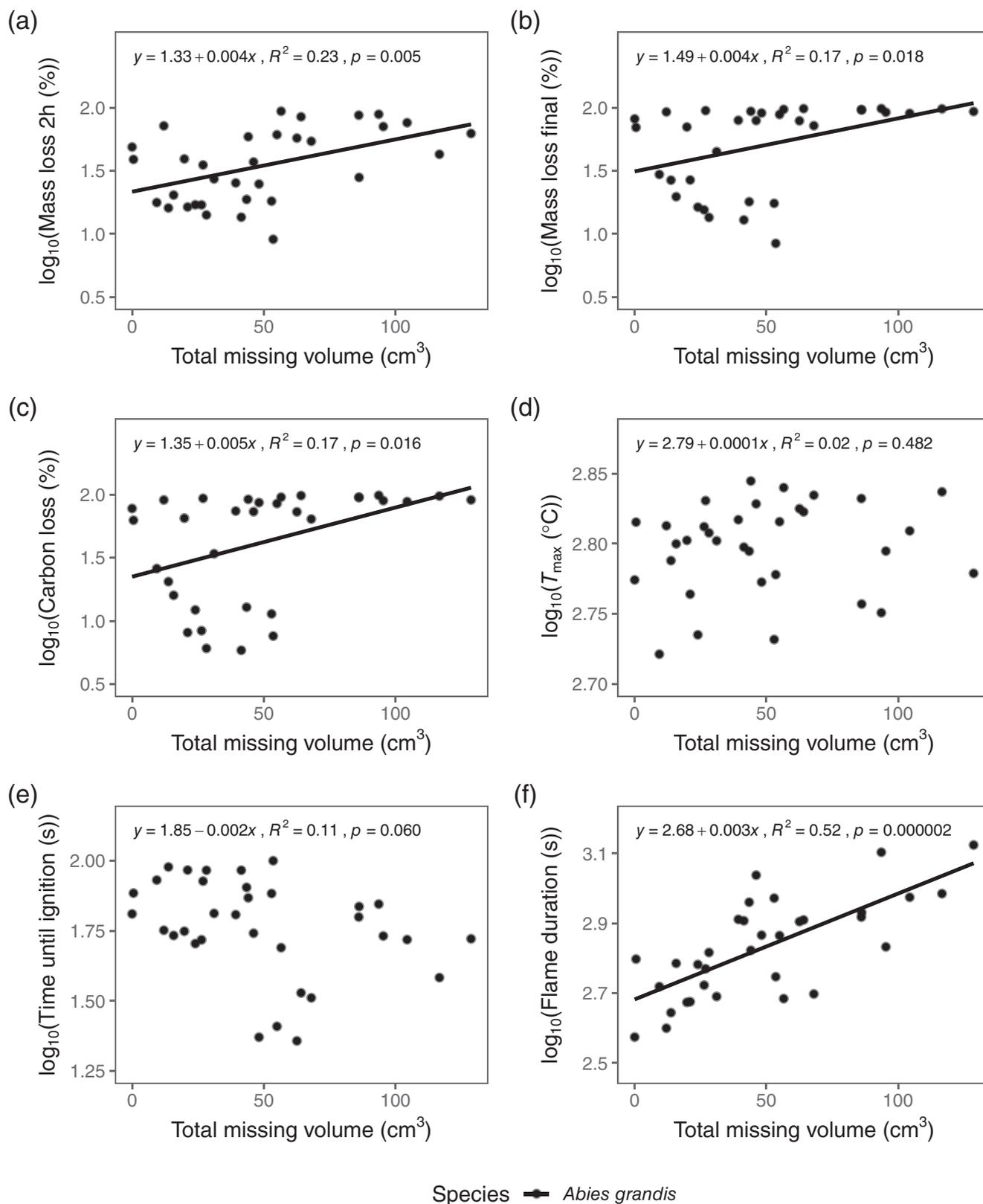


**FIGURE 3** (a) Boxplot showing the distribution of crack volume per log in *Abies grandis* and *Picea abies*. Dots are raw data. (b) Relationships between wood density and crack volume of *Abies grandis*.  $R^2$  and  $p$  values are given (see Appendix S1: Table S5). (c) Example of flame appearing from the sample crack. (d) Example of smoldering in the sample crack. Pictures in (c) and (d) were taken by Shudong Zhang.

considered the few very small cracks in *P. abies* logs as negligible and therefore excluded *P. abies* from further analyses.  $V_{\text{crack}}$  of *A. grandis* showed a significant negative correlation with wood density (Figure 3b).  $V_{\text{total}}$  in *A. grandis* was also significantly correlated with most flammability parameters (Figure 4).

## DISCUSSION

To our knowledge, this is the first study to provide empirical evidence that the presence of beetle holes in deadwood increases its flammability. Across two species, in support of our hypothesis, the radial hole treatment



**FIGURE 4** Relationships between total missing volume per log (due to cracks and drilled holes) and six flammability parameters of *Abies grandis*.  $R^2$  and  $p$  values are given. Only significant linear relations are shown with regression lines (see Appendix S1: Table S6). Mass loss 2 h represents percentage mass loss after 2 h (in percentage), mass loss final represents final percentage mass loss (in percentage), and  $T_{\max}$  represents mean maximum temperature (in degrees Celsius).

significantly increased sustainability and consumability of deadwood (Figure 1; Appendix S1: Tables S2 and S3).  $T_{\max}$ , TUI, and FD were not significantly influenced by the beetle hole treatment, which implies that beetle holes may not promote ignitability and intensity of the surface wildfire. An explanation for this may be that the deadwood structure itself makes it hard to catch and maintain a fire even with the help of beetle holes. However, the radial holes did promote deadwood smoldering, which means that deadwood invaded by wood-boring beetles will release more carbon into the atmosphere during burning.

### The key factor for CWD flammability: Ventilation

An increased surface-to-air ratio would improve wood internal ventilation, which, in turn, leads to increased flammability. All of our results supported previous studies that ventilation is the key factor for deadwood flammability (Cornelissen et al., 2017; Rothermel, 1972). Indeed, the beetle hole treatments, as well as the wood density,  $V_{\text{crack}}$ , and  $V_{\text{total}}$  we measured in this study, could all be assumed to be linked with oxygen availability in the wood. However, our results showed that, compared with the control treatment, only the radial hole treatment significantly increased part of the flammability variables of deadwood. The direction of radial holes may provide a favorable condition for air exchange as the hot air tends to rise upward; for example, smoke could be observed rising from the radial holes with the hot airflow (see Figure 3d; Appendix S1: Figure S4d). This difference may be the main reason why the radial hole treatment could significantly promote the deadwood smoldering process and associated  $C_{\text{loss}}$ . As the airflow in the fume hood was mainly upward from the logs, we expect that the longitudinal holes would have promoted smoldering and  $C_{\text{loss}}$  if positioned upright. In future research, it would therefore be relevant to incorporate both positions in the experimental design, as these positions should represent downed versus standing deadwood in the field. Meanwhile, as we set the same depth for radial and longitudinal holes, the effect of longitudinal holes could be weakened as considering the relatively longer log length in the longitudinal direction compared with the radial direction, the longitudinal side could have deeper holes. This is consistent with our anecdotal field observations of deeper natural longitudinal holes in some cases. Thus, future research should also check whether deeper longitudinal holes have a similar effect as radial holes.

Wood density, as an indicator of internal ventilation at the wood tissue scale, has been shown comprehensively

to be strongly correlated with deadwood flammability (Hyde et al., 2011, 2012; Zhao et al., 2018). In line with this, our results showed that density was negatively correlated with deadwood smoldering (Figure 2; Appendix S1: Figure S5). An interesting finding was that the correlations between wood density and flammability variables seemed to have been weakened by the radial hole treatment across species (Figure 2a,d; Appendix S1: Figure S5b). This would suggest that radial holes improved deadwood internal ventilation somehow (especially at higher wood densities), which then caused higher mass and C loss.

A wood crack (split) appears when wood shrinks as it dries, which is an inevitable natural process under pre-fire abiotic conditions. Formation of the crack can depend strongly on the species of wood, as different species of wood vary in their structure (e.g., in wood density). In our study, *A. grandis* had a lower density than *P. abies*, and *P. abies* deadwood barely cracked compared with *A. grandis*. This is probably caused by high density wood having low shrinkage rate due to its dense structure. The significant negative relationship between density and  $V_{\text{crack}}$  within wood of *A. grandis* is also in line with this pattern. Based on our observation in this study, the wood cracks increased the opportunities of a fire reaching into the wood. These cracks usually promoted the smoldering process of the wood. Together with the simulated beetle holes, their  $V_{\text{total}}$  influenced most flammability variable.

### The ecological meaning of experimental burns with CWD

Due to the compact shape and internal structure of coarse deadwood, it is difficult to get it to start burning by itself. Moreover, although Pinaceae species like *A. grandis* and *P. abies* have soft wood with lower wood density than most angiosperm species, they are more persistent on the forest floor owing to their low decomposition rates (Chang et al., 2020). This makes CWD of these species a substrate for both biological decomposition and wildfire on the soil surface. Meanwhile, leaf litter of *A. grandis* and *P. abies* tends to accumulate and form dense leaf litter layers due to their low decomposability (Zhang et al., 2023; Zuo et al., 2018). Although the dense litter bed structure reduces their litter layer flammability (Cornelissen et al., 2017; Zhang et al., 2023), under extreme conditions (drought combined with strong wind), the large fine litter fuel loads will still create severe fires which should provide enough heat to start and maintain CWD burning. Facilitated by the wood-boring beetle holes, CWD could lose part of its carbon sink function and could turn into a carbon source with its increased

flammability. This scenario is more and more likely to become a reality, as the ongoing climate change is turning our planet into a fire-prone world with frequent and unpredictable extreme weather including drought episodes (Ellis et al., 2022; Jain et al., 2022).

However, for a more comprehensive understanding of the role of wood-boring holes on the forest C balance, we need to also study their effect on CWD decomposition as the alternative C emission process. At the landscape scale, when tree mortality rates increase due to drought or other unfavorable climate events, the load of CWD on the forest surface will increase. Subsequently, as the CWD provides habitat and energy (as the food source) for wood-boring beetles, the populations of wood-boring beetles should also increase. With the holes they create, the CWD decomposition would be accelerated (which means lower wood density), as beetle holes could not only improve ventilation but also facilitate fungal and macro-detritivore colonization and stimulate wood breakdown (Jacobsen et al., 2017; Ulyshen, 2016).

In conclusion, our study has shown that wood-boring beetle holes increase deadwood flammability, with radial holes significantly enhancing smoldering and carbon release. Wood density and cracks also significantly affect deadwood flammability. Even when accounting for these factors, these radial holes continued to have a notable impact on deadwood flammability. Based on our findings (i.e., no treatment effect on fire temperatures), these beetle infections in wood would not make the wildfire more intense, but the increased amount of C released during wildfire may still contribute to further climate warming.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Zhang et al., 2024) are available in Figshare at <https://doi.org/10.6084/m9.figshare.26300371.v1>.

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## REFERENCES

- Anderegg, W. R. L., J. A. Hicke, R. A. Fisher, C. D. Allen, J. Aukema, B. Bentz, S. Hood, et al. 2015. "Tree Mortality from Drought, Insects, and Their Interactions in a Changing Climate." *New Phytologist* 208: 674–683.
- Anderson, H. E. 1970. "Forest Fuel Ignitibility." *Fire Technology* 6: 312–19.
- Arora, V. K., Y. Peng, W. A. Kurz, J. C. Fyfe, B. Hawkins, and A. T. Werner. 2016. "Potential Near-Future Carbon Uptake Overcomes Losses from a Large Insect Outbreak in British Columbia, Canada." *Geophysical Research Letters* 43: 2590–98.
- Brovkin, V., P. M. van Bodegom, T. Kleinen, C. Wirth, W. K. Cornwell, J. H. C. Cornelissen, and J. Kattge. 2012. "Plant-Driven Variation in Decomposition Rates Improves Projections of Global Litter Stock Distribution." *Biogeosciences* 9: 565–576.
- Canadell, J. G., and M. R. Raupach. 2008. "Managing Forests for Climate Change Mitigation." *Science* 320: 1456–57.
- Chang, C., R. S. P. van Logtestijn, L. Goudzwaard, J. van Hal, J. Zuo, M. Hefting, U. Sass-Klaassen, et al. 2020. "Methodology Matters for Comparing Coarse Wood and Bark Decay Rates across Tree Species." *Methods in Ecology and Evolution* 11: 828–838.
- Cornelissen, J. H. C., S. Grootemaat, L. M. Verheijen, W. K. Cornwell, P. M. van Bodegom, R. van der Wal, and R. Aerts. 2017. "Are Litter Decomposition and Fire Linked through Plant Species Traits?" *New Phytologist* 216: 653–669.
- Cornelissen, J. H. C., U. Sass-Klaassen, L. Poorter, K. van Geffen, R. S. P. van Logtestijn, J. van Hal, L. Goudzwaard, et al. 2012. "Controls on Coarse Wood Decay in Temperate Tree Species: Birth of the LOGLIFE Experiment." *Ambio* 41: 231–245.
- Cornwell, W. K., J. H. C. Cornelissen, S. D. Allison, J. Bauhus, P. Eggleton, C. M. Preston, F. Scarff, J. T. Weedon, C. Wirth, and A. E. Zanne. 2009. "Plant Traits and Wood Fates across the Globe: Rotted, Burned, or Consumed?" *Global Change Biology* 15: 2431–49.
- Ellis, T. M., D. M. J. S. Bowman, P. Jain, M. D. Flannigan, and G. J. Williamson. 2022. "Global Increase in Wildfire Risk Due to Climate-Driven Declines in Fuel Moisture." *Global Change Biology* 28: 1544–59.
- Harvey, B. J., D. C. Donato, W. H. Romme, and M. G. Turner. 2013. "Influence of Recent Bark Beetle Outbreak on Fire Severity and Postfire Tree Regeneration in Montane Douglas-Fir Forests." *Ecology* 94: 2475–86.
- Hlásny, T., S. Zimová, and B. Bentz. 2021. "Scientific Response to Intensifying Bark Beetle Outbreaks in Europe and North America." *Forest Ecology and Management* 499: 119599.
- Hurteau, M., and M. North. 2009. "Fuel Treatment Effects on Tree-Based Forest Carbon Storage and Emissions under Modeled Wildfire Scenarios." *Frontiers in Ecology and the Environment* 7: 409–414.
- Hurteau, M. D., G. W. Koch, and B. A. Hungate. 2008. "Carbon Protection and Fire Risk Reduction: Toward a Full Accounting of Forest Carbon Offsets." *Frontiers in Ecology and the Environment* 6: 493–98.
- Hyde, J. C., A. M. S. Smith, and R. D. Ottmar. 2012. "Properties Affecting the Consumption of Sound and Rotten Coarse

- Woody Debris in Northern Idaho: A Preliminary Investigation Using Laboratory Fires.” *International Journal of Wildland Fire* 21: 596–608.
- Hyde, J. C., A. M. S. Smith, R. D. Ottmar, E. C. Alvarado, and P. Morgan. 2011. “The Combustion of Sound and Rotten Coarse Woody Debris: A Review.” *International Journal of Wildland Fire* 20: 163–174.
- IPCC. 2021. *The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press.
- Jacobsen, R. M., H. Kauserud, A. Sverdrup-Thygeson, M. M. Bjorbækmo, and T. Birkemoe. 2017. “Wood-Inhabiting Insects Can Function as Targeted Vectors for Decomposer Fungi.” *Fungal Ecology* 29: 76–84.
- Jain, P., D. Castellanos-Acuna, S. C. P. Coogan, J. T. Abatzoglou, and M. D. Flannigan. 2022. “Observed Increases in Extreme Fire Weather Driven by Atmospheric Humidity and Temperature.” *Nature Climate Change* 12: 63–70.
- Kenward, M. G., and J. H. Roger. 1997. “Small Sample Inference for Fixed Effects from Restricted Maximum Likelihood.” *Biometrics* 53: 983–997.
- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. “Mountain Pine Beetle and Forest Carbon Feedback to Climate Change.” *Nature* 452: 987–990.
- Kurz, W. A., G. Stinson, G. J. Rampley, C. C. Dymond, and E. T. Neilson. 2008. “Risk of Natural Disturbances Makes Future Contribution of Canada’s Forests to the Global Carbon Cycle Highly Uncertain.” *Proceedings of the National Academy of Sciences of the United States of America* 105: 1551–55.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software* 82: 1–26.
- Lindner, M., M. Maroschek, S. Netherer, A. Kremer, A. Barbati, J. Garcia-Gonzalo, R. Seidl, et al. 2010. “Climate Change Impacts, Adaptive Capacity, and Vulnerability of European Forest Ecosystems.” *Forest Ecology and Management* 259: 698–709.
- Logan, J. A., J. Régnière, and J. A. Powell. 2003. “Assessing the Impacts of Global Warming on Forest Pest Dynamics.” *Frontiers in Ecology and the Environment* 1: 130–37.
- Luyssaert, S., G. Marie, A. Valade, Y.-Y. Chen, S. Njakou Djomo, J. Ryder, J. Otto, et al. 2018. “Trade-Offs in Using European Forests to Meet Climate Objectives.” *Nature* 562: 259–262.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Robbins, Z. J., C. Xu, B. H. Aukema, P. C. Buotte, R. Chitra-Tarak, C. J. Fettig, M. L. Goulden, et al. 2022. “Warming Increased Bark Beetle-Induced Tree Mortality by 30% during an Extreme Drought in California.” *Global Change Biology* 28: 509–523.
- Rothermel, R. C. 1972. *A Mathematical Model for Predicting Fire Spread in Wildland Fuels*. Res. Pap. INT-115. Ogden, UT: U.S. Department of Agriculture, Intermountain Forest and Range Experiment Station.
- Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, et al. 2017. “Forest Disturbances under Climate Change.” *Nature Climate Change* 7: 395–402.
- Sommerfeld, A., W. Rammer, M. Heurich, T. Hilmers, J. Müller, and R. Seidl. 2021. “Do Bark Beetle Outbreaks Amplify or Dampen Future Bark Beetle Disturbances in Central Europe?” *Journal of Ecology* 109: 737–749.
- Ulyshen, M. D. 2016. “Wood Decomposition as Influenced by Invertebrates.” *Biological Reviews* 91: 70–85.
- Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. “Consequences of Climate Change for Biotic Disturbances in North American Forests.” *Ecological Monographs* 83: 441–470.
- Wijas, B. J., S. D. Allison, A. T. Austin, W. K. Cornwell, J. H. C. Cornelissen, P. Eggleton, S. Fraver, et al. 2024. “The Role of Deadwood in the Carbon Cycle: Implications for Models, Forest Management, and Future Climates.” *Annual Review of Ecology, Evolution, and Systematics*. 55: 133–155.
- Zhang, S., W. K. Cornwell, W. Zhao, R. S. P. van Logtestijn, E. J. Krab, R. Aerts, and J. H. C. Cornelissen. 2023. “Experimental Evidence that Leaf Litter Decomposability and Flammability Are Decoupled across Gymnosperm Species.” *Journal of Ecology* 111: 761–772.
- Zhang, S., F. Dekker, R. S. P. van Logtestijn, and J. H. C. Cornelissen. 2024. “Do Wood-Boring Beetles Influence the Flammability of Deadwood? Figshare.” Dataset. <https://doi.org/10.6084/m9.figshare.26300371.v1>.
- Zhao, W., R. S. P. van Logtestijn, G. R. van der Werf, J. R. van Hal, and J. H. C. Cornelissen. 2018. “Disentangling Effects of Key Coarse Woody Debris Fuel Properties on Its Combustion, Consumption and Carbon Gas Emissions during Experimental Laboratory Fire.” *Forest Ecology and Management* 427: 275–288.
- Zuo, J., M. M. Hefting, M. P. Berg, R. S. P. van Logtestijn, J. van Hal, L. Goudzwaard, J.-C. Liu, et al. 2018. “Is There a Tree Economics Spectrum of Decomposability?” *Soil Biology and Biochemistry* 119: 135–142.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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