

ARTICLE

Variation in the contribution of macroinvertebrates to wood decomposition as it progresses

Melanie K. Taylor^{1,2}  | Michael D. Ulyshen¹ | Scott Horn¹ |
Emilee M. Poole¹ | Mac A. Callaham Jr.¹

¹USDA Forest Service, Southern Research Station, Athens, Georgia, USA

²Odum School of Ecology, University of Georgia, Athens, Georgia, USA

Correspondence

Melanie K. Taylor

Email: melanie.k.taylor@usda.gov

Funding information

Southern Research Station (SRS)

Handling Editor: Robert R. Parmenter

Abstract

Although necromass decay rates are limited by the slowest portions to decompose, most decomposition studies examine only the earliest stage of decay. As such, these studies run the risk of yielding misleading results regarding the relative contributions of different decomposers. For example, the contributions of macroinvertebrates to wood decomposition remain mostly unknown beyond the first 50% of mass lost, despite drastic changes in substrate conditions over time. We sought to clarify how the macroinvertebrate contribution to decay changes over the course of wood decomposition in the Southeastern United States—a region with a long history of wood decomposition research. To this end, we (1) compiled data from published studies comparing wood decay with and without macroinvertebrates; and (2) conducted a field study assessing wood mass loss, with and without macroinvertebrate access, at three sites across the region over four years. With these combined data, we analyzed macroinvertebrate contribution as decay progressed, revealing a quadratic relationship, wherein macroinvertebrate contribution increased early in decomposition and then began to decline as decay progressed. Strong local site effects, particularly the abundance and activity of termites, determine the time required for wood to reach this point of mass loss.

KEYWORDS

Blattodea, carbon cycling, carbon storage, ecosystem service, insects, saproxylic, termite

INTRODUCTION

Dead and decaying material (necromass) represents a substantial fraction of terrestrial carbon, and its decomposition is the primary pathway by which this carbon moves from the biosphere to the atmosphere (Pan et al., 2011; Schlesinger & Bernhardt, 2013). Although necromass consists of both labile and recalcitrant fractions, the decay rates of these different components can vary greatly

(Benbow et al., 2019), and the decay rate of the recalcitrant portions ultimately determines the rate of the overall process. For example, as wood decays, the softest and most nutritious components (e.g., sapwood) decompose first, while the more recalcitrant portions (e.g., heartwood or the late-season layers of annual growth rings) are the slowest to decompose (i.e., the rate-determining step; Ulyshen, 2016). Although wood decomposition is largely driven by microbes, particularly fungi enzymatically

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Published 2023. This article is a U.S. Government work and is in the public domain in the USA. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

capable of catabolizing lignocellulose, there is a growing awareness that wood-feeding macroinvertebrates, especially termites, are a major driver of wood decay rates. Two recent global experiments, for instance, estimated that insects may account for 29% of the carbon flux from dead wood globally (Seibold et al., 2021), and that the temperature sensitivity of termites largely drives rates of wood decay (Zanne et al., 2022).

Although recent studies have made it clear that macroinvertebrates are a major determinant of wood decay rates, most studies of wood decomposition measure only one time point and therefore fail to follow the decay process as it progresses (Oberle et al., 2020). While this is understandable, given that wood can require (depending on climate, wood species, soil contact, etc.) decades or even centuries to decompose completely, the short duration of most studies ultimately fails to address questions about the contributions of macroinvertebrates over the entire decay process. The issue of study length is critical because wood experiences significant chemical and physical changes as it decomposes, and as such, findings based on the early phases of decomposition cannot be reliably applied (or assumed) to be representative of the entire process. For instance, macroinvertebrates may contribute more to decomposition at certain stages than others due to wood changes over time that make it more or less hospitable, which may also depend on substrate quality (Guo et al., 2021). If the contribution of macroinvertebrates does change as decay progresses, studies focused only on the early stages of decay will not accurately reflect the contributions of macroinvertebrates to the entire process, and as a result, they risk over- or underestimating rates of wood decay, which could cause misestimation of carbon pools represented by dead wood.

Previous research on the topic has largely focused on termites and found that wood traits are a strong driver of their contribution to decomposition. For instance, Liu et al. (2015) found that termites preferentially consume wood with a lower initial density (soft wood). Further research showed that tree species traits associated with the wood economics spectrum—from acquisitive to conservative tree species—determined wood decomposition attributable to termites (Guo et al., 2021). A subsequent study found that wood traits were predictive of microbial, but not termite-driven decay (Law et al., 2023), suggesting results may be dependent on species (trees and termites) and/or climatic variables. Guo et al. (2021) also found that termite-driven decomposition was higher in lower quality wood (from conservative tree species) later in the decay process, suggesting that some degree of microbial decay may make wood more palatable for termites, highlighting likely interactions among different groups of decomposers.

In this research, we sought to better understand how the contributions of macroinvertebrates to wood decomposition change from early- to late stages of decay. To that end, we compiled data from literature on studies comparing wood decay with and without macroinvertebrates. We focused on the Southeastern United States (hereafter southeast), which is a well-studied region in this regard, providing many observations of wood decay over time for analysis. We used wood mass loss data from these studies to calculate the macroinvertebrate contribution to mass loss as decay progressed. To provide additional data points at later stages of decay, we measured wood mass loss (with and without macroinvertebrate access) over four years in three physiographic provinces of the southeast (Blue Ridge Mountains, Piedmont, and Atlantic Coastal Plain). Because we expected that macroinvertebrates, particularly termites, might contribute more to decay in the early than later stages, we hypothesized that the macroinvertebrate contribution would exhibit a quadratic relationship with wood mass loss, where the macroinvertebrate contribution increased to a point, and then declined as decay progressed. We further hypothesized that no such relationship would exist with time, that is, year of observation.

MATERIALS AND METHODS

To determine the pattern of macroinvertebrate contribution to mass loss as decay progressed in the southeast, we utilized multiple datasets (Appendix S1: Table S1) from the region (Appendix S1: Figure S1) that measured wood mass loss with and without macroinvertebrates. From each dataset, we extracted the average mass loss data for each wood species, each treatment (or only experimental controls if treatments involved manipulation, e.g., sealing of wood), and each site, for each time of observation (if multiple included), with and without macroinvertebrates. We then calculated the percentage of mass loss attributable to macroinvertebrates (hereafter macroinvertebrate contribution) using Equation (1).

$$\text{Macroinvertebrate contribution (\% of mass loss)} = \left(\frac{\% \text{ mass loss (Macroinvertebrate included)} - \% \text{ mass loss (Macroinvertebrate excluded)}}{\% \text{ mass loss (Macroinvertebrate included)}} \right) \times 100. \quad (1)$$

To add additional mass loss values at later stages of decay to our analysis, we measured mass loss of Monterey pine (*Pinus radiata*) D. Donn. in three physiographic provinces of the southeast (Appendix S1:

Figure S1): (1) Blue Ridge Mountains (Coweeta Experimental Forest, NC; hereafter Coweeta), (2) Piedmont (Hitchiti Experimental Forest, GA; hereafter Hitchiti), and (3) Atlantic Coastal Plain (Savannah River Site, SC; hereafter SRS). Both Hitchiti and SRS have mixed pine–oak overstory vegetation, while Coweeta has a mixed oak–hickory–tulip poplar overstory. Coweeta has an elevation of 1158 m with a mean annual temperature (MAT) of 13.7°C and mean annual precipitation (MAP) of 183.3 cm (NCEI, 2021). Hitchiti and SRS have similar climates (Hitchiti: MAT 18.6°C, MAP 119.2 cm; SRS: MAT 17.7°C, MAP 119.8 cm; NCEI, 2021) but differing elevations (Hitchiti: 113.1 m; SRS: 61 m).

At each site, we set out paired baits (with and without macroinvertebrate access) consisting of blocks (two pieces of stacked, untreated, planed, dried, and weighed *P. radiata* wood; measuring 16.7 cm long × 6.3 cm wide × 1.8 cm deep for a total bait volume of 378.76 cm³) enveloped in nylon mesh (300 μm), following the protocol used in Zanne et al. (2022). The mesh allowed fungal hyphae to penetrate but not macroinvertebrates. In half the baits, 10 holes (5 mm) were placed on the soil-facing side of the mesh bag to allow colonization by soil-dwelling macroinvertebrates. Eighty pairs of baits were deployed in January 2017 at all sites with one pair every 5 m in straight transects (Appendix S1: Figure S2), with plans to collect 20 pairs every year for four years. Baits were placed on the soil surface after removing the leaf litter layer by hand. Once the baits were placed, a shade cloth (70%) was placed over them and pinned to the ground.

We collected pairs of baits from each site in January 2018, 2019, 2020, and 2021. Upon collection, the remaining wood from each bait was dried (105°C for 72 h) and weighed to determine the percentage of mass loss. For baits that had heavy termite usage, soil was manually removed before weighing. The mesh of some baits was noticeably damaged (likely from animal chewing) and these were not included in the analyses. Others were missing entirely, and at Hitchiti, most of the remaining baits were destroyed in a fire that occurred in the spring of 2018 (see Appendix S1: Table S2 for the number of baits included in the analyses). For each recovered bait, termite and fungal impacts were scored on a scale from 0 to 4 (Appendix S1: Figures S3–S6), wherein 0 was assigned to sound wood, 1 to perceptible but very limited changes, 2 to clear changes to a moderate extent, 3 to severe changes, and 4 to breakage, in accordance with the methods of Davies et al. (1999). For those blocks with active termites, we identified them all to be *Reticulitermes virginicus* Banks, 1907 using the key in Lim and Forschler (2012).

Statistical analyses

Using our compilation of data (Taylor et al., 2023) from the southeast and our added measurements, we created two linear mixed-effects models (all analyses conducted using R version 4.2.2; R Core Team, 2022; lmer function in lme4 package; Bates et al., 2014). The first, “mass loss model,” examined the macroinvertebrate contribution at observed values of mass loss. In this model, we used the percentage of mass loss (invertebrates included) and the squared percentage of mass loss ([% mass loss]²) as non-interacting fixed effects. The second, “year model,” examined the macroinvertebrate contribution at year of observation. Similarly, in this model, we used the year of observation and the squared year of observation ([year of observation]²) as non-interacting fixed effects. For both models, wood species and the study from which the data were extracted were included as non-interacting random intercepts. Random effects that explained no variance were removed from the model. Significance was assessed using the Wald χ^2 test (Anova function in car package; Fox & Weisberg, 2019), and model fit was assessed by conditional R^2 (r.squaredGLMM function in MuMIn package; Bartoń, 2022).

To compare our additional wood mass loss data in the three physiographic provinces of the southeast, we analyzed wood mass loss percentage using a linear model where location, macroinvertebrate access, and year were treated as explanatory variables. Significance was assessed using ANOVA (Anova function in car; Fox & Weisberg, 2019). Post hoc comparisons of year 4 data were conducted using estimated marginal means (emmeans function in emmeans package; Lenth, 2022) with the Sidak adjustments for multiple comparisons.

RESULTS

In our compiled dataset from the southeast along with our added measurements, we analyzed 41 observations of wood mass loss (average mass loss: 40.4%, average year of observation: 2.0). From the mass loss model (conditional $R^2 = 0.32$; Table 1), we found that the

TABLE 1 Results from the fixed effects of our model of macroinvertebrate contributions to wood mass loss as explained by mass loss in the Southeastern United States.

Fixed effects	Estimate	SE	χ^2 (df)	p
Intercept	−7.37	7.22	...	...
% mass loss	0.86	0.34	6.38 (1)	0.01
(% mass loss) ²	−0.01	0.004	3.40 (1)	0.07

contributions of macroinvertebrates to decay increased with increasing mass loss before beginning a downward trend (Figure 1a), consistent with our hypothesis. The mass loss model predicted that the macroinvertebrate contribution to wood decay peaks at 20.8% when mass loss reaches 64.0% before declining to 16.7% at 89% mass

loss. The study from which the data were extracted accounted for 14.2% of the random effect variance. Wood species did not account for any random effect variance in either model and was removed from the final version. From the year model (conditional $R^2 = 0.15$; Table 2), we found no relationship between the

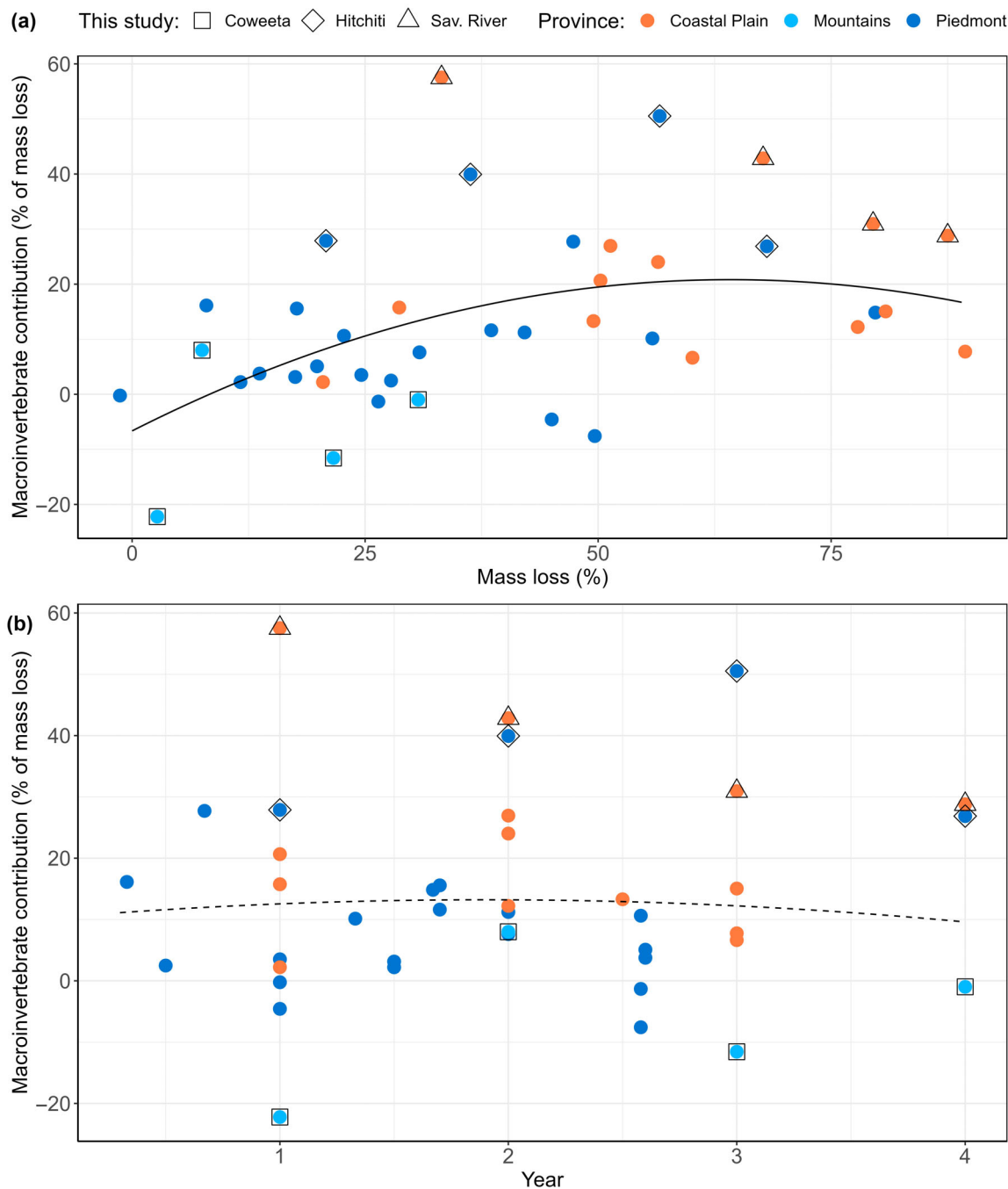


FIGURE 1 Macroinvertebrate contribution to mass loss over the course of decay: (a) average percentage of mass loss and (b) year, for studies conducted in the Southeastern United States. Colors denote the physiographic province in which the study occurred. Symbols represent the data from the three locations added in this study. Lines represent the quadratic model predictions ($R^2 = 0.32$ in panel a; $R^2 = 0.15$ in panel b) and significance is denoted by a solid line. Negative values of macroinvertebrate contribution result from the percentage of mass loss without invertebrate access being greater than those with macroinvertebrate access (see Equation 1).

contributions of macroinvertebrates to decay and year of observation (Figure 2), in support of our hypothesis. The study from which the data were extracted accounted for 15% of the random effect variance of this model.

Of the provinces represented by observations of wood decomposition in our compiled dataset, most (56.1%) were from studies conducted on the Piedmont, while 34.1% were from the Coastal Plain, and only the sites from the study presented herein were available from the Blue Ridge Mountains (9.8%; Figure 1). Among the three locations sampled in the current study, the quadratic relationship was most striking at the SRS (Figure 1a). There, the macroinvertebrate contribution decreased from 58% after one year to only 29% after four years. The pattern at Hitchiti was less dramatic, possibly due to lower termite activity relative to SRS, but was still

consistent with the quadratic relationship detected in our analysis.

We found that within our added data from the three provinces of the southeast, the wood mass loss percentage differed significantly among locations ($F_{2,370} = 168.7$, $p < 0.001$), macroinvertebrate access ($F_{1,370} = 41.4$, $p < 0.001$), and years ($F_{3,370} = 92.9$, $p < 0.001$; overall model adjusted $R^2 = 0.63$; Figure 2). For those baits with macroinvertebrate access, at the end of the study, mean wood mass loss at SRS was 2.9 times greater than at Coweeta and 1.3 times greater than at Hitchiti. For those baits without macroinvertebrate access, at the end of the study, mean wood mass loss at SRS was 2 times greater than at Coweeta and 1.3 times greater than at Hitchiti. Post hoc comparisons of the final year of the study revealed that there was an effect of macroinvertebrate access at SRS and Hitchiti ($t = 4.18$, $df = 81$, $p < 0.001$; $t = 2.34$, $df = 81$, $p = 0.06$), but not at Coweeta ($p > 0.1$). Examination of termite and fungal degradation categories further highlights the effects of location and year. These data indicate that termites discovered all blocks at SRS during the first year, fewer than half at Hitchiti, and none at Coweeta (Figure 3). Microbial decomposition followed a similar pattern, showing the fastest decay at SRS, followed by Hitchiti, and then Coweeta (Figure 4).

TABLE 2 Results from the fixed effects of our model of macroinvertebrate contributions to wood mass loss as explained by year in the Southeastern United States.

Fixed effects	Estimate	SE	χ^2 (df)	p
Intercept	10.19	11.45	...	...
Year	3.12	11.06	0.08 (1)	0.78
Year ²	−0.82	2.49	0.11 (1)	0.74

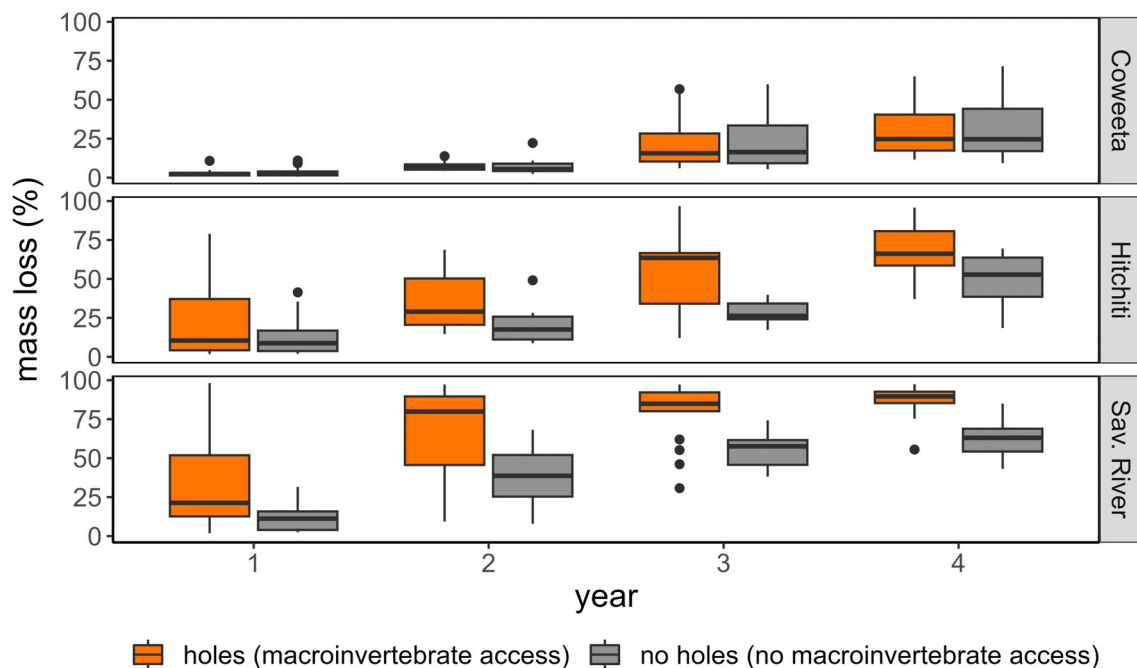


FIGURE 2 Mass loss percentage in three physiographic provinces of the Southeastern United States across four years with and without macroinvertebrate access. Each box represents the interquartile range (IQR) and the horizontal line inside each box is the median value. The whiskers on each box represent the minimum and maximum values that are within $1.5 \times$ IQR. Points that fall beyond those values are plotted individually.

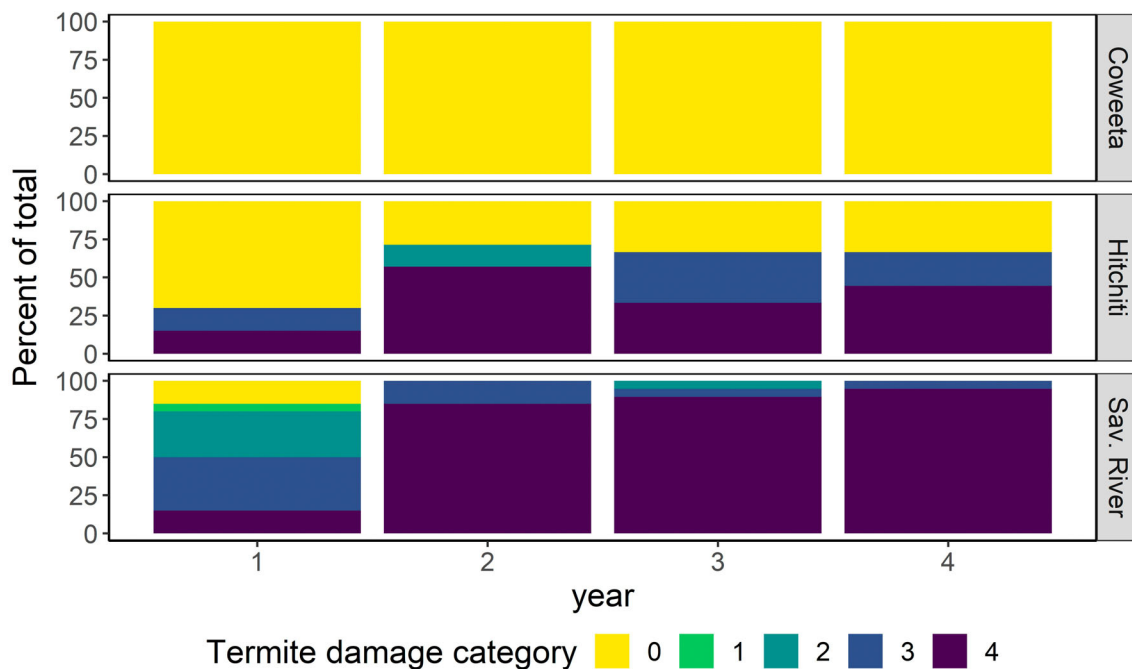


FIGURE 3 The percentage of total baits (with macroinvertebrate access) in different categories of termite damage in three physiographic provinces of the Southeastern United States across four years. Termite damage was rated from 0 (sound wood) to 4 (breakage) for each bait.

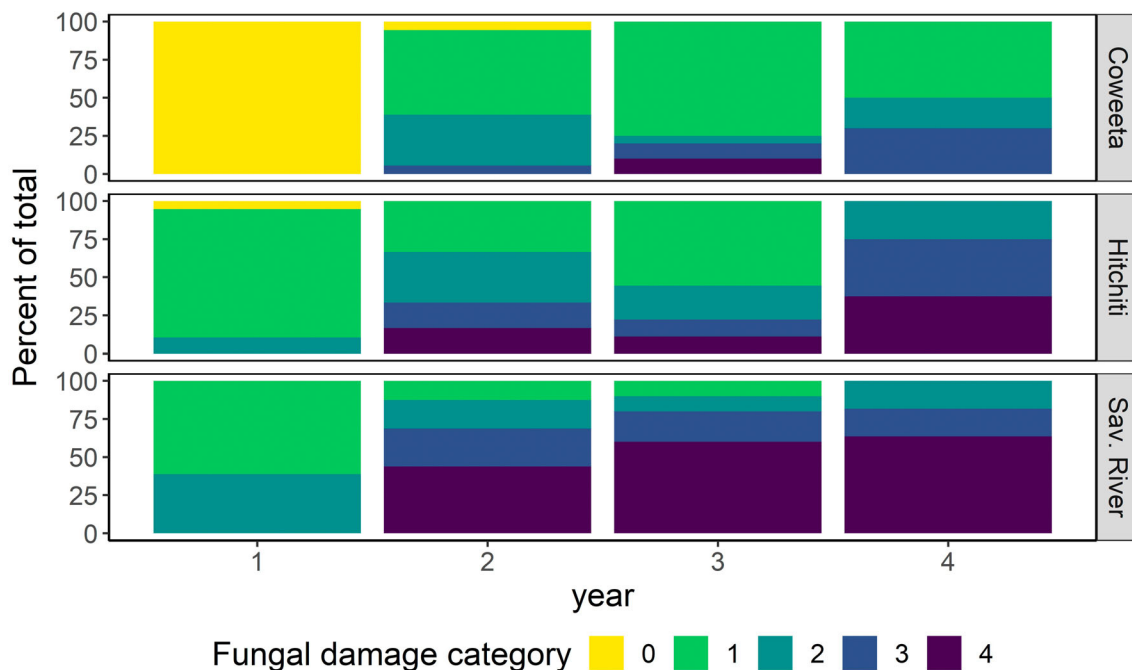


FIGURE 4 The percentage of total baits (without macroinvertebrate access) in different categories of fungal damage in three physiographic provinces of the Southeastern United States across four years. Fungal damage was rated from 0 (sound wood) to 4 (breakage) for each bait.

DISCUSSION

The main objective of this study was to clarify how the contributions of macroinvertebrates to wood decomposition

varied as decomposition proceeded. We did this by (1) comparing macroinvertebrate contribution to wood mass loss from several studies in the southeast and (2) measuring wood decay, with and without macroinvertebrate access,

yearly for four years in three physiographic provinces of the region. Our results demonstrate, for the first time, that a quadratic relationship exists between macroinvertebrate contribution and stage of decomposition (i.e., % mass loss; Figure 1a).

Our findings are consistent with the idea that macroinvertebrates, particularly termites, are discriminant feeders that play a lesser role in wood decomposition after the softer and more nutritious portions have been consumed. Support for this comes from work from Mississippi where Ulyshen et al. (2014) found that termites preferentially consumed the softer portions of annual growth rings while leaving the denser portions relatively intact. Moreover, it is not uncommon for termites to abandon logs at later stages of decay (Oberst et al., 2018), leaving further decomposition to microbial activity. Thus, the completion of decomposition by fungi and various microbes may erode the perceived impact of termites at later stages of decay. Although these results indicate that macroinvertebrates may be less important to wood decomposition overall than suggested by short-term studies, it is important to note that macroinvertebrates still contributed significantly to decomposition after four years in this study. For example, at SRS, about 29% of mass loss was still attributable to macroinvertebrates after four years (>80% mass loss; Figure 1b), suggesting that the accelerative effects of these insects on wood decomposition can be detected even at the end of the decomposition process.

Our wood mass loss data from the three physiographic provinces of the southeast provide further evidence that strong local site characteristics are largely responsible for observed patterns in wood decay (Bradford et al., 2014). We found that wood decayed faster at SRS than at Hitchiti, and experienced faster termite and fungal degradation (Figures 3 and 4), though the two sites have similar climates. One potential explanation for this difference is that termites are more abundant or active at SRS than at Hitchiti. This is supported by the rapidity with which termites encountered and damaged baits at SRS compared to Hitchiti (Figure 3), though the reason for this difference is unclear. One potential explanation for this difference in termite abundance/activity is that regular fires at Hitchiti alter fungal communities in ways that inhibit fungal decay (Oliver et al., 2015) and impact termite activity, particularly given that some fungi may have an inhibitory effect on termites (Kirker et al., 2012). Wood decay proceeded most slowly at Coweeta, where we observed mass loss of only 31% after four years (Figure 1b) and no termite damage (Figure 3), suggesting very low abundances or activities of termites.

There are caveats and limitations to our findings. First, our results are from one region of North America,

and may not extend to other parts of the world. For example, termites are known to contribute substantially to wood decomposition in tropical and arid climates (Zanne et al., 2022), and more so than in subtropical and temperate areas. A fruitful area for future research could be in determining whether a quadratic relationship such as the one observed here is found in other climates. Another limitation we acknowledge is that our added data from the three provinces of the southeast used only one wood species. The trajectory of wood decomposition is influenced by plant traits (Guo et al., 2021), the effects of which change over the course of decomposition (Oberle et al., 2020). Further research may consider whether tree species effects alter the observed relationship we report here. A further methodological limitation is that studies included here using mesh bags (Appendix S1: Table S1) that fully encapsulate wood and provide belowground openings do not allow macroinvertebrate access from above, which likely underestimates the total macroinvertebrate contribution to decomposition.

Our findings support the conclusion that macroinvertebrates accelerate wood decomposition, but indicate that studies measuring macroinvertebrate effects on decay in the early stages of mass loss may overestimate their importance. We suspect that this pattern may be common among decomposer communities, wherein the early stages of decomposition are characterized by intense competition between invertebrates and other taxa for the most nutritious or easily digestible components while later stages may be dominated by specialist taxa better equipped to utilize late-stage substrates. Although the results from this study suggest invertebrates may become less important to wood decomposition near the end of the process, this may not be the case for all decomposing matter, or even for all forms of woody debris. Among carrion-feeders, for instance, certain beetle species (e.g., Trogidae) are known to play a key role in the consumption of hide, hair, and feathers remaining at the end of the decomposition process (Horenstein & Linhares, 2011). Similarly, insects may play a more important role at late stages of wood decomposition under certain conditions than suggested by the current study. For example, Ulyshen and Sheehan (2021) suggested that termites or carpenter ants may be important players in the degradation of longleaf pine heartwood in the Southeastern United States. Because the wooden blocks used in the current study lacked heartwood, further research is needed to explore this question.

ACKNOWLEDGMENTS

We thank the USDA Forest Service Southern Research Station (SRS) for funding this work and SRS's Experimental

Forest Network and the Department of Energy's Savannah River Site for serving as experiment locations. We are grateful to Amy Zanne for the protocol for the baits, to Amy Janvier and Xiumin Yan for assistance processing wood blocks, to Nina Wurzbürger for helpful conversations regarding the analyses, and to Lee Dietterich for suggestions on an earlier version of the manuscript. Two anonymous reviewers provided substantial feedback, which greatly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Taylor et al., 2023) are available from the USDA Forest Service Research Data Archive: <https://doi.org/10.2737/RDS-2023-0056>.

ORCID

Melanie K. Taylor  <https://orcid.org/0000-0003-4611-5156>

REFERENCES

- Bartoń, K. 2022. "MuMIn: Multi-Model Inference." R Package Version 1.46.0. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "Fitting Linear Mixed-Effects Models Using lme4." arXiv Preprint arXiv:1406.5823.
- Benbow, M. E., P. S. Barton, M. D. Ulyshen, J. C. Beasley, T. L. DeVault, M. S. Strickland, J. K. Tomberlin, H. R. Jordan, and J. L. Pechal. 2019. "Necrobiome Framework for Bridging Decomposition Ecology of Autotrophically and Heterotrophically Derived Organic Matter." *Ecological Monographs* 89(1): e01331.
- Bradford, M. A., R. J. Warren, II, P. Baldrian, T. W. Crowther, D. S. Maynard, E. E. Oldfield, W. R. Wieder, S. A. Wood, and J. R. King. 2014. "Climate Fails to Predict Wood Decomposition at Regional Scales." *Nature Climate Change* 4(7): 625–630.
- Davies, R. G., P. Eggleton, L. Dibog, J. H. Lawton, D. E. Bignell, A. Brauman, C. Hartmann, L. Nunes, J. Holt, and C. Rouland. 1999. "Successional Response of a Tropical Forest Termite Assemblage to Experimental Habitat Perturbation." *Journal of Applied Ecology* 36(6): 946–962.
- Fox, J., and S. Weisberg. 2019. *An {R} Companion to Applied Regression*, 3rd ed. Thousand Oaks, CA: Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.
- Guo, C., B. Tuo, H. Ci, E. R. Yan, and J. H. Cornelissen. 2021. "Dynamic Feedbacks among Tree Functional Traits, Termite Populations and Deadwood Turnover." *Journal of Ecology* 109(4): 1578–90.
- Horenstein, B. M., and A. X. Linhares. 2011. "Seasonal Composition and Temporal Succession of Necrophagous and Predator Beetles on Pig Carrion in Central Argentina." *Medical and Veterinary Entomology* 25: 395–401. <https://doi.org/10.1111/j.1365-2915.2011.00969.x>.
- Kirker, G. T., T. L. Wagner, and S. V. Diehl. 2012. "Relationship between Wood-Inhabiting Fungi and *Reticulitermes* spp. in Four Forest Habitats of Northeastern Mississippi." *International Biodeterioration & Biodegradation* 72: 18–25.
- Law, S., H. Flores-Moreno, A. W. Cheesman, R. Clement, M. Rosenfield, A. Yatsko, L. A. Cernusak, et al. 2023. "Wood Traits Explain Microbial but Not Termite-Driven Decay in Australian Tropical Rainforest and Savanna." *Journal of Ecology* 111(5): 982–993.
- Lenth, R. 2022. "emmeans: Estimated Marginal Means, aka Least-Squares Means." R Package Version 1.7.3. <https://CRAN.R-project.org/package=emmeans>.
- Lim, S. Y., and B. T. Forschler. 2012. "*Reticulitermes nelsonae*, a New Species of Subterranean Termite (Rhinotermitidae) from the Southeastern United States." *Insects* 3(1): 62–90. <https://doi.org/10.3390/insects3010062>.
- Liu, G., W. K. Cornwell, K. Cao, Y. Hu, R. S. Van Logtestijn, S. Yang, X. Xie, et al. 2015. "Termites Amplify the Effects of Wood Traits on Decomposition Rates among Multiple Bamboo and Dicot Woody Species." *Journal of Ecology* 103(5): 1214–23.
- National Centers for Environmental Information (NCEI). 2021. "National Oceanic and Atmospheric Administration (NOAA)." <https://www.ncei.noaa.gov/access/us-climate-normals/>.
- Oberle, B., M. R. Lee, J. A. Myers, O. L. Osazuwa-Peters, M. J. Spasojevic, M. L. Walton, D. F. Young, and A. E. Zanne. 2020. "Accurate Forest Projections Require Long-Term Wood Decay Experiments because Plant Trait Effects Change through Time." *Global Change Biology* 26(2): 864–875.
- Oberst, S., J. C. Lai, and T. A. Evans. 2018. "Key Physical Wood Properties in Termite Foraging Decisions." *Journal of the Royal Society Interface* 15(149): 20180505.
- Oliver, A. K., M. A. Callaham, Jr., and A. Jumpponen. 2015. "Soil Fungal Communities Respond Compositionally to Recurring Frequent Prescribed Burning in a Managed Southeastern US Forest Ecosystem." *Forest Ecology and Management* 345: 1–9.
- Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, P. E. Kauppi, W. A. Kurz, O. L. Phillips, et al. 2011. "A Large and Persistent Carbon Sink in the World's Forests." *Science* 333(6045): 988–993.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Schlesinger, W. H., and E. S. Bernhardt. 2013. *Biogeochemistry: An Analysis of Global Change*. New York: Academic Press.
- Seibold, S., W. Rammer, R. Hothorn, R. Seidl, M. D. Ulyshen, J. Lorz, M. W. Cadotte, et al. 2021. "The Contribution of Insects to Global Forest Deadwood Decomposition." *Nature* 597(7874): 77–81.
- Taylor, M. K., M. D. Ulyshen, S. Horn, E. M. Poole, and M. A. Callaham, Jr. 2023. *Macroinvertebrate Contributions to Wood Decomposition as It Progresses in the Southeastern USA*. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2023-0056>.
- Ulyshen, M. D. 2016. "Wood Decomposition as Influenced by Invertebrates." *Biological Reviews* 91(1): 70–85.
- Ulyshen, M. D., and T. N. Sheehan. 2021. "The Importance of Termites and Fire to Dead Wood Consumption in the Longleaf Pine Ecosystem." *Scientific Reports* 11(1): 1–7.

- Ulyshen, M. D., T. L. Wagner, and J. E. Mulrooney. 2014. "Contrasting Effects of Insect Exclusion on Wood Loss in a Temperate Forest." *Ecosphere* 5(4): 1–15.
- Zanne, A. E., H. Flores-Moreno, J. R. Powell, W. K. Cornwell, J. W. Dalling, A. T. Austin, A. T. Classen, et al. 2022. "Termite Sensitivity to Temperature Affects Global Wood Decay Rates." *Science* 377(6613): 1440–44.

SUPPORTING INFORMATION

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

How to cite this article: Taylor, Melanie K., Michael D. Ulyshen, Scott Horn, Emilee M. Poole, and Mac A. Callaham Jr.. 2024. "Variation in the Contribution of Macroinvertebrates to Wood Decomposition as it Progresses." *Ecosphere* 15(2): e4714. <https://doi.org/10.1002/ecs2.4714>