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**ADVANCED REVIEW**

A little relief: Ecological functions and autogenesis of wetland microtopography

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Abstract

Microtopography, or the small-scale variation in ground surface height (10^{-1} – 10^0 m) over short (10^0 – 10^2 m) spatial scales, is a ubiquitous feature of wetlands globally. This variation in elevation, characterized by local high (“hummocks”) and low (“hollows”) patches, is more structured than what is observed in uplands, and is intertwined with concordantly structured spatiotemporal variability in hydrologic regimes and associated ecological processes. The importance of microtopography in wetlands is manifold, with critical influence on local hydrological, biogeochemical, and biological processes. Further, the creation and maintenance of wetland microtopography is a balance between activation processes (i.e., those that induce random elevation variation) and autogenic reinforcement processes (i.e., those that provide the feedbacks necessary for the persistence of microtopography). While there are many mechanisms that create vertical structure (e.g., tree falls, accumulation of roots and soil organic matter, and sediment deposition), they all yield a similar core feedback to enhance and sustain microtopographic structure. Finally, microtopography contributes to spatial patterning that confers emergent ecosystem-scale functions such as hydrologic storage and flows, carbon cycling, organism dispersal, and biodiversity. There is an ongoing need to study the origins and implications of this fine-scale variation in elevation, as well as the utility of including microtopography in model predictions and ecological restoration efforts.

This article is categorized under:

Water and Life > Conservation, Management, and Awareness

KEYWORDS

ecohydrology, feedback, hollow, hummock, wetland

1 | INTRODUCTION

Wetlands are ecosystems characterized by seasonal to permanent inundation or soil saturation, hydrophytic vegetation, and hydric soils (Tiner, 1999), and cover more than 12.1 million km² around the globe (Ramsar Convention on Wetlands, 2018). They are hotspots of biodiversity, nutrient cycling, and water storage, and are thus important in

providing habitat for species, water quality improvement, climate regulation, and floodwater attenuation (Millennium Ecosystem Assessment (MEA), 2005; Ramsar Convention on Wetlands, 2018). A common feature in wetlands globally is microtopography, the vertical variation in the soil surface occurring at centimeter to meter scales. Microtopography has been described in fens (Sullivan, Arens, Chimner, & Welker, 2008), peat bogs (Malmer & Wallén, 1999; Nungesser, 2003), arctic and alpine tundra ecosystems (Biasi et al., 2005; Gao, Hu, Li, & Li, 2020), forested swamps (Bledsoe & Shear, 2000), tidal freshwater swamps (Casey & Ewel, 2006; Duberstein, Krauss, Conner, Bridges, & Shelburne, 2013), freshwater marshes (van de Koppel & Crain, 2006; Watts, Cohen, Heffernan, & Osborne, 2010), and coastal marshes (Fogel, Crain, & Bertness, 2004; Posey, Alphin, Meyer, & Johnson, 2003; Stribling, Cornwell, & Glahn, 2007; Figure 1).

Although microtopography itself is not unique to wetland systems, the expression and influence of fine-scale topographic variation in wetlands is unique in several important ways. Specifically, wetland microtopography: (i) creates greater small-scale topographic heterogeneity than in uplands (e.g., Harman, Lohse, Troch, & Sivapalan, 2014; Thompson, Katul, & Porporato, 2010), (ii) induces hydrologic variability, with important consequences for biological and biogeochemical processes, and (iii) appears to be structured (i.e., nonrandom), implying autogenic origins and supporting emergent, ecosystem-scale functions.

While microtopographic structure varies among wetlands, a common convention is to use binary nomenclature to distinguish between distinct high and low elevation patches. These include categories such as “hummock and hollow,” “mound and lawn,” “ridge and slough,” “tussock and pool,” and others. Topographic differentiation of elevated microsites is also system-dependent (Table 1). Generally, higher-microsite features (e.g., “hummocks”) are convex and embedded within otherwise lower areas (e.g., “hollows”) (Cantelmo Jr. & Ehrenfeld, 1999; Duberstein & Conner, 2009), which are typically flat or concave spaces (Nungesser, 2003; Stribling et al., 2007). The resulting spatial mosaic of topographic variation is among the hallmark features of many wetlands. For consistency, we hereafter refer to all elevated microsites as “hummocks” and the lower-elevation matrix as “hollows.” We acknowledge that this heuristic

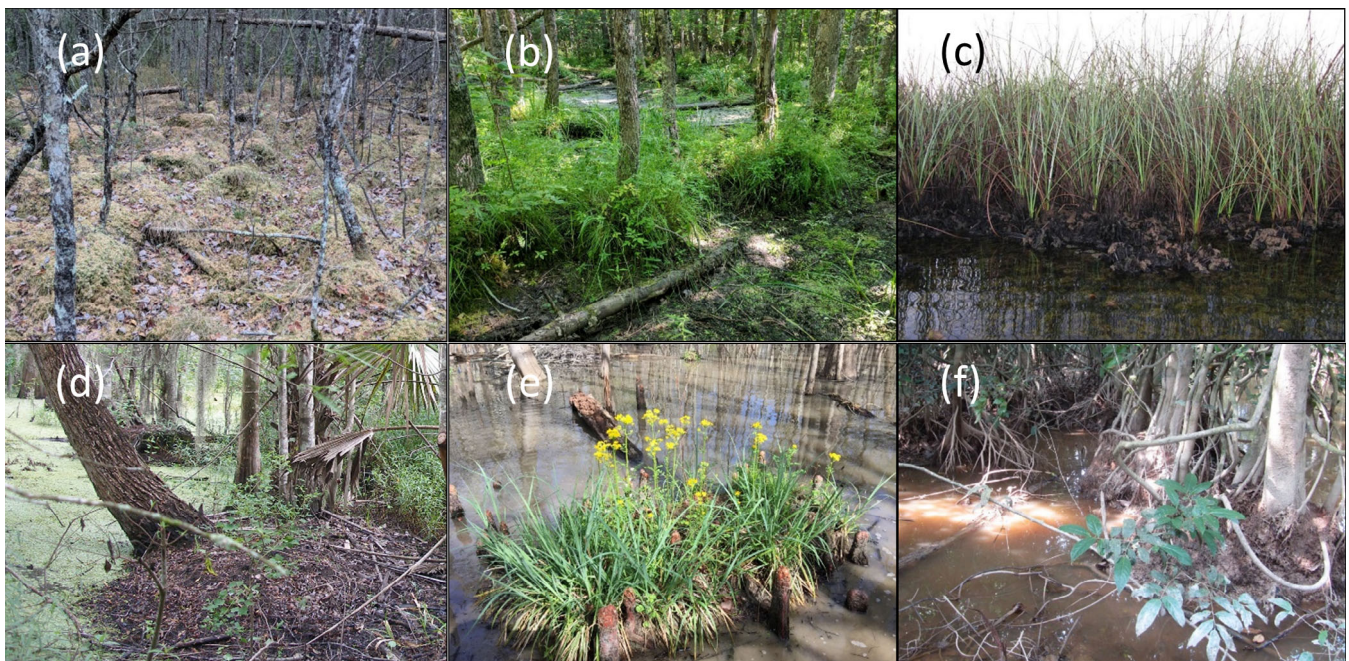


FIGURE 1 FExamples of wetland microtopography. (a) spruce (*Picea mariana*) bog with small *Sphagnum* spp. moss hummocks in northern MN (photo credit: Jacob S. Diamond); (b) black ash (*Fraxinus nigra*) swamp with hummocks associated with black ash trees interspersed among un-vegetated hollows in northern MN (photo credit: Jacob S. Diamond); (c) sawgrass (*Cladium jamaicense*) ridge rising above an inundated slough (hollow) in Everglades, FL (photo credit: Danielle Watts); (d) mixed water tupelo (*Nyssa aquatica*) swamp with mounded hummock amidst inundated hollows, FL (photo credit: Amy Washuta); (e) small vegetated hummock associated with knees of baldcypress (*Taxodium distichum*) in a cypress/tupelo swamp in the Spanish Lake Basin of Mississippi River delta, USA (photo credit: Richard Keim); (f) Beriah tropical peat swamp forest in the floodplain of the Kerian River, Perak state, Malaysia (photo credit: Richard Keim)

TABLE 1 Characteristics of hummocks across systems

System type	Wetland, location	Reported heights (cm)	Reported areas (m ²)	Initiation and autogenic mechanisms	Vegetation	References
Non-forested freshwater	Wet meadows, WI	10–20	0.3–0.8	Initiated by rhizomes; sediment/organic matter accretion	<i>Carex stricta</i>	Costello (1936)
	Wet tundra, AK/Siberia, Russia	11–38/40–60	0.03/0.7–7	Initiated by rhizomes; sediment accretion and differential freeze–thaw/organic matter accretion	<i>Eriophorum vaginatum</i>	Mark, Fetcher, Shaver, and Chapin III (1985), Biasi et al. (2005)
	Peatland, Qinghai-Tibetan Plateau, Tibet	10–30	0.16–1.57	Initiated by differential freeze–thaw; production-decomposition feedback and freeze–thaw feedback	<i>Kobresia sp.</i> , <i>Primula nutans</i> , <i>Carex allivescens</i>	Shen, Tang, and Washitani (2006), Deng, Cui, Hernández, and Dumont (2014), Gao et al. (2020)
	Polygonal bogs/frozen bogs/raised bogs Siberia, Russia	24–110/33–49	50–100	Initiated by differential freeze–thaw; production-decomposition feedback	<i>Carex spp.</i> , <i>Sphagnum spp.</i> , <i>Eriophorum spp.</i>	Biasi, et al., (2005)
	Floating fen, Ireland	15–30	NA	Initiated by differential freeze–thaw; production-decomposition feedback	<i>Sphagnum spp.</i> , <i>Schoenus nigricans</i>	van Bergen et al. (2020)
Nonforested saltwater	Salt marsh, Gulf of Mexico	7–13	NA	Initiated by rhizomes; sediment accretion	<i>Spartina alterniflora</i> and <i>Spartina patens</i>	Stribling et al. (2007)
	Pannes, ME	7	NA	Initiated by rhizomes; diversity-productivity feedback	<i>Triglochin maritima</i>	Fogel et al. (2004)
	Intertidal marsh, Netherlands	5–35	1–20	Initiated by rhizomes; sediment accretion	<i>Spartina anglica</i>	van Hulzen et al. (2007)
Forested freshwater	Bay or Hudson River, USA/Georgia or South Carolina, USA	15–20/4–18	1–10/1–10	Initiated as fallen tree trunks or large branches; organic matter accretion and root expansion	<i>Fraxinus</i> and <i>Nyssa spp.</i> , <i>Acer rubrum</i> , <i>Liquidambar styraciflua</i> / <i>Taxodium distichum</i> , <i>Nyssa aquatica</i> and <i>biflora</i> , <i>Quercus nigra</i>	Courtwright and Findlay (2011), Peterson and Baldwin (2004), Rheinhardt (1992), Rheinhardt and Hershner (1992)/Duberstein et al. (2013), Noe, Krauss, Lockaby, Conner, and Hupp (2013)
	Spruce peat bogs, ME or MN, USA and ON, Canada	20–50	0.1–16	Initiated from <i>Sphagnum</i> production and decomposition; low <i>Sphagnum</i> decomposition rates on hummocks versus the surrounding environment	<i>Picea mariana</i> , <i>Sphagnum spp.</i>	Rocheftort, Vitt, and Bayley (1990), Nungesser (2003), Graham, Glenn, Spaete, and Hanson (2020)
	Ombrotrophic bogs, Sweden and Estonia	20–40	NA	Initiated from <i>Sphagnum</i> production and decomposition	<i>Sphagnum spp.</i>	Johnson, Damman, and Malmer (1990), Karofeld (1998), Malmer and Wallén (1999)
	Tropical peat swamp, Sumatra, Indonesia	10–40	NA	Initiated around tree buttresses; organic matter accretion	<i>Shorea teysmanniana</i>	Shimamura and Momose (2005, 2007)
	Freshwater swamps, NJ/MN	22–123/20–50	1–1.5/0.1–10	Initiated from woody debris and large structural roots of trees and shrubs; sediment/organic matter accumulation	<i>Chamaecyparis thyoides</i> , <i>Kalmia angustifolia</i> , <i>Vaccinium corymbosum</i> , <i>Rhododendron viscosum</i> / <i>Fraxinus nigra</i>	Ehrenfeld (1995), Ehrenfeld and Schneider (1993)/Diamond, McLaughlin, Slesak, and Stovall (2020)

(Continues)

TABLE 1 (Continued)

System type	Wetland, location	Reported heights (cm)	Reported areas (m ²)	Initiation and autogenic mechanisms	Vegetation	References
	Mesotrophic or oligotrophic fen, Newfoundland and Alberta, Canada/Finland	20–50	NA		<i>Sphagnum spp.</i> , <i>Picea mariana</i>	Bateman and Davis (1980), Lieffers, Caners, and Ge (2017), Saarnio et al. (1997)
	Tree islands, FL	100	10e6–7	Initiated by erosion and sedimentation by river flow; phosphorus redistribution	<i>Chrysobalanus icaco</i> , <i>Myrica cerifera</i> , <i>Salix caroliniana</i> , and <i>Schinus terebinthifolius</i>	Sklar and van der Valk (2012), Wetzel et al. (2005)
Forested saltwater	Mangroves, Australia, New Zealand	5–20	0.5–1	Initiated from crab/lobster burrows; sedimentation trapped by prop root system	<i>Avicennia spp.</i>	Griffin et al. (2010), Knight et al. (2009), Lindquist et al. (2009)
	Brackish marsh/swamp, Australia	40–70	NA	Initiated by rhizomes/roots; organic matter accumulation, increased productivity from guano deposition	<i>Melaleuca ericifolia</i> and <i>Phragmites australis</i>	Wallis and Raulings (2011)

simplification does not apply to all wetlands, which can indeed be composed of more than two microtopographic modes (Graham et al., 2020; Moore et al., 2019).

Despite the prevalence of wetland microtopography, efforts to synthesize the attendant hydrological, biogeochemical, and biological processes have been limited, as have efforts to generalize initiation and reinforcement mechanisms. The pressing need to protect and restore wetland functions (Creed et al., 2017; Sullivan, Rains, & Rodewald, 2019) motivates this review on the ecological importance of wetland microtopography, and mechanisms that control initiation and reinforcement. We approach this review from a systems perspective, emphasizing the feedbacks between hydrology, biota, and physical accretion that underlie wetland processes and appear crucial for the genesis, persistence, and patterning of microtopography.

2 | MICROTOPOGRAPHIC INFLUENCE ON WETLAND PROCESSES

In wetlands, even limited microtopographic relief may alter local inundation and soil moisture dynamics that in turn regulate elemental cycling, metabolic processing, and site suitability for flora and fauna (Table 2). There are thus often striking differences in local habitat and biogeochemical processes between hummocks and hollows (Conner, 1995; Titus, 1990). These short-range differences are ecologically relevant at larger scales because they induce coupling dynamics that scale-up to increase net ecosystem productivity, biodiversity, and resilience (Larkin, Vivian-Smith, & Zedler, 2006). In this section, we review the influence of microtopography on key wetland hydrologic, biogeochemical, and biological processes at multiple spatial and temporal scales.

2.1 | Hydrologic processes

Microtopography directly influences the timing and spatial distribution of hydrologic storages and fluxes in a wetland at multiple scales. Wetlands are fundamentally defined by their hydrologic regime (Rodriguez-Iturbe, D'Odorico, Laio, Ridolfi, & Tamea, 2007), which is both a function of external drivers (such as climate, regional topography and geology, and landscape position) and of internal properties (such as vegetation type and distribution, soil properties, and basin morphology). Among these internal properties, microtopography adds complexity to wetland basin morphology, structuring hydrologic processes at the point scale (e.g., soil moisture spatial patterns; Zona et al., 2011) and system scale (e.g., storage capacity and drainage patterns; Dettmann & Bechtold, 2016; Quinton, Gray, & Marsh, 2000). Therefore,

TABLE 2 Variation in wetland processes and functions between hummocks and hollows

Function	Effect of microtopography	References
Plant diversity/ species richness	Higher vegetative diversity on hummocks.	Vivian-Smith (1997), Bukata (1999), Fogel et al. (2004), Koponen, Nygren, Sabatier, Rousteau, and Saur (2004), Yasuhiro, Hirofumi, and Kihachiro (2004), Duberstein and Kitchens (2007), Økland, Rydgren, and Kland (2008), Courtwright and Findlay (2011), Washuta (2011)
	Higher vegetative diversity in hollows.	Peterson and Baldwin (2004), Givnish et al. (2008)
Seedling/root/stem density	Higher density on hummocks	Titus (1990), Jordan and Hartman (1995), Jones, Lockaby, and Somers (1996), Jones, Henson, and Somers (2000), Duberstein and Conner (2009), Courtwright and Findlay (2011), Washuta (2011), Lampela et al. (2016), Lieffers et al. (2017)
	Higher density in hollows	No references found
Soil moisture variability	Higher variability on hummocks	Bubier, Costello, Moore, Roulet, and Savage (1993), Lindholm and Markkula (1984), Zona, Lipson, Zulueta, Oberbauer, and Oechel (2011)
	Higher variability in hollows	No references found
Nutrient accumulation	Higher nutrient accumulation on hummocks	Sullivan et al. (2008) (nitrogen and carbon), Jones et al. (1996), Wetzel et al. (2005), Eppinga et al. (2008) (phosphorus)
	Higher nutrient accumulation in hollows	Stoeckel and Miller-Goodman (2001) (nitrogen and phosphorus in floodplain systems)
Greenhouse gas emissions	Higher carbon dioxide emissions on hummocks	Bubier, Crill, Moore, Savage, and Varner (1998)
	Higher methane emissions in hollows	Bubier et al. (1993), MacDonald et al. (1998), Waddington and Roulet (1996), Saarnio et al. (1997)

the spatial arrangement and extent of microtopography plays an integral role in the degree to which it influences inundation and soil moisture patterns, water storage, and flow regimes.

At the point scale, the relative elevation of any microtopographic feature largely controls soil moisture and inundation dynamics. Because of the high hydraulic conductivity of many organic wetland soils, water tables are much flatter than the surface microtopographic variation (Cobb et al., 2017; Nungesser, 2003). Therefore, variation in soil surface height represents equivalent variation in distance to the water table (Wallis & Raulings, 2011). Hummocks then tend to be sites of consistently reduced inundation and lower soil moisture relative to hollows (Bubier et al., 1993; Lindholm & Markkula, 1984; Zona et al., 2011). Hummocks may also exhibit more temporal variation in soil moisture than hollows as a result of greater relative sensitivity to rainfall inputs, particularly during drier periods (Lindholm & Markkula, 1984). In contrast, soil moisture regimes in hollows are less variable because they are typically saturated for extended periods (even semi-aquatic or buoyant) and thus depend more on shallow water table variations.

Microtopography also exerts system-scale controls on inundation and soil moisture regimes by regulating wetland stage response to inputs (e.g., precipitation) and outputs (e.g., evapotranspiration; ET). Water levels in topographically homogeneous wetlands are likely to be highly dynamic near the mean elevation of the sediment–water interface (Daly, Zinger, Deletic, & Fletcher, 2009; Tamea, Muneeppeerakul, Laio, Ridolfi, & Rodriguez-Iturbe, 2010). This phenomenon is expected because the specific yield (i.e., the inverse of the stage response to a unit volume change; Childs, 1960) approaches zero, amplifying the stage response to water inputs or losses (Cheng, Wang, Duan, Chen, & Yang, 2015; Nachabe, 2002). While this has been observed in unusually topographically uniform settings, it has not been observed more broadly (McLaughlin & Cohen, 2014; McLaughlin, Diamond, Quintero, Heffernan, & Cohen, 2019). The most likely explanation is that in wetlands with significant microtopography, the soil surface occurs over a range of elevations rather than just one, the spatial integration of which dramatically dampens the near-zero specific yield effect, thereby stabilizing water level dynamics (Dettmann & Bechtold, 2016; Sumner, 2007). Intriguingly, although microtopography mutes expected stage dynamics at the hollow surface, it also amplifies stage dynamics beyond flat-surface expectations when water levels are slightly higher. The combination of these two effects is important for interpreting

stage response dynamics to hydroclimatic forcing, and thus critical to predicting how wetland water levels respond to climate change (e.g., errors up to 4 m without considering microtopography; Cresto Aleina et al., 2015; Shi et al., 2015).

At the system scale, microtopography also regulates wetland hydrology by modulating water storage capacity and surface flow paths. While hummocks can reduce the available volume for static water storage by up to 30% (Diamond, McLaughlin, Slesak, & Stovall, 2019), their influence on stage dynamics (see previous paragraph) actually increases dynamic water storage leading to reduced outflows compared to basins without microtopography (Tweedy & Evans, 2001). Indeed, some researchers have likened gaps between hummocks to v-notch weirs (Dommain, Couwenberg, & Joosten, 2010) that alter surface flowpaths and prolong wetland storage through storm flow attenuation (Kværner & Kløve, 2008). Accordingly, modeling suggests that wetland microtopography induces more-variable surface water outflows relative to topographically homogenous surfaces: at high stage, discharge is rapid, but as stage lowers, discharge can occur through progressively smaller surface channels between hummock features (van der Ploeg et al., 2012). Further, the degree to which microtopography influences water flows and thus water storage can be sensitive to the orientation and spatial arrangement of hummocks and hollows (Frei et al., 2010; Kaplan, Paudel, Cohen, & Jawitz, 2012). As such, wetland microtopography largely regulates water storage and export, with implications for broader landscape hydrology.

2.2 | Biogeochemical processes

Microtopographic variability allows wetlands to host a profusion of biogeochemical processes, many of which enable important landscape and watershed functions (Golden et al., 2019; Marton et al., 2015). The diversity of biogeochemical processes in wetlands arises from spatiotemporal gradients in microbially driven reduction–oxidation (redox) reactions. Local soil saturation and soil properties (e.g., texture, organic matter content) are primary controls on the gradients and speciation of electron acceptors and donors (DeLaune & Reddy, 2008), and thus they are primary controls on the prevailing redox conditions throughout a wetland. Through its influence on soil saturation and the unique substrata and organisms associated with hummocks and hollows, microtopography can control the point-scale distribution of wetland biogeochemical processes and how these processes are coupled between adjacent contrasting settings (i.e., hummocks and hollows) to drive emergent, wetland-scale biogeochemical phenomena.

At the point scale, microtopographically induced variation in redox state leads to spatially dynamic carbon processing. In general, wetlands are associated with reduced redox states, where the availability of oxygen for root respiration (and thus primary productivity) and decomposition is low. Primary productivity increases with distance from the water table (Belyea & Clymo, 2001; Jones et al., 2000), meaning that hummocks are often loci of high primary productivity compared to hollows (Strack, Waddington, Rochefort, & Tuittila, 2006; Sullivan et al., 2008). This difference in primary productivity is balanced by coincidentally greater decomposition rates in hummocks relative to hollows due to their more consistently oxygenated condition (Courtwright & Findlay, 2011). Decomposition end-products also depend on microtopography, with greater methane emissions from hollows (Bubier et al., 1993; MacDonald et al., 1998; Saarnio et al., 1997; Waddington & Roulet, 1996) and greater carbon dioxide emissions from hummocks (Bubier et al., 1998; Schneider, Kutzbach, & Wilmking, 2012). Even fluxes of trace gases show spatial patterns. For example, isoprene emissions (an important aerosol precursor) from hollows exceed hummocks by two orders of magnitude (Janson & Serves, 1998). Although many studies of greenhouse and trace gas flux from wetlands do not explicitly parse differences in gas emissions between topographic microsites, the well-known controls of soil saturation/redox on these fluxes (Bridgman, Cadillo-Quiroz, Keller, & Zhuang, 2013; Turetsky et al., 2014; Yvon-Durocher et al., 2014) support the hypothesis of strong spatial divergence in gas emission composition and magnitude.

Differences in primary production and decomposition attributed to microtopographic variation often result in associated spatial variation in nutrient availability and fluxes. Nutrient concentrations are typically greater in hummocks than hollows (Bruland & Richardson, 2005; Diamond et al., 2020; Noe & Hupp, 2005; Wolf, Ahn, & Noe, 2011), with up to four times more nitrogen, carbon, and root mass (Sullivan et al., 2008) and up to five times more phosphorus (Jones et al., 1996). Increased nutrient abundance and availability in hummocks relative to hollows may be attributed to: (1) accumulation of debris and litter (Stine, Resler, & Campbell, 2011), (2) incremental nutrient concentration due to evapotranspiration differences between hummocks and hollows (Eppinga, Rietkerk, Wassen, & De Ruiter, 2009; Troxler & Childers, 2009; Wang, 2011; Wetzel et al., 2005), or (3) higher turnover and cycling rates (Lampela, Jauhiainen, & Vasander, 2014; Wetzel et al., 2005). Even mycorrhizal activity (Cantelmo Jr. & Ehrenfeld, 1999) and

absorptive root biomass (Li et al., 2019) are greater in hummocks than hollows, which may be important for phosphorus acquisition from ferric-bound particles and nutrient harvesting for plants. Hummocks may also host significantly greater soil microbial diversity than hollows (Ahn, Gillevet, Sikaroodi, & Wolf, 2009), likely resulting in a greater diversity of biogeochemical processes (e.g., bacterial photoautotrophy; Burke, Gorham, & Pratt, 1974) that drive elemental turnover. Across most systems, microtopographic variation in nutrient cycling appears related to internal biotic processes as opposed to external drivers such as spatially variable atmospheric deposition (e.g., Moore, Blodau, Turunen, Roulet, & Richard, 2005). We note that the importance of internal processes is likely greater in low energy systems; floodplain systems, in contrast, may concentrate N and P into lower swale features due to externally-driven redistribution of fine-textured sediment (Stoekel & Miller-Goodman, 2001), although denitrification and export of P by redox-driven dissolution of orthophosphates (Scott, Keim, Edwards, Jones, & Kroes, 2014) may counteract this tendency. Additionally, there are many understudied elements for which biogeochemical cycles in wetlands are of global importance (e.g., silica; Struyf & Conley, 2009) where microtopography could be influential.

The higher redox potential in hummocks may also limit concentrations of ions and toxic solutes common in wetland systems. For example, because methylation of mercury (resulting in methylmercury, a toxic organometallic cation) occurs under low redox conditions, it may be 2–3.5 times more concentrated in hollows than in hummocks (Branfireun, 2004). Higher redox potentials in hummocks favor nontoxic and insoluble Fe^{3+} rather than the phytotoxic and soluble Fe^{2+} in more reduced conditions. Similarly, reduced sulfur can reach toxic levels in salt marshes, but aerobic oxidation in hummocks can lower concentrations by up to an order of magnitude compared to hollows (Stribling et al., 2007). Conversely, hummocks may also concentrate certain toxic compounds or elements. For example, selenium, which is toxic at levels found in some wetlands, is mobilized, bioavailable, and taken up by plants in oxidizing conditions (Hansen, Duda, Zayed, & Terry, 1998; Masscheleyn & Patrick, 1993).

By increasing heterogeneity in redox states and associated elemental cycling, microtopography has a clear capacity to regulate ecosystem-scale biogeochemical processes. Models and empirical observations demonstrate clear hummock-hollow biogeochemical coupling, where electron acceptors and donors are generated in and subsequently exchanged between oxidized and reduced zones (Devito & Hill, 1999; Frei, Knorr, Peiffer, & Fleckenstein, 2012; Ulanowski & Branfireun, 2013). For example, nitrification rates can be up to twice as high in hummocks as in hollows (Noe et al., 2013), suggesting hummocks are nitrate sources and thus donors to denitrifiers in the more-saturated hollows (Seitzinger et al., 2006). Redox coupling may occur in the opposite direction as well; much of the methane generated by methanogens in hollows is likely consumed by methanotrophs in hummocks (Bubier, Moore, Bellisario, Comer, & Crill, 1995; Deng et al., 2014). Further, microtopography expands the effective soil surface up to 42% for redox gradients and exchange interfaces (Diamond et al., 2019). 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; Bruland, Richardson, & Whalen, 2006; McClain et al., 2003), greater effective surface area enhances overall wetland biogeochemical reactivity (Marton et al., 2015).

2.3 | Biotic composition

The structured variability in hydrology and biogeochemical processes resulting from microtopography increases the variety of microhabitats available for flora and fauna within a wetland. Depending on specific environmental tolerances and optimal growth conditions, wetland flora and fauna may occupy distinct niches defined by hummocks or hollows (Beatty, 1984; Koponen et al., 2004; Raulings, Morris, Roache, & Boon, 2010). Because microtopographic variation enhances habitat complexity, it has important implications for floral and faunal communities.

It is well established that hummocks provide refuge from hydrologic stressors experienced by wetland plants, commonly leading to higher growth and regeneration on hummocks compared to hollows (Moeslund, Arge, Bøcher, Dalgaard, & Svenning, 2013 and references therein). For example, in fluvial systems, hummocks provide local physical protection from floating woody debris (Huenneke & Sharitz, 1986), and in coastal systems hummocks reduce stress from salinity (Hsueh, Chambers, Krauss, Allen, & Keim, 2016). However, the most salient stress relief that hummocks provide is likely abatement from saturated soils and their anaerobic conditions, because distance to the water table appears to be the most important control on wetland vegetation community structure (Araya et al., 2011; Malhotra, Roulet, Wilson, Giroux-Bougard, & Harris, 2016). Consequently, hummock height is positively associated with greater relative growth and biomass (Diamond et al., 2020; Roy, Bernier, Plamondon, & Ruel, 1999; Stoffella et al., 2010), foliar

nutrient concentrations (Roy et al., 1999), and seedling regeneration success (Blood & Titus, 2010; Chimner & Hart, 1996; Titus, 1990). Indeed, the greater success of seedlings on hummocks (Gengarely & Lee, 2005; Shida & Nakamura, 2011) has led to the consensus that restoration plantings on hummocks fare better than in hollows (Anderson, Landi, & Marks, 2009; Battaglia, Sharitz, & Minchin, 1999; Simmons, Wu, & Whisenant, 2011). Consequently, restoring microtopography is an emerging priority for wetland restoration projects (Bannister, Coopman, Donoso, & Bauhus, 2013; Conner, 1995; Larkin et al., 2006; Lieffers et al., 2017).

In addition to higher plant growth and recruitment, hummocks typically support higher plant density and diversity than hollows. This microtopographic control on plant density and diversity is evident across systems: in the U.S. southeastern coastal plain (Anderson et al., 2009; Duberstein & Conner, 2009), northeastern U.S. tidal freshwater swamps (Courtwright & Findlay, 2011; Hörnberg, Ohlson, & Zackrisson, 1997; Økland et al., 2008), tropical freshwater swamp forests (Koponen et al., 2004), and tropical ombrotrophic peat swamps (Lampela et al., 2014). The preference for hummocks is particularly true for woody midstory and overstory species, but hummocks also exhibit greater understory diversity of both vascular plants and mosses (Diamond et al., 2020; but see Peterson & Baldwin, 2004). While not as pronounced as differences in woody vegetation, in some systems like salt and freshwater marshes that lack woody vegetation, hummocks are also associated with greater abundances of herbaceous species than hollows (Fogel et al., 2004; Langlois, Bonis, & Bouzillé, 2003; Shen et al., 2006). On the other hand, some floodplain tree species in the peat swamps of Indonesia (Freund, Harsanto, Purwanto, Takahashi, & Harrison, 2018; Shimamura & Momose, 2005) may not prefer hummocks, and perhaps have developed adaptations to hydrologically dynamic environments. However, the increased density and diversity observed on wetland hummocks in most systems suggest these features to be important in governing community assembly and metapopulation stability.

While hummocks often have higher plant diversity and density, certain species may preferentially occupy lower and wetter hollow positions. Because plants on hummocks likely face greater root competition (Windham, 1999), hollows allow for flood-tolerant species to flourish. Consequently, hollows often support a higher density of obligate wetland species, including some woody species (Duberstein & Conner, 2009; Koponen et al., 2004) and a large variety of emergent, floating, and submerged herbaceous species (Anderson & Lockaby, 2007; Leck, Baldwin, Parker, Schile, & Whigham, 2009). Likewise, floral diversity in the low elevation sloughs of the Everglades is far higher, and spans a broader array of herbaceous growth forms, than in the adjacent higher elevation ridges (Givnish et al., 2008); note that the still higher elevation tree islands are among the most diverse patches in the Greater Everglades system (see Box 1).

At the wetland scale, the presence of both hummocks and hollows provides diverse niches that enable higher overall wetland species richness, evenness, and abundance compared to wetlands without microtopography (Smith, Meiman, & Brummer, 2012; Vivian-Smith, 1997). Numerous studies have observed a positive correlation between microtopographic heterogeneity and species richness (Higo & Okada, 2018; Paratley & Fahey, 1986; Raulings et al., 2010; Ritchie & Olson, 2015). Small-scale environmental heterogeneity potentially enhances the coexistence of facultative and obligate wetland species (e.g., in temperate swamp and boreal forest wetland systems; Paratley & Fahey, 1986), aligning with expectations from the habitat heterogeneity hypothesis (Douda, Doudová-Kochánková, Boublík, & Drašnarová, 2012). Notably, the microtopographic enhancement of species richness may not be evident from sampling at larger scales (Johnson, 1996).

The spatial mosaic of wetland hummocks and hollows often provides ideal habitat and specific microsite conditions for multiple faunal groups (Batzer & Wissinger, 1996; Spitzer & Danks, 2006). In this regard, wetland fauna are not typically associated with particular hummock or hollow microsites (but see Fairchild, Cruz, Faulds, Short, & Matta, 2003), but instead often rely on the incidence of both high and low sites to meet their time-varying needs for refugia, food sources, and habitat structure under variable hydrologic conditions (Čelik & Vreš, 2018). As such, faunal diversity increases with topographic diversity at the microsite scale (Angradi, Hagan, & Able, 2001; Karunaratne, Darby, & Bennetts, 2006). For example, crustaceans may occupy slightly drier microsites during inundated conditions, but retreat to hollows with persistent inundation or simply higher soil moisture during drier conditions (Strachan, Chester, & Robson, 2014). Likewise, both hummocks and hollows provide important habitat for snail kites in the Everglades: birds use trees on high elevation sites (i.e., tree islands) for nesting and sites of lower elevation (i.e., sloughs) for snail foraging (Bennetts, Darby, & Karunaratne, 2006; Dreitz, Bennetts, Toland, Kitchens, & Collopy, 2001). Microtopography is also important for ant and rotifer habitat diversity in northern peat fens (Bateman & Davis, 1980; Lesica & Kanno, 1998), insect diversity within boreal peat bogs (Spitzer & Danks, 2006), and for small mammals such as mice and voles that may benefit from microsite variability for foraging, protection, and reproduction (Bias & Morrison, 2006; Rossell & Rossell, 1999; Seagle, 1985). During dry periods, hollows with sustained inundation serve as refugia for fish and amphibians (Larkin, Madon, West, & Zedler, 2008) and foraging

BOX 1. TREE ISLANDS IN THE EVERGLADES, FL



Front to back: slough, sawgrass (*Cladium jamaicense*) ridge, and tree island in Everglades, FL (Photo credit: Jacob S. Diamond).

The persistence and potential vulnerability of microtopography is exemplified by tree islands in the Everglades, FL. The mechanisms of tree island persistence include ecohydrological feedbacks among hydrology, nutrient availability, tree production, and soil/peat accumulation (Espinar, Ross, & Sah, 2011; Troxler & Childers, 2009). Tree islands are nutrient hotspots, having 6–100 times more phosphorus than the surrounding P-limited marshes and sloughs (Noe, Childers, & Jones, 2001; Wetzel et al., 2005). Evidence suggests there is a persistent groundwater head gradient toward the tree islands from the surrounding marsh because of specific yield differences and evapotranspiration gradients between the two habitats (Rodriguez, Serna, & Scinto, 2014; Ross et al., 2006). Localized nutrient enrichment on tree islands is also plausibly attributable to animal movement, particularly nesting by wading birds (Givnish et al., 2008; Wetzel et al., 2005). Regardless of the enrichment mechanism, the phosphorus surplus enhances woody plant production, which increases litter and root mass accumulation, entraining a positive feedback that both reinforces phosphorus enrichment and creates and maintains tree island height (Hanan & Ross, 2010). Soil height stabilizes when soil oxidation equilibrates with soil carbon accretion. However, modifications to regional hydrology have likely altered these feedbacks, as evidenced by recent observations of woody vegetation mortality and the loss of many tree islands (Carr, D'Odorico, Engel, & Redwine, 2016; Ruiz, Sah, Ross, & Spitzig, 2013; Wu, Rutchey, Guan, Vilchek, & Sklar, 2002). Tree island loss or conversion to treeless “ghost islands” has raised concerns over habitat diversity loss and speculation that there may ultimately be transition to a marsh state over time (D'Odorico et al., 2011; Troxler & Childers, 2009). Although efforts are in place to restore historical hydrology in the hopes of reinvigorating processes leading to microtopography, recovery may be unrealistic in the presence of new feedbacks that develop in this bi-stable system (Heffernan, Watts, & Cohen, 2013).

sites for wading birds and turtles (Rice & Mazzotti, 2004). Microtopography thus greatly expands available niches even within small wetlands.

3 | INITIATION AND REINFORCEMENT OF MICROTOPOGRAPHY

The development of microtopographic structure in many wetlands appears to be self-reinforcing. The question naturally arises, what came first: hummocks that led to increased primary production, or vegetation growth that induced hummocks (or something else entirely)? Here, we seek to clarify this issue by distinguishing between random environmental

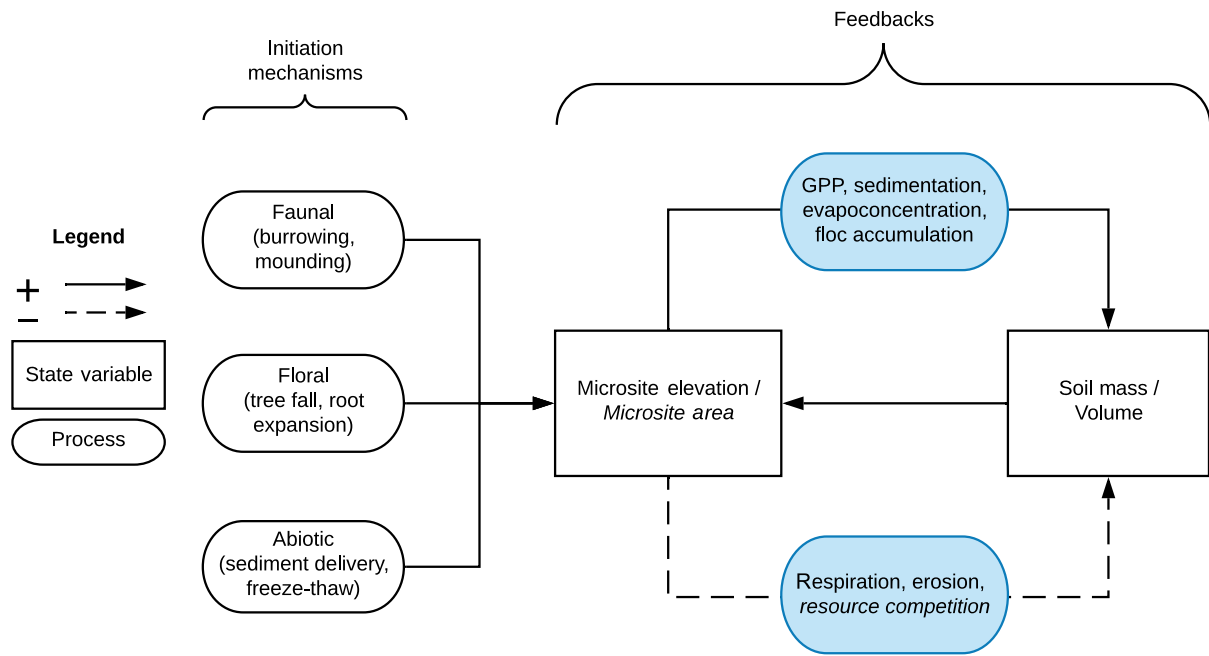


FIGURE 2 Conceptual model for hummock initiation and maintenance in wetlands (Reprinted with permission from Diamond et al. (2020)). Initiation mechanisms create small-scale variation in soil elevation that is amplified by feedbacks that grow and maintain elevated hummock structures. Solid lines indicate positive feedback loops and dashed lines indicate negative feedback loops. Italics denote feedback processes hypothesized to only affect lateral hummock extent (thus hummock area), whereas nonitalics indicate mechanisms that affect both vertical and lateral hummock extent. Blue shading indicates mechanisms influenced by hydrology. Soil mass can include mineral and organic matter. GPP refers to gross primary production

processes that induce incipient microtopography, and the processes that augment and reinforce these random microtopographic variations through ecological and hydrological feedbacks. While there are numerous mechanisms that initiate microtopographic variation, persistent wetland microtopography requires the same core processes to enhance and sustain vertical structure; these processes largely arise from feedbacks between plant growth, hydrology, and material accrual rates that are self-reinforcing, or *autogenic* (Figure 2). In this section, we review these initiation and reinforcing processes and their consequences for emergent microtopographic patterns.

3.1 | Initiation

There are myriad ways to initiate vertical topographic heterogeneity in wetlands (Smith et al., 2012 and references therein; Figure 2). Incipient processes are often biogenic, where plant growth and death are probably the most common hummock initiation processes. Through the expansion of roots (e.g., Keough, Thompson, Guntenspergen, & Wilcox, 1999; Lawrence, Fahey, & Zedler, 2013; Stribling et al., 2007) and shoots (Yabe, 1985), and downed woody debris and tree falls (Beatty, 1984), plants create zones of accumulation for sediment and organic matter (Anderson & Lockaby, 2007; Peterson & Baldwin, 2004). Animal activity can also initiate microtopographic development. Through their burrowing action, crabs create microtopography in many coastal systems, like mangrove swamps (Minchinton, 2001; Warren & Underwood, 1986). In swamps and marshes of the southeastern US, American alligators (*Alligator mississippiensis*) create local depressions by redistributing sediment or peat, leading to raised topographic mounding at the margins of these depressions (Palmer & Mazzotti, 2004). Similarly, Botswana hippo (*Hippopotamus amphibius*) movement develops incised channels with sediment redistributed to the edges of channels in the Okavango Delta (McCarthy, Ellery, & Bloem, 1998). Also in the Okavango, termites (*Macrotermes michaelseni*) initiate hummocks through mound-building (McCarthy, Ellery, & Dangerfield, 1998).

Microtopography can also be initiated through abiotic processes, such as freeze–thaw cycles (Ogata, 2005; Smith et al., 2012; Tsuyuzaki, 2006), bedrock outcropping (Wetzel, 2002), and preferential sediment delivery and accretion (Werner & Zedler, 2002). For example, in high-latitude and alpine regions, microtopography may arise from differential

responses of soil macropores to soil moisture variability during freeze–thaw events, with a higher soil water content being associated with hummock formation (Gao et al., 2020). Additionally, vegetated islands can develop on small bedrock or mineral soil outcrops, or even on “pop-up” islands of floating peat freed from the soil surface (Wetzel, 2002). In high-energy wetlands like floodplains, scour and deposition can induce microtopographic variation (Hardin & Wistendahl, 1983; Lewin & Ashworth, 2014). Even in low-gradient systems like the Everglades, velocities on the order of 1 cm s^{-1} may be enough to redistribute sediments to sites with emergent vegetation where reduced flow velocities can induce deposition (Larsen & Harvey, 2010). Small-scale variability of soil hydraulic properties such as infiltration capacity can influence local runoff, erosion, and ponding, which may also affect sediment redistribution and result in hollow and hummock initiation (Bledsoe & Shear, 2000). While these initiation processes vary in their driving mechanism, the resulting creation of vertical structure is common.

3.2 | Reinforcement and persistence

Microtopographic initiation, regardless of process, requires maintenance for structural longevity. Wetland microtopographic reinforcement and persistence results from positive feedbacks that promote divergence into hummocks and hollows, and negative feedbacks that constrain the magnitude of this separation. The nature of these feedbacks controls the prevalence and distinctness, as well as the spatial pattern, of hummock-hollow features within a wetland. Net hummock growth occurs when soil organic matter and/or sediment accretion exceeds local depletion (Couwenberg & Joosten, 2005), and hummock size is stable when the two are in balance with one another (Rietkerk, Dekker, Wassen, et al., 2004; Stribling et al., 2007; Figure 2). In most wetlands, we submit that this core feedback is autogenic, where increased primary production and soil organic matter accumulation on hummocks is compensated by the soil respiration cost of being drier and more oxidized. However, in many floodplain systems, microtopographic features can be predominately allogenic, and feedbacks on microtopographic formation can be positive or negative, depending on sediment deposition and erosion patterns driven by fluvial processes (Lewin & Ashworth, 2014; Walling & He, 1998).

The positive feedbacks on hummocks that increase topographic divergence in most wetlands are primarily driven either by favorable redox conditions or by favorable nutrient availability. Slightly elevated microsites (arising from any of the aforementioned initiation processes) provide relief from adverse hydrologic and redox conditions, promoting plant establishment and production. Plant growth increases organic matter accumulation (Conner, 1995; Hanan & Ross, 2010; Stribling et al., 2007) along with sediment trapping around stems and roots (Barry, Garlo, & Wood, 1996), increasing the local surface elevation. Nutrients can also accumulate on hummocks via evapoconcentration, enhancing plant growth and subsequent increase in hummock mass through root expansion (Eppinga et al., 2008, 2009; Rietkerk, Dekker, Wassen, et al., 2004). This mechanism is observed in several systems including the extreme case of the Okavango Delta, where a hydraulic head gradient induced by transpiration on elevated microsites causes massive evapoconcentration of solutes (concentrations 500–1,000 times the adjacent marsh) and mineral precipitates at the centers of tree-island hummocks (Gumbrecht, McCarthy, & Bauer, 2005; McCarthy, Ellery, & Ellery, 1993). Importantly, this general positive growth feedback is not activated in uplands or in drier wetlands (Diamond et al., 2019; Tsuyuzaki, Haraguchi, & Kanda, 2004; Watts et al., 2010; Yabe & Uemura, 2001), underscoring the dependence of hummock autogenesis on hydrology.

In some hummocks, surface elevation gain is not necessarily accompanied by mass gain. Ehrenfeld 1995 and Hsueh et al. (2016) both described hummocks containing considerable void space in coastal, forested wetlands of the eastern US. This shell-like morphology presumably results from oxidation of organic matter in the hummock interior and maintenance or gain in hummock surface elevation by recent organic accumulation. Mass of the hummock may thus increase more slowly relative to surface elevation in shell-like hummocks as compared to solid hummocks. Organic accumulation is likely enhanced near hummock surfaces because of enhanced root exploitation relative to lower, wetter substrates (Hsueh et al., 2016), especially if peat and bryophyte characteristics are conducive to mesic moisture regimes (Ehrenfeld, 1995). It is not clear why some hummocks form shell-like morphology, but they likely cannot persist if hummock-interior water is necessary to subsidize plant growth.

Ultimately, where biota augment material accumulation, compensatory negative feedbacks arise that limit accumulation and elevation. The primary negative feedback that limits vertical hummock growth in most organic matter-accumulating systems is respiration from increasingly oxidized soil (Belyea & Clymo, 2001; Couwenberg & Joosten, 2005; Nungesser, 2003). As hummocks grow, their organic substrate becomes drier and more prone to aerobic

decomposition; this feedback likely describes many hummock-hollow landscapes across the globe (e.g., Belyea & Malmer, 2004; Watts et al., 2010). Negative feedbacks to lateral expansion also commonly accompany these limits to vertical growth. For example, in lotic wetlands, hummocks may induce higher velocity flows at their boundaries, leading to accelerated erosion (Larsen & Harvey, 2010). Competition for light may also result in negative feedbacks to lateral hummock growth, for example in tussock systems (Peach & Zedler, 2006) and likely in forested systems (Diamond et al., 2019). In salt marshes, crabs preferentially consume propagules and seedlings on hummocks (that are also created by crab burrowing) as opposed to hollows, indirectly controlling subsequent lateral vegetative reinforcement of microtopography (Lindquist et al., 2009).

A key feature of wetland microtopography across systems is that it is persistent at both local and system scales. Local persistence is the propensity for microtopographic structure to remain or regenerate after a disturbance, which is likely as long as the core reinforcing processes persist (Benscoter, Vitt, et al., 2005; Benscoter, Wieder, et al., 2005; Ehrenfeld, 1995). One may consider three potential responses of a disturbed microtopographic feature: (1) complete reversal or loss (i.e., a hummock becomes a hollow), (2) resistance, where a hummock may reduce in size temporarily, but maintains production-respiration feedbacks that prevent complete loss, or (3) regeneration after loss (i.e., resilience). Each of these responses were observed 40 years after a major peat bog fire, where hollows tended to remain, and individual hummocks exhibited equal chances for complete reversal and regeneration (Benscoter, Vitt, et al., 2005; Benscoter, Wieder, et al., 2005). The observation that hummocks can spontaneously regenerate and then persist after a large pulse disturbance provides clear support for the conclusion that feedbacks control hummock growth and maintenance.

At the system scale, wetland microtopography is persistent when overall hummock-hollow structure is maintained after disturbance, whether or not individual hummocks are lost. If a disturbance alters local features (i.e., converts hummocks to hollows), but the overall (often bimodal) elevation distribution remains, wetland microtopography can be considered metastable (Heffernan et al., 2013), and thus resilient to disturbance. Metastability is probably common to wetlands that develop with periodic pulse disturbances such as fire or catastrophic wind events, where internal feedbacks persist after disturbance (Ehrenfeld, 1995). If, on the other hand, wetland microtopography is substantially shifted to a new stable topographic configuration following disturbance (e.g., the soil surface flattens), the system is bi-stable (Rietkerk, Dekker, De Ruiter, et al.,), occupying either a hummock-hollow system state, or a state where topographic divergence is lost (i.e., all hollows). Bi-stability of wetland microtopography may be common to many systems, but its presence is only revealed following massive pulse disturbances or continuous press disturbances that exceed resilience thresholds (Heffernan et al., 2013). For example, large-scale hydrologic modification in the Everglades has resulted in loss of historic microtopography at very dry and very wet sites (Watts et al., 2010; Zweig, Newman, Saunders, Sklar, & Kitchens, 2018). However, the commonality of wetland microtopography across systems and its persistence throughout time is a clear indicator of its broad resilience to disturbance.

3.3 | Microtopographic pattern development

The elevation distributions and spatial arrangement of wetland microtopography are often nonrandom. Elevations are frequently bi-modal (Diamond et al., 2019; Watts et al., 2010) and hummocks are typically spaced further apart than would be expected by random chance (i.e., hummocks are spatially overdispersed; Diamond et al., 2019; Kenkel, 1988). The resulting pattern can be visually apparent, including maze-like structures and linear banding patterns (Casey, Cohen, Acharya, Kaplan, & Jawitz, 2016; Rietkerk, Dekker, Wassen, et al., 2004). Whereas the vertical structure of wetland microtopography is a function of linked positive (organic matter accumulation) and negative (respiration) feedbacks that regulate hummock formation, the horizontal spatial structure of wetland microtopography is a combination of additional feedback processes operating at different spatial scales. Specifically, hummock lateral expansion is limited by an inhibitory feedback, often biotic competition for resources (e.g., light, nutrients; Rietkerk & van de Koppel, 2008). Without this inhibitory feedback, which may exhibit a characteristic spatial scale (i.e., it may be “scale-dependent”) or may operate at the entire system scale (i.e., “global”), hummocks would continue to expand laterally. As such, lateral inhibitory feedbacks ultimately control emergent microtopographic spatial patterns. In this section, we review how such feedbacks (either scale-dependent or global) yield the wide array of extant spatial patterns in wetland microtopography.

Scale-dependent feedbacks are necessary to produce regular patterning, in which the size of and spacing between hummocks is highly consistent. The presence of scale-dependent feedbacks in a system may be difficult to

experimentally assess, but the patterns produced have two important features: (1) regular spacing of hummocks and (2) limits to hummock radial size (Casey et al., 2016; Diamond et al., 2019). The presence of characteristic spacing and size for pattern features (i.e., hummocks) arises from the nature of the inhibitory feedback. As such, the spatial scale of patterning can be used to inform which feedbacks operate. For example, increased vegetative growth on hummocks may limit local light availability as a result of shading or crown competition in the case of forested systems (as suggested by Diamond et al., 2019), or by accumulation of dead biomass as is the case for some salt marsh tussocks (van de Koppel & Crain, 2006; van Wesenbeeck, Koppel, Herman, & Bouma, 2008). Lower light availability, in turn, inhibits vegetation growth at some spatial extent around a hummock; notably, this local constraint is relieved at some further distance. Consequently, competition for light and rooting space on a hummock may promote even spacing between hummocks, with a length scale defined by the extent of canopy shading effects. This same principle extends to wetlands where elemental resource competition is high, as is the case for peat bogs where bioavailable phosphorus limits plant growth (Rietkerk, Dekker, Wassen, et al., 2004). In these systems, head gradients maintained by differential evaporation and specific yield effects between hummocks and hollows, as well as high P recycling efficiency within hummocks, concentrate phosphorus on hummocks (Eppinga et al., 2008). As previously discussed, this accelerates on-hummock primary production, but it also depletes P from the nearby hollows, extending over a spatial scale defined by P transport, and this leads to regular hummock patterning (Eppinga et al., 2008, 2009; Rietkerk, Dekker, Wassen, et al., 2004).

The negative feedbacks that constrain patch expansion can exhibit a characteristic spatial scale, resulting in regular pattern, or they can arise at the system scale (i.e., global feedbacks), with no regular spatial structure. A global feedback mechanism occurs when local growth of hummocks induces competition for, or alters the distribution of, some resource that affects all hummocks in a wetland equally. This global inhibition ultimately limits the total occupancy of hummocks at the system-scale, but not their individual sizes (*sensu* Pascual, Roy, Guichard, & Flierl, 2002; Scanlon, Caylor, Levin, & Rodriguez-Iturbe, 2007). Such a global feedback has been invoked in describing the ridge-slough mosaic patterning in the Everglades, where the spatial arrangement and sizes of individual ridge and slough patches (i.e., hummocks and hollows) follow power law scaling and exhibit no characteristic spatial scale or wavelength (Casey et al., 2016). Models that include global feedbacks to explain ridge-slough patterning suggest that as hummocks form and grow they reduce the accommodation space available for water, thereby increasing water levels throughout the system (Heffernan et al., 2013; Kaplan et al., 2012). In this way, hummock expansion alters landscape hydrology (extending inundation uniformly) in a way that incrementally inhibits further expansion. The predicted consequence of such a global negative feedback is a hummock-hollow pattern that lacks spatial regularity (i.e., pattern wavelength) and a characteristic hummock size. Such global feedbacks may be common in other highly inundated systems, like tropical peat swamp forests, where no spatial patterns in microtopography are detected (Lampela et al., 2016).

Spatial patterns of wetland microtopography can be irregular/scale-free (via global inhibition) or regular (via scale-dependent inhibition), both of which confer emergent landscape functions. Examples include organism dispersal (Schofield et al., 2018), augmented biodiversity (Foti, del Jesus, Rinaldo, & Rodriguez-Iturbe, 2012), carbon sequestration capacity (Sullivan et al., 2008), and water storage and conveyance (Kaplan et al., 2012; Yuan et al., 2015). Hence, it is critical to understand and maintain these patterns through effective management of the underlying processes that maintain microtopographic feedbacks. Fortunately, detailed topographic data sets like those currently emerging (Graham et al., 2020; Stovall, Diamond, Slesak, McLaughlin, & Shugart, 2019) are becoming more widely available to better assess where different patterns occur (Diamond et al., 2020) and to infer the underlying processes from which they arise (Acharya et al., 2017; Rietkerk, Dekker, De Ruiter, et al.,). We suggest that diagnosing microtopographic pattern to understand feedback processes can help inform model predictions, management decisions, and restoration efforts.

4 | CONCLUSION

This review illustrates that wetland microtopography is a fundamental, ecologically important, and persistent element of many wetlands, underscoring the need to better understand the origins and consequences of a little vertical relief. Wetland microtopography is, in many cases, a clear and emergent signature of feedbacks between biota, hydrology, and local landform. While biogeomorphic landscape features are not confined to wetlands, microtopography in wetlands may be more ecologically relevant than elsewhere. Unlike well-drained upland systems, in the shallow water table

environments that characterize wetland systems, small changes in elevation translate into dramatic differences in hydrologic regimes, vegetation composition and productivity, and biogeochemical processes.

Several consequences of wetland microtopography are clear across scales. Examples include controls on water flux and storage, nutrient cycling, and carbon budgets. Despite their importance, these emergent outcomes of microtopography are rarely included in ecosystem management and models. Our review makes clear that hummock-hollow microtopography supports habitat heterogeneity and ecosystem functioning and thus can serve a crucial role in wetland management, restoration, and mitigation (Bannister et al., 2013; Bledsoe & Shear, 2000; Bruland & Richardson, 2005; Doherty & Zedler, 2015). In addition to considering microtopography during restoration design, we argue that microtopography should be regularly incorporated into constructed wetlands to increase the diversity of redox conditions and flow velocities for efficient processing of nutrients (Keefe et al., 2010; Moser, Ahn, & Noe, 2009; Wolf et al., 2011). We also emphasize the need to better model microtopographic features and their influence on ecological processes and, by extension, how the loss of microtopography may alter ecosystem function, resilience, and stability. Improving our understanding of the feedbacks that create and maintain microtopography, as well as the thresholds beyond which wetland topographic patterning is lost, will be useful in predicting how wetlands will respond to regional and global change (Rietkerk & van de Koppel, 2008; Scheffer et al., 2012).

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Jamie Duberstein: Conceptualization; formal analysis; visualization; writing-original draft; writing-review and editing. **Joshua Epstein:** Conceptualization; data curation; formal analysis; investigation; supervision; visualization; writing-original draft; writing-review and editing. **Daniel McLaughlin:** Conceptualization; formal analysis; visualization; writing-original draft; writing-review and editing. **Matthew Cohen:** Conceptualization; formal analysis; writing-original draft; writing-review and editing. **Richard Keim:** Conceptualization; formal analysis; visualization; writing-original draft; writing-review and editing. **Yu-Hsin Hsueh:** Conceptualization; writing-original draft; writing-review and editing.

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