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Forest cover buffers microclimate and increases fuel moisture in northern conifer forests: a terrestrial laser scanning approach

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Abstract

Background Weather and fuels are among the critical, interacting factors that drive wildland fire behavior, and thus are primary factors in fire operations planning and decision support tools. In mesic forests, variation in stand structure may lead to heterogeneous microclimate and fuel moisture conditions in the understory where fires often ignite and spread. However, such variation in fuel availability is often overlooked by fire behavior models that assume spatially uniform weather and fuel conditions. In this study, we analyze a combination of field-based understory meteorology and fuel moisture data with terrestrial laser scanning (TLS) and traditional forest inventory data to develop new knowledge about relationships between forest structure, microclimate, and dead fuel moisture in USA northern conifer forests that can inform fire operations planning and decision support.

Results We found that open canopy plots were significantly warmer (+ 7.82 °C average daily maximum air temperature) and drier (-24.1% average daily relative humidity) and with drier fuels (+ 8.03% fuel moisture) at midday in summer compared to closed canopy plots. Directly using microclimate variables (i.e., air temperature and relative humidity) resulted in better predictions of dead fuel moisture content (mean $R^2 = 0.88$) than using forest structure variables such as canopy openness ($R^2 = 0.60$). Furthermore, forest structure variables derived from TLS were better predictors of dead fuel moisture content ($R^2 = 0.74$) than traditional forest inventory metrics.

Conclusions Our study used multi-modal measurements to demonstrate that dense forest cover linearly reduces fuel availability by buffering microclimate and maintaining fuel moisture. This research can be used to develop thinning prescriptions to achieve certain thresholds of understory temperature, relative humidity, and dead fuel moisture. Moreover, our results highlight the microclimate buffering effect of shaded fuel breaks used in fire suppression and containment tactics. Finally, our work suggests that tools like TLS can be used to fine tune fuel-weather relationships in fire behavior models that use spatially explicit fuels data to inform planning and predict fuels treatment effectiveness. This research enhances fire managers' ability to plan and implement fuel treatments by highlighting how changes in forest stand structure drive fine scale heterogeneity in fuel availability.

Keywords Canopy openness, Fire environment, Fuel availability, Fuel moisture, Microclimate, Northeastern USA, Stand density

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Resumen

Antecedentes El tiempo meteorológico y los combustibles vegetales son los factores interactivos críticos que condicionan el comportamiento de los fuegos de vegetación, y por lo tanto los factores primarios a considerar en el planeamiento de las operaciones y en las decisiones sobre las herramientas de soporte a usar. En bosques mésicos, la variación en la estructura de los rodales puede generar microclimas heterogéneos y diferentes condiciones de humedad de los combustibles en el sotobosque, que es donde frecuentemente los fuegos se inician y propagan. Sin embargo, esta variación en la disponibilidad del combustible es frecuentemente pasada por alto en los modelos de comportamiento, que suponen condiciones uniformes tanto en el tiempo meteorológico como en las de los combustibles. En este estudio, analizamos una combinación de condiciones meteorológicas del sotobosque medidas a campo y datos de humedad de los combustibles con un escáner láser terrestre (TLS), junto con datos de inventario tomados de manera tradicional, para desarrollar nuevos conocimientos sobre las relaciones entre la estructura forestal, el microclima, y la humedad de los combustibles muertos en bosques de coníferas del norte de los EEUU. Esto servirá para aportar información para planificar las operaciones y apoyar las decisiones de manejo.

Resultados Encontramos que parcelas con doseles abiertos tuvieron temperaturas significativamente más cálidas (+7.82 °C en promedio de la temperatura máxima diaria), más secas (-24.1% en el promedio de la humedad relativa diaria) y con combustibles más secos (8.03% menos en la humedad del combustible) al mediodía en el verano comparado con parcelas con doseles más cerrados. El uso directo de variables microclimáticas (i.e. temperatura del aire y humedad relativa) resultó en mejores predicciones del contenido de humedad del combustible muerto (promedio del $R2 = 0{,}88$) que usando una variable de la estructura forestal tal como lo es la apertura del dosel ($R2 = 0{,}60$). Además, las variables derivadas del TLS predijeron mejor el contenido de humedad del combustible muerto ($R2 = 0{,}74$) que las métricas tradicionales usadas en los inventarios forestales.

Conclusiones Nuestro estudio usó mediciones multimodales para demostrar que los bosques con coberturas densas reducen la disponibilidad de los combustibles mediante un efecto buffer (atemperador) de las variables microclimáticas y manteniendo la humedad del combustible. Esta investigación puede usarse para desarrollar prescripciones de raleos o aclareos para lograr ciertos umbrales de temperatura en el sotobosque, humedad relativa del ambiente, y humedad del combustible. Asimismo, nuestros resultados subrayan el efecto buffer de barreras de combustibles sombreadas usadas en la supresión de fuegos y en las tácticas de contención. Finalmente, nuestro trabajo sugiere que herramientas como el TLS puede ser usado como hacer una sintonía fina en la relación entre variables meteorológicas y de combustibles en modelos de comportamiento que usan datos explícitos de combustibles e informar sobre el planeamiento y predecir la efectividad de los tratamientos de combustibles. Esta investigación aumenta la habilidad de los gestores de incendios para planificar e implementar tratamientos de combustibles, subrayando cómo cambios en la estructura de los rodales afecta la heterogeneidad a pequeña escala sobre la disponibilidad de los combustibles.

Background

Monitoring and predicting fuel and weather conditions that contribute to fire spread are central to fire planning, staffing, and other preparedness strategies that often consider those variables via their integration into decision support frameworks (Holden and Jolly 2011; Schroeder and Buck 1983). For example, fire behavior models with weather, fuels, and topographic inputs predict potential fire behavior for an area to inform management decisions for wildfire and prescribed fire operations (Cohen and Deeming 1985; Rothermel 1983). Traditional fire behavior models and model parameterization tools assume weather and dead fuel moisture to be spatially uniform over a given area of interest (Andrews 2014; Pinto and Fernandes 2014; Hiers et al. 2020). However, in forested systems variation in stand structure and topography can contribute to spatial heterogeneity in microclimate (i.e., temperature and moisture) and fuel moisture in the understory where fires often ignite and spread (Kane 2021; Pickering et al. 2021; Ma et al. 2010; Geiger et al. 2012). Furthermore, the effects of forest cover on understory fuel availability are particularly pronounced in mesic systems (Nowacki and Abrams 2008; Barberá et al. 2023; Estes et al. 2012; Faiella and Bailey 2007), like those of the northeastern USA where fire research is limited but support for fire management is increasing (Regmi et al. 2024; Wu et al. 2022). As new approaches for improving model parameterization develop, there is a need to refine knowledge of fuel and weather dynamics and incorporate it in these tools and approaches for them to fully meet their potential for decision support

(Marcozzi et al. 2025; Bonner et al. 2024; Hiers et al. 2020).

Tree canopies can buffer understories from broader macroclimate conditions that occur outside of forests (De Frenne et al. 2019; De Lombaerde et al. 2022; Geiger et al. 2012). This buffering effect is driven in part by canopy leaves and branches absorbing solar radiation that would otherwise penetrate the forest understory (Hardy et al. 2004; Aussenac 2000; Geiger et al. 2012), which reduces radiative heat transfer to the ground and near-ground air (Bristow and Campbell 1984; Gaudio et al. 2017). This effect on incoming radiation, as well as reduced air mixing with nearby open areas, often leads to closed canopy understories having lower maximum temperatures and higher minimum humidities in summer compared to open areas (von Arx et al. 2013; Zellweger et al. 2019). In mesic forests, dense cover also tends to increase dead fuel moisture (Barberá et al. 2023; Cawson et al. 2017; Tanskanen et al. 2006), due to the influence of latent heat flux on microclimate buffering (Davis et al. 2019) and fuel availability. In practice, achieving desired effects from prescribed fire in mesic forests of the eastern USA often depends on pre-fire thinning, which opens the canopy to reduce microclimate buffering and increase fuel availability (Hutchinson et al. 2012; Arthur et al. 2021; Nowacki and Abrams 2008; Brose et al. 1999). Consequently, the relationships between forest structure and understory temperature and moisture conditions are central to effective fire management in mesic forests.

Despite the strong influence of within-stand structural variation on understory microclimate and fuel moisture, quantifying forest structure can be challenging and time consuming with traditional forest inventory methods. Terrestrial laser scanning (TLS) is maturing as an approach in forest and fire monitoring that addresses this issue by using ground-based light detection and ranging (lidar) to capture structural variability that would otherwise be difficult to quantify with traditional methods (Pokswinski et al. 2021; Tenny et al. 2025; Maeda et al. 2025; Murphy et al. 2024). Lidar is a promising tool for estimating forest structure (Molina-Valero et al. 2022; De Conto et al. 2017) and its effects on understory microclimate (Wang et al. 2025; Vandewiele et al. 2023; Menge et al. 2023) and fuel moisture (Batchelor et al. 2023; Brown et al. 2021) but more research is needed to assess these relationships in a variety of forest types. Therefore, using emerging technologies to disentangle the interactions between forest structure, microclimate, and fuel moisture can improve pre-fire planning and operational decision making in mesic forests of the northeastern USA where research on this topic is limited.

In this study, we collected and analyzed field-based micro-meteorology sensor data, physically measured fuel moisture data, TLS data, and traditional forest inventory measurements to better understand relationships between forest structure, microclimate, and fuel moisture in northeastern USA conifer forests while also assessing next-generation tools for management. We addressed this goal by pursuing three research objectives: (1) evaluate the extent to which forest structure influences microclimate across a diverse range of managed stands; (2) determine the effectiveness of TLS-derived forest inventory data for predicting traditional forest inventory metrics in the northeastern USA; and (3) evaluate the effectiveness of microclimate measurements, TLS-derived forest inventory data, and traditional forest inventory data for predicting fuel moisture in northeastern forest types (Fig. 1). The results from this research can enhance fire managers' ability to plan and implement fuel treatments by highlighting how changes in forest stand structure drive fine scale heterogeneity in fuel availability.

Methods

Study areas and plot selection

This study focused on two areas in the northeastern USA: the Penobscot Experimental Forest (PEF) in central Maine and Zealand (ZEL) in northern New Hampshire (Fig. 2) that provide a broad range of canopy structures and compositions with minimal topographic variation. The PEF is the site of long-term silvicultural research

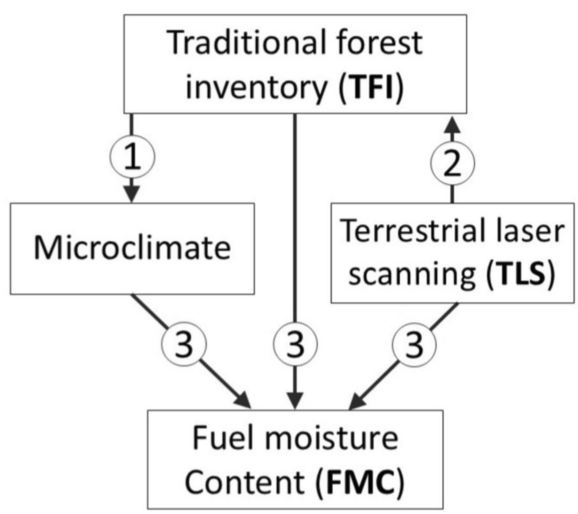

Fig. 1 Conceptual depiction of study objectives. Objective 1: evaluate the extent to which forest structure impacts microclimate across a diverse range of managed stands; Objective 2: determine the effectiveness of TLS-derived forest inventory data for predicting traditional forest inventory metrics in the northeastern USA; and Objective 3: evaluate the effectiveness of microclimate measurements, TLS-derived forest inventory data, and traditional forest inventory data for predicting fuel moisture in northeastern forest types

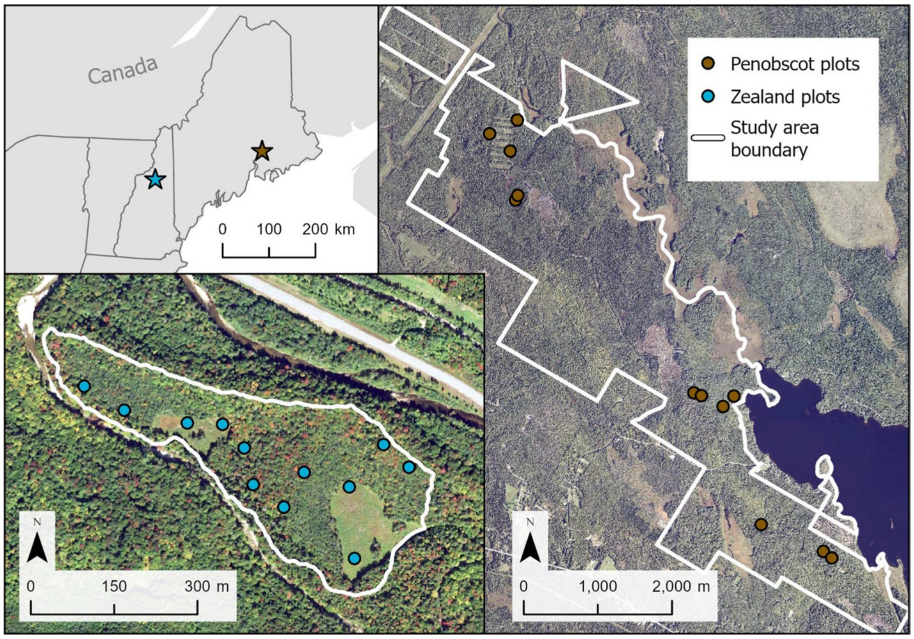

Fig. 2 Study area map showing Zealand (bottom left) and the Penobscot Experimental Forest (right), as well as their respective locations in New Hampshire and Maine in the northeastern USA (top left). Colored points depict 24 study plots (12 at each study location) established across a broad range of forest structures. Each plot included a nested 10- and 6-m fixed radius forest inventory with a microclimate sensor and fuel moisture array located at plot center (Figure S1)

by the USDA Forest Service, Northern Research Station (Kenefic and Brissette 2014). The PEF contains over 50 individual management units that have received a range of experimental harvesting treatments, from high basal area removal (i.e., clearcut) to low basal area removal (i.e., single tree selection), as well as intermediate treatments (i.e., thinning) and untreated areas. Additionally, stand-level species composition ranges from pure evergreen needle-leaved to pure deciduous broadleaved, with many mixed stands interspersed. Common species include red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.)), northern white-cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), paper birch (*Betula papyrifera* Marsh.), bigtooth aspen (*Populus grandidentata* Michx.), and American beech (*Fagus grandifolia* Ehrh.). The PEF is located among forested rolling hills in central Maine and the elevation at the PEF ranges from 8 to 80 m above sea level. It is approximately 66 km from the coast of the Atlantic Ocean.

ZEL is part of the White Mountain National Forest, which is managed by the USDA Forest Service. ZEL is actively managed for recreational trails and wildlife habitat, with approximately 14% of the area maintained as early successional habitat (DeGraaf et al. 2006) through prescribed burning and mowing. The remainder of ZEL is dominated by semi-closed and closed canopy forest, with common species including white spruce (*Picea glauca* (Moench) Voss), red spruce, balsam fir, eastern white pine, black cherry (*Prunus serotina* Ehrh.), red maple, bigtooth aspen, sugar maple (*Acer saccharum* Marsh.), paper birch, and American beech. The study area is located in a mountain valley in the north central portion of the White Mountains and the elevation at ZEL ranges from 400 to 450 m above sea level. ZEL is approximately 125 km from the coast of the Atlantic Ocean.

Historically, northern New England experienced return intervals for stand-replacing fire as long as 800 years (Lorimer 1977). The extent of Indigenous fire use in the region remains controversial (Day 1953; Russell 1983; Oswald et al. 2020a, b; Roos 2020; Abrams and Nowacki 2020) and likely exhibited geographic variability (Patterson and Sassaman 1988; Russell 1983; Roos 2020). Although fire occurrence increased dramatically following widespread European colonial settlement (Parshall and Foster 2002; Hawes 1925), fire suppression since the early twentieth century has greatly reduced the annual area burned (Fahey and Reiners 1981). However, climate change projections for this region point to a doubling in wildfire occurrence by year 2100 (Gao et al. 2021). This projection, coupled with a projected increase in wind-caused forest disturbance worldwide (McDowell et al. 2020)—thereby increasing fuel loads—suggests the need to better understand potential fire behavior and fuel moisture in this region. This information is particularly relevant given the increased support for prescribed burning in the region (Regmi et al. 2024; Northeast Regional Strategy Committee 2020).

Since canopy openness is suggested to strongly influence microclimate and fuel moisture (Brown et al. 2022; De Frenne et al. 2019), we established 24 study plots (12 at PEF and 12 at ZEL) to capture a broad range of canopy structures, from fully open to fully closed canopies. To do this, we used satellite imagery and field visits to identify and verify polygons of potential sampling areas (size range 3500 to 8000 m^2) that represented three strata of canopy openness (i.e., open, intermediate, and closed, see below). Additional criteria for sampling areas dictated that they must be at least 30 m from a major gravel road and at least 30 m from a major water body to avoid edge influence. Once we identified potential sampling area polygons at each location (7 areas in each canopy stratum at PEF for 21 total; 6 in each canopy stratum at ZEL for 18 total), we conducted stratified random sampling to determine plot locations. First, we randomly selected an area from a stratum, then used a 5 × 5-m gridded overlay (based on functional accuracy of handheld GPS) to randomly select a plot location within the pre-identified sampling area polygon. Once a plot location was randomly selected, we ground-validated the location to ensure that (1) it met the canopy stratum requirements (i.e., greater than 66% canopy openness for open plots; 33–66% canopy openness for intermediate plots; less than 33% canopy openness for closed plots); (2) it had no evidence of standing water (i.e., not a forested wetland); and (3) the plot edge was at least 50 m from the edge of a previously selected plot. If any of these criteria were not met, we repeated the selection process within the selected sampling area until all criteria were met. No plot centers were occupied by vegetation that would interfere with our equipment. At each chosen plot location, we established a 10-m fixed radius forest plot in which we conducted microclimate, fuel moisture, and forest structure measurements.

Microclimate data

To quantify microclimate conditions at each plot, we measured air temperature and relative humidity every hour using iButton data loggers (Hygrochron model DS1923, resolution 0.5 °C and 0.6% RH; Maxim Integrated Products, Inc., Sunnyvale, California). To minimize exposure to solar radiation and precipitation while allowing for adequate air mixing, each iButton logger was suspended inside a vented radiation shield with additional overhead radiation cover (modified from Wason et al. 2017) and fastened to a wooden post 1.0 m above the ground (pictured in Figure S1). Posts were placed in the center of each plot and oriented so that radiation shields were on the south side of the stake. Sensors remained in the field from July to December 2023. All microclimate time series data were inspected prior to analysis. Our final dataset included hourly measurements of temperature and relative humidity from 7 July 2023 to 5 September 2023 for all plots.

Fuel moisture data

To quantify fuel moisture content (FMC) at each plot, we placed 10-h fuel stick arrays directly below the microclimate sensor (Figure S1) in late June and early July. Fuel stick arrays consisted of four rectangular (1.9 × 1.9 × 41 cm) pieces of jack pine (*Pinus banksiana* Lamb.) fastened to a plastic frame that facilitated airflow around the sticks (Figure S1). Prior to placing them in the field, we oven dried the fuel sticks at 100 °C until they reached constant mass (> 120 h) to obtain dry mass (range 52.02–73.30 g). Twice throughout the study period we measured the field mass of the sticks: once at 2 days since rain (DSR; sampled on 13 July 2023 at PEF and 24 July 2023 at ZEL) and once at 6 DSR (sampled on 3 September 2023 at PEF and 2 September 2023 at ZEL). At each study area, each round of field mass measurements was collected in a single day between 1200 and 1500. FMC was calculated as (field mass−dry mass)/dry mass, expressed as a percent.

Traditional forest inventory data

To acquire traditional forest inventory (TFI) measurements at each plot, we conducted fixed-radius, nested plot surveys (10-m outer radius; 6-m nested radius) in August 2023. We recorded diameter at breast height (DBH) and species of all trees greater than 11 cm DBH within each 10-m radius plot, and all trees between 1- and 11-cm DBH within each 6-m radius plot. For each plot, we calculated total basal area, trees per hectare, and evergreen cover basal area (Table S1). We also estimated canopy openness as the mean of four measurements taken in cardinal directions with a spherical densiometer (Forestry Suppliers Spherical Crown Densiometer, Convex Model A; see Beeles et al. 2022) held directly over each iButton logger (Figure S1).

Terrestrial laser scanning data

To estimate forest structure from terrestrial laser scanning (TLS), we scanned each plot with a BLK360 G1 TLS (Leica Geosystems, Heerbrugg, Switzerland) in August 2023. The TLS unit operated from a tripod at plot center that was tall enough to be placed over the microclimate and fuel moisture array so that they were not captured in the scan. For each plot, the TLS unit collected a 360° panoramic RGB image followed by a full 360° spherical lidar scan to produce a three-dimensional point cloud. We clipped all point clouds to a cylinder with a 10-m radius in order to match our TFI plots. Next, we classified points into ground and non-ground, which were further used to produce a digital terrain model (DTM) and normalized point cloud (Maxwell et al. 2023; Loudermilk et al. 2022; Gallagher et al. 2021). We used the normalized point cloud to generate height and intensity metrics (Roussel et al. 2020), as well as a suite of custom metrics that capture a wide range of forest structural characteristics (Table S2; also see Gallagher et al. 2021; Maxwell et al. 2023).

Data analyses

To characterize air temperature and moisture for each plot we calculated daily values of maximum temperature (T_{max}; Fig. 3a shows mean of all plots at each location) and minimum relative humidity (RH_{min}; Fig. 3b shows mean of all plots at each location), as well as mean values of T_{max} and RH_{min} for the entire study period (Table S3). For each round of fuel moisture measurements at each plot, we calculated plot-level means of FMC from the four fuel sticks in each array.

To determine how microclimate buffering was driven by TFI metrics (Objective 1), we built a set of linear mixed-effects models (LMEs) predicting mean values of T_{max} and RH_{min} for the entire study period as a function of canopy openness, basal area per hectare, and trees per hectare. We included a random effect for study area (i.e., PEF vs. ZEL) to account for the locations having different climates during the study period (Fig. 3, Table S3). We built models with all possible combinations of predictors (but no interactions due to our limited sample), then ranked the models based on values of corrected Akaike Information Criterion (AIC_c) and selected only models within 10 ΔAIC_c of the highest ranked model (Table S4, Table S5). We assessed performance using mean conditional R^2 (R^2_c; includes fixed and random

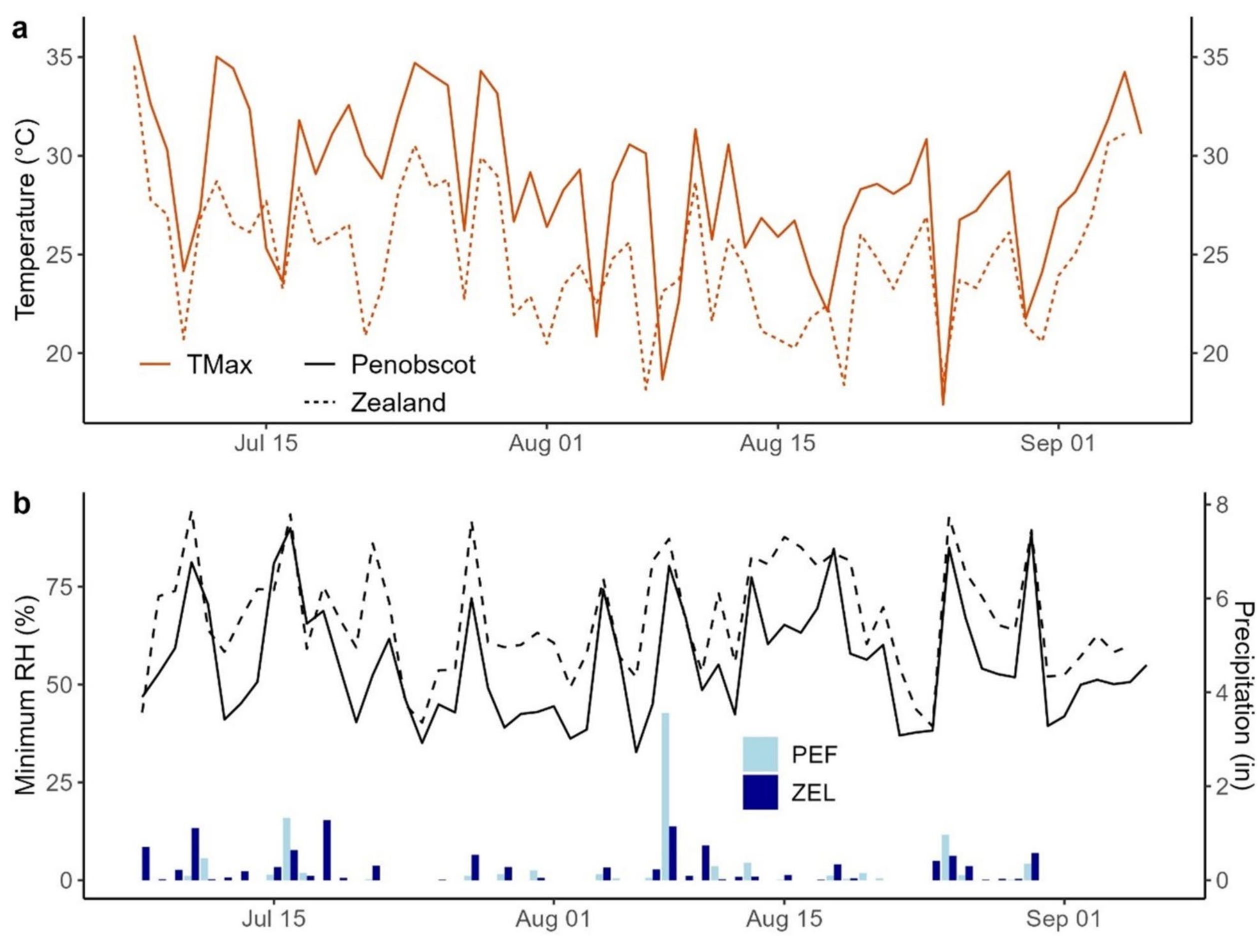

Fig. 3 Microclimate summaries for each study location. **a** Daily values of maximum air temperature (T_{max}) and **b** minimum relative humidity (RH_{min}) averaged across all plots at each study location. Daily precipitation totals from the nearest National Weather Service station to the Penobscot (PEF) and Zealand (ZEL) are shown on the bottom of panel b

effects), marginal R^2 (R^2_m; includes only fixed effects), and root mean square error (RMSE) of all the candidate models. To compare model performance across response variables with different units (T_{max} and RH_{min}) we used normalized root mean square error ($_n$RMSE), which is standardized by the mean of the response variable. Additionally, to focus on the effect of canopy openness on microclimate, we built linear models predicting mean values of T_{max} and RH_{min} for the entire study period as a function of canopy openness. To assess this relationship across our two study areas, we included an interaction term for study location and removed the interaction if not significant ($p > 0.05$).

To determine effectiveness of TLS-derived forest inventory data for predicting TFI metrics (Objective 2), we first identified important variables for modeling canopy openness, basal area per hectare, and trees per hectare as response variables. Due to the large number of TLS metrics (> 200) relative to the number of plots (24) for predicting TFI metrics, we conducted a variable selection process using random forests (VSURF (Genuer et al. 2013)) to identify important TLS variables to include in our models. Once TLS-derived predictor variables were identified, we ran multiple linear models with each TFI metric as the response variable and used values of R^2, RMSE, and percent agreement between observed and predicted values to assess performance. Additionally, to visualize relationships between each TFI response variable and its top TLS-derived predictor variable, we ran bivariate linear models and used R^2 to assess the relationship.

When predicting FMC from TFI, microclimate, or TLS (Objective 3), we accounted for impacts of recent precipitation on dead fuel moisture by including a random effect for days since rain (DSR; 2 observations per plot over the study period) nested within study area in all models. This was based on preliminary analyses showing similar slopes to the regression lines among sites and DSR. To determine how fuel moisture could be predicted by TFI metrics (Objective 3), we used the same approach as above to build a set of LMEs predicting FMC as a function of canopy openness, basal area per hectare, and trees per hectare. We used the same AIC_c selection process as above to rank and choose model predictors (Table S6). When building LMEs to model FMC from microclimate variables (Objective 3), we accounted for impact of recent weather conditions on dead fuel moisture by calculating means of daily maximum temperature and daily minimum relative humidity for the 5 days prior to each round of fuel moisture measurements, which we then used to predict corresponding FMC values. While our previous analyses from Objective 1 used seasonal mean values of T_{max} and RH_{min} as response variables for modeling microclimate from TFI metrics that are relatively static over a summer season, our analyses using microclimate to predict FMC only included 5-day antecedent averages of daily maximum temperature ($T_{max,ant}$) and daily minimum relative humidity ($RH_{min,ant}$). We then used the same AIC_c selection process as above to rank and choose model predictors (Table S7). To predict FMC from TLS (Objective 3), we used VSURF (Genuer et al. 2013) to identify important TLS variables for predicting FMC. Once these variables were identified, we carried out the same AIC_c selection process to rank and choose the top LMEs (Table S8). Additionally, to visualize the relationships between FMC and the top predictor variable from each data source (i.e., microclimate, TLS, and TFI), we ran bivariate linear models and used R^2 to assess performance. To assess these relationships across our two study areas, we included an interaction term for study location and removed the interaction if not significant.

For every model, we checked normality of residuals with the Shapiro–Wilk test. We used variance inflation factor (VIF) to test collinearity of predictors and removed all models with VIF greater than 4. All analyses were run in R using RStudio (ver. 4.2.3, R Core Team 2023; RStudio Team 2023) and models were generated using packages nlme (Pinheiro et al. 1999), and VSURF (Genuer et al. 2013).

Results

We found that forest structure strongly influences understory microclimate. Our LMEs predicting microclimate from TFI metrics consistently explained over 85% of the variation in daily averages of T_{max} (mean R^2_c of 0.87; Table S4) and RH_{min} (mean R^2_c of 0.88; Table S5). On average, the fixed effects of forest structure (i.e., canopy openness, basal area per hectare, and trees per hectare) explained 41% of the variation (R^2_m) in T_{max} and RH_{min}, while the random effect for study area explained 46% of the variation in T_{max} and RH_{min} (Figure S2). Canopy openness and basal area were the most prominent TFI predictor variables and occurred in the top models of both T_{max} and RH_{min} from our AIC selection process. We found a significant effect of canopy openness on mean daily T_{max} (slope, 0.078 ± 0.015 °C*%$^{-1}$, p-value < 0.001; $R^2 = 0.54$) causing an overall increase from open to closed stand of 7.82 °C (Fig. 4a). We also found a significant effect of canopy openness on mean daily RH_{min} (slope, -0.241 ± 0.048%*%$^{-1}$, p-value < 0.001; $R^2 = 0.55$) causing an overall decrease from open to closed stand of 24.1% (Fig. 4b). The relationships between canopy openness and microclimate were consistent across our two study areas (no significant interaction between canopy openness and location) despite the PEF being generally warmer and

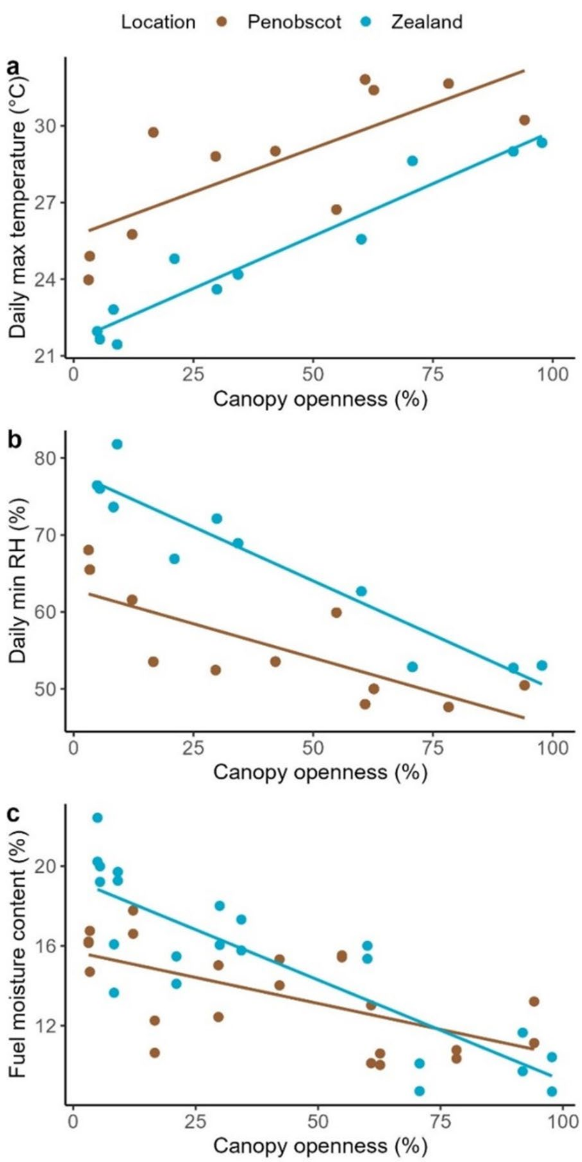

Fig. 4 Microclimate and fuel moisture variables as a function of canopy openness. **a** Mean seasonal daily maximum temperature (T_{max}), **b** mean seasonal daily minimum relative humidity (RH_{min}), and **c** fuel moisture content (FMC) as a function of canopy openness. Lines represent separate simple linear regressions for each study location for visualization. However, we used linear mixed effects models to test these effects and found that canopy openness was a significant predictor of both variables

less humid than ZEL over the study period (Fig. 4a, b; Table S3).

TLS metrics were generally able to predict TFI variables of canopy openness, basal area per hectare, and trees per hectare (Fig. 5, Figure S4). For each TFI response variable, the VSURF selection process revealed two TLS-derived predictor variables that were important for modelling the response variable (Table S9). Our multiple linear models predicting each TFI response variable showed that TLS-derived predictors explained 91% of variation in canopy openness (Table S10), 91% of variation in basal area per hectare (Table S11), and 82% of variation in trees per hectare (Table S12). When plotting the top TLS-derived predictors with their respective response variables, we found that individual TLS metrics explained 89% of variation in canopy openness, 76% of variation in basal area per hectare, and 78% of variation in trees per hectare (Fig. 5).

We found directly using microclimate variables to predict FMC explained more variation (mean R^2_c of 0.87; Fig. 6, Table S7) than using forest structure variables whether measured by TLS (mean R^2_c of 0.74; Fig. 6, Table S8) or traditional forest inventory (mean R^2_c of 0.60; Fig. 6, Table S6). On average, the fixed effects of microclimate or forest structure explained the majority of the variation in FMC (mean R^2_m of 0.59), while the random effects for days since rain (DSR) and study location on average explained 14% of the variation in FMC (Fig. 6). Of our chosen microclimate variables used to predict FMC, we found that $T_{max,ant}$ explained the most variation in FMC when plotted in a bivariate model ($R^2 = 0.71$; Fig. 7a; no significant interaction with study location). For our TLS variables used to model FMC, percent gap fraction explained the most variation in FMC ($R^2 = 0.53$; Fig. 7b; no significant interaction with study location). Finally, of our TFI predictors used to model FMC, we found that canopy openness explained the most variation in FMC ($R^2 = 0.55$; Fig. 7c). We found that the strong influence of forest structure on microclimate also led to a significant effect on FMC (slope, $-0.080 \pm 0.011\%{*}\%^{-1}$, p-value < 0.001; $R^2 = 0.55$) causing an overall decrease from open to closed stand of 8.03% (Fig. 7c). Interestingly, the decline in FMC with increasing canopy openness at ZEL was stronger (more negative) compared to the PEF (significant interaction, p-value 0.021; Fig. 7c).

Discussion

Our findings support previous research from mesic systems demonstrating that dense forest cover reduces fuel availability by buffering microclimate (De Lombaerde et al. 2022; Pickering et al. 2021; Brown et al. 2022) and increasing dead fuel moisture (Barberá et al. 2023; Brown et al. 2022; Cawson et al. 2017; Tanskanen et al. 2006). This finding also supports previous research demonstrating that forest structure interacts with the fire environment beyond just fuel considerations (Loudermilk et al. 2022; Mitchell et al. 2009). We found that canopy openness was a prominent structural driver of these effects on understory conditions (von Arx et al. 2013). The strong influence of forest structure on understory microclimate

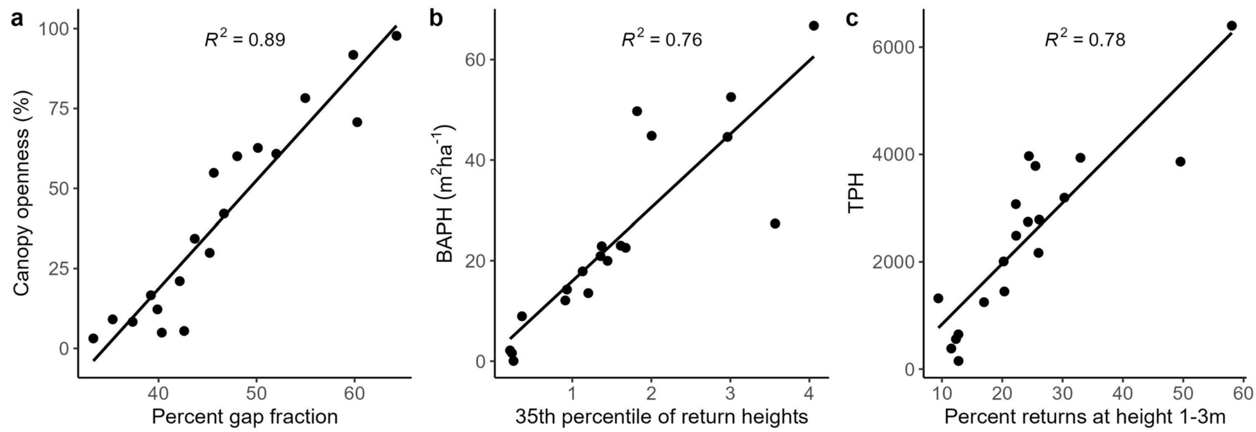

Fig. 5 Bivariate relationships between each traditional forest inventory (TFI) response variable and its top terrestrial laser scanning (TLS) predictor variable identified from variable selection using random forests. Each panel shows the top TLS-derived individual predictors of **a** canopy openness, **b** basal area per hectare (BAPH), and **c** trees per hectare (TPH)

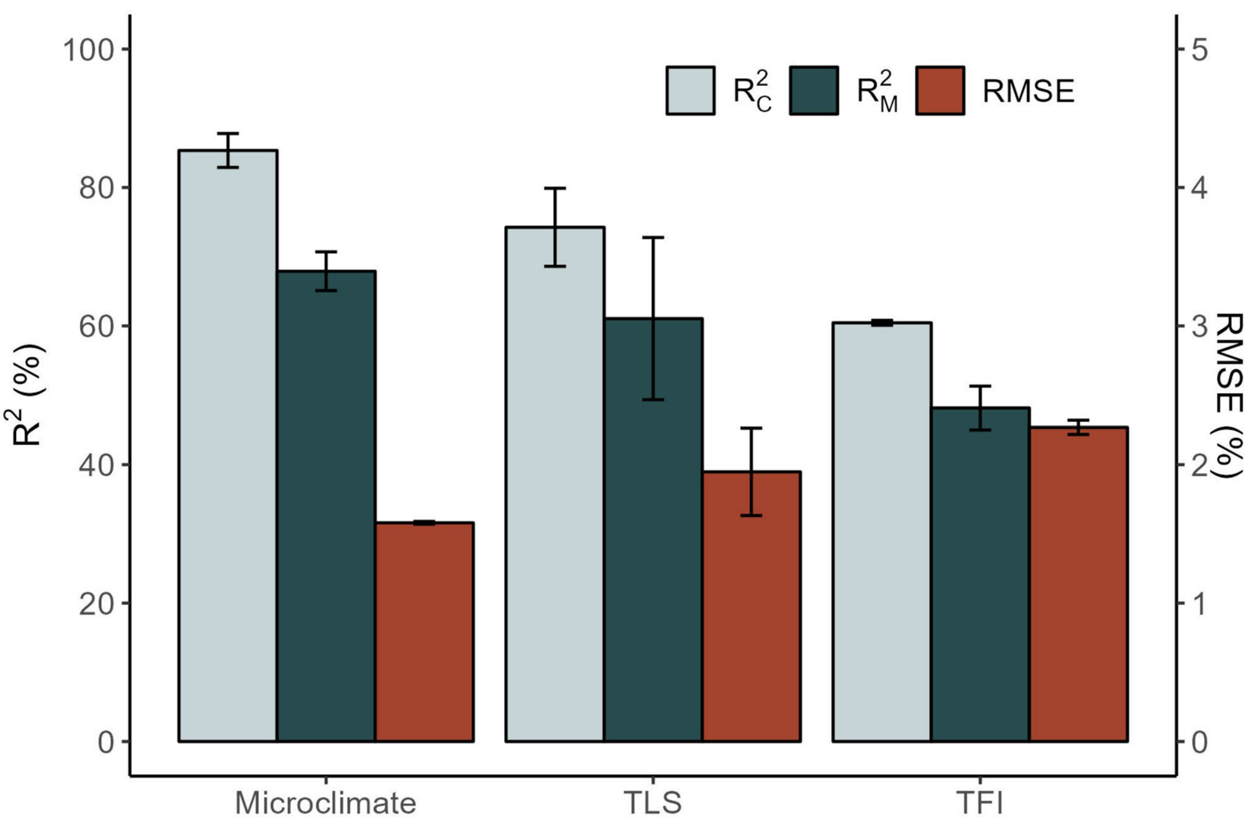

Fig. 6 Performance from linear mixed models predicting fuel moisture content from variables derived from microclimate, terrestrial laser scanning (TLS), or traditional forest inventory (TFI) measurements. Error bars depict one standard error. For each set of predictor variables, we ran all LMEs within 10 ΔAIC of the top model (n = 2 for all sets of predictors). The figure shows the mean output of these models. All models included a random effect for days since rain nested within study location. Conditional R^2 (R^2_c) depicts the total variation explained by fixed and random effects, while marginal R^2 (R^2_m) depicts the variation explained by fixed effects. Root mean square error (RMSE) is a measure of model error

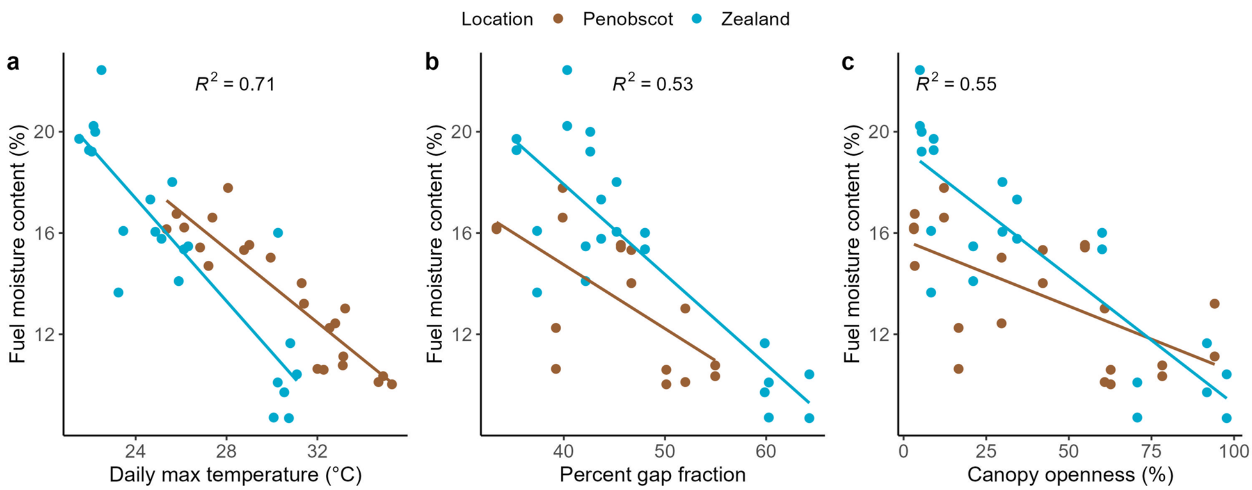

Fig. 7 Bivariate relationships of the top individual predictors of fuel moisture content (FMC) from **a** microclimate variables, **b** terrestrial laser scanning (TLS) variables, and **c** ground-based forest structure variables. For panel **a**, the x-axis represents the 5-day antecedent average of daily maximum temperature. Lines represent linear regressions for each location, while R^2 values in each panel correspond to the overall relationship not accounting for study location

and dead fuel moisture was further supported by our models that used TLS-derived variables as predictors. In fact, TLS-derived variables were better predictors of dead fuel moisture than traditional forest inventory metrics. As further discussed below, we presume this is because our TLS-derived predictors of dead fuel moisture captured additional canopy structure that was not measured in our traditional inventories.

Canopy openness and basal area were the top TFI-derived predictors of seasonal microclimate. Canopy openness has emerged in our study, and others (von Arx et al. 2013; Brown et al. 2022), as a robust predictor of both understory temperature and relative humidity. Here we provide new estimates for the strength of this relationship and our findings suggest that this relationship may be consistent across locations (i.e., no significant interaction between canopy openness and location across our two study areas). Basal area was also a robust predictor of understory microclimate (Díaz-Calafat et al. 2023), presumably due to collinearity with canopy openness (Figure S3) and the relationship between tree diameter and crown size (Hemery et al. 2005; Russell and Weiskittel 2011). Trees per hectare was not a prominent predictor of microclimate because this metric is highly sensitive to smaller sapling-size trees that did not directly shade the microclimate sensor, as shown by its lower correlation with canopy openness compared to basal area (Figure S3). While evergreen basal area can be a prominent predictor of microclimate in mixed stands during leaf-off seasons (Díaz-Calafat et al. 2023), it was not a significant predictor in our study that occurred during summer. Although topography is known to affect microclimate (Dobrowski 2011; Fridley 2009; Jucker et al. 2018), it was not included in our predictors since elevation differences within both our study areas were less than 80 m. Our model selection process included all possible combinations of predictors for modeling microclimate, but all models with multiple TFI terms were eventually removed due to high collinearity among predictors. Regardless, our results suggest that in many cases there are existing forest metrics already available from traditional forest inventories that can be used to predict both microclimate and, as discussed later, fuel moisture.

We found that TLS provided reliable estimates of three commonly used TFI metrics. When predicting canopy openness, the top TLS variables included percent gap fraction and the 5th percentile of height distribution of returns. While gap fraction represents variation in lidar reflectance from the forest canopy (Danson et al. 2007), the 5th percentile of height distribution of returns is indirectly related to canopy openness by representing the relationship between overstory cover and understory productivity. TLS variables used to predict basal area and trees per hectare represented lower strata of returns, which appear to be physically related to lower sections of the forest. For basal area, the top predictor was the 35th percentile of height distribution of returns, which likely corresponds to lidar reflectance capturing both tree stem diameter and crown width. For trees per hectare, the top predictor was the percent of returns recorded at 1–3 m height, which likely represents lidar reflectance capturing tree stem density within the plot scan. Despite the large number (> 200) of potential TLS predictors, it is encouraging that we found linkages between TLS metrics and

TFI metrics in our study areas. While future research could use larger datasets and a variety of models to establish clear mechanistic links between TLS and TFI metrics, our findings contribute to the growing body of research highlighting the utility of this emerging technology in forest monitoring (De Conto et al. 2017; Maeda et al. 2025; Molina-Valero et al. 2022; Tenny et al. 2025).

Our results support the underlying theory of models that predict dead fuel moisture from weather conditions (Cohen and Deeming 1985; Rothermel 1983) by demonstrating that microclimate variables were better predictors of dead fuel moisture than forest structure variables, regardless of whether they were measured by TLS or TFI. Although $T_{max,ant}$ was the top microclimate predictor of FMC from our model selection process, $RH_{min,ant}$ influenced FMC to nearly the same degree due to their interrelated nature and direct effects on dead fuel moisture. Even though the lag times from our custom fuel sticks may have been slightly longer compared to standard 10-h fuel sticks, we equipped all plots similarly and our models show that microclimate consistently provided strong predictions of dead fuel moisture. Additionally, while our study measured dead fuel moisture at only two different levels of days since rain, fire management in mesic systems would benefit from future research that more closely examines the relationships between fuel conditions, antecedent moisture, and forest structure.

Although microclimate was the most prominent driver of FMC in our study, we also found that microclimate and fuel moisture can vary markedly within the same stand, due to spatial variability in forest cover (Geiger et al. 2012; Tanskanen et al. 2006; Zellweger et al. 2020). While canopy openness and basal area both occurred in our top models of microclimate and FMC, we focus more on canopy openness due to the known mechanisms of canopy traits (such as leaf area index) affecting understory conditions through interception of solar radiation (von Arx et al. 2013; Hardy et al. 2004). Our finding that basal area strongly influenced microclimate and FMC is likely due to higher basal area being related to greater crown coverage (Hemery et al. 2005; Russell and Weiskittel 2011), as is shown by its high collinearity with canopy openness in our dataset (Figure S3). This is further supported by our TLS metrics. Of our 200+ candidate TLS-derived predictors of FMC, the top two identified from VSURF are canopy-related. Percent gap fraction is highly correlated with canopy openness (Danson et al. 2007) and standard deviation of returns above 2 m describes variation in canopy layering, which relates to live crown ratio and leaf area index. Therefore, the accuracy of models predicting dead fuel moisture at management-relevant scales could be improved by incorporating adjustments for forest cover (Tanskanen et al. 2006), since canopy traits can be mapped from airborne lidar to predict understory conditions (Menge et al. 2023; Jucker et al. 2018; Vandewiele et al. 2023). Given the ease, efficiency, and effectiveness of using TLS to estimate forest structure, our results support the use of this technology at the plot level. Future research that combines forest structure estimates from TLS with those from airborne lidar could scale up models of microclimate and dead fuel moisture to improve fire and fuels management.

The relationships between forest structure and understory conditions can be used to fine tune a variety of targets related to fire and fuels management. In fire-excluded systems that have been colonized by fire-intolerant plant species (i.e., mesophication), mechanical thinning is often needed prior to prescribed burning in situations where managers aim to restore fire-adapted ecosystems (Nowacki and Abrams 2008). Our results can provide a foundation for identifying target stand conditions that may produce desirable understory microclimates for conducting prescribed fire. Future research could build on our findings by measuring microclimate and fuel moisture before and after specific fuel treatments, across a wider range of fuel sizes, and in relation to observed fire behavior. Our findings demonstrating the strength of canopy openness and related TLS metrics for explaining variation in understory microclimate and FMC may support the use of shaded fuel breaks (also called green fuel breaks) in fire suppression operations, which reduce fuel availability by maintaining a semi-closed canopy in order to retain some level of buffering for microclimate and dead fuel moisture (Agee et al. 2000; St. John and Ogle 2009). Our findings regarding the effect of forest cover on understory microclimate can inform thinning prescriptions that seek to achieve certain thresholds of understory temperature, relative humidity, and dead fuel moisture by highlighting the link between canopy openness and surface fuel availability. Further, the results of our study demonstrate the importance of incorporating spatially dynamic fuel and weather conditions into fire behavior tools to fine tune operational decision making and planning.

Conclusions

Our study used multi-modal measurements to demonstrate that forest structure strongly affects understory microclimate, with open canopy plots having predicted maximum temperatures 7.82 °C warmer and predicted relative humidity 24.1% lower compared to closed canopy plots. The effects of forest structure on understory microclimate extend to dead fuel moisture, where open canopy plots had predicted fuel moisture content 8.03% drier than closed canopy plots. TLS-derived variables were better predictors of dead fuel moisture than traditional forest inventory metrics, presumably due to their ability to capture structural variation in the canopy that is otherwise difficult to measure. Our models showed consistent linear relationships between forest structure and microclimate at two study areas in northern New England, which suggests our results may be transferable to new areas with similar mesic forest types. Our results demonstrate the importance of thinning for optimizing fuel availability for prescribed fire in mesic forests, and our models suggest that fuel moisture content responds linearly to canopy openness. While within-stand heterogeneity in forest structure may be difficult and time consuming to measure with traditional methods, TLS is effective for estimating forest structure, as well as microclimate and dead fuel moisture. Therefore, our results support the use of TLS for monitoring stand structure, as well as fuels management operations that consider the effect of canopy buffering on understory microclimate and dead fuel moisture.

Abbreviations

TLS	Terrestrial laser scanning
PEF	Penobscot experimental forest study area
ZEL	Zealand study area
FMC	Fuel moisture content
TFI	Traditional forest inventory
DBH	Diameter at breast height
DTM	Digital terrain model
AIC	Akaike Information Criterion
RMSE	Root mean square error
T_{max}	Daily maximum temperature
RH_{min}	Daily minimum relative humidity
T_{max}	$_{Ant}$: 5-day antecedent daily maximum temperature
RH_{min}	$_{Ant}$: 5-day antecedent daily minimum humidity
LME	Linear mixed-effects model
DSR	Days since rain
VSURF	Variable selection using random forests

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00480-w.

Additional file 1: Supplemental tables and figures.

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Authors' contributions
PB and JW conceptualized the study, collected data, interpreted data, and were major contributors in writing the manuscript. SF, LK, MG, and EL provided guidance on study design, data collection, data interpretation, and writing. JN provided guidance on study design, data collection, and writing.

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Data availability
Data is publicly available on Dryad (DOI: https://doi.org/10.5061/dryad.83bk3jb74).

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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