Microtopography is a fundamental organizing structure in black ash wetlands

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Abstract. All wetland ecosystems are controlled by water table and soil saturation dynamics, so any local scale deviation in soil elevation represents variability in this primary control. Wetland microtopography is the structured variability in soil elevation, and is typically categorized into a binary classification of local high points ("hummocks") and local low points ("hollows"). Although the influence of microtopography on vegetation composition and biogeochemical processes has received attention in wetlands around the globe, its role in forested wetlands is still poorly understood. We studied relationships among microtopography on understory vegetation communities, tree biomass, and soil chemistry in 10 black ash (*Fraxinus nigra* Marshall) wetlands in northern Minnesota, U.S.A. To do so, we combined a 1-cm resolution surface elevation model generated from terrestrial laser scanning (TLS) with co-located water table, vegetation, and soil measurements. We observed that microtopography was an important structural element across sites, where hummocks were loci of greater species richness, greater midstory and canopy basal area, and higher soil concentrations of chloride, phosphorus, and base cations. In contrast, hollows were associated with higher soil nitrate and sulfate concentrations. We also found that the effect of microtopography on vegetation and soils was greater at wetter sites than at drier sites, suggesting that distance to mean water table is a primary determinant of wetland biogeochemistry. These findings highlight clear controls of mictopography on vegetation and soil distributions, while also supporting the notion that microtopography arises from feedbacks that concentrate biomass, soil nutrients, and productivity on microsite highs, especially in otherwise wet conditions. We therefore conclude that microtopography is a fundamental organizing structure in black ash wetlands.

1 Introduction

Microtopography is a key component of wetland ecology, influencing a host of fundamental wetland processes. This results from the primacy of shallow water table and soil saturation dynamics in driving wetland dynamics (Rodriguez-Iturbe et al. 2007); any variability in soil elevation therefore represents coincident variability in this control (Wallis and Raulings 2011). For example, perhaps incredibly, experimental treatments have demonstrated that even soil surface variability of 2 cm can dramatically increase wetland vegetation germination, overall biomass, and species richness relative to flat soil surfaces

(Vivian-Smith 1997). This microtopographic effect on vegetation community structure is also borne out in real wetlands (though with elevation variation on the order of 10–50 cm), ranging from freshwater sedge meadows (Werner and Zedler 2002, Peach and Zedler 2006) to salt marshes (Windham et al. 1999, Fogel et al. 2004). Further, in many wetlands, primary productivity tends to increase with distance from the water table (Belyea and Clymo 2001), and high points are often loci of

35   greater primary productivity compared to low points (Strack et al. 2006, Sullivan et al. 2008). Microtopography also augments the spatial extent of soil redox gradients (Frei et al. 2012), which largely control wetland biogeochemical processing (DeLaune & Reddy 2008). However, by far, most studies on wetland microtopography have focused on herbaceous wetlands or northern bog systems dominated by *Sphagnum spp.* mosses, leaving open questions regarding the commonality of microtopographic influence on wetland processes in forested systems.

40   The relationship between wetland process and microtopography is thought to be reciprocal, where vegetation and biogeochemical interactions can in turn support expansion of microtopographic features (Eppinga et al. 2009). That is, wetland microtopography can result from feedbacks among hydrology, vegetation, and soil processes that induce soil elevation divergence into two modes: 1) a high elevation mode ("hummocks") and 2) a low elevation mode ("hollows") (Rietkerk et al. 2004, Eppinga et al. 2008, Heffernan et al. 2013). In previous work, we observed clear microtopographic patterns that we

45   propose arise from these types of ecohydrological feedbacks (Diamond et al. in review). If these microtopographic patterns are in fact a result of proposed ecohydrological feedbacks, we therefore expect there to be concordant microtopographic differences in vegetation and soils.

The primary hypothesized feedback that results in observed hummock hollow microtopography is the productivity-respiration feedback. Preferential colonization by plants on slightly elevated sites leads to local buildup of organic matter via primary

50   productivity and sediment accretion around roots, and further increased elevation (Gunnarsson and Rydin 1998, Pouliot et al. 2011). Increased elevation reduces anaerobic stress to plants and improves local redox conditions, leading to further increases in vegetative productivity. This productivity-elevation positive feedback is ultimately constrained and stabilized by increased decomposition rates of accumulated organic matter as hummocks become more aerobic (Belyea and Clymo 2001, Watts et al. 2010). Additional negative feedbacks to hummock growth can include increased instability in substrate and consequent erosion

55   (Larsen and Harvey 2010), or resource limitations (e.g., nutrients; Wetzel et al. 2005). The resulting microtopography often displays a clear structure, with observations of marked spatial patterns in open bog (Eppinga et al. 2009) and marsh systems (Casey et al. 2016), and potentially in swamp systems as well (Diamond et al. in review). If these feedbacks are operating in wetlands, the expectation is greater vegetation biomass and productivity on hummocks rather than hollows.

An additional feedback mechanism that can reinforce and maintain wetland microtopography is preferential hummock

60   evapoconcentration of nutrients. Greater productivity and thus greater evapotranspiration rates on hummocks compared to hollows drive a net flow of water and dissolved nutrients toward hummocks (Rietkerk et al. 2004, Wetzel et al. 2005, Eppinga et al. 2008, Eppinga et al. 2009). Nutrients are consequently rapidly cycled through vascular plant uptake and plant litter mineralization on the more aerobic hummocks (Malmer et al. 2003), leading to local nutrient concentration effects. This localized nutrient concentration purportedly leads to increased primary productivity, which leads to more nutrient

65 evapoconcentration, and so on (Ross et al. 2006). In other words, hummocks may harvest nutrients from hollows, concentrating them there. One clear prediction from this hypothesis is greater nutrient—and conservative water tracer—concentrations in hummock soil relative to hollow soil. To the best of our knowledge, this mechanism remains untested in forested wetlands with hummock-hollow terrain.

In this work, we assessed microtopographic influences on vegetation and soil chemistry in black ash (*Fraxinus nigra* Marshall)
70 wetlands in northern Minnesota, U.S.A. In a complimentary study (or Paper I), we observed evident hummock-hollow structure in these systems, but this microtopography was more pronounced at wetter sites. Here, we ask the question: to what extent do the integrated controls of water table regimes and microtopography determine spatial variation in vegetation and soil properties?

Specifically we tested the overall hypothesis that elevation relative to water table is the primary control on understory
75 composition, tree biomass, and soil chemistry, with the following specific predictions:

1) Understory richness and diversity will be: a) greater at drier sites compared to wetter sites, b) greater on hummocks than hollows, and c) positively correlated with elevation relative to water table.

2) Mid- and canopy-level basal area will be: a) greater at drier sites compared to wetter sites, b) greater on hummocks than hollows, and c) positively correlated with elevation relative to water table.

80 3) Soil nutrient and conservative tracer (chloride) concentrations will be: a) less variable on drier sites than wetter sites, b) greater on hummocks than hollows, and c) positively correlated with elevation relative to water table.

2 Methods

2.1 Site descriptions

To test our hypotheses, we investigated ten black ash wetlands of varying size (0.5–15.6 ha) and hydrogeomorphic landscape
85 position in northern Minnesota, U.S.A. (Figure 1). Black ash trees are unique among ash species because they often occur in nearly pure stands (i.e., over 90% canopy cover) in wetland conditions with very little regeneration of other tree species (Palik et al. 2012). In previous work (Diamont et al. in review) and as part of a larger project (D'Amato et al. 2018), we categorized and grouped each wetland by its hydrogeomorphic characteristics as follows: 1) depression sites ("D", n = 4) characterized by a convex, pool-type geometry with geographical isolation from other surface water bodies, 2) lowland sites ("L", n = 3)
90 characterized by flat, gently sloping topography, and 3) transition sites ("T", n = 3) characterized as flat, linear features between uplands and black spruce (*Picea mariana* Mill. Britton) bogs. Additional detail on site characteristics are provided in Diamond et al. (in review), but briefly, we believe that our sites are late successional or climax communities and have not been harvested for at least a century. Soils are primarily organic Histosols characterized by deep mucky peats underlain by silty clay mineral horizons, with depression and transition sites having deeper organic layers than lowland sites. We also previously characterized
95 hydrology at these sites using ground water wells and rain gages (Diamond et al. [in review]) and found that lowland sites were considerably drier on average than depression or transition sites (note hydroperiods in Figure 1), and exhibited much

more water table variability. Depression sites were typically wetter than transition sites and were more frequently inundated. Depression and transition sites also exhibited significantly more microtopographic structure than lowland sites, with over twice as much elevation variability on average.

100 2.2 Field measurements

We conducted field sampling campaigns to characterize vegetation and soil properties of our study systems. We then coupled these data to previously characterized water table and elevation data (Diamond et al., in review) to address our hypothesis and predictions. Elevation data were collected using high-resolution terrestrial laser scanning (TLS) measurements within three, 300 m² circular plots at each site. These data were then used to create1-cm digital elevation models and to delineate hummock

105 versus hollow features (see method details in Diamond et al., in review and Stovall et al. 2019). With these data and three-year records of daily water table levels, we were able to calculate a relative elevation above mean water table for each vegetation/soil sampling point, and categorize each sampling point as a hummock or hollow.

2.2.1 Understory composition

We characterized understory vegetation at each site to test the prediction that understory richness and diversity will be greater

110 on higher elevation features. To do so, we used a quasi-random walk sampling scheme within the plots (3 per site) previously used for elevation measurements. We term the study design quasi-random because we constrained the random sampling locations by quadrant, allowing us to sample each quadrant of a circular plot approximately equally (13 points per plot, Figure S1). At each sampling point, we used a 0.25 m² square quadrat to classify vascular and moss individuals to the species level, visually estimated their percent foliar cover, and recorded stem count (if possible) for vascular species. We chose a 0.25 m²

115 size quadrat as it corresponded to the smallest hummock areas that we observed in the field, and thus was on the scale of elevation variation at each site. Vegetation surveys occurred during July 2017, coinciding with peak vegetation presence. Species that we were unable to identify in the field were assigned a genus or standard unknown code and collected in a bag for later identification.

2.2.2 Tree biomass

120 To assess the prediction that midstory and canopy basal area will be greater on higher elevation features, we used data from two parts of a larger study investigating black ash wetlands. The first data source was stand-level metrics, including species, basal area and trees per hectare for both the midstory (2.5≤ diameter at breast height (DBH) ≤10 cm) and canopy level (>10 cm DBH), for each site. We calculated site-level basal area for each midstory and canopy species.

The second data source was plot-scale point clouds of forest structure from the aforementioned TLS campaign at six of the ten

125 sites (see Stovall et al. 2019). We estimated overstory DBH (i.e., > 2.5 cm) from these TLS point clouds with the SimpleTree algorithm implemented in CompuTree (Hackenberg et al. 2015). We were only able to apply the algorithm on a fraction of our scanned areas (approximately 300 m² at each of the six sites) due to resolution issues and understory noise that precluded DBH

analysis. The SimpleTree algorithm models trees as cylinders by segmenting trees using an iterative nearest neighbor approach that moves vertically from an initial seed point along the stem while expanding in area with increasing crown size. The best least squares cylinder at approximately 1.3 m above ground provided estimates of DBH. Following DBH analysis, we matched each processed tree with an elevation value associated with surface models from our TLS analysis (Stovall et al. 2019).

2.2.3 Soil chemistry

To assess the prediction that soil chemistry heterogeneity will covary with elevation variability, we cored soil at a subsample of the 390 sampling points in the previously described quasi-random walk sampling design. We determined the subsampling points prior to site arrival with the intention to sample all points at a minimum of one plot (13 points) per site. We sampled one plot at sites D2, D3, D4, and T3, but two plots at the remaining sites for a total of 208 sampling points out of our original 390. We first removed the top layer of moss and litter, and used a 15-cm beveled and serrated soil knife to extract our soil samples to a depth of 10 cm.

We air-dried soil samples over 2 weeks, removed visible roots (typically greater than 2 mm in diameter), and hand-ground, mixed, and sieved soils to pass a 2 mm mesh to create a representative sample of the 10 cm soil increment. Total carbon and nitrogen concentrations were determined with dry combustion on 0.25 g subsamples with a CN Elemental Analyzer (Elementar Analysensysteme GmbH vario Max; Langenselbold, Germany). For anions and cations, we used a modified water extraction method (Jones and Willett 2006). Nitrate (NO_3^-) and phosphate (PO_4^{3-}) were analyzed colorimetrically with a segmented flow analyzer (SEAL AA3; SEAL Analytical, Mequon, WI) using equipment methods G-200-97 and G-175-96, respectively. Chloride (Cl^-), sulfate (SO_4^{2-}), calcium (Ca^{2+}), and magnesium (Mg^{2+}) were analyzed with ion chromatography (Standard Methods 4110, Dionex ICS 3000; Thermo Fisher Scientific, Waltham, MA).

2.3 Data analysis

Across our different environmental variables, we took the following general approach: 1) test for site-scale differences focusing on site hydrologic metrics as predicting variables, 2) test for microsite-scale (hummock vs. hollow) categorical differences, and 3) test for point-scale influences of elevation relative to water table.

2.3.1 Understory composition

To test our prediction that site hydrology is a strong control on understory composition, we regressed mean (n=3 plots) site-level richness and diversity with site-level hydrology metrics using simple linear regression.

To assess categorical differences in vegetation composition among both sites and microsites (i.e., hummock vs. hollow), we first classified understory vegetation in ordination space using nonmetric multi-dimensional scaling (NMDS). Prior to analysis, we removed rare species (<1% presence overall) from the understory community matrix (McCune and Grace 2002). We then aggregated point-scale measurements to site-level hummock and hollow values by averaging species' percent cover for hummocks and hollows within each site. We used *metaMDS* function from the *vegan* package (Oksanen et al. 2018) in the R

statistical software (R Core Team 2018) to conduct the ordination analyses, and tested for understory community differences

160 among sites and microsites using a multivariate permutational analysis of variance (PerMANOVA) with the *adonis* function from the same package.

We also evaluated species fidelity and association to particular sites and microsites (hummocks versus hollows). Indicator species analysis was conducted using the function *multipatt* from the *indicspecies* R package (De Caceres and Legendre 2009). This analysis generates an indicator value index (IV) for each species within each category (e.g., site or microsite). We used

165 the function standard 1,000 Monte Carlo simulations with permutationally randomized data to test the null hypothesis that the observed species IV is not significantly greater than a value produced with randomized data. To remove the influence of rare species on the indicator analysis, we limited the candidate species to those that were present in more than 10% of its identified microsite or site category. Using this reduced sample, we identified species or species combinations that had a specificity of at least 0.80 and a sensitivity of at least 0.20. We based these thresholds on observations of clear delineations in the indicator

170 species output and from guidance in package materials (Cáceres 2013).

To test categorical differences in richness between hummocks and hollows, we calculated Welch's two sample t-tests on richness between hummocks and hollows for each site. We additionally calculated hummock-hollow Bray-Curtis community dissimilarity indices using the *vegdist* function. This dissimilarity index falls between 0 and 1, where 1 indicates complete dissimilarity and 0 indicates identical communities. The t-test allowed us to test our prediction that hummocks were more

175 diverse than hollows within a site, and the dissimilarity index allowed us to further determine how different the vegetation communities were. To examine differences in moss and vascular plant communities, we conducted this analysis for both 1) moss and vascular plants separately, and 2) moss and vascular plants combined.

Lastly, we analyzed within-site relationships between point-scale understory richness and point-scale elevation relative to mean water table using a generalized linear mixed effect model (GLMM). We conducted GLMM analysis with the *lme4* R

180 package (Bates et al. 2015) using suggested methods for Poisson distributions from Bolker et al. (2009). We compared the following richness-elevation models and chose the best model based on a combination of the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC): 1) random site-level intercept, 2) random site-level intercept and slope, 3) random site-level intercept and slope with plots nested in sites, 4) inclusion of "moss" binary covariate (1 for moss, 0 for not moss) with random site-level intercept, 5) inclusion of "moss" binary covariate with random site-level intercept and slope.

185 **2.3.2 Tree biomass**

We tested our hypothesis that site-scale hydrology influences tree biomass by regressing site-scale (midstory + canopy) basal area with site-scale hydrology. To determine categorical differences in tree biomass between hummocks and hollows, we used individual tree DBH data (from the TLS scan data) and summed the cumulative basal area between hummocks and hollows. We then estimated a fraction of trees at each site that occupied hummocks relative to hollows.

190 Finally, we analyzed within-site relationships between point-scale DBH (from the TLS data) and point-scale elevations relative to water table. To do so, we used a linear mixed effect model to regress within-site individual tree DBH versus estimated tree

base elevation from digital elevation models derived from TLS point clouds, which serves as a proxy for tree distance from the mean water table. The linear mixed effect model used allowed for uncorrelated random slopes and intercepts across sites.

2.3.3 Soil chemistry

195   To test the prediction that there would be less variation in soil chemistry at drier sites compared to wetter sites, we conducted standard ANOVA and post-hoc Tukey's Honestly Significant Difference t-test on soil extraction chemistry. We first examined differences among hydrogeomorphic categories, and then tested differences among individual sites. To assess soil chemistry variation among groups, we conducted a Levene test on hydrogeomorphic group variances for each analyte.

To test the overall importance of microsite influence on soil extraction chemistry, we examined differences between hummocks

200   and hollows, averaged across sites. Across-site comparison of hummocks and hollows (as opposed to within-site comparison) increased the power of our inference because, due to our random sampling, some sites did not have equal measurements of hummocks and hollows. Prior to averaging across sites, we normalized soil extraction concentrations to site-level average concentration for each analyte. This allowed us to compare relative differences between hummocks and hollows across sites, even when absolute concentrations differed among sites. We then used these normalized concentrations to compare hummocks

205   and hollows across sites using Welch's two-sample t-tests. We also used a simple ratio of hollow to hummock normalized concentrations to contextualize differences between microsites, regardless of among site variability in absolute concentrations. Finally, we regressed point-scale soil analyte concentrations versus local elevation relative to water table. We used a similar method to our richness-elevation analysis, where we chose a best-fit linear mixed-effect model (using the *lme4* R package, Bates et al. 2015) based on the following possibilities: 1) random site-level intercept, 2) random site-level intercept and slope,

210   and 3) random site level intercept and slope with uncorrelated random effects for slope and intercept.

3 Results

3.1 Understory composition

Across all sites (30 plots), we observed 95 distinct understory species: nine moss species, 85 vascular species, and one liverwort species. The most common vascular species were sedges of the *Carex* genus, grasses of the *Glyceria* genus, *Impatiens capensis*

215   Meerb., *Aster lateriflorus* (L.) Britton, and *Caltha palustris* (L.). The most common mosses were *Calliergon cordifolium* (Hedw.) Kindb., *Thuidium delicatulum* (Hedw.) Schimp., and *Rhizomnium magnifolium* (Horik.) T. Kop.

We observed a clear influence of site-scale hydrology on site-scale community composition. Median daily water table was a linear predictor of both richness (p = 0.003) and diversity (p<0.001) for understory vegetation (Figure 2). Mean water table, to a lesser extent, also explained similar amounts of site-level variance in richness (R^2=0.25) or diversity (R^2=0.29). Lowland

220   sites and transition sites tended to clump together in this relationship, but depression sites exhibited far more intra- and across-site variability in richness and hydrology.

Our NMDS model demonstrated clear ordinal separation of our understory community matrix between hummocks and hollows across sites (p = 0.002) and between hummocks and hollows within sites (p=0.001; Figure 3). Hummocks and hollows were more similar for lowland sites, particularly L1 and L3, compared to depression and transition sites (Figure 3).

225 Our indicator species analysis revealed that four moss species (*Climacium dendroides* [Hedw.] F. Weber & D. Mohr*, Funaria hygrometrica* Hedw.*, Rhizomnium magnifolium* [Horik.] T. Kop., and *Thuidium delicatulum* [Hedw.] Schimp.) were the most distinguishing species of hummocks across sites (Table 1). The best hummock indicator species was *Climacium dendroides* (Hedw.) F. Weber & D. Mohr with it having an 87% chance of indicating that a sampling point is on a hummock (specificity), and having a 59% chance that it will be present at a point, given that the point is a hummock (sensitivity). Similarly, for

230 hollows, a moss species (*Calliergon cordifolium* [Hedw.] Kindb.) was the best indicator species, although common duckweed (*Lemna minor* L.) had a nearly perfect (99%) chance of indicating that a sampling point is a hollow. When we removed the criteria for across-site species presence (>10%), we observed approximately an order of magnitude more candidate indicator species for hummocks than for hollows, with most species having very high specificity (Table S1).

We also observed distinct differences in richness between hummock and hollow microsites. Hummocks were nearly always

235 locations of both greater moss species richness and greater understory vascular plant species richness (Figure 4). This pattern was identical when also combining both moss and vascular plants (Figure S2). We found the greatest hummock-hollow differences in understory species richness in depression sites (mean water table = 0.01 m), with less difference in transition sites (mean water table = -0.04 m) and lowland sites (mean water table = -0.32 m). Bray-Curtis dissimilarities for both mosses and understory vascular plants were greatest for depression and transition sites (BC values in Figure 4).

240 At the point scale, we found that the best-fit GLMM model for richness *versus* elevation relative to mean water table was one with site-level random effects for both intercept and slope, as well as a dummy variable for moss (contrasted with vascular understory vegetation). Although random site effects modulated the richness-elevation relationship, all site slopes were significantly greater than zero (Table 2, and see site-specific fits in Figure S3), implying positive association between richness and elevation across sites. Importantly, we found that drier lowland sites had lower overall slopes (i.e., more negative random

245 slope effects) compared to wetter sites (Figure S3a), indicating less rapid increases in richness with elevation at dry sites. Overall, we observed that moss richness increased approximately 22% less than vascular plant richness with increasing elevation.

To visualize more clearly the results from this point-scale analysis, we plotted GLMM-predicted richness values as a function of relative elevation above water table without considering site effects (Figure 5). Both moss and vascular plants exhibited

250 only one or two species when at sampling points near or below the mean water table, but species counts increased rapidly beginning near the mean water table, notably for vascular plants.

3.2 Tree biomass

There was no strong relationship (p < 0.05) between basal area and hydrologic metrics for either the canopy or midstory level, at the site-scale. Median water table was the best predictor of basal area out of the metrics tested (Figure 6). We observed that

255   T1 was a major outlier in the midstory basal area-elevation relationship (Figure 6), but its omission did not result in a significant fit (p = 0.137).

Using our TLS-derived DBH data at a subset of sites, we further assessed differences between hummocks and hollows. Total basal area was disproportionately (by two orders of magnitude) associated with hummocks at the wettest sites (D1, D3, D4, and T1), but the relative lack of hummocks at the drier sites (L1 and L2) inverted this relationship (Table 3). Further, across

260   all size classes, we found that trees in the wettest sites (depression and transition) occupied hummocks 83–94% of the time (Figure 7). We also observed size-dependent association with hummocks, especially for sites D1, D3, and T1, where larger trees (i.e., trees with DBH>20 cm) were 2–3x more likely to exist on hummocks compared to hollows (Figure 7). This is in contrast to drier lowland sites, where trees do not prefer hummocks to hollows, at least not in our subsampled areas.

Point-scale linear mixed effect models of DBH *versus* relative elevation did not reveal any significant (p>0.05) trends see

265   Figure S4). We note here, however, that the matching procedures to tie digital elevation models from TLS to tree base height elevations likely has high uncertainty.

3.3 Soil chemistry

There were clear differences in soil chemistry among site hydrogeomorphic groups and among individual sites for all analytes (p < 0.01, Figure 8). Depression sites had the lowest soil base cation concentrations (Ca^{2+} and Mg^{2+}), followed by lowland and

270   then transition sites. Depression sites and transition sites had considerably less $NO_3^-–N$ than lowland sites, but somewhat more $PO_4^{3-}–P$, and clearly higher C:N. However, we observed more variability among sites than among hydrogeomorphic site groupings. There was some indication that drier lowland sites exhibited less variability in soil chemistry than wetter transition and depression sites, but this trend was not consistent across analytes (Table S3). In fact, we observed significantly greater variance in %C, $NO_3^-–N$, and SO_4^{2-} in drier lowland sites than in wetter sites (Table S3).

275   We also found differences (p<0.05) in soil chemistry between hummocks and hollows for seven out of nine analytes (Figure 9). Except for $NO_3^-–N$, %N, and SO_4^{2-}, hummocks had higher analyte concentrations than hollows. Relative across-site hummock-hollow differences in mean concentrations ranged from -27% for $NO_3^-–N$ to +23% for Cl^-. Although some sites varied in their relative differences between hummock and hollow analyte concentrations (Table S4), broad patterns were still discernible wherein hummocks were generally loci of higher Ca^{2+}, Cl^-, Mg^{2+}, $PO_4^{3-}–P$, C, and C:N (though only by 4%) relative

280   to hollows.

We found linear relationships (p<0.05) between concentration and relative elevation above water table at the sample point scale for six out of nine soil chemistry analytes. The linear mixed effect models were fit with a restricted maximum likelihood estimation with uncorrelated random intercepts and slopes; standardized residuals were normally distributed about zero (Table S5). Random site effects modulated the overall concentration-elevation relationship, implying large variability in responses

285   (direction and magnitude) among sites. We did not observe clear patterns in random effects relating to sites or site hydrogeomorphic groupings (Figure S5), indicating no obvious control of hydrology or setting on the strength of these relationships. However, relationships for $PO_4^{3-}-P$ and Cl^- were similar in wetter depression and transition sites in contrast to

drier lowland sites, which did not have as steeply positive linear relationships with elevation. Results from this point-scale linear fitting align with categorical results from hummock and hollow analysis. For illustration, Figure 10 presents results

290 using predicted concentrations from the model fit, without taking into account site level random effects. Some analytes varied much more among sites in the concentration-elevation relationship than others, leading to large variability in some best-fit lines (e.g., Ca^{2+}, NO^{3-}–N), but most analyte concentrations had clear linear relationships with elevation (Figure 10).

4 Discussion

Using integrated measures of fine-scale topography, water table regimes, and vegetation and soil attributes, our work highlights

295 the primary control of elevation and microsite position in black ash wetlands. Findings demonstrate these controls on vegetation distributions, tree biomass, and soil chemistry at both site- and within-site scales, driven by distance to water table and thus decreased anaerobic stress at drier sites and on elevated hummocks at wetter sites. We suggest that these results support biotically driven feedback models of hummock development and maintenance, where increased vegetative productivity at higher microsites leads to increased microsite elevation that is eventually limited by increased soil

300 decomposition in drier conditions.

4.1 Controls on understory composition

Site-scale hydrologic behavior of black ash wetlands is a major determinant of site-scale understory richness and diversity. We found that even a simple hydrologic metric like mean water table could explain 30% of inter-site understory richness variability (Figure 2). For example, our wettest site had half of the species richness as our driest site, and was two-thirds as

305 diverse. Numerous other studies have observed the influence of hydrologic regime on site-scale species richness (e.g., van der Valk et al. 1994, Nielsen and Chick 1997, Nielsen et al. 2013), but most have been based on treatment studies of expected hydrologic change or in riparian systems dominated by flood pulses. This study demonstrates that black ash wetlands, which are abundant ecosystems in the Great Lakes region (e.g., they cover approximately 5% of forested land in Minnesota, Michigan, and Wisconsin; USDA Forest Service 2016), may exhibit similar hydrology-richness responses as other studied wetland

310 systems, and further solidifies hydrology as the primary determinant of understory species distributions in wetlands.

Despite clear broad site-scale controls on understory richness, we also observed a dominant microsite-scale influence on community composition. Our NMDS analysis indicated that hummocks and hollows separated along community structure, but also that the degree of this separation was highly site dependent. For example, drier lowland sites (especially L1 and L3) had considerably less understory community variation between microsites than the wetter depression or transition sites, supporting

315 the notion that distinct and functionally important microsite states arise in response to wet conditions. Likewise, Bray-Curtis dissimilatory index testing at our wettest sites indicated that understory vegetation communities between hummocks and hollows were highly dissimilar (i.e., BC closer to 1), with little overlap in species.

Assessment of species fidelity to specific microsites provided further support that hummocks and hollows are discrete ecosystem states (*cf.* Watts et al. 2010). Using indicator species analysis, we found that mosses were the most discriminative
320   understory growth form for parsing hummocks from hollows (Table 2). This finding garners more evidence for the contention that hummocks provide hydrologic stress relief for vegetation, as moss species are highly sensitive to soil moisture regimes (i.e., they are poikilohydric; Busby et al. 1978, Proctor 1990). We suggest that the presence of microtopography increases overall site richness, because some species show clear affinity for microsite type, a finding supported by similar studies of richness and microsite variability (Beatty 1984, Vivian-Smith, 1997; Bruland and Richardson, 2005). Therefore,
325   microtopography greatly expands potential hydrologic and associated habitat niches.

In addition to different community structure between hummocks and hollows, we found strong evidence for our prediction that hummocks support a higher number and greater diversity of understory vegetation species than hollows. In our systems, hummocks were loci for approximately 60% of total sampled species per site, with larger richness differences between hummocks and hollows in wetter sites. This finding aligns with field observations of visually distinct breaks between the
330   relatively bare organic surface of hollows and the verdant structure of hummocks. We suggest that greater understory richness on hummocks may imply greater understory GPP vis-à-vis the richness-productivity relationship (Olde Venterink et al. 2003, van Ruijven and Berendse 2005), lending credence to productivity-elevation feedback. Adding further support, modeling demonstrated clear increases in richness with elevation, where the slope of this relationship was greatest in the wettest sites (Figure S3). Perhaps these are not surprising results given that distance to water table may be the most important control on
335   wetland community structure (Bubier et al. 2006, Økland et al. 2008, Malhotra et al. 2016). Our results add black ash swamps to a number of wetland ecosystems with similar understory microtopography-richness structure, including salt marshes (Stribling et al. 2006), alluvial swamps (Bledsoe and Shear 2000), tidal freshwater swamps (Dubertstein and Connor 2009, Courtwright and Findlay 2011), tropical swamps (Koponen et al. 2004), boreal swamps (Økland et al. 2008), and northern sedge meadows (Peach and Zedler 2006). The concordance of similar observations across systems substantiates hypotheses
340   that hummocks play a critical role in supporting wetland plant diversity.

Lastly, we note that while hollows have less species on average than hummocks, they are not devoid of understory productivity. At some sites, we observed large swaths of *Carex spp.* in the hollow understory, whose thick stems and spanning rhizomes would have contributed to high primary productivity. Follow-up studies could focus on this aspect of hummock-hollow differences in these and other systems.

345   **4.2 Controls on tree biomass**

Although not a significant direct association, we found indirect evidence that links site-scale hydrology to tree basal area. The driest sites (lowland sites) had the greatest basal area, supporting observations from floodplain wetlands where sites that received less inundation were more productive and had greater basal area than intermediately or regularly inundated sites (Megonigal et al. 1997). However, other drivers may be also influence these differences, including variability in disturbance
350   regime or pedological characteristics that were outside the scope of this study.

Our findings also highlight local hydrologic influences and demonstrate that trees at wetter sites almost exclusively occupy raised hummocks; almost the entirety of live basal area corresponded directly to elevated hummock structures in the wettest black ash systems. A recent study of canopy competition in black ash wetlands acknowledged this importance of microsite variation in explaining lack of predicted competition and subsequent tree size distributions among black ash trees (Looney et al. 2016). In contrast to our findings at the site level, we did not find support for our prediction that basal area would correlate with tree base elevation within sites. However, this may not be surprising for three primary reasons: 1) black ash trees are extremely slow growing and there can be very little discernible variability in DBH across trees of different age classes (D'Amato et al. 2018, Looney et al. 2018), 2) hummock heights (and thus tree base elevation), while centered around some site mean, exhibit variation within a site, leading to a range of elevations supporting trees with similar DBH, and 3) tree base elevations were extremely difficult to ascertain using our TLS matching method, leading to high uncertainty in elevation measurements. Perhaps in wetter black ash systems, it is merely the fact that trees are alive (and on hummocks) that is important. In other words, trees that establish and survive eventually reach similar sizes based on resource constraints or growth patterns, but it is more common that they establish and survive on hummocks at the wettest sites.

4.3 Controls on soil chemistry

We observed clear and significant differences in soil chemistry among sites that could broadly be attributed to site-scale hydrology and site hydrogeomorphic category. For example, the drier lowland sites had an order of magnitude greater NO_3^-–N soil concentrations than wetter depression or transition sites (Figure 8) despite having nearly equal soil total N (CV = 0.1). We suggest that water table regimes of our sites correspond directly with expected water-table- and soil-specific shifts in N-processing. Where water tables are deeper below ground surface (e.g., by 30 cm or more), net nitrification dominates and where water tables are shallower (e.g., within 10 cm of the surface), net ammonification dominates (Hefting et al. 2003). Specific to our prediction, we found some support that within site variation in analytes (specifically for Cl^-, PO_4^{3-}-P, C:N, %N, and Mg^{2+}) was greater at wetter sites, suggestive of more variable redox conditions and biogeochemical processing.

We found some support that hummocks can act as evapo-concentrators of mobile soil chemical pools. We observed this hummock-hollow soil chemistry separation at all sites, regardless of variability in absolute concentrations among sites. The strongest evidence for this comes from the relatively high level of the conservative tracer, chloride, in hummocks relative to hollows (23% greater on average). We can surmise few biogeochemical mechanisms, if any, apart from preferential hydraulic flow from that would result in such a locally disproportionate concentration of chloride. Chloride is commonly used across scales and systems as a hydrologic tracer to evaluate hydrologic storage and transport processes (Kirchner 2000, Kirchner et al. 2010), and its concentration in terrestrial waters is widely attributed to evaporation effects (e.g., Thorslund et al. 2018). Further, we believe that our chloride values may be a conservative estimate of differences between hummocks and hollows, because our sampling occurred after leaf-off and approximately one week after a series of rainfall events, the combination of which likely flushed solutes from hummocks towards hollows. As a reference, these systems have on average an order of magnitude higher chloride concentrations than rainfall in the region (<0.1 mg L^{-1}, NADP 2019), indicating that evaporation is

major component of their water cycle–a prerequisite for the evapoconcentration hypothesis. In northern bog wetlands,
385   encroachment or presence of woody vascular plants can dramatically increase evapotranspiration losses (Takagi et al. 1999,
Frankl and Schmeidl 2000) aligning with results here suggesting presence of black ash trees and their associated understory
hummock species may be significant drivers of evapotranspiration on hummocks.

The significantly greater amounts of soil phosphorus on hummocks indicates directional concentration from hollows to
hummocks. However, in addition to evapoconcentration, the mechanisms of increased nutrient availability in hummocks
390   relative to hollows may be also attributed to accumulation of debris and litter (Resler and Stine 2009), and/or higher turnover
and cycling rates (Wetzel et al. 2005). Even mycorrhizal activity is greater in hummocks than hollows, which may be important
in P acquisition from ferric-bound particles (Cantelmo and Ehrenfeld 1999). Eppinga et al. (2008) were the first to empirically
test and provide evidence for hummock evapoconcentration of limiting nutrients, which had previously been suggested as a
mechanism inducing greater phosphorus on tree islands in the Everglades, FL (Wetzel et al. 2005, Ross et al. 2006). Although
395   we do not have direct evidence that 1) black ash wetlands are phosphorus limited or 2) phosphorus is driven into hummocks
via evapotranspiration gradients (e.g., as opposed to local resource recycling only), our phosphorus and chloride results
comport with modeled hummock-hollow system responses under the evapoconcentration assumption (e.g., Eppinga et al. 2008,
Ross et al. 2006). Hence, while we cannot definitively reject other mechanisms of nutrient enhancement on hummocks, this
study adds further support for the evapoconcentration hypothesis. Overall, our finding of greater phosphorus on hummocks
400   aligns with numerous studies where hummocks are consistently found to be zones of greater phosphorus concentrations than
hollows (Jones et al. 1996, Wetzel et al. 2005, Eppinga et al. 2008).

Hummocks were also enriched in base cations compared to hollows. We postulate that this base cation enrichment effect may
be a result of preferential uptake and rapid nutrient recycling by black ash trees located on hummocks. Black ash trees are
known to exhibit considerably higher Ca^{2+} and Mg^{2+} in live tissues than neighboring species at the same site, or in other nearby
405   ecosystems (Reiners and Reiners 1970), indicating preferential uptake of these nutrients relative to other species.

In contrast, we observed that hummocks were sites of lower nitrate concentrations. These findings are in contrast to most
microtopographic studies, where hummocks often have higher nitrate than hollows (e.g., Bruland and Richardson 2005).
However, Courtwright and Findlay (2011) also observed hollow nitrate enrichment, which they attributed to biologically
mediated effects such as enhanced uptake on hummocks and coupled nitrification-denitrification (Courtwright and Findlay
410   2011). In this model, high nitrification rates on aerobic hummocks (Noe et al. 2013) may result in diffusive transport of mobile
nitrate to hollows, where it is subsequently denitrified under hydrologically induced anaerobic conditions (Wolf et al. 2011).
It seems likely that coupled nitrification-denitrification resulting from distinct hummock-hollow microtopography in wetter
transition and depression sites limits nitrate buildup in these systems, in contrast to the drier sites with less topographic relief
(see Diamond et al. [in review]) where we observed lower concentrations. However, the unexpected NO_3^-–N enrichment on
415   hollows in this study may simply be due to sampling after leaf fall, which may have transferred NO_3^-–N to hollows, or perhaps
because soils were recently aerobic, allowing for nitrification to proceed in hollows.

Results for SO_4^{2-} were also in contrast to what we expected. We surmised that oxidized SO_4^{2-} would be greater in aerobic hummocks than in more anaerobic hollows. However, we observed consistently less soil SO_4^{2-} in hummocks than in hollows, which we tentatively attribute to either diffusive transport from hummocks to hollows or assimilatory sulfate reduction in

420   hummocks. Our results also contrast with observations in saltwater systems, where vegetated zones are areas of increased SO_4^{2-} due to root-zone oxygenation of reduced toxic suflides (Hsieh and Yang 1997, Madureira et al 1997, Ferreira et al. 2007). Clearly, we are missing a piece of the puzzle with respect to sulfur cycling in hummock-hollow systems, because our results are also in stark opposition to expected results from coupled sulfur-hydrology-microtopography modeling exercises for freshwater systems (Frei et al. 2012).

425   We found some evidence for our hypothesis that relative elevation, as opposed to simply microsite position, was a major control on soil chemical pools in black ash wetlands. Unsurprisingly, all analyte-elevation trends directly corresponded with categorical hummock-hollow trends, both in direction and in strength. We also observed some indication that Cl^- and PO_4^{3-}-P exhibited more similar and more positive relationships with elevation in wetter sites compared to drier sites (Figure S5), potentially indicating enhanced evapoconcentration at wetter sites. Whereas most other studies examining relative elevation

430   effects on soil chemistry use sample depth to water table as their elevation measurement (e.g., Bubier et al. 2006, Stribling et al. 2006), our study took a combined approach where we monitored water table regimes at one location, but measured relative surface elevation in high-resolution at all points. Hence, a major underlying assumption in our approach is that the water table is flat across our study area, and that capillary fringe and/or hydraulic redistribution effects are negligible in comparison to water table fluctuations. We concede that this approach may be inappropriate for other systems with less organic soils or more

435   undulating terrain, but note that it appeared to provide reasonable and practical results in our case.

Our work here provides a strong foundation for viewing microtopography as a primary control on vegetation and soil distributions in black ash wetlands, while also suggesting that it arises from biogeomorphic feedback processes that concentrate biomass and nutrients into hummock structures. Future studies could explore differences in evapotranspiration rates between hummocks and hollows for further elucidation of evapoconcentration differences. Inferences along these lines would also be

440   bolstered by leaf tissue measurements on hummocks and hollows to test for limiting nutrients. We also suggest investigating, at the microsite-level, additional species of nitrogen (e.g., ammonium), sulfur (e.g., sulfide), and other important redox compounds (e.g., iron) and biogeochemical processes (e.g., denitrification) that may explain observed trends in soil chemistry.

5 Conclusions

This work provides support for ecosystem engineering by vegetation in swamps, where vegetation capitalizes on and amplifies

445   small changes in surface elevation. The result of this engineering is hummock-hollow microtopography, where hummocks and hollows are distinct, self-organized ecosystem states. Here we used the case study of black ash wetlands to illustrate this possibility. Importantly, we found that black ash hummocks are characterized by increased local species richness, biomass, and nutrient availability, all of which are likely due to reduced hydrologic stress. We conclude the following: 1) vegetation,

and in particular black ash trees, occupy and reinforce hummock structure, and 2) hummock and hollow microtopography
450   yields predictable patterns of understory richness, biomass, and soil chemistry. Therefore, we infer that microtopography is a
fundamental organizing structure of many black ash wetlands, particularly those that undergo wetter conditions and shallow
water tables.

Code and data availability

All data and code for analysis are available from the authors by request.

455   **Author contribution**

JSD, DLM, and RAS designed the study, and JSD carried it out. JSD conducted all analyses with input from all authors. JSD
prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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Table 1 Indicator species analysis for hummocks and hollows across sites. Species indicator values (IV) range from 0–1, and are the product of specificity and sensitivity conditional probabilities. Specificity is the conditional probability that the sampling point belongs to a particular microsite, given the fact that a particular species was found there, and sensitivity is the conditional probability of finding a particular species in a sampling point, given that the sampling point belongs to a particular microsite.

Microsite	Species	Specificity	Sensitivity	IV
Hummock	*Climacium dendroides* (Hedw.) F.Weber & D. Mohr	0.87	0.59	0.51
	Funaria hygrometrica Hedw.+ *Rhizomnium magnifolium* (Horik.) T.Kop.	0.85	0.27	0.23
	Rhizomnium magnifolium (Horik.) T.Kop.+ *Thuidium delicatulum* (Hedw.) Schimp	0.90	0.24	0.21
Hollow	*Calliergon cordifolium* (Hedw.) Kindb.	0.79	0.61	0.48
	Lemna minor L.	0.99	0.27	0.27
	Carex tuckermanii Boott	0.58	0.29	0.17
	Glyceria striata (Lam.) Hitchc.	0.77	0.21	0.16

615

Table 2: GLMM model results for species richness versus relative elevation

Effect	Term	Estimate	SE	Z-score	P(Z>|z|)
Fixed	Intercept	1.07	0.09	11.62	<<0.0001
	z	2.04	0.31	6.66	<<0.0001
	moss	-0.45	0.04	-10.17	<<0.0001
Random	SD Intercept	0.26			
	SD z	0.74			
	Cor (z-intercept)	-0.69			

Note: Random effects are presented here as the standard deviation (SD) of all site effects on intercept and slope, with correlation (Cor) between random intercept and slopes. Figure S3 has individual site effects.

Table 3: Cumulative sum of basal area by hummock and hollow across sites.

Site	Hummock basal area (m² per 300 m²)	Hollow basal area (m² per 300 m²)
D1	23.33	0.36
D3	26.00	0.26
D4	20.37	0.11
L1	0.16	20.09
L2	no data	17.55
T1	27.13	0.17

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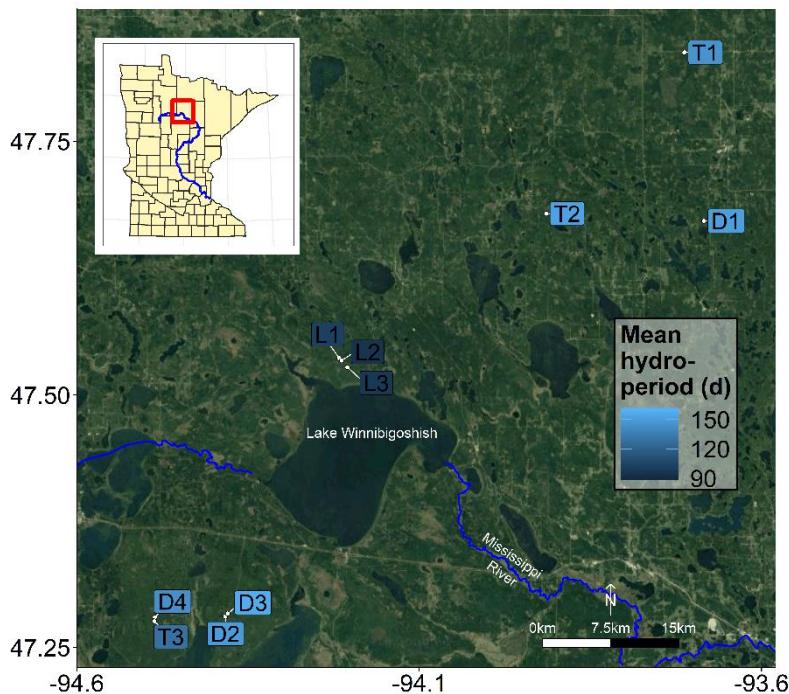


Figure 1: Map of the ten black ash study wetlands in northern Minnesota, U.S.A., with sites colored by average annual hydroperiod (i.e., number of surface-inundation days per year from the May to November) for 2015–2018. © Google Maps 2019.

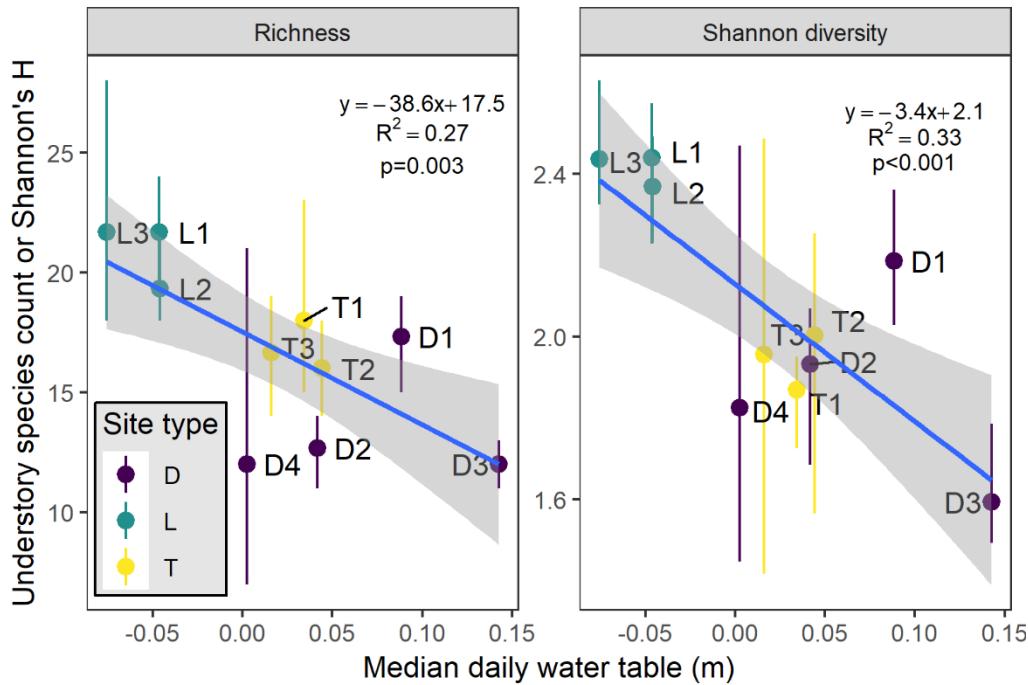



Figure 2: Plot level richness or diversity, aggregated by site, as a function of site level median water table relative to the ground surface (negative values indicate belowground). Vertical bars on points indicate bootstrapped 95% credible intervals calculated from the three plot measurements per site. Linear regression model results presented are also shown. Hydrology summaries provided in Table S3.

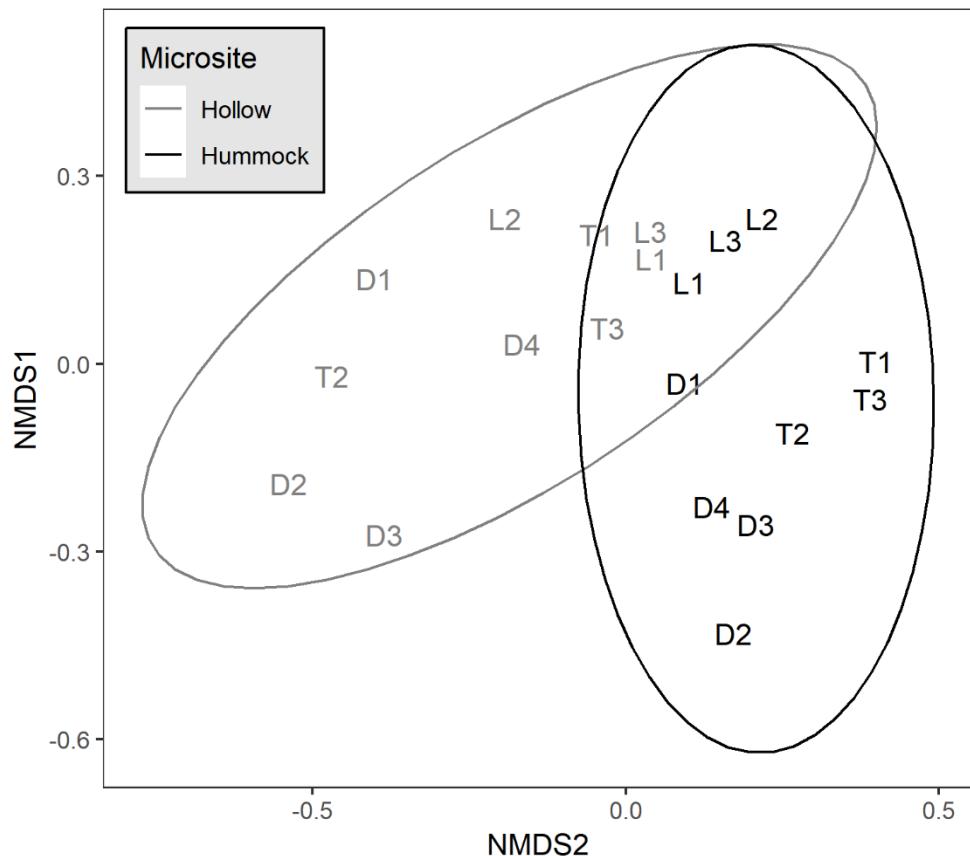
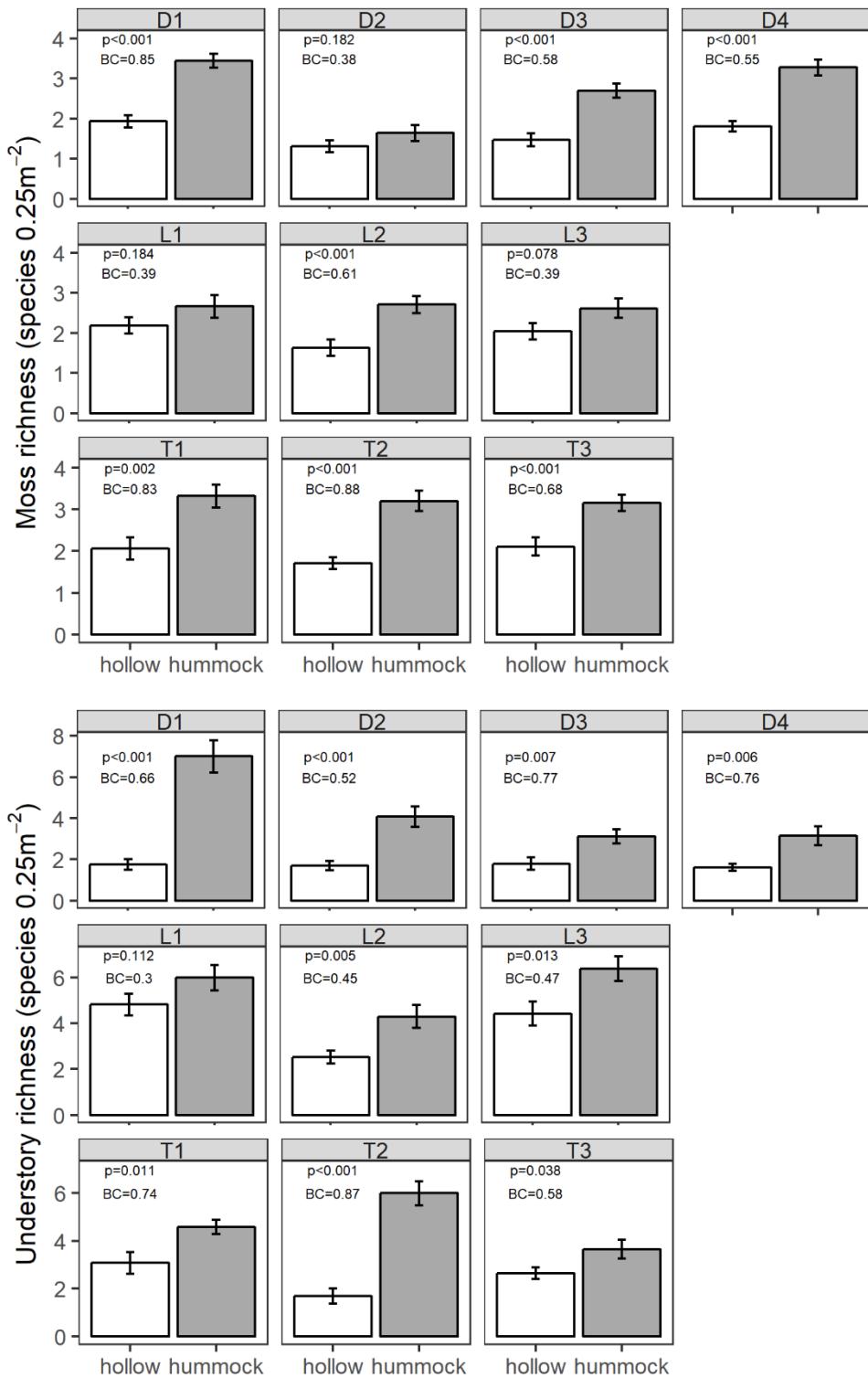



Figure 3: NMDS ordination of understory vegetation communities, grouped by sites (text labels) and microsites, with hummocks in black and hollows in grey. Ellipses indicate 95% credible intervals around the group centroid.

635 **Figure 4: Understory species richness on hummocks and hollows for (top) mosses and (bottom) understory vascular plants for each study site. BC text values indicate Bray-Curtis dissimilarity, with a 0–1 range, spanning identical (0) to completely dissimilar (1) vegetation communities. p-values indicate Welch's two sample t-test significances.**

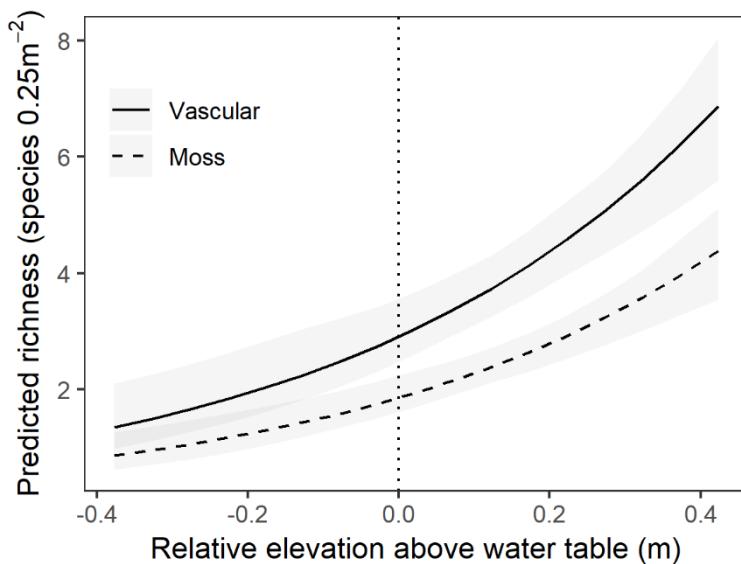



Figure 5: Predicted understory species richness as a function of elevation above mean water table, split by moss and vascular species
640 **components. Shaded ribbons indicate 95% confidence intervals about the estimate.**

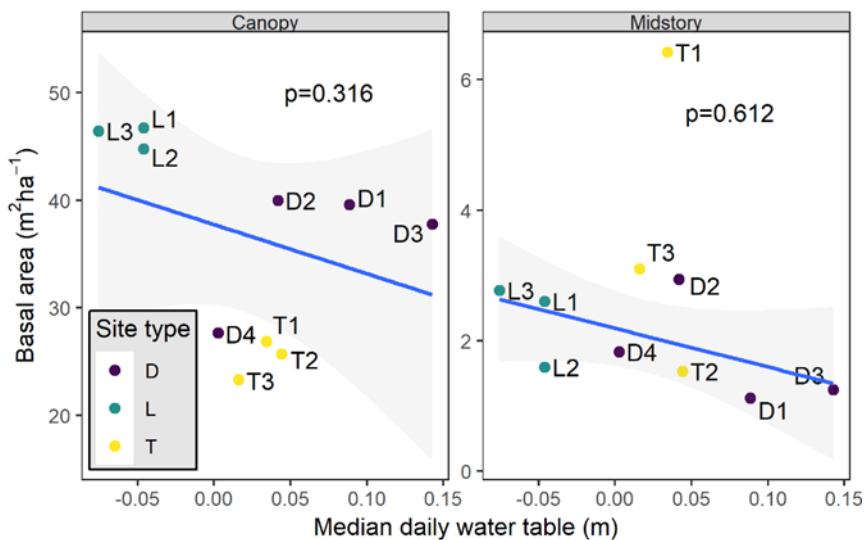



Figure 6 Site-scale basal area in the canopy and midstory versus median water table linear regression, with sites labeled and colored by hydrogeomorphic category. p-values indicate p-values for linear regression and shaded region indicates 95% credible interval about the best-fit line. Stand structure and hydrology summaries can be found in Table S2.

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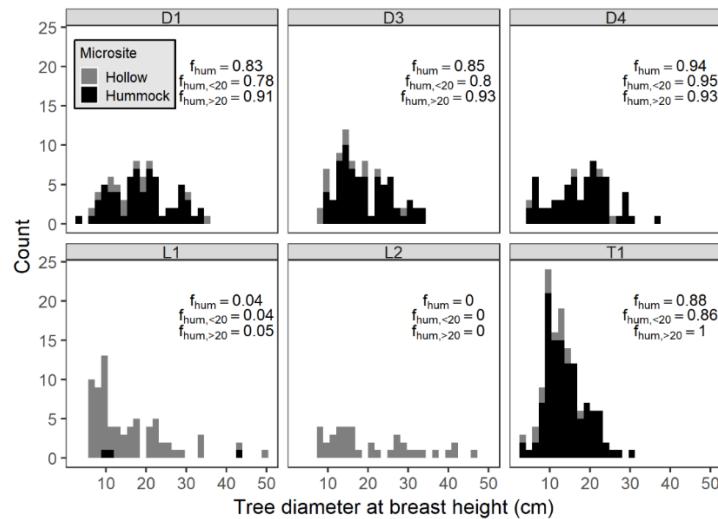
Figure 7: Stacked histograms of DBH size classes across sites. Black bars represent trees on hummocks and grey bars represent the remaining proportion of trees on hollows. Fraction of bars that are black indicate the fraction of trees that are on hummocks in that DBH size bin. Text refers to the fraction of observed trees that occupy hummocks at each sampling area for 1) the total sampling distribution (f_{hum}), 2) the sampling distribution for trees ≤ 20cm DBH ($f_{hum,<20}$), and 3) the sampling distribution for trees >20 cm DBH ($f_{hum,>20}$).

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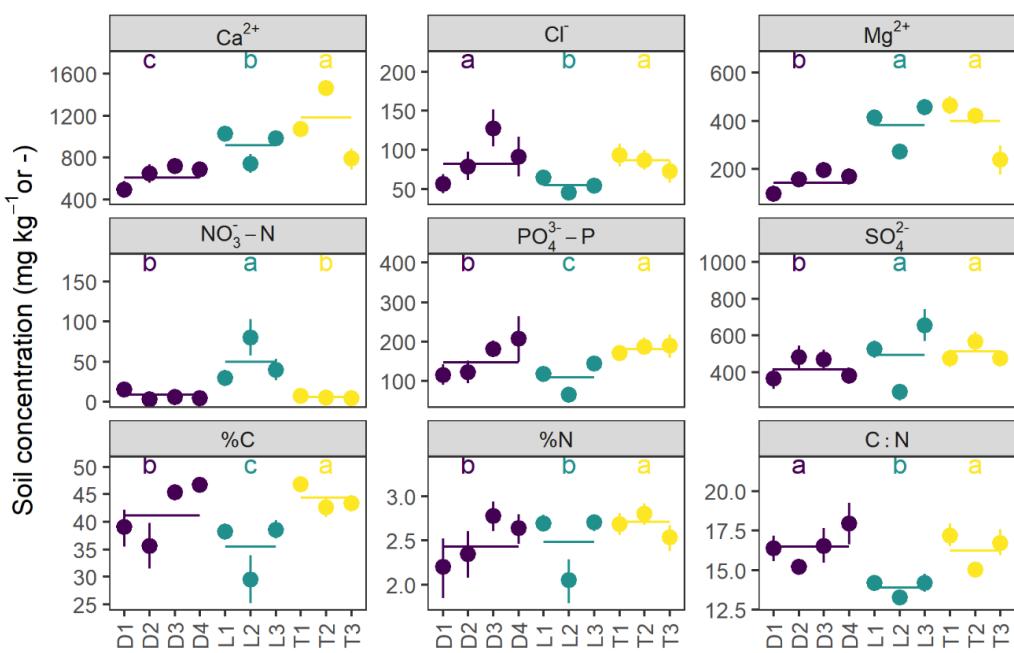
Figure 8: Average soil extraction concentrations for every site and solute analyzed. Colors indicate site type, vertical bars indicate bootstrapped 95% confidence intervals about the mean for each site, and horizontal bars indicate means within groups. If vertical intervals among sites do not overlap, they are significantly different at p = 0.05. Significantly different groups at p=0.05 are labeled with letters. Note: %C, %N, and CN are unitless (-) and are determined from combustion, not soil extraction.

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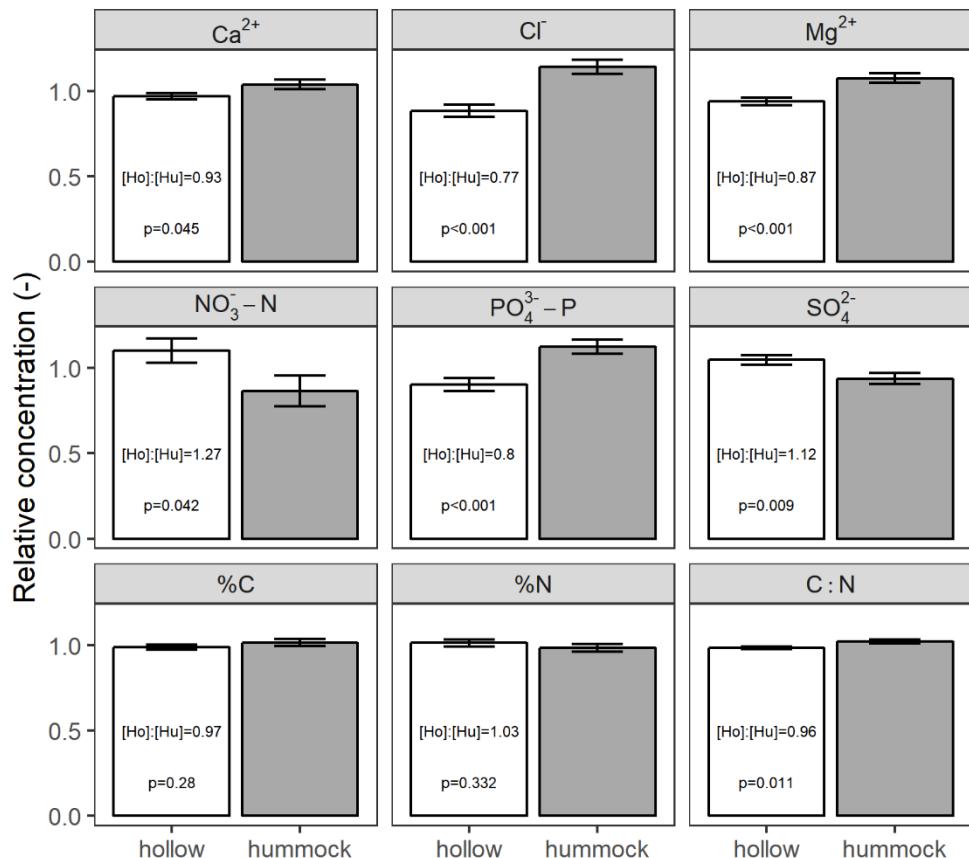
Figure 9: Across-site comparison between hummocks and hollows of relative concentrations of soil analytes. Relative concentration
660 **for any particular sample is normalized to its site average concentration. Text in each panel refers to the across-site ratio of hollow**
to hummock relative concentrations and the Welch's two sample t-test of hollow and hummock means.
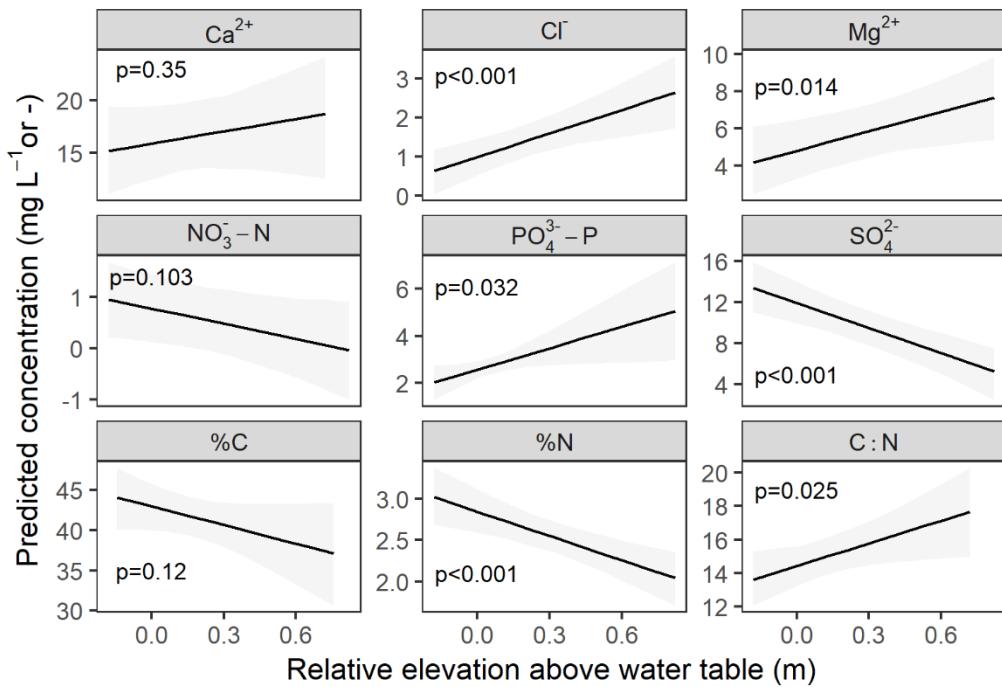
Figure 10: Linear mixed effects model-predicted soil extract concentration as a function of elevation above mean water table, split by analyte, without random site effects. Shaded ribbons indicate 95% confidence intervals about the estimate. Text are p-values for linear mixed effects model regressions.

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