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Original Articles

Flatlining fens? Small-scale variations in peat properties and microtopography as indicators of ecosystem homogenisation

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ABSTRACT

Fens, groundwater-fed mires, are important hotspots of biodiversity, carbon storage, and water regulation, but many have been degraded through drainage for agriculture, reducing their multifunctionality. Restoration efforts, particularly rewetting, are gaining attention in Europe, but understanding small-scale spatial processes driving ecosystem recovery remains limited. To explore spatial structure in soil properties and microtopography as indicators of ecosystem homogenisation, we collected ~200 georeferenced soil samples from a near-natural alkaline fen and a degraded counterpart. Variogram analysis revealed distinct spatial structures in peat properties according to ecosystem status. The degraded fen exhibited longer autocorrelation ranges for soil organic matter (SOM), moisture, carbonate content, and surface microelevation, suggesting higher homogeneity compared to the near-natural fen. In addition, higher SOM was associated with higher surface microelevation and moisture content at both sites, highlighting the role of peat accumulation in shaping microtopography. The relationship between soil properties and microelevation showed stronger association and greater non-linearity in the near-intact fen compared to the degraded one. The variogram range appears to be a useful indicator of ecosystem status and homogeneity, providing valuable insights into the dynamics of fen degradation and restoration.

1. Introduction

1.1. Background

Alkaline fens are groundwater fed peat-forming wetlands (mires) that support diverse plant communities, primarily composed of small sedges and brown moss communities on permanently waterlogged soils. These ecosystems thrive in areas where the water supply is base-rich, and the water table is consistently at or close to the peat surface. They can be classified as soligenous, where vertical water movement predominates, or topogenous, where horizontal water movement is significant and often associated with slopes or flushes (O'Neill et al., 2023). The vegetation in alkaline fens often includes calciphytes, which are adapted to alkaline conditions such as various types of *Carex* (Seer and Schrautzer, 2014; O'Neill et al., 2023).

While soil organic matter (SOM) and water availability are core indicators of peatland health (Lasota and Błońska, 2021), carbonate content plays a particularly important role in alkaline fens (Glina et al., 2019). These ecosystems are often characterised by variable calcium carbonate content, ranging from trace amounts to very high levels. Under specific conditions, alkaline fens are also associated with tufa deposition. This process occurs when groundwater rich in dissolved calcium (Ca^{2+}) and bicarbonate (HCO_3^-) reaches the surface and soil-generated CO_2 escapes (degasses) into the atmosphere. This leads to oversaturation of $CaCO_3$ in the water, resulting in its precipitation as tufa (Grootjans et al., 2021; Apolinarska et al., 2023; Apolinarska et al., 2024).

Alkaline fens are relatively rare among mire ecosystems and are considered one of the most threatened ecosystems in Europe (Seer and Schrautzer, 2014). Their decline is largely driven by the intensification of artificial drainage and fertilisation, which facilitates their transition into highly productive grasslands (Seer and Schrautzer, 2014). As fens

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undergo drainage, increased aerobic conditions lead to a higher rate of peat decomposition (SOM mineralisation, see Łachacz et al., 2024) and a loss of buoyant force (Strack et al., 2005; Liu et al., 2020). This results in the collapse of pore spaces, consolidation, compaction, and surface elevation loss (Rezanezhad et al., 2017; Liu et al., 2020) affecting their hydraulic functions (Ahmad et al., 2020c) among other effects. Fen plant assemblages are influenced by two main stress factors, anoxia in the root zone (due to high water tables) and low nutrient availability (due to nutrient-poor, mineral-rich groundwater) (Kotowski et al., 2010; Glina et al., 2019). These stressors also regulate vegetation dynamics and prevent the domination of competitive plant species. However, as fens degrade and these stressors are removed, stress-tolerant species are replaced by more competitive plants, resulting in a shift in vegetation composition (Klimkowska et al., 2019). These changes alter the spatial patterns of ecosystem properties and functions across multiple scales (Luscombe et al., 2016) and are likely to lead to a transition from a complex and heterogeneous system to one that is increasingly simplified (Peipoch et al., 2015) and homogeneous (Stover and Henry, 2018). Thus, spatial patterns hold important information regarding the state of an ecosystem and its functionality.

1.2. Spatial heterogeneity, functionality, and ecosystem homogenisation

Heterogeneity refers to the spatial variability within an environment, often characterised by a combination of gradients, networks and patches (White and Brown, 2005). It can be represented as discrete units, such as hummocks and hollows (microforms) or as continuous variation across ecosystems (Turner and Chapin III, 2005) – such as variability in surface microelevation – commonly termed as microtopography in peatland studies (Moore et al., 2019). Increased environmental heterogeneity plays a key role in determining species diversity by creating a variety of conditions that can support a wider range of species with diverse ecological requirements (Allouche et al., 2012). Heterogeneity influences multifunctionality, the ability of ecosystems to perform many functions, at various scales, including habitats, ecosystems and landscapes (van der Plas et al., 2016; Alsterberg et al., 2017). However, the relationship between heterogeneity and multifunctionality may depend on factors such as the nature or intensity of land use (Crouzat et al., 2015; Lavorel et al., 2017). Moreover, heterogeneity has been shown to modulate biodiversity-ecosystem functioning relationships, with the scale of these relationships being influenced by the degree of autocorrelation in environmental conditions (Thompson et al., 2021). Heterogeneity in any factor influencing the variation in ecosystem services, whether land-use, dominance of keystone species, soil properties, climate, or altitude, can enhance landscape multifunctionality, provided that the ecosystem driver strongly impacts ecosystem services and leads to trade-offs among them (van der Plas et al., 2016). The reduction in heterogeneity in both physical habitats and biotic communities, therefore, contributes to a loss of ecosystem multifunctionality. This loss of multifunctionality over time due to decreased variability in physical, chemical, and biological characteristics has been referred to as ecosystem homogenisation (McLean et al., 2022). Worldwide, ecosystems are facing homogenisation due to human activities (Alsterberg et al., 2017).

Over the last 200 years peatlands, including bogs and fens, have been facing widespread degradation, turning these efficient carbon sinks into sources of carbon emissions (Leifeld et al., 2019). Although efforts to restore fen peatlands are increasing, predominantly through rewetting (i.e. raising the water table), such efforts do not necessarily "return drained fens to their old selves" (Kreyling et al., 2021). Nevertheless, such restoration efforts may result in some recovery of ecosystem functionality (Glina et al., 2018; Klimkowska et al., 2019). To better inform successful restoration efforts, understanding restoration requires an improved understanding of the process of degradation through studying spatial patterns hinting at underlying soil-hydrological processes. In peatlands, studying spatial heterogeneity of soil properties and surface microelevation is vital to identify hotspots of peat accumulation (Ahmad et al., 2020b) and organic matter decomposition (Briones et al., 2022). Furthermore, spatial variability of organic matter properties can determine methane fluxes (Girkin et al., 2019) while surface microelevation heterogeneity stimulates the regeneration of bryophytes and vascular plants on disturbed fens (Caners et al., 2019).

To explore spatial heterogeneity of soil properties, spatial autocorrelation should be considered. Spatial autocorrelation refers to the degree to which values that are closer in space are more similar than those further apart (for the same variable). Low autocorrelation indicates high rates of change in environmental conditions over short distances leading to rapid decay in similarity (Thompson et al., 2021). The variogram range, i.e., the separation distance at which spatial autocorrelation ceases, provides insights into ecosystem heterogeneity. A shorter range suggests a more heterogenous ecosystem, whereas a longer range indicates greater homogeneity.

1.3. Research gap and hypotheses

Peat properties such as organic matter content and moisture content are critical for peatland health. Higher organic matter helps to retain more water, and higher moisture content (close to or at saturation) slows down the process of decomposition as water forms a barrier for oxygen diffusion, leading to anaerobic conditions (Clymo et al., 1998). While peat hydro-physical properties (e.g., bulk density, saturated hydraulic conductivity, water storage capacity) and chemical composition (such as SOM or carbon content) have been widely recognised as indicators of the degradation status of peatlands (Frolking et al., 2010; Krüger et al., 2015; Liu and Lennartz, 2019; Leifeld et al., 2020), such measures often rely on point measurements with limited spatial representation.

However, given the high heterogeneity of peat properties within even a single ecosystem (Lewis et al., 2012; Negassa et al., 2019; Ahmad et al., 2020b; Wang et al., 2021; Wang et al., 2023), such assumptions often may not hold. Peatland research has made significant progress through remote sensing and mapping techniques (e.g., Habib and Connolly, 2023, Habib et al., 2024, Minasny et al., 2024) and microtopography (e.g., Graham et al., 2020) and habitat classification (Bhatnagar et al., 2021), but studies exploring small-scale variability (from less than a meter to hundreds of metres) remain much more sparse, yet necessary to bridge knowledge gaps between large scale and pore-scale investigation (e.g., Rezanezhad et al., 2016, Rezanezhad et al., 2017, Wang et al., 2020). This may provide new insights to the issue of scaling complex biogeochemical and ecohydrological processes and their interactions such as water storage changes, peat accumulation rates and microtopography formation, among others.

Microtopography plays a major role in influencing ecological processes associated with peatland biogeochemistry and hydrology (Arsenault et al., 2019; Graham et al., 2020). However, long-term studies on microtopography formation are challenging because its development spans several decades (Arsenault et al., 2019). By analysing key variables such as peat properties in relation to surface elevation at small spatial scales, insights can be gained into processes underlying peat accumulation and microtopography formation. Comparing peatlands of differing degradation statuses or management regimes can provide valuable insights into ecosystem homogenisation, degradation processes and the restoration potential of fens.

Most studies on peatland microtopography are based on bogs (e.g., Nungesser, 2003; Mäkilä et al., 2018; Harris and Baird, 2019; Graham et al., 2020; Stastney and Black, 2020; Graham et al., 2022) while research on fen microtopography remains comparatively limited. This knowledge gap presents opportunities to improve our understanding of microtopography formation and alterations, their influence on and interaction with habitat diversity, peat accumulation, carbonate deposition and hydraulic functions, as well as how these relationships are modified by ecosystem degradation characterised by homogenisation. Globally, while bogs cover an area of around 2.1 million km^2, fens cover almost half of that (1.1 Mkm^2, Loisel and Bunsen, 2020). Generally, fens harbour larger plant diversity per unit area than bogs, making them highly valuable ecosystems. We are particularly interested in alkaline fens, due to their limited occurrence because they are threatened ecosystems and remain understudied, but also because there has been considerably less attention on the homogenisation of freshwater wetlands including mire ecosystems (McLean et al., 2022). Microtopographic variation has been proposed as a potential early indicator of ecosystem state change in salt marshes (Smith et al., 2024), but limited studies exist on its use as an indicator of fen peatland homogenisation and degradation. Our study is the first to apply variogram ranges of microtopography and soil properties as indicators of ecosystem homogenisation of alkaline fens.

This study aims to compare a drained and degraded alkaline fen with a near-intact one in Ireland, focusing on the spatial variability of peat properties (including SOM, water content, and carbonate content) and peat surface microelevation (microtopography).

We propose the following hypotheses:

(1) **Ecosystem homogenisation**: The degraded fen will exhibit a larger variogram range compared to the near-intact site, as an increased range is indicative of spatial autocorrelation occurring over longer distances, reflecting spatial homogenisation due to ecosystem degradation.
(2) **Ecosystem simplification:** The more homogenous fen will display more linear (less complex) associations among soil properties and microtopography compared to the near-natural fen. As fens undergo degradation and homogenisation, the complexity of the association between soil properties and microtopography decreases. This results in changes to hydrology, organic matter accumulation and biogeochemical cycling, leading to a simplified ecosystem where the interdependence of soil and microtopography weakens.

2. Material and methods

2.1. Study areas

Alkaline fens in Ireland have been estimated to cover approximately 12,531 ha, of which 52% are under Special Areas of Conservation (SAC) (Central Statistics Office Ireland, 2018). The study sites include a rewetted near-intact alkaline fen (Ballymore SAC) and a degraded alkaline fen (Tory Hill SAC) located in counties Westmeath and Limerick in the Republic of Ireland, respectively. Both peatlands are under similar meteorological conditions and maritime temperate climate and are under designated as SAC. Fig. 1 shows the locations of the study sites in Ireland and the sampling frames within each site. Table. 1 summarises the site characteristics based on Regan and Conaghan (2017), Regan and Conaghan (2016), Bijkerk et al. (2022) and Bijkerk (2021).

2.1.1. The Near-Intact fen – Ballymore SAC

Ballymore Fen (53°29′N, 7°38′W) covers 42.7 ha at an elevation of 90–110 m above sea level (m asl). It is designated as a Special Area of Conservation (SAC) that includes transition mires and quaking bogs (habitat code 7140). It covers approximately 11 ha, of which about 4.8 ha forms a mosaic with alkaline fen (habitat code 7230) (Regan and

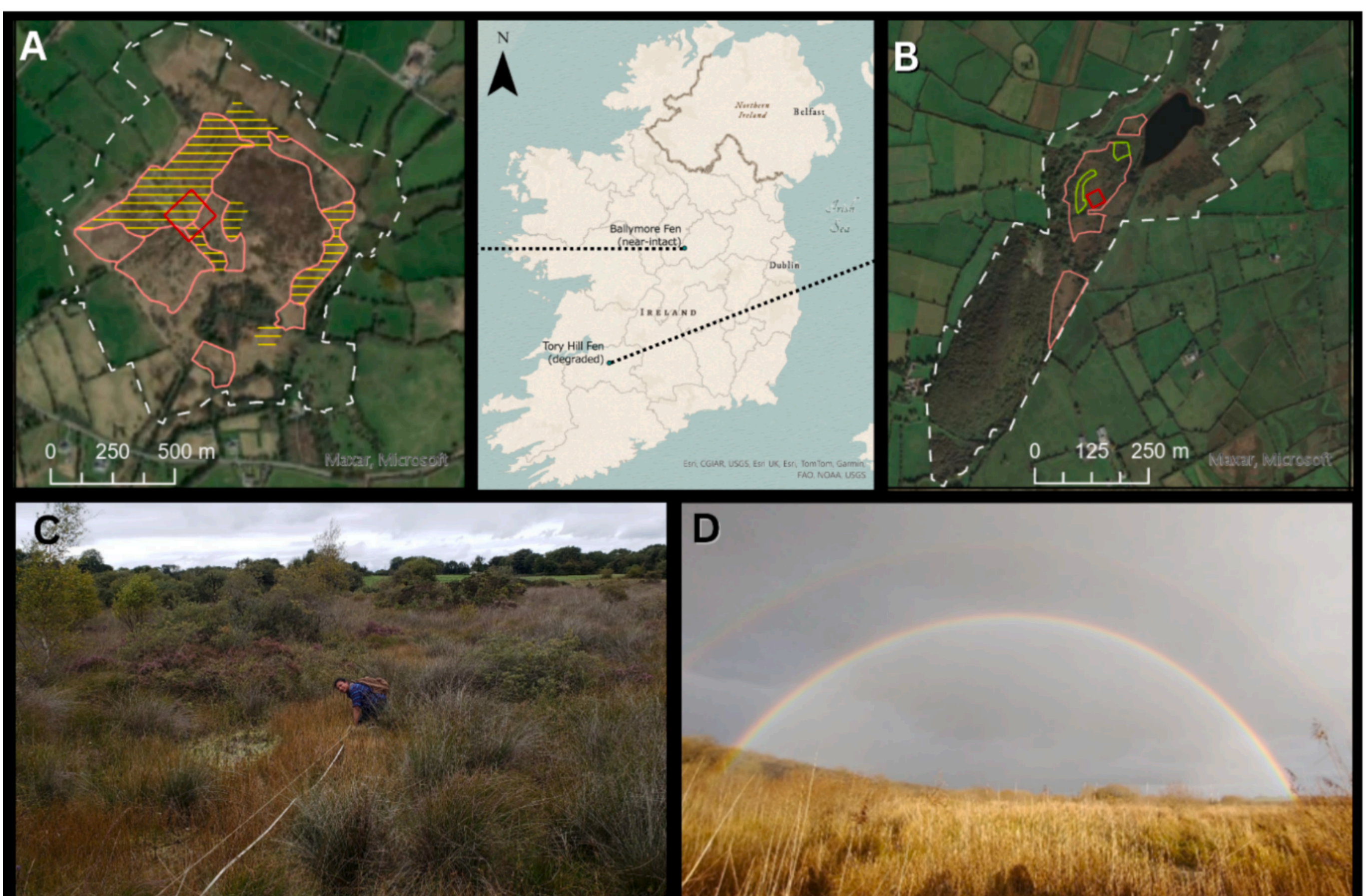


Fig. 1. Map of the study areas **(A)** Ballymore SAC (near-natural alkaline fens) – hatched yellow patterns indicate alkaline fen (7230) and the orange lines denote transition mires (7140). **(B)** Tory Hill SAC (degraded alkaline fen) – orange shades show alkaline fen (7230) and the light green lines indicate *Cladium* fens (7210). Their views from the ground are shown in **C** and **D,** respectively. The study plots are indicated by the red square frames.

Table 1
Summary of study sites.

Description	Ballymore SAC	Tory Hill SAC
Status	Near-intact	Degraded
Location	County West Meath	County Limerick
Designation	Special Area of Conservation (SAC)	SAC
Areal extent	42.71 ha	78.20 ha
Threats and Pressures	Diffuse agricultural pollution	Drainage; Infilling; Grazing
Peat Depth / Thickness	0.6 – 0.8 *m*	0.5 m (on average)
pH	7.12 – 7.34	7.20 – 7.29
Plant diversity in the study plot	12 to 27 species (per 4 m^2 plot)	9 to 17 species (per 4 m^2 plot)
Vegetation habitat diversity	4 (for the study plot)	1 (for the study plot)
Total phosphorus in groundwater (median)	0.8 mg/L	0.1 mg/L
Percentage of time the water-level is above the peat surface	> 90 – 100 % of the year	~ 37 % of the year (fen part)

Conaghan, 2017).

We established a sampling plot (45 m × 45 m) near the centre of the site, the majority of which consists of a mosaic of *Schoenus-Carex* fen and *Menyanthes* pool. A smaller portion is composed of a *Carex-Menyanthes* transition mire, with similarly small portions consisting of a *Carex-Menyanthes* and *Filipendula-Holcus* community, and a tiny portion of *Juncus subnodulosus* fen communities (based on survey maps by Regan and Conaghan, 2017). Most of these communities are relatively species rich ranging from 12 to 27 species in a plot of 4 m^2 (Regan and Conaghan, 2017).

The landscape surrounding the SAC is primarily agricultural grasslands, including pastures and wet grasslands, with smaller patches of cultivated land and forests.

2.1.2. The degraded fen – Tory Hill SAC

Tory Hill (52°32′N, 8°41′W) covers 78.2 ha at 25 – 112 m asl. Tory Hill is a SAC designed to protect three habitats listed on the Annex I of the EU Habitats Directive: orchid-rich calcareous grassland (habitat code 6210), *Cladium* fens (7210), and Alkaline fens (7230). The wetland orchid *Epipactis palustris* is scattered throughout these areas. We established a study plot (45 m × 45 m) at the centre-north part of the SAC, in a flat area of the alkaline fen, which consists of tall herb fen *Filipendula-Lythrum* communities. These communities consist of 9 to 17 species per 4 m^2 plots (Regan and Conaghan, 2016, Table 5). Brown moss species such as *Campylium stellaum* and *Drepanocladus revolvens*, which are typical of high-quality rich fen habitats, are very rare at Tory Hill (Regan and Conaghan, 2016). Tory Hill fen is considered to be ecologically degraded (Bijkerk et al., 2022), due to a lack of fen indicator species. The SAC is surrounded by a landscape of agricultural grasslands, including pastures and impacted by drainage and infilling (Bijkerk et al., 2022). A natural stream channel (taking water from the northerly lake) was cut much deeper to drain the adjacent land to prevent flooding. This drainage channel significantly lowered the overall water level in the study site.

The site descriptions are summarised in Table 1 based on Regan and Conaghan (2016), Regan and Conaghan (2017), and Bijkerk et al.

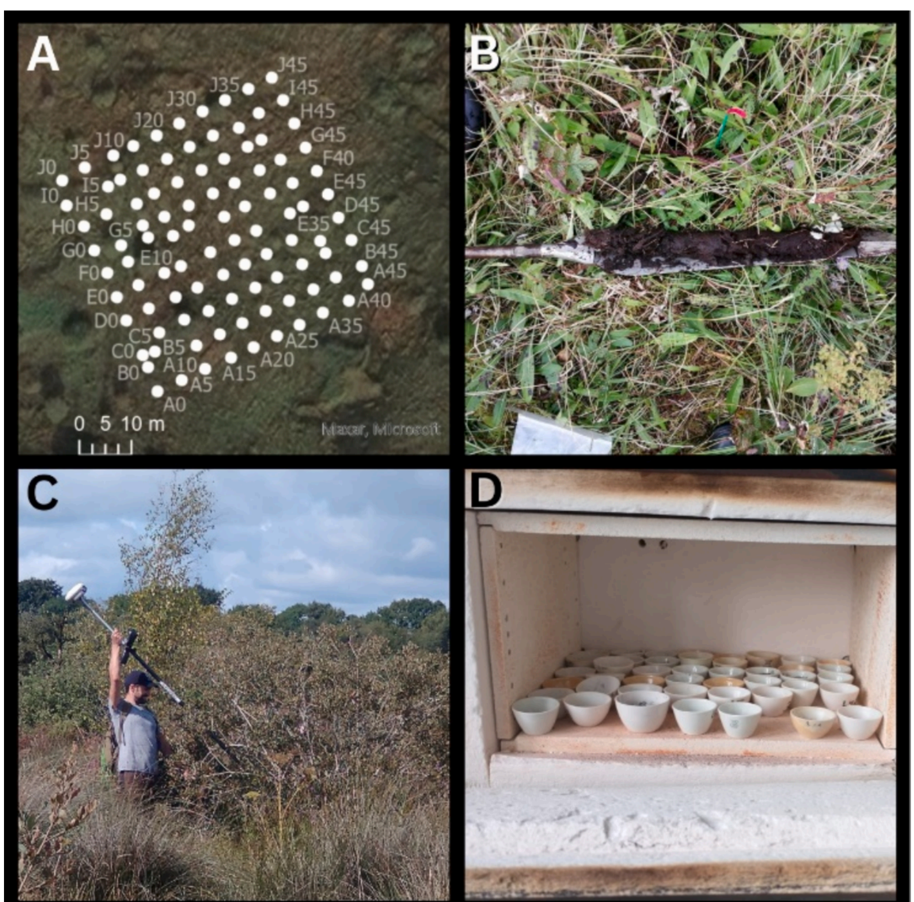


Fig. 2. Field and lab methods used for determining peat properties (topsoil) and surface microelevation. (A) Lattice plus close-pairs sampling with random replacements locations (example of sampling at Tory Hill Fen). (B) Peat sample collected using the Russian Peat Auger (C) Use of Trimble R8 GNSS for recording high precision geolocation including microelevation. (D) Muffle furnace used to conduct sequential loss-on-ignition to determine soil organic matter and carbonate content in peat within the topsoil horizon.

(2022).

2.2. Peat sampling and sampling design

The sampling approach for both sites was based on a lattice-plus-close-pairs design (Diggle and Lophaven, 2006) with random replacements (Bijleveld et al., 2012). A lattice of 45 m × 45 m was constructed of 100 points spaced at regular intervals of 5 m (Fig. 2A). Twenty percent of the sampling points were randomly selected and replaced with nearby points based on (1) a direction randomly chosen from 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315° angles, and (2) a distance randomly selected between 0.5 m and 2.5 m in increments of 0.5 m. This type of sampling reduces the number of samples required without compromising effectiveness and representativeness. Furthermore, it incorporates a wide range of separation distances and therefore reduces the nugget effect and increases the likelihood of capturing the range at which autocorrelation levels off (see subsection 2.4).

For determining soil properties such as organic matter (SOM), moisture and carbonate content, peat samples at a depth of about 10–15 cm from the peat surface were collected using a peat-auger (Fig. 2B). The exact sampling location (latitude, longitude) and the microelevation of the peat surface were recorded at high precision using Trimble GNSS (model R8s), which has a horizontal precision of 3 mm + 0.1 ppm RMS and a vertical precision of 3.5 mm + 0.4 ppm RMS (Fig. 2C).

2.3. Determination of soil properties

Soil moisture content and SOM were determined following the protocol made for peat by Chambers et al. (2011). Wet samples were weighed and then dried overnight at 100 °C and reweighed to determine the soil moisture content (calculated both as wet basis as well as dry basis). SOM content was determined by loss-on-ignition (LOI) at 550 °C for 4 h in a muffle furnace and expressed as dry weight percent (%w/w) (Fig. 2D). The benefits of this method include the ability to run many samples simultaneously and its low equipment cost (Vos et al., 2005). The remaining residues after LOI at 550 °C were re-ignited at 950 °C for 1 h to estimate carbonate content following Bhatti and Bauer (2002).

2.4. Geospatial analysis

Geolocation data including the microelevations (as metres above geoid), were merged with soil data for each point, and loaded onto ArcGIS Pro 3.3 for geospatial analysis. Variograms were constructed for each variable using simple kriging in the Geostatistical Wizard. Variables which were non-normally distributed (such as SOM, soil moisture and carbonate content) were transformed using normal score transformation combined with multiplicative skewing before generating empirical variograms and fitting model variograms.

The range is the separation distance (lag distance) where the model first flattens out, indicating the limit of spatial autocorrelation. Beyond this distance the variable in question shows no spatial dependence. As we are interested in comparing the variogram ranges of soil properties and surface microelevation between the degraded and the near-intact fen, we constructed the empirical variograms using the same lag size (2 m) and number of lags (19) for both sites. Model variograms were fitted to the empirical variograms to determine the variogram range of each variable for both sites. Detailed justification for the choice of lag size and number of lags can be found in **Supplementary Material 1**.

2.5. Statistical analysis

For data analysis which did not involve variogram models, RStudio (R-version 4.3.3) was used (R Core Team, 2024). To analyse the bivariate relationship between ecosystem degradation status and soil properties Welch Two-Sample t-tests were performed (Welch, 1947). Violins with mean and error plot were generated using 'ggplot2' package (Wickham et al., 2023) for graphical comparisons.

To analyse the relationship of soil moisture and microtopography with SOM content, we employed two separate Generalized Additive Models (GAM, one for each site) using a Beta regression framework with a logit link function in RStudio using the 'gratia' package (Simpson, 2024). GAMs are particularly suited for this analysis because they allow for the inclusion of non-linear relationships between the dependent and independent variables (Guisan et al., 2002), which is often the case with ecological data. SOM (% dry weight) was set as the dependent variable, while the smooth terms of soil moisture content (% dry weight) and surface microelevation (relative to the site mean elevation) were included as predictors. Additionally, the smooth function of the interaction between latitude and longitude, s(X,Y), was included to statistically control for spatial effects.

Model diagnostics, including the residual deviance and R-squared values, were used to evaluate model fit. The adjusted R-squared value was reported to account for the complexity of the model. The proportion of deviance explained by the model was also assessed. The model fit was assessed through adjusted R-squared and deviance explained, which quantifies the proportion of variation in the data explained by the model. The model was considered an appropriate fit if it explained a substantial proportion of the deviance and showed significant relationships between the response variable and predictor terms. For each significant smooth term, we interpreted the direction and nature of the relationship by plotting the smooth function estimates, which provide insight into the non-linear effects of each predictor. The diagnostic plots can be found in Supplementary Material 2(Fig. S1).

3. Results

3.1. Aspatial differences in soil properties between the drained and the near-intact fen

The degraded fen exhibits a higher mean soil organic matter (SOM) content (78% vs. 73%) but less variability compared to the near-intact fen, as indicated by the coefficient of variation (CV: 13% vs. 28%, Table 2). However, this difference is not statistically significant (Fig. 3A). Both sites have high and comparable carbonate content (~18%), although the peat in the near-intact fen shows substantially greater variability in this parameter (CV: 67% vs. 37%, Table 2). Additionally, the near-intact fen has significantly higher soil moisture content (835% vs. 610% dry weight in the degraded fen; Welch's *t*-test = −7.06, df = 182, $p < 0.001$). The degraded fen is situated at a lower elevation than the near-intact fen, but their CVs for elevation are similarly small (less than 1%). While these aspatial statistics provide a useful starting point for comparing ecosystem properties and conditions, a deeper investigation into their spatial structure is essential for understanding the spatial organization of their variability.

3.2. Spatial structures of peat properties and microtopography

The empirical variograms and fitting model variograms for SOM content, carbonate, and moisture content along with the surface microelevation representing the microtopography revealed that the degraded site exhibits a longer variogram range compared to the near-intact fen.

At the near-intact fen, the spatial autocorrelation of SOM ceases at a separation distance of 7.8 m, while at the degraded fen, the SOM gammavariance flattens at a lag distance of 23.75 m (Fig. 4A). Similarly, for soil moisture content, microtopography, and carbonate content, the variogram ranges are 8.51 m, 10.14 m, and 9.75 m, respectively, at the near-intact fen (first panels of Fig. 4B–D). In contrast, at the degraded fen, the spatial range extends to 38 m for soil moisture and microtopography, and 28.87 m for carbonate content (second panels of Fig. 4B–D).

Table 2
Summary statistics of the peat properties and surface microelevation.

Variable	Near-Intact (n = 99)				Degraded (n = 100)			
	mean	*median*	*SD*	*CV*	*mean*	*median*	*SD*	*CV*
SOM (%)	73.3	81.8	20.5	27.9	78.0	81.9	10.4	13.4
Carbonate Content (%)	18.3	13.9	12.26	67.1	17.5	15.5	6.53	37.3
Moisture Content (% dry basis)	835	814	254	30.4	610	582	191	31.3
Moisture Content (% wet basis)	88.3	89.1	4.21	4.77	84.9	85.3	4.11	4.84
microelevation (masl)	90.42	90.39	0.12	0.13	26.55	26.55	0.10	0.38

Note: All values, except for microelevation, are reported to three significant figures.

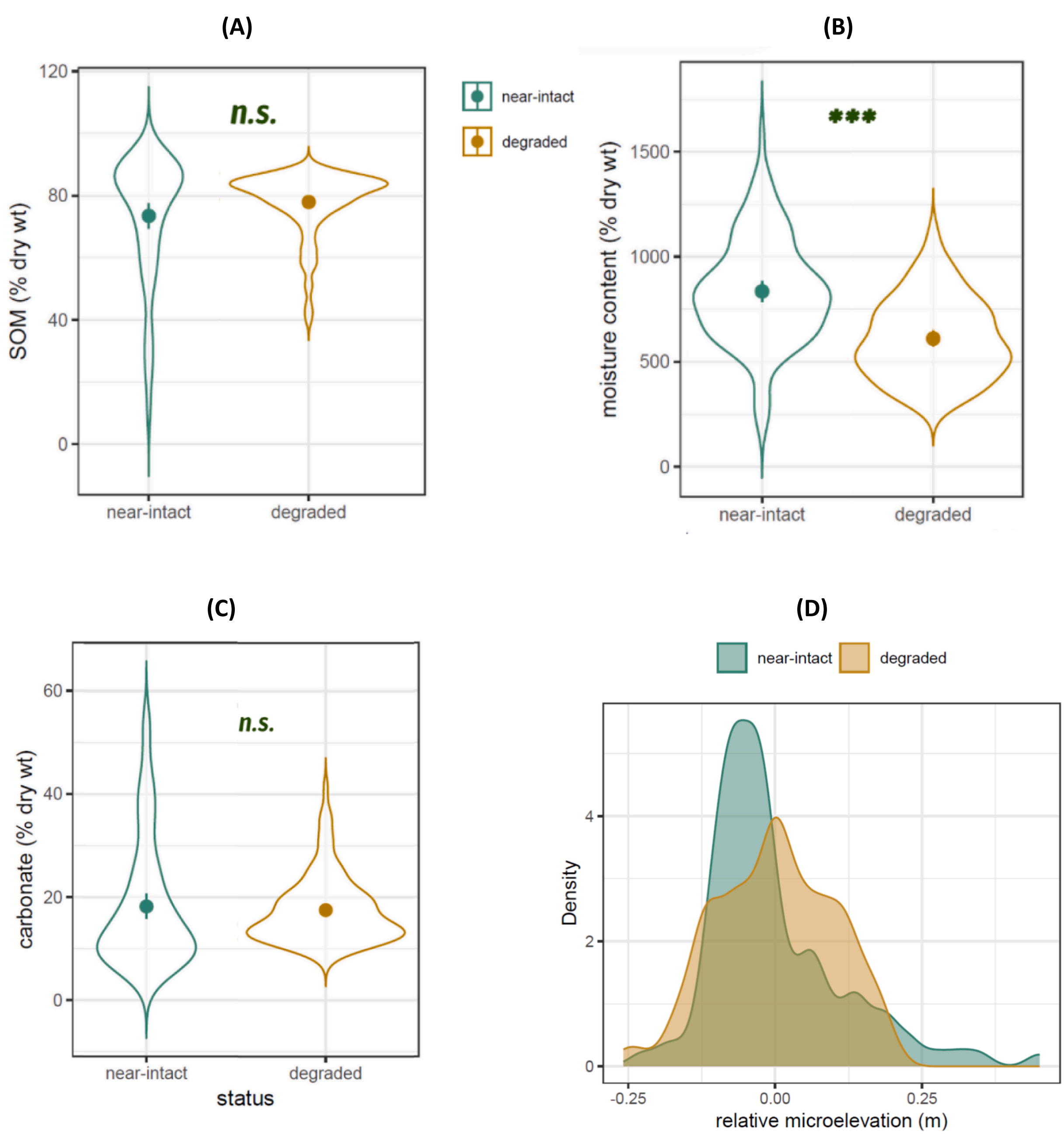


Fig. 3. Comparison of peat properties according to ecosystem status in terms of **(A)** SOM **(B)** Soil Moisture Content **(C)** Carbonate Content **(D)** microtopography (relative surface microelevation, centred around mean of each site). The shape of the violin plots (**A–C**) shows the density distribution (mirrored) while the point and error bars represent the mean and 95 % confidence intervals, respectively. Kernel density estimates (KDE) were used to smooth the distribution of the data. Statistically significant differences ($p < 0.001$) are denoted with "***", and non-significant results are indicated as "***n.s.***".

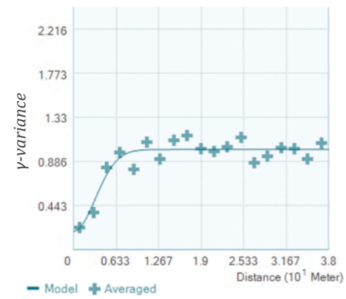
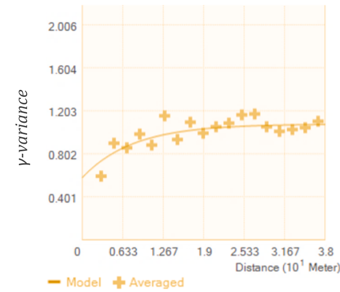
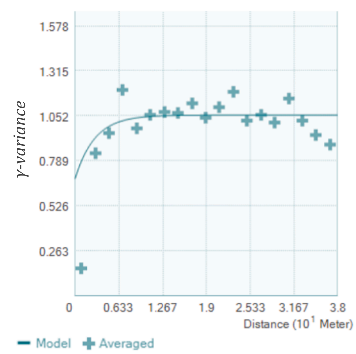
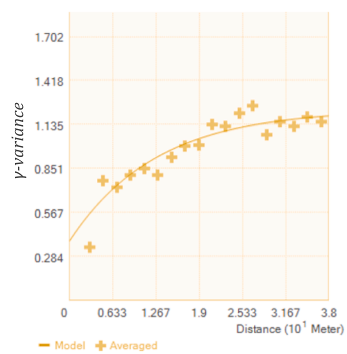
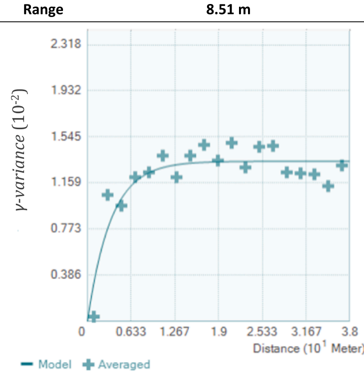
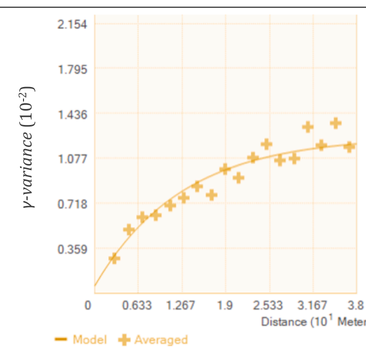
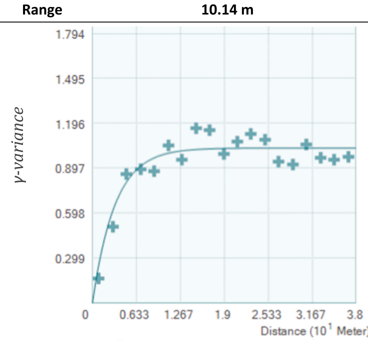
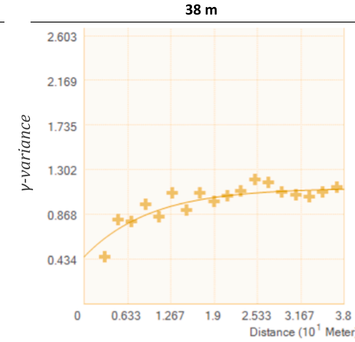
Variables	Ecosystem Status	
	Near-Intact Fen	**Degraded Fen**
(A) SOM (% dry weight)		
Model	0.19*Nugget+0.82*Gaussian(7.88)	0.58*Nugget+0.50*Exponential(23.75)
Range	**7.8 m**	**23.75 m**
(B) Soil Water Content (%, dry basis)		
Model	0.68*Nugget+0.37*Exponential (8.51)	0.38*Nugget+0.85*Exponential (38)
Range	**8.51 m**	**38 m**
(C) Microtopography (masl)		
Model	0*Nugget+0.01*Exponential (10.14)	0*Nugget+0.01*Exponential (38)
Range	**10.14 m**	**38 m**
(D) Carbonate Content (% dry basis)		
Model	0*Nugget+1.03*Exponential (9.75)	0.46*Nugget+0.67*Exponential (28.87)
Range	**9.75 m**	**28.87 m**

Fig. 4. Variograms of **(A)** SOM **(B)** Soil Wate Content **(C)** Microtopography and **(D)** Carbonate Content according to ecosystem status. The y-axis shows the gammavariance *(γ)* for the binned separation distances (x-axis). The main parameter of interest is the range, determined from the model variograms. All values have been rounded to 2 decimal places.

3.3. The association of SOM with moisture content and surface microelevation

In addition to comparing the spatial structures of soil properties and microtopography across both sites, we investigated differences in the small-scale associations between SOM and soil moisture content, and surface microelevation, while statistically controlling for the spatial location of each sample. The results of the generalised additive models (GAMs) for the near-intact fen and degraded fen are summarized in Fig. 5. The GAM for the near-intact fen explains 78% of the deviance, whereas the model for the degraded fen explains 58%.

For both sites, SOM is positively associated with soil moisture content. However, in the near-intact fen, the association sharply decreases beyond approximately 900% soil moisture content (dry weight), likely due to saturation effects in the peat. This non-linear relationship is evident from the higher effective degrees of freedom (EDF = 4.07) in the near-intact fen, compared to the degraded fen (EDF = 1.69), where the association is closer to linear.

Similarly, SOM shows a positive association with microelevation at both sites. However, in the near-intact fen, the positive association is observed only when the microelevation is above the mean level (0 m). Once again, the association is non-linear in the near-intact fen (EDF = 2.89), whereas it is less non-linear in the degraded fen (EDF = 1.88).

For both soil moisture content and surface microelevation, the associations are weaker in the degraded fen compared to the near-intact fen as indicated by the range of the partial effects (y-axis, see Fig. 5.).

4. Discussion

Our research highlights the importance of understanding the small-scale associations among soil organic matter (SOM), moisture content, and peat surface microelevation, particularly in the context of degradation and homogenisation.

4.1. Similar SOM but contrasting water storage in near-intact and degraded fens

Contrary to our expectations, both sites exhibited similarly high SOM (median = 82 %w/w for both). Nevertheless, as anticipated, soil moisture content was significantly lower in the degraded fen (*median values: degraded = 582 dry basis %w/w; 85% wet basis %w/w versus near-intact = 814 dry basis %w/w; 89 wet basis %w/w*). This suggests that for a similar quantity of organic matter, the peat in the near-intact site holds more water than in the degraded site. This could indicate a lower bulk density

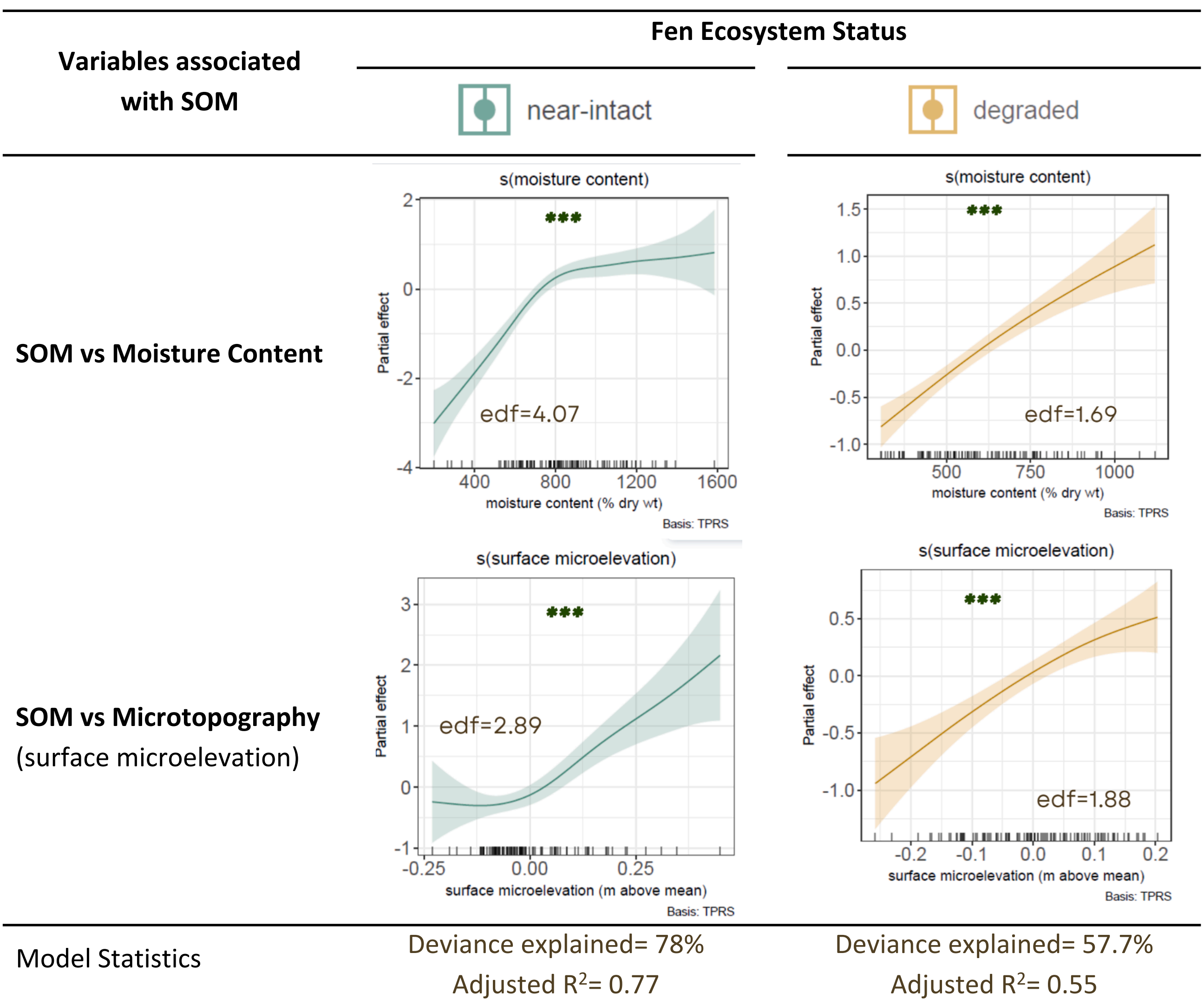


Fig. 5. Results of the generalised additive models to estimate how soil moisture and microtopography is associated with soil organic matter content (SOM). High precision latitude and longitude were kept in each model to control for spatial autocorrelation. '***' indicates $p < 0.001$.

in the near-intact site, as a lower bulk density means more pore space, allowing for greater water storage. Peat degradation via artificial drainage involves not only SOM mineralisation through aerobic decomposition but also shrinkage due to drying, the collapse of pore structures, leading to consolidation, compaction and surface elevation loss (Liu et al., 2020). These processes increase bulk density and decrease porosity, impairing hydrological functioning (Liu and Lennartz, 2019; Ahmad et al., 2020c; Liu et al., 2020; Ahmad et al., 2021). Although bulk density has been shown to be an effective indicator of peatland degradation (Liu and Lennartz, 2019), unfortunately, for our study areas (especially the near-intact site), it was not possible to collect undisturbed soil samples to determine bulk density – due to the nature of the peat (very loose and of high quality in the near-intact site).

Organic matter decomposition in peatlands is often conceptualised as a two phase process (Jayasekara et al., 2024): an aerobic phase in the acrotelm and an anaerobic phase in the catotelm. In the context of our study, although the degraded fen is subject to aerobic decomposition more than the near-intact site, nevertheless for an estimated 37% of the year, the water table is at or above the peat surface, and at or above 30 cm depth for 80% of the time, as illustrated by Fig. 9.30 in Bijkerk (2021, p. 282). Thus, under such shallow drainage the peat in our study plot of the degraded site is subject to aerobic decomposition for around 60% of the year. This is a likely explanation for the similarly high SOM content in the degraded fen (median = 82 *%w/w*), which is not significantly different from that of the near-intact fen (Ballymore), despite drainage. However, average values do not capture the spatial variation in ecosystem properties, underscoring the importance of analysing spatial heterogeneity.

4.2. Drainage and degradation may lead to ecosystem homogenisation

For all soil properties (SOM, moisture, and carbonate content) as well as microtopography, the variogram ranges (the separation distance at which the variogram levels off) are substantially larger in the degraded fen, exceeding twice the magnitude observed in the near-intact fen. Given the historical similarities between the two sites, including shared alkaline fen vegetation, groundwater-dependent hydrology and hydrodynamics, and lime-rich substrates (Regan and Conaghan, 2016; Regan and Conaghan, 2017), the near-intact Ballymore fen may serve as a reference for the past state of Tory Hill fen before the introduction of artificial drainage in the 1830s (Regan and Conaghan, 2016; Bijkerk, 2021).

Our results show that the near-natural fen exhibits higher rates of change in soil properties and surface microtopography over shorter distances leading to a more rapid decrease in similarity compared to the degraded fen. This pattern, with shorter variogram ranges in the near-intact fen and longer ranges in the degraded fen, likely reflects a process of ecosystem degradation accompanied by spatial homogenisation, where the fen's properties become more uniform across space.

Given that there are no significant differences in SOM between the two sites, and that the degraded site is subject only to shallow drainage (likely not experiencing prolonged drainage, as indicated by the depth duration frequency curves), it is unlikely that organic carbon mineralisation through aerobic decomposition is the only driver of these changes. It is possible for peat structure to be altered following drainage without substantial carbon mineralisation. During dry periods or when the water table is significantly below the soil surface, peat shrinkage occurs, and the weight of the unsaturated peat compresses the lower "layers", potentially 'flattening' microtopographic features. This can be driven by a reduction of buoyant force (see Strack et al., 2005, for a detail discussion on peat buoyancy) which may be followed by hysteresis (e.g., Waddington et al., 2010).

Spatial heterogeneity in peat properties may also be driven by spatially differential processes:

(1) **Plant biomass production rates:** Variations in plant productivity across microtopographic features can create heterogeneity in peat accumulation. Elevated areas (e.g., hummocks) often support species with higher biomass production, which can contribute to localized peat accumulation.
(2) **Decomposition Rates and Biomass Quality:** Decomposition rates are influenced by the inherent characteristics of plant material, such as biomass quality. Traits like high carbon-to-nitrogen (C:N) ratios, lignin content, and other recalcitrant compounds increase decomposition resistance, slowing organic matter breakdown and facilitating peat accumulation (Chaudhary et al., 2018).

However, the relationship between decomposition rates and microtopography remains unresolved. Some studies have suggested that differential decomposition across microforms leads to increased surface heterogeneity. For example, microform type and position are significant predictors of peat hydrophysical properties and as such, peatland microtopography is often said to be "self-reinforcing through ecological feedbacks" (Waddington et al., 2010). Others propose that it may result in surface flattening over time (Chaudhary et al., 2018).

Notably, the degraded site, which exhibits greater homogeneity, also has lower plant and habitat diversity compared to the near-intact fen (see Table 1). This observation raises a key question: does biotic homogeneity lead to abiotic homogeneity, or vice versa? It is plausible that if a relationship exists, it is bidirectional. Interestingly, the variogram ranges for all soil properties and microtopography are similar (approximately 8 to 10 m) for the near-intact fen which indicates that the ecological processes that potentially link these properties are operating at the same spatial scale. In contrast, this pattern is less evident in the degraded fen. The autocorrelation range for SOM is 23 m, which is noticeably lower compared to those of microtopography and soil moisture, both of which have ranges of ≥38 m.

4.3. Degradation and homogenisation may alter soil property-microtopography relationship

The generalised additive models revealed that higher moisture content is associated with SOM content in both drained and near-intact fens (controlling for space and peat surface microelevation). This relationship arises for two reasons: (1) organic matter has a high capacity to retain moisture (Hudson, 1994), and (2) higher water content promotes anaerobic conditions, under which decomposition rates slow down and organic carbon mineralization becomes limited (Clymo et al., 1998). These conditions are conducive to peat formation and accumulation.

Higher microelevations exhibit significantly higher SOM (controlling for spatial position and soil moisture content). In many peatland ecosystems, higher elevations (e.g., coastal or inland peatlands) are often hotspots of decomposition and carbon mineralisation due to reduced water saturation (Ahmad et al., 2020b) while lower elevations with wetter conditions accumulate peat (Wang et al., 2023). However, in our study, contrary to expectations, higher microelevations correspond to areas of accumulated peat which has higher organic matter content and lower areas indicate lower peat accumulation and consequently lower SOM. Nevertheless, at such small-scales associations between ecosystem properties are likely to be different than at a larger scale. In this context, where soil moisture is sufficient to lead to anaerobic decomposition (slower), plant biomass production may play a more crucial role in organic carbon dynamics than decomposition in maintaining a peat accumulating system or at the least, a system where peat loss is limited. Thus, the positive relationship between SOM and microelevation highlights the role of peat accumulation in shaping the microtopography at such small scale. For bogs, studies (Johnson et al., 1990; Johnson and Damman, 1991) have found that inherent characteristics related to decomposition rate starkly differ between hummock and hollow *Sphagnum* species. Hummock species decay more slowly than hollow species (Mäkilä et al., 2018) and retain their structure longer, after entering the peat horizon. This slower decay results in a faster peat accumulation in hummocks, a pattern also observed by Ohlson and Dahlberg (1991) and described by Nungesser (2003). Similarly, in a poor fen, Rochefort et al. (1990) had found that decomposition rate of peat is lower in hummocks compared to hollows concluding that peat accumulation rate should be higher in hummocks. Chaudhary et al. (2018) states, "…litter derived from plant species growing in hollow areas decomposes more quickly than that derived from vegetation of hummocks and intermediate areas…".

Furthermore, we found that small-scale relationships between SOM and microelevation, as well as SOM and soil moisture exhibit greater non-linearity in the near-intact fen compared to the degraded fen. As non-linear relationships between the properties of an ecosystem are one of the key features of a complex system (Riva et al., 2023), our results suggest that the near-intact fen maintains a higher degree of ecosystem complexity. Thus, if we were to consider the degraded site as a future state of the near-intact fen (post-degradation), it is interesting to consider how interventions such as drainage, may result in a simplification (see Peipoch et al., 2015) of relationships between ecosystem properties. The absence of a levelling-off effect for soil moisture suggests that the degraded fen may lack the same saturation dynamics as the near-intact fen. Furthermore, the range of partial effects in the GAM models is smaller in the degraded site compared to the near-intact fen, indicating weaker associations between variables. This is because the predicted effect of a given variable on the response variable varies less across its range, meaning that changes in the predictor have a relatively weaker influence on the response. This is also indicated by the overall lower deviance explained by the model.

4.4. Ecosystem homogenisation in peatlands: Limitations and future directions

We acknowledge that our interpretation is limited to only the two study sites. Furthermore, we were able to capture only a snapshot of the two sites which limits our ability to understand ecosystem dynamics. For example soil moisture content varies over time and is affected by meteorological factors such as precipitation, temperature, wind speed and solar radiation as these in turn influence hydrological processes such as infiltration, recharge and evapotranspiration (Ahmad et al., 2020a) and consequently groundwater fluctuation (Ahmad et al., 2021) and consequently surface runoff (Holden, 2005).

Nevertheless, our general observation opens several exciting avenues for further investigation:

(1) **Generalisability:** Do degraded fens commonly exhibit more spatially homogeneous soil properties and microtopography compared to their near-intact counterparts? Can various levels of spatial homogeneity be observed along a degradation gradient?
(2) **Differential decomposition vs. differential production:** Under what circumstances does differentiated decomposability of plant material play a larger role than differentiated plant biomass productivity in creating heterogeneous fen peatlands? What role do plant traits (e.g., biomass quality, lignin content; sphagnan content; C:N ratio) play in this process?
(3) **Biotic-abiotic coupling:** To what extent are biotic and abiotic homogenisation processes interconnected? What factors might lead to their decoupling?
(4) **Scale dependence – microtopography vs. macrotopography:** Is the association of fen microtopography with soil properties (especially SOM) dependant on the spatial scale of investigation?

Addressing these questions requires larger number of study sites, along with equal consideration for soil-hydrological and vegetation data. Long-term observation of fens and bogs should incorporate not only water-table monitoring and vegetation surveys but also repeated measurements of surface microelevation (see Graham et al., 2020).

It is well known that fens and bogs, especially in pristine conditions with high peat depths, experience dynamic changes due to shrinkage and swelling cycles (Eiselen, 1802) – often referred to as mire breathing, surface oscillation (Howie and Hebda, 2018) or "*Mooratmung*" (Seidel et al., 2023). Recent advancements in characterising peat surface oscillation and microtopography through remote sensing techniques (such as InSAR, Hrysiewicz et al., 2024) as well as structure-from-motion methods (e.g., Li et al., 2019) and terrestrial LiDAR scanning (e.g. Graham et al., 2020) have shown great promise. In addition identification of peat soils using radiometric data at multiple scales (e.g., O'Leary et al., 2025) may help to characterise spatial patterns of peat accumulation. These approaches should be integrated with high-precision GPS measurements (e.g., Wang et al., 2023) as well as camera system methods (e.g., Evans et al., 2021).

Incorporating abiotic properties into ecosystem homogenisation frameworks is essential, as current definitions often focus on biotic factors, overlooking the interconnectedness of physical and biological processes. Even the recently developed "ecosystem homogenisation index" (Sweet et al., 2021), while providing a way forward, insufficiently integrates abiotic homogenisation treating it primarily in terms of environmental gradients. While preferences for focusing on one or the other is often influenced by the specialisation of the researcher, Arthur Tansley's definition of "the ecosystem" which includes "…not only the organism-complex, but also the whole complex of physical factors…" (Tansley, 1935, p.299), is undermined if the study of ecosystem homogenisation fails to adequately address abiotic factors or treats them as secondary. Just as plant, soil and water interact, so too should soil scientists, plant ecologists and hydrologists, as it would lead to more holistic investigation of fen peatlands.

This consideration is particularly vital in peatlands, where plant-soil–water interactions are intricately linked and shape microtopography (and vice-versa). These interactions engage in a dynamic feedback that maintain ecosystem functioning, involving processes collectively referred to as 'self-organisation' (Couwenberg and Joosten, 2005) and self-regulation (Dommain et al., 2010). One need only examine the seven figures produced by Waddington et al. (2015, Figs. 1-7), illustrating different hydrological feedbacks in peatlands, to recognise that undisturbed peatlands differ profoundly from other terrestrial ecosystems. In these systems, homogenisation of one factor likely triggers cascading feedbacks that may lead to homogenisation of other properties.

5. Conclusion

Our findings highlight the importance of small-scale associations among soil organic matter (SOM), moisture content, and peat surface microelevation, especially in the context of degradation. We found that both study sites exhibited similar SOM levels, but the degraded fen had significantly lower moisture content, suggesting poorer water retention and hydrological functioning. Degradation processes, including drainage and compression, likely contribute to these differences. Higher moisture content was positively associated with higher SOM, as organic matter retains moisture, and anaerobic conditions slow decomposition, promoting peat formation. We also observed that higher microelevations corresponded to areas of greater peat accumulation, indicating a link between microtopography and SOM. The degraded fen, however, showed weaker and more linear associations between variables, suggesting lower ecosystem complexity. Our variogram analysis showed that the degraded fen had more homogenised soil properties and microtopography, with a much larger variogram range. This supports the idea that degradation is accompanied by ecosystem homogenisation and that variogram range of soil properties and microtopography is an effective indicator of ecosystem homogenisation in fen peatlands. The results align with generalised additive models, reinforcing the observed trends.

These findings raise several important questions for future research: Do other degraded fens show similar spatial homogenisation? How do decomposition rates and plant diversity contribute to peatland heterogeneity? What are the interconnections between biotic and abiotic processes in shaping peatland ecosystems? Addressing these questions requires a broader approach, including more study sites and a balance of soil-hydrological and vegetation data. Long-term monitoring and advanced remote sensing techniques can help track dynamic changes in peatlands, informing better management and restoration strategies.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT-3.5 in order to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT authorship contribution statement

Sate Ahmad: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing, Software, Visualization. **Miaorun Wang:** Formal analysis, Software, Writing – original draft, Writing – review & editing. **Adam Bates:** Investigation, Project administration, Writing – review & editing. **Francesco Martini:** Investigation, Writing – review & editing. **Shane Regan:** Resources, Writing – review & editing. **Matthew Saunders:** Resources, Writing – review & editing. **Haojie Liu:** Writing – review & editing. **Jennifer McElwain:** Writing – review & editing. **Laurence Gill:** Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113317.

Data availability

Data will be made available on request.

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