Journal: HESS
Title: A microtopographic signature of life: Ecohydrologic feedbacks structure wetland microtopography
Author(s): Jacob S. Diamond et al.
MS No.: hess-2019-239
MS Type: Research article

Authors Response

Dear HESS editorial review board,

We thank the reviewers and editors at HESS 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 two anonymous reviewers and Dr. Lieffers, 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

Response to Short Comment

Victor Lieffers:

We thank Dr. Lieffers for his detailed review of our manuscript. We have broken out your individual comments and responded to each accordingly. We hope that our comments address and clarify any issues or concerns that they may have.

Overall comments:

SC1: I am, however, not convinced that this work shows 'that the structure and regular patterning of wetland microtopography is an autogenic response to hydrology.' On (L635-36). There are a variety of external influences such as frost/ice, severe disturbance in drought, floods, wind that could be influencing these wetlands.

AC1: We acknowledge that other external influences may influence microtopography in these systems. Black ash wetlands are a relatively understudied ecosystem relative to other wetlands, but we believe we can discount each of the listed influences as being more important than hydrology for the maintenance and persistence of hummock hollow microtopography.

Frost and ice: it is possible that frost preferentially affects soil expansion and contraction in these systems thereby leading to regular horizontal and vertical patterning, but this mechanism would have to persist throughout the growing season and among years. We expect that the organic nature of these soils and the regular inundation in the growing season would likely erase any frost-based microtopographic signature on a yearly basis. In contrast, the observed persistence of microtopographic features in our system and in numerous other documented wetlands more strongly point to a balance between increased soil organic matter production from vegetation on local high points that is eventually balanced by increased soil organic matter respiration due to aerobic conditions. This mechanism would persist throughout years, and would unlikely be erased due to frost upheaval.

Drought: we are unsure through what mechanism that drought may induce microtopography in wetlands, but of course, we are open to alternative hypotheses.

Floods: while our wetlands experience regular inundation throughout frost-free season, they rarely experience high-energy flood events that could reorganize soil structure.

Wind: black ash wetlands are susceptible to tree fall by extreme wind events, which can create microtopography (indeed, as initiators in our conceptual model, Figure 1). However, we suggest that the patterns of tree fall alone are highly unlikely to explain our observation of regular spatial patterning (i.e., common spacing between hummocks, and a characteristic hummock size).

A less complex hypothesis, and one that we believe is supported by our multiple lines of evidence, and by previous studies in wetland systems, is that hydrology (the primary physical control in wetlands) is a major driver of microtopographic structure through our proposed feedbacks.

SC2: Some of the basic questions posed in this study seem rather simplistic and most folks who have worked in peatland systems would already know this. Indeed figures 5, 6 and 7 would be predicted by simple logic before collecting and analyzing such data. As a consequence, I rate the novelty of this work as rather low. I suggest that the authors refocus their data on the detailed spatial arrangement of hummock and hollows and stay away from this autogenic feedback idea – because frankly, I am unconvinced from what is presented.

AC2: The authors strongly disagree that the results presented could have been easily ascertained a priori. We are unsure what simple logic the commenter is referring to with regards to Figures 5, 6, and 7. In this work, we uniquely extended concepts from landscape ecology to assess microtopographic patterning and potential feedbacks, a novel application. Hence, our unique contribution is the observations of patterned signatures that are reflective of coupled feedbacks. We systematically test these signatures with commonly applied diagnostics by evaluating elevation bimodality, characteristic patch spacing (hummock nearest neighbor distances), and truncated hummock size distributions. We have made edits in the Introduction and throughout to more clearly point out that underlying processes can be inferred through spatial pattern analysis. Specifically, we have simplified our description of processes and re-crafted language throughout to more specifically link our (well-established) methods to our modes of inference.

Figure 5, shows elevation bimodality at our sites (with the strongest bimodality occurring in our wettest sites and the least bimodality occurring in our driest sites). We did not know a priori that 1) we would observe any bimodality at our sites, or 2) that hydrology would be as strong a predictor for the differences in bimodality and hummock area among sites. Bimodality on its own is evidence of autogenic feedbacks that create and maintain hummock structure, as has been illustrated in analogous non-forested systems, but is by no means a commonly measured or reported finding in the literature. We also reiterate that our finding of elevation bimodality being limited to our wettest sites further indicates that hydrology is a major driver of topographic divergence into hummocks and hollows. Again, we have clarified how we arrive at our inference in the Introduction, and added a section in the Discussion "Evidence for patch self-organization" to more thoroughly walk through our findings.

Figure 6 is a direct test of whether surface microtopography represents subsurface mineral microtopography or whether it is decoupled from subsurface structure (thereby indicating it is generated by surface processes, supporting our hypotheses), but we did not know whether this would be true before we tested it. We also did not know what the distribution of organic matter depths were in these wetlands because this is invisible to the eye and inherently non-obvious.

Figure 7 provides direct support for hummock height being a function of local hydrologic conditions, both at the system and at the microsite scale. If this were simple logic, according to the commenter, then it would also be simple logic that hydrology drives hummock structure, thereby negating the first comment presented indicating that the results were unconvincing in this regard. We however agree with the original commenter's first comment that there could be many reasons for wetland microtopographic structure, but we hypothesized that it was driven by hydrology and we directly tested that hypothesis here.

We have made revisions throughout the manuscript, but primarily in the Introduction and Discussion, more clearly present our evidence, which we contend supports the autogenic hypothesis of hummock development.

SC3: I would have expected some more information on the types of vegetation on the tops and sides of hummocks vs the sides and bottoms of hollows.

AC3: We are now referencing a companion text (in review) that directly measures vegetation communities and soil chemistry on microsites throughout our study systems. In that work, we find further support for the hypotheses presented here (i.e., that hummocks are maintained by vegetation through an organic matter production-respiration feedback that depends on hydrology). We reference this companion text as Diamond et al., 2019 throughout the document.

SC4: L141 Prediction 1 that elevation distribution will be bimodal in a hummock hollow system seems to be a rather mundane prediction as you selected the study site with such characteristics.

AC4: We did not select study sites with elevation bimodality a priori; in fact, we would argue that three of our sites exhibited very weak bimodality. We were working in these systems as part of a separate, larger work studying black ash systems in detail due to their vulnerability to loss from the emerald ash borer (Diamond et al. 2018, Slesak et al. 2014, Looney et al. 2015). In the course of our work, we observed the hummock-hollow microtopography of these systems, which we selected for further study. We are also unsure how one would know if a system had bimodal elevation without actually measuring it.

SC5: L145 Prediction 2. This would only be relevant with shallow peat. There are plenty of studies that show that peatlands often spread across the landscape over thousands of years of peat accumulation so there is very little reason to think depth is that important, after a minimum depth of peat is achieved.

AC5: What is the minimum peat depth that the commenter thinks is relevant to our hypothesis? We, of course, could not know ahead of time what the peat depth of these systems were. For instance, peat depths varied by over 1m across our sites, and although all sites had some degree of organic soil, not all sites had actual peat; some were more mucky mineral, and some were more sapric. By no means are all black ash wetlands considered peatlands, but that we observed more microtopography in sites with the most organic soils (which corresponded to wettest sites) is further evidence for our proposed feedback to the vertical structure of microtopography. (Plant production of organic matter preferentially builds up around plant stems/roots builds, but this production is ultimately constrained in height by aerobic soil respiration when the hummock becomes too dry).

SC6: L153. It would be good to have a better understanding of the negative process that maintains a hollow part of the landscape. If there is not a powerful process that tears these substrates apart, what will maintain the hollows over the decades?

AC6: We have clearly not done an adequate job of explaining the hypothesized feedbacks that maintain hummock-hollow structure in wetlands, and will improve this in the upcoming revisions. We do not believe there is a "powerful process that tears [hollow] substrates apart". In our conceptual model, hollows are areas of mean/base elevation within the wetland, whereas hummocks are local high points raised above this mean/base elevation. Hence, hollow maintenance is essentially just lack of "invasion" by hummocks, which themselves cannot grow to infinite size (as shown in Figure 8 and 9) due to negative feedbacks to their expansion (e.g., crown competition for light).

SC7: L181-190 I did not really understand the description of the hydrology of these sites. These are quite generic descriptions of these landforms. It is would be nice to know more about the freeze-thaw cycle of the peat and how this might be a factor in hummock hollow distribution and the types of disturbances that might periodically affect these wetlands. What is the frequency of extreme flooding and drought in these systems? Could flooding be a primary reason for maintenance of patterns and hence be linked to wetness? What is the lateral flow of water through the peatlands and does this have any effect on the physical movement of the hummocks during times of extreme flood? Further, later in the paper there is a statement that hummocks are often associated with an ash stem. Perhaps this is an important mechanism that should have been explored in your spatial study.

AC7: We will add some information about freeze-thaw cycles in the upcoming revision, but note that black ash wetlands are understudied with respect to most other northern peatlands, so much remains *to be discovered. We would be open to a mechanistic hypothesis that links flooding to observed patterns (hummocks in these systems do not physically move to the best of our knowledge), but we consider our conceptual feedback model to be appropriate and supported by evidence presented here, in the companion paper in review that we will now reference, and in other low-energy wetland systems. Lateral flow through these wetlands (not peatlands) is primarily groundwater, and other related work indicates that this is a small fraction of the total water budget compared to precipitation and evapotranspiration. The fact that hummocks are associated with an ash stem is actually the primary rationale behind our proposed feedback model and subsequent hypotheses, and we reference this throughout the manuscript. We will be more explicit in revisions to address this issue.*

SC8: L195-205 What is the density of trees? Canopy cover or leaf area index of the forest? I would like to know what sort of substrate this forest is growing on. Is it Sphagnum peat or Carex or feather moss? Paper like this needs some discussion of the mosses/herbs and graminoids that cover the ground surface in such places.

AC8: This data is presented in our companion paper, but we will include some basic information here for reference in the Methods section. We have added forestry and understory information as requested in the Methods section.

SC9: L319 Using a steel rod and resistance to pushing down - how was buried wood distinguished from mineral soil at the base of the peat? If wood was encountered, then averaging with 3 other nearby spots will produce an underestimate of the true depth. Incidentally, it is traditional to use a spoon-like end on such probes to bring up a bit of mineral soil to confirm that it has been reached.

AC9: Buried wood was clearly distinguishable from mineral soil by touch and when it was encountered, the rod could easily penetrate further in the nearby vicinity to reach the mineral layer. We are removing this sentence from the next revision because it overcomplicates the issue…buried wood was rarely encountered in our fieldwork. This sentence was removed.

SC10: L325-30 You did not really tell us where the well was positioned relative to hummock hollow system. What was the control height to which you were defining the water level? I could not figure this out from the datum description.

*AC10: We placed the well at “*the approximate geographic center of each site” (Line 329–330). “We referenced each site to a datum located at each site’s base well elevation.” (Line 227). *So, the well was essentially in the middle of the site and we referenced all elevation to the base of the well. We will try to be more clear in revisions. We added clarifying text to this section “Ground surface at the well served as each site’s datum (i.e., elevation = 0 m).”*

SC11: L339 What is the elevation of the well and what is ground surface (mineral soil or top of hummock)?

AC11: The elevation of the well is our datum, so 0 m, and ground surface is the boundary between the soil and the atmosphere. See above comment.

SC12: L141 The hydroperiod is based upon 1 year (I think?). Given the dynamics of moisture from one year to the next, is this long enough? Also was this a typical year. I expect that very wet years might influence the dynamics of these stems for years after.

AC12: The hydroperiod is based on 3 years of data (2016–2018); we will be more explicit here. We added the parenthetical (2016–2018) to this sentence for clarity.

SC13: Fig. 5. Please remind us what the O elevation means.

AC13: We will clarify in the figure caption. We added that 0 elevation is the elevation is the base of the well.

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.

Overall comments:

RC1: I find the introduction to be quite lengthy though (see comments below). I also found that the introduction could be better organized to more clearly present the hypotheses.

AC1: We will revise the introduction to be shortened and to more clearly present the hypotheses, leaving any mention of hypotheses until the last paragraph; see responses to comments below. We have thoroughly revised the Introduction as requested.

RC2: It seems to me the authors have mainly described the distribution (spatial and size) of microtopographic features and potential drivers of microtopographic features (e.g. water table depth, subsurface mineral soil depth), but have not, in my opinion, provided substantial evidence that these features lead to self-organization as suggested (L502-507). Particularly the feedbacks between plants and microtopography was not even studied, although it was mentioned frequently in the introduction and speculated about in the discussion. I believe the author's story would be much stronger, in regards to self-organization, if some attempt to quantify plant communities was made.

AC2: We agree with the reviewer that without some more context that the results presented are not in of themselves evidence of hummock self-organization. We will now discuss in text that this manuscript is coupled to a sister study (in review) that examined in detail the vegetation communities and soil chemistry of hummocks and hollows in these wetlands. That work further supports our hypothesis that hummocks are indeed self-organizing as a biotic response to inundated conditions. The depth and breadth of results from both studies are too much to present in one manuscript, thus the two separate manuscripts. We will emphasize this and that our overarching objective for the coupled studies was to explore patterning and its drivers. We also realize that the some of the diagnostics that we used to assess self-organization (i.e., nearest-neighbor distances, size distributions, bimodality) may be unfamiliar to some of the audience. However, these are commonly used in the literature as strong indicators of self-organization and feedbacks, so we have more effectively conveyed their usage as such in the Introduction and throughout the manuscript.

Specifically, we will revise the introduction to more clearly establish how diagnostics from the field of landscape ecology can suggest patterning mechanisms but that measures of patterning should be coupled with those of hypothesized drivers. We will then scope this paper's objective as focused on the former while referencing our sister study as one that focuses on the latter. Our overarching objective was to use both studies to explore microtopographic patterning and its drivers. We will also re-organize discussion text to first present our observations, emphasizing patterning and how it varies within and across systems as a function of water table position, and then present what the observed patterning suggests using well-established diagnostics from landscape ecology and when considering our complimentary observations (from the sister study) on vegetation and soil properties on hummocks vs. hollows. Again, we heavily revised the Introduction to more clearly and simply state that the diagnostic measures that we use to evaluate hummock self-organization have strong basis in the literature. While we also edited much of the Discussion text, we also believe that the edits to the Introduction more readily prepare the reader for our interpretation of results in the Discussion.

RC3: It would be interesting to see a study that actually looked at formation of microtopographic features over time (maybe using a chronosequence).

AC3: We agree, but these features can take decades or more to form. Some work has been done by Benscoter et al. (2005) after fire in peat bogs, and some work also has been done using geochronology in salt marshes by Stribling et al. (2007). We have now added discussion about the difficulty in such studies, but that the few have done it have shown further support the general hypothesis that wetland hummocks are relatively stable, long-lived, and generated and sustained by plant action. This specific text was added to the discussion "Future efforts could leverage time-series observations of hummock properties (e.g., area, height and volume), but we note the likely decadal time-scales required to detect hummock growth or shrinkage (Benscoter et al., 2005; Stribling et al., 2007)."

RC4: I suggest the authors acknowledge some of the limitations of the study in testing the self organizing hypothesis (primarily no plant-soil-microtopography feedbacks were measured, and changes in hummock hollow size/distribution etc. was not measured).

AC4: We will be sure to include more limitations of the inferences allowable by this study in the Discussion and Conclusion. We note again that we will also reference our companion study that does measure plant and soil properties of these systems. We reference our companion study, Diamond et al., 2019, throughout to support our inferences made with techniques used in this work.

RC5: I would like to see more reference to other forested wetlands, as I feel that was somewhat lacking.

AC5: We conducted extensive literature reviews as part of this work, and one of the reasons the findings are novel is that this is one of the few instances of microtopography being measured in this way in forested wetlands. The primary systems that have focused on self-organizing microtopography have been Sphagnum moss bogs, fens, and marshes.

Detailed Comments:

Abstract:

RC6: I find the second half of the abstract to be quite vague with no data/percentages or any other time of numerical evidence for all the findings the authors "showed". I would suggest putting a little bit more information on the actual findings in the abstract so the reader has something to pull them in.

AC6: We will update the abstract to include more specific numerical findings as suggested. Updated to include more numerical findings as requested.

RC7: Each of the last six sentences begin with "we. . ." Although I don't mind some use of personal pronouns, this seems excessive and detracts from the writing. I would suggest changing at least a few of the sentence structure to avoid this.

AC7: The authors acknowledge the comment and will reconsider the stylistic choices for the use of "we".

RC8: What is meant by "base elevation"?

AC8: We will clarify that "base elevation" refers to the average elevation of the hollow surface. We changed this to be "low" elevation instead of base elevation.

RC9: L27 What is meant by "reactive surfaces" of hummocks? Reactive with what? Does this mean biogeochemically reactive? Or reactive with the plants?

AC9: We will clarify that "reactive surfaces" refers to the effective soil surface for redox gradients and exchange interfaces. Because many of the coupled redox reactions (e.g., nitrification and denitrification) happen at soil-water interfaces (where there are steep gradients in reactant concentrations), the expansion of the effective surface area enhances overall wetland biogeochemical reactivity. Changed to "Hummocks increase the effective soil surface area for redox gradients and exchange interfaces in black ash wetlands by up to 32%..."

RC10: L27-28 What is meant by specific yield in reference to surface water dynamics?

AC10: Specific yield is a common term in hydrology which can be (for wetlands) defined as the ratio of input (precipitation) or output (ET) depth relative to the induced water level rise or fall (e.g., if 1 inch of rain causes a 2 inch water level change, specific yield = 0.5). For the sake of brevity in the Abstract, we will most likely keep this term as is, but more clearly explain it in the Broader Implications section, where the term is introduced.

Introduction:

RC11: The introduction is too long and needs to flow better. Some of the paragraphs become quite redundant and could be greatly shortened or condensed. For example, the paragraph from L63-77 discuss positive and negative feedback loops on formation and maintenance of microtopographical features. L98-115 the authors again discuss feedback loops with very similar. It seems like this could be condensed into one paragraph or two smaller paragraphs (one for positive feedbacks and one for negative feedbacks, or one paragraph for both).

AC11: We will make efforts to condense and simplify the explanation presented in the introduction as it is clearly a source of confusion. We note that there are two types of feedbacks discussed in the two paragraphs: (L63-77) refers to horizontal organization of microtopography and how to diagnose patch dynamics, and (L98-115) refers to vertical organization of microtopography. Still, we will clarify and simplify these points, which will hopefully help convince readers that our methodology for diagnosing self-organization is based on precedent and substantial theory. We have substantially shortened and clarified the Introduction as described here.

RC12: L86 "which are frequently modelled with powerlaw functions". I am not sure what this adds to this paragraph, if anything I found it to be a disruption to the flow of the paragraph. L89-97 typically hypotheses are presented in the final paragraph. In this case the authors present a hypothesis, and then go onto numerous more paragraphs describing feedbacks in the formation of microtopography. I would suggest moving hypotheses to the final paragraph after all justification for the hypotheses has been given previously.

AC12: We understand the frustration with the flow of the introductory narrative, and we will work to simplify and clarify. Briefly, we will note that introducing modeling of size distributions for hummock patches provides insight into the feedback processes that maintain their sizes: power law distributions indicate system-scale negative feedbacks to hummock expansion, and exponential distributions indicate hummock-scale negative feedbacks to hummock expansion. Further, as mentioned in a previous and later response, we will hold presentation of hypotheses for the end of the introduction. We have revised as described and also left all hypotheses to the end of the Introduction.

RC13: L121 "unsaturated soils compared to unsaturated soils"...change one of the unsaturated to saturated

AC13: Thank you for finding this error; we have corrected it. Corrected.

RC14: L129-135 I am not sure what this paragraph adds to the introduction. Do the authors plan to test the null hypothesis? If so, why not just move/incorporate that first sentence into the concluding paragraph (with other hypotheses, as already suggested)? I would also suggest stating all the hypothesis similarly. Either state all as null or state as the alternate, I prefer the latter.

AC14: We do test this hypothesis specifically (hypothesis 2), line 145. Either way, this is clearly confusing and we will work to clarify the Introduction. We will now reserve all mention of hypotheses for the end of the introduction.

RC15: L153 "regularly spatial patterned" awkward wording.

AC15: Acknowledged, but this is a common term in the self-organization literature, so we have elected to keep it as written.

RC16: L136-165 Here the authors do provide a detailed list of their hypotheses, which is what I would expect. But mixed in with all the other hypotheses the authors present in the introduction (scattered throughout) it is confusing as the reader to know which hypotheses are being tested and which are not. I think all mention of hypotheses should be removed from the introduction, other than the final paragraph. The authors should streamline the introduction to better guide the reader through the main arguments they are making that set the stage for the hypotheses in the final paragraph.

AC15: All of the hypotheses listed here are the ones we explicitly tested. We will clarify the rest of the Introduction so there is no confusion on this matter. We think that this upfront clarification may help with all of the rest of the comments throughout this review, as well. Hypotheses were clarified as suggested.

Methods:

RC16: L175 I don't think ET was previously defined. . ..it is actually defined on L190.

AC16: Thank you, we will fix this. Now defined.

RC17: L319-320 I am confused by this sentence. The authors say there was a clear difference in resistance when a mineral soil layer was reached. So the authors are saying that the rod method is quite unreliable? Or are the authors just stating that this is why they took 2-3 measurements per area? Just want to clarify.

AC17: The rod method is very reliable, but we wanted to acknowledge that occasionally we would hit some buried wood or a tree root (which was obvious by feel). In these rare instances we would sample depth in the near vicinity to avoid the root and to ensure we were reaching a mineral layer. We will remove this sentence because it just adds confusion and is not important to the results. Sentence was removed.

Results:

RC18: L421-422 I don't see a figure showing seasonal water table depth

AC18: Table 2 contains the hydrology metrics for each site. We do not have a figure for seasonal water depth because it is not a result that we thought contributed to the overall manuscript. We can provide a supplementary figure of water table time series if the editors deem it necessary, but all relevant hydrology metrics used are presented in Table 2.

RC19: L423-433 It sure would be nice if the authors had real data on hummock plant species taxonomy, biomass, etc. It would strengthen the manuscript significantly and really help support some of their conjectures on plant feedbacks with microtopography. Do the authors have any data on this? If not, is this section necessary, as it is observational and not technically data driven?

AC19: We do have this data in a companion study that we will now reference and summarize findings in the discussion. The companion study is now referenced in the Introduction to justify some of our hypotheses, Methods to list vegetation findings, and Discussion to support our inferences from this work.

RC20: L460 Why "possibly"? It either is or isn't. Looks to me that L2 is definitely not and D1 is not if you are considering alpha of P<0.05 as significant. It is if you are using P<0.1 as significant. I actually am not sure I saw any mention of that in the methods section..

AC20: We agree with the reviewer have deleted the word "possibly" and replaced it with "except for D1 and L2". Changed as described.

RC21: L471 Add "7" to "(Figure)". It would be helpful to also identify here that the authors (I think) are referring to the top panel of Figure 7.

AC21: Thank you for finding this omission; we have clarified as requested. Fixed all missing figure numbers.

RC22: L487 Add "8" to "(Figure)".

AC22: Thank you for finding this omission; we have clarified as requested. Fixed all missing figure numbers.

Discussion:

RC23: L520 which figure?

AC23: This should be Figure 6, thank you for finding this omission. Fixed all missing figure numbers.

RC24: L524 what ecosystem/wetland type is Watts et al. 2014? In forested wetlands, there may be much more propensity for formation of microtopographic features, particularly because trees typically root more heavily in the elevated/aerated hummocks which likely further raises the elevation of these features. I wonder how that would differ in a different wetland type.

AC24: The wetland in Watts et al. 2014 is the ridge-slough mosaic of the Everglades, FL, and have now added this clarifying information. We agree with the reviewer that it seems reasonable that there may be more propensity for formation of microtopographic features in forested wetlands, but most research on this topic has occurred in non-forested wetlands, so there are still open questions in this regard. We suggest that a major difference between microtopography in forested versus non-forested wetland systems will be the size distributions and spacing of hummocks. In forested systems, hummocks associated with trees will likely be limited in size, exhibiting characteristic sizes and spacing due to local negative feedbacks from the crown competition. In contrast, non-forested wetland hummocks may have a much wider distribution of size classes. Negative feedbacks to non-forested hummock expansion may range from local nutrient competition effects (e.g., Eppinga et al. 2008), or system-scale inundation effects, where hummock presence increases overall water levels through displacement (Heffernan et al. 2013). We have added the clarifying information about the type of system in Watts et al. 2014 and also added text at the end of Discussion section 4.2 regarding differences. "Therefore, based on evidence and observations presented here and in Diamond et al.

(2019), we suggest that a major difference between microtopography in forested versus non-forested wetland systems will be the size distributions and spacing of hummocks. In other forested systems, hummocks associated with trees will likely be limited in size, exhibiting characteristic sizes and spacing due to local negative feedbacks from the crown competition. In contrast, non-forested wetland hummocks may have a much wider distribution of size classes, where negative feedbacks to hummock expansion may be largely due to local nutrient competition effects (e.g., Eppinga et al. 2008)."

RC25: L525 What other surface level processes?

AC25: We will be more explicit that we are referring to soil production processes that result from hypothesized feedbacks between increased organic matter production (and therefore increased soil height) on hummocks. Updated text to be: "This implies that deviations from this smooth surfaceorganic soil surfaces are related to other surface-level processes, such as spatial variation in organic matter accumulation resulting from hypothesized elevation-productivity feedbacks."

RC26: L531-534 how would you measure what "state" a hummock is in? This seems like it would be the ideal experiment to test your self organizing hypothesis, ie to test over time (or using some well thought out chronosequence of sites) the formation/change in microtopography (or repeat this study in x amount of years).

AC26: We agree with the referee that a time series experiment with and without disturbance would be ideal to test this hypothesis and we will add text to suggest this idea for future work. Hummock state could be measured through time series of production (potentially measured with hummock volume and hummock soil bulk density) and respiration (potentially measured with chamber methods). When production exceeds respiration, the hummock is in a "growing" state, and when production equals respiration, the hummock is in an "equilibrium" state. Text added: "From our feedback model (Figure 1) it seems reasonable that within a site, some hummocks may be in growing states (e.g., increasing in height over time via the elevation-productivity positive feedback) and some may be in shrinking states if hydrologic conditions have recently become drier (e.g., decreasing in height via the elevation-respiration negative feedback), the combination of which may result in a distribution of hummock heights centered around an equilibrium hummock height. Future efforts could leverage time-series observations of hummock properties (e.g., area, height and volume), but we note the likely decadal time-scales required to detect hummock growth or shrinkage (Benscoter et al., 2005; Stribling et al., 2007)."

RC27: L613 here and other places, seem to lack some of the more current publications in forested wetlands on microtopography. For instance, researchers out of John King's lab group at North Carolina State University have many numerous publications from forested wetlands in coastal NC on hummock-hollow microtopographical distribution and also effects of this on soil and plant processes. Not sure if this work would help but there seems to be only comparisons in the manuscript to northern, non forested wetlands. It would be nice to see some inclusion of more relevant literature cited.

AC27: We have now included the following recommended publications in our discussion of forested wetlands, each of which supports our conceptual model that although local organic matter production is higher on hummocks, leading to increased hummock height/volume/area, greater respiration due to unsaturated conditions eventually balances these increases:

Minick, K. J., Mitra, B., Li, X., Noormets, A., & King, J. (2019). Water table drawdown alters soil and microbial carbon pool size and isotope composition in coastal freshwater forested wetlands. Frontiers *in Forests and Global Change, 2, 7. This work provides observational support for our contention that hummocks are loci for increased soil organic matter and soil organic matter processing (respiration) relative to hollows, a finding which is also common to non-forested wetland systems.*

Miao, G., Noormets, A., Domec, J. C., Trettin, C. C., McNulty, S. G., Sun, G., & King, J. S. (2013). The effect of water table fluctuation on soil respiration in a lower coastal plain forested wetland in the southeastern US. Journal of Geophysical Research: Biogeosciences, 118(4), 1748-1762. This work similarly supports the notion that respiration is higher on drier hummock microsites compared to wetter hollows, which is a key feature of our conceptual model.

Miao, G., Noormets, A., Domec, J. C., Fuentes, M., Trettin, C. C., Sun, G., ... & King, J. S. (2017). Hydrology and microtopography control carbon dynamics in wetlands: Implications in partitioning ecosystem respiration in a coastal plain forested wetland. Agricultural and forest meteorology, 247, 343-355.

Minick, K. J., Kelley, A. M., Miao, G., Li, X., Noormets, A., Mitra, B., & King, J. S. (2019). Microtopography Alters Hydrology, Phenol Oxidase Activity and Nutrient Availability in Organic Soils of a Coastal Freshwater Forested Wetland. Wetlands, 39(2), 263-273.

These publications were added and referenced throughout the manuscript.

RC28: L629 what does EAB stand for?

AC28: Emerald ash borer, an invasive beetle that causes extreme ash tree mortality. We will add this information. Clarified as requested.

RC29: L623-631 I am thinking that some of this information would best to put more upfront in the discussion, and maybe in the introduction. The fact that the authors did not measure (or present) any vegetation data but rely heavily on their interpretation of microtopographical features is somewhat problematic. Therefore, it is important to alleviate the readers concern that there was no need to measure this. Can the authors comment on why no vegetation measurements were taken in the current study?

AC29: Yes, as noted throughout, we will reference the companion study.

RC30: L633-L638 Seems like the concluding section is too short. I think it could just be wrapped into the previous section on Broader Implications or expounded upon to make the conclusions a little more impactful.

AC30: Noted, we will consider these options in our rewrite of the Discussion. Conclusions section was eliminated and combined into broader Discussion.

Tables and Figures:

RC31: Figure 1. Add space before Incipient in caption. What is meant by soil mass? Is this specifically referring to the amount of soil or just to the soil as a whole? Also, I wonder if arrows between the incipient events are needed. For instance, tree fall could of course be caused during extreme weather events.

AC31: We will add the space. Soil mass refers to the amount of soil, which we will clarify in the caption. Done as requested.

Anonymous Referee #2:

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

Overall comments:

RC1: I find the research to be technically sound, but some of the narrative of the paper goes beyond what is directly supported and sort of distracts from the good descriptive work that the authors have done. For example, one big finding here is that degree of hummock formation is a function of inundation. (The authors' "Lowland" sites being less-developed with regard to hummocks due to intermittent inundation shows this really well). That kind of simple finding is basic but noteworthy in my opinion. I'd support the authors developing that point more and drawing in similar findings from the literature. Instead the authors often seem to veer into discussions of causal mechanisms for such patterns, and that's where I'd say they go beyond what the data collected can really support and what can really be claimed.

AC1: We appreciate that without additional context, the conclusions and mechanisms discussed in this paper may seem to reach beyond the results presented. We will do a better job in the Introduction and throughout to justify our inferences and rationale for causal mechanisms. First, we will now mention in text that this manuscript is coupled to a sister study (in review) that examined in detail the vegetation communities and soil chemistry of hummocks and hollows in these wetlands. That work further supports our hypothesis that hummocks are indeed self-organizing as a biotic response to inundated conditions. We also realize that some of the diagnostics that we used to assess self-organization (i.e., nearest-neighbor distances, size distributions, bimodality) may be unfamiliar to some of the audience. However, these are commonly used in landscape ecology literature as strong indicators of self-organization and feedbacks, so we will be sure to more effectively convey their usage as such in the Introduction and throughout the manuscript. We further believe that addressing the causal mechanisms is what makes this work relevant and interesting because these mechanisms are present in most wetlands, and therefore the invoked feedback loops are applicable in most wetlands to understand vegetation-soil-water feedbacks. Last, we agree that we could emphasize our finding of less microtopographic structure in drier sites; indeed, this finding is consistent with our proposed causal mechanisms.

Specifically, we will revise the introduction to more clearly establish how diagnostics from the field of landscape ecology can suggest patterning mechanisms but that measures of patterning should be coupled with those of hypothesized drivers. We will then scope this paper's objective as focused on the former while referencing our sister study as one that focuses on the latter. (The extent of results from both papers precluded presentation in one paper.) Our overarching objective was to use both studies to explore microtopographic patterning and its drivers. We will also re-organize discussion text to first present our observations, emphasizing patterning and how it varies within and across systems as a function of water table position, and then present what the observed patterning suggests using well-established diagnostics from landscape ecology and when considering our complimentary observations (from the sister study) on vegetation and soil properties on hummocks vs. hollows. We have thoroughly revised the Introduction as suggested to more clearly present our hypotheses and rationale for using the (well-established) methods to infer process from pattern in these systems.

RC2: That leads to some slightly overstated conclusions, such as on Line 634. I agree that structure and pattern were well described in a new and interesting way. However, I disagree with the idea that drivers of wetland microtopography were detailed in this study; some leads were generated here (hummocks are not probably not a mere addition to subsoil microtopography and it seems to be all about hydrologic regime. and the authors are clearly aware of the many candidate parameters that could affect hummock formation... they simply were not studied in detail within this particular paper).

AC2: We will temper our conclusions to more accurately reflect what was specifically found in this work (i.e., by focusing on specific patterning and patch metrics). In our edits to the Introduction and Discussion, we will also more strongly present that in this work we aimed to infer process from pattern, using site differences in hydrology as a test of our hypothesized driver for microtopography. We note again that this work has a companion study (in review) that more thoroughly addresses drivers and consequences of wetland microtopography in these systems, the results of which are bolstered by analogous findings in non-forested wetlands. We have slightly tempered our conclusions as suggested, but also believe that our revisions to the Introduction and our reference to supporting results in a companion study help bolster our arguments presented.

RC3: I think the Intro and discussions of this paper need to be steered back toward the descriptive results at hand rather than the often vegetation-based mechanisms that *might* be at work. I tried to suggest a few changes that would help that shift in my comments below.

AC3: We appreciate the Referee's intention here, and we will reorganize and edit the Introduction and Discussion to better prepare the reader for the results presented and the mechanisms invoked; see AC1. Edited as discussed. We note that the objective was not for the results to be simply descriptive, but instead for the results to support a (very well-established) "process-from-pattern" approach that we believe is now more clearly described.

RC4: The title is too broad and emphasizes the part of this work that is less known (i.e., the mechanistic nature of feedbacks that maintain hummocks); and this is about hummocks in Fraxinus nigra forests, as opposed to all other types of wetland microtopography so more specificity is warranted in the title.

AC4: We have changed the title to: "Pattern and structure of microtopography implies autogenic origins in forested wetlands". While we still believe that our results are largely consistent with the original title, we have revised it to be more tempered ('implies') and specific to forested wetlands . However, we do not think that just because our study focuses on one type of ecosystem (as the vast majority of studies are) that it is limited in scope of inference. Indeed, the mechanisms invoked are consistent with microtopography studies in wetlands throughout the globe and our approach adds to these studies by using a theoretical landscape ecology perspective to further evince the self-organizing properties of wetland microtopography in forested wetlands.

Abstract:

RC3: The third sentence of the abstract introduces a complex vegetation-centric hypothesis that the current study seems unable to really address or resolve. This idea of testing microsite preference is an example of something that I would bring up in the discussion as a possible next venue for research, but raising it in the abstract seems out of place since it is certainly not at the center of this research effort.

AC3: We agree with the reviewer that this sentence is out of place with this work and we will focus the abstract on microtopography structure and patterning. We will save this type of language for future work in the discussion. Sentence was removed.

Introduction:

RC4: Very broad start to the introduction, I think the first paragraph or two could be shortened.

AC4: Acknowledged; we will rewrite this section to be more clear as to the intent of the paper. Paragraph removed.

RC5: The paragraph beginning on line 53 seems to set up two non-exclusive scenarios. plants find their preferred microsite on existing substrates or plants create hummocks. Can't it be a little bit of both? Showing that hummocks are self-organizing doesn't change the fact that various species may be "hummock specialists" once the pattern is set.

*AC5: Agreed, and we try to be mindful of this through our language in this paragraph (e.g., the words "*the degree*" in "*wetland vegetation simply preferentially occupies hummocks (*sensu* Jackson & Caldwell 1996) *versus* the degree to which wetland vegetation reinforces and maintains its own hummock microtopography"). *We do not mean to suggest that it is one or the other, but only that through examining spatial patterns of hummocks that we can make inferences about the mechanisms that lead to their persistence throughout time.*

RC6: I like the development of positive and negative feedbacks idea around lines 70-77, this is great as context for the patterning, even tho I don't think the present approach really allows us to discern what mechanisms are at play.... in the following paragraph tho the authors go on to say that previous authors have argued that overdispersion of patches can be taken as evidence of negative feedbacks (which I think makes sense). If others have already made the case well, the authors should dig in and say a little bit more about how this connection of pattern and mechanism has been argued previously. (connect the dots a little bit more for the reader about how these "inferences" are made.).

AC6: We will work to make our application of these ideas and previously established diagnostic tests are more clear for the reader throughout the Manuscript, but especially in this part of the Introduction. The Introduction has been thoroughly revised.

RC7: Lines 116 and 117 of the introduction cite a figure (which is fairly uncommon in intros). I happen to like the model, but I think it should be used differently. At present, the authors seem to work in this order: 1) propose a model based on previous work in the literature early in the intro, 2) state more specific/basic hypotheses about that patterns they are likely to see (e.g., taller hummocks in more inundated sites), 3) present findings and discuss. . . .. I suggest doing part 2 in the intro, part 3 thereafter, and weaving part 1 into the discussion (maybe put the figure into supplemental material but reference it); that way the paper moves efficiently through the topography-centric research and ends with some broader (untested) ideas about what's really going on via specific mechanisms involving plants/soils/water on the ground.

AC7: We have considered the reviewer's suggestion for reorganization, but opted to keep the current organization as is. We believe that with planned substantial edits to the Introduction and Discussion based on the constructive comments in this review that the text will now flow more naturally. We submit that the current organization most accurately aligns with the history of this work. The hypotheses and conceptual model came from initial observations of microtopography in our model systems (black ash wetlands), but also from literature and previous experience in other wetlands. We then sought to test this conceptual model using a novel approach using concepts from landscape ecology and patterned landscapes. In other words, the conceptual model is intricately linked to, and *in fact informs, our hypotheses. Again, we hope that with the planned edits that this will be clearer in the revised work.*

Methods:

RC8: I found the hummock area calculation curious (Line 271). Was this just a best-guess method by the authors? when they say that their method provided a conservative estimate of height are they comparing that to a field-based measurment with an autolevel or a meter stick or something? (obviously this might be a best-guess scenario, but I'm just curious).

AC8: We agree and have now changed the text and side area calculation to be based on a conical shape (a reasonable estimate for hummock shape), where we estimate lateral area from measured volumes and heights. Updated calculations are approximately 50% larger than the initial 20-percentile height, which was a best-guess conservative estimate to calculate hummock side area. We chose this initially rather than, say, using the median or average height of the hummock because hummocks are not perfect cylinders (they are more tapered at the top). Hence, we were trying to provide a lower bound for what we expect the additional hummock side area is. We believe the new approach (cone shape assumption) to be conservative based on our observations of hummock shapes, which tend to be have more undulating edges (as opposed to simple conical sides) that would lead to further increases in area above the conical estimation.

Results:

RC9: The contention that hummocks plot above the -1:1 line in all sites (in manuscript lines 466 and 467) does not seem to be supported by sites L1 and L3. (as far as I can see in Figure 6). Result may need to be stated differently there. (it's also problematic in view of the fact that approximately one and a half sites lacked data b/c the horizon was below detection with your depth to refusal rod method. I think the authors did the correct thing by omitting those data, but it further weakens that claim that "all sites" showed this trend.)

AC10: We thank the reviewer for the careful attention to detail here. We appreciate the reviewer's point, and we will add text to refine our presentation of results by noting that not every measured point exhibited this trend. We note here that at sites L1 and L3, only 1 hummock plots below the 1:1 line (at approximately -0.5m mineral layer elevation at site L1), so we believe our overall statement is well supported. Moreover, that the drier lowland (L) sites had less clear patterns in this regard than our considerably wetter depression (D) or transition (T) sites supports our hydrology-driven hypothesis for hummock development. We believe that because some of the points were too deep to reach with our rod (particularly at site T1) is more likely further evidence for our contention that hummocks are self-organized mounds on a smooth surface of organic soil, rather than an argument against it. If we had a longer rod, the chances that a point would plot below the -1:1 line at these highly organic sites are exceedingly small because the buildup of organic matter to a thickness of greater than 1.2m will almost certainly be smoothed out by physical processes like flooding and wind over long time-scales. We think that this is an important point that could have been better presented; we will revise text to emphasize what these deep (non-data) points suggest. Text clarified and some text added to Discussion 4.1 "Moreover, drier lowland (L) sites had less clear patterns in this regard than the wetter depression (D) or transition (T) sites, supporting our hypothesis for hydrology driven hummock development. We also note that some measurement locations had deeper organic soils than we could measure with our rod (particularly at our wettest sites) and that this is likely further evidence for our contention that hummocks are self-organized mounds on a smooth surface of organic soil, rather than an argument against it."

Discussion:

RC11: Lines 545-560 are great, but this is where I would suggest the authors actually speculate more about what drives hummock formation and what is the same or different about hummock formation in forested systems and others. For example, the authors cite work by Lawrence and Zedler 2011, which showed that inundation drove tussock formation and correlated with tussock height (just like the present study); those authors also showed that the tussocks they studied were majority organic (so I wouldn't lump them in with "soil building" as stated in Line 558). I think the authors ought to capitalize on an opportunity to compare and contrast more... drawing out with what is same/different from the hummock literature vs. their results.

AC11: We will edit this section to more clearly draw similarities and distinctions between our study and others. We will also clarify that we included organic matter as part of conceptualization of "soil building" here because hummocks in our system are also primarily organic matter. We heavily updated the Discussion text to more clearly present our arguments and differences between forested and non-forested systems. Especially at Discussion 4.2 "Therefore, based on evidence and observations presented here and in Diamond et al. (2019), we suggest that a major difference between microtopography in forested versus non-forested wetland systems will be the size distributions and spacing of hummocks. In other forested systems, hummocks associated with trees will likely be limited in size, exhibiting characteristic sizes and spacing due to local negative feedbacks from the crown competition. In contrast, non-forested wetland hummocks may have a much wider distribution of size classes, where negative feedbacks to hummock expansion may be largely due to local nutrient competition effects (e.g., Eppinga et al. 2008)."

RC12: Line 567 and 568 makes a claim that "this study is the first..." I'm not so sure that's the case. I recall a paper by Bruland and Richardson in 2005 (not cited here) that looked at hummock and hollows in natural wetlands as a natural counterpart to similar features a restoration site study. And more broadly, the authors might want to check the most recent Foundations of Restoration book chapter by Bruland and Zedler (because it's a review chapter of wetland microtopography) as a way of seeing if they truly are the "first".

*AC12: The authors have conducted extensive literature reviews as part of this work and are familiar with both the Bruland and Richardson 2005 study and the Bruland and Zedler book chapter, and acknowledge that our study is not the first to examine microtopography in forested wetlands. Our language is precise regarding what we studied (i.e., regular patterning and hydrologic control), and we believe it is accurate to the best of our knowledge: "*but to our knowledge, this study is the first to demonstrate regular patterning in forested wetland microtopography and the hydrologic control on this regular pattern emergence*." To avoid any issues, however, we have revised the text to temper the language:* "Regular patterning of landscape elements is observed across climates, regions, and ecosystems (Rietkerk and van de Koppel 2008), and here we demonstrate such patterning for forested wetland microtopography and, importantly, demonstrate the hydrologic controls on its patterning and structure.*"*

RC13: I think the authors should reconsider what they present in paper vs. in supplement. The star example of this is Figure S2. As a first-time reader of this paper, I'm most eager to see what the impressively data-rich TLS approach turned up and to see what the hummock pattern looks like!!! I want to see Figure S2... I would include that one (and possibly Figure S1) in the paper itself, even if it means shunting other tables and figures into the supplementary materials; (something like Fig 9 is extremely cool to be able to draw, but to me it's far less important to the main theme of the paper).

AC13: We also share the reviewer's excitement regarding the TLS approach and its applicability. The initial presentation of these results and the TLS methodology was presented in previous paper, Stovall et al. (2019; DOI: 10.1016/j.rse.2019.111271), which is why we did not add it initially. We will now add a portion of them to Figure 3 to create a 6 panel figure showing both photos and TLS results. We note Figure 9 is a critical finding that supports our hypotheses by inferring process from pattern. We acknowledge that we have not done a good job of highlighting this, and will make edits accordingly to support the inclusion of Figure 9 as a critical result. He have updated the figure as requested.

Specific comments:

RC14: Eppinga et al. 2008 is first referenced on page 2, and several times after that, but there is only one Eppinga ref in the ref list dated as 2009. Please double check the citations here as it's unclear if the intent is to cite a single paper or two.

AC14: Thank you for finding this error, we have corrected these references. Reference corrected.

RC15: Line 96, it would be useful to say more than "meaningful structure." Is there a more specific signature that the authors would assert represents autogenic feedbacks at work? I'm not sure why the burrowing, litter accumulation, and erosion would preclude regular spacing (overdispersion) of hummocks.

AC15: We will be more specific with this phrase in our edits. There are three signatures that represent autogenic feedbacks: one vertical (bimodality), and two lateral (overdispersion of patches and characteristic patch sizes); we test each of these in this work. Regular spacing induced by random processes would be extremely rare, and the probability of this is testable using metrics and methods which we discuss later in the Introduction and Methods. Introduction and abstract clarified in this regard.

RC16: On line 102 I see a reference to a familiar citation (Barry et al. 1996) about hummock formation in forested wetlands, but the citation does not appear in the ref list.

AC16: Thank you for finding this omission, we will add this to the references. Added.

RC17: Eliminate "just" in line 130 (redundant).

AC17: We have deleted this word.

RC18: I like the explanation of HGM categories (Line 180-185), very helpful.

AC18: Thank you!

RC19: Results section 3.5 is really neat. I see it as a strength of this paper that the lowland sites (with their less inundated hydrologic regime) showed a different (essentially less hummocky) topography. very cool!

AC20: We agree, and we suggest that this finding (hydrologic control on microtopographic structure) has similar support with all of our results.

RC21: Line 545 says "(Figure);" A figure number is needed there.

AC21: Noted, have fixed this; should be Figure 9. All missing figure numbers updated.

RC22: Line 560 has an extra comma in the last citation.

AC22: Noted, we will delete this comma. Deleted.

RC23: In the Figure 3 caption, refer to each individual photo by its caption (e.g. D2) and remind the reader what D, L, and T denote.

AC23: Noted, we have added these recommendations and also updated the figure to include Figure S2 as additional panels. Edited as suggested.

~~A microtopographic signature of life: Ecohydrologic feedbacks~~ Pattern and structure ~~wetland~~of microtopography implies autogenic origins in forested wetlands

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Abstract

~~Microtopography in wetlands can be~~Wetland microtopography is a visually striking ~~landscape~~ feature, ~~and~~but also critically influences biogeochemical processes at both the scale of its observation (10^{-2}–10^{2} m^2) and at aggregate scales (10^{2}–10^{4} m^2). However, relatively little is known about how wetland microtopography develops ~~in wetlands~~ or the factors ~~that influence~~influencing its structure and pattern. ~~For example, wetland vegetation appears to have a strong affinity to elevated microsites, but the degree to which wetland vegetation simply preferentially occupies elevated microsites ("hummocks") versus the degree to which wetland vegetation reinforces and maintains these elevated microsites is not clear.~~ Growing research across different ecosystems suggests that ~~such~~ reinforcing processes may be common between plants and their environment, resulting in self-organized patch features, like hummocks. Here, we ~~made use of~~used landscape ecology ~~techniques~~metrics and diagnostics to evaluate the plausibility of plant-environment feedback mechanisms in the maintenance of wetland microtopography. ~~Using a novel~~We used terrestrial laser scanning ~~dataset, we were able~~(TLS) to quantify the sizing and spatial distribution of hummocks in 10 black ash (*Fraxinus nigra* Marshall) wetlands in northern Minnesota, U.S.A. We observed clear elevation bimodality in our wettest sites, indicating microsite divergence into two states: elevated hummocks and ~~base~~low elevation hollows. We coupled the TLS dataset to a three-year water ~~table~~level record and soil-depth measurements, and showed that hummock height (mean = 0.31±0.06 m) variability is largely predicted by mean water ~~table~~level depth~~,~~ (R^2=0.8 at the site scale, 0.12–0.56 at the hummock scale), with little influence of subsurface microtopography on surface microtopography. ~~We further show that hummocks~~Hummocks in wetter sites ~~exhibit~~exhibited regular spatial patterning (i.e., regular spacing of ca. 1.5 meters, 25–30% further apart than expected by chance) in contrast to ~~hummocks in drier sites, which exhibit~~the more random spatial arrangements~~. We show that hummock~~ of hummocks in drier sites. Hummock size distributions (perimeters, areas, and volumes) ~~are~~were lognormal, ~~and that hummocks exhibit~~with a characteristic patch area of approximately 1 m^2 across sites. ~~Finally, we show that hummocks may be responsible for increased reactive~~Hummocks increase the effective soil surface area for redox gradients and exchange interfaces in black ash wetlands by up to 32%, and ~~may~~ also influence surface water dynamics through modulation of specific yield by up to 30%. ~~We suggest~~Taken together, the data indicates that vegetation develops and maintains hummocks in response to anaerobic stresses from saturated soils, leading to a microtopographic signature of life.

Key words: hummocks, hollows, black ash, Fraxinus nigra, wetlands, ecohydrology, TLS

1 Introduction

~~Biota permeate the Earth's surface, exerting direct control on surface processes and topographic features. Although topographic signatures of life at landscape scales remain elusive (Dietrich and Perron 2006), there is clear evidence of a biotic imprint on the land surface at the scale of biota (10^{1} m; Lashermes et al., 2007, Roering et al., 2010), attributed to both animal (e.g., 1 m hill structures via burrowing; Gabet et al., 2014) and vegetative actions (e.g., 20–40 cm elevated ridges via organic inputs; Watts et al., 2010). Recently, vegetation's role in affecting critical zone processes and resulting structure has received considerable research attention (Amundson et al., 2007, Reinhardt et al., 2010, Corenblit et al., 2011). However, despite general understanding of the broad, directional effects that vegetation~~

~~imposes on the critical zone environment (e.g., bedrock weathering and soil development), less is known regarding the reciprocal feedbacks that develop between vegetation and their environment (Pawlik et al., 2016, Brantley et al., 2017). Some of these feedbacks may lead to reinforced and biotically maintained topographic structure (Eppinga et al., 2008), resulting in diagnostic (micro)topographic fingerprints of plants.~~

~~Microtopography~~ Wetland microtopography changes the spatial distribution of relative water ~~table~~levels, affecting vegetative composition and growth ~~in wetlands. However, the degree to~~, which ~~wetland vegetation simply preferentially occupies hummocks (*sensu* Jackson & Caldwell 1996) *versus* the degree to which wetland vegetation reinforces and maintains its own hummock microtopography (and thus preferred environmental conditions) is not clear.~~, in turn, may reinforce microtopographic development. For example, seedlings ~~may simply~~often fare better on elevated microtopographic features such as downed woody debris or tree-fall mounds (Huenneke & Sharitz, 1990). ~~On the other hand,~~The resulting increased vegetation root growth and associated organic matter inputs ~~may~~on such features may subsequently support hummock expansion. In this way, vegetation may reinforce and maintain its own hummock microtopography (and thus preferred environmental conditions). Growing research across different ecosystems suggests that such reinforcing processes, or feedback loops, may be common between ~~plants~~biota and their environment, and may result in characteristic, self-organized patch features (Rietkerk and van de Koppel, 2008; Bertolini et al., 2019). By quantifying the structure and patterning of these features, we may therefore make process-based inferences about ~~the~~ latent feedback mechanisms (Turner, 2005; Quintero and Cohen 2019).

~~Several diagnostic features implicate feedback mechanisms in the reinforcement and maintenance~~Spatial patterning of landscape patches~~, like~~ has been observed in many systems, such as the striping of vegetated patches in arid settings or maze-like patterns in mussel beds (Rietkerk and van de Koppel, 2008~~).~~), where researchers have inferred responsible feedback mechanisms (as opposed to random processes) using a suite of diagnostic indicators. There is a large body of literature where such measurements are used to identify patterned systems and to infer their latent feedbacks (see Pascual et al., 2002; Pascual and Guichard, 2005; Kefi et al., 2011; Kéfi et al., 2014; Quinton and Cohen, 2019 and references therein). We suggest that ~~such~~these diagnostic ~~features from landscape ecology~~indicators are extensible to analysis of wetland microtopography, thereby allowing us to assess mechanisms ~~of potential~~that maintain and reinforce patterns of hummock ~~self-organization. For example~~patches. Here, we focus on three common methods of inference. First, multimodal distributions in environmental variables, such as vegetation composition, soil texture, and, in our case, elevation (and see Rietkerk et al., 2004~~,~~; Eppinga et al., 2008~~,~~; Watts et al., 2010), indicate ~~patch self-organization (Scheffer and Carpenter 2003). Hypothesized mechanisms for patch self-organization rely on~~ positive feedbacks ~~that support so-called "local facilitation" (Pugnaire et al., 1996),~~to patch growth, where ~~vegetation improves growth~~ local patch conditions ~~locally by modifying plant-scale soil properties (e.g., soil nutrients, hydraulic conductivity) or structure (elevation). This local facilitation then leads to greater vegetation growth,~~promote further ~~soil modification, and thus reinforced~~ patch expansion~~. However, this~~

[illegible]

implies that limits to patch growth operate at local~~, or patch~~ scales as opposed to system scales (Manor and Shnerb, 2008~~,~~; von Hardenberg et al., 2010). Limited patch growth results in a distinct absence of large patches, and a thus a truncation of the size distribution~~, which is modeled with a power law or exponential function~~ (Kéfi et al., 2014; Watts et al., 2014)~~. Characteristic patch sizes are also commonly accompanied by~~ Thi regular spatial patterning of patches (Rietkerk et al., 2004), or spatial overdispersion of patches (i.e., uniformity of patch spacing is greater than expected by chance), ~~which further~~ implies a coupling of both local-scale positive feedbacks to patch growth and local-scale negative feedbacks to patch expansion (Watts et al., [illegible] patterning~~) to test predictions concerning the generation~~ and infer genesis and ~~maintenance~~ persistence of wetland microtopography.

~~Our broad hypothesis is that while there are many mechanisms that may initiate wetland microtopographic variation, structured and persistent (and possibly patterned) wetland microtopography results from self-organizing, reciprocal feedbacks between plant growth and hydrology (Figure 1). Microtopographic initiation mechanisms may include~~Our conceptual model of wetland microtopographic development posits elevation-plant productivity feedbacks that result in elevation bimodality, characteristic patch sizes, and patch overdispersion (Figure 1). We suggest that many mechanisms may initiate microtopographic development, including direct actions from biota (e.g., burrowing or mounding), indirect actions from biota (e.g., tree falls or preferential litter accumulation), and abiotic events that redistribute soils and sediment (e.g., extreme weather events). However, ~~without reinforcement, or autogenic feedbacks~~regardless of initiation mechanism, we hypothesize that ~~maintain such variations in soil elevation, this type of microtopography would be unstructured—indistinguishable from the random processes that create it, both vertically and laterally. On other hand, when operated on by autogenic feedbacks, these variations may take on a meaningful structure resulting from ecosystem processes.~~

~~In wetlands, the posited positive and negative feedback loops that grow and maintain hummocks are likely under the strong influence of both site- and hummock-scale hydrology (blue shading in Figure 1). Consequently, we hypothesize that soil wetness is predictive of the strength of the autogenic processes that structure wetland microtopography. For example, drier sites may obviate the feedback loop between elevation and productivity/decomposition (*cf.* Watts et al., 2010), because soils are nearly always unsaturated and aerobic. Additionally, dissolved solutes may less easily flow along directional hydraulic routes in unsaturated soils compared to unsaturated soils, reducing the evapoconcentration effect. In contrast, we predict that in wetter sites both the elevation-productivity and evapoconcentration feedbacks will be more important, and will therefore lead to more clear and structured hummock-hollow features. In this framework, we view wetland hummocks as self-organizing, created autogenically by bidirectional feedbacks among vegetation, soil, and hydrology. Although our broad hypothesis has previously been tested in non-forested peatland environments (Belyea and Baird 2006, Eppinga et al., 2009), we seek here to expand and more directly quantify our understanding of the pattern and development of wetland microtopography in forested-wetland systems with a focus on hydrologic controls.~~

1. [illegible] variability in ~~Figure 1), and therefore suggest biotically controlled hummock development~~ elevation will be greater in wetter sites than drier sites.
2. Surface ~~soil depth will exhibit a -1:1 relationship with underlying mineral layer~~ topography~~, but~~ [illegible] subsurface [illegible] topography, but instead [illegible] representative of self-organizing processes at the soil surface ~~level self-organization of soil elevation~~.

~~1. [illegible]~~

4. Hummock patches will exhibit spatial overdispersion, which will be more evident at wetter sites.

~~3.~~5. Cumulative ~~distribution (cdf)~~distributions of ~~individual~~ hummock areas (and perimeters and volumes) will correspond to a family of [illegible] sites exhibiting more large area hummocks than drier sites.

2 Methods

2.1 Site descriptions

To test our hypotheses, we investigated ten black ash ~~(*Fraxinus nigra* Marshall)~~ wetlands of varying size and hydrogeomorphic landscape position in northern Minnesota, U.S.A. ~~(Figure~~ (Figure 2; ~~Table 1).~~Table 1). Thousands of meters of sedimentary rocks overlay an Archean granite bedrock geology in this region. Study sites are located on 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. The climate is continental, with mean annual precipitation of 700 mm and a mean growing season (May–October) temperature of 14.3°C (mean annual temperature = -1.1°C – 4.8°C; WRCC 2019). Annual precipitation is approximately two-thirds rain and one-third snowfall. Potential ~~ET~~evapotranspiration (PET) is approximately 600–650 mm per year (Sebestyen et al., 2011). Detailed site histories were unavailable for the ten study wetlands, but silvicultural practices in black ash wetlands have been historically limited in extent (D'Amato et al., 2018). Based on the available information (e.g., Erdmann et al., 1987~~,~~; Kurmis and Kim, 1989), we surmise that our sites are late successional or climax communities and have not been harvested for at least a century.

As part of a larger effort to understand and characterize black ash wetlands (D'Amato et al., 2018), we categorized and grouped each wetland by its hydrogeomorphic characteristics as follows: 1) depression sites ("D", n = 4) characterized by a convex, pool-type geometry with geographical isolation from other surface water bodies and surrounded by uplands, 2) lowland sites ("L", n = 3) characterized by extensive wetland complexes on flat, gently sloping topography, and 3) transition sites ("T", n = 3) characterized as flat, linear boundaries between uplands and black spruce (*Picea mariana* Mill. Britton) bogs ~~(Figure~~ (Figure 3). The three lowland sites were control plots from a long-term experimental randomized block design on black ash wetlands (blocks 1, 3, and 6; Slesak et al., 2014~~,~~; Diamond et al., 2018). We considered hydrogeomorphic variability among sites an important criterion, as it allowed us to capture expected differences in hydrologic regime and thus differences in the strength of our predicted control on microtopographic generation ~~(Figure 1).~~(Figure 1). Ground slopes across sites ranged from 0–1%. ~~Hydrology of black~~Black ash wetlands ~~is~~are typically ~~dominated by~~hydrologically disconnected from regional groundwater and other surface water bodies, resulting in precipitation and evapotranspiration (ET~~),~~) as dominant components of the water budget, with ~~shallow water tables following~~no indication of extreme surface flows (Slesak et al., 2014). Water levels follow a common annual trajectory of late-spring/early-summer inundation (10–50 cm) followed by ET-induced summer drawdown ~~from ET~~and belowground water levels (Slesak et al., 2014~~,~~; Diamond et al., 2018). However, the degree of drawdown depends on local hydrogeomorphic setting; we observed considerably wetter conditions at depression ~~sites~~ and transition sites than at lowland sites.

2.1.1 Vegetation

Overstory vegetation at the ten sites is dominated by black ash~~.~~, with tree densities ranging from 650 stems ha^{-1} (basal area = 195 m^{2} ha^{-1}) at the driest lowland site to 1600 stems ha^{-1} (basal area = 40 m^{2} ha^{-1}) at a much wetter depression site (across-site mean = 942 stems ha^{-1}; Diamond et al. 2019). 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). Except at one transition site (T1), where northern white cedar represented a significant overstory component, black ash represented over 75% of overstory cover across all sites. Black ash also made up the dominant midstory component in each site, but was regularly found with balsam fir (*Abies balsamea* L. Mill.) and speckled alder (*Alnus incana* L. Moench) in minor components, and greater abundances of American elm (*Ulmus Americana* L.) at lowland sites. Black ash stands are commonly highly uneven-aged (Erdmann et al., 1987), with canopy tree 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). The relatively open canopies of black ash wetlands (leaf area index < 2.5; Telander et al., 2015) allow for a variety of graminoids, shrubs, and mosses to grow in the understory. However, the majority of understory diversity and biomass tends to occur on hummocks that are occupied by black ash trees (Diamond et al., 2019). Hollows exhibit relatively little plant cover and are typically bare soil areas, but may be covered at times of the year by sedges (*Carex spp.*) or layers of duckweed (*Lemna minor* L.), especially after recent inundation.

2.1.2 Soils

Soils in black ash wetlands in this region tend to be Histosols characterized by deep mucky peats underlain by silty clay mineral horizons, although there were clear differences among site groups (NRCS 2019). Depression sites were commonly associated with Terric haplosaprists of the poorly drained Cathro or Rifle series with O horizons approximately 30–150 cm deep ~~(Table 1).~~(Table 1). Lowland sites were associated with lowland Histic inceptisols of the Wildwood series, which consist of deep, poorly drained mineral soils with a thin O horizon (< 10 cm) underlain by clayey till or glacial lacustrine sediments. Transition sites typically had the deepest O horizons (> 100 cm), and were associated with typic haplosaprists of the Seelyeville series and Typic haplohemists (NRCS 2019). Both depression and transition sites had much deeper O horizons than lowland sites, but depression site organic soils were typically muckier and more decomposed than more peat-like transition site ~~organic~~ soils.

2.2 TLS

2.2.1 Data collection

To characterize the microtopography of our sites, we conducted a terrestrial laser scanning (TLS) campaign from October 20–24, 2017. We chose this period to ensure high-quality TLS acquisitions, as it coincided with the time of least vegetative cover and the least likelihood for inundated conditions. During scanning, leaves from all deciduous canopy trees had fallen and grasses had largely senesced. Standing water was present at portions of three of the sites and was typically dispersed across the site in small pools (*ca*. 0.5–2 m^2) less than 10 cm deep. We used a Faro Focus 120 3D phase-shift TLS (905 nm λ) to scan three randomly established, 10 m diameter sampling plots at each site (see Stovall et al., ~~[in revision]~~2019 for exact methodological details). For each site, we merged our plot-level TLS data to a single ~900 m^2 site-level point-cloud using 30 strategically placed and scanned 7.62 cm radius polystyrene registration spheres set atop 1.2 m stakes. We referenced each site to a datum located at each site's base well elevation~~.~~ (see section 2.3.1).

~~We~~To validate the TLS surface model products, we installed sixty 2.54 cm radius spheres on fiberglass stakes exactly 1.2 m above ground surface at each site~~ to validate the TLS surface model products.~~. With the validation locations we could easily calculate the exact surface elevation (i.e., 1.2 m below a scanned sphere) of 60 points in space. We installed 39 (13 at each plot) validation spheres at points according to a random walk sampling design, and placed 21 (7 at each plot) validation spheres on distinctive hummock-hollow transitions. We placed the 1.2 m tall validation spheres approximately plumb to reduce errors due to horizontal misalignment.

We processed the point clouds generated from the TLS sampling campaign to generate two products: 1) site-level 1~~-~~-cm resolution ground surface models, and 2) site-level delineations of hummocks and hollows. The details and validation of this method are described completely in Stovall et al~~., (in review~~. (2019), but a brief summary is provided here.

2.2.2 Surface model processing and validation

For each site, we first filtered the site-level point-clouds in the CloudCompare software (Othmani et al., 2011) and created an initial surface model with the absolute minima in a moving 0.5 cm grid. We removed tree trunks from this initial surface model using a slope analysis and implemented a final outlier removal filter to ensure all points above ground level were excluded. Our final site-level surface models meshed the remaining slope-filtered point cloud using a local minima approach at 1 cm resolution. We validated this final 1~~-~~-cm surface model using the 60 validation spheres per site.

Before we analyzed surface models from each site, we first detrended sites that exhibited site-scale elevation gradients (e.g., 0.02 cm m^{-1}). These gradients may obscure analysis of site-level relative elevation distributions (Planchon et al., 2002), and our hypothesis relates to relative elevations of hummocks and hollows and not their absolute elevations. We chose the best-detrended surface model based on adjusted R^2 values and observation of resultant residuals and elevation distributions from three options: no detrend, linear detrend, and quadratic detrend~~ (P~~. Five sites were detrended: L2 was detrended with a linear model, and D1, D2, D4, and T1 were detrended with quadratic models. We then subsampled each surface model to 10,000 points to speed up processing time as original surface models were approximately 100,000,000 points. We observed no significant difference in results from the original surface model based on our subsampling routine.

2.2.3 Hummock delineation and validation

We classified the final surface model into two elevation categories: hummocks and hollows. We first classified hollows using a combination of normalized elevation and slope thresholds; hollows have less than average elevation and less than average slope. This combined elevation and slope approach avoided confounding hollows with the tops of hummocks since the tops of hummocks are typically flat or shallow sloped. We removed hollows and used the remaining area as our domain of potential hummocks.

Within the potential hummock domain, we segmented hummocks into individual features using a novel approach – TopoSeg (Stovall et al., ~~in revision~~2019) – and thereby created a hummock-level surface model for each site. We first used the local maximum (Roussel and Auty, 2018) of a moving window to identify potential microtopographic structures for segmentation. The local maximum served as the “seed point” from which we then applied a modified watershed delineation approach (Pau et al., 2010). The watershed delineation inverts convex topographic features and finds the edge of the “watershed”, which in our case are hummock edges. The defined boundary was used to clip and segment hummock features into individual hummock surface models.

For each delineated hummock within all sites, we calculated perimeter length, total area, volume, and height distributions relative both to local hollow datum and to a site level datum. To calculate area, we summed total number of points in each hummock raster multiplied by the model resolution (1 cm^2). We calculated volume using the same method as area, but multiplied by each points’ height above the hollow surface. Perimeter was conservatively estimated by converting our raster-based hummock features into polygons and extracting the edge length from each hummock. We estimated ~~side~~lateral hummock area ~~(analogous to~~by modelling each hummock as a simple cone, and calculating the lateral surface area ~~of a cylinder without a top or bottom) by multiplying the perimeter of each hummock by its 20th percentile~~from previously estimated volume and height~~, which we determined~~. We believe this conical estimation method to be a conservative representation of the average height around the perimeter of the hummock because real hummock shapes are more undulating and complex than simple cones. We elected not to use a cylindrical model because we observed some tapering of hummocks from their base to their top. We note that a cylindrical model would increase lateral surface area estimation by approximately 15% compared to the conical model and therefore may provide an upper bound on our conservative estimates.

To validate the hummock delineation, we compared manually delineated and automatically delineated hummock size distributions at one depression site (D2) and one transition site (T1), both with clearly defined hummock features. We omitted using a lowland site for validation because none of these sites had obvious hummock features that we could manually delineate with confidence. We manually delineated hummocks for the D2 and T1 sites with a qualitative visual analysis of raw TLS scans using the clipping tool in CloudCompare (2018). Stovall et al~~.,~~. (2019) found no significant differences between the manual and automatically segmented hummock distributions, and feature geometry had an RMSE of less than ~20%.

After the automatic delineation procedure and subsequent validation, we performed a data cleaning procedure by manually inspecting outputs in the CloudCompare software. We eliminated clear hummock mischaracterization that was especially prevalent at the edges of sites, where point densities were low. We also excluded downed woody debris from further hummock analysis because, although these features may serve as nucleation points for future hummocks, they are not traditionally considered hummocks and their distribution does not relate to our broad hypotheses. Finally, we excluded delineated hummocks that were less than 0.1 m^2 in area because we did not observe hummocks less than this size during our field visits. This delineation and manual cleaning process yielded point clouds of hummocks and hollows for every site that could be further analyzed.

2.2.4 Surface model performance

Validation of surface models using the validation spheres indicated that surface models were precise (RMSE = 3.67 ± 1 cm) and accurate (bias = 1.26 ± 0.1 cm) across all sites (Stovall et al~~., in revision~~. 2019). The gently sloping lowland sites (L) had substantially higher RMSE and bias than the transition (T) and depression (D) sites. The relatively high error of lowland site validation points resulted from either low point density or a complete absence of LiDAR returns. We observed overestimation of the surface model when TLS scans were unable to reach the ground surface, leading to the greatest overestimations in sites with dense grass cover (lowland sites). Overestimation was also common in locations with no LiDAR returns, such as small hollows, where the scanner's oblique view angle was unable to reach. Nonetheless, examination of the surface models indicated clear ability of the TLS to capture surface microtopography (Figure S1).

2.2.5 Hummock delineation performance

Hummocks delineated from our algorithm were generally consistent in distribution and dimension with manually delineated hummocks. However, the automatic delineation located hundreds of small (<0.1 m^2) "hummock" features that were not captured with manual delineation, which we attribute to our detrending procedure. We did not consider automatically delineated hummocks less than 0.1 m^2 in further analyses, as we did not observe hummocks smaller than this in the field. Both area and volume size distributions from the manual and automatic delineations were statistically indistinguishable for both t-test (p-value = 0.84 and 0.51, respectively) and Kolmogorov-Smirnov test (p-value = 0.40 and 0.88, respectively). Automatically delineated hummock area, perimeter:area, and volume estimates had 23%, 19.6%, and 24.1% RMSE, respectively, and the estimates were either unbiased or slightly negatively biased (-9.8 %, 0.2 %, and -11.9 %, respectively). We consider these errors to be well within the range of plausibility, especially considering the uncertainty involved in manual delineation of hummocks, both in the field and on the computer. Final delineations showed clear visual differences among site types in the spatial distributions of hummocks (Figure S2).

2.3 Field data collection

~~2.3.1~~1.1.1 ~~Mineral layer depth measurements~~

To address our hypothesis that hydrology is a controlling variable of microtopographic expression in black ash wetlands, we instrumented all 10 sites to continuously monitor water level dynamics and ~~continuous~~ precipitation. Three sites (L1, L2, and L3; Slesak et al., 2014) were instrumented in 2011 and seven in June 2016 following the same protocols. ~~-~~At each site, we placed a fully-slotted observation well (schedule 40 PVC, 2-inch diameter, 0.010-inch-wide slots) at approximately the lowest elevation; at the flatter L sites, wells were placed at the approximate geographic center of each site. Ground surface at the well served as each site's datum (i.e., elevation = 0 m). We instrumented each well with a high-resolution total pressure transducer (HOBO U20L-04, resolution = 0.14 cm, average error = 0.4 cm) to record water level time series at 15-minute intervals. We dug each well with a hand auger to a depth associated with the local clay mineral layer and did not penetrate the mineral layer, which ranged from

30 cm below the soil surface to depths greater than 200 cm. We then backfilled each well with a clean, fine sand (20-40 grade). At each site, we also placed a dry well with the same pressure transducer model to measure temperature-buffered barometric pressure and frequency for barometric pressure compensation (McLaughlin and Cohen, 2011).

2.3.2 Mineral layer depth measurements

To quantify the control that underlying mineral layer microtopography has on surface microtopography, we conducted synoptic measurements of mineral layer depth and thus organic soil thickness at each site. Within each of the 10 m diameter plots used for TLS at each site, we took 13 measurements (co-located with the randomly established validation spheres) of depth to mineral layer using a steel 1.2 m rod. At each point the steel rod was gently pushed into the soil with consistent pressure until resistance was met and the depth to resistance was recorded (resolution = 1 cm) as the depth to mineral layer. We then associated each of these depth-to-mineral-layer measurements with a soil elevation based on TLS data and the site-level datum (i.e., elevation at the base of each site's well).

2.4 Data analysis

2.4.1 Hydrology

We calculated simple hydrologic metrics based on the three years (2016–2018) of water ~~table~~level data for each site. For each site, we calculated the mean and variance of water ~~table~~level elevation relative to ground surface at the well~~. A positive water table value indicates that the water table is above the soil surface (inundated conditions), and a~~, where negative ~~water table indicates that the water table is below the soil surface~~values represent belowground water levels and positive values indicate inundation. We also calculated the average hydroperiod of each site by counting the number of days that the mean daily water ~~table~~level was above the soil surface at the well each year, and averaging across years.

2.4.2 Elevation distributions

Our first line of inquiry was to evaluate the general spatial distribution of elevation at each site. We first calculated site-level omni-directional and directional (0°, 45°, 90°, 135°) semivariograms using the *gstat* package in R (Pebesma 2004 and Gräler, 2016). We calculated directional variograms to test for effects of anisotropy (directional dependence) of elevation. Semivariogram analysis is regularly used in spatial ecology to determine spatial correlation between measurements (Ettema and Wardle, 2002). The sill, which is the horizontal asymptote of the semivariogram, is approximately the total variance in parameter measurements. The nugget is the semivariogram y-intercept, and it represents the parameter variance due to sampling error or the inability of sampling resolution to capture parameter variance at small scales. The larger the difference between the sill and the nugget (the "partial sill"), the more spatially predictable the parameter. If the semivariogram is entirely represented by the nugget (i.e., slope = 0), the parameter is randomly spatially distributed. The semivariogram range is the distance where the semivariogram reaches its sill, and it represents the spatial extent (patch size) of heterogeneity, beyond which data are randomly distributed. When spatial dependence is present, semivariance will be low at short distances, increase for intermediate distances, and reach its sill when data are separated by large distances. We used detrended elevation models for this analysis to assess more directly the importance of microtopography on elevation variation as opposed to having it obscured by site-level elevation gradients. From these semivariograms we calculated the best-fit semivariogram model among exponential, Matérn, or Matérn with Stein parameterization model forms (Minasny and McBratney, 2005). We also extracted semivariogram nuggets, ranges, sills, and partial sills.

Our second line of inquiry was to evaluate the degree of elevation bimodality in these systems, which is indicative of a positive feedback between hummock growth and hummock height (Eppinga et al., 2008). Based on the classification into hummock or hollow from our delineation algorithm, we plotted site-level detrended elevation distributions for hummocks and hollows and determined a best-fit Gaussian mixture model with Bayesian Information Criteria (BIC) using the *mclust* package (Scrucca et al., 2016) in R (R Core Team, 2018), which uses an expectation-maximization algorithm. Mixture models were allowed to have either equal or unequal variance, and were constrained to a comparison of bimodal versus a unimodal mixture distribution.

2.4.3 Subsurface topographic control on microtopography

We assessed the importance of mineral layer microtopography on soil surface microtopography by comparing the depth-to-mineral-layer measurements with the soil surface elevation TLS measurements. We first calculated the elevation of the mineral layer relative to each site-level datum by subtracting the depth-to-mineral-layer measurement from its co-located soil elevation measurement estimated from the TLS campaign. We then plotted the depth-to-mineral-layer measurement (hereafter referred to as “organic soil thickness”) as a function of this mineral layer elevation, noting which points were on hummocks or hollows as determined from the TLS delineation algorithm. We fit linear models to these points and compared the regression slopes to the expected slopes from: 1) a scenario where surface microtopography is simply a reflection of subsurface microtopography (slope = 0, or constant organic soil thickness), and 2) a scenario of flat soil surface where organic soil thickness negatively corresponds to varying mineral layer elevation (slope = -1, or varying soil thickness). ~~Again, the~~The first ~~observation~~scenario would ~~suggest~~indicate that surface microtopography mimics subsurface microtopography, whereas the second would ~~suggest~~indicate organic matter/surface soil accumulation and smoothing over a varying subsurface topography. Observations above the -1:1 line would indicate surface processes that increase elevation above expectations for a flat surface.

2.4.4 Hydrologic controls on ~~microtopography~~hummock height

To test our hypothesis that hydrology is a broad, site-level control on hummock height, we first regressed site mean hummock height against site mean daily water ~~table~~level. We also conducted a within-site regression of individual hummock heights against their local mean daily water ~~table~~level. To do so, we first calculated a local relative mean water ~~table~~level for each delineated hummock location by subtracting the elevation minimum of the hummock (i.e., the elevation at the base of the hummock) from the site-level mean water ~~table.~~level elevation. This calculation assumes that the water ~~table~~level is flat across the site, which is likely valid for the high permeability organic soils at each site, low slopes (<1%), and relatively small areas that we assessed. This within-site regression allowed us to understand more local-scale controls on hummock height.

2.4.5 Hummock spatial distributions

To test whether there was regular spatial patterning of hummocks at each site, we compared the observed distribution of hummocks against a theoretical distribution of hummocks subject to complete spatial randomness (CSR) with the R package *spatstat* (Baddeley et al., 2015). We first extracted the centroids and areas of the hummocks using TopoSeg (Stovall et al., 2019) and created a marked point pattern of the data. Using this point pattern, we conducted a nearest-neighbor analysis (Diggle, 2002), which evaluates the degree of dispersion in a spatial point process (i.e., how far apart on average hummocks are from each other). If hummocks are on average further apart (using the mean nearest neighbor distance, μ_{NN}) compared to what would be expected under CSR (μ_{exp}), the hummocks are said to be overdispersed and subject to regular spacing; if hummocks are closer together than what CSR predicts, they are said to be underdispersed and subject to clustering. We compared the ratio of μ_{NN} and μ_{exp}, where values greater than 1 indicate overdispersion and values below 1 indicate clustering, and calculated a z-score (z_{ANN}) and subsequent p-value to evaluate the significance of overdispersion or clustering (Diggle, 2002, Watts et al., 2014). ~~We~~Z-scores were computed~~ the z-score~~ from the difference between μ_{NN} and μ_{exp} scaled by the standard error. We also evaluated the probability distribution of observed nearest neighbor distances to visualize further the dispersion of wetlands in the landscape.

2.4.6 Hummock size distributions

To test the prediction that hummock sizes are constrained by patch-scale negative feedbacks, we plotted site-level rank-frequency curves (inverse cumulative distribution functions) for hummock perimeter, area, and volume. These curves trace the cumulative probability of a hummock dimension (perimeter, area, or volume) being greater than or equal to a certain value ($P[X \geq x]$). We then compared best-fit power ($P[X \geq x] = \alpha X^{\beta}$), log-normal ($P[X \geq x] = \beta \ln(X) + \beta_0$), and exponential ($P[X \geq x] = \alpha e^{\beta X}$) distributions for these curves using AIC values. Power-scaling of these curves occurs where negative feedbacks to hummock size are controlled at the landscape-scale (i.e., hummocks have approximately equal probability to be found at all size classes). Truncated scaling of these curves, as in the case of exponential or lognormal distributions, occurs when negative feedbacks to hummock size are controlled at the patch-scale (Scanlon et al., 2007, Watts et al., 2014).

3 Results

3.1 Hydrology

Hydrology varied across sites, but largely corresponded to hydrogeomorphic categories (~~Table 2).~~Table 2). Depressions sites were the wettest sites (mean daily water ~~table~~level = -0.~~010~~01 m), followed by transition sites (-0.~~039~~04 m), and lowland sites (-0.~~324~~32 m). Lowland sites also exhibited significantly more water level variability ~~in water table~~ than transition or depression sites, whose water ~~tables~~levels were consistently within 0.4 m of the soil surface. Although lowland sites exhibited greater water ~~table~~level drawdown during the growing season, they were able to rapidly ~~re-wet~~rise after rain events.

3.2 Elevation distributions

~~During field sampling, we observed distinct differences in microtopography among site categories. Depression sites were dominated by hollow features that were punctuated with hummocks associated~~

[illegible]

sites than at lowland sites (~~Figure 4).~~Figure 4). In general, lowland sites reached overall site elevation variance (sills, horizontal dashed lines) within 5 meters, but best-fit ranges (dotted vertical lines in ~~Figure 4~~Figure 4) were less than 1 m. In contrast, best-fit semivariogram ranges for depression and transition sites were several times greater. Therefore, depression and transitions sites have much larger ranges of spatial autocorrelation for elevation than lowland sites. Semivariograms were all best fit with Matérn models with Stein parameterizations, and nugget effects were extremely small in all cases (average <0.001), which we attribute to the very high precision of the TLS method. As such, partial sills were quite large (i.e., the difference between the sill and nugget), indicating that very little elevation variation is at scales less than our surface model resolution (1 cm); the remaining variation is found over site-level ranges of autocorrelation. We did not observe major differences in directional semivariograms compared to the omnidirectional semivariogram, implying isotropic variability in elevation, and do not present them here.

We observed bimodal elevation distributions at every site, with hummocks clearly belonging to a distinct elevation class separate from hollows ~~(Figure 5).~~(Figure 5). Bimodal mixture models of two normal distributions were always better fit to the data than unimodal models based on BIC values. Differences in mean elevations between these two classes ranged from 12 cm at the lowland sites to 20 cm at depression sites, and hummock elevations were more variable than hollow elevations across sites. Across sites, 27±10% of all elevations did not fall into either a hummock or a hollow category, with lowland sites having considerably more elevations ~~failing to fall into~~not in these binary categories (36–44%) ~~than~~compared to depression (22–27%) or transition sites (16–22%). However, we emphasize that even when considering the entire site elevation distribution (i.e., including elevations that did not fall into a hummock or hollow category), bimodal fits were still better than unimodal fits, but to a lesser extent for lowland sites (Figure S3). Delineated hummocks varied in number and size across and within sites. We observed the greatest number of hummocks in the depression and transition sites, with approximately an order of magnitude less hummocks found in lowland sites ~~(Figure 5).~~(Figure 5).

3.3 Subsurface topographic control on microtopography

Across sites, ~~depth to resistance (“~~organic soil thickness~~”)~~ varied and was greatest at the lowest mineral layer elevations, indicating that surface microtopography is not simply a reflection of subsurface mineral layer topography with constant overlying organic thickness (as illustrated with 0-slope line in ~~Figure~~ Figure 6). In contrast, at most sites, except for ~~possibly~~ D1 and L2, there was a strong negative linear relationship between soil thickness and mineral layer elevation, with five sites exhibiting slopes near -1, which we define as the smooth surface model of soil elevation (dashed -1:1 line in ~~Figure~~ Figure 6). If only hollows (open circles; ~~Figure~~ Figure 6) were used in the regression, then D1 also exhibited a significant ($p<0.001$) negative slope in this relationship (-0.4, $R^2 = 0.52$). A majority of depth to mineral layer measurements at D3 were below detection limit with our 1.~~5~~2 m steel rod, and all but one measurement at T1 were below detection limit. At sites D2 and L2, there was indication that some hollows were actually better represented by the subsurface reflection model (i.e., slope = 0). However, at all sites, though to a lesser extent at lowland sites~~,~~ (e.g., L1 and L3), hummocks (closed circles; ~~Figure~~ Figure 6) tend to plot above hollows and above the -1:1 line, ~~even when at the same soil thickness as hollows,~~ indicating that their elevation is greater than would be expected for a smooth surface model.

3.4 Hydrologic control on ~~microtopography~~hummock height

We observed a significant (p<0.001) positive linear relationship between site level mean hummock height and site level mean daily water ~~table (Figure).~~level (Figure 7, top panel). Because lowland sites were clearly influential points on this linear relationship, we also conducted this regression excluding the lowland sites and still found a significant (p = 0.007) positive linear trend between these variables with reasonable predictive power (R^2=0.8) — wetter sites have on average have taller hummocks than drier sites. We found very little variability in average hummock heights across sites when relative to site-level mean water ~~table~~level elevation (mean normalized hummock height = 0.31±0.06 m), indicating that hummocks were generally about 30 cm higher than the site mean water ~~table~~level.

Within sites, we also observed clear positive relationships between individual hummock heights and their local mean daily water ~~table (Figure 7).~~level (Figure 7, bottom panel). At all but two of the sites (D4 and L1), individual hummock heights within a site were significantly (p<0.01) taller at wetter locations than drier locations. Slopes for these individual hummock regressions varied among sites, ranging from 0.4–1.1 (mean±sd = 0.7±0.2), and local hummock mean water ~~table~~level was able to explain 12–56% (mean±sd = 0.36±0.14) of variability in hummock height within a site.

3.5 Hummock spatial distributions

All sites characterized as depressions or transitions exhibited significant (p <0.001) overdispersion of hummocks compared to what would be predicted under complete spatial randomness ~~(Figure 8).~~(Figure 8). For these sites, the nearest neighbor ratios (μ_{NN}:μ_{exp}) indicated that hummocks are 25–30% further apart than would be expected with complete spatial randomness, with spacing ca. 1.5 meters, as evidenced by the narrow distributions in nearest neighbor histograms ~~(Figure).~~(Figure 8). In contrast, all lowland sites, while having hummock nearest neighbor distances 2–3 times as far apart as depression of transition sites, were not significantly different than what would be predicted under complete spatial randomness (p = 0.129, 0.125, 0.04 for sites L1, L2, and L3, respectively).

3.6 Hummock size distributions

Hummock dimensions (perimeter, area, and volume) were strongly lognormally distributed across sites (Figure 9), though exponential models were typically only slightly worse fits. For each hummock dimension, site fits were similar within site hydrogeomorphic categories, but drier lowland site distributions were clearly different from wetter depression and transition site distributions, which were more similar (Figure 9). Lowland sites had significantly lower (p < 0.05) coefficients for hummock property model fits than depression or transition sites, with slopes approximately 20% more negative on average, indicating more rapid truncation of size distributions. Across sites, average hummock perimeter was 4.2±0.8 m, average hummock area was 1.7±0.5 m^2, and average hummock volume was 0.17±0.06 m^3. Hummock areas were typically less than 1 m^2 in size at all sites (Figure 9). Similar to hummock spatial density, hummock area per site (ratio of hummock area to site area) was lower at drier lowland sites (2–5%) compared to wetter depression and transition sites (12–22%) (Figure 5).

4 Discussion

We tested our hypothesis that microtopography in black ash wetlands self-organizes in response to hydrologic drivers ~~(Figure 1)~~(Figure 1) using an array of commonly used diagnostic tests from landscape ecology, including analyses of multimodal elevation distributions, spatial patterning, and patch size distributions. We further analyzed the influence of hydrology on these diagnostic measures and tested a potential null hypothesis that surface microtopography was simply a reflection of subsurface microtopography. Diagnostic test results ~~and~~of elevation bimodality, hummock spatial overdispersion, and truncated hummock areas along with clear hydrologic influence on microtopographic structure provide strong support for our hypothesis.

4.1 Controls on microtopographic structure

Bimodal soil elevation distributions at all sites suggest that the microsite separation into hummocks and hollows is a common attribute of black ash wetlands. Soil elevation bimodality was most evident at the wetter depression and transition sites, where hummocks were more numerous and occupied a higher fraction of overall site area (15–20%). Sharp boundaries between hummocks and hollows were not always observed in soil elevation probability densities ~~(Figure 5),~~(Figure 5), which may be indicative of ~~weaker-than-predicted~~weak positive feedbacks between primary productivity and elevation (Rietkerk et al., 2004; ~~Figure 1).~~Figure 1). On the other hand, modeling predictions indicate that if evapoconcentration feedbacks (i.e., that hummocks harvest nutrients from hollows through hydraulic gradients driven by hummock-hollow ET differences) are strong, boundaries between hummocks and hollows will be less sharp (Eppinga et al., 2009), possibly implicating hummock evapoconcentration as an additional feedback to hummock maintenance ~~(Figure 1).~~(Figure 1). Greater levels of soil chloride in hummocks relative to hollows in these systems may be an additional layer of evidence for this mechanism (Diamond et al., 2019).

~~Our results provide~~We also observed clear evidence of decoupling between surface microtopography and mineral layer microtopography at all of our sites. ~~A~~Hollows were best represented by a smooth surface model, with a relatively constant surface elevation despite variable underlying mineral soil elevation~~, best represented hollows.~~. Importantly, we also observed that regardless of underlying mineral layer, hummocks had greater soil thickness than hollows ~~did (Figure). To clarify~~(Figure 6). That is, irrespective of mineral layer microtopography, hummocks are maintained at local elevations that are higher than would be predicted for a smooth soil surface. ~~We interpret this as evidence for self-organization of wetland microtopography.~~Moreover, drier lowland (L) sites had less clear patterns in this regard than the wetter depression (D) or transition (T) sites, supporting our hypothesis for hydrology driven hummock development. We also note that some measurement locations had deeper organic soils than we could measure with our rod (particularly at our wettest sites) and that this is likely further evidence for our contention that hummocks are self-organized mounds on a smooth surface of organic soil, rather than an argument against it. Smoothing of soil surfaces relative to variability in underlying mineral layers or bedrock is observed in other wetland systems where soil creation is dominated by organic matter accumulation (e.g., the Everglades, Watts et al., 2014~~), implying~~). This implies that deviations from this smooth ~~surface~~organic soil surfaces are related to other surface-level processes, such as spatial variation in organic matter accumulation resulting from hypothesized elevation-productivity feedbacks.

Hummock heights relative to mean site-level water ~~table~~level were approximately 30 cm, aligning with field observations of relatively constant hummock height within sites. Generally consistent hummock height across sites in conjunction with clear bimodality in soil elevations supports the contention that hummocks and hollows are discrete, self-organized ecosystem states (*sensu* Watts et al., 2010). However, variability in site-level hummock heights–especially at depression and transition sites–may partially be attributable to hummocks in non-equilibrium states. From our feedback model ~~(Figure 1),~~(Figure 1), it seems reasonable that within a site, some hummocks may be in growing states (e.g., increasing in height over time via the elevation-~~GPP~~productivity positive feedback) and some may be in shrinking states if hydrologic conditions have recently become drier (e.g., decreasing in height via the elevation-respiration negative feedback), the combination of which may result in a distribution of hummock heights centered around an equilibrium hummock height. Future efforts could leverage time-series observations of hummock properties (e.g., area, height and volume), but we note the likely decadal time-scales required to detect hummock growth or shrinkage (Benscoter et al., 2005; Stribling et al., 2007).

~~We observed strong control of local~~Local hydrology exhibited clear control on hummock height, providing evidence for our hypothesis that hummocks are a biogeomorphic response to hydrologic ~~stresses~~stress in wetlands. ~~Vegetation patches like hummocks are most commonly found in conditions with strong environmental stressors. In particular, water stress—both too little (Deblauwe et al., 2008, Scanlon et al., 2007) and too much (Eppinga et al., 2009)—appears to be an important regulator of microhabitat size and its spatial distribution across the landscape. Wetlands are characterized by regular water stresses from periodic inundation with nearly all biogeochemical processes under the fundamental influence of hydrology (Rodriguez-Iturbe et al., 2007). It is therefore perhaps unsurprising that hydrology also controls the scale-dependent feedbacks that create and maintain hummock sizes and their spatial patterning.~~ We found support for this contention at both the site level and at the hummock level~~, with the~~. The tallest hummocks ~~being found~~were consistently located in the wettest sites and in the wettest zones within sites. ~~In fact, distance from~~ At the site-scale, 85% of the variance in average hummock height could be explained by mean water ~~table~~level alone. Within sites, local mean water level explained on average 35% of the variability in hummock height ~~(Figure);~~(Figure 7); prevalence of non-equilibrium hummock states may explain much of the additional variability. The considerable variation in the ability of ~~hydrology~~local water levels to explain hummock height within sites (adjusted R^2 =0.12–0.56), and ~~also~~ in the strength of that relationship (linear regression slopes=0.4–1.1) may be attributed to two factors: 1) the across-site flat water ~~table~~level assumption, and 2) lack of long trends for hydrology. The flat water ~~table~~level assumption is likely to be a minor effect in transition sites with deep organic wetland soils (e.g., Nungesser, 2003~~,~~; Wallis and Raulings, 2011~~,~~; Cobb et al., 2017~~),~~) but could be significant at depression and lowland sites with shallower O horizons. Lack of sufficient data to characterize mean water ~~table~~level may also be an issue at several of our sites, because hummocks likely develop over the course of decades or more, whereas our hydrology data only span three years.

4.2 Controls on microtopographic patterning

We found clear support for our hypothesis that hummocks are non-randomly distributed in ~~the~~our wettest ~~sites of our~~ study ~~area, further supporting the posited interactions among hydrology, vegetation, and soils.~~sites. Hummocks exhibited spatial overdispersion ~~in~~at all sites, but this overdispersion was only significant at depression and transition sites ~~(Figure).~~(Figure 8). Significant spatial overdispersion ~~is indicative of~~indicates regular hummock spacing in contrast to clustered distributions or completely random placement. Regular patterning of landscape elements is observed across climates, regions, and ecosystems (Rietkerk and van de Koppel, 2008), ~~but to our knowledge, this study~~and is ~~the first to demonstrate regular~~indicative of negative feedbacks that limit patch expansion (Quinton and Cohen 2019). Our results indicate similar patterning ~~in~~for forested wetland microtopography and~~.~~, importantly, demonstrate the hydrologic ~~control~~controls on ~~this regular pattern emergence~~that patterning. Hydrology appears to be a common driver in regular pattern formation in wetlands (Heffernan et al., 2013~~),~~) and drylands (Scanlon et al., 2007~~), and tidal flats (Weerman)~~. Thus, water stress—both too much (Eppinga [illegible] regulator of patch distribution across the ~~importance of biota in structuring their own environment~~landscape.

We observed lognormal hummock size distributions, suggesting that some hummocks may attain very large areas (i.e., over 10 m^2), but the majority of hummocks (~80%) are less than 1 m^2 (Figure 9). This finding aligns with field observations, where most hummocks were associated with a single black ash tree, but some hummocks appeared to have merged ~~over time~~ to create large patches. Truncated patch size distributions are common in other systems as well, ~~like~~such as the stretched exponential distribution for geographically isolated wetlands (Watts et al., 2014) or the lognormal distribution for desert soil crusts (Bowker et al., 2013). These types of distributions have ~~much~~ fewer large patches than would be expected for systems without patch-scale negative feedbacks, and have a central tendency towards a common patch size. Hence, truncation in hummock size distributions comports with hypothesized patch-scale negative feedbacks (i.e., tree competition for light and/or nutrients) that inhibit expansion. Hummocks at drier lowland sites did not conform to size distributions ~~or spatial patterns from~~for wetter depression and transition sites, supporting our hypothesis that the feedbacks that control hummock maintenance and distribution are governed by hydrology and amplified in wetter conditions~~. Larger hummock patches were especially obvious at transition sites that had significant *Sphagnum spp.* moss cover, which tended to blend and expand hummock areas.~~.. This work adds to recent efforts across climates and systems to use patch size distributions to infer drivers ~~and processes~~ of ecosystem self-organization and response to environmental conditions ~~and abiotic drivers~~ (Kefi et al., 2007~~,~~; Maestre and Escudero, 2009~~,~~; Weerman et al., 2011~~,~~; Schoelynck et al., 2012~~,~~; Tamarelli et al., 2017).

Characteristic hummock sizes in association with overdispersion in black ash wetlands suggest that hummocks are laterally limited in size by negative feedbacks on the scale of meters (Manor and Shnerb, 2008). We posit that there are two patch-scale negative feedbacks: 1) overstory competition for nutrients and 2) understory and overstory competition for light. Hummocks associated with black ash trees, which account for more than 85% of measured hummocks, are likely limited in area by the radial growth of the tree's root system. Evapoconcentration feedbacks bring nutrients to the tree roots, limiting the degree to which roots must search for them (Karban, 2008), and therefore limiting root lateral expansion. Indeed, evidence suggests that a majority of fine tree roots occur within hummocks in forested wetland systems (Jones et al., 1996; Jones et al., 2000). Moreover, finite nutrient pools may lead to development of similarly sized nutrient source basins for each hummock, further limiting lateral hummock expansion (Rietkerk et al., 2004~~,~~; Eppinga et al., 2008). Black ash trees must also compete for light with other ash trees, but leaf area is typically low in these systems ~~(<2.5 leaf area index [LAI];~~ (Telander et al., 2015). Low LAI and observed ~~canopy~~crown shyness (*sensu* Long and Smith, 1992) in black ash wetlands may imply less competition among individuals than would be expected in mixed stands (Franco, 1986). On the other hand, ~~low~~less-than-expected canopy competition for light in the overstory may increase light availability for understory hummock species, and therefore allow subsequent hummock expansion from the understory. Therefore, based on evidence and observations presented here and in Diamond et al. (2019), we suggest that a major difference between microtopography in forested versus non-forested wetland systems will be the size distributions and spacing of hummocks. In other forested systems, hummocks associated with trees will likely be limited in size, exhibiting characteristic sizes and spacing due to local negative feedbacks from the crown competition. In contrast, non-forested wetland hummocks may have a much wider distribution of size classes, where negative feedbacks to hummock expansion may be largely due to local nutrient competition effects (e.g., Eppinga et al. 2008).

4.3 Evidence for patch self-organization

In this work, we used common landscape ecology diagnostics to characterize microtopographic pattern and infer responsible reinforcing processes, including analyses of multimodal distributions of elevation, spatial patterns of hummock patches, and hummock size distributions. Other recent work has used nearly identical diagnostic measurements to infer self-organization of depressional wetland features (~100 m wide) in a karst landscape (Quinton and Cohen 2019), demonstrating the broad utility of the approach and the various spatial scales that pattern may manifest. However, we note that this diagnostic approach alone does not directly implicate hypothesized mechanisms of hummock persistence, and that more measurements are required to support inferences made here. To that end, in complementary work we observed support for the elevation-productivity feedback, where we found hummocks to be loci of higher tree occurrence and biomass, more understory diversity, and greater phosphorus and base cation soil concentrations (Diamond et al., 2019). Further, these associations were most evident in the wettest sites, concordant with the hydrologic controls observed here for hummock height, pattern, and size distributions. Together, these multiple lines of evidence lend strong support for the hydrologically driven self-organization hypothesis of hummock growth and persistence (Figure 1).

~~4.3~~4.4 Broader implications

The consequences of wetland microtopography are clear at small scales, but ~~there is~~can also ~~some evidence that the presence of microtopography has~~scale to influence site- and regional-scale ~~importance~~processes. For example, microtopographic expression results in a drastic increase in surface area within wetlands. We conservatively estimate an average of ~~19~~22% and up to ~~32~~42% relative increase in surface area due to the presence of hummocks (i.e., ~~that~~ additional surface area provided by the sides of hummocks; ~~Table 23).~~Table 3). These estimates comport with studies in tussock meadows ~~that found~~, where tussocks ~~of an average of~~(ca. 20 cm tall) increased surface area by up to 40% (Peach and Zedler, 2006). ~~Increases~~Further, increases in the diversity of biogeochemical processes occurring at the individual hummock or hollow scale (Deng et al., 2014) likely aggregate to influence ecosystem functioning at large scales. For example, microtopographic niche expansion allows for local material and solute exchange between hummocks and hollows, creating coupled aerobic-anaerobic conditions with emergent outcomes for denitrification (Frei et al., 2012) and carbon emission (Bubier et al., 1995; Minick et al. 2019ab).

While our results implicate hydrology as a major determinant of microtopographic structure and pattern, microtopography can reciprocally influence system-scale hydraulic properties. Results from our hummock property analysis indicate that hummock volume displacement may be a significant factor in water ~~table~~level dynamics of wetlands. ~~-~~Specific yield, which ~~controls~~governs water ~~table~~level response to hydrologic fluxes, is commonly assumed to be unity when wetlands are inundated. However, inclusion of microtopography may render this assumption invalid, with hummock volumes up to 30% of site volumes (~~Table 4).~~Table 4). These observations are supported in other studies of microtopographic effects of specific yield (Sumner, 2007~~,~~; McLaughlin and Cohen, 2014~~,~~; Dettmann and Bechtold, 2016). Therefore, while hydrology exerts clear control on the geometry of hummocks, hummocks may exert reciprocal control on hydrology by amplifying small hydrologic fluxes into large water ~~table~~level variations.

Last, black ash hummocks ~~also~~ provide unique microsite conditions that support increased vegetation growth and diversity (Diamond et al. 2019), aligning with observations in other wetland systems (Bledsoe and Shear, 2000~~,~~; Peach and Zedler, 2006~~,~~; Økland et al., 2008). ~~Evidence abounds for both increased understory richness and improved seedling regeneration on hummocks relative to hollows (Koponen et al., 2004, Dubertstein and Connor 2009, Courtwright and Findlay 2011). To this point~~Accordingly, recent wetland restoration efforts have begun to use microtopography as a ~~restoration~~ strategy to promote ~~planted~~ seedling success and long-term project viability (Larkin et al., 2006; Bannister et al., 2013; Lieffers et al., 2017). ~~Indeed,~~Specific to our focal system, there are increasing efforts to mitigate potential black ash loss due to the emerald ash borer and ~~in light of recent concerns over~~possible regime ~~shift~~shifts to marsh~~-~~-like states ~~from black ash loss to EAB~~ (Diamond et al., 2018~~), we~~). We posit that hummock presence and persistence may allow for future tree seedlings to survive wetting up periods following this ash loss (Slesak et al., 2014), and for consequent resilience of ~~swamp~~forested ecosystem states.

~~5 Conclusions~~

~~6~~5 Code and data availability

The authors will provide code and data upon request, and will upload code to Github upon acceptance of the manuscript. The algorithm for delineating hummocks and hollows (“TopoSeg”) can be found at: https://github.com/aestovall/TopoSeg.

~~7~~6 Author contribution

JD and DM created the conceptual framework, questions, and hypotheses. AS and JD developed the TLS procedure and carried out measurements and subsequent analysis/code; JD and RS carried out hydrology measurements. JD conducted all data analysis and wrote the manuscript. All co-authors contributed significantly to editing the manuscript.

~~8~~7 Competing interests

The authors declare that they have no conflict of interest.

~~9~~8 Acknowledgments

This project was funded by the Minnesota Environmental and Natural Resources Trust Fund, the USDA Forest Service Northern Research Station, and the Minnesota Forest Resources Council. Additional funding was provided by the Virginia Tech Forest Resources and Environmental Conservation department, the Virginia Tech Institute for Critical Technology and Applied Science, and the Virginia Tech William J. Dann Fellowship. JD is supported by POI FEDER Loire n°2017-EX001784, Water Agency of Loire Catchment AELB, and University of Tours. We gratefully acknowledge the field work and data collection assistance provided by Mitch Slater, Alan Toczydlowksi, and Hannah Friesen. The authors also acknowledge two anonymous reviewers and Dr. Victor Lieffers, whose comments and suggestions improved this manuscript.

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~~11~~10 Tables

Table ~~1~~1 Site information for ten black ash study wetlands

Site	Latitude	Longitude	Elevation (m ASL)	Size (ha)	Average organic horizon depth (cm)
D1	47.67168	-93.68438	447	5.697	28.9 ± 9.1
D2	47.28097	-94.38353	425	6.499	27.7 ± 11.3
D3	47.28380	-94.37992	429	6.062	105.3 ± 32.2
D4	47.28021	-94.48627	442	0.491	60.6 ± 22.1
L1	47.53685	-94.21786	403	2.191	28.8 ± 9.5
L2	47.53444	-94.21320	391	6.845	19.6 ± 7.2
L3	47.52744	-94.20573	394	1.455	24.5 ± 10.1
T1	47.83737	-93.71288	424	15.659	129.4 ± 3.6
T2	47.67887	-93.91441	447	8.618	84 ± 26.2
T3	47.27623	-94.48689	432	1.938	53.6 ± 28.5

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Table 2 Daily water ~~table~~level summary statistics for black ash study wetlands

Site	Mean (m)	Median (m)	Standard deviation (m)	Mean hydroperiod (d)
D1	0.012	0.088	0.179	105
D2	-0.098	0.042	0.156	96
D3	0.053	0.143	0.196	117
D4	-0.008	0.003	0.151	77
L1	-0.255	-0.046	0.462	67
L2	-0.346	-0.046	0.543	77
L3	-0.370	-0.076	0.502	61
T1	-0.001	0.034	0.125	105
T2	-0.048	0.044	0.202	101
T3	-0.069	0.016	0.217	84

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Table 3 Relative area increase by hummocks across sites

Site	Survey area (m^2~~)~~)[†]	Hummock side surface area (m^2~~)~~)[‡]	Relative area increase by hummocks
D1	1045~~1234~~	~~175~~267	0.~~17~~26
D2	1041~~919~~	~~151~~258	0.~~14~~25
D3	1093~~1221~~	~~223~~311	0.~~20~~28
D4	1164~~1045~~	~~107~~217	0.~~09~~19
L1	1234~~1041~~	~~55~~92	0.~~04~~07
L2	919~~1093~~	~~40~~34	0.04
L3	1221~~1164~~	~~41~~56	0.~~03~~05
T1	731	~~237~~304	0.~~32~~42
T2	994	~~227~~376	0.~~23~~38
T3	1198	~~179~~308	0.~~15~~26
Average		~~144±74~~	
(Average, no L)	~~(186±44~~222±114 (291±47)	0.~~14~~22±0.~~09~~13 (0.~~19~~29±0.07)

[†] Survey area is the area scanned by TLS

[‡] Hummock side surface area is calculated from measured volumes and heights using a cone model

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Table 4 Hummock volume displacement ratios for all sites

Site	Site height[†] (m)	Site volume[‡] (m^3)	Hummock volume (m^3)	Hummock volume displacement ratio
D1	0.17	179	33	0.18
D2	0.15	155	26	0.17
D3	0.21	233	41	0.18
D4	0.17	200	24	0.12
L1	0.15	181	10	0.05
L2	0.26	242	5	0.02
L3	0.21	255	6	0.02
T1	0.18	134	37	0.28
T2	0.16	157	46	0.30
T3	0.17	199	37	0.18
Average			**27±14**	**0.15±0.09**
(Average, no L)			**(35±7)**	**(0.20±0.06)**

[†] Site height is estimated as the mean 80th percentile of hummock heights across the site

[‡] Site volume is estimated as by multiplying site height by site area

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~~12~~11 Figures

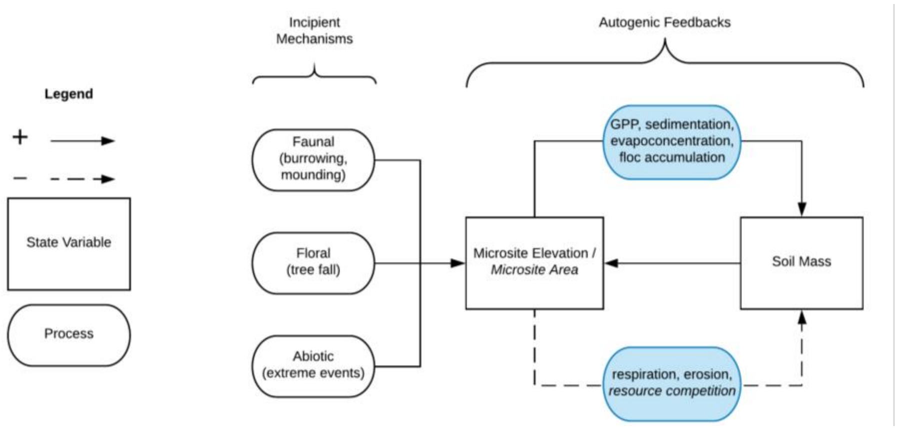


Figure ~~1.~~1. Conceptual model for autogenic hummock maintenance in wetlands. Incipient mechanisms create small-scale variation in soil elevation that is amplified by autogenic feedbacks, which grow and maintain elevated hummock structures. Solid lines indicate positive feedback loops and dashed lines indicate negative feedback loops. Font in italics refer to feedback processes hypothesized to only affect lateral hummock extent (thus hummock area), whereas non-italic font indicates mechanisms that affect both vertical and lateral hummock extent. Processes in blue indicate that these mechanisms are influenced by hydrology.

Soil mass refers to the amount of (organic) soil in a hummock, which can include roots, leaves, and decaying organic matter.

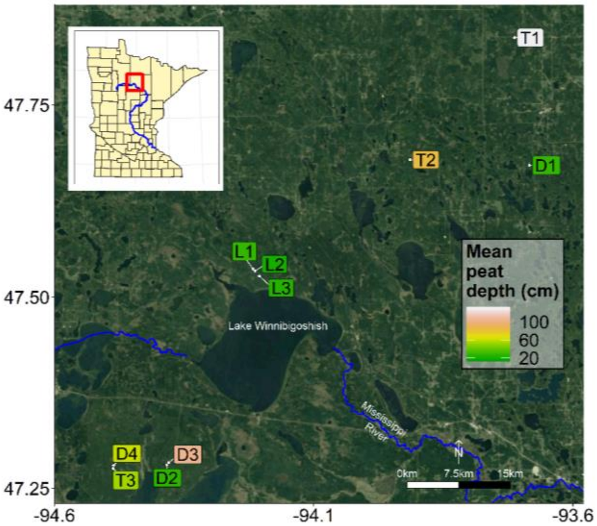
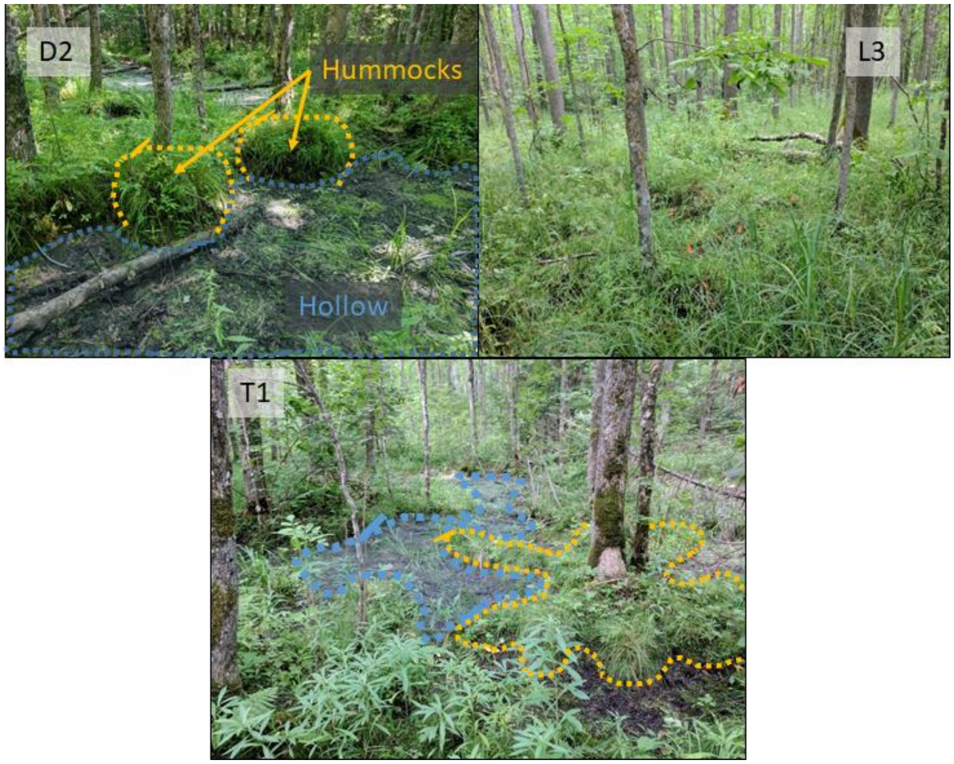


Figure 2. Map of black ash wetland sites. Sites are colored by their mean organic horizon depth.


D2
Hummocks
Hollow
L3
T1

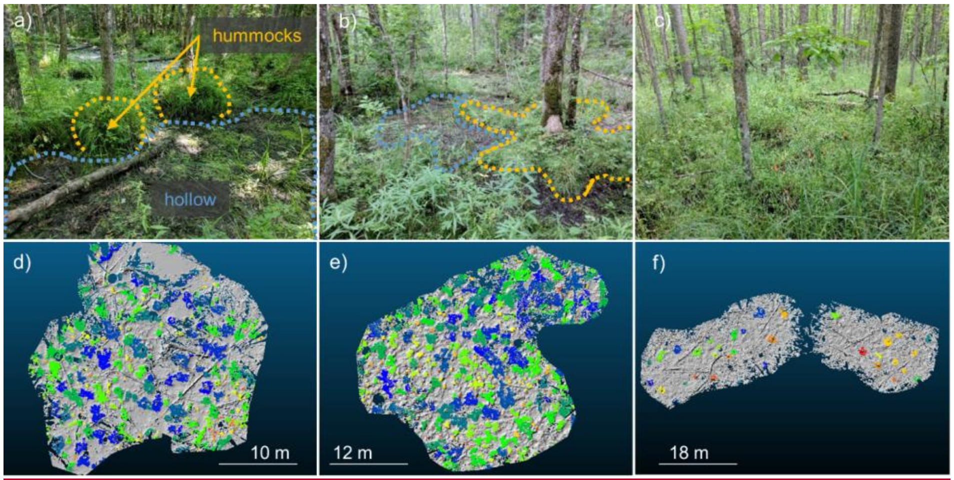

a)
hummocks
hollow
b)
c)
d)
10 m
e)
12 m
f)
18 m

Figure 3. (a–c) Photos of observed black ash wetland microtopography from a site in each hydrogeomorphic category: a) depression site D2, b) transition site T1, and c) lowland site L3. Hummocks are outlined in yellow/orange dashed lines, and hollows are outlined and lightly shaded in blue. Lowland (L1) site hummocks and hollows are difficult to discern in summer time due to heavy understory cover and are additionally less pronounced, so they are not drawn here. In contrast, depression (D2) and transition (T1) site hummocks were typically more visually distinct from hollow surfaces. (d–e) Corresponding automatically delineated hummocks for every site with hill-shaded surface models in the background: d) D2, e) T1, and f) L3. Hummocks are colored in each site by a unique identifier. Although some hummocks have similar colors to their neighbors indicating that they are the same hummock, if they are separated by grey space (hollows), they are unique.

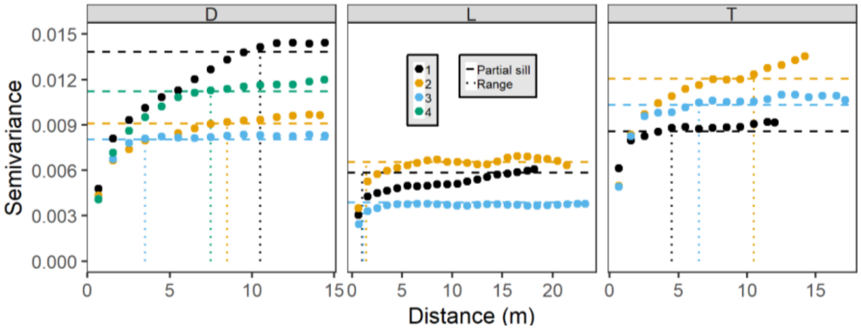


Figure 4. Omni-directional semivariograms for site elevations by hydrogeomorphic category (D = depression, L = lowland, T = transition). Sites are colored according to their number within their hydrogeomorphic category. Dotted vertical lines indicate best-fit ranges and horizontal dashed lines indicate best-fit partial sills (sill – nugget).

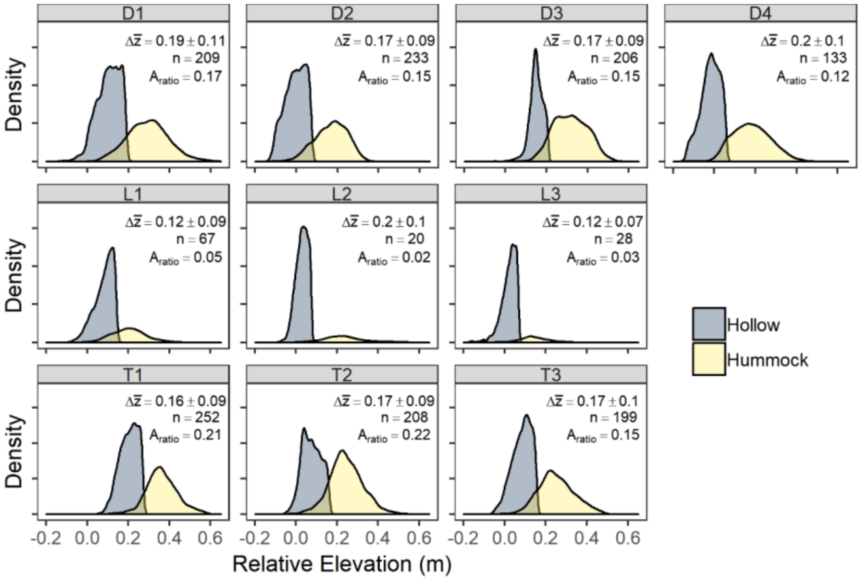


Figure 5. Relative elevation probability densities for each site, colored by hummock and hollow. Text indicates the difference in mean elevation (Δz; m) between hummock and hollow at each site (± standard deviation), the total number of hummocks identified at each site (n), and the ratio of hummock area to total site area (A_{ratio}). Depression sites (D) occupy the top row, followed by lowland sites (L), and transition sites (T). Elevations are relative to the base of the well at each site, which was approximately the lowest elevation at each site.

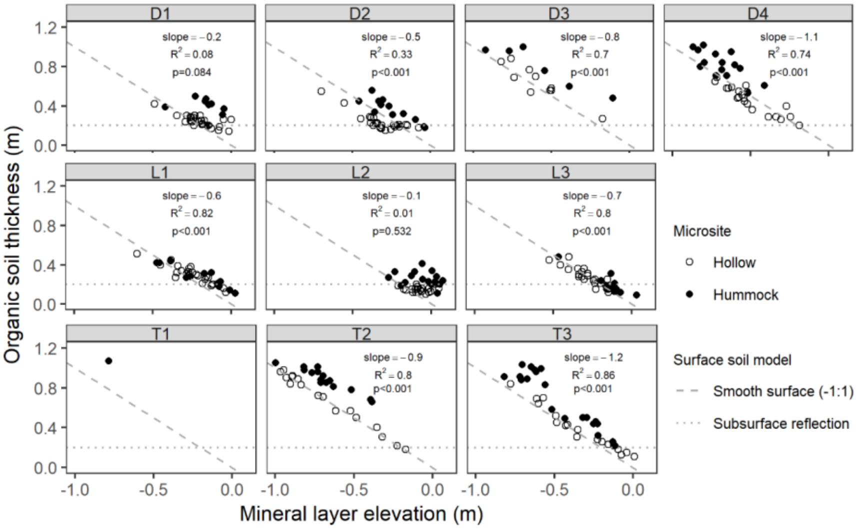


Figure 6. Organic soil thickness (measured as depth to resistance) as a function of mineral layer elevation. Points are filled by their microsite. Dashed -1:1 line indicates a smooth surface soil model and dotted horizontal line indicates a subsurface reflection model. Text values are slopes, R^2, and p-value of best-fit linear model for aggregated hummock and hollow points.

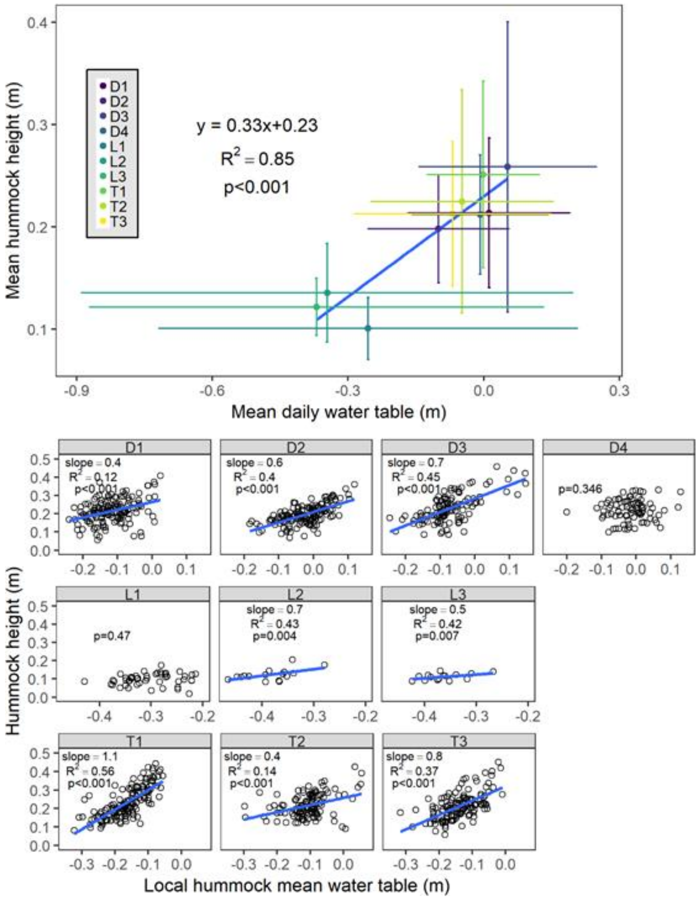


Figure 7. Hummock height as a function of mean water ~~table~~level. (Top) mean site-level hummock height (± sd) versus mean site-level daily water ~~table~~level (± sd), and (Bottom) individual hummock height versus local daily mean water ~~table~~level. Slope, R2, and p-value for best fit linear model (blue line) presented.

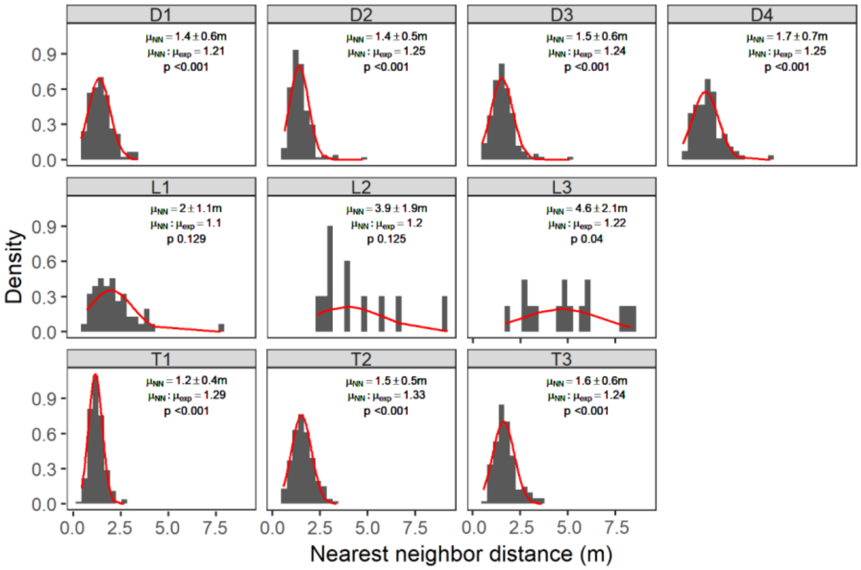


Figure 8. Hummock nearest-neighbor distance distributions across sites. Bars are scaled density histograms overlain with best-fit normal distributions (red lines). Text indicates the mean nearest-neighbor distance (μ_{NN} ± standard error); the ratio of the measured mean nearest-neighbor distance and the expected nearest neighbor distance for complete spatial randomness (μ_{exp}); and the p-value for a z-score comparison between μ_{NN} and μ_{exp}. p-values less than 0.001 indicate that hummocks are significantly overdispersed.

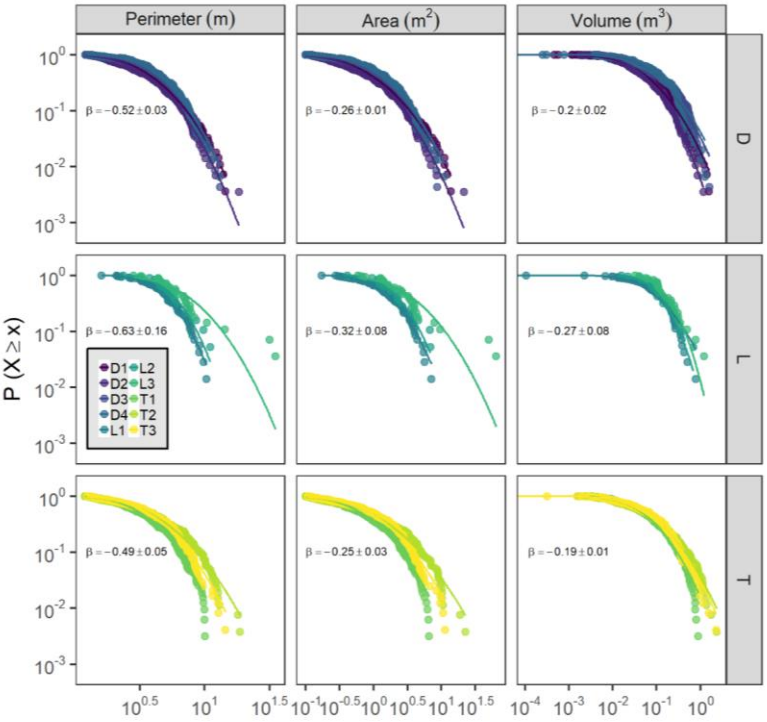


Figure 9. Inverse cumulative distributions of hummock dimensions (perimeter, area, and volume) across sites (points), split by hummock dimension and site type. The y-axis is the probability that a hummock dimension value is greater than or equal to the corresponding value on the x-axis. Best-fit lognormal distributions are shown for each site as lines. All fits were highly significant ($p<<0.001$). Text indicates mean (±sd) within-group coefficient for a model of the form $P(X\geq x)=\beta*\ln(\text{dimension\_value}) + \beta0$.