Journal: BG
Title: Microtopography is a fundamental organizing structure in black ash wetlands
Author(s): Jacob S. Diamond et al.
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Authors Response

Dear Biogeosciences editorial review board,

We thank the reviewers and editors at Biogeosciences for the opportunity to respond to comments and to revise our manuscript based on those comments. We believe the manuscript is greatly improved thanks to the careful attention paid by the three anonymous reviewers, and we present our updated manuscript below. First, we show our previously made point-by-point response to reviewers, but now also include in red text the direct changes that were made to the manuscript. We hope that this will serve as a specific list of the changes made as requested by the editor.

Sincerely,

Jake Diamond and co-authors

Responses to Referees

Anonymous Referee #1:

We thank Referee #1 for their detailed review of our manuscript. We have broken out your individual comments (RC) and responded to each accordingly (AC). We hope that our comments address and clarify any issues or concerns that they may have.

Detailed comments:

Title/Abstract:

RC1: …organizing structure of WHAT?

AC1: Our intent was that "organizing structure" refer to the structural backbone of ecosystem function in black ash wetlands, as is often mentioned in the ecological literature (i.e., "structure and function of ecosystems"). We understand that this may be ambiguous to some and we will amend the title to "Microtopography is a fundamental organizing structure of vegetation and soil chemistry in black ash wetlands".

RC2: By the definition wetlands are also coastal areas and shallow water bodies up to the depth of 6 m. This paper is about peatlands or mires. Please change through the text!

AC2: We respectfully disagree with the Referee comment on the necessity of changing the word "wetland" for two reasons. First, we are specific in our usage of the term "black ash wetlands", as opposed to simply "wetlands", and this term is in common usage in the literature. Second, we appreciate the reviewer's attention to word choice, but we further note that our study systems are not peatlands or mires; the similarity among our study sites is that they are dominated by black ash trees, not that they are peatlands (which the majority are not). We recognize this is not entirely clear and will add more detail in our site description section to address this oversight.

Lines 75–78: Black ash wetlands are common features throughout the north-eastern U.S. and south-eastern Canada that range in soil type (e.g., from mineral to peat) and hydrology (e.g., from intermittent to ephemeral). Despite the range in habitat, most late-successional black ash wetlands *are characterized by nearly pure black ash stands (i.e., over 90% canopy cover) with very little regeneration of other tree species (Palik et al. 2012).*

RC3: Are [wetland ecosystems] “controlled” or influenced, ruled or governed?

AC3: We are comfortable with our use of the word “controlled” in this context.

RC4: What was the resolution for [TLS] scanning?

AC4: The ranging error for the TLS used in this study is on the order of 5 mm, but we did not feel that including this information in the abstract was important or relevant, at least not nearly as important as describing the resolution of the surface model, which we note as 1-cm previously in the sentence.

RC5: Or something is causing the formation of microtopography and only then it will influence peat chemistry, vegetation etc?

AC5: We agree, and make this same argument in the previous sentence. Our perspective, which is well-supported in the literature, is that microtopography is created and maintained through feedbacks between biota and hydrology.

Introduction:

RC6: It is so in peatlands only up to the certain height above WT, whereas in wet lawns productivity can be higher than on dry hummocks.

AC6: We do not dispute this, and we provide direct references to support our statements, and state that “in many wetlands” this is true, not in all wetlands.

RC7: [Strack et al. 2006; Sullivan et al. 2008] Both missing from References! For citations missing from References it is shown here only once.

AC7: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Strack, M., Waddington, J.M., Rochefort, L. and Tuittila, E.S., 2006. Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. Journal of Geophysical Research: Biogeosciences, 111(G2).

Sullivan, P.F., Arens, S.J., Chimner, R.A. and Welker, J.M., 2008. Temperature and microtopography interact to control carbon cycling in a high arctic fen. Ecosystems, 11(1), pp.61-76.

RC8: [Rietkerk et al. 2004] Missing from References!

AC8: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Rietkerk, M., Dekker, S.C., Wassen, M.J., Verkroost, A.W.M. and Bierkens, M.F.P., 2004. A putative mechanism for bog patterning. The American Naturalist, 163(5), pp.699-708.

RC9: [Heffernan et al. 2013] Missing from References!

AC9: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Heffernan, J.B., Watts, D.L. and Cohen, M.J., 2013. Discharge competence and pattern formation in peatlands: a meta-ecosystem model of the Everglades ridge-slough landscape. PloS one, 8(5), p.e64174.

RC10: [Casey et al. 2016] Missing from References!

AC10: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Casey, S.T., Cohen, M.J., Acharya, S., Kaplan, D.A. and Jawitz, J.W., 2016. Hydrologic controls on aperiodic spatial organization of the ridge–slough patterned landscape. Hydrology and Earth System Sciences, 20(11), pp.4457-4467.

RC11: Mostly evapotranspiration from hollows is greater than from hummocks!

AC11: We provide four references that support our statement that ET is higher on hummocks relative to hollows. If the Referee has a reference for the opposite, we would be happy to include it as an in-text parenthetical exception.

RC12: What is Paper I?

AC12: Apologies, Paper I is:

Diamond, J.S., McLaughlin, D.M., Slesak, R.A., and Stovall, A. Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences, 2019.

Methods:

RC13: If this paper is not published yet then it can not cited for Methods. Please give details here.

AC13: The paper is now published, and can be found at:

Diamond, J.S., McLaughlin, D.M., Slesak, R.A., and Stovall, A. Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences, 2019.

RC14: Please give peat depth, peat type, vegetation etc on studied sites-

AC14: We will include this summary information in our revisions, and we hope it also will clarify previous concerns the Referee had with our use of the word "black ash wetlands".

Lines 109–114: "…but we provide a brief summary of their characteristics here. The study wetlands varied in soil type, organic layer depth, hydrology, and vegetation, but were all characterized by having black ash canopy dominance of at least 75%. At the lowland sites, other overstory species were negligible, but at the depression and transition sites there were minor cohorts of northern white-cedar (Thuja occidentalis L.), green ash (Fraxinus pennsylvanica Marshall), red maple (Acer rubrum L.), yellow birch (Betula alleghaniensis Britt.), balsam poplar (Populus balsamifera L.), and black spruce (Picea mariana Mill. Britton)."

Lines 117–123: "Depression sites were commonly associated with Terric haplosaprists with O horizons 30–150 cm deep; lowland sites were associated with poorly drained mineral Histic inceptisols with thin O horizons (< 10 cm) underlain by clayey till; transition sites typically had the deepest O horizons (> 100 cm), and were associated with Typic haplosaprists or Typic haplohemists (Soil Survey Staff 2019). Although depression and transition sites had thicker O horizons than lowland sites, depression site organic soils were typically muckier and more decomposed than more peat-like transition site soils. We previously characterized hydrology at these sites (Diamond et al. 2019)…"

RC15: [Stovall et al. 2019] Missing from References!

AC15: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Stovall, A.E., Diamond, J.S., Slesak, R.A., McLaughlin, D.L. and Shugart, H., 2019. Quantifying wetland microtopography with terrestrial laser scanning. Remote Sensing of Environment, 232, p.111271.

RC16: Size of plots?

AC16: We refer to the size of the plots in the previous section 2.2 on line 106; …"within three, 300 m^2 circular plots", but we added a reference to their size again in the parentheses after this comment (Line 141).

RC17: Sampling depth and area?

AC17: We added that the area of sample was a circle 5 cm in diameter (Line 176), but describe the remaining information already in the same paragraph as this comment: at least 13 points per site, 10 cm depth.

RC18: Samples were nor dried to constant weight to get concentration of chemicals per gram?

AC18: The samples were air-dried in a climate controlled room to constant weight. We added this information in our revisions (Line 177).

RC19: … water table depth? Or where there other parameters studied?

AC19: Water table depth was our state variable, but several simple statistical metrics were calculated from it. We will be more specific in our language in our revisions, and note that median and mean water table were the most predictive of our independent variables.

Line 186:"… on site water table metrics (e.g., mean, median and variance)…"

RC20: [De Caceres and Legendre 2009] Missing from References!

AC20: We sincerely apologize for the multiple issues with references. We will fix this in the revisions. This is already currently in the references as:

Cáceres, M.D. and Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology, 90(12), pp.3566-3574.

RC21: [Caceres 2013] Missing from References!

AC21: We sincerely apologize for the multiple issues with references. We will fix this in the revisions. This is already currently in the references as:

De Cáceres, M., 2013. How to use the indicspecies package (ver. 1.7. 1). R Proj, 29.

Discussion:

RC22: [Duberstein and Connor 2009] Missing from References!

AC22: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Duberstein, J.A. and Conner, W.H., 2009. Use of hummocks and hollows by trees in tidal freshwater forested wetlands along the Savannah River. Forest Ecology and Management, 258(7), pp.1613-1618.

RC23: But what is causing higher species diversity on hummocks?

AC23: As we discuss throughout the manuscript, and in particular in the previous paragraphs (lines 302–341), the preponderance of literature evidence suggests that hummocks provide hydrologic stress relief for vegetation allowing for both obligate and facultative species to grow. We also suggest *that there is a productivity-elevation feedback that as hummocks increase in height, they increase local productivity/nutrient cycling on the hummock, further relaxing constraints on plant growth.*

RC24: Can there be several "water tables" or still in each site only one?

AC24: In this case we referring to "water tables" in the broad, across-site sense. We rephrased to improve clarity.

RC25: [Kirchner 2000] Missing from References!

AC25: We sincerely apologize for the multiple issues with references. We will fix this in the revisions. This should actually be "Kirchner et al. 2000" in text.

RC26: [In northern bog wetlands] This is the total mess of terms!

AC26: We rephrased to "northern bogs".

RC27: There are opposite results published as well. See Limpens et al, 2014.

AC27: Without a specific reference from the referee, we can only assume that they are referring to:

Limpens, J., Holmgren, M., Jacobs, C.M., Van der Zee, S.E., Karofeld, E. and Berendse, F., 2014. How does tree density affect water loss of peatlands? A mesocosm experiment. PloS one, 9(3), p.e91748.

If this is true, the results from this study are not in opposition to our statement (which we support with citations from two studies). Limpens et al. 2014 show that compared to a control mesocosm, a treatment of low-density trees (analogous to tree encroachment in a bog) can produce lower water levels at the end of a growing season. They conclude that low-densities of trees produce a drying effect, but that if there are many trees and the canopy closes, this effect may be offset in the future.

RC28: [Cantelmo and Ehrenfeld 1999] Missing from References!

AC28: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Cantelmo Jr, A.J. and Ehrenfeld, J.G., 1999. Effects of microtopography on mycorrhizal infection in Atlantic white cedar (Chamaecyparis thyoides (L.) Mills.). Mycorrhiza, 8(4), pp.175-180.

RC29: [Jones et al. 1996] Missing from References!

AC29: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Jones, R.H., Lockaby, B.G. and Somers, G.L., 1996. Effects of microtopography and disturbance on fine-root dynamics in wetland forests of low-order stream floodplains. American Midland Naturalist, pp.57-71.

RC30: There is too much of repetition of results in Discussion.

AC30: In our revisions, we will reduce repetition of Results in the Discussion (see edits throughout).

RC31: Is there any measurements to approve it?

AC31: Apart from our field observations, we do not have any publishable results to confirm that water tables are indeed flat across the study areas. We will add more attention to this limitation here (Line 504).

Conclusions:

RC32: But vegetation "occupied" hollows as well?

AC32: Yes, vegetation occupies hollows as well. We will refine our language here to be less ambiguous.
Line 522: "…vegetation preferentially occupy…"

References:

RC33: [Cohen et al 2016] Citation missing from the text

AC33: Thank you for finding this omission. We removed this citation.

RC34: Are these two the same person or not? If not then put Caceres .. in right place in alphabetical order.

AC34: Yes, they are same person. We fixed this error.

RC35: [Huenneke and Sharitz 1986] Citation missing from the text

AC35: Thank you for finding this omission. We removed this citation.

RC36: [Iremonger and Kelly 1988] Citation missing from the text

AC36: Thank you for finding this omission. We removed this citation.

RC37: [Wilson and Agnew 1992] Citation missing from the text

AC37: Thank you for finding this omission. We removed this citation.

Figures:

RC38: [Figure 4] "..richness" or "species number?

AC38: Species richness is equivalent to the number of different species.

Anonymous Referee #2:

We thank Referee #2 for their detailed review of our manuscript. We have broken out your individual comments (RC) and responded to each accordingly (AC). We hope that our comments address and clarify any issues or concerns that they may have.

Overall comments:

RC1: This work presents an interesting question and is within the scope of Biogeosciences. It is well written and the conclusions are sound, however care should be taken in how the story is presented. I don't think it's quite as black and white as the authors seem to state regarding microtopography being primary control on vegetation communities.

AC1: We appreciate the Referee's careful consideration of our interpretations, and we will be sure to temper language throughout in accordance with the Referees recommendations.

RC2: I believe it will be a useful addition to the literature after some major revisions. The manuscript is rather long and could do with being streamlined, especially in the methods and results section. In particular I found it difficult to follow section 2.3 (Data analysis). Although the methods used are sound and appropriate, it was very difficult to follow to see what was done where. There was also a little bit of repetition throughout this section where the authors would state why they are going to use a test multiple times

AC2: We are happy to streamline the text, especially in the Methods and Results to improve readability. See numerous changes throughout Methods and Results.

RC3: One of my major concerns throughout this manuscript was the frequent absence of citations in the reference list, that are referred throughout the paper. A thorough check of this is needed. Conversely, there are citations in the reference list that are not included in the main body of the text. Also, it is not clear to me whether Diamond et al. In Review which is referenced many times throughout this work has been submitted to the same journal? The authors make reference to a complimentary paper (Paper I) in line 70 but I am unsure if this is the same paper. There is no guarantee that paper will be published before this one, therefore I think it is important that the authors remove reference to this paper in review and expand where necessary in the main body of the text. It can not be expected that readers just assume a paper will be published in due course and be OK with lacking details within this one.

AC3: We sincerely apologize for the numerous issues associated with citations throughout our manuscript; this was noticed by the other Referees as well. We have fixed all citation issues and note them here in our response, and note that Diamond et al. [in Review] (accidentally referred to Diamont et al. at one point) is published now as:

Diamond, J.S., McLaughlin, D.M., Slesak, R.A., and Stovall, A. Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences 2019.

Detailed comments:

Title and Abstract:

RC4: Title: Organizing structure of what? The title does not link well with the main results of the text. I believe more reference to the influence on vegetation communities might be clearer here.

AC4: Our intent was that "organizing structure" refer to the structural backbone of ecosystem function of black ash wetlands, as is often mentioned in the ecological literature (i.e., "structure and function of ecosystems"). We understand that this may be ambiguous to some and we will amend the title to "Microtopography is a fundamental organizing structure of vegetation and soil chemistry in black ash wetlands".

RC5: Line 10-11: Local deviation in soil soil elevation sounds awkward – do you mean deviation above the water table?

AC5: Yes, good catch, and made this change.

Introduction:

RC6: Line 30: This is the main organizing structure – or is it the water table position is – and that just influences everything else?

AC6: Our perspective is that microtopography modulates local water table position, thereby affecting and organizing all processes that are influenced by soil moisture.

RC7: Line 35: Strack reference and Sullivan reference are missing from reference list

AC7: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Strack, M., Waddington, J.M., Rochefort, L. and Tuittila, E.S., 2006. Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. Journal of Geophysical Research: Biogeosciences, 111(G2).

Sullivan, P.F., Arens, S.J., Chimner, R.A. and Welker, J.M., 2008. Temperature and microtopography interact to control carbon cycling in a high arctic fen. Ecosystems, 11(1), pp.61-76.

RC8: Line 43-44: All these references are missing. This is happening throughout the paper – please check and amend.

AC8: We sincerely apologize for the multiple issues with references. We will fix this in the revisions.

Rietkerk, M., Dekker, S.C., Wassen, M.J., Verkroost, A.W.M. and Bierkens, M.F.P., 2004. A putative mechanism for bog patterning. The American Naturalist, 163(5), pp.699-708.

Heffernan, J.B., Watts, D.L. and Cohen, M.J., 2013. Discharge competence and pattern formation in peatlands: a meta-ecosystem model of the Everglades ridge-slough landscape. PloS one, 8(5), p.e64174.

RC9: Line 48: / missing between hummock and hollow

AC9: Thank you, we added a dash ("-") between these words.

RC10: Line 70: What paper is Paper I? Is it in review in same journal? I don't think it's clear to refer to this paper in this way, unless they were submitted together?

AC10: We will fix this in revisions, but Paper I is:

Diamond, J.S., McLaughlin, D.M., Slesak, R.A., and Stovall, A. Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences, 2019.

Methods:

RC11: Section 2.1: You need to give more background information. I am still unclear whether these wetlands are peatlands or mineral wetlands? This has not been defined anywhere. It would be really useful to give the depth of organic matter, the dominant vegetation communities present, meteorological conditions etc.

AC11: We will include all of this information in our revisions, which we cover in more detail in previous work. The wetlands vary between their soil types, depth of organic matter, but are all dominated (75–100% cover) by black ash.

Lines 75–78: Black ash wetlands are common features throughout the north-eastern U.S. and south-eastern Canada that range in soil type (e.g., from mineral to peat) and hydrology (e.g., from intermittent to ephemeral). Despite the range in habitat, most late-successional black ash wetlands are characterized by nearly pure black ash stands (i.e., over 90% canopy cover) with very little regeneration of other tree species (Palik et al. 2012).

And additional text throughout 2.1 Site descriptions.

RC12: Line 95: You can't expect the reader to go and read an unpublished paper. You need to expand the methods here.

AC12: That paper is published now. We elect to not expand the hydrology methods here because it will increase the length of the paper (which was requested to be shortened by the reviewer), and because those methods are detailed in their entirety in this work:

Diamond, J.S., McLaughlin, D.M., Slesak, R.A., and Stovall, A. Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences, 2019.

RC13: Line 104: Space needed between create and 1cm

AC13: Thank you, we corrected this.

RC14: Line110: How big are these plots? Are they the same plots as the 300m2 circular plots used in the elevation data collection

AC14: Yes, these are the same plots; we clarified this in our revisions.

RC15: Line 117-118: What was used if you did not know the species? It would be useful to include a sentence such as "Vascular plant identification were made according to X and non-vascular plant identification according to Y".

What nomenclature was used? What was the breakdown for percent foliar cover – 1, 3, 5 and then to the nearest 5%?

AC15: We discuss at the end of this paragraph that "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."

We will include in our revisions a sentence for the tools used for identification, but note here that we used two main sources: 1) a local wetland plant/moss identification manual, and 2) a regional wetland plant identification guide. (Lines 148–149).

The nomenclature used depended on the species (for example, see Table 1) because not all species had the same nomenclature system (particularly for mosses), but we included nomenclature in all of our identification.

Indeed, we used the 1, 2, 5, and nearest 5% approach for percent foliar cover and will note this in our revisions. (Line 145)

RC16: Line 139: Does air-drying allow for a consistent drying method? Why not use an oven?

AC16: To the best of our knowledge, air-drying wetland soil is a common method used across many wetland systems and recommended by Reddy and DeLaune, Biogeochemistry of Wetlands: Science and Applications. We further note that soils were air-dried to constant weight, and were extremely friable when we ground them. We will include a discussion of possible artifacts of this method in the Discussion (Lines 493–494). We do not believe that our approach is dubious or that alternative drying methods would substantially change our results, particularly for our most compelling results for Cl and PO_4^{3-}.

RC17: Line 149: Hydrologic metrics? Do you just mean water table depth?

AC17: Water table depth was our state variable, but several simple statistical metrics were calculated from it. We will be more specific in our language in our revisions, and note that median and mean water table were the most predictive of our independent variables (e.g., Lines 188 and 264–265).

RC18: 2.3. Data analysis: This whole section is really quite confusing and very wordy–I think it would be useful to streamline this without losing the integrity of the work.

AC18: We will reduce the text here and streamline this section in our revisions. For example, we reduced much of the methodological specifics in the Understory composition section (2.3.1) and the Soil chemistry section (2.3.3).

Results:

RC19: Lines 218, 224, 253, 269 (and any I missed): This is not enough information for the results of a statistical test. It's also unclear what test has been used. The correct way to present this data would be, for example; (ANOVA, F=0.12, p < 0.0001). Please correct throughout.

AC19: On line 218, we are referring to the OLS in Figure 2, and will include the F values for the linear regression in our parenthetical reference; and the same for line 253. On line 224, we will include the F values for the PerMANOVA test in our parenthetical reference. In line 269 we are referring to an ANOVA, and will report the F value, as well.

Discussion:

RC20: It's still unclear to me what type of wetlands these are? This needs to be made explicitly clear.

AC20: The commonality in our study sites is that they are all black ash wetlands, but have variable soils and hydrogeomorphic settings. We were much more explicit here and also in the Site Descriptions so that there is no ambiguity.

RC21: Line 385: This is where it would be useful to make it clear what type of wetlands these are. The term northern bog wetlands is awkward – bogs are peatlands, therefore wetlands.

AC21: We rephrased to say "northern bogs". Our wetlands are not bogs; we only use these references in this sentence to support the notion that areas with trees (cf. hummocks in our study systems) can be sites of increased evapotranspiration relative to areas without trees (cf. hollows in our study system).

RC22: Line 434: Is it microtopography or is it water table as the primary control? I understand that this is a useful study and I don't dispute the findings, but I wonder if stating that microtopgraphy is the primary control is not exactly what is shown – rather water table depth and vegetation community dictate microtopography?

AC22: We agree entirely, and try to point to this later in the sentence with "…while also suggesting that it arises from biogeomorphic feedback processes that concentrate biomass and nutrients into hummock structures." We will refine our language here to better reflect this perspective: that microtopography is created and maintained through feedbacks between hydrology, vegetation, and soil (organic matter). So, microtopography controls the vegetation and soil, but water table and vegetation/soil also control the size and distribution of microtopography.

Figures

RC23: Ten figure seems excessive – and they are hard to follow. Could a few be sent to the supplementary information without losing the story?

AC23: We agree, and moved Figures 3, 6, 7, and 10 to the supplementary information.

RC24: Figure 1: An inset figure of where Minnesota is in context of the United States would be very useful These sites are quite far north.

AC24: We did not include an inset of Minnesota in a new map because it was too cluttered and we additionally include latitude and longitude, which we consider to be sufficient.

RC25: Figure 2: The Y axes of these plots are not the same, so sharing an axis title is rather confusing. They are on a different scale. Define what D, L and T are again in the figure caption.

AC25: We split the y-axes and defined what D, L, and T are in the caption.

RC26: Figure 3: The ellipses used in this figure are very hard to tell apart–please use another colour or line type.

AC26: We did not change these colors, as we moved the figure to the supplement.

RC27: Figure 4: This could be moved to the supplementary information

AC27: We disagreed and found this figure to be critical to the results, but we made it simpler.

RC28: Figure 6: Again, define D, L, T in figure caption

AC28: We defined these in the caption, and also moved to supplementary information.

RC29: Figure 7: This could be moved to the supplementary information.

AC29: Agreed, wel moved this to the supplementary.

RC30: Figure 8: You have no legend as to what the colours mean in this figure.

AC30: In the caption we indicate that “colors indicate site type”.

RC31: Figure 9: This could be moved to supplementary information

AC31: We disagree with the Referee here, and think this is important to include in the manuscript, but we appreciate the importance of reducing the total figure count.

RC32: Figure 10: This could be moved to supplementary information

AC32: We moved this figure to supplementary.

Anonymous Referee #3:

We thank Referee #3 for their detailed review of our manuscript. We have broken out your individual comments (RC) and responded to each accordingly (AC). We hope that our comments address and clarify any issues or concerns that they may have.

Detailed comments:

Introduction:

RC1: When talking about primary production and distance from WT, it's a bit odd not to mention drainage of peatlands for forestry which has been thoroughly studied

AC1: We included some references to these works in our revisions (Lines 38–39).

RC2: As the Diamond (referred to at times as "Diamont") et al. in review is a discussion paper, it can of course be referred to, but a link to the paper should be found in the references!

AC2: We sincerely apologize for the numerous issues associated with citations throughout our manuscript; this was noticed by the other Referees as well. We have fixed all citation issues and note them here in our response, and note that Diamond et al. [in Review] (accidentally referred to Diamont et al. at one point) is published now as:

Diamond, J.S., McLaughlin, D.M., Slesak, R.A., and Stovall, A. Pattern and structure of microtopography implies autogenic origins in forested wetlands. Hydrology and Earth System Sciences, 2019.

Methods:

RC3: 2.1 Site descriptions How were the measurement plots placed in the sites? How far from each other were they? The area variation in the sites is large; is there some correlation between site type and area? These things should be explained in the text at least briefly even if they are available in another article.

AC3: We included more detailed information on site characteristics and plot locations in our revisions. The measurement plots were randomly placed throughout the sites (by means of a pre-field random placement algorithm), typically less than 50 meters from one another (Lines 133–135).

RC4: 2.2 Field measurements The WTL monitoring setup should be described in detail already in the methods section-now the fact that WTL was measured in only one location per site(?) only comes up in the Discussion. If indeed WTL was only measured at one location in a site of over 15 hectares, this is quite a problematic approach. The water retention characteristics of peat can vary by a lot based on how decomposed it is and what it is composed of. Also, the water in a peatland system is never at a steady state; it is always on the move and therefore there are always differences in the pressure head inside the ecosystem. This hampers the tests on species richness and basal area, a fact which should be noted in the text. The fact that the TLS measurements were only conducted on six of the sites should be mentioned already here.

AC4: We will be more detailed here, as it is clearly confusing as written. The note that site areas were 0.5–15.6 ha is misleading and we amended it (Line 92). Those site areas were estimated from earlier survey approaches and are not representative of our actual study areas. The actual study areas within sites only varied between 0.07 and 0.12 ha, as we did not sample the entire previously estimated site area. Hence, we believe that measured water tables are quite representative of our small study areas. We measured water table every 15-minutes at our sites for 3 years and so we believe have a good *general understanding of overall water table behavior and dynamics at our sites (Lines 131–133). Overall, the goal was to sample areas that we could also measure with our TLS approach, which was indeed measured at all 10 sites. Still, we point to limitations of this approach in the Methods and will increase focus on these limitations in the Discussion text.*

RC5: 2.2.1 For the species richness, the importance of each microform to landscape level biodiversity would be interesting; even though areas higher from the WTL host more species than those closer to the WTL, their species composition might be closer to that of the surrounding upland forests. This could be discussed.

AC5: We agree that this is a very interesting perspective and will include a brief discussion of the potential for this future work in the Discussion (Lines 385–387). However, we are unable to assess this importance with our current datasets.

RC6: 2.2.2 These two paragraphs are really hard to understand. How were the stand-level metrics for the first data source measured? Is there some reference available?

AC6: We agree that this is the most confusing part of our methods, and did our best to clarify (Lines 153–167). The stand-level metrics were measured with standard forestry methods. There is no direct reference available for these data, but we will provide them as part of open access in this journal.

Essentially, the first, forestry/stand-based data source is useful for site-level understanding, but the second, TLS data source is useful for microform-level understanding. With the TLS data source we can tie a specific tree to a specific microform.

RC7: 2.2.3 Why would you air-dry the samples? Bringing moist peat samples to warm conditions is sure to alter their composition, with high microbial activity breaking down organic matter, and nitrification-denitrification processes running wild. This casts doubt on the whole soil chemistry part of the manuscript and should at least be discussed. The different times it takes for the peat samples with different pore size distribution to dry and thus the different amounts of microbial activity that has gone on in the samples will cause the carbon and available phosphate content and nitrogen fractions to differ between the samples.

AC7: To the best of our knowledge, air-drying wetland soil is a common method used across many wetland systems and recommended by Reddy and DeLaune, Biogeochemistry of Wetlands: Science and Applications. We will further note that soils were air-dried to constant weight, and were extremely friable when we ground them. We will include a discussion of possible artifacts of this method in the Discussion (Lines 493–494).

RC8: 2.3 The three-level approach to the dataset is good and the applied statistical methods seem appropriate for each sub-analysis

AC8: Thank you.

Methods:

RC9: 3.2 If you take the p-value approach to significance of effects, you should use the wording "no statistically significant relationship".

AC9: We made this change.

RC10: 3.3 The problems with sample processing should be addressed. Bulk density and other physical characteristics representing the state of decomposition of the peat in each location would be useful and potentially another explanation for some of the chemical differences observed.

AC10: We will include a discussion of potential artifacts of the approach in the Discussion (Lines 493–494).

Discussion:

RC11: The various problems of sampling and sample processing mentioned above and their effects on the observed results should be discussed here.

AC11: We will include a brief discussion of potential artifacts from sample processing here (Lines 493–494).

Microtopography is a fundamental organizing structure of vegetation and soil chemistry in black ash wetlands

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Mis en forme : Exposant

Abstract. All wetland ecosystems are controlled by water table and soil saturation dynamics, so any local scale deviation in soil elevation and thus water table position 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~~less understood. We studied relationships among microtopography ~~on~~and 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~~microtopography 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 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~~vegetation composition and growth and biogeochemical processes (Rodríguez-Iturbe et al. 2007); any variability in soil elevation therefore represents coincident variability in this hydrologic control (Wallis and Raulings 2011). For example, perhaps incredibly, ~~experimental treatments~~experiments 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 greater primary productivity compared to low points (Strack et al. 2006, Sullivan et al. ~~2008).~~2008), driving the rationale behind wetland drainage for increased forestry yields (Laine et al. 1995; Mäkiranta et al. 2010). 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.

The relationship between wetland ~~process~~processes 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 propose arise from these types of ecohydrological feedbacks (Diamond et al. ~~in review~~2019). 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~~elevation feedback. Preferential colonization by plants on slightly elevated sites leads to local buildup of organic matter via primary 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 (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~~2019). 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 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 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) ~~wetlands~~swamps in northern Minnesota, U.S.A. Black ash wetlands are common features throughout the north-eastern U.S. and south-eastern Canada that range in soil type (e.g., from mineral to peat) and hydrology (e.g., from intermittent to ephemeral). Despite the range in habitat, most late-successional black ash wetlands are characterized by nearly pure black ash stands (i.e., over 90% canopy cover) with very little regeneration of other tree species (Palik et al. 2012). In a complimentary study (~~or Paper I~~Diamond et al. 2019), we observed evident hummock-hollow structure in these systems, ~~but this microtopography~~which 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 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.
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 2 Methods

2.1 2.1 Site descriptions

~~To test~~We tested our ~~hypotheses, we investigated~~hypothesis in ten black ash wetlands of varying size (0.~~5–15.6~~07–0.12 ha) and hydrogeomorphic landscape position in northern Minnesota, U.S.A. (Figure 1). The study region is characterized by a glacial moraine landscape (400–430 m ASL) that is flat to gently rolling, with the black ash wetlands found in lower landscape positions that commonly grade into aspen or pine-dominated upland forests. Climate is continental with mean annual precipitation of 700 mm and a mean growing season (May–October) temperature of 14.3°C (WRCC 2019). Annual precipitation is approximately two-thirds rain and one-third snowfall, and potential evapotranspiration is 600–650 mm per year (Sebestyen et al., 2011).

Black ash ~~trees are unique among ash species because they often occur in nearly pure~~ stands ~~(i.e., over 90%~~are commonly highly uneven-aged (Erdmann et al., 1987), with canopy ~~cover) in wetland conditions with very little regeneration of other~~ tree ~~species (Palik et al.~~ ages ranging from 130–232 years, and stand development under a gap-scale disturbance regime (D'Amato et al., 2018). Black ash are also typically slow-growing, achieving heights of only 10–15 m and diameters at breast height of only 25–30 cm after 100 years (Erdmann et al., 1987).

~~2012).~~ In previous work (~~Diamont~~Diamond et al. ~~in review~~2019) and as part of a larger project (D'Amato et al. 2018), we categorized and grouped each wetland site 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) 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~~(2019), but we provide a brief summary of their characteristics here. The study wetlands varied in soil type, organic layer depth, hydrology, and vegetation, but were all characterized by having black ash canopy dominance of at least 75%. At the lowland sites, other overstory species were negligible, but at the depression and transition sites there were minor cohorts of northern white-cedar (*Thuja occidentalis* L.), green ash (*Fraxinus pennsylvanica* Marshall), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britt.), balsam poplar (*Populus balsamifera* L.), and black spruce (*Picea mariana* Mill. Britton). 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 hydrology at these sites using ground-water wells and rain gages (Diamond et al. [in review])~~ (Soil Survey Staff 2019). Depression sites were commonly associated with Terric haplosaprists with O horizons 30–150 cm deep; lowland sites were associated with poorly drained mineral Histic inceptisols with thin O horizons (< 10 cm) underlain by clayey till; transition sites typically had the deepest O horizons (> 100 cm), and were associated with Typic haplosaprists or Typic haplohemists (Soil Survey Staff 2019). Although depression and transition sites had thicker O horizons than lowland sites, depression site organic soils were typically muckier and more decomposed than more peat-like transition site soils. We previously characterized hydrology at these sites (Diamond et al. 2019) 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~~.~~ (Diamond et al. 2019).

2.2 2.2 Field measurements

We conducted field sampling campaigns to characterize vegetation and soil ~~properties~~chemistry of our study systems. We then coupled these data to previously ~~characterized~~ collected water table and elevation data (Diamond et al., ~~in review~~2019) to address our hypothesis and predictions. Water table data (15-minute measurement intervals) were collected at each of our ten sites from 2016–2018, where negative values represent belowground water levels and positive values represent aboveground levels (see Diamond et al. 2019 for details). Elevation data were collected in 2017 using high-resolution terrestrial laser scanning (TLS) measurements within three, randomly placed 300 m^2 circular plots at each site~~.~~ (plots were placed at most 50 m from each other to ensure overlap of TLS scans). These data were then used to ~~create1~~create 1-cm digital elevation models and to delineate hummock versus hollow features (see method details in Diamond et al~~., in review~~. 2019 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 to categorize each sampling point as a hummock or hollow.

2.2.1 2.2.1 Understory composition

We characterized understory vegetation at each site to test the prediction that understory richness and diversity will be greater on higher elevation features. To do so, we used a quasi-random walk sampling scheme within the 300 m^2 plots (3 per site) previously used for TLS elevation measurements. We term the ~~study~~sampling 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 m^2 square quadrat to classify vascular and moss individuals to the species level, visually estimated their percent foliar cover~~,~~ (1%, 2%, and nearest 5%), and recorded stem count (if possible) for vascular species. We chose a 0.25 m^2 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. Vascular plant identifications were made according to Eggers and Reed (1988), and non-vascular plant (liverworts and mosses) identifications were made according to Jannsens (2014). 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 2.2.2 Tree biomass

~~To~~We used two different data sources 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~~ comprised standard stand~~-level~~ metrics~~, including~~ and was used for our site-level comparisons. These stand data were collected as part of a larger study by the USDA Northern Research Station in Grand Rapids, Minnesota and included species, basal area, and ~~trees per hectare~~density 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 used to relate specific trees and their basal area to a specific base elevation relative to water table, and employed plot-scale point clouds of forest structure from the aforementioned TLS campaign ~~at six of the ten 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 m^2 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 original TLS analysis (Stovall et al. 2019). We were only able to apply the SimpleTree algorithm at six of our sites, and only on a fraction of our scanned areas at those sites (approximately 300 m^2 at each of the six sites), due to resolution issues and understory noise.

2.2.3 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 then used a 15-cm beveled and serrated soil knife to extract our soil samples (approximately 5 cm in diameter at the soil surface) to a depth of 10 cm.

~~We~~Following standard methods (DeLaune and Reddy 2008; USEPA 2008), 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 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~~water table metrics (e.g., mean, median and variance) 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 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 understory vegetation composition among both sites and microsites (i.e., hummock vs. hollow), we ~~first classified~~used a multivariate permutational analysis of variance (PerMANOVA) on understory vegetation in ordination space~~ using~~. For ordination, we used nonmetric multi-dimensional scaling (NMDS~~).~~) with the *vegan* package (Oksanen et al. 2018) in the R statistical software (R Core Team 2018). Prior to

~~analysis~~ordination, 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 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~~Cáceres and Legendre 2009). This analysis generates an indicator value index (IV) for each species within each category (e.g., site or microsite~~). We used 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.~~) based on two metrics: specificity (i.e., the probability that a sample point belongs to a particular group, given that the species was found there) and sensitivity (i.e., the probability that the species is found in sample points belonging to a particular group). 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 species output and from guidance in package materials (Cáceres 2013).

~~To test categorical differences in richness between hummocks and hollows, we calculated~~ We also conducted Welch's two sample t-tests on richness between hummocks and hollows for each site~~. We additionally~~ and calculated hummock-hollow Bray-Curtis community dissimilarity indices ~~using the *vegdist* function. This dissimilarity index falls~~, which fall 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 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~~Last, 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 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.~~).

2.3.2 2.3.2 Tree biomass

We tested our ~~hypothesis~~prediction that site-scale hydrology influences tree biomass by regressing site-scale (midstory + canopy) basal area with site-scale ~~hydrology.~~water table metrics. To determine categorical differences in tree biomass between hummocks and hollows, we used individual tree DBH data (from the TLS scan data) and ~~summed~~compared the cumulative basal area between hummocks and hollows. We then estimated ~~a~~the fraction of ~~trees~~tree basal area at each site that occupied hummocks relative to hollows. Finally, we analyzed within-site relationships between point-scale DBH (from the TLS data) and tree base elevations relative to mean water table using a linear mixed effect model (using the *lme4* R package, Bates et al. 2015).

~~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 2.3.3 Soil chemistry

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 in each analyte among hydrogeomorphic categories~~,~~ (via Levene test on group variance), 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 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~~Normalized concentrations ~~to compare~~ were compared between hummocks and hollows across sites using Welch's two-sample t-tests~~. We~~; we also ~~used a simple ratio~~calculated ratios of hollow to hummock ~~normalized~~ concentrations to ~~contextualize~~assess 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~~ using best-fit linear mixed-effect ~~model (using~~ modeling (via 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, and 3) random site level intercept and slope with uncorrelated random effects for slope and intercept.~~).

3 3 Results

3.1 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* 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~~.~~, with mean and median daily water table being the best predictors. Median daily water table was a linear predictor of both understory richness ($F_{2,28}$ = 10.6, p = 0.003) and diversity ($F_{2,28}$ = 13.6, 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 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~~the understory community matrix between hummocks and hollows across sites (PerMANOVA, $F_{1,18}$ = 4.07, p = 0.002) and between hummocks and hollows within sites (PerMANOVA, $F_{1,18}$ = 4.76, p=0.001; Figure ~~3~~S2). Hummocks and hollows were more similar for lowland sites, particularly L1 and L3, compared to depression and transition sites (Figure ~~3~~S2).

~~Our indicator~~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 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 understory richness between hummock and hollow microsites. Hummocks were nearly always locations of ~~both~~ greater combined moss ~~species richness and greater understory~~ and vascular plant species richness (Figure ~~4~~3). This pattern was identical when ~~also combining both moss and~~separating mosses from vascular plants (Figure ~~S2~~S3). 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~~).~~; see Table S2 for site hydrology summaries). Bray-Curtis dissimilarities for both mosses and understory vascular plants were greatest for depression and transition sites (BC values in ~~Figure 4~~Figures 3 and S3).

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) (Table 2). 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~~S4), 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 slope effects) compared to wetter sites (Figure ~~S3a~~S4a), indicating less rapid increases in richness with increased 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~~4). Both moss and vascular plants exhibited 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 3.2 Tree biomass

There was no ~~strong~~significant linear 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 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~~,~~ (n=6), we further assessed differences between hummocks and hollows. Total basal area was disproportionately (by ~~two orders~~an order 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 all size classes, we found that trees in the wettest sites (depression and transition) occupied hummocks 83–94% of the time (Figure ~~7~~S5). 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~~S5). 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~~relationship (fixed effect = 2.2±2.8 cm m^{-1}, t = 0.77; and see Figure ~~S4~~S6). 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 3.3 Soil chemistry

There were clear differences in soil chemistry among site hydrogeomorphic groups and among individual sites for all analytes (ANOVA, $F_{2,184–202} = 5.1–143.8$, $p < 0.01$, Figure ~~8~~5). Depression sites had the lowest soil base cation concentrations (Ca^{2+} and Mg^{2+}), followed by lowland and 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~~there was 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~~For example, we observed significantly greater variance in %C, NO_3^{-}~~–~~–N, and SO_4^{2-} in drier lowland sites than in wetter sites (Table S3).

We also found differences (Welch’s two-sample t-test, $p<0.05$) in soil chemistry between hummocks and hollows for seven out of nine analytes (Figure ~~9~~6). Except for NO_3^-–N, %N, and SO_4^{2-}, hummocks had higher analyte concentrations than hollows. ~~Relative across~~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 to hollows.

We found strong 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 (Figure S7, S8). Results from this point-scale linear fitting align with categorical results from hummock and hollow analysis (Figure S8). 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 ~~.~~S7). 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 (direction and magnitude) among sites~~.~~ (Table S5). We did not observe clear patterns in random effects relating to sites or site hydrogeomorphic groupings (Figure ~~S5~~S7), 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 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 4 Discussion

Using integrated measures of fine-scale topography, water table regimes, and vegetation and soil attributes, our work highlights 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-hollow development ~~and maintenance~~, where increased vegetative productivity at higher microsites leads to increased microsite elevation ~~that is eventually limited by increased soil decomposition in drier conditions~~with reciprocal controls on vegetation composition and soil chemistry at site- and microsite-scales.

4.1 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~~median 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 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~~experimental 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 systems, and further solidifies hydrology as the primary determinant of understory species distributions in wetlands.

Despite clear ~~broad~~ site-scale hydrologic controls on understory richness, we also observed a dominant microsite-scale influence on community composition. ~~Our~~Both NMDS analysis and Bray-Curtis dissimilatory indices 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 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 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~~We suggest that the presence of microtopography increases overall site richness, a finding supported by similar studies of richness and microsite variability (Beatty 1984, Vivian-Smith, 1997; Bruland and Richardson, 2005). Therefore, microtopography greatly expands potential hydrologic and associated habitat niches. It would be informative to take a larger scale perspective by assessing the importance of each microsite to overall landscape level biodiversity, and through comparison of hummock species compositions to those of surrounding upland forests.

Mis en forme : Anglais (États-Unis)

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~~.~~ (Figure 3). 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 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 a 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~~Figures 4 and S4). Perhaps these are not surprising results given that distance to water table may be the most important control on 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~~Conner 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 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.

4.2 4.2 Controls on tree biomass

Although not a significant direct association, we found some indirect evidence that links site-scale hydrology to tree basal area. The driest sites (lowland sites) had the greatest basal area~~,~~ (Table S2), 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 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~~.~~ (Figure S5). 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 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~~5) 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~~In general, 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~~2004). 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.~~; Figure 6). Chloride is commonly used across scales and systems as a hydrologic tracer to evaluate hydrologic storage and transport processes (Kirchner et al. 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~~In northern bogs, encroachment or presence of woody vascular plants can dramatically increase evapotranspiration losses (Takagi et al. 1999, Frankl and Schmeidl 2000~~)~~), aligning with results here and 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 also indicates directional concentration from hollows to hummocks. 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~~However,~~ in the Everglades, FL (Wetzel et al. 2005, Ross et al. 2006).

In addition to evapoconcentration,~~ the~~ mechanisms of increased nutrient availability in hummocks 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~~Both the mass of absorptive fine roots (Li et al. in press) and mycorrhizal activity ~~is~~are 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 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 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 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~~, which contrasts with findings ~~are in contrast to most~~from other 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 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 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. Additionally, sample drying procedures may have led to relatively greater oxidation of ammonium in hollow samples compared to hummock samples.

Results for SO_4^{2-} were also in contrast to what we expected~~. We~~, as we had 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 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~~sulfides (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~~2007), and also ~~in stark opposition to expected results from~~contrast with coupled sulfur-hydrology-microtopography modeling exercises for freshwater systems (Frei et al. ~~2012).~~2012). Similar to nitrate, some of this discordance may be attributed to soil drying procedures, which could have allowed time for oxidation of previously reduced sulfur compounds in hollow samples.

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~~.~~ (Figures S7 and S8). 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 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. Apart from field observations, we cannot verify this assumption, but believe it is reasonable considering the relatively small site areas and flat terrain. We concede that this approach may be inappropriate for other systems with less organic soils or more 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~~determinant of soil chemistry 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 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 5 Conclusions

This work provides support for ecosystem engineering by vegetation in ~~swamps~~forested wetlands, where vegetation capitalizes on and amplifies 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~~understory species richness, tree 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,~~ preferentially occupy and reinforce hummock structure, and 2) hummock and hollow microtopography yields predictable patterns of ~~understory richness, biomass,~~vegetation 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.

Author contribution

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

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 (m^2 per 300 m^2)**	**Hollow basal area (m^2 per 300 m^2)**
D1	~~23~~2.33	0.36
D3	~~26.00~~2.60	0.~~26~~27
D4	~~20.37~~2.04	0.11
L1	0.16	~~20.09~~2.01
L2	no data	~~17.55~~1.76
T1	~~27.13~~2.71	0.17

810

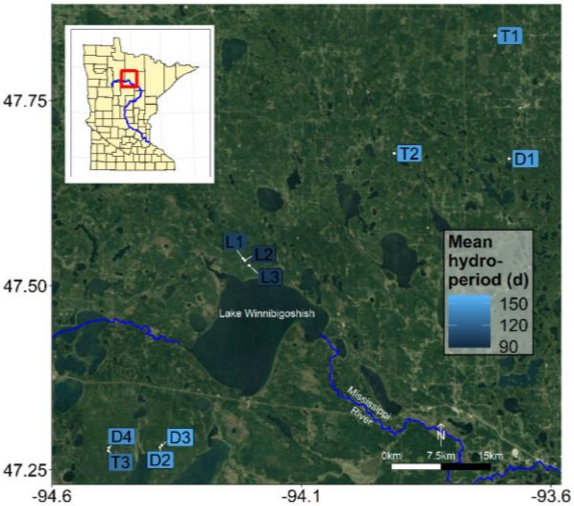
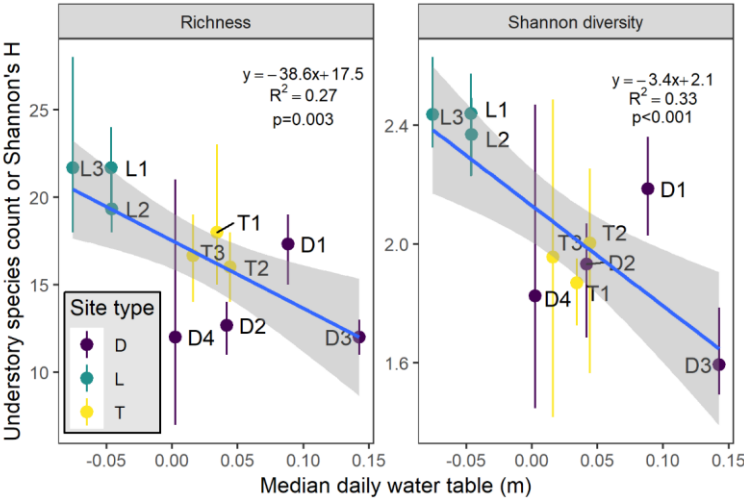


Figure 1: Map of the ten black ash study wetlands in northern Minnesota, U.S.A., with sites colored by average annual hydroperiod (i.e., number of surface-inundation days per year from the May to November) for 2015–2018. © Google Maps 2019.



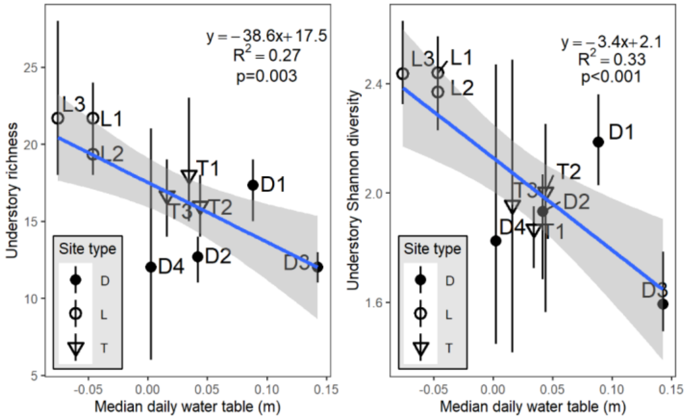
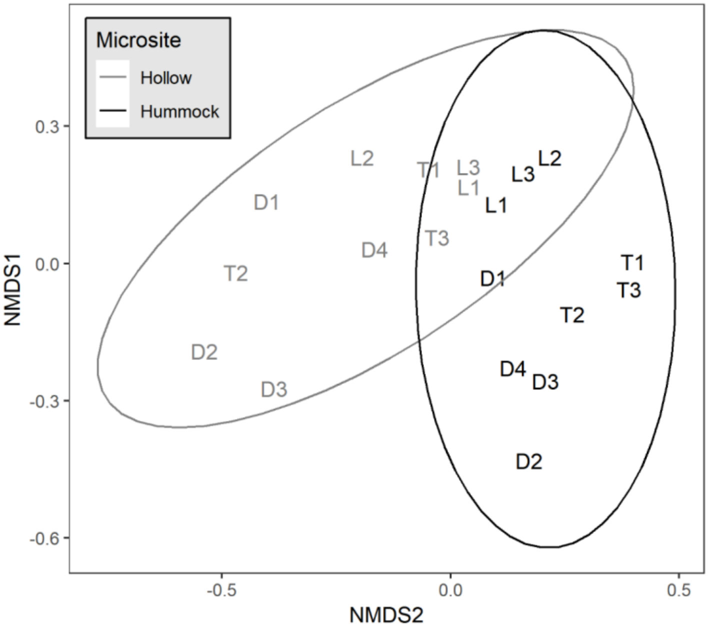


Figure 2: Plot level richness or diversity, aggregated by site, as a function of site level median water table relative to the ground surface (negative values indicate belowground). Letters and symbols refer to hydrogeomorphic site types: D refers to depression sites, L refers to lowland sites, and T refers to transition sites. Vertical bars on points indicate bootstrapped 95% credible intervals

820 **calculated from the three plot measurements per site. Linear regression model results presented are also shown. Hydrology summaries provided in Table ~~S3~~S2.**



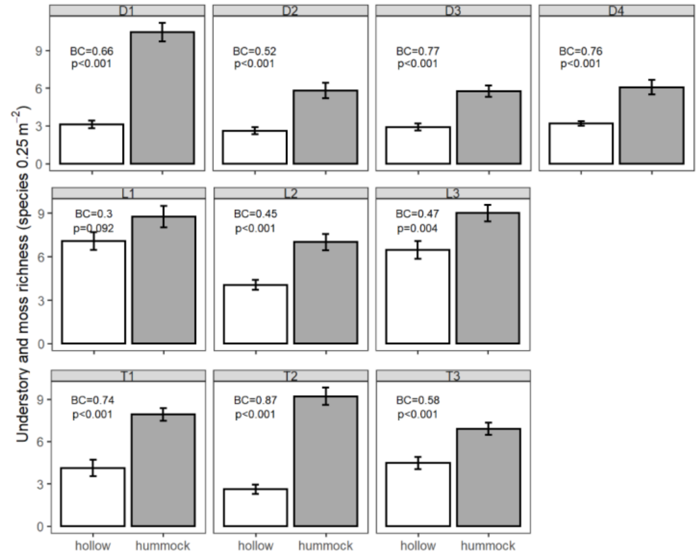


Figure 3: ~~NMDS ordination of~~Combined understory ~~vegetation communities, grouped by sites (text labels)~~vascular and ~~microsites, with hummocks in black~~moss richness hummock and ~~hollows in grey. Ellipses~~hollow comparison. Text values indicate ~~95% credible intervals around the group centroid.~~

Mis en forme : Anglais (États-Unis)

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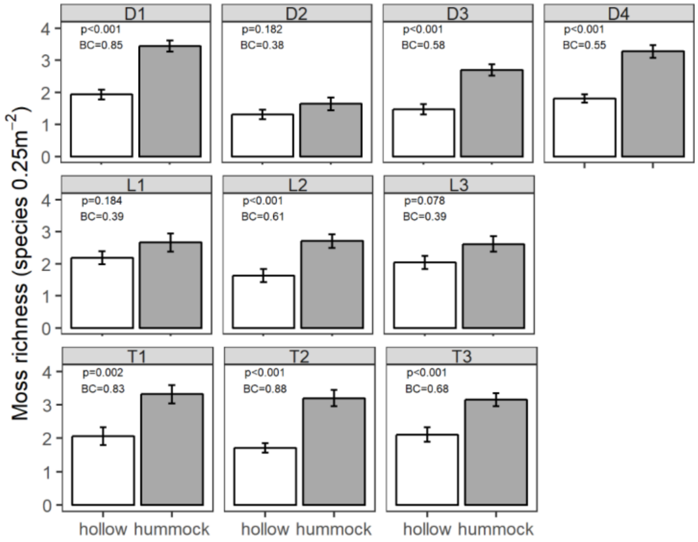
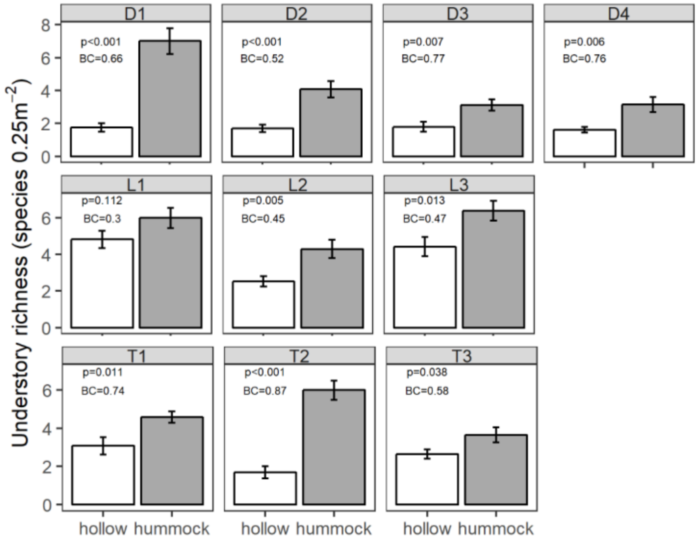

Moss richness (species 0.25m^{-2})
D1
p<0.001
BC=0.85
D2
p=0.182
BC=0.38
D3
p<0.001
BC=0.58
D4
p<0.001
BC=0.55
L1
p=0.184
BC=0.39
L2
p<0.001
BC=0.61
L3
p=0.078
BC=0.39
T1
p=0.002
BC=0.83
T2
p<0.001
BC=0.88
T3
p<0.001
BC=0.68
0
1
2
3
4
hollow
hummock


Understory richness (species 0.25m^{-2})
D1
p<0.001
BC=0.66
D2
p<0.001
BC=0.52
D3
p=0.007
BC=0.77
D4
p=0.006
BC=0.76
L1
p=0.112
BC=0.3
L2
p=0.005
BC=0.45
L3
p=0.013
BC=0.47
T1
p=0.011
BC=0.74
T2
p<0.001
BC=0.87
T3
p=0.038
BC=0.58
0
2
4
6
8
hollow
hummock

~~Figure 4: Understory species richness on hummocks~~Sorensen dissimilarity indices and ~~hollows for (top) mosses and (bottom) understory vascular plants for each study site~~Welch's two sample t-test results. 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.~~.

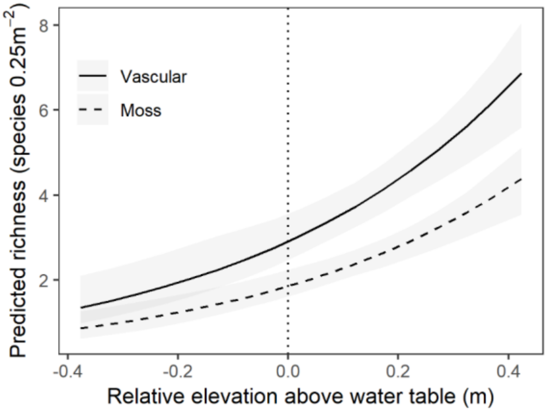
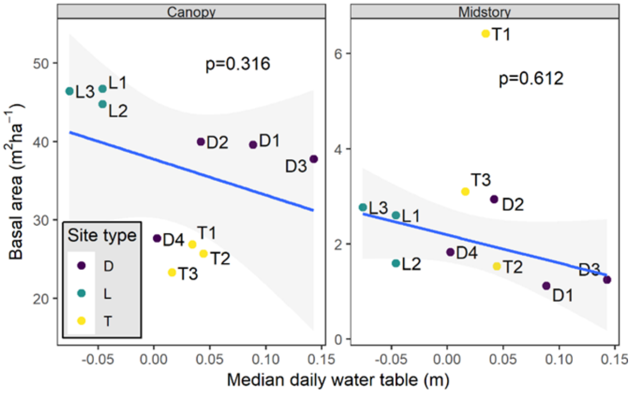


Figure ~~5~~4: Predicted understory species richness as a function of elevation above mean water table based on GLMM model without random site effects included, split by moss and vascular species components. Shaded ribbons indicate 95% confidence intervals about the estimate.



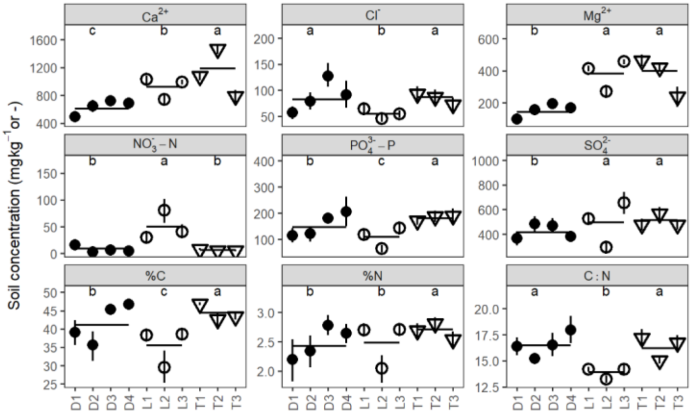
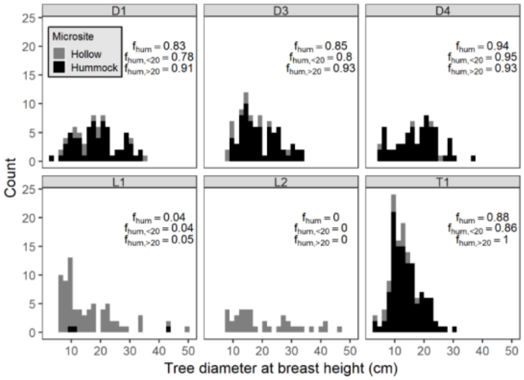
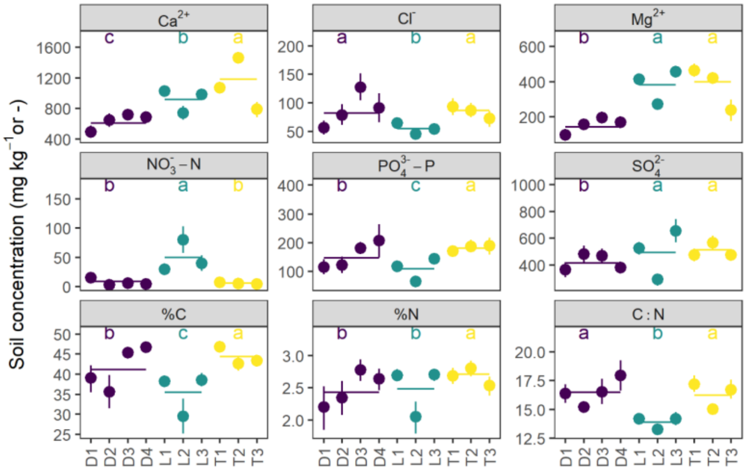


Figure ~~6 Site-scale basal area in the canopy and midstory versus median water table linear regression, with sites labeled and colored by hydrogeomorphic category. p-values indicate p-values for linear regression and shaded region indicates 95% credible interval about the best-fit line. Stand structure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



~~**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 ($f_{hum,>20}$).**~~



~~Figure 8~~5: Average soil extraction concentrations for every site and solute analyzed. ~~Colors indicate~~ Shapes correspond with site hydrogeomorphic 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.

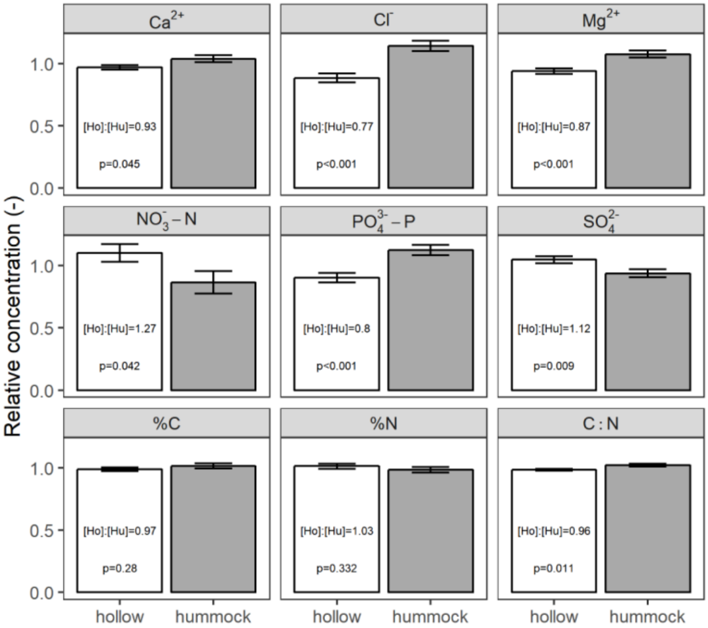
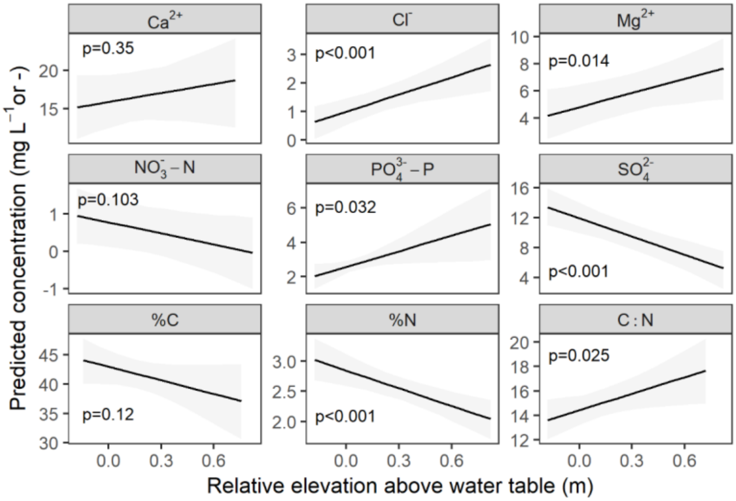


Figure ~~9~~6: Across-site comparison between hummocks and hollows of relative concentrations of soil analytes. Relative concentration for any particular sample is normalized to its site average concentration. Text in each panel refers to the across-site ratio of hollow to hummock relative concentrations 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.**~~