



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

Christian Hettwer¹, Kathleen Savage², Andrew Ouimette³, Jay Wason¹, Roel Ruzol¹, and Shawn Fraver¹

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

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

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

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

Received: 18 July 2025 – Discussion started: 8 August 2025

Revised: 20 November 2025 – Accepted: 21 November 2025 – Published: 9 December 2025

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 (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 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, confirming 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 CH₄ emission) occurred at ~60 % soil moisture. Compared to other substrates at the site, including soils, living trees, and various deadwood, snags were the largest emitters of CO₂ and second-largest emitters of CH₄. We present direct measurements of gas exchange from snags along a moisture and temperature gradient, providing new insights into CO₂ and CH₄ fluxes from snags.

1 Introduction

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 forests with high snag densities or recent disturbances, where deadwood volumes are elevated (Kipping et al., 2022; Yatskov et al., 2022). The issue of greenhouse gas fluxes from snags will likely gain future importance as we anticipate climate-change increases in forest disturbance (Seidl et al., 2017; McDowell et al., 2020) and hence snag abundance. 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 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). 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).

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 and Megonigal, 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 co-vary 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.

Here we describe CO₂ and CH₄ fluxes from repeated measurements on a series of 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 shed light on the importance of snags in ecosystem carbon dynamics, their dependence on environmental conditions, and their significance in GHG fluxes.

2 Methods

2.1 Site Description

This study was conducted at Howland Research Forest of central Maine, USA (45.2041° N 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 ± 0.8 °C and mean precipitation of 112 ± 21 cm yr⁻¹ 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 period, daily precipitation ranged from 0 to 41.3 mm with a mean of 2.5 mm. Peak temperature occurred on 2 August and peak precipitation occurred on 9 August.

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 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 snags was 8 cm (Table A1). Snags account for roughly 35 % (440 ± 20 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., 2025a). 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 (Fig. 1). 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 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 CO₂ and CH₄ flux from snag surfaces, we affixed custom-fitted PVC collars to snags with pure silicone at 50 cm stem height (Hettwer et al., 2025b). All collars were checked for leaks before each measurement by exhaling around the collar, with additional silicone applied as neces-

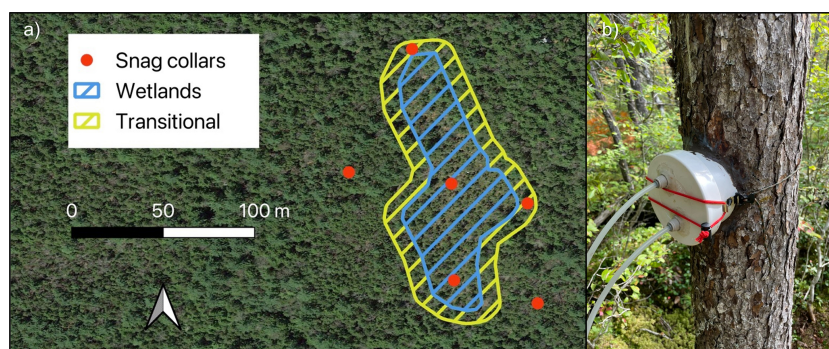


Figure 1. (a) Sampling collar locations for gas flux measurements throughout the designated wetlands, transitional areas, and uplands. (b) Chamber design with inlet and outlet tubes for connecting to a gas analyzer.

sary. CO₂ and CH₄ concentrations were measured by sealing each collar with a custom PVC chamber lid, connected via 3 m of 6.4 mm (1/4 in.) 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 6 min intervals (Hutchinson et al., 2000) per observation and processed as described below. Fluxes were also periodically measured from a set of decay class two ($N = 6$) and decay class four ($N = 6$) *P. rubens* logs, decay class four *P. rubens* stumps ($N = 6$), and soils according to the same protocol and at the same site.

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 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 measurements. Hemispherical photographs were taken at three points around each snag (2 m 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 min intervals. For each flux measurement, the 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 (Eq. 1), where $PV = nRT$ (P = barometric pressure, atm, V = chamber volume, L (liters), R (gas constant) = 0.08206 L atm mol⁻¹ K⁻¹, T = temperature, °C).

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

The rate of change in gas concentration over time (dC/dt) was calculated from 90 to 345 s 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 concentration surges commonly seen in wetland trees (Yong et al., 2024). Barometric pressure (P) was paired with the nearest 30 min 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 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).

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 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 generated interpretable non-linear models by automatically developing numerous candidate models and ranking them based on AICc scores (Cramer, 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 (Eq. 2).

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

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 μmol m⁻² s⁻¹ (mean ± SD = 2.26 ± 2.34) and CH₄ fluxes ranged from −0.21 to 2.46 nmol m⁻² s⁻¹ (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. 2). 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. In comparing fluxes from various substrates at Howland Research Forest, upland snags emerged as the largest emitters of CO₂ (Table 1). Wetland snags were the second-largest emitter of CH₄ behind wetland soils.

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

Table 1. Summary of CO₂ and CH₄ fluxes (mean ± SD) from snags, logs, stumps, soils, and living tree stems during the 2024 growing season at Howland Research Forest in central Maine. Data for living tree stem (*Picea rubens*) fluxes is from Hettwer et al. (2025a).

Substrate	CO ₂ flux (μmol m ⁻² s ⁻¹)	CH ₄ flux (nmol m ⁻² s ⁻¹)
Upland snags	2.53 ± 2.15	0.030 ± 0.020
Wetland snags	0.69 ± 0.47	0.77 ± 0.55
Decay class 2 logs	1.27 ± 1.13	0.016 ± 0.014
Decay class 4 logs	1.41 ± 1.13	−0.046 ± 0.10
Decay class 4 stumps	0.91 ± 0.88	−0.0031 ± 0.055
Upland soils	1.58 ± 0.83	−0.47 ± 0.47
Wetland soils	2.14 ± 1.91	289 ± 137
Upland living tree stems	0.41 ± 0.27	0.0090 ± 0.0063
Wetland living tree stems	0.68 ± 0.67	0.091 ± 0.083

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 2, Fig. 3a). Importantly, this model has the potential for negative, or antagonistic, interaction between predictors. CH₄ flux responded to soil moisture and soil temperature as a rational function where flux changed slowly until soil moisture approached a critical value (~ 60 %), above which it increased dramatically, although modulated by soil temperature (Table 2, Fig. 3b).

Modeling based on partial derivatives highlighted distinct response surfaces for the two gases while revealing interactive effects between the predictors for each (Fig. 3). 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 ($\partial^2 y / \partial x_1 \partial x_2 = 0.05 \mu\text{mol m}^{-2} \text{s}^{-1} (\% \text{VWC } ^\circ\text{C})^{-1}$) 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 highlighted the relationship between CO₂ and CH₄ fluxes along the upland-to-wetland moisture gradient (Fig. 4). CO₂ flux peaked at approximately 30 % soil moisture, then declined exponentially until becoming negligible at approximately 60 % soil moisture, where CH₄ fluxes exhibited a sharp increase at that soil moisture level.

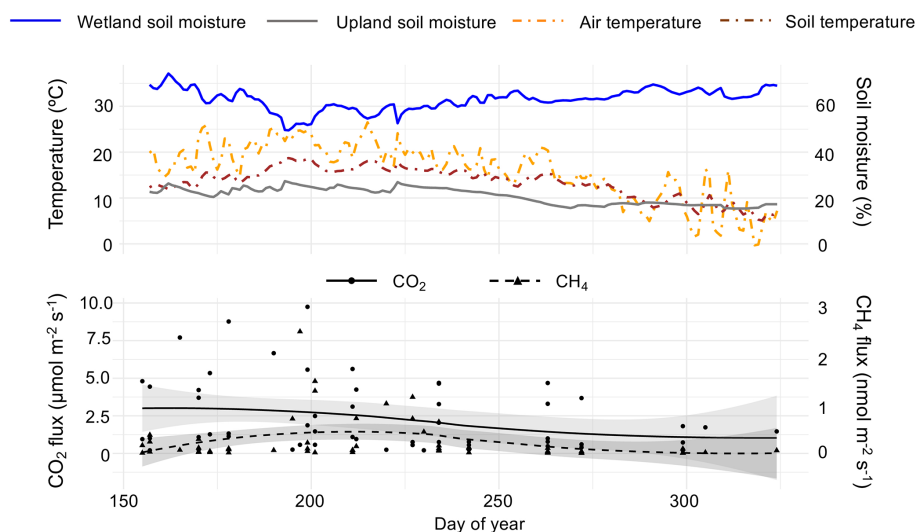


Figure 2. Top pane shows environmental conditions (temperature and soil moisture) throughout the sampling period, obtained from on-site eddy-covariance tower. Bottom pane shows observed CO₂ (primary y-axis) and CH₄ (secondary y-axis) fluxes vs. day of year. The shaded regions around each spline represent the 95 % confidence interval, calculated using standard errors from the smoothing model.

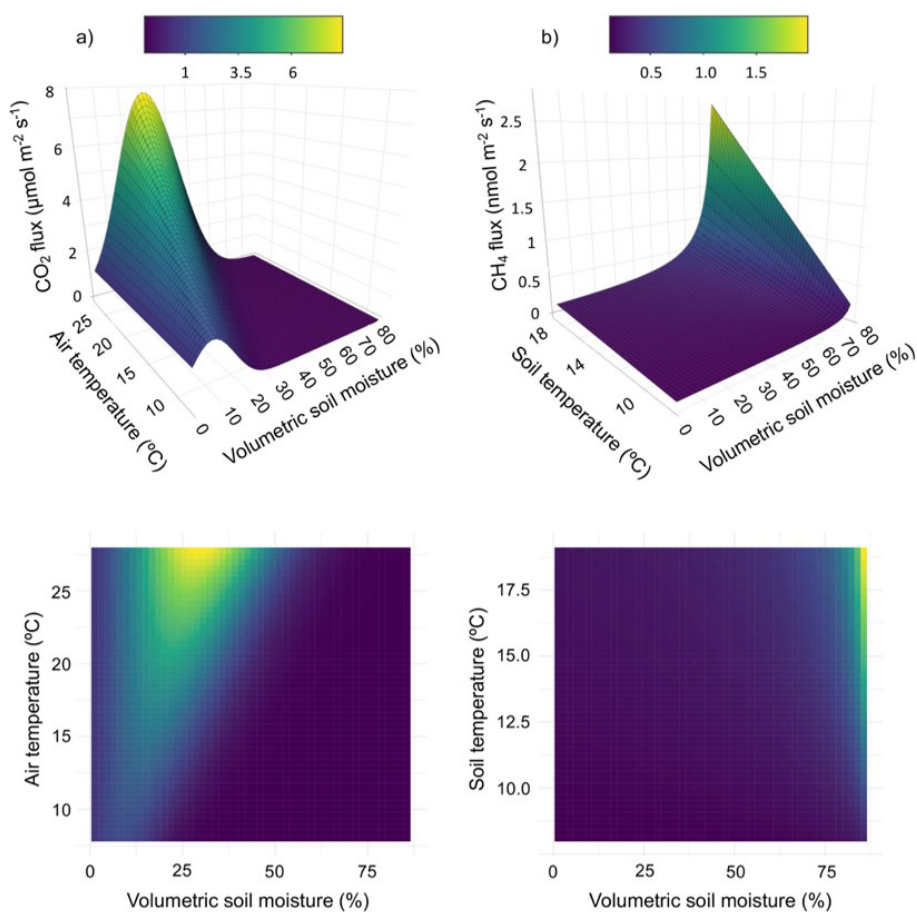


Figure 3. Modeled relationships between (a) CO₂ and (b) CH₄ snag fluxes and top environmental variables, highlighting the important interactions between predictors for each gas. Color scales correspond to CO₂ ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and CH₄ ($\text{nmol m}^{-2} \text{s}^{-1}$) units. Top pane shows 3D surface plots and bottom pane shows 2D heatmaps.

Table 2. 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	$y = e^{a \cdot x_1 \cdot \left(b - \frac{x_1}{x_2}\right)}$	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

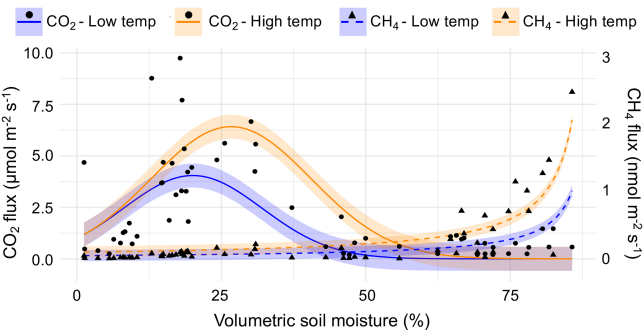


Figure 4. Observed snag CO₂ and CH₄ fluxes along a soil-moisture gradient, with curve fits corresponding to top-performing nonlinear models. Temperature (air temperature for CO₂, soil temperature for CH₄) was held constant at low (25th percentile) and high (75th percentile) values for predicting curves. 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 ($p < 0.001$), indicating that the positive effect of soil moisture on CH₄ flux weakened as CO₂ flux increased. Regardless of temperature percentile, 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 mois-

ture 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. These drivers, identified by random forest, seem reasonable based on the differing origins of the emissions. CO₂ emissions result from aerobic microbial respiration within the deadwood itself, and are thus more influenced by air temperature. In contrast, CH₄ emissions result from anaerobic methanogenesis in the saturated soils at the snag base, with the gas then transported upward through the snag stem (Covey et al., 2016).

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 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 and living tree stems increase dramatically (von Fischer and Hedin, 2007; Hettwer et al., 2025b). While a positive relationship between CH₄ flux and moisture has been observed from soils and other deadwood forms (Covey and Magonigal, 2019; Kipping et al., 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, 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 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.

In addition to exhibiting complex relationships between gas fluxes and environmental drivers, snags may also emit higher rates of CO₂ and CH₄ than other forest surfaces. Several studies report that snags can emit CO₂ and CH₄ at rates comparable to or greater than those from downed wood and living trees. Martinez et al. (2022) measured average wetland snag flux rates of 0.73 μmol CO₂ m⁻² s⁻¹ and 5.21 nmol CH₄ m⁻² s⁻¹, and Carmichael et al. (2018) measured 0.72 μmol CO₂ m⁻² s⁻¹ and 6.94 nmol CH₄ m⁻² s⁻¹. While snag CH₄ emissions were not this large at our site, they still exceeded those from living trees, revealing a pattern not previously documented. Emphasized by their magnitude of CO₂ and CH₄ fluxes and relationships with environmental predictors, snags represent an important and understudied component of forest biogeochemical exchange, particularly across drainage gradients where CO₂ and CH₄ emissions will vary independently. The conifer forest of this region may be at particular risk of increased snag abundance, an in turn increased GHG emissions, because of current spruce budworm (*Choristoneura fumiferana*) outbreaks in adjacent Canadian Provinces and growing budworm populations in northern Maine (Spruce Budworm Task Force 2023 Update, 2023).

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 under certain conditions. Our results de-

rive 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 wood traits, stem height, stages of snag decay, and fungal community composition.

5 Conclusions

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 %), after which emissions increased sharply, modulated by soil temperature. The observed negative correlation between CO₂ and CH₄ fluxes, along with evidence of an interaction between CO₂ flux and soil moisture in predicting CH₄ flux, suggests that the two gases respond divergently along the upland-to-wetland gradient. In comparing various substrates at our site, snags emerged as the largest emitters of CO₂ and the second-largest emitters of CH₄ behind soils. These environmentally-driven patterns reveal that GHG fluxes from snags behaved similarly to those from soils. Future research should incorporate simultaneous measurements of CO₂ and CH₄ fluxes from snags and their surrounding soils to elucidate the relative contributions of soil- versus snag-derived emissions.

Overall, these findings highlight the complexity of greenhouse gas emissions from snags and underscore the importance of considering interactive environmental drivers when modeling their contributions to forest carbon dynamics. These results are especially important because of climate-change increases in forest disturbance, particularly spruce budworm in this region, leading to increased snag abundance. Further research is needed to clarify how snag species and their associated microbial consortia influence gaseous fluxes. Additionally, quantifying snag CO₂ and CH₄ emissions across various ecosystems and regions remains a critical gap. Addressing these uncertainties is essential for integrating snag fluxes into ecosystem- and landscape-scale carbon budgets.

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, 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. The datasets generated and analyzed during the current study have been made available in the Environmental Data Initiative (EDI) repository (<https://doi.org/10.6073/pasta/60ef923f4f82f8931bd904ebb36a8bd7>; Hettwer et al., 2025b).

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

Competing interests. The contact author has declared that none of the authors has any competing interests.

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Acknowledgements. We would like to thank Ivan Fernandez, Jonathan Gewirtzman, and Rachel Poppe for their help with this manuscript.

Financial support. This research has been supported by the National Science Foundation (DEB Award nos. 2208658 and 2208655), the U.S. Department of Energy, Office of Science (AmeriFlux core site (US-Ho1)), the U.S. Forest Service, Northern Research Station (grant no. JVA 25-JV-11242306-009), and the Maine Agricultural and Forest Experiment Station (grant nos. ME042612 and ME042121).

Review statement. This paper was edited by Paul Stoy and reviewed by two anonymous referees.

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