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Landscape controls on fuel moisture variability in fire-prone heathland and peatland landscapes

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Abstract

Background Cross-landscape fuel moisture content is highly variable but not considered in existing fire danger assessments. Capturing fuel moisture complexity and its associated controls is critical for understanding wildfire behavior and danger in emerging fire-prone environments that are influenced by local heterogeneity. This is particularly true for temperate heathland and peatland landscapes that exhibit spatial differences in the vulnerability of their globally important carbon stores to wildfire. Here we quantified the range of variability in the live and dead fuel moisture of *Calluna vulgaris* across a temperate fire-prone landscape through an intensive fuel moisture sampling campaign conducted in the North Yorkshire Moors, UK. We also evaluated the landscape (soil texture, canopy age, aspect, and slope) and micrometeorological (temperature, relative humidity, vapor pressure deficit, and windspeed) drivers of landscape fuel moisture variability for temperate heathlands and peatlands for the first time.

Results We observed high cross-landscape fuel moisture variation, which created a spatial discontinuity in the availability of live fuels for wildfire spread (fuel moisture < 65%) and vulnerability of the organic layer to smoldering combustion (fuel moisture < 250%). This heterogeneity was most important in spring, which is also the peak wildfire season in these temperate ecosystems. Landscape and micrometeorological factors explained up to 72% of spatial fuel moisture variation and were season- and fuel-layer-dependent. Landscape factors predominantly controlled spatial fuel moisture content beyond modifying local micrometeorology. Accounting for direct landscape—fuel moisture relationships could improve fuel moisture estimates, as existing estimates derived solely from micrometeorological observations will exclude the underlying influence of landscape characteristics. We hypothesize that differences in soil texture, canopy age, and aspect play important roles across the fuel layers examined, with the main differences in processes arising between live, dead, and surface/ground fuels. We also highlight the critical role of fuel phenology in assessing landscape fuel moisture variations in temperate environments.

Conclusions Understanding the mechanisms driving fuel moisture variability opens opportunities to develop locally robust fuel models for input into wildfire danger rating systems, adding versatility to wildfire danger assessments as a management tool.

Keywords *Calluna vulgaris*, Fire danger, Fire weather, Landscape ecology, Phenology, Spatial controls, Temperate ecosystems, United Kingdom, Wildfire

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Resumen

Antecedentes El contenido de humedad de los combustibles a través del paisaje es altamente variable, aunque no es considerado en las determinaciones actuales del peligro de incendio. Capturar la complejidad y sus controles asociados es crítico para entender el comportamiento del fuego y el peligro de incendios en ambientes propensos al fuego, que son influenciados por heterogeneidades locales. Esto es particularmente cierto para ambientes de brezales (i.e. comunidades de plantas leñosas de bajo crecimiento generalmente de la familia *Ericaceae*) y turberas, que exhiben diferencias espaciales en su vulnerabilidad en cuanto a su importancia global como almacenes de carbono en relación con los incendios. Cuantificamos acá el rango de variabilidad en el combustible vivo y muerto de *Calluna vulgaris* a lo largo de un paisaje propenso al fuego mediante una campaña de muestreo intensivo de la humedad de combustible conducido en los Páramos de Yorkshire del Norte, en el Reino Unido (*North Yorkshire Moors, UK.*) Evaluamos asimismo por vez primera, el paisaje (textura del suelo, edad del dosel, aspecto y pendiente), y los factores micro meteorológicos (temperatura, humedad relativa, déficit de vapor de difusión, y velocidad del viento) que influyen en la variación de la humedad de estos brezales y turberas templados.

Resultados Observamos una alta variación en la humedad del combustible a través del paisaje, lo cual crea una discontinuidad espacial en la disponibilidad de combustibles vivos para la propagación del fuego (humedad del combustible < 65%) y vulnerabilidad del estrato orgánico a la combustión latente (humedad del combustible del < 250%). Esta heterogeneidad fue más importante en primavera, que es también el pico de la estación de fuegos en estos ecosistemas templados. El paisaje y los factores micro meteorológicos explicaron hasta un 72% de la variación espacial del contenido de humedad de los combustibles, y fueron dependientes del estrato de combustibles y de la estación del año. Los factores del paisaje controlaron predominantemente el contenido de humedad a nivel espacial, más allá de modificar la micro meteorología local. El contar con las relaciones directas entre paisaje-humedad del combustible puede mejorar la estimación de la humedad del combustible, dado que las estimaciones existentes basadas solamente en observaciones micro meteorológicas excluirán la marcada influencia de las características del paisaje. Hipotetizamos que las diferencias en la textura del suelo, la edad del dosel, y el aspecto juegan roles importantes en todos los estratos examinados con las principales diferencias que surgen entre los combustibles vivos y muertos y los superficiales (aéreos) y rastreros (que tocan el suelo). También enfatizamos el rol crítico de la fenología de los combustibles en la determinación de la variación de la humedad de los combustibles a escala de paisaje en estos ecosistemas templados.

Conclusiones El entender los mecanismos de determinan la variabilidad en la humedad de los combustibles abre la oportunidad para desarrollar modelos robustos de combustibles locales como input para sistemas de peligro de incendios, adicionando versatilidad a las determinaciones de peligro de incendios como una herramienta de manejo.

Background

Temperate peatlands and heathlands contain globally important carbon stores that are becoming increasingly susceptible to wildfires under climate and land use change (Page and Baird 2016; Kirkland et al 2023). Peatlands store 550 gigatons of organic soil carbon globally, and approximately 0.19–0.88 million km² of these peatlands are found in temperate latitudes (30-50°) (Batjes 1996; Yu 2012). Surface wildfires can lead to the smoldering combustion of carbon-rich peatland soils (Kirkland et al 2023). These fires are resource-intensive to extinguish and can result in significant carbon emissions (Mickler 2021). Fuel moisture is a key component of fuel flammability, ignition probability, and subsequent wildfire behavior (Matthews 2014; Scarff et al 2021). As such, fuel moisture content is important for determining peatland and heathland wildfire danger—the combination of factors affecting the initiation, spread, and ease of control of a wildfire (Natural Resources Canada 2021).

Existing operational fire weather indices across northwest Europe (e.g., EFFIS: San-Miguel-Ayanz et al (2012)) use weather information to predict the danger of a successful ignition, drawing on regional assessments of fuel moisture (for example the Fine Fuel Moisture Code of the Canadian Fire Weather Index System (CFWIS)). However, fuel moisture content can be highly spatially variable at the landscape level (Nyman et al 2015; Walsh et al 2017). Regional estimates do not capture this spatial heterogeneity of fuel moisture and consequently may not reflect local conditions (Nyman et al 2018; Matthews et al 2019). Current risk assessments therefore do not account for fuel-driven within-landscape vulnerability to wildfires and their consequent ecological, biogeochemical, or socioeconomic impacts (Davies et al 2016; Hokanson et al 2016).

Studies that have captured the extent of fuel moisture variability at the landscape level using direct measurement techniques are rare and have not been conducted Little et al. Fire Ecology (2024) 20:14 Page 3 of 13

within temperate peatland and heathland landscapes. Previous research has utilized indirect measures of fuel moisture content such as soil and litter moisture sensors to quantify the moisture variability of fire-prone forest litter layers (Nyman et al 2015; Slijepcevic et al 2018). However, in dwarf shrub Calluna vulgaris dominated temperate peatland and heathlands, both the dead and live vegetation are important for wildfire ignition and spread, with live fuels often comprising the largest component of the fuel load (Davies and Legg 2008, Davies and Legg 2010). The magnitude of fuel moisture variability at the landscape scale and the controls on that variability will therefore strongly differ from forest ecosystems (Dickman et al 2023). Further, fuel moisture within the surface moss, litter, and organic soils is important for determining the potential for smoldering combustion and the associated fire severity (Grau-Andrés et al 2018). Low organic soil moisture (<250%) facilitates belowground smoldering and consequent loss of carbon to the atmosphere (Lukenbach et al 2015).

In addition to the quantification of cross-landscape fuel moisture variability, the landscape characteristics that control this variability have not yet been fully resolved. Average regional-scale fuel moisture is likely modulated by landscape-scale variability in hydrology, meteorology, ecology, and plant physiology. Again, previous research into how landscape characteristics control fuel moisture content has primarily focused on forested fuels and landscapes. Four key landscape characteristics have emerged: soil properties, landscape position, topography/aspect, and vegetation structure (see references within Table 1). The extent to which these landscape characteristics are important for fuel moisture within temperate peatland and heathland fuels is unknown. The complexity of landscape ecological field studies has also meant that landscape characteristics can be confounded and difficult to isolate (e.g., all of the south-facing sites contained all of the highest porosity soils, and the link between vegetation cover on equatorial versus polar-facing slopes Nyman et al 2015; Slijepcevic et al 2018)).

Cross-landscape differences in fire behavior and fire danger are particularly relevant to consider in emerging fire-prone environments, where fire behavior, including wildfire spread through live fuels and smoldering combustion of organic soils, can be influenced by small-scale heterogeneity in landscape characteristics. It is therefore important to understand fuel moisture dynamics at the landscape level to develop appropriate fuel models for inclusion in fire danger assessments in temperate ecosystems. To this end, we assess (1) what is the range of variability in the live and dead fuel moisture content of *Calluna vulgaris* across a temperate fire-prone landscape? and (2) what are the relative contributions of

landscape and micrometeorological drivers of fuel moisture variability at the landscape scale? In doing so, we provide the critical understanding necessary to develop tailored fuel moisture models for input in wildfire danger rating systems, to support local-scale fire management decisions.

Methods

Study region

Our study region was the North Yorkshire Moors National Park, UK (Fig. 1). The dwarf shrub Calluna vulgaris is abundant in peatlands and heathlands that form large areas of fire-prone landscapes across north-western Europe, including the UK (Gimingham et al 1979; Glaves et al 2020). Upland areas of the North Yorkshire Moors comprise extensively managed Calluna vulgaris-dominated peatland and wet heathland ecosystems (Simmons 1990). Calluna has been burned on rotation, creating a patchwork mosaic of homogenous Calluna plots of different ages across the landscape, allowing the role of vegetation structure and topography/aspect that have previously been confounded to be isolated (Nyman et al 2015; Slijepcevic et al 2018). The landscape also consists of a diversity of soil textures and associated geologies, slopes, aspect, and landscape positions, within the given regional moist, maritime climate. As such, the region provides an ideal location to examine the underlying controls on spatial fuel moisture variability in critical fireprone temperate landscapes.

Experimental design and site selection

We selected 36 plots across the North Yorkshire Moors. The plot dimensions were approximately 20×20 m of homogenous Calluna as this was the size burned by land managers to create the patchwork mosaic of Calluna across the landscape. We decided on 36 plots as this allowed each plot to contain a unique combination of the four landscape factors hypothesized to be important for spatial fuel moisture variability based on previous research: soil texture, canopy age, aspect, and hillslope position (Fig. 2; Table 1). We selected potential plots by overlaying the source maps from Table 1 to identify areas that contained all possible combinations of landscape factors. We then visited the areas to identify suitable plots with land managers. The criteria for the 36 plots were as follows: (1) each plot must possess a unique combination of landscape factors, (2) plots must be sufficiently accessible to allow sampling to be carried out at all plots on the same day (using multiple samplers), and (3) plots must meet requirements of land managers (e.g., minimize disruption to nesting birds or land management activities). Fuel moisture sampling is intensive, so we selected plots that were sufficiently close to allow field

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Table 1 The hypothesized landscape drivers of fuel moisture variability examined for plot selection. We classified landscape drivers using the provided sources and validated these with field assessments

Driver	Classification (number of sites in each classification, $n=36$ sites)	Source	Significance (hypothesized from previous research)
Soil texture	Coarse: Freely draining very acid sandy and loamy soils (12 sites) Fine: Slightly acid loamy and clayey soils with impeded drainage; slowly permeable seasonally wet acid loamy and clayey soils (12 sites) Peat: Blanket bog peat soils and slowly permeable wet very acid upland soils with a peaty surface (12 sites)	Soilscapes class numbers (Farewell et al 2011)	Soil texture captures the soil hydraulic traits (e.g., soil depth, porosity, permeability, drainage flow paths, and water table depth) hypothesized to control water availability to dead fuels via capillary action and live fuels via water uptake by roots (Nyman et al 2015; Matthews 2014)
Canopy age	Building: 5–10 years since last burn, 30 cm height (18 sites) Mature: 15–20 years since last burn, 60 cm height (18 sites)	Land managers' records and satellite imagery	Fuel age and height influence fuel moisture by creating differences in shading, fuel structure, and plant hydraulic traits. Live fuel canopy cover and biomass have been shown to regulate the moisture content of underlying fuels (Nyman et al 2018, Brown et al 2022b). But also within the same species, variability in biomass, age, and the proportion of live-to-dead material influence the moisture content of live fuels themselves (Davies and Legg 2011; Brown et al 2022a)
Hillslope position	Hillslope position Low: low plateau (12 sites) Medium: mid-slope (12 sites) High: high plateau (12 sites)	OS Terrain® 50 DTM OS data © Crown copyright and database right 2022	Hillslope position influences drainage flow paths across the landscape and thus the availability of water to live fuels (Tromp-van Meerveld and McDonnell 2006)
Aspect	North (18 sites) South (18 sites)	OS Terrain® 50 DTM OS data © Crown copyright and database right 2022	North and south aspects capture the range of variation in incoming solar radiation to dry out fuels. Topography and aspect influence fuel moisture through the formulation of complex microclimates that modify the meteorological controls on drying (humidity, temperature, windspeed) (Nyman et al 2015, 2018; Brown et al 2022b). Dead fine fuels are typically drier on equatorial than polar facing slopes (Nyman et al 2015; Walsh et al 2017; Slijepcevic et al 2018) where spatial differences driven by variations in incoming solar radiation between polar and equatorial facing slopes are created

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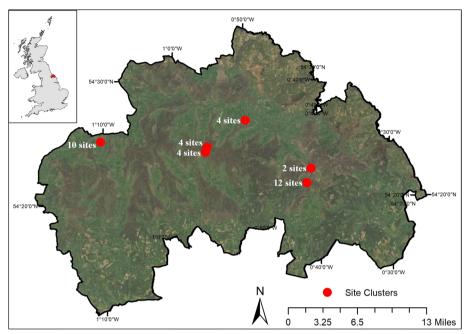


Fig. 1 The North Yorkshire Moors National Park study region situated in northeast England. We established 36 measurement plots clustered in six key areas of the national park. Source: Esri, Maxar, Earthstar Geographics, and the GIS User Community. © Natural England copyright. Contains Ordnance Survey data © Crown copyright and database right 2022

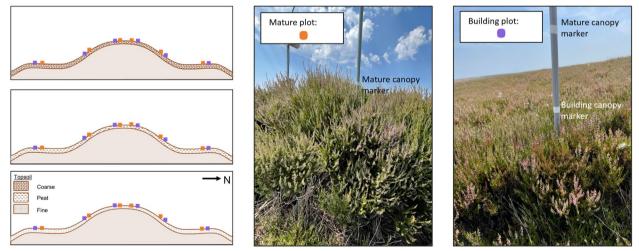


Fig. 2 Conceptual figure of the 36 sample plots (colored circles) comprising each possible combination of hypothesized landscape drivers: soil texture (coarse, peat, or fine); canopy age (building or mature); hillslope position (low, medium, or high); and aspect (north or south). We installed weather stations next to each pair of building and mature Calluna plots

campaigns to be conducted within a single day in accessible locations, while capturing the diversity of soils that tend to be spatially disparate.

We identified coarse, fine, and peaty textured soils using Soilscapes, a classification derived from the detailed National Soil Map for England and Wales (Farewell et al 2011). We validated soil texture

classifications with manual textural assessments of soil samples collected in the field (Thien 1979). We selected plots on north- and south-facing hillslopes using the OS Terrain® 50 DTM (Ordnance Survey 2019). In the North Yorkshire Moors, peatland and heathland land covers transition to grassland/agricultural land prior to reaching the topographic low, so the hillslope position

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in these ecosystems is defined as follows: high, the plateau on the hilltop; mid, the hillslope below this plateau; and low, a plateau below a slope.

We examined the combined influence of fuel age and height between contrasting building and mature heather canopies. We used these terms to represent the two different classes of younger (shorter) and older (taller) heather life stages. Previous research has established the significance of Calluna biomass, proportion of live and dead fuel, and life stage for fuel moisture content and wildfire behavior (Gimingham 1992; Davies and Legg 2011; Santana and Marrs 2014; Log 2020). Within the constraints of the landscape, we selected existing building and mature Calluna plots side by side to isolate canopy differences from our other landscape factors of interest. We distinguished age using timesince-last-burn records held by land managers. Mature canopy plots were last burned 15-20 years ago and had an average height of 60 cm and accumulated moss/litter layer depth of 5 cm. Building canopy plots were burned in the last 5-10 years and had an average height of 30 cm and accumulated moss/litter layer depth of 2.5 cm. This classification allowed us to (1) maximize differences between the two categories of interest, so the building canopy plots were distinctly different from the mature canopy plots; (2) ensure consistency across sites as all sites within each category have a similar age, height, structure, and management approach; and (3) ensure within-plot variation is low relative to between-plot variation.

Data collection

Fuel moisture sampling

Wildfires generally occur across two fire seasons in northwestern temperate Europe, a primary peak season in spring and a secondary season in summer (Belcher et al 2021; Cardíl et al 2023). To capture the temporal variations in landscape controls on a phenological timescale, we collected fuel moisture samples in hot, dry fire weather conditions across the spring and summer fire seasons (Fig S1). We collected three sets of samples across a 1-week drying period in April 2021, during the peak spring wildfire season, and two further sets in June

Fuel moisture exhibits vertical variation from the organic to the canopy layer that is relevant for determining wildfire behavior. For example, fires will often burn through the canopy of *Calluna* without involving litter and ground fuels. Therefore, in each plot, we sampled seven fuel layers: *Calluna* live canopy, live stems (<2 mm diameter), dead canopy, dead stems (<2 mm diameter), surface moss (top 2 cm), litter (top 2 cm), and the organic layer beneath the *Calluna* (top 5 cm of organic material above mineral soil). We combined lower canopy material with live stems following a study by Davies and Legg (2011), in which a factor analysis grouped these two fuel layers together, separate from the upper canopy.

We collected samples following the sampling protocol of Little et al. (2024), modified from Norum and Miller (1984). We set out a 25-m transect through each plot and walked along it, collecting fuel clippings from ca. 10 different plants into one aluminum tin (250 ml) with a screw-fit lid sealed with masking tape. We collected the same amount of biomass from each plant along the transect, filling the 250 ml tin ¾ full. We selected plants haphazardly, as the aim was to ensure samples were representative of within-plot variability rather than individual plants. We collected Calluna canopy and stem material by clipping sprigs with stem diameter < 2 mm and separating the leafy canopy material from the woody lower stems. We collected the top 2 cm of surface moss and litter at 10 points along the transect, removing any highly decomposed material from the base of the layer. Finally, after exposing the material beneath the surface moss and litter, we extracted the top 5 cm of organic material at five points along the transect using a small corer.

We measured gravimetric fuel moisture content (mass of water per mass of dried sample, %, referred to throughout as fuel moisture content (Eq. 1)) following the same protocol. Briefly, we weighed the tinned samples (wet weight) as soon as possible after collection, and within a maximum of 24 h. We subsequently dried the samples for at least 48 h at 80 °C, consistent with previous *Calluna vulgaris* fuel moisture studies (e.g., Davies et al 2010), and then reweighed the samples (dry weight).

$$Fuel moisture content = \frac{(sample wet weight - sample dry weight)}{(sample dry weight - container tare weight)} * 100$$
 (1)

and July 2021, respectively, during the secondary summer wildfire season. During each campaign, we collected samples within each of the 36 plots between 1100 and 1700, randomizing the order of sampling as much as logistically possible.

Micrometeorological variables

We recorded 1.25-m air temperature and relative humidity at 15-min intervals at each pair of building and mature *Calluna* sites with HOBO U23-001A PRO

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V2 (Onset Computer Corporation, Bourne, MA) sensors housed within radiation shields. We installed Davis Vantage Pro wind anemometers (Davis Instruments) at 2 m on the north and south sides of the three main hillslopes at equivalent elevations to monitor wind speed and direction at 1-min intervals.

Data analysis

Each of the 36 sites represented a unique combination of the four landscape factors of interest. This experimental design allowed us to use linear regression models to assess the influence of landscape factors without confounding between our hypothesized drivers. We developed three linear regression models to assess the influence of landscape factors, micrometeorological factors, and the overall contribution of both groups of factors on fuel moisture variation. We ran these three models for each combination of fuel layer and sampling month to examine fuel layer and season-dependent relationships (21 variations of each model).

The landscape model was defined by the hypothesized controls on landscape-scale fuel moisture variability, as identified from the literature—soil texture, canopy cover, hillslope position, and aspect. To define the micrometeorological model, we first selected parameters considered to be important for fire weather to investigate—temperature, relative humidity, wind speed, and vapor pressure deficit. We included vapor pressure deficit (calculated from air temperature and relative humidity measurements) based on recent demonstrations of its importance for live fuel moisture content (Griebel et al 2023). We then evaluated different lag periods and parameters to derive the best relationship between the micrometeorological variables and fuel moisture, with micrometeorological variables averaged 5-h before time-of-sampling performing best (Table S1). We excluded uneven precipitation distribution as a significant control on spatial fuel moisture variability in this study, as we targeted the driest periods of the fire season and monitoring of precipitation using hand gauges at each pair of sites throughout the sampling period did not reveal any major between-site differences. We also considered relationships between fuel moisture content and the Canadian Fire Weather Index System (CFWIS) as this is the system currently used within the UK Met Office Fire Severity Index (MOFSI) to assess aspects of fire weather (Arnell et al 2021). However, we excluded these from the main analyses due to their comparatively poorer performance (Fig S2).

We used variance partitioning to understand the relative importance of landscape or micrometeorological variables for fuel moisture content (Nakagawa and Schielzeth 2013). We calculated the variance explained (R^2)

for the landscape (soil texture, canopy age, hillslope position, and aspect), micrometeorological (1.25-m air temperature, relative humidity, vapor pressure deficit, and wind speed averaged 5-h before time-of-sampling), and combined (both landscape and micrometeorological factors) statistical models. We calculated the independent contributions of landscape and micrometeorological models as $R_{\rm full}^2 - R_{\rm met}^2$ and $R_{\rm full}^2 - R_{\rm landscape}^2$, respectively. The shared variance explained was the difference between the total variance explained and the independent contributions of the two sub-models.

We used weighted effect coding on individual regression models (21 variations of four landscape models) for each landscape factor to narrow in on the role of landscape drivers by producing model estimates as deviations from the sample mean (Sweeney and Ulveling 1972). We tested the assumptions of all of the linear models by producing Q-Q plots (for normality) and residual vs predicted plots (for heteroscedasticity) using the DHARMa R package (Hartig 2022). No significant deviations from the assumptions were seen in the majority of the 147 models (Fig S3). To test for spatial autocorrelation we calculated Moran's I using the lctools R package (Kalogirou 2020). No significant deviations from the assumptions were found for the majority of the models (Table S3-S5). We conducted all statistical analyses in R version 4.1.2 (R Core Team 2022), using packages cffdrs (Wang et al 2017), plantecophys (Duursma 2015), and wec (Grotenhuis et al 2016).

Results

Fuel moisture variability

Fuel moisture content was highly spatially variable across the 36 plots in the North Yorkshire Moors. Observed fuel moisture variability was the season- and fuel-layerdependent (Fig. 3). Live *Calluna* fuel moisture content was the lowest and least variable in spring. Live fuel moisture content varied by 54% (percentage points) for Calluna canopy between the driest and wettest site in spring, increasing to 97% by July. Previous research has developed fuel moisture thresholds for certain fuel layers that indicate the fuel moisture content below which a fire is likely to sustain ignition (vertical lines in Fig. 3). Live fuel moisture content was found to vary across the 47-65% threshold for sustained fire ignition (Taylor et al 2021), particularly in spring (Fig. 3 dashed vertical lines on live canopy graph). Cross-landscape organic layer fuel moisture content varied across the 250% fuel moisture threshold for smoldering combustion (Lukenbach et al 2015) during both spring and summer (Fig. 3 vertical dashed line on organic layer graph). Dead *Calluna*, moss, litter, and organic layers were more variable in spring than summer. Surface moss and litter layer fuel moisture

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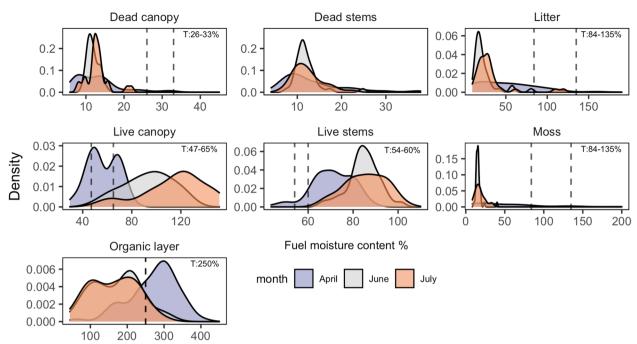


Fig. 3 Density plots of fuel moisture distribution for *Calluna vulgaris* fuel layers across the 36 plots in the North Yorkshire Moors during hot, dry conditions April–July 2021 (number of samples for each fuel layer panel = ca. 180). Dashed vertical lines depict fuel moisture thresholds for sustained ignition within the different fuel layers based on previous research (Lukenbach et al 2015; Taylor et al 2021). One line = threshold; two lines = range of lower and upper threshold; no line = no conclusive threshold for this species

content spanned a range of 191 and 156%, respectively, between the driest and wettest sites.

Landscape and micrometeorological drivers of fuel moisture variability

Combined landscape and micrometeorological factors explain 16-72% of the total cross-landscape fuel moisture variability (Fig. 4). Overall, the landscape models tend to outperform the micrometeorological models in explaining the spatial distribution of fuel moisture. However, the importance of landscape and micrometeorological factors show differences between fuel layers and seasons. The overlap between the landscape and micrometeorological models in Fig. 4 shows the shared variance explained between the models. For live Calluna canopy fuel moisture, the shared variance exceeds the individual variance of each model, which suggests there is an interaction between landscape and micrometeorological factors. Landscape factors are consistently more important drivers of dead Calluna and litter layer fuel moisture. The total variance explained for dead Calluna is higher in summer (50-72%) than in spring. Where landscape factors drive fuel moisture variability, the individual contribution of the landscape model largely outweighs the shared variance, indicating that landscape factors control fuel moisture variation beyond simply modifying local micrometeorology. The micrometeorological model only outperforms the landscape model for the moss layer in April (21%) and June (45%), the live canopy in April (47%), and the organic layer in July (22%). There is no clear difference in the importance of landscape and micrometeorological factors for organic layer fuel moisture variation outside of July.

Linear regression models quantified the deviation in fuel moisture percentage from the sample mean associated with specific landscape factors (Table S2). Soil texture exerts the greatest control on the spatial distribution of fuel moisture content for all layers except dead Calluna. Live Calluna canopy material is up to 20% drier than average on fine-textured soils and up to 19% wetter than average on coarse-textured soils, resulting in a 39% percentage point difference in fuel moisture estimates across the landscape. This magnitude of difference increases through summer. Live Calluna stems show a seasonal reversal in relationship with soil texture, where fuel moisture is highest (lowest) on fine soils in April (June and July). There are also some instances where relationships between landscape factors and fuel moisture switch backwards and forwards inconsistently across the sampling period (e.g., moss, litter, and organic layer

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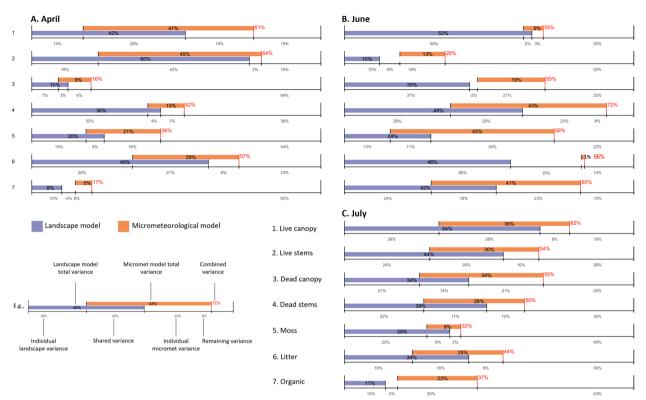


Fig. 4 Spatial variation in fuel moisture that can be explained by the landscape and micrometeorological linear regression models. Variance partitioning for the **a** April, **b** June, and **c** July sample sets, showing the contribution of the overall linear regression model towards explaining fuel moisture variation (red) and the total variance explained by the landscape factors (purple) and micrometeorological factors (orange)

relationships with soil texture). In July, organic layer fuel moisture is significantly (46.6%) lower than average on coarse soils.

Canopy age consistently controls fuel moisture variation across all fuel layers. Live *Calluna* canopy is up to 9% drier in mature *Calluna*, increasing in magnitude from spring to summer. Dead *Calluna* and organic layer fuels are driest in building *Calluna* (organic layer fuel moisture is 20–29% lower in summer). The influence of aspect varies between live *Calluna* and surface fuels. Live canopy fuel moisture content is up to 9% wetter on south slopes in summer. Surface fuels in contrast are driest on south slopes, except for June, where all fuel layers are wetter on south slopes than on north slopes. The influence of slope position is least clear, though *Calluna* live stems and the organic layer are consistently driest at low hillslope positions. Conversely, *Calluna* live canopy is wettest at low hillslope positions.

Discussion

Cross-landscape fuel moisture is highly variable

Plant phenology drives fuel moisture variability in live *Calluna*. Fuel moisture content is low in spring following winter dormancy, resulting in a high load of fuel in

an ignitable state. As temperatures increase and sap flow restarts in Calluna, a "green-up" is observed where new leaf and shoot growth increases fuel moisture content (Bannister 1964b; Davies et al 2010). There is an important spatial dimension to this recognized temporal variability in fuel moisture. Live fuel moisture content was found to be most variable in summer, linked to observations of spatial variation in the timing of Calluna green-up across the landscape. However, it is the spatial variation in live fuel moisture in the peak wildfire season of spring in the UK (Belcher et al 2021) that is especially important from a wildfire danger perspective. On the days sampled, live canopy fuel moisture content varied across the threshold for sustained ignition (47–65%) identified by Taylor et al. (2021). Due to landscape heterogeneity, live Calluna fuel moisture was below the threshold for contributing to wildfire spread in some locations and above it in others (Fig. 3). Moreover, live Calluna can form a major component of the available fuel for wildfire spread and can behave independently akin to a mini-crown fire (Fernandes et al 2000; Davies and Legg 2016). Similarly, fuel moisture in the organic layer was distributed above and below the 250% threshold for smoldering combustion (Lukenbach et al 2015; Little et al. Fire Ecology (2024) 20:14 Page 10 of 13

Fig. 3), indicating the differential potential for higher severity wildfires due to smoldering combustion across the landscape.

Landscape factors drive fuel moisture variability

Spatial variation in the distribution of fuel moisture creates a cross-landscape on/off thresholding of fuel availability. It is clear from our results that regional estimates of fuel moisture will not capture important local spatial variability driven by either landscape or micrometeorological factors. Overall, landscape factors were found to be more important drivers of fuel moisture variation than micrometeorological factors. There are a small number of instances where the shared variance outweighs the individual contributions of each model, suggesting there may be some form of interaction between landscape and micrometeorological factors, such as the landscape factors modifying micrometeorology. However, for the most part, landscape factors control fuel moisture content beyond simply modifying micrometeorology. This is a key insight towards improving the accuracy of fuel moisture estimates by accounting for landscape-fuel moisture relationships directly, as estimates derived solely from micrometeorological observations will exclude the underlying influence of landscape controls. Fire weather index systems that are based on weather parameters alone will have limited ability to provide fire managers with accurate predictions in these ecosystems.

We hypothesize that soil texture differences are important controls on fuel moisture variability. We observed higher live canopy fuel moisture content on coarse-textured soils than fine-textured soils and blanket peat, with the magnitude of difference increasing through summer, which is consistent with our field observations of Calluna green-up occurring earlier over coarse soils. Fine textured soil and blanket peat more effectively retain water, but this water is not necessarily available for plants to uptake (Easton and Bock 2016). Moreover, it may be that the North Yorkshire Moors did not experience a sufficiently moisture-limited state during field sampling to observe the expected impact of soil drainage properties on live fuel moisture. These results likely reflect the complexity of soil-fuel moisture relationships beyond simply water availability and are hypothesized to be related to both plant adaptive and soil hydraulic traits.

Ecophysiological research has demonstrated the importance of soil and plant hydraulic traits in regulating live fuel moisture content (Scarff et al 2021; Brown et al 2022a; Nolan et al 2022; Rao et al 2022; Ruffault et al 2022). This may provide a useful framework to simulate the moisture of temperate fuels like *Calluna*, building

on pioneering physiological (Bannister 1964a; 1964b) and more recent live fuel moisture modeling (Davies and Legg 2008). Ecophysiological traits governing fuel moisture variability have been explored temporally for *Calluna* (Davies and Legg 2008; Davies et al 2010) and between different species (Brown et al 2022a; Rao et al 2022); however, the ecophysiological controls on the spatial distribution of within-species fuel moisture as quantified here have not yet been unraveled. Collaboration between wildfire scientists and plant physiologists remains (cf. Davies and Legg 2008; Dickman et al 2023) highly important for discerning the cross-landscape controls on live fuel moisture and therefore wildfire danger in temperate fire-prone landscapes.

We observed a fuel layer-dependent relationship between canopy age and fuel moisture content. Live fuel moisture content was found to be lower in mature Calluna plant canopies and is linked to a greater proportion of old growth and a lower proportion of new growth when compared to younger Calluna plants. Conversely, in the dead fuel components of the canopy and organic layer, fuel moisture contents were found to be lower in the building stage of Calluna. These findings suggest that the Calluna canopy (that is elevated above the ground) acts in a similar manner to that of the overstory in forested fuels, that form a boundary between the atmosphere and underlying surface fuels (Brown et al 2022b; Nyman et al 2018; Walsh et al 2017). Contrary to previous studies, aspect and slope were found to play a smaller role in influencing cross-landscape fuel moisture variation. However, this could be due to the absence of sufficiently steep slopes in the study region such that we did not observe large differences between sites. On steeper gradients and in more complex environments, we would expect these factors to be more important. We were able to separate the correlation between denser vegetation cover on polar aspects that likely amplified the "aspect effect" in previous research (Slijepcevic et al 2018). Therefore, it is not particularly surprising that we observed a smaller influence of aspect when isolated from other landscape factors.

While the role of phenology in the temporal variability of live *Calluna* fuel moisture has been well documented (Davies and Legg 2008), it is clear that there is also an important phenological component to the spatial distribution of live fuel moisture variability. We have demonstrated that the direction of landscape—fuel moisture relationships can switch between spring and summer, highlighting the importance of accounting for plant phenology in wildfire danger assessments in temperate environments. Understanding how landscape and

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micrometeorological factors modulate cross-landscape differences in the timing of green-up may aid the development of live fuel moisture models for assessing wildfire danger and behavior.

We hypothesize that cross-landscape fuel moisture variability is associated with specific landscape controls through careful experimental design, literature-based model selection, and interpretation based on our scientific understanding of landscape processes. However, we acknowledge that inherent variability within natural landscapes means there may be unknown spatial controls not accounted for that may impact our findings. In particular, plots tended to be clustered around soil textures as soil properties are spatially disparate by nature. Future research could narrow in on specific landscape controls of interest like soil texture to validate our hypotheses. These sorts of experimental studies are critical for advancing our understanding of landscape processes and disturbances and provide valuable insights despite the spatial complexity (Davies and Gray 2015).

Implications

Landscape fuel moisture variability can create spatial discontinuity in the availability of fuel that is in the correct state for ignition (surface fuels) and wildfire spread (live fuels), including the potential for spot-fires in extreme conditions, and vulnerability of the organic layer to smoldering (Finney et al 2021). Spatial heterogeneity in fuel moisture can therefore influence how a fire will propagate across the landscape. For example, the percolation threshold describes the point at which a fire will spread continuously throughout the landscape irrespective of landscape connectivity (Gardner et al 1987). Knowing the magnitude of fuel moisture variability may allow for spatial pattern analyses of the role of fuel moisture in landscape connectivity, as well as targeting fire prevention in areas where this threshold for continuous fire spread may be breached (Rahimi and Salman Mahini 2018; Duane et al 2021). Fuel moisture models should therefore have high spatial fidelity to capture cross-landscape fuel moisture variation and dynamics, which can then be integrated into fire behavior modeling systems (Dickman et al 2023).

Tailored fuel moisture models of *Calluna*-dominated landscapes that sit within systems that predict fire behavior during incidents may aid wildfire event decision-making for fire managers by informing resource deployment (particularly where locations may be vulnerable to smoldering) and identifying suppression opportunities. We suggest that by knowing the specific landscape characteristics of an area of interest, a lookup tool could be applied to adjust fuel moisture estimates to local conditions by land managers or fire and

rescue services. For example, controlled burns in the UK are typically small-scale where accurate estimates of local fuel moisture variability may help to identify the best burn locations if seeking to reduce the risk of out-of-control fires or failed ignitions for land managers. Beyond this, the availability of digital landscape information (e.g., elevation models and soil maps) opens opportunities to enhance the spatial resolution of regional fuel moisture estimates to better reflect local conditions. Such downscaling has previously been used to account for the effect of topography on net radiation and aridity (Nyman et al 2014) and has subsequently been developed to downscale regional weather observations for wildfire management (Nyman et al 2015; Walsh et al 2017). The recently developed Australian Fire Danger Rating System is the first to forecast wildfire danger at an improved spatial resolution of 1.5×1.5 km (Matthews et al 2019), highlighting recent recognition of the need for operational wildfire danger forecasts at the local scale.

Conclusions

We have quantified the magnitude of cross-landscape fuel moisture variability and the extent to which this is driven by landscape scale and micrometeorological factors in temperate peatlands and heathlands, finding:

- 1. Within the landscape scale, variations in fuel moisture content create spatial discontinuity in the availability of live fuels for wildfire spread and vulnerability of the organic layer to high-severity smoldering.
- 2. Within the landscape scale, fuel moisture variation is controlled by both landscape and micrometeorological factors, though landscape factors show greater overall performance (beyond modifying local micrometeorology).
- 3. Accounting for within landscape—fuel moisture relationships directly will improve the accuracy of fuel moisture estimates because estimates derived solely from micrometeorological observations will exclude the underlying influence of landscape-scale controls.
- 4. Differences in soil texture, shrub canopy age, and slope aspect are hypothesized to be important within landscape scale controls.
- 5. Phenology is capable of switching within landscapescale fuel moisture variability between spring and summer.

Our work thus sets the scene for a new avenue of landscape-scale wildfire danger research to support regionalscale predictions, recognizing that fire danger ratings and fire behavior models may require different levels of detail for the different functions they perform. Little et al. Fire Ecology (2024) 20:14 Page 12 of 13

Supplementary Information

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Additional file 1. Supplementary material. Supplementary Figures. Supplementary Tables.

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Authors' contributions

KL, LG, and NK developed the experimental design and analyses. KL analysed the data and led the writing of the manuscript. LG and NK supervised the research. All authors contributed to interpretation of data and editing of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets generated during the current study will be made publicly available at time of publication. The data and code that support this publication are available at: https://doi.org/10.6084/m9.figshare.25041644.v1.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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