



CO₂ and CH₄ fluxes from standing dead trees in a northern conifer forest

5 Christian Hettwer ¹, Kathleen Savage ², Andrew Ouimette ³, Jay Wason ¹, Roel Ruzol ¹, Shawn Fraver ¹

¹ School of Forest Resources, University of Maine, Orono, ME 04469, USA

² Woodwell Climate Research Center, Falmouth, MA 02540, USA

³ USDA Forest Service, Northern Research Station, Durham, NH 03825, USA

Correspondence to: Christian Hettwer (christian.hettwer@maine.edu)



10 **Abstract.** Representing 15 – 20% of aboveground biomass in forests, deadwood is an important,
yet understudied, component of ecosystem greenhouse gas (GHG) fluxes. In particular, standing
dead trees (snags) can serve as conduits for the atmospheric flux of carbon dioxide (CO₂) and
methane (CH₄), with fluxes varying according to environmental conditions. We measured CO₂ and
CH₄ fluxes from six snags along an upland-to-wetland gradient at Howland Research Forest
15 (Maine, USA) with measurements made every two weeks from April to November 2024. Using
nonlinear models, we quantified flux responses to environmental predictors including soil
moisture, soil temperature, and air temperature. Gas fluxes increased with increasing temperature,
yet CO₂ flux peaked at moderate soil moisture (~ 30%), while CH₄ peaked at the highest moisture
levels. CH₄ fluxes were overwhelmingly net positive, suggesting that snags are important
20 pathways for wetland gas emission. CH₄ flux was relatively insensitive under low soil moisture
and temperature, but increased with rising soil temperature when soil moisture was high,
suggesting that methanogenesis depends on anaerobic moisture conditions. Results also suggest
that CO₂ flux co-varied with CH₄ flux from snags, with decreases in CO₂ flux associated with
increases in CH₄ flux. As soil moisture increased, a pronounced shift in gas fluxes (from CO₂ to
25 CH₄ emission) occurred at ~ 60% soil moisture. These results, which align with those from
previous studies establishing anaerobic moisture thresholds and provide new insights into CO₂ and
CH₄ fluxes from snags, present direct measurements of gas exchange from snags along a moisture
and temperature gradient.



1 Introduction

30 Deadwood can represent as much as 20% of aboveground biomass in forests, thereby contributing significantly to global carbon dynamics (Komposch et al., 2022; Russell et al., 2015; Woodall et al., 2015). Among deadwood components, standing dead trees, or snags, are particularly important because they remain upright for years, decaying and releasing gases slower than other types of deadwood (Hararuk et al., 2020; Onega and Eickmeier, 1991). This is particularly important in
35 forests with high snag densities or recent disturbances, where deadwood volumes are elevated (Kipping et al., 2022; Yatskov et al., 2022). Snags also influence carbon flux dynamics by serving as a conduit for atmospheric flux of carbon dioxide (CO₂) and methane (CH₄), transporting soil-generated gases and also producing within-stem gases (Carmichael et al., 2018). Relatively few studies have addressed greenhouse gas (GHG) fluxes from snags, despite their acknowledged
40 importance in ecosystem functioning and forest carbon dynamics.

Snags emit CO₂ as the result of heterotrophic respiration. As fungi decompose wood, environmental factors, including soil moisture and temperature, influence CO₂ flux rates (Mukhortova et al., 2021; Noh et al., 2019). CO₂ flux from snags is positively influenced by temperature, as warmer conditions generally enhance decomposition (Renninger et al., 2014).
45 While moisture is known to have a positive relationship with CO₂ flux from deadwood (Olajuyigbe et al., 2012), excessive moisture can limit oxygen diffusion in snag stems, reducing CO₂ emissions (Oberle et al., 2018). Snag CO₂ emissions (per unit area) are typically smaller in magnitude than those from soils; however, emissions from the two sources are often positively correlated, as both arise from similar biological processes and environmental drivers (Perreault et al., 2021).

50 Even less well understood is CH₄ flux from snags, which can arise through two primary pathways: passive transport of soil-generated CH₄ through the stem and *in situ* production within the stem.



In water-saturated soils, methanogenic archaea anaerobically produce CH₄, primarily by reducing CO₂ (Conrad, 2020). Internal conduits, particularly in trees with compromised xylem structure, can transport CH₄ upward through the stem to be diffused to the atmosphere (Keppler et al., 2006; Pangala et al., 2013). This mechanism is well documented in living trees (Barba et al., 2019; Pangala et al., 2015), and emerging evidence suggests that snags can similarly serve as conduits for soil-emitted CH₄ (Carmichael et al. 2018). However, because snags have the potential to host both methanogenic (CH₄ emitting) and methanotrophic (CH₄ consuming) communities, they may act as net CH₄ sources or sinks under certain conditions (Carmichael et al., 2024; Martinez et al., 2022). In the limited studies available on this topic, the balance between methanogenesis and methanotrophy in snags appears to be strongly influenced by moisture availability and oxygen levels (Terazawa et al., 2021). Thus, in drier, well-aerated upland conditions, methanotrophic activity may dominate, leading to CH₄ uptake; in contrast, in saturated lowlands or wetlands, anaerobic conditions support CH₄ production, leading to net emission.

Despite their clear contribution to GHG budgets of forests, differences in gas fluxes between living and dead tree stems remain poorly understood. CH₄ emissions are generally higher in living than dead stems, depending on stage of decay (Covey et al., 2016; Covey & Magonigal, 2019). CO₂ emissions from deadwood are typically higher than those from living stems, but smaller than soil emissions (Warner et al., 2017). Nonetheless, snags remain active sites of biogeochemical exchange of CO₂ and CH₄ due to their unique microbial composition. GHG fluxes may also covary in ways that reflect underlying environmental controls such as moisture and temperature. Thus, snags may represent a significant, yet often overlooked, component of GHG fluxes in forest ecosystems.



In this technical note, we describe CO₂ and CH₄ fluxes from repeated measurements on a series of
75 snags along an upland-to-wetland gradient in a northern temperate conifer forest. Our objectives
were to (1) identify the important drivers of CO₂ and CH₄ fluxes from snags, (2) illustrate how
these fluxes respond to key environmental variables, and (3) determine if fluxes co-vary along an
upland-to-wetland gradient. In doing so, we clarify the importance of snags in ecosystem carbon
dynamics, their dependence on environmental conditions, and their significance in GHG fluxes.

80

2 Methods

2.1 Site Description

This study was conducted at Howland Research Forest of central Maine, USA (45.2041°N
85 68.7402°W, elevation 60 m above sea level), located in the transition zone between deciduous and
boreal forests in northeastern North America. The climate is damp and cool, with average annual
temperatures of $5.9 \pm 0.8^{\circ}\text{C}$ and mean precipitation of 112 ± 21 cm/year that is evenly distributed
throughout the year (Daly et al., 2008). Mean daily temperature ranged from -1.2 to 26.6°C with
an average of 15.2°C from May to November, 2024, when this study took place. During this same
90 period, daily precipitation ranged from 0 to 41.3 mm with a mean of 2.5 mm. Peak temperature
occurred on August 2nd and peak precipitation occurred on August 9th.

The mature, multi-aged forest is composed of approximately 90% conifers, primarily red spruce
(*Picea rubens*), which accounts for 51% of the site's basal area. The forest has not been actively
95 managed since a partial harvest in the 1920s and now displays late-successional features, including
large, old trees (over 200 years), a variety of tree diameters, and diverse stages of coarse woody
debris decomposition (Fien et al., 2019). Soils in the area developed from coarse-loamy granitic



basal till and vary in drainage from well-drained to poorly drained across short distances along upland-to-wetland transitions (Fernandez et al., 1993). Average soil organic layer depth at the six
100 snags was 8 cm (Table A1). Snags account for roughly 35% ($440 \pm 20 \text{ g C m}^{-2}$) of deadwood biomass and 3% of total aboveground biomass at this site (Hollinger et al., 2021).

2.2 Data Collection

We randomly selected six standing dead red spruce stems for gas flux sampling (Hettwer et al.,
105 2025). The snags were within decay classes two and three, based on the five-class system of Sollins (1982), where one is recently dead wood and five is heavily decomposed. Snags spanned an upland-to-wetland drainage gradient, where two were in uplands, two in transitional drainage, and two in an wetlands. Drainage classes (wetland, transitional, upland) were assigned based on soil moisture data obtained from 100 randomly placed soil moisture sensors, as well as a National
110 Wetlands Inventory wetland delineation. All analyses were conducted across continuous predictor variables (e.g., soil moisture, temperature); drainage classes were used solely to guide snag selection and were not used as grouping factors in the data analyses.

To measure CO_2 and CH_4 flux from snag surfaces, we affixed custom-fitted PVC collars to snags with pure silicone at 50 cm stem height. All collars were checked for leaks before each
115 measurement by exhaling around the collar, with additional silicone applied as necessary. CO_2 and CH_4 concentrations were measured by sealing each collar with a custom PVC chamber lid, connected via 3 meters of 6.4 mm ($\frac{1}{4}$ -inch) Bev-A-Line tubing to a LI-7810 analyzer (LI-COR Biosciences, Lincoln, NE, USA). Ambient air was flushed through the system until gas concentrations stabilized, after which manual fluxes were recorded at a frequency of 1 Hz for six-
120 minute intervals (Hutchinson et al., 2000) per observation and processed as described below, along



with spot measurements of air temperature, soil temperature, and volumetric soil moisture (%). While obtaining flux measurements from each snag, instantaneous air temperature was measured with radiation shielding (Precision Lollipop Digital Thermometer, Traceable), while soil moisture and soil temperature were recorded at three locations around the snag at a depth of 15 cm (True
125 TDR-315N Soil Moisture Sensor, Acclima). While we did not directly measure snag moisture, previous work has shown that snag volumetric water content closely tracks that of surface soil (Green et al., 2022). This makes soil moisture, a more widely available and routinely measured environmental variable, a reasonable proxy for snag moisture in our study. Flux and environmental data were collected every two weeks from May through November 2024, resulting in a total of 76
130 measurements. Hemispherical photographs were taken at three points around each snag (two meters from stem, at bearings 0, 120 and 240°) and processed using Gap Light Analyzer software (Frazer et al., 1999) to yield canopy openness values. Relative humidity was measured using a platinum resistance thermometer (EE181-L, Campbell Scientific) from an on-site flux tower, with data scanned every minute and averaged over 30-minute intervals. For each flux measurement, the
135 closest corresponding humidity measurement in time was selected.

2.3 Data Processing

Fluxes for CO₂ (μmol m⁻² s⁻¹) and CH₄ (nmol m⁻² s⁻¹) were calculated from the gas analyzer output using the ideal gas law (Equation 1), where $PV = nRT$ (P = barometric pressure, atm, V = chamber
140 volume, L (liters), R (gas constant) = 0.08206 L·atm/mol·K, T = temperature, °C).

$$Flux = \left(\frac{dC}{dt} \right) \left(\frac{V}{A} \right) \frac{P}{(R \cdot (T + 273.15))} \quad (1)$$

The rate of change in gas concentration over time (dC/dt) was calculated from 90 to 345 seconds for each sampling event, using gas concentration versus time data obtained from the gas analyzer.



This timeframe was chosen to reduce the influence of chamber sealing artifacts and initial
145 concentration surges commonly seen in wetland trees (Yong et al., 2024). Barometric pressure (P)
was paired with the nearest 30-minute measurement recorded by an on-site pressure sensor.
Chamber volumes (V) were determined in the lab for each chamber size by sealing the tree-facing
side with a contour-fitting cover, filling the chamber with quinoa seeds, and measuring the
displaced volume. Surface areas (A) of tree stems within the chambers were also calculated for
150 each template size. Air temperature (°C) at the time of sampling was converted to Kelvin (K)
before calculating fluxes. The minimum detectable flux was estimated for each measurement
following methods from Christiansen et al. (2015) and Nickerson (2016) with all measured fluxes
falling within detectable limits. Data processing was performed in R (version 4.5.0) (R Core Team,
2024) using RStudio (Posit Team, 2024).

155

2.4 Data Analysis

To investigate the environmental drivers of CO₂ and CH₄ fluxes from snags, we conducted a series
of statistical and predictive modeling approaches. Random forest analysis, using the *Boruta*
package in R (Kursa and Rudnicki, 2010), allowed us to identify the most influential
160 environmental predictors associated with each gas flux. These potential predictors included air
temperature, soil temperature, volumetric soil moisture, relative humidity, organic soil pH,
diameter at breast height, and canopy openness. We then used symbolic regression in Python
(PySR) to determine mathematical models that best describe the relationships between top
environmental predictors and gas fluxes (separate models for CO₂ and CH₄). This algorithm
165 generated interpretable nonlinear models by automatically developing numerous candidate models
and ranking them based on AICc scores (Cranmer, 2023).



To evaluate the strength of nonlinear interaction effects between predictor variables, we computed the second-order mixed partial derivatives ($\partial^2 y / \partial x_1 \partial x_2$) of the fitted nonlinear response surfaces. Doing so allowed us to assess how the effect of one predictor (e.g., soil moisture) on the response (e.g., CO₂ or CH₄ flux) changed depending on the level of another predictor (e.g., soil or air temperature). By calculating these interaction terms across a grid of observed data ranges, we identified regions where interactions were strongest, which may indicate synergistic or antagonistic environmental effects on gas fluxes. Given the response curve, we determined the optimal soil moisture (x_1) for maximizing CO₂ flux (y) by setting the derivative of $\ln(y)$ with respect to x_1 to 0 (Equation 2).

$$\frac{d}{dx_1} \ln(y) = ab - 2a \frac{x_1}{x_2} = 0 \rightarrow x_1 = \frac{bx_2}{2} \quad (2)$$

To determine if the relationship between CO₂ and CH₄ fluxes varied across the soil moisture gradient, we fit linear models with CH₄ flux as a response to the interaction between soil moisture and CO₂ flux. For CO₂ and CH₄ fluxes in this two-gas model, we used our top-performing nonlinear models and held temperature constant at low (25th percentile) and high (75th percentile) values. We then used a multivariate analysis of variance (MANOVA) to test whether soil moisture jointly influenced CO₂ and CH₄ fluxes, treating both gases as simultaneous response variables, at low and high temperatures. Lastly, we used Pearson tests on raw data to determine the correlation between CO₂ and CH₄ fluxes.

3 Results

Sampling period snag CO₂ fluxes ranged from 0.20 to 9.75 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (mean = 2.26 ± 2.34) and CH₄ fluxes ranged from -0.21 to 2.46 $\text{nmol m}^{-2} \text{s}^{-1}$ (mean = 0.25 ± 0.44). CO₂ emissions were highest from late-June to late-July and CH₄ emissions were highest from mid-July to mid-August



(Fig. 1). Minor CH₄ uptake was observed only three times out of 72 measurements throughout the sampling period, all of which occurred on upland snags. Mean CO₂ and CH₄ fluxes approached zero between October (day of year 275) and November.

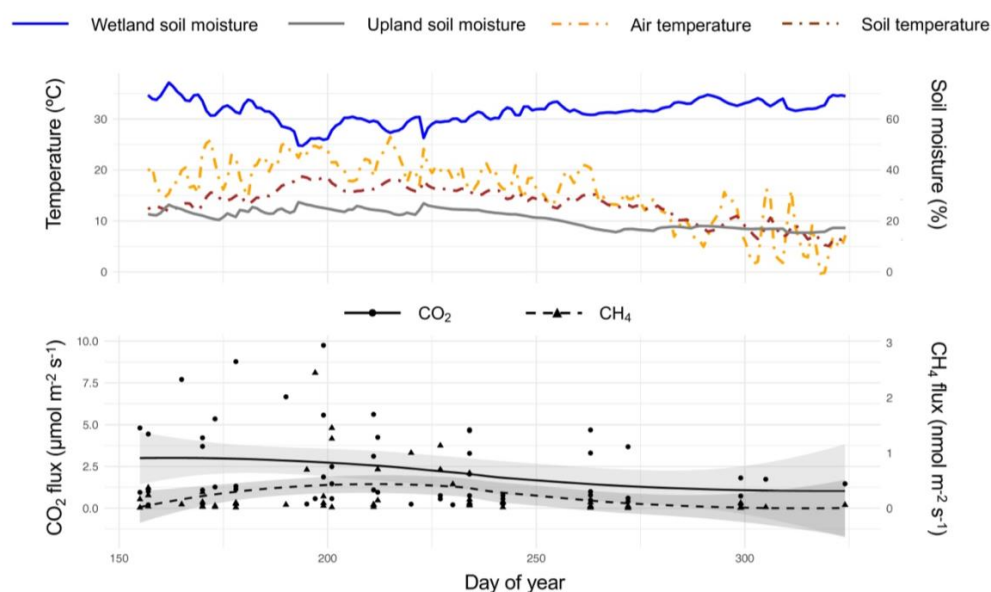


Figure 1: Top pane shows environmental conditions (temperature and soil moisture) throughout the sampling period, obtained from on-site eddy-covariance tower. Bottom pane shows observed CO₂ (primary y-axis) and CH₄ (secondary y-axis) fluxes vs. day of year. The shaded regions around each spline represent the 95% confidence interval, calculated using standard errors from the smoothing model.

Based on random forest analysis, soil moisture, air temperature, and canopy openness were deemed important for CO₂ flux, and soil moisture, soil temperature, and canopy openness for CH₄ flux. Canopy openness was strongly correlated with soil moisture ($r = 0.74$) and was therefore omitted from subsequent analyses. Relative humidity and stem diameter were classified as unimportant and were also omitted. Results from our nonlinear model fitting suggested that CO₂ flux followed an exponential increase or decrease depending on the relative values of soil moisture and air temperature (Table 1, Fig. 2). Importantly, this model has the potential for negative, or antagonistic, interaction between predictors. CH₄ flux responded to soil moisture and soil



Table 1: Top-performing nonlinear models for CO₂ flux (μmol m⁻² s⁻¹) and CH₄ flux (nmol m⁻² s⁻¹) from snags with the functional forms of each model, the estimated parameters, and associated coefficients of determination (R²).

Response (y)	Predictors (x ₁ , x ₂)	Model form	a	b	R ²
CO ₂ flux	Soil moisture, Air temperature	$y = e^{a \cdot x_1 \cdot (b - \frac{x_1}{x_2})}$	0.0657	2.119	0.62
CH ₄ flux	Soil moisture, Soil temperature	$y = \frac{x_2 + a}{b - x_1}$	-7.0015	89.999	0.90

temperature as a rational function where flux changed slowly until soil moisture approached a critical value, above which it increased dramatically, although modulated by soil temperature (Table 1, Fig. 2).

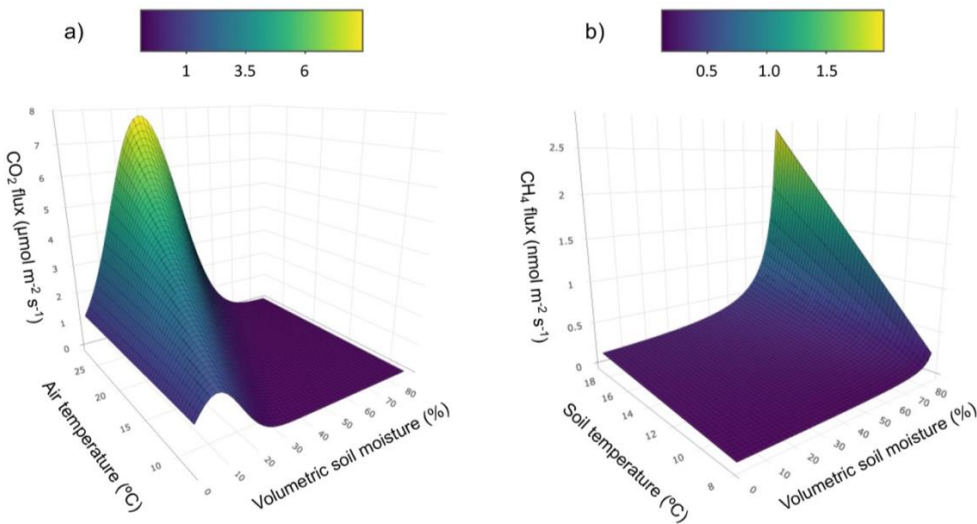


Figure 2: Modeled relationships between (a) CO₂ and (b) CH₄ snag fluxes and top environmental variables, highlighting the important interactions between predictors for each gas. Color scales correspond to CO₂ (μmol m⁻² s⁻¹) and CH₄ (nmol m⁻² s⁻¹) units.

Modeling based on partial derivatives highlighted distinct response surfaces for the two gases while revealing interactive effects between the predictors for each (Fig. 2). The highest CO₂ fluxes occurred at intermediate soil moisture levels (25 – 35% volumetric soil moisture) and elevated temperatures (> 20 °C). The strongest positive interaction for predicting CO₂ flux ($\partial^2 y / \partial x_1 \partial x_2 =$

$0.05 \frac{\mu\text{mol m}^{-2} \text{ s}^{-1}}{\% \text{VWC} \cdot ^\circ\text{C}}$) occurred at 27% soil moisture and 28 °C air temperature (maximum observed



value). The strongest negative interaction occurred at 53% soil moisture and 28 °C air temperature. Assuming maximum observed air temperature, CO₂ flux reached its maximum at 30% volumetric soil moisture. The nonlinear models also highlight the relationship between CO₂ and CH₄ fluxes along the upland-to-wetland moisture gradient (Fig. 3). CO₂ flux peaked at approximately 25% soil moisture, then declined exponentially until becoming negligible at approximately 60% soil moisture, where CH₄ fluxes exhibited a sharp increase.

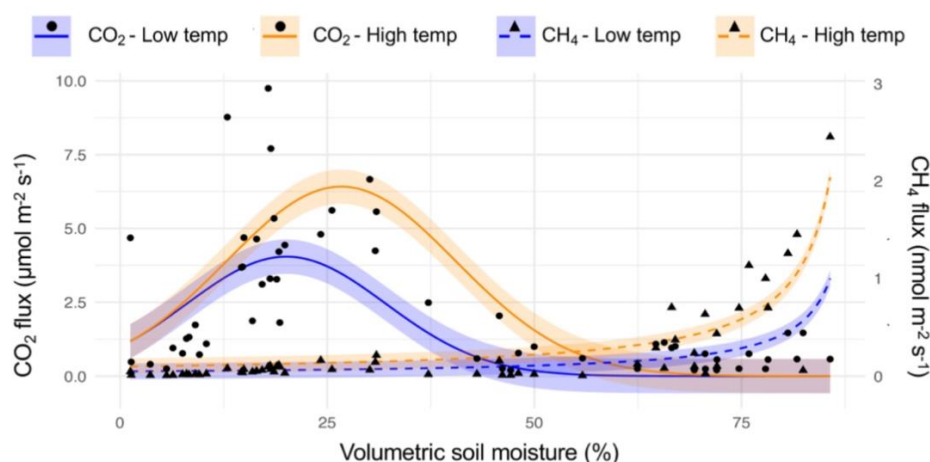


Figure 3: Observed snag CO₂ and CH₄ fluxes along a soil-moisture gradient, with curve fits corresponding to top-performing nonlinear models. Temperature (air temperature for CO₂, soil temperature for CH₄) was held constant at low (25th percentile) and high (75th percentile) values for predicting curves. Shaded regions around each curve represent the 95% confidence intervals.

CH₄ fluxes increased sharply with higher soil moisture levels (~ 60%) and exhibited negligible response to increases in soil temperature, except when soil moisture was high. The strongest interaction effect between predictors was observed at 86% soil moisture (maximum observed value) and 17 °C soil temperature, while the weakest interaction occurred at 1% soil moisture (minimum observed value) and 14 °C soil temperature.



The two-gas model revealed a significant negative interaction between CO₂ flux and soil moisture in predicting CH₄ flux ($p < 0.001$), regardless of temperature percentile, indicating that the relationship between the two gases varied along the soil moisture gradient. Specifically, CH₄ flux increased when CO₂ flux decreased under increasing moisture conditions. Furthermore, the MANOVA results show that CO₂ and CH₄ fluxes were jointly influenced by soil moisture ($p < 0.001$). CH₄ and CO₂ fluxes were negatively correlated ($r = -0.53$), suggesting they respond differently along the soil moisture gradient.

4 Discussion

Our results highlight the strong influence that soil moisture and temperature exert on gas fluxes from snags, demonstrating these responses along an upland-to-wetland moisture gradient. CO₂ fluxes peaked at intermediate soil moisture (~ 30%) and high temperatures, showing a significant interaction between soil moisture and air temperature. CH₄ fluxes rose sharply at high soil moisture (~ 60%) and were primarily driven by soil moisture, with a strong interaction between soil moisture and soil temperature.

CO₂ flux increased as air temperature increased, in agreement with previous studies (Boddy, 1983; Noh et al., 2019), but it also depended on soil moisture. As soil moisture deviated in either direction from that of maximum CO₂ flux (~ 30%), flux decreased towards zero. Therefore, our results suggest that fungal activity in snags, and in turn CO₂ emissions, may be inhibited at both low and high moisture conditions. The finding of reduced deadwood CO₂ flux under low moisture conditions has been reported in previous studies (Boddy, 1983; Hicks et al., 2003). The finding of reduced CO₂ flux at high moisture conditions corroborates several deadwood studies (Meyer and



260 Brischke, 2015; Progar et al., 2000) but contrasts with others (Forrester et al., 2012; Gough et al., 2007).

CH₄ flux increased sharply with rising soil moisture when soil temperature was high, indicating a synergistic effect between the two variables. Similarly, CH₄ flux became more responsive to increases in soil temperature when soil moisture was high, suggesting that optimal conditions for CH₄ emission occurred when both predictors were elevated. CH₄ flux rates, as well as interaction effects of predictor variables, were negligible in drier, cooler conditions. The insensitivity of CH₄ flux to increasing soil moisture, even at high temperatures, aligns with findings of a volumetric soil moisture threshold of ~ 60% beyond which CH₄ flux rates from soils increase dramatically (von Fischer and Hedin, 2007). While a positive relationship between CH₄ flux and moisture has been observed from soils and other deadwood forms (Covey & Megonigal, 2019; Kipping et al., 270 2022), the dynamics of snag CH₄ flux and its dependence on moisture remain poorly understood, perhaps due to the challenge of directly measuring internal snag moisture (Green et al., 2022).

Our results point to a complex, moisture-sensitive relationship between CO₂ and CH₄ fluxes in the studied ecosystem. The significant interaction between CO₂ flux and soil moisture in predicting CH₄ flux suggests that the behavior of one gas flux may be linked to the other, especially under varying moisture conditions. As soil moisture increased, CO₂ flux declined while CH₄ flux rose, 275 indicating a possible transition from aerobic to anaerobic microbial processes. The negative correlation between CO₂ and CH₄ fluxes, combined with MANOVA results showing soil moisture as a joint flux driver, reinforces the assumption that the coupling of these gas fluxes is moisture dependent. Furthermore, the shift in positive CO₂ to CH₄ fluxes between 60 – 70% moisture aligns 280 with reported values for volumetric water content at which conditions shift from aerobic to anaerobic (Długosz et al., 2024; Fairbairn et al., 2023; Schlüter et al., 2025). Overall, these findings



underscore the importance of soil moisture in regulating greenhouse gas dynamics in forested systems and the value of using a two-gas framework to understand GHG fluxes as they pertain to radiative forcing and climate change.

285 In summary, we found that moisture and temperature interact in complex ways to govern both CO₂ and CH₄ fluxes from snags. Both gas fluxes increased with increasing temperature, yet CO₂ flux peaked at moderate moisture levels, while CH₄ peaked at the highest moisture recorded. CH₄ fluxes were overwhelmingly net positive (i.e., sources to the atmosphere), suggesting that snags represent an important pathway for wetland gas production; however, they may serve as CH₄ sinks
290 under certain conditions. Our results derive from a small number of snags, yet they provide compelling evidence for the importance of snag fluxes in the forest carbon cycle, particularly considering projected increases in regional temperature and precipitation (Fernandez et al., 2020). Our results identify further knowledge gaps regarding the influence of snag species (via wood anatomy), stem height, and stages of snag decay. Our results also point to the need for methods of
295 measuring internal snag moisture, rather than relying on soil moisture as a proxy. Finally, phylogenetic sequencing of the bacterial and fungal communities residing in snags would clarify the mechanisms driving the variations in CO₂ and CH₄ fluxes from snags.

Conclusions

300 These results demonstrate that standing dead trees (snags) in northern conifer forests emit both CO₂ and CH₄, with flux dynamics strongly regulated by environmental gradients, particularly soil moisture. CO₂ flux peaked at intermediate soil moisture (~ 30%) and warm air temperatures, following a rational response shaped by interactive effects between soil moisture and air temperature. In contrast, CH₄ flux remained low until soil moisture exceeded a threshold (~ 60%),



305 after which emissions increased sharply, modulated by soil temperature. The observed negative
correlation between CO₂ and CH₄ fluxes, along with evidence of antagonistic interactions between
CO₂ flux and soil moisture in predicting CH₄ flux, suggests that the two gases respond divergently
along the upland-to-wetland gradient. Overall, these findings highlight the complexity of
greenhouse gas emissions from snags and underscore the importance of considering interactive
310 environmental drivers when modeling their contributions to forest carbon dynamics.

Appendix A

Table A1: Organic layer depth (mean of three points) for each snag and mean soil moisture and
snag fluxes across the sampling period. Also reported are the standard deviations for soil moisture,
315 CH₄ flux, and CO₂ flux.

Snag	Mean soil organic layer depth (cm)	Mean soil moisture (%)	Mean CH ₄ flux (nmol m ⁻² s ⁻¹)	Mean CO ₂ flux (μmol m ⁻² s ⁻¹)
1	7.62	67.9 ± 12.9	0.628 ± 0.708	0.536 ± 0.492
2	10.16	64.4 ± 12.9	0.493 ± 0.444	0.875 ± 0.395
3	8.23	19.2 ± 9.5	0.085 ± 0.028	5.070 ± 3.040
4	9.53	23.1 ± 5.7	0.133 ± 0.043	3.890 ± 1.220
5	5.56	7.46 ± 4.2	0.017 ± 0.011	0.933 ± 0.519
6	6.99	15.6 ± 6.9	0.045 ± 0.017	4.590 ± 1.580

Data availability

320 The datasets generated and analyzed during the current study have been made available in the
Environmental Data Initiative (EDI) repository. Refer to the citation for Hettwer et al., 2025 in the
references.

Competing interests

325 The authors declare that they have no conflicts of interest.

Acknowledgements

We would like to thank Ivan Fernandez, Jonathan Gewirtzman, and Rachel Poppe for their help
with this manuscript. This research was supported in part by the U.S. National Science Foundation
330 (DEB Award #2208658, 2208655), the U.S. Department of Energy's Office of Science (AmeriFlux
core site), the U.S. Forest Service, Northern Research Station (JVA #25-JV-11242306-009), and
the Maine Agricultural and Forest Experiment Station (ME042612, ME042121).



335 **Author contributions**

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Christian Hettwer. The first draft of the manuscript was written by Christian Hettwer and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.



340 References

- Barba, J., Bradford, M. A., Brewer, P. E., Bruhn, D., Covey, K., van Haren, J., Megonigal, J. P., Mikkelsen, T. N., Pangala, S. R., Pihlatie, M., Poulter, B., Rivas-Ubach, A., Schadt, C. W., Terazawa, K., Warner, D. L., Zhang, Z., and Vargas, R.: Methane emissions from tree
345 stems: a new frontier in the global carbon cycle, *New Phytologist*, 222, 18–28, <https://doi.org/https://doi.org/10.1111/nph.15582>, 2019.
- Boddy, L.: Carbon dioxide release from decomposing wood: Effect of water content and temperature, *Soil Biol Biochem*, 15, 501–510, [https://doi.org/https://doi.org/10.1016/0038-0717\(83\)90042-1](https://doi.org/https://doi.org/10.1016/0038-0717(83)90042-1), 1983.
- 350 Carmichael, M. J., Helton, A. M., White, J. C., and Smith, W. K.: Standing Dead Trees are a Conduit for the Atmospheric Flux of CH₄ and CO₂ from Wetlands, *Wetlands*, 38, 133–143, <https://doi.org/10.1007/s13157-017-0963-8>, 2018.
- Carmichael, M. J., Martinez, M., Bräuer, S. L., and Ardón, M.: Microbial Communities in
355 Standing Dead Trees in Ghost Forests are Largely Aerobic, Saprophytic, and Methanotrophic, *Curr Microbiol*, 81, 229, <https://doi.org/10.1007/s00284-024-03767-w>, 2024.
- Christiansen, J., Outhwaite, J., and Smukler, S.: Comparison of CO₂, CH₄ and N₂O soil-atmosphere exchange measured in static chambers with cavity ring-down spectroscopy and gas chromatography, *Agric For Meteorol*, 211,
360 <https://doi.org/10.1016/j.agrformet.2015.06.004>, 2015.
- Conrad, R.: Methane Production in Soil Environments—Anaerobic Biogeochemistry and Microbial Life between Flooding and Desiccation, *Microorganisms*, 8, 881, <https://doi.org/10.3390/microorganisms8060881>, 2020.
- Covey, K. R. and Megonigal, J. P.: Methane production and emissions in trees and forests, *New
365 Phytologist*, 222, 35–51, <https://doi.org/10.1111/nph.15624>, 2019.
- Covey, K. R., de Mesquita, C. P. B., Oberle, B., Maynard, D. S., Bettigole, C., Crowther, T. W., Duguid, M. C., Steven, B., Zanne, A. E., Lapin, M., Ashton, M. S., Oliver, C. D., Lee, X., and Bradford, M. A.: Greenhouse trace gases in deadwood, *Biogeochemistry*, 130, 215–226, <https://doi.org/10.1007/s10533-016-0253-1>, 2016.
- 370 Cranmer, M.: Interpretable Machine Learning for Science with PySR and SymbolicRegression.jl, <https://arxiv.org/abs/2305.01582>, 2023.
- Daly, C., Halbleib, M. D., Smith, J. I., Gibson, W., Doggett, M. K., Taylor, G. H., Curtis, J. M., and Pasteris, P. P.: Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States, *International Journal of Climatology*,
375 28, 2031–2064, <https://doi.org/10.1002/joc.1688>, 2008.
- Długosz, J., Piotrowska-Długosz, A., and Breza-Boruta, B.: The effect of differences in soil water content on microbial and enzymatic properties across the soil profiles, *Ecohydrology & Hydrobiology*, 24, 547–556, <https://doi.org/https://doi.org/10.1016/j.ecohyd.2023.06.010>, 2024.
- 380 Fairbairn, L., Rezanezhad, F., Gharasoo, M., Parsons, C. T., Macrae, M. L., Slowinski, S., and Van Cappellen, P.: Relationship between soil CO₂ fluxes and soil moisture: Anaerobic sources explain fluxes at high water content, *Geoderma*, 434, 116493, <https://doi.org/https://doi.org/10.1016/j.geoderma.2023.116493>, 2023.
- Fernandez, I. J., Son, Y., Kraske, C. R., Rustad, L. E., and David, M. B.: Soil Carbon Dioxide
385 Characteristics under Different Forest Types and after Harvest, *Soil Science Society of*



- America Journal, 57, 1115–1121,
<https://doi.org/https://doi.org/10.2136/sssaj1993.03615995005700040039x>, 1993.
- Fernandez, I. J., Birkel, S., Schmitt, C. V., Simonson, J., Lyon, B., Pershing, A., Stancioff, E., and Jacobson, G. L.: Maine’s climate future: 2020 update,
390 <https://doi.org/10.13140/RG.2.2.24401.07521>, 2020.
- Fien, E. K. P., Fraver, S., Teets, A., Weiskittel, A. R., and Hollinger, D. Y.: Drivers of individual tree growth and mortality in an uneven-aged, mixed-species conifer forest, For Ecol Manage, 449, 117446, <https://doi.org/10.1016/j.foreco.2019.06.043>, 2019.
- von Fischer, J. C. and Hedin, L. O.: Controls on soil methane fluxes: Tests of biophysical mechanisms using stable isotope tracers, Global Biogeochem Cycles, 21, GB2007,
395 <https://doi.org/https://doi.org/10.1029/2006GB002687>, 2007.
- Forrester, J., Mladenoff, D., Gower, S., and Stoffel, J.: Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps, For Ecol Manage, 265, 124–132, <https://doi.org/10.1016/j.foreco.2011.10.038>, 2012.
- 400 Frazer, G. W., Canham, C. D., and Lertzman, K. P.: Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation, 1999.
- Gough, C., Vogel, C., Kazanski, C., Nagel, L., Flower, C., and Curtis, P.: Coarse woody debris and the carbon balance of a north temperate forest, For Ecol Manage, 244, 60–67,
405 <https://doi.org/10.1016/j.foreco.2007.03.039>, 2007.
- Green, M. B., Fraver, S., Lutz, D. A., Woodall, C. W., D’Amato, A. W., and Evans, D. M.: Does deadwood moisture vary jointly with surface soil water content?, Soil Science Society of America Journal, 86, 1113–1121, <https://doi.org/https://doi.org/10.1002/saj2.20413>, 2022.
- Hararuk, O., Kurz, W. A., and Didion, M.: Dynamics of dead wood decay in Swiss forests, For Ecosyst, 7, 36, <https://doi.org/10.1186/s40663-020-00248-x>, 2020.
- 410 Hettwer, C., Fraver, S., and Savage, K.: CO₂ and CH₄ fluxes from living and standing dead trees in Howland Research Forest, Maine USA, 2024, Environmental Data Initiative, <https://doi.org/https://doi.org/10.6073/pasta/03586624214245c96a0399509ab4e3cb>, 2025.
- Hicks, W., Harmon, M., and Griffiths, R.: Abiotic controls on nitrogen fixation and respiration in selected woody debris from the Pacific Northwest, U.S.A, Ecoscience, 10, 66–73,
415 <https://doi.org/10.1080/11956860.2003.11682752>, 2003.
- Hollinger, D. Y., Davidson, E. A., Fraver, S., Hughes, H., Lee, J. T., Richardson, A. D., Savage, K., Sihi, D., and Teets, A.: Multi-Decadal Carbon Cycle Measurements Indicate Resistance to External Drivers of Change at the Howland Forest AmeriFlux Site, J Geophys Res Biogeosci, 126, e2021JG006276, <https://doi.org/10.1029/2021JG006276>, 2021.
- 420 Hutchinson, G. L., Livingston, G. P., Healy, R. W., and Striegl, R. G.: Chamber measurement of surface-atmosphere trace gas exchange: Numerical evaluation of dependence on soil, interfacial layer, and source/sink properties, Journal of Geophysical Research: Atmospheres, 105, 8865–8875, <https://doi.org/https://doi.org/10.1029/1999JD901204>,
425 2000.
- Keppler, F., Hamilton, J. T. G., Braß, M., and Röckmann, T.: Methane emissions from terrestrial plants under aerobic conditions, Nature, 439, 187–191,
<https://doi.org/10.1038/nature04420>, 2006.
- Kipping, L., Gossner, M. M., Koschorreck, M., Muszynski, S., Maurer, F., Weisser, W. W., Jehmlich, N., and Noll, M.: Emission of CO₂ and CH₄ From 13 Deadwood Tree Species Is
430 Linked to Tree Species Identity and Management Intensity in Forest and Grassland



- Habitats, *Global Biogeochem Cycles*, 36, e2021GB007143, <https://doi.org/10.1029/2021GB007143>, 2022.
- 435 Komposch, A., Ensslin, A., Fischer, M., and Hemp, A.: Aboveground Deadwood Biomass and Composition Along Elevation and Land-Use Gradients at Mount Kilimanjaro, *Front Ecol Evol*, 9, <https://doi.org/10.3389/fevo.2021.732092>, 2022.
- Kursa, M. B. and Rudnicki, W. R.: Feature Selection with the Boruta Package, *J Stat Softw*, 36, 1–13, <https://doi.org/10.18637/jss.v036.i11>, 2010.
- 440 Martinez, M., Ardón, M., and Carmichael, M. J.: Identifying Sources and Oxidation of Methane in Standing Dead Trees in Freshwater Forested Wetlands, *Front Environ Sci*, 9, <https://doi.org/10.3389/fenvs.2021.737379>, 2022.
- Meyer, L. and Brischke, C.: Fungal decay at different moisture levels of selected European-grown wood species, *Int Biodeterior Biodegradation*, 103, 23–29, <https://doi.org/10.1016/j.ibiod.2015.04.009>, 2015.
- 445 Mukhortova, L., Pashenova, N., Meteleva, M., Krivobokov, L., and Guggenberger, G.: Temperature sensitivity of CO₂ and CH₄ fluxes from coarse woody debris in northern boreal forests, *Forests*, 12, 624, <https://doi.org/10.3390/f12050624>, 2021.
- Nickerson, N.: Evaluating gas emission measurements using Minimum Detectable Flux (MDF), <https://doi.org/10.13140/RG.2.1.4149.2089>, 2016.
- 450 Noh, N. J., Shannon, J. P., Bolton, N. W., Davis, J. C., Van Grinsven, M. J., Pypker, T. G., Kolka, R. K., and Wagenbrenner, J. W.: Temperature responses of carbon dioxide fluxes from coarse dead wood in a black ash wetland, *Wetl Ecol Manag*, 27, 157–170, <https://doi.org/10.1007/s11273-018-9649-0>, 2019.
- Oberle, B., Ogle, K., Zanne, A., and Woodall, C.: When a tree falls: Controls on wood decay predict standing dead tree fall and new risks in changing forests, *PLoS One*, 13, e0196712, <https://doi.org/10.1371/journal.pone.0196712>, 2018.
- Olajuyigbe, S., Tobin, B., and Nieuwenhuis, M.: Temperature and moisture effects on respiration rate of decomposing logs in a Sitka spruce plantation in Ireland, *Forestry: An International Journal of Forest Research*, 85, 485–496, <https://doi.org/10.1093/forestry/CPS045>, 2012.
- 460 Onega, T. L. and Eickmeier, W. G.: Woody Detritus Inputs and Decomposition Kinetics in a Southern Temperate Deciduous Forest, *Bulletin of the Torrey Botanical Club*, 118, 52–57, <https://doi.org/10.2307/2996975>, 1991.
- Pangala, S. R., Moore, S., Hornibrook, E. R. C., and Gauci, V.: Trees are major conduits for methane egress from tropical forested wetlands, *New Phytologist*, 197, 524–531, <https://doi.org/10.1111/nph.12031>, 2013.
- 465 Pangala, S. R., Hornibrook, E. R. C., Gowing, D. J., and Gauci, V.: The contribution of trees to ecosystem methane emissions in a temperate forested wetland, *Glob Chang Biol*, 21, 2642–2654, <https://doi.org/10.1111/gcb.12891>, 2015.
- Perreault, L., Forrester, J. A., Mladenoff, D. J., and Gower, S. T.: Linking deadwood and soil GHG fluxes in a second growth north temperate deciduous forest (Upper Midwest USA), *Biogeochemistry*, 156, 177–194, <https://doi.org/10.1007/s10533-021-00839-y>, 2021.
- Posit Team: RStudio: Integrated Development Environment for R, <https://posit.co/>, 2024.
- Progar, R. A., Schowalter, T. D., Freitag, C. M., and Morrell, J. J.: Respiration from coarse woody debris as affected by moisture and saprotroph functional diversity in Western
- 475 Oregon, *Oecologia*, 124, 426–431, <https://doi.org/10.1007/PL00008868>, 2000.
- R Core Team: R: A language and environment for statistical computing, <https://www.R-project.org/>, 2024.



- Renninger, H. J., Carlo, N., Clark, K. L., and Schäfer, K. V. R.: Modeling respiration from snags
and coarse woody debris before and after an invasive gypsy moth disturbance, *J Geophys*
480 *Res Biogeosci*, 119, 630–644, <https://doi.org/10.1002/2013JG002542>, 2014.
- Russell, M. B., Fraver, S., Aakala, T., Gove, J. H., Woodall, C. W., D’Amato, A. W., and Ducey,
M. J.: Quantifying carbon stores and decomposition in dead wood: A review, *For Ecol*
Manage, 350, 107–128, <https://doi.org/10.1016/j.foreco.2015.04.033>, 2015.
- Schlüter, S., Lucas, M., Grosz, B., Ippisch, O., Zawallich, J., He, H., Dechow, R., Kraus, D.,
485 Blagodatsky, S., Senbayram, M., Kravchenko, A., Vogel, H.-J., and Well, R.: The anaerobic
soil volume as a controlling factor of denitrification: a review, *Biol Fertil Soils*, 61, 343–
365, <https://doi.org/10.1007/s00374-024-01819-8>, 2025.
- Sollins, P.: Input and decay of coarse woody debris in coniferous stands in western Oregon and
Washington, *Canadian Journal of Forest Research*, 12, 18–28, [https://doi.org/10.1139/x82-](https://doi.org/10.1139/x82-003)
490 003, 1982.
- Terazawa, K., Tokida, T., Sakata, T., Yamada, K., and Ishizuka, S.: Seasonal and weather-related
controls on methane emissions from the stems of mature trees in a cool-temperate forested
wetland, *Biogeochemistry*, 156, 1–20, <https://doi.org/10.1007/s10533-021-00841-4>, 2021.
- Warner, D. L., Villarreal, S., McWilliams, K., Inamdar, S., and Vargas, R.: Carbon Dioxide and
495 Methane Fluxes From Tree Stems, Coarse Woody Debris, and Soils in an Upland
Temperate Forest, *Ecosystems*, 20, 1205–1216, <https://doi.org/10.1007/s10021-016-0106-8>,
2017.
- Woodall, C. W., Russell, M. B., Walters, B. F., D’Amato, A. W., Fraver, S., and Domke, G. M.:
Net carbon flux of dead wood in forests of the Eastern US, *Oecologia*, 177, 861–874,
500 <https://doi.org/10.1007/s00442-014-3171-8>, 2015.
- Yatskov, M. A., Harmon, M. E., Fasth, B., Sexton, J., Hoyman, T. L., and Dudoit, C. M.:
Decomposition differences between snags and logs in forests of Kenai Peninsula, Alaska,
Canadian Journal of Forest Research, 52, 727–742, <https://doi.org/10.1139/cjfr-2021-0208>,
2022.
- 505 Yong, Z.-J., Lin, W.-J., Lin, C.-W., and Lin, H.-J.: Tidal influence on carbon dioxide and
methane fluxes from tree stems and soils in mangrove forests, *Biogeosciences*, 21, 5247–
5260, <https://doi.org/10.5194/bg-21-5247-2024>, 2024.