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ASSESSING THE PEATLAND HUMMOCK-HOLLOW CLASSIFICATION FRAMEWORK USING HIGH-RESOLUTION ELEVATION MODELS: IMPLICATIONS FOR APPROPRIATE COMPLEXITY ECOSYSTEM MODELLING

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ABSTRACT

The hummock-hollow classification framework used to categorize peatland ecosystem microtopography is pervasive throughout peatland experimental designs and current peatland ecosystem modelling approaches. However, identifying what constitutes a representative hummock-hollow pair within a site and characterizing hummock-hollow variability within or between peatlands remains largely unassessed. Using structure-from-motion (SfM), high resolution digital elevation models (DEM) of hummock-hollow microtopography were used to: 1) examined how much area needs to be sampled to characterize site-level microtopographic variation; and 2) examine the potential role of microtopographic shape/structure on biogeochemical fluxes using data from 9 norther peatlands. To capture 95% of site-level microtopographic variability, on average an aggregate sampling area of 32 m^2 composed of ten randomly located plots with vegetation removed was required. We further present non-destructive transect-based results as an alternative to the SfM approach. Microtopography at the plot-level was often found to be non-bimodal, as assessed using a Gaussian mixture model (GMM). Our findings suggest that the non-bimodal distribution of microtopography at the plot-level may result in an under-sampling of intermediate topographic position. Extended to the modelling domain, an under-representation of intermediate microtopographic positions is shown to lead to large flux biases over a wide range of water table positions for ecosystem processes which are non-linearly related to water and energy availability at the moss surface. A range of tools examined herein can be used to easily parameterize peatland models, from GMMs used as simple transfer functions, to spatially explicit fractal landscapes based on simple power law relations between

microtopographic variability and scale.

INTRODUCTION

Northern peatlands in the maritime-temperate, boreal, and subarctic have been persistent terrestrial sinks for carbon throughout the Holocene, storing approximately one-third of all global soil carbon (Yu, 2012). However, these peatland carbon stores are now considered to be at risk from the effects of climate change due to warmer temperatures and prolonged periods of drought which would increase carbon loss through decomposition and increased wildfire consumption (Moore et al., 1998; Yu et al., 2009; Turetsky et al., 2002; Kettridge et al., 2015). While these positive feedbacks cause carbon loss (*e.g.* Ise et al., 2008; Blodau et al., 2004), the long-term stability of peatland carbon may be maintained by negative ecohydrological feedbacks that promote resilience to environmental change (Belyea and Clymo, 2001; Waddington et al., 2015; Hodgkins et al., 2018). These negative feedbacks depend, in part, on the presence of microtopography (microforms) that provides spatial diversity in ecohydrological structure and biogeochemical function across a peatland (Belyea and Clymo, 2001; Belyea and Malmer, 2004; Eppinga et al., 2008; Pedrotti et al., 2014; Malhotra et al., 2016).

Peatland microform classification is typically defined by their proximity to the water table and characteristic vegetation assemblages, such as different species of *Sphagnum* moss and cover of woody shrubs (Andrus et al., 1983; Rydin and McDonald, 1985; Belyea and Clymo, 1998). Hummocks and hollows occur at a spatial scale of 1 to 10 m

(S2 – Belyea and Baird, 2006), with the surface of hummocks usually covering an area on the order of 1 m^2. The hummock surface is typically located ~0.20 m or higher above the water table (Belyea and Clymo 1998; Malhotra et al., 2016). Hollows are closer to the water table and may occasionally be inundated, and 'lawns' are intermediate to hummocks and hollows (Belyea and Clymo, 1998).

Conceptualizing and qualitatively classifying complex peatland microtopography as hummocks and hollows is common in peatland research (*e.g.* Waddington and Roulet 1996; Belyea and Clymo 2001; Nungesser 2003; Benscoter et al., 2005; Bruland and Richardson 2005; Moser et al., 2007) as it is simple and allows for straightforward sampling designs, however, the visual characterization of hummocks and hollows is subjective and has the potential to produce biased results for several reasons. First, although microform vegetation and hydrology may be included in detailed study site/method descriptions, these characteristics may be quite different for microforms classified as hummocks at one study site compared to hummocks at a different study site. Biogeochemical function (ecosystem fluxes) may differ for microforms within a site (*e.g.* Bubier et al., 1993; Pelletier et al., 2011), but if the vegetation and hydrology of those microforms vary for different peatlands, assumptions for hummock and hollow biogeochemical function at one site may not be applicable to other peatlands. Given that there may also be large differences in the relative/absolute height and surface roughness of microforms between sites, comparing studies with hummock and hollow microforms as a central component of the sampling design can be problematic. Moreover, the surface area, spatial distribution, and relative proportion of hummock and hollow microforms present within a peatland also vary between sites (*e.g.* Moore et al., 2015), which may introduce bias into sampling design. For example, researchers may over-sample the visually obvious extremes of the hummock-hollow continuum. Given that several peatland hydrological and ecosystem carbon models parameterize peat decomposition, production and hydraulic properties based on peatland microform classification (*e.g*. Dimitrov et al., 2010; Sonnentag et al., 2008), the aforementioned sampling and classification biases may also lead to issues in determining the scale and complexity required for ecosystem modelling (*e.g.* Larsen et al., 2016).

The construction of a digital elevation model (DEM) in a peatland allows for the classification of microforms based on quantitative measures (*e.g.* relative position, slope, or roughness) (*e.g.* Mercer and Westbrook, 2016; Rahman et al., 2017) rather than relying on qualitative/visual methods. Given the wide use and adoption of the hummock-hollow conceptual framework, we examine the potential utility of DEM quantitative techniques to overcome the concerns with the dominant qualitative hummock and hollow framework/classification scheme. As such, the two main objectives of this study were to: (i) provide a geostatistical/geospatial description of plot scale microtopographic variation in peatlands; and (ii) to use simple physically-based and empirical models to examine the effect of measured microtopographic complexity on ecosystem fluxes. For the first objective, our two main focuses were: i) using a case-study approach, assess how much area needs to be sampled in order to be able to adequately quantify microtopographic variability within an unpatterned peatland; and ii) using multi-site plot-scale sampling, explore DEM-derived morphometric properties (*e.g.* microtopography

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height distribution, slope, and roughness) of peatland microforms which may be useful as microtopographic metrics.

METHODS

Experimental design

We first evaluated how much sampling area is needed to capture the overall microtopographic variation of an unpatterned site using both structure-from-motion (SfM) (see Brown and Lowe 2005; Mercer and Westbrook 2016) and a transect based sampling approach. To accomplish this, we randomly sampled 50 plots for SfM reconstruction in a peatland near Red Earth Creek, AB (56.54°N 115.22°W) (hereafter referred to as site-level). In addition, we manually measured surface elevation along several 50 m transects at 0.05 m intervals covering the plot area at the Red Earth Creek site. Secondly, we used SfM to examine morphometric properties at the plot scale in 9 boreal/hemi-boreal, non-permafrost, ombrotrophic peatlands (4 in Canada, 4 in USA, 1 in Sweden; see Table 1) using two different approaches. The first approach involved randomly selecting 9 plot locations within a single site and creating a plot around the random location which was perceived to contain a hummock-hollow pair. The second approach involved qualitatively choosing what was perceived to be a representative hummock-hollow pair at 9 different sites. The aim of our approach was to highlight the potential breadth of variation in morphometric properties which might be observed either within a site (*i.e.* implications for small sample size) or across sites (*i.e.* highlight potential challenges with site inter-comparisons without supporting information of peatland microtopographic metrics). For both randomly located plots and qualitatively chosen plots, individuals were asked to identify a central point for a hummock and hollow subplot within the larger microtopography plot.

Site preparation and image acquisition protocol

All vascular vegetation was removed from the plot area using scissors and hand pruners in order to provide an unobstructed view of the surface microtopographic variation (moss surface) for imaging. Matte-colored discs (n=20) of 0.04 m diameter were placed randomly on the clipped surface to provide reference points for better correlation between images. To provide absolute scale and orientation, two boxes of known dimensions (0.1×0.1×0.1 m) were placed in each plot and levelled prior to image acquisition. Images of each target area were taken via at least two circuits around the plot, with images taken from two separate vertical viewing angles (see http://www.cs.cmu.edu/~reconstruction/basic_workflow.html for third party description of general workflow). Distance to target area was set so that a large portion of the clipped area was visible in each image. To produce different horizontal viewing angles, images were taken every one or two paces around the perimeter of the plot. This procedure yielded 41 to 282 overlapping images from multiple view-points of the plot areas, which ranged in size from 3.2 to 10.1 m^2 (Table 1). Images were taken during either clear-sky or over-cast conditions near mid-day during the summer to avoid changing lighting conditions and to limit self-shadowing of the surface. Images were captured with digital cameras using automatic exposure settings. Prior to analysis, all images were downscaled where necessary to a common resolution of 2048 x 1536 using a Lanczos3 filter.

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Digital elevation models of microtopography

A point-cloud of the moss surface was generated using an SfM approach (Brown and Lowe 2005; Mercer and Westbrook 2016) using the program Visual SfM (Wu, 2011). Visual SfM identifies image features for cross-comparison using a scale-invariant feature transform (Lowe, 1999), and then matches features between images in a pairwise manner. Effectively, this creates multiple stereo-pairs from which camera position and scene geometry can be estimated through triangulation. This procedure yielded average point cloud densities ranging from 3-59 pixels cm^{-2} for the imaged plots (Table 1).

Prior to generating the DEMs, point clouds were cropped to the region of interest (*i.e.* area of clipped vegetation), then scaled, levelled, and oriented using the rendered reference objects. DEMs were produced using the MATLAB function *TriScatteredInterp* (MATLAB R2010a, The Mathworks), which performs Delaunay triangulation of the point clouds. DEMs were generated on a 0.01 x 0.01 m grid using natural neighbor (Voronoi) interpolation. The DEMs were smoothed using a mean filter window with a size of 0.03 x 0.03 m. Finally, a mask was applied to the DEMs to remove reference objects.

Capturing site-level microtopographic variation

Plots from the Red Earth Creek peatland were ~3.5 m^2 and differences between plot elevation for the 50 plots were surveyed using a Smart Leveler digital water level (accuracy ±2.5 mm), with offsets applied to DEMs. A Monte Carlo re-sampling approach was used to evaluate how total variance in microtopographic elevation increased with

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increasing sample size. For each sample size (*i.e.* 1-50), 200 random re-samplings were performed. To estimate the change in variance with increasing sample size, a rectangular hyperbola was fit to the mean variance (y) versus sample size (x):

$$y = \frac{ax+b-\sqrt{(ax+b)^2-4axbc}}{2c}$$

where *b* is the estimated maximum total variance, and *a* and *c* are initial slope and concavity parameters.

To evaluate the dominant scale of microtopographic variation which contributes to total variance, a fast Fourier transform (*fft* function in MATLAB) was used to estimate the power spectral density (PSD) of microtopographic variation along an artificially constructed 300 m long transect (combination of multiple transects). Manual measurements of moss surface elevation were taken every 0.05 m along six 50 m transects at the Red Earth Creek, AB and Nobel, ON site using the Smart Leveler.

Plot-level microtopographic variation

Plot-level microtopographic variation was analyzed using randomly and qualitatively chosen plot locations listed in Table 1. Based on the hummock-hollow conceptual model, our *a priori* assumption was that a hummock-hollow pair would have a bi-modal distribution of surface elevation. Our null hypothesis was that microtopography would follow a bi-modal distribution, so we evaluated DEM height distributions using 1– to 3–member Gaussian mixture models (GMM) to evaluate whether 2-member GMMs would best explain height distributions. GMMs were fit to DEM height distributions using the MATLAB function *gmmdistribution.fit*, which uses an iterative expectation maximization

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algorithm to determine GMM parameters representing maximum likelihood estimates. The GMM fit function was seeded with initial parameter estimates using *k*–means cluster analysis. The best model was decided based on the minimum Akaike information criteria (AIC).

Surface slope and aspect were evaluated using the computed surface normals for each point and eight connected neighbours of the DEM. The fractal dimension of plots was evaluated using radially averaged PSD derived from an *fft* of elevation data. The Hurst (*H*) exponent (values of 0–1) presented herein is related to fractal dimension as 3-*H*, where the slope of the PSD curve in log space is -2(H+1).

Modelled moss surface insolation and productivity

Potential moss surface insolation was modelled using the formulation presented in Kumar et al. (1997) to account for earth-sun geometry, surface slope and aspect, and diffuse radiation under clear-sky conditions. Total potential insolation was evaluated on an annual basis and normalized relative to total insolation on a flat surface for each plot location.

For moss net primary productivity (NPP) and capitula water content (*WC*), each plot was classified into three units based on relative elevation which notionally correspond with hollow/lawn, low hummock, high hummock. K-means clustering was used to perform unsupervised classification of microtopographic elevation (Figure S1). A separate parameterization for moss NPP and WC was used for each elevation cluster.

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Parameterizations for hollow/lawn, low hummock, and high hummock were obtained from *Sphagnum* species of the section Cuspidata, Sphagnum, and Acutifolia, respectively (Figure S2). An empirical relation between WC and water table depth (WTD) was modelled as follows:

$$WC = p_1 \cdot \ln(p_2 \cdot WTD) + p_3$$

where WC is in $g_{water}\ g^{-1}{}_{dry\ weight}$, and $p_{1\text{-}3}$ are fitted parameters. WC was restricted to a range of 1–25 $g_{water}\ g^{-1}{}_{dry\ weiight}$. A rational function was used to model the relation between moss capitula NPP and WC:

$$NPP_{pot} = 100 \cdot \left(\frac{p_4 \cdot x^2 + p_5 \cdot x + p_6}{x^2 + p_7 \cdot x + p_8} \right) \cdot NPP_{max}^{-1}$$

where NPP_{pot} represents % of maximum NPP, and $p_{4\text{-}8}$ are fitted parameters. Estimates of 83, 170, and 198 g m^{-2} mo^{-1} for NPP_{max} were used to represent *Sphagnum* species of section Cuspidata, Sphagnum, and Acutifolia, respectively (Nungesser, 2003).

RESULTS

Site-level microtopographic variation

In characterizing microtopographic variability across the Red Earth Creek site, our data shows that variability in surface elevation increases asymptotically with sample size (*i.e.* area sampled) and is well predicted by a rectangular hyperbola (r^2=0.98; p<<0.01) (Fig. 1). Based on the asymptote of the fitted rectangular hyperbola (0.147 m), Figure 1 shows that on average an area of 32 m^2 (*i.e.* 9 random plots of ~3.5 m^2 size) contains roughly 95% of the predicted site-scale microtopographic variability. Even though increasing the number of plots by a factor of 5 (*i.e.* ~50 plots) has little effect on the average variance in surface elevation, the range associated with re-sampling is reduced by about half (Fig. 1 – shaded area).

While the Red Earth Creek multi-plot DEM data provides the ability to assess the area required to capture site-scale microtopographic variability for a small unpatterned Alberta peatland, it does not directly provide information on what spatial scales contribute most to overall variability. The power spectral density (PSD) of manual elevation transects from both the Red Earth Creek and Nobel sites suggests that most of the microtopographic variation for these two surveyed sites occurs at spatial scales between 1–10 m (Fig. 2 – cumulative curves). Both sites have qualitatively similar PSD curves in log-space with a roll-off at spatial scales between 2.6–3.1 m (break point of piecewise regression). Moreover, the PSD of microtopographic variation appears to be well described by a power law (*i.e.* relatively smooth slope in log space) at small spatial scales resulting in a Hurst exponent (see Methods for relation to fractal dimension) between 0.61–0.79.

Plot-level hypsometry and fractal dimension

There is a characteristic difference in the elevation distribution of whole-plots compared to that of the corresponding hummock-hollow subplots for both qualitatively (Fig. 3) and randomly (Fig. 4) chosen plot locations. The elevation distributions for hummock-hollow subplots tend to have a clear separation of modes (Fig. 3-4 B-panels). The degree of separation in modes has a weak (r^2 = 0.31) but significant linear relation (F_{16} = 7.1, p = 0.017) with the microtopographic range in the whole plot. On average, the elevation

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range absent from the hummock-hollow subplots represents roughly 25% of the microtopographic range of the whole plot. When all hummock-hollow subplots are aggregated across randomly selected plots (*i.e.* Nobel, ON site), the whole elevation distribution is captured (Fig. S3). However, there remains a bias towards higher elevations being sampled in the aggregated subplot elevation distribution compared to the aggregated whole plot elevation distribution.

In testing the null hypothesis of bimodally distributed relative surface elevation at the plot scale, we examined the goodness of fit of one-, two-, and three-member GMMs. An assessment of all 18 plots suggests that two- or three-member GMMs tend to provide a better fit to reconstructed elevation distributions compared to a one-member (*i.e.* normal) distribution. Based on AIC values, the one-member GMM was best for only 3 plots, while two- and three-member GMMs were best for 6 and 9 plots, respectively (Table 2). In contrast, when GMMs were fit to hummock-hollow subplot data, the two-member GMM tended to outperform one- and three-member GMMs.

The mean (μ) and standard deviation of elevation for hummock and hollow subplots were grouped and compared according to plot selection method (*i.e.* random within site versus qualitative between site selection). Since the μ parameter corresponds with relative elevation, we took the difference between the two members (*i.e.* μ_{hum}–μ_{hol}) for comparison purposes. Overall, the qualitatively chosen plots appear to have similar ($F_{1,16}$=0.2; p=0.68) relative hummock heights (μ_{hum}–μ_{hol}) (0.21±0.08 m) compared to the randomly chosen plots. (0.19±0.09 m). Variation in elevation tended to be lower in

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hollow subplots (0.032±0.012 m) compared to hummock subplots (0.022±0.009 m) (microform; $F_{1,32}$=9.0, p=0.005), where the difference between hummock and hollow subplots was similar when comparing qualitatively and randomly chosen sites (microform × plot type; $F_{1,32}$=0.02; p=0.89).

Depending on the underlying structure of spatial variability, surface roughness can be highly dependent on the scale of analysis. A two-dimensional power spectral density of elevation provides a means to formally describe the change in roughness with scale (Fig. 5). The power spectral density of elevation was found to be a linear function of length-scale across the 0.05–1 m range in log–log space (r^2_{adj}>0.96) and is the basis for the Hurst exponent (*H*) (see methods for relation to fractal dimension). While the distribution of *H* for qualitatively chosen plots (0.73±0.18) was higher compared to randomly chosen plots (0.60±0.11) (*i.e.* comparatively less 'complexity' at finer spatial scales), the difference was not strongly significant ($F_{1,16}$ = 3.63; p = 0.075).

Plot-level slope, aspect and solar insolation

A Weibull distribution provided a good fit to the slopes for the reconstructed DEMs (Fig. S4), where the average, maximum, and minimum RMSE were 0.10%, 0.14%, and 0.06%, respectively, based on a relative frequency distribution with 1° bin sizes. When grouped according to qualitatively versus randomly chosen plots, the modal slope for whole plots was 21.5±4.4° and 23.4±5.7°, respectively. Similarly, the distribution of standard deviation in slope for randomly and qualitatively chosen plots was 14.6±1.3° and 14.5±2.1°, respectively. Comparing the parameter distributions from the Weibull fit

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for qualitatively and randomly chosen plots, it was found that there was no significant difference in the mean scale (analogous to mode) and shape (analogous to standard deviation) parameters (scale: p=0.44, $F_{1,16}$=0.62; shape: p=0.88, $F_{1,16}$=0.02).

While modal slope tended to only be slightly higher in the hummock subplots (22.9±6.8°) versus hollow subplots (19.5±6.0°), there was greater distinction in the prevalence of steep slopes (*i.e*. >45°) in hummock subplots (14.8±10.4%) versus hollow subplots (8.4±9.5%) (Fig. S5). Comparing slope in the hummock/hollow subplots to the 3-member GMM clusters (high, intermediate, and low elevations – for example see Fig. S1), we see that the subplots tend to be somewhat flatter compared to the rest of the plot, particularly for hollow subplots (Fig. S5).

Figure 7 shows how slope and aspect affect potential solar insolation at the moss surface under ideal conditions (i.e. clear-sky, sparse vegetation). Potential solar insolation is significantly affected by aspect ($F_{7,60820} \geq 290.8$, $p<<0.01$) and its interaction with slope ($F_{7,45606} \geq 7043.7$, $p<<0.01$), where on average, south facing slopes receive double the potential solar insolation compared to north facing slopes. Based on measured slope and aspect at randomly and qualitatively chosen plots, median potential solar insolation for a south aspect is 12-24% greater compared to a flat surface. Similarly, for a north-facing aspect, median potential solar insolation is 18-40% lower (Figure S6).

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Plot-level empirical model of moss productivity using high resolution DEMs

Assuming a flat water table at the plot-level, Figure 8 shows how modelled NPP_{pot} varies with WTD relative to the average hollow surface. Hollows tend to have a comparatively narrow range of WTD (i.e. 0–0.15 m) over which the moss is expected to be highly productive compared to hummocks. Despite using species-dependent NPP_{pot}-WC relations, the large differences in water table range over which hummock and hollow NPP_{pot} is high is largely driven by the WC-WTD relations (Figure S2). Where moss species have large differences in NPP_{max} and different characteristic water retention, NPP_{pot} rarely overlaps between microtopographic classes (Figure 8). If we ignore the effect of species-dependent characteristics (i.e. NPP_{max}, NPP_{pot}–WC, and WC–WTD) and use a single average parameterization, differences between microtopographic classes tend to be smaller for shallow water table conditions (Figure S7), yet there remains a characteristic difference in mean NPP_{pot} between microtopographic classes.

From a scaling perspective, modelled NPP_{pot} (Figure 8 and S7) were used to compare spatially explicit estimates with plot averages based on the notional chamber subplot (i.e. pre-determined 0.37 m^2 area in perceived hummock and hollow — see methods). In general, spatially explicit NPP_{pot} estimates tended to be higher/lower than the hummock-hollow estimates depending on whether the water table was relatively shallow/deep (Figure 9a). The maximum positive bias between the spatially explicit and hummock–hollow NPP_{pot} values ranged from 21.1–40.1 g m^{-2} mo^{-1}, while the negative bias ranged from -5.9 to -40.9 g m^{-2} mo^{-1}. Using a single average parameterization for

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NPP_{pot} tends to result overwhelmingly in positive bias between the spatially explicit and hummock-hollow models, where maximum bias ranges from 22.7 to 58.9 g m^{-2} mo^{-1}. Averaged across all 18 plots, the subjective hummock subplot broadly overlapped with the k-means high-hummock classification (94%), with only small portions overlapping with the low-hummock classification (6%). Similarly, the subjective hollow subplot broadly overlapped with the k-means hollow/lawn classification (79%), with only small portions overlapping with the low-hummock classification (20%). In this study, our results indicate that the subjective choice of hummock and hollow subplot location (e.g. for chamber flux measurement) systematically under samples intermediate topographic positions. This is exemplified in Figure S8 which shows the spatial distribution of NPP_{pot} for one of the plots. For the NPP_{pot} model using separate parameterization for the microtopography classes, the low-hummock class remains distinct from both the hollow/lawn and high-hummock class except under very dry conditions. For the uniform parameterization, the low-hummock classification is distinct from the other two classes under wet conditions, behaves like the hollow/lawn under moderately dry conditions, and behaves like a hummock under very dry conditions.

DISCUSSION

Assessing microform representativeness

In studies which use the hummock-hollow microtopography classification as part of their sampling design, there are many cases in which the plot choice is said to be representative (*e.g.* Kettridge and Baird 2008; Laing et al., 2008; Nijp et al., 2014), but

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often lacks detail on how representativeness was assessed. For example, when characterizing the surface within an eddy covariance flux measurement footprint, it is common to only sample one or few hummock-hollow pair(s) (*e.g.* Lafleur et al., 2003; Humphreys et al., 2006; Peichl et al., 2014; Moore et al., 2015). Similarly, for direct measurements of surface fluxes where microtopography is considered explicitly, chamber-based measurements typically use between four and eight replicates (*e.g.* Frenzel and Karofeld 2000; Turetsky et al., 2002; Forbrich et al., 2011; Petrone et al., 2011) per microtopographic unit. For peatland studies which use random plots, as many as 30 plots per site have been reported (*i.e.* Wieder et al., 2009), yet earlier studies have reported using as few as one to four plots to characterize a site (*e.g.* Crill et al., 1988; Shannon and White 1994; Regina et al., 1996). Using the Red Earth Creek results as a reference, for studies which have 4-8 replicates, 2-3 microtopographic units (*e.g*. hummock, lawn, hollow), and the more common chamber size of roughly 0.6 x 0.6 m, we would infer from our results that the typical total sample area for chamber flux measurements in a peatland ecosystem would capture on the order of 70-86% of site-scale microtopographic variability in their plots. It should be noted however that the simple assessment above assumes that chamber placement is random. In cases with lower replication of two microtopographic units, our results suggest that the uncertainty associated with repeated sampling is relatively high (Fig. 1 – shaded area) and that the choice of two microtopographic units could lead to an under-sampling of intermediate topographic positions (*e.g.* Fig. 3-4 B-panels). When the ecosystem processes of interest are not measured across the range of variability observed at the site-scale, particularly for non-linear processes, then scaling from process-based, or simply plot-

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scale measurements, is at risk of being biased. Our simple empirical model of moss NPP_{pot} demonstrates that flux bias can be large relative to NPP_{max} and is strongly dependent on water table depth (Figure 9). Although NPP_{pot} estimates are strongly influenced by the parameterization used (e.g. Figure 8 and S7), there remains a large bias between the spatially explicit and hummock-hollow NPP_{pot} models.

To upscale models or plot-scale measurements it is important to determine the microtopographic structure and variability of a peatland. There were often non-bimodal distributions of microtopography in our study sites (Fig. 3–4 A-panels and Table 2) where the more continuous distribution of elevation at the plot scale suggests that when experimental designs use hummock-hollow pairs as the primary experimental unit (Fig. 3–4 B-panels) they have a tendency to capture the ends of the distribution, omitting on average 25% of the elevation distribution at the plot scale (see also Figure S3). In this study we clipped vegetation in 50 small random plots to produce very high resolution DEMs for assessing microtope-scale (*i.e.* S3 hummock-hollow complex, *cf*. Belyea and Baird, 2006) variability, yet surface vegetation removal will generally be undesirable. Ground- or drone-based SfM approaches have been used to produce a digital surface model (DSM – vegetation present) for alpine (Mercer and Westbrook, 2016) and blanket (Harris and Baird, 2018) peatlands with reasonable accuracy (e.g. mean absolute error of ~0.08 m, and normalized median absolute deviation of ~0.11 m for the alpine and blanket peatlands, respectively). In situations where surface vegetation removal is not possible or desirable and/or where drone-based imagery is hampered (*e.g.* treed peatlands), a survey of height distribution along one or several transects would provide an alternative to assessing microtope to mesotope-scale (S3–S4 Belyea and Baird, 2006) microtopographic variability. The power spectral density of transect data would suggest that, for absolute height, a sampling interval of less than 1 m (*e.g.* 0.5 m) for several 50 m transects would capture the scales of variability which contribute most to total height variance (Fig. 2 and 5) since this corresponds to ~90% of measured microtopographic variation and provide sufficient fine-scale data to estimate the fractal dimension of microtopography. Information on height distributions could provide the basis for plot selection, where plots could be chosen to deliberately span the range of variability, or to avoid oversampling extremes. Information on the height distribution would furthermore provide the ability to scale up findings from the plot level given their relative position in the wider distribution of microtopographic variability (*cf. Griffis* et al., 2000).

Despite the variety of site characteristics observed, our plots were limited to bogs and poor fens, and did not include sites with ridge and pool patterning. Nevertheless, our results would suggest that generalizations based on a hummock-hollow classification, either to the site-scale, or to hummocks-hollow pairs across sites should be viewed with a degree of skepticism when sample size is low, or when a general microtopographic survey is absent/unreported. Thus, for wider inter-comparability of peatland studies, SfM or transect-based approaches of measuring and reporting on one or several morphometric properties of microtopography could provide a more comprehensive dataset to aid in future meta-analysis/synthesis.

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Implications for appropriate complexity ecosystem modelling in peatlands

The complex shape/structure of peatland microtopography has generally been ignored from a modelling standpoint, but several studies have shown, for example, that slope and aspect may affect peat temperature (Kettridge and Baird 2010). Under clear-sky conditions, modelled annual total solar insolation differs from a flat surface by roughly ±20% in our measured plots, where our study sites span 43° to 60°N latitude (Figure S6). For north and south facing slopes, this effect is amplified (Figure 7) particularly for high- and low-hummock microtopographic classes (e.g. Figure S1) which tend to have greater average slope compared to the hollow/lawn classification (Figure S5). While our study sites are limited to the non-permafrost boreal region, the applicability of slope and aspect considerations to modelling tundra tussocks in arctic and permafrost regions is also relevant (*e.g.* De Baets et al., 2016). Based on the results of empirical studies, the shape of microtopographic features aught to play a role in ecosystem fluxes due to the effect of shortwave radiation on surface evaporation (Kettridge and Baird, 2010), photosynthetically active radiation on moss production (Harley et al., 1989; Loisel et al., 2012), and soil temperature on methane production and respiration (*e.g.* Lafleur et al., 2005; Waddington et al., 2009). It is important to note, however, that under cloudy conditions the increasing proportion of total insolation from diffuse radiation decreases the disparity in insolation associated with slope and aspect. Furthermore, in peatlands where substantial tree, shrub, or graminoid cover exists, the importance of slope and aspect on soil heating or ecosystem fluxes is likely to be low since insolation decreases exponentially with increasing vascular leaf area.

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In addition to microtopographic shape/structure, the size of microtopographic features and their small-scale variability can similarly affect ecosystem fluxes, where height above water table imposes a first order control on water availability. Methane fluxes from peatlands, for example, have been shown to vary logarithmically over 0.1 m scales (Turetsky, 2014). Water availability at the moss surface has been shown to be both species-dependent and strongly affected by water table (Hayward and Clymo, 1982; Rydin, 1985), where moss species and water availability has been linked to many ecohydrological processes such as surface evaporation (Kettridge and Waddington, 2014), productivity (Williams and Flanagan, 1998; Strack and Price, 2009), and hydrophobicity (Moore et al., 2017). We show that when microtopographic variability is explicitly modelled, complex patterns of potential moss productivity emerge (Figure S8) which are not captured by a hummock-hollow model (Figure 9), and that the presence of bias is independent of whether moss species niche partitioning is considered.

The SfM method is a potentially useful tool for examining both how morphometric properties of the surface which affect ecohydrological processes vary within a site. Moreover, information on microtopographic variability and structure from SfM-derived DEMs can be used to further examine the potential role of fine-scale microtopographic variability on biogeochemical processes within a modelling domain. The GMM is a simple way to include a more realistic description of height distributions within distributed peatland models (*e.g*. Dimitrov et al., 2010), or extend from the meso- to micro-scale (Sonnentag et al., 2008). Computationally, GMMs are a relatively efficient way of representing microtopographic variability, needing only two parameters per

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member of the GMM distribution. Conceptually, the GMM distribution can be applied directly in distributed peatland models to populate relative heights of individual cells. In the case of one-dimensional models, a GMM distribution can be used as a transfer function for any water table dependent processes, particularly in cases where the relation is non-linear. Alternatively, a small number of parameters from the PSD of microtopographic elevation (*e.g.* variance, Hurst exponent, and spatial scale of break point), be it from a DEM (Fig. S4) or transect (Fig. 2), can be used to generate 'synthetic' microtopography which includes spatial structure in elevation change rather than just the distribution.

CONCLUSIONS

The magnitude of variation in assessed morphometric properties within a site (randomly chosen plots) is commensurate with the range across sites (qualitative plots) where mean differences are comparatively small. With a small effect size, our results highlight the need for adequate spatial sampling in process-based studies of microform function, particularly when upscaling to the whole peatland or in order to make broader inferences regarding peatland microforms in general. The SfM technique provides very high resolution and accurate DEMs relatively quickly and easily. For studies which focus on processes which are correlated with microtopographic position, a DEM or DSM derived from ground- or drone-based imagery provides valuable information on microtopographic variability and structure which can help inform plot selection, be used for upscaling results, and quantify well defined morphometric and topographic variables to aid in study inter-comparisons. Conversely, height measurements (*e.g.* using a dGPS or other survey method) along a transect of at least 100 m with measurements taken at an interval of less than 1 m provides sufficient information to describe a number of peatland morphometric properties (*e.g.* hypsometry, roughness, fractal dimension, etc.).

Our study highlights the need to critically assess sampling approaches in peatland ecosystem science where we show that a strict hummock-hollow classification tends to under-sample intermediate topographic positions. While the discretization of peatland ecosystems into microtopographic units has facilitated the understanding of peatland processes in the context of species niche partitioning and their covariates such as water table position, we now have techniques to better quantify variability with relative ease. Consequently, techniques such as SfM enable us to consider peatland ecosystem processes as part of a continuum. We must recognize that our conceptualizations, while perhaps representing necessary simplifications, ought to be scrutinized to ensure that elements of peatland complexity are not omitted. By considering microtopography explicitly, we may be better able to understand how ecosystem complexity subsumed within current microtopographic classifications might represent an important unquantified confounding variable which limits our ability to adequately resolve and thus understand certain peatland processes.

DATA AVAILABILITY

The post-processed point clouds used to generate digital elevation models which were analysed in this study are available online at: [File are currently uploaded to a project

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Table 1: Summary information on sample locations and SfM reconstructions of microtopographic variation for target areas for randomly and qualitatively chosen plot locations within a site.

Location	Plot Name	Lat. (°N)	Lon. (°W)	Plot Area (m^2)	Number of Images Used	Point Cloud Density (m^{-2})
Random						
Nobel, ON[1]	Alpha	45.434	80.081	4.6	47	6.04×10^4
--	Beta	--	--	3.8	41	7.83×10^4
--	Gamma	--	--	4.1	44	6.68×10^4
--	Epsilon	--	--	5.2	53	8.38×10^4
--	Zeta	--	--	6.12	66	1.60×10^5
--	Eta	--	--	5.74	60	1.42×10^5
--	Iota	--	--	5.66	49	3.23×10^4
--	Kappa	--	--	5.53	66	1.77×10^5
--	Theta	--	--	5.48	59	1.38×10^5
--	Lambda	--	--	8.2	61	1.18×10^5
Qualitative						
Caribou Bog, MN[2]	Maine	44.83	68.75	10.1	79	3.75×10^4
James Bay, ON[3]	JamesBay	52.846	83.930	7.6	82	1.97×10^5
Ottawa, ON	Limerick	44.877	75.609	9.0	282	5.94×10^5
Puslinch, ON[4]	Puslinch	43.407	80.264	6.45	109	1.12×10^5
Rödmossen, SWE[5]	Sweden	60.013	-17.355	10.6	105	4.71×10^4
Seney, MI[6]	WET	46.190	86.019	7.7	135	1.12×10^5
Seney, MI[6]	INT	46.192	86.019	7.0	109	9.44×10^4
Seney, MI[6]	DRY	46.186	86.015	7.3	62	8.89×10^4
Nobel, ON[1]	Lambda	45.434	80.081	8.2	61	1.18×10^4

For detailed site information see the following studies: 1. Moore et al., (2019); 2. Kettridge et al. (2008); 3. Ulanowski and Branfireuen (2013); 4. Campbell et al. (1997); 5. Granath et al. (2009); 6. Moore et al. (2015).

Table 2: Estimated parameters for one-, two-, or three-member Gaussian mixture model (GMM) fit to DEM elevations. Results are presented for the GMM which minimizes AIC. Plots are separated into those chosen at random versus qualitatively at their respective site.

Location	Plot Name	1st distribution			2nd distribution			3rd distribution		
		Mean	SD	Scale	Mean	SD	Scale	Mean	SD	Scale
Random										
Nobel, ON	Alpha	0.11	0.03	0.23	0.20	0.03	0.36	0.28	0.06	0.41
--	Beta	0.13	0.04	0.37	0.18	0.03	0.53	0.29	0.04	0.10
--	Epsilon	0.07	0.02	0.06	0.18	0.05	0.30	0.31	0.05	0.64
--	Gamma	0.19	0.08	0.23	0.26	0.04	0.59	0.44	0.06	0.18
--	Zeta	0.11	0.03	1	—	—	—	—	—	—
--	Eta	0.13	0.04	0.82	0.25	0.05	0.18	—	—	—
--	Iota	0.11	0.03	0.24	0.19	0.06	0.76	—	—	—
--	Kappa	0.11	0.04	0.23	0.23	0.06	0.60	0.42	0.05	0.06
--	Theta	0.16	0.03	0.84	0.25	0.04	0.16	—	—	—
Qualitative										
Caribou Bog, ME	Maine	0.07	0.02	0.15	0.16	0.02	0.55	0.28	0.07	0.30
James Bay, ON	JamesBay	0.17	0.08	1	—	—	—	—	—	—
Ottawa, ON	Limerick	0.08	0.02	0.38	0.15	0.05	0.62			
Puslinch, ON	Puslinch	0.14	0.053	1	—	—	—	—	—	—
Rödmossen	Sweden	0.17	0.05	0.87	0.36	0.04	0.13	—	—	—
Seney, MI	WET	0.23	0.08	0.59	0.36	0.05	0.25	0.44	0.03	0.16
Seney, MI	INT	0.25	0.07	0.51	0.45	0.06	0.40	0.53	0.02	0.09
Seney, MI	DRY	0.08	0.03	0.05	0.21	0.04	0.45	0.34	0.05	0.50
Nobel, ON	Lambda	0.05	0.02	0.46	0.20	0.08	0.54	—	—	—

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LIST OF FIGURES:

Figure 1: Relation between standard deviation of microtopographic variation based on total sample area for the Red Earth Creek site based on fifty ~3.5 m^2 plots. The grey shaded area represents the 2.5 and 97.5 percentile of standard deviation from the Monte Carlo resampling procedure.

Figure 2: Absolute (solid lines) and cumulative (dashed lines) power spectral density of height along a 300 m transect for the Red Earth Creek, AB (red) and Nobel, ON (black) sites.

Figure 3: Relative frequency distribution of height in plots where a perceived representative hummock and adjacent hollow was subjectively chosen for a given site. Relative height distributions are shown for the entire plot (A) and for a hummock and hollow subplot (B) whose area corresponds to the size of a large flux measurement chamber. Elevations are referenced to the lowest point of the reconstructed surface and set to zero.

Figure 4: Relative frequency distribution of height in plots with randomly chosen locations within a site containing a perceived hummock and adjacent hollow. Relative height distributions are shown for the entire plot (A) and for a hummock and hollow subplot (B) whose area corresponds to the size of a large flux measurement chamber. Elevations are referenced to the lowest point of the reconstructed surface and set to zero.

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Figure 5: Radially averaged power spectral density for randomly– (left panel) and qualitatively– (right panel) chosen plots representing the change in elevation variability with length scale. The slope between the power spectral density and wavevector (2×π/wavelength) in log-log space corresponds with the Hurst exponent (H), where slope = -2(H+1); and is related to the fractal dimension as 3-H.

Figure 6: Weibull probability density function of slope derived from surface normal of a planar fit to elevation in a moving 0.03 m x 0.03 m window for all DEMs. Panels (a) and (b) separate the randomly and qualitatively chosen plots, respectively.

Figure 7: Variation in potential solar insolation relative to a flat surface based on aspect (a) and slope (b). Boxplots shows median and inter-quartile range, with outliers shown as dots. Insolation as a function of slope has been bin averaged per cardinal direction, where each point represents 100 data points. Slope and aspect data are for the Seney, WET plot.

Figure 8: Mean potential net photosynthesis (NPP) for three microtopographic classes (i.e. high-hummock, low-hummock, and lawn/hollow — see supplementary figure 1) derived from spatially explicit elevation data for random (a,c) and qualitatively chosen (b,d) plots. NPP-WC and WC-WTD relations are based on separate parameterization for each microtopography class (see supplementary figure 2).

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Figure 9: Difference in maximum potential net photosynthesis (NPP_{pot}) between models using the measured distribution of elevation over the entire SfM-derived DEM and the measured distribution within hummock-hollow subplots. NPP_{pot} is modelled using separate parameterization (Figure S2) for each microtopography class (a), as well as a uniform (low-hummock) parameterization across microtopography classes (b).

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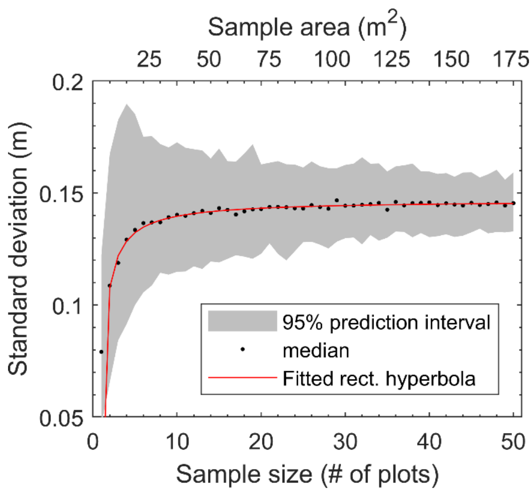
[Figure 1]



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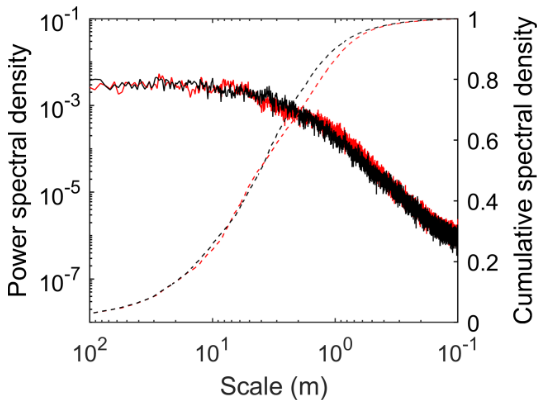
[Figure 2]



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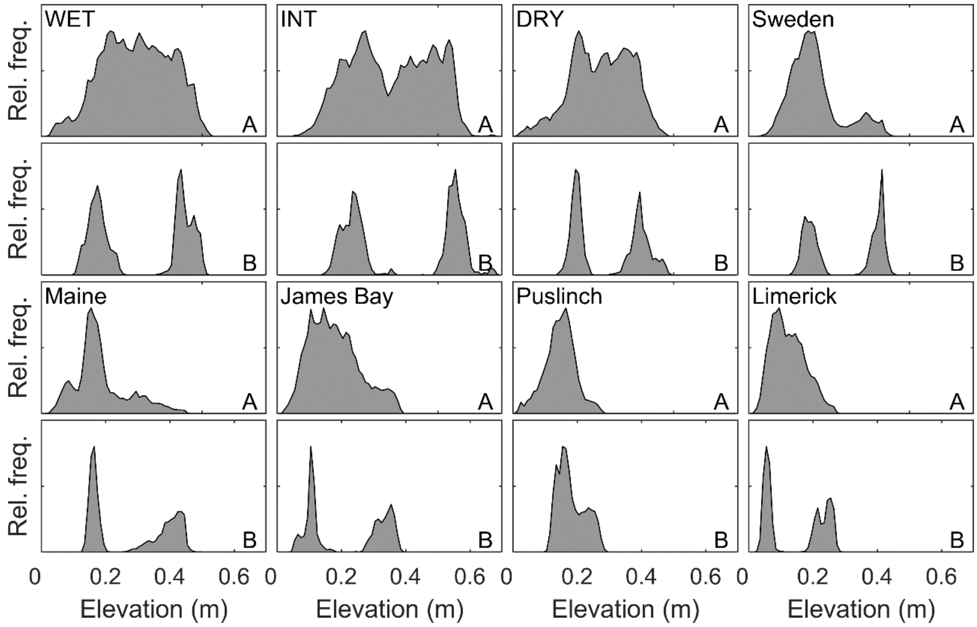
848 [Figure 3]



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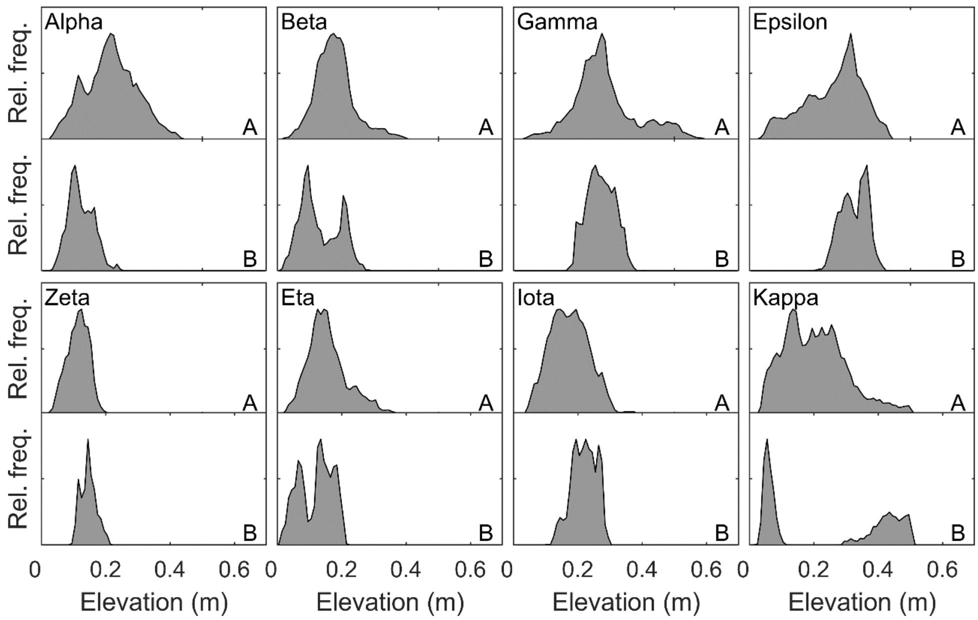
851 [Figure 4]



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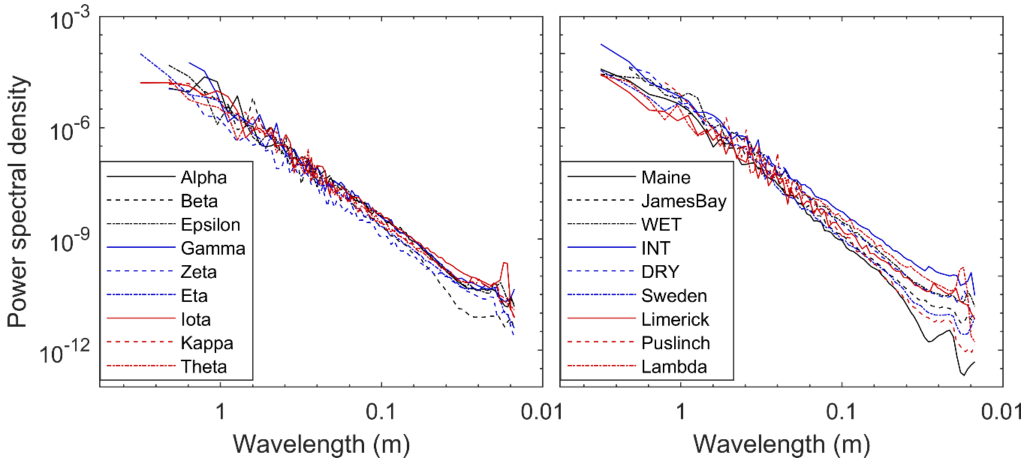
[Figure 5]



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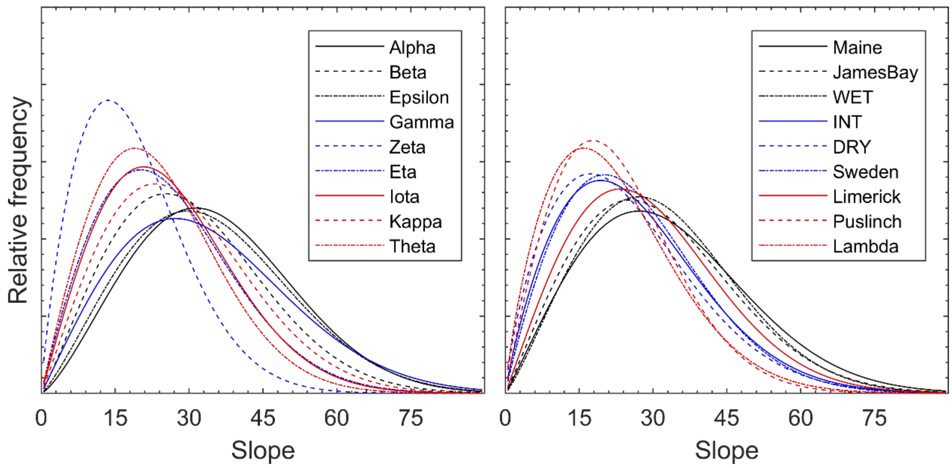
857 [Figure 6]



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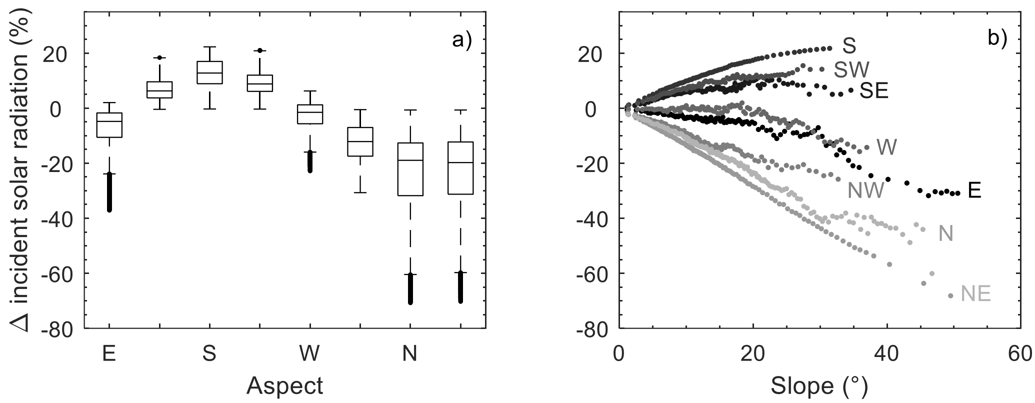
[Figure 7]



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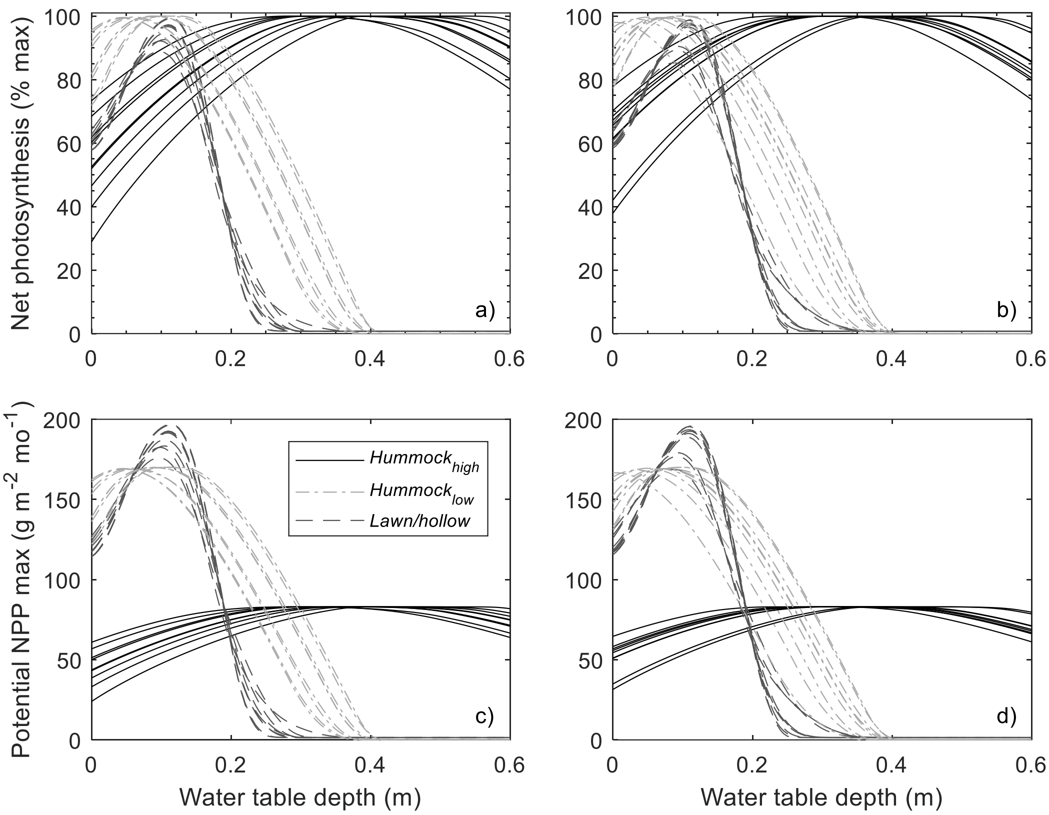
[Figure 8]



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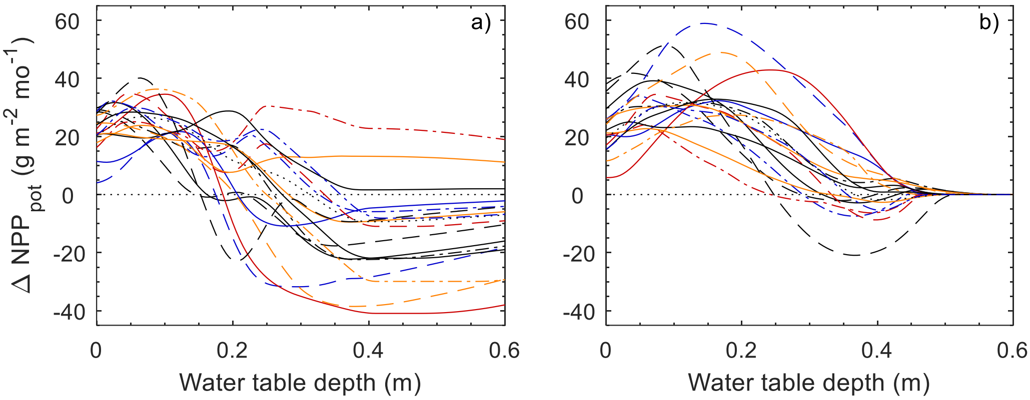
869 [Figure 9]



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