Impacts of old, comparatively stable, treethrow microtopography on soils and forest dynamics in the northern hardwoods of Michigan, USA

Pavel Šamonil [a,*], Martin Valtera [a], Randall J. Schaetzl [b], Dušan Adam [a], Ivana Vašíčková [a,c], Pavel Daněk [a,d], David Janík [a], Václav Tejnecký [e]

[a] Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Lidická 25/27, 602 00 Brno, Czech Republic
[b] Department of Geography, Michigan State University, 128 Geography Building, East Lansing, MI 48824, USA
[c] Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemedelska 1, 613 00 Brno, Czech Republic
[d] Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 267/2, 611 37 Brno, Czech Republic
[e] Department of Soil Science and Soil Protection, The Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Praha 6, Czech Republic

ABSTRACT

Uprooting represents a key disturbance process in forests, forming pit-mound microtopography, which can then dramatically impact pedogenesis and the forest ecology. At our study sites in northern Michigan, where well-drained, sandy Spodosols dominate, pit-mound microtopography tends to persist for millennia. Because of its persistence, the influence of this type of microtopography is greater here than in most forests. In that respect, our sites represent an end member along a continuum of forest soil disturbance by uprooting. We studied post-uprooting pedogenesis (at 14 dated pit-mound pairs), mapped and characterized the pit-mound topography (over 2.8 ha), the soils below (within 317 soil profiles), and the trees above, to better understand the complex interactions among this type of disturbance regime and forest dynamics.

We used a pair correlation function and chi-square test approach to study the relationships between treethrow features and the living trees at one of these sites. Soil variability as affected by microtopography, was studied using geostatistics.

Pit-mound microtopography here covers 17% of the surface and are generally randomly distributed across the forest floor. Mounds are more prominent features of the forest floor than are pits. Pits infill with sediment and litter, obscuring them, whereas mounds persist for millennia in the sandy sediment because runoff is limited, and litter forms a protective armor. Treethrow features had volumes of roughly 214–225 m³/ha, and on average, each uprooting event translocated 0.6 m³ of soil about 0.8 m laterally and 0.1–0.2 m vertically. Areas of the pit-mound features did not differ between slope aspects, supporting an idea that on the gentle slopes of the study sites, uprooting does little to affect the movement of sediment downslope. The exceptional longevity of the treethrow features is probably a factor in the statistical randomness with which treethrow features are distributed on the forest floor, as footprints of many uprooting events are interlaced across the forest floor.

As reported elsewhere, soil development was accelerated in pits, leading to increasingly greater differences in soil development between pits and mounds, over time, and illustrating the concept of locally divergent pedogenesis. In older pits, the abnormally thick soil profiles extent so far below the depth of rooting that they are unlikely to be disturbed by future uprooting events. On the coarser spatial scale of the forest stand, uprooting decreased the ranges and increased the sills of spatial autocorrelation for O, E and Bhs horizon thicknesses. The effect of treethrow dynamics on soil characteristics was greatest and statistically most significant for E horizon thicknesses, where the range was decreased from 13 m to 10 m, whereas the maximal level of semivariance (sill) increased by 42%. All tree species preferred treethrow mounds to pits or undisturbed microsite for regeneration, especially *Acer saccharum*.

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1. Introduction

Tree uprooting represents a key disturbance process in many forests (see reviews by Schaetzl et al., 1989a, 1989b; Ulanova, 2000; Šamonil et al., 2010b; Pawlik, 2013). For example, in some European temperate forests, a third of all trees die due to uprooting and the entire area is so disturbed every 900–1400 years, i.e., its turnover period (Šamonil et al., 2009, 2013). In Alaska (USA), the rotation period of this phenomenon is even much shorter — only 200–400 years (Bormann et al., 1995). Under this type of disturbance regime, soil texture represents an important modifying factor, as it impacts post-disturbance pedogenesis as well

as post-disturbance erosion and sedimentation processes (e.g. Šamonil et al., 2015). Microtopography caused by uprooting also causes unique microclimate conditions within pits and on mounds (Beatty and Stone, 1986; Clinton and Baker, 2000). Pit–mound microtopography also dramatically influences localized pedogenesis (e.g. Schaetzl, 1990; Šamonil et al., 2010a; Tejnecký et al., 2015) as well as the biodiversity of organisms that eventually inhabit the microsites (e.g. Nachtergale et al., 2002; von Oheimb et al., 2007; Lõhmus et al., 2010; Simon et al., 2011; Šebková et al., 2012).

In northern Michigan (Fig. 1), many forests are developed on nutrient-poor, sandy outwash. These parent materials, when combined with mixed coniferous-deciduous forest, thick snow cover in winter, and a strong leaching regime, have led to strongly developed Spodosols (Schaetzl and Isard, 1996; Schaetzl et al., 2015). The coarse parent materials not only enhance deep percolation and leaching, but they probably also minimize runoff and hence, slow the leveling of the pit-mound microtopography. As a result, the oldest known treethrow features reported to date, older than 6000 years, exist in this area (Šamonil et al., 2013). In comparable studies from other regions, the longevity of treethrow pit–mounds commonly reaches only about 500–2000 years, and often considerably shorter (see review by Šamonil et al., 2010b).

In our study, we reasoned that sandy textures, and great pit-mound longevity derived probably from this texture (studied in detail by Šamonil et al., 2013), act to modify the role of uprooting-related disturbances in forest dynamics. For example, long-lasting pits and mounds could dramatically impact seedling establishment and mortality and hence, overstory tree composition and distribution. Thus, one of our study goals was to examine the density and distribution of these long-lived pit–mound features in forest stands, and to determine (statistically) their impact on the forest. Spatial relationships between soils, treethrow disturbances and woody species community have never been studied in this region.

A key aspect of long-lived microtopography is its impact on soil properties over short-distances and small scales (in Michigan studied in detail by Šamonil et al., 2015). Some studies of the effects of pit–mound microtopography on soil development (see review by Šamonil et al., 2010b) have shown that pits tend to be sites of enhanced leaching, and thus old pits may have the strongest developed soils on such landscapes (e.g. Schaetzl, 1990). Conversely, mounds tend to be site of less intense leaching and weakly developed soils. Šamonil et al. (2015), suggested based an analysis of soil morphology, that post-disturbance pedogenesis could be divergent within the pit–mound pairs in regions

undergoing podzolization. Microtopography also affects other soil parameters that can also impact forest ecology, such as soil temperature and moisture conditions, litter depth, and nutrient accessibility (e.g. Clinton and Baker, 2000). All of these impacts are likely to be more pronounced when the microtopography is more semi-permanent on the landscape, as at our study sites. Thus, a second goal of our study was to examine local soil development using soil morphological and chemical analyses, and to examine soil variability, as affected by microtopography. We will compare our results with studies from the other regions (e.g. Putz, 1983; Shubayeva and Karpachevskiy, 1983; Small et al., 1990; Vassenev and Targulian, 1995; Šamonil et al., 2008, 2010a, 2015; Ulanova, 2000; Pawlik, 2013) to help understand the role of bioturbation on forest ecosystem dynamics, and on soil evolution.

2. Materials and methods

2.1. Study sites

To obtain more generalizable results we collected data on three study sites located in forest stands near the cities of Munising, Strongs, and Brimley, in the Upper Peninsula of Michigan, USA (Fig. 1). According to the World Reference Base for Soil Resources (FAO, 2014) soils here are primarily Albic Podzols (Typic Haplorthods and Durorthods according to Soil Taxonomy, Soil Survey Staff, 2014). The soils at our study sites have developed on sandy glacial outwash under a mixed northern hardwood stand dominated by maple (*Acer saccharum* Marsh., *Acer rubrum* L.) followed by red oak, black cherry, eastern hemlock and pine (*Quercus rubra* L., *Prunus serotina* Ehrh., *Tsuga canadensis* (L.) Carr. and *Pinus* spp.). The climate here is cool and humid, with a frigid soil temperature regime and an udic–aquic soil moisture regime (Soil Survey Staff, 2014). The National Weather Service (NWS) station at Newberry, nearest to the three study sites, reports an average of 812 mm of annual precipitation and a mean annual temperature of 4.7 °C. The area lies within a Lake Superior snowbelt, with Newberry receiving annually an average of 255 cm of snowfall (Schaetzl et al., 2015). The average seasonal maximum snow cover often exceeds 1.25 m. Tree uprooting is the most important disturbance process in these forest ecosystems, although rare fires or infrequent mammalian burrowing occurs as well. All three study sites are located within managed forests that were last cut no later than 40 years ago. The Munising site has had the least
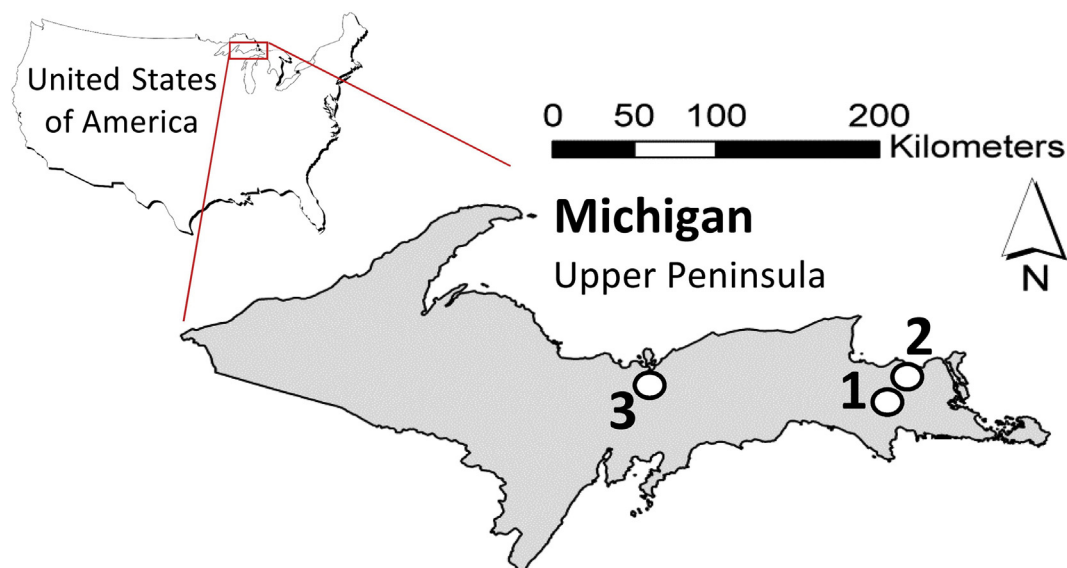

Fig. 1. Locations of the study sites: (1) Strongs (46.44°N, 84.82°W), and (2) Brimley (46.32°N, 85.06°W), (3) Munising (46.37°N, 86.70°W).

amount of cutting and had been minimally managed in the past (selective cutting and natural regeneration).

2.2. Field methods

2.2.1. Analysis of soils at fine scales (pit-mound pairs)

In a past study (Šamonil et al., 2013), we dated 14 treethrow pit–mound pairs across the three study sites, using dendrochronological and radiometric (^{210}Pb, ^{137}Cs, ^{226}Ra, ^{14}C isotopes) methods. For dating, we used remnants of uprooted tree trunks, material from buried A horizons within the mound, or material from the sedimentation funnel in the pits as well as radial growth responses of surrounding trees to uprooting event. These dating procedures confirmed the exceptional longevity of the treethrow pit–mound pairs in the study area, with some exceeding 6000 years in age.

Evaluation of soil mixing and pedogenesis, as affected by tree uprooting and post-uprooting microtopography, was performed at all three sites and partially published by Šamonil et al. (2015). Within this paper, we will focus on selected soil properties in three additional pit–mound pairs — 170, 910, 5230 years old, to illustrate the podzolization process in northern Michigan. The pit–mound pairs were excavated via hand-dug trenches, 1.5 m deep and 0.6 m wide, opened along their axes, following Šamonil et al. (2015). Soils within the pit, beneath the mound and in the adjacent undisturbed (reference) pedons were sampled at 5, 15, 30, 50 and 100 cm depths. In addition, horizon-based samples were recovered where appropriate. On these 56 samples, various lab analyses were run, with the intention of determining the extent to which transformation and translocation of organic compounds (e.g. humification), weathering, leaching, (mineral formation and alteration, podzolization) and oxidation–reduction processes had been operative.

2.2.2. Forest stand scale: pit-mound microtopography and tree-soil interaction

Over time, treethrow pit–mound features erode, collapse and deteriorate, making their detection and measurement difficult and imprecise. However, careful identification of the position of coarse woody debris or rock fragments within the soil can help to identify these forms, even if old (Schaetzl and Follmer, 1990; Šamonil et al., 2010a, 2010b, 2015).

We used our experience to identify pits and mounds at the study sites, determine their locations, and examine their relationships to topography. At the Munising and Strongs sites, we first outlined a 1-ha square plot. Around this plot we then laid out circular plots. At the Strongs site we used four circular plots of 1000 m^2 each, whereas at Munising we used eight plots of 500 m^2 each. In total, 1.4 ha of forest area was assessed in this way at each of the two sites (Appendixes A–C). All microtopographic features recognized as pits or mounds (with a minimal height or depth of 15 cm) were located within these plots, using Field-Map technology (http://field-mapping.com). For each, we measured their dimensions and the slope gradient across the entire 1.4 ha at the site as well as the position of undisturbed land surface. The areas of the pits and mounds were approximated as ellipses (Skvorcova et al., 1983; Šamonil et al., 2009). We next calculated the volumes of soil affected by treethrow dynamics as the sum of all the individual mounds plus pit volumes in situations where the companion mound is no longer present. Treethrow features were approximated by a half of an ellipsoid (e.g. Norman et al., 1995; Kabrick et al., 1997; Pawlik, 2013) and volume (V) was calculated using equation $V = \pi whl/6$ where w is width, h is height (or depth in case of alone pits, where mound is missing) and l is length of the treethrow mound (or alone pit). The horizontal distances between the bottoms of the pits and the tops of the corresponding mounds were used to approximate their centers of gravity, which was then used to estimate the distances over which the soil material had been moved by the uprooting event. Knowing the regional slope gradient, we were then able to determine the direction of the "moved" material, relative to the local slope.

At the Munising site, we also determined the locations, sizes and species of all trees, living and dead, and their diameters at breast height (DBH) ≥ 10 cm, again using Field-Map technology. Individual tree locations were assessed in relation to pit–mound microtopography. We cored 12 trees to study their age relationship to DBH.

Soil spatial variability and its relationship to pit–mound features were also evaluated at the Munising site, using a combination of regular and random soil sampling (Appendix A). At this site, we sampled 317 pedons and recorded their thicknesses of organic (O), upper mineral (A), eluvial (E), upper illuvial spodic (Bhs, Bhsm) and lower illivial spodic (Bs, Bsm) horizons, as determined from 0.7 m deep excavations and 1.5 m deep cores.

2.3. Data analysis

2.3.1. Pedogenesis: laboratory soil analysis

All 317 soil samples were analyzed according to the procedures reported in Zbíral (2002, 2003) and Zbíral et al. (2004). We measured the characteristics of the sorption complex, including exchangeable cations, exchangeable acidity (Al + H) and effective cation exchange capacity (ECEC) according to Gillman and Sumpter (1986; BaCl$_2$-compulsive exchange procedure, native pH). Samples were also analyzed for oxidizable C (Cox) — spectrophotometrically after oxidation by H$_2$SO$_4$ + K$_2$Cr$_2$O$_7$ (Anonymous, 1995); conventional C content in humic acids (C–HA) and in fulvic acids (C–FA) — all in Na$_4$P$_2$O$_7$ (Kononova and Bel'chikova, 1961); color quotient (Q4/6) calculated based on Q4/6 = E465/E665, where E465 and E665 are the extinctions (Na$_4$P$_2$O$_7$ extract) at wavelengths 465 and 665 nm (Chen et al., 1977); total N content according to Kjeldahl (Bremner, 1996); exchange soil reaction (pH-KCl) — 0.2 M KCl; and particle-size distribution according to Casagrande (Bernhardt, 1994). Elemental concentrations in liquid extracts were measured using an atomic absorption spectrophotometer (GBC 932 AB Plus) and a Specol 221 UV–VIS spectrophotometer.

To assess the degree of podzolization, the contents of Fe, Al, Mn and Si were determined for all samples by standard extraction methods (McKeague and Day, 1966; McKeague et al., 1971; Drábek et al., 2003, 2005; Courchesne and Turmel, 2008). The amount of crystalline forms (Al$_d$, Fe$_d$) was determined by extraction with a dithionite–citrate solution (DC) at a ratio of 0.5:25 (w/v). The proportion of amorphous forms and organic complexes (Al$_{ox}$, Fe$_{ox}$, Si$_{ox}$) was determined with an acid ammonium oxalate extract. The extraction was carried out in the dark with 0.2 M of ammonium oxalate at pH 3 (at a ratio of 0.25:10, w/v). The content of labile forms (Al$_k$, Fe$_k$) was determined by using 0.5 M KCl (1:10, v/w).

2.3.2. Soil variability and tree–soil interactions

Spatial data were analyzed at the stand level by basic descriptive statistics, simple regression models, and geostatistics. Our goal was to determine the variability of soil horizon thicknesses within and outside of pit–mound microtopographical forms, and to use these data to better understand the interactions between tree uprooting and soil spatial variability. We employed semivariance analysis on the untransformed thickness data from O, A, E and Bhs horizons, and Box–Cox transformed data on E/Bhs horizon thickness ratios, which can be used as an indicator of non-linear podzolization rates (see Šamonil et al., 2015). The lags for variogram calculation were set by 1 m increments, starting at 1 and progressing to 15 m, and by 5 m at distances from 15 to 75 m. We separately constructed semivariograms for (i) all 317 soil profiles (pits, mounds and undisturbed positions), (ii) undisturbed positions, and (iii) positions within the pits and mounds. On each of the experimental variograms, a variety of standardized semivariogram models (nugget, linear, spherical, exponential, Gaussian, power, periodic/cosine) were fitted using nonlinear least-squares methods (Webster and Oliver, 2007). The best-fit model selection was based on: (i) the AICc selection criterion, with the threshold value delta AICc = 2.0, and (ii) the mean and median square deviation ratios (MSDR, mSDR) after leave-one-

out cross validation (e.g. Lark, 2000; Valtera et al., 2013). Total differences in soil horizon thicknesses between studied microsites were tested using Kruskal–Wallis test.

We also studied the relationships between treethrow microtopography and landform constitution. The cumulative areas affected by pit–mounds on different slopes and aspects were tested against a random model. Slopes and aspects were divided into regular five and eight (according to the eight cardinal directions) categories, respectively, and the observed cumulative sums of pit–mound areas in these categories were compared to the distribution of expected sums derived from 10,000 random assignments of pit–mounds into these categories, while taking into consideration the area the categories occupied. The difference between observed and expected area for a group was considered significant if the observed value lied outside the middle (100–5/B)% randomized values, where B is a Bonferroni correction parameter equal to the number of groups.

A Chi square test was used to investigate the spatial relationships between trees and treethrow microtopography. The null hypothesis posited equal frequencies of trees on all microsites, i.e., proportional to the area that each microsite occupies. To capture the spatial interactions between trees and treethrow mounds, we used the "i-to-j" pair correlation function, which is the extended $g(r)$ function to multitype point patterns (Baddeley, 2008; Stoyan and Stoyan, 1994). We tested the null hypothesis that trees and treethrow features were independent. In a randomization test of the independence-of-components hypothesis, the simulated patterns are generated from the dataset by splitting the data into sub-patterns of points of one type, and by randomly shifting these sub-patterns independently of each other (Baddeley, 2008). We generated 199 simulations of this null model to obtain pointwise critical envelopes for $g(r)$. Edge effects were corrected using Ripley's isotropic correction (Ripley, 1988).

3. Results

3.1. Local-scale pedogenesis

Selected soil data within disturbed (pit and mound sites) and undisturbed soils confirm that post-uprooting as well as "intact", pedogenesis are dominated by weathering and vertical translocation processes, mainly associated with podzolization (Fig. 2, Table 1). Detailed chemical analyses confirmed the low cation exchange capacities in these sandy soils (Table 1). The sorption complex was only partly saturated, mainly by Ca, in all microsites. Exchange pH ranged between 3.5 and 4.9 in these acidic, sandy soils. As expected in soils undergoing podzolization, fulvic acids predominated over humic acids, and crystalline and amorphous forms of Al and Fe predominated over labile forms (Table 1). Chemical soil data suggest that podzolization here is driven mainly by chelation, rather than migration of Fe and Al as inorganic sols

(Buurman, 1984; Buurman and Jongmans, 2005; Schaetzl and Harris, 2011).

Podzolization is more rapid within pits than beneath mounds of relevant age (Schaetzl, 1990). The differences between pits and mounds in soil development also increase with age, as evidenced by sites where thicknesses of E horizons within older pits are much greater than beneath mounds of the same age. In the oldest pits, E horizons were even thicker than in control pedons undisturbed for long periods of time (Fig. 2). The increasingly greater differences in soil morphology as well as soil chemistry in profile development between microsites, over time, illustrates locally divergent soil evolution (Phillips, 2001; Šamonil et al., 2015), a process that can significantly increase local soil variability.

As expected, E horizons had lower content of all forms of Al, Fe, and Si, as well as soil nutrients, when compared to B horizons (such as Bhs, Bs) below (Table 1) and the A horizons above. The latter comparison is less significant because at many sites A horizons were thin or absent, even in reference pedons. The Bhs and Bs horizons represented key sources of nutrients for plant communities in this landscape. These horizons were easily accessible for plant roots in mounds of all ages. However, these horizons were deeper and hence, almost inaccessible in the soils beneath the oldest treethrow pits (see root border in Fig. 2). Some Bs horizons had even higher amounts of these soil compounds than the overlying Bhs horizons (Table 1). Illuviation of humusosesquioxides in primarily non-illuvial Bs horizons is not easily detectable using terrain soil morphology. Initial stages of illuviation of organometallic complexes in Bs horizons were differentiable using chemical analyses such as forms of Fe or Al in laboratory, but not in terrain using soil morphology (see also Šamonil et al., 2015; Schaetzl and Thompson, 2015).

3.2. The level of forest stand

3.2.1. Pit–mound microtopography

Treethrow microtopography covered 16.9% of the surface at both the Munising and Strongs sites. Mounds occupied a higher proportion of the forest floor at both sites, covering 12.7% and 12.4% of area at Munising and Strongs, respectively, whereas pits covered only 4.2% and 4.5% of the surface, respectively (Appendixes B, C). Using 10,000 random iterations (Section 2.3) we did not find any statistically significant relationship between the area affected by pit-mound features and landform aspect and steepness. Treethrow features were generally distributed randomly across the surface, with a slight tendency toward a regular distribution on distances <1.5 m, and with a tendency toward a clustered distribution on distances from 3 to 5 m (Fig. 3).

Treethrow features had a total volume of 225 m³/ha at Munising and 214 m³/ha at Strongs. The volume of soil up to the genetic soil depth (i.e. horizons influenced by pedogenesis; calculated using the distributions
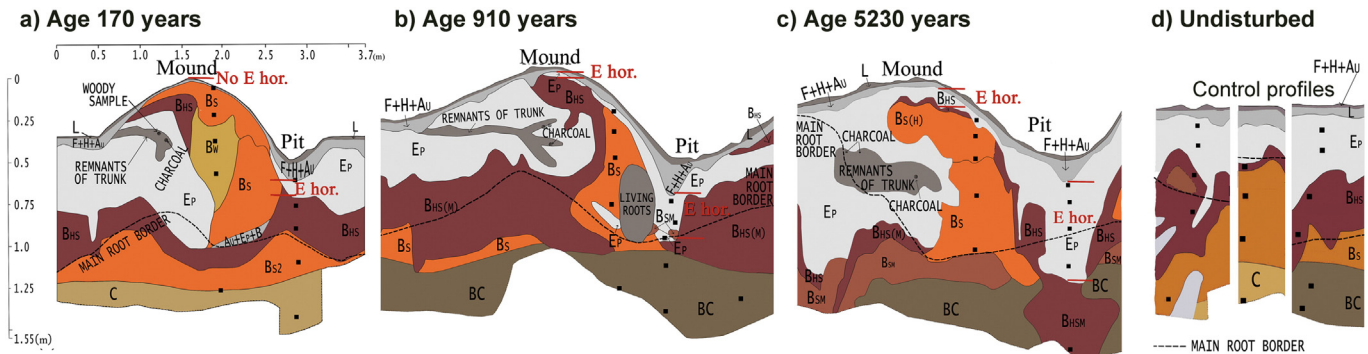

Fig. 2. Soil horizonation resulted from soil mixing due to uprooting and post-disturbance pedogenesis in selected treethrow pit-mound pairs from (a) Brimley, (b) Strongs, and (c) Munising. Part (d) shows the morphology of the selected reference soil profiles at the same sites. Ages are derived from dendrochronology and radiometry data (Šamonil et al., 2013, 2015).

Table 1
Soil chemical properties for disturbed and adjacent undisturbed soil profiles.

Age of pit-mound pair	Microsite	Horizon	Sample depth	Ca^{++}	Mg^{++}	Al + H	ECEC	pH$_{KCl}$	Q4/6	Cox	Nt	C-HA	C-FA	Al$_K$	Fe$_K$	Al$_{ox}$	Fe$_{ox}$	Al$_d$	Fe$_d$	Si$_{ox}$
			cm	(mmol$^+$/kg)	(mmol$^+$/kg)	(mmol$^+$/kg)	(mmol$^+$/kg)	(/)	(/)	(%)	(%)	(%)	(%)	mg/Kg	mg/Kg	mg/kg	mg/kg	mg/kg	mg/kg	mg/kg
170 years	Pit	A(E)	0–5	9.8	2.9	18.3	31.6	3.7	5.6	1.0	0.1	0.1	0.2	47.5	21.32	740	1361	465	1979	44.0
		Bhs	15	9.2	2.2	18.8	40.2	3.9	5.9	0.6	0.1	0.1	0.2	82.9	12.64	1209	3334	1305	4085	112.0
		Bhs	30	6.6	2.1	18.0	33.0	4.3	6.5	0.7	0.1	0.1	0.3	67.6	10.64	11,077	21,974	8770	19,792	400.0
		Bs	50	8.4	3.2	11.4	28.9	4.6	8.2	0.5	0.0	<0.03	0.3	57.9	25.03	18,516	15,660	14,180	16,175	2604.0
		C	80	6.6	2.8	7.1	19.8	4.7	9.1	0.4	0.0	<0.03	0.1	31.9	3.25	906	571	1150	1469	148.0
	Mound	A(E)	0–5	12.4	3.0	35.5	53.5	4.1	8.2	2.1	0.2	0.2	0.4	141.9	11.33	5640	8807	4090	8431	324.0
		Bs	15	11.0	3.0	26.0	43.2	4.3	8.8	1.7	0.1	0.2	0.7	138.2	8.56	5589	6429	8140	18,177	184.0
		Bw	30	8.0	2.7	21.8	38.4	4.2	7.0	1.5	0.1	0.1	0.4	109.5	49.97	2923	5462	2335	5475	92.0
		Bw	50	8.8	1.8	20.7	35.9	4.2	7.1	0.9	0.1	<0.03	0.2	101.5	32.63	2026	5981	1400	5917	84.0
		C	115	8.6	2.5	10.4	24.6	4.7	6.2	0.3	0.0	<0.03	0.1	28.8	2.83	2518	1049	1530	1225	584.0
	Undisturbed control	(A)E	0–5	8.6	3.0	9.8	34.2	3.5	4.7	0.6	0.1	<0.03	0.1	20.7	9.27	175	185	280	1049	0.0
		E	15	4.8	1.7	11.6	35.8	3.9	5.0	0.3	0.0	<0.03	0.1	32.7	6.21	332	435	445	1444	8.0
		E	30	7.8	2.8	17.2	28.7	3.9	5.3	0.4	0.0	<0.03	0.1	55.0	13.96	649	1463	695	2357	28.0
		Bhs	50	8.4	2.0	17.2	35.2	4.3	7.4	0.5	0.1	<0.03	0.3	84.3	11.17	11,201	20,922	4925	7266	460.0
		Bs	80	7.4	2.5	12.2	29.5	4.6	7.8	0.5	0.0	<0.03	0.2	46.9	4.28	20,617	16,233	16,865	16,870	2788.0
		C	100	5.6	2.1	6.0	23.4	4.7	5.6	0.3	0.0	<0.03	0.1	26.6	1.22	799	102	685	124	196.0
910 years	Pit	AE	0–5	17.4	4.2	3.6	42.7	4.7	4.9	0.8	0.1	0.1	0.1	12.0	0.29	239	1432	90	2445	44.0
		E	15	9.4	2.8	4.2	43.4	4.2	4.9	0.5	0.0	0.1	0.1	15.8	0.44	166	472	15	1094	32.0
		E	30	7.6	1.9	5.0	28.7	4.4	6.0	0.4	0.0	0.1	0.1	25.7	0.54	582	1762	125	2151	40.0
		Bs(h)	50	20.7	2.5	6.4	36.8	4.9	6.3	0.6	0.1	0.1	0.2	20.9	0.86	2216	2438	1335	2494	372.0
		BCx	100	5.4	1.6	4.4	26.3	4.8	7.9	0.2	0.0	0.1	0.1	14.0	0.35	702	472	500	567	164.0
	Mound	Ae	0–5	24.2	3.5	10.0	62.6	4.1	6.1	1.2	0.0	0.1	0.2	31.6	1.66	904	4437	950	5756	44.0
		Bs	15	9.8	2.9	16.6	77.8	4.5	6.7	0.8	0.1	0.1	0.3	75.6	1.18	4936	4190	3195	3701	480.0
		Bs	30	8.0	2.6	14.9	29.8	4.5	6.6	0.8	0.1	0.1	0.3	62.6	0.79	4886	3299	2905	3039	580.0
		Bs	50	4.4	1.5	14.6	26.4	4.5	6.8	0.8	0.0	0.1	0.3	69.0	0.8	4683	2936	2700	2981	628.0
		2BC	100	7.2	2.1	5.8	25.1	4.8	8.0	0.5	0.0	0.0	0.1	24.9	0.43	1193	664	800	775	212.0
	Undisturbed control	E	0–5	21.0	3.6	3.4	39.2	4.1	4.4	0.8	0.1	0.0	0.1	0.0	0.73	72	189	100	921	36.0
		E	15	13.6	2.8	2.1	36.1	4.3	4.2	0.4	0.0	0.1	<0.03	0.0	0.1	3	51	−20	726	24.0
		Bhs(m)	35	30.9	3.6	25.6	66.1	4.2	6.6	2.1	0.1	0.2	0.5	83.1	17.48	5143	8835	4760	9833	348.0
		Bhs(m)	50	17.4	2.9	20.0	90.8	4.4	6.9	1.8	0.1	0.2	0.5	80.3	4.55	4365	5341	3520	5965	276.0
		BC	100	11.4	2.4	5.4	41.4	4.6	7.5	0.4	0.0	0.1	0.2	26.6	1.34	1382	902	1155	1091	264.0
5230 years	Pit	AE	0–5	13.6	4.1	6.6	30.2	3.8	2.6	0.7	0.1	0.1	0.1	0.0	0.68	66	113	190	1400	20.0
		E	15	12.4	3.6	3.0	22.2	3.9	2.0	0.2	0.0	0.0	0.1	0.0	0.99	14	64	265	1369	4.0
		E	30	12.6	2.9	4.0	22.5	3.8	1.7	0.2	0.0	0.0	0.0	14.6	0.99	10	92	275	1435	0.0
		E	50	9.4	3.2	4.8	23.8	3.8	1.8	0.3	0.0	0.0	0.1	31.0	0.99	62	138	315	1817	0.0
		Bhsm	95	10.6	1.9	12.8	29.4	4.3	7.7	0.6	0.0	0.1	0.1	67.1	3.55	1532	751	1320	2279	172.0
	Mound	E	0–5	12.0	3.4	6.0	26.1	3.8	4.6	0.5	0.0	<0.03	0.1	0.0	2.6	82	91	255	1499	16.0
		Bhs	15	6.0	1.1	17.6	29.6	4.4	7.3	1.1	0.1	0.1	0.4	99.2	0.94	4538	2094	3540	3291	472.0
		Bs	30	6.8	1.8	12.2	27.4	4.5	7.3	0.8	0.1	0.1	0.3	78.8	1.1	4520	2281	3710	3406	536.0
		Bs	50	6.0	1.3	10.4	24.0	4.5	7.1	0.8	0.1	0.1	0.3	71.8	1.23	4161	2237	3840	3892	516.0
		Bs	80	10.0	2.6	11.6	28.3	4.5	7.4	1.1	0.1	0.1	0.4	83.5	0.72	6086	2808	5080	4182	504.0
	Undisturbed control	E	0–5	12.0	3.3	3.8	24.1	3.9	3.1	0.5	0.1	0.0	0.1	0.0	0.8	52	67	1605	1640	12.0
		E	15	11.6	3.3	3.2	28.2	3.9	3.6	0.3	0.0	<0.03	0.0	0.0	0.72	49	70	1715	1674	24.0
		Bhs	30	10.8	2.7	21.8	38.9	4.2	7.6	1.5	0.1	0.1	0.5	165.1	7.61	5279	5281	5860	7194	280.0
		Bhsm	50	13.8	3.7	15.8	36.6	4.5	7.7	1.0	0.1	0.1	0.4	92.4	2.9	4826	2722	5470	4323	420.0
		Bs	100	10.8	3.1	6.2	28.4	4.7	8.3	0.4	0.0	<0.03	0.1	31.1	1.66	1599	418	2930	1680	264.0

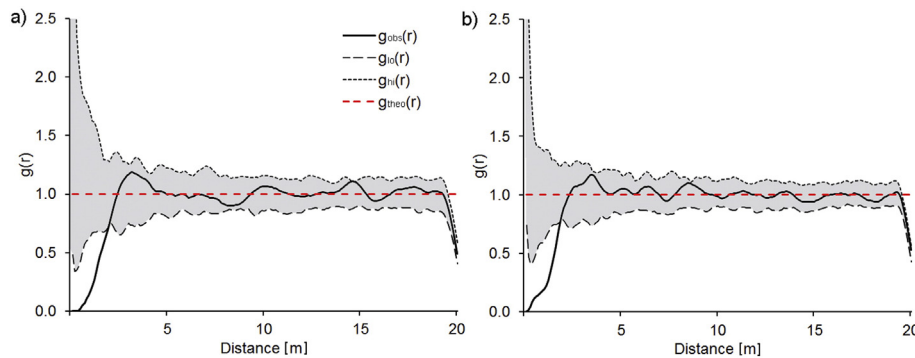**Fig. 3.** Spatial patterns of treethrow features at Strongs (a) and Munising (b). We used the pair correlation function g(r). $g_{obs}(r)$ — observed function, $g_{lo}(r)$, $g_{hi}(r)$ — the lower and upper pointwise envelopes resulting from 199 Monte Carlo simulations of the null model of complete spatial randomness. If the value of $g_{obs}(r)$ is larger than the value of the $g_{hi}(r)$, then the treethrow features show significant clustering. If the $g_{obs}(r)$ is smaller than value of the $g_{lo}(r)$ then the treethrow features show a regular distribution. Within the gray zone, we cannot reject the null hypothesis of spatial randomness.

of the depth transitions between B and C horizons in soil profiles) exceeds 1500 m³/ha in both sites (Table 2; Šamonil et al., 2015). On average, an uprooting event translocated 0.6 m³ of soil about 0.8 m laterally (see volumes of treethrow features and distances of soil movement in Fig. 4). Because treethrow pit–mounds were oriented in a multitude of directions, relative to slope inclination, vertical movement of soil material was relatively limited, being on average 0.1 m downslope at the Munising site and 0.2 upslope at the flatter Strongs site (Fig. 4). Although tree uprooting sometimes represents an important lateral biogeomorphological process, by facilitating the downslope movement of soil and regolith (see below; Norman et al., 1995; Gabet and Mudd, 2010; Phillips, 2010), at our sites the low slope gradient does not cause trees to preferentially fall downslope. Thus, lateral translocation of sediment is fairly random and tree uprooting is not probably a major factor in sediment transfer downslope. In these sandy soils, the material disturbed and shifted by uprooting quickly becomes stabilized and covered with forest litter, further limiting downslope transfer.

3.2.2. Soil variability

Uprooting microtopography had a statistically significant effect on soil horizon thicknesses and their spatial variability at the study sites (Table 2, Fig. 5). As has been documented elsewhere (Schaetzl, 1986; Šamonil et al., 2008, 2015), the thickness of the forest floor (O horizons) differed significantly between all three kinds of sites. O horizons were thinnest on mounds and thickest in the pits; E and Bhs horizon thicknesses differed significantly only between mound and other microsites; pits exhibited relatively high internal variability in horizon thicknesses (Table 2). The ages of individual pit–mound features (Šamonil et al., 2013) were an important source of soil variability; horizon thicknesses change quickly with time in preferred microsites (Šamonil et al., 2015). The E/B horizon thickness ratio was significantly greater at undisturbed microsites compared to mounds (Table 2).

Variograms revealed that soils within pits and mounds exhibited a higher level of variability, particularly in E horizon thickness, as measured by the level of semivariance, when compared to undisturbed areas (Fig. 5). These differences were only statistically significant in E horizons at distances between 33 and 70 m (Fig. 5a), in contrast to the wider confidence intervals of the O, A and Bhs horizons for pit and mound sites (Fig. 5b). Soil disturbances significantly shortened the range of spatial autocorrelation of thicknesses of majority the soil horizons we examined. For example, whereas no spatial autocorrelation was observed between eluvial horizon thicknesses in disturbed positions (i.e. pure nugget), the range at about 10 m was observed in all positions regardless of former disturbances, and the range at about 13 m was observed separately for undisturbed positions (Fig. 5). Wetting front instability (i.e. fingered flow) and its morphological feedbacks could also influence the local scale where nugget variance rules, whereas topography and soil texture could be more important on coarser scales.

3.2.3. Relationships between trees and treethrow microtopography

The frequency of trees on mounds was more than double what is predicted by the null model, particularly in case of large trees (Chi-square = 153.7, p-value <0.001). In contrast, the frequency of trees growing within pits was only ≈20% of the null model (Chi-square 25.2, p-value <0.001). The disproportionally high numbers of trees on mounds was observed for all categories of tree diameter (Fig. 6), although the frequencies were highest for the thickest (oldest) trees. Most trees of DBH >40 cm were at least 88 years old (a *T. canadensis* tree of DBH = 68 cm and an *A. saccharum* tree of DBH = 52 were 236 years and 260 years old, respectively). The strong positive spatial correlation between trees and mounds was valid for the majority of tree species (*Betula alleghaniensis*, *P.s serotina*, *T. canadensis*) but was the most statistically significant for *A. rubrum* and *A. saccharum* (Fig. 7).

4. Discussion

We believe that the well drained, sandy nature of the soils at our study sites has accentuated the longevity of the pit–mound microtopography here. A similar finding was observed by Schaetzl and Follmer (1990), on sandy soils in a nearby setting. Great longevities of treethrow features normally lead to high densities as well. Karpachevskiy et al. (1980) found almost 90% of his study area coved by pits and mounds in podzolic soils in Siberia. The 17% of land surface covered by pit–mound features at our sites is well above average, when compared to other studies (see review by Šamonil et al., 2010b). Moreover, other researchers that have canvassed pit–mound features have employed smaller sample plots (e.g. Shubayeva and Karpachevskiy, 1983; Kabrick et al., 1997), possibly leading to over-estimates of pit–mound microtopography.
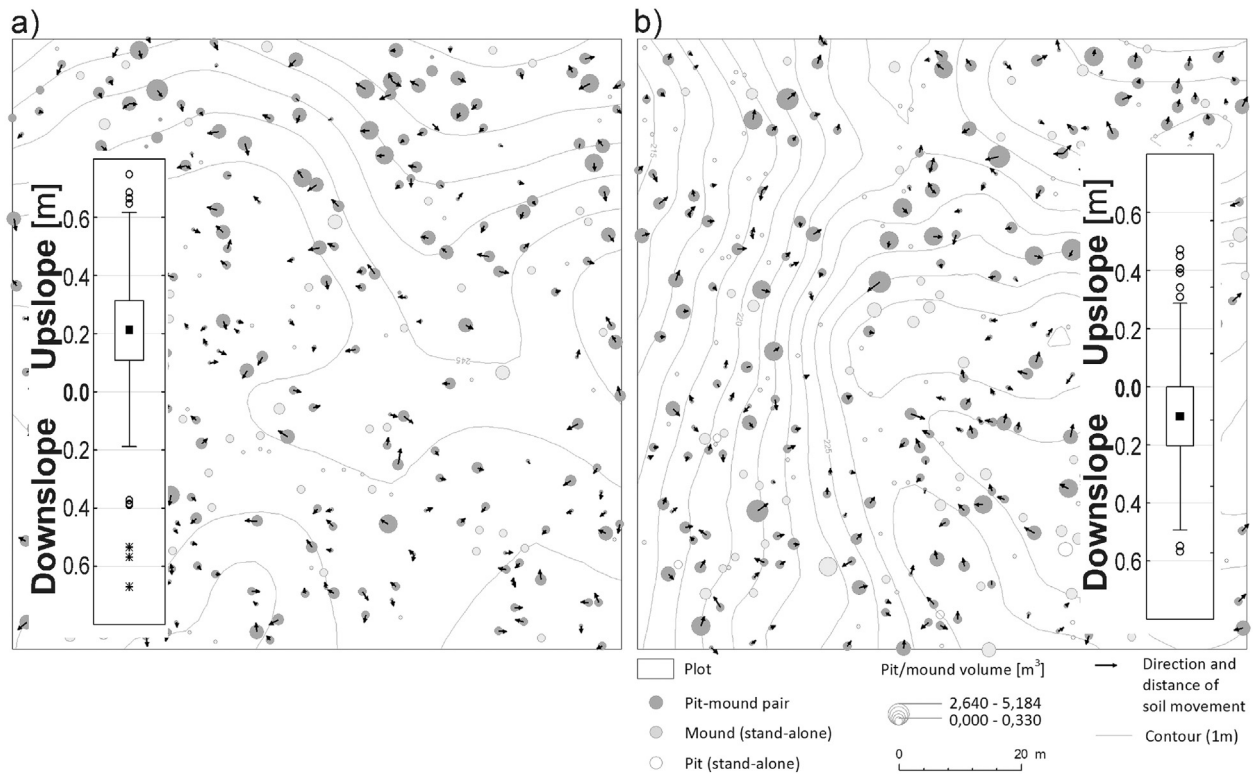
Table 2
Mean soil horizon thicknesses and variation within individual microsites at the Munising site. All units are in mm; SD — standard deviation; NA — not evaluated. Within a row, numbers with different letters significantly differ at α = 0.05 (Kruslal–Wallis test was used).

Horizon		Mound		Pit		Undisturbed	
		Mean	SD	Mean	SD	Mean	SD
O	Organic	45[a]	28	77[b]	31	58[c]	26
A	Upper mineral	14[a]	13	12[a]	11	11[a]	11
E	Eluvial	197[a]	198	346[b]	284	276[b]	147
Bhs	Spodic illuvial	126[a]	96	204[b]	122	182[b]	97
Bs	Spodic	NA		NA		1075	367
E/Bhs	Ratio of E and Bhs thicknesses	1.36[a]	0.9	1.68[ab]	0.92	1.78[b]	1.79

Fig. 4. Volumes of individual treethrow features and the various vectors of soil movement at the 1-ha plots at Strongs (a) and Munising (b). Arrows represent distance from pit bottom to corresponding mound peak, and the direction of mass movement. Box-plots represents main characteristics of vertical soil movement distribution; full squares — median, open boxes —interquartile range (25%–75%), whiskers — non-outlier range (coefficient 1), open circles — outliers, stars — extremes.

We suggest that the greater proportion of mounds (vs. pits) on the landscape here (in total, 2.8 ha were evaluated) is due to the rapid, partial filling of pits by mound material during (see "rotational tree falls" in Norman et al., 1995) and shortly after the uprooting event, rather than from subsequent erosion processes on the undisturbed landscape. The sandy soils here are highly permeable, implying that little runoff occurs, and thus, limited potential exists for slope wash to bring sediment from upslope areas into pits. Additionally, pits are sites of rapid and thick accumulation of litter (Schaetzl et al., 1990). Thus, it is likely that some small pits — too small to be mapped — exist in our study area but have so much litter within them that they fall below our 15-cm depth threshold. Erosion of mounds in these sandy soils is minimal, explaining why they persist and hence, are so common on the landscape. The lack of runoff and the dominance of vertical percolation processes can be demonstrated by absence of lateral podzolization (sensu Sommer et al., 2001) outside pit–mound pairs in our sites.

Pit–mound areas did not significantly differ either by slope aspect or gradient. On sandy or coarse silty soils in Wisconsin, Kabrick et al. (1997) observed more pit–mound features on NW-facing backslopes, when compared to SE-facing backslopes and summits. However, the differences were not statistically significant. Indeed, differences in pit–mound density as a function of landscape segments in regions of podzolic soils has been found only in steeper, mountainous terrain (Valtera et al., 2015). On finer-textured soils, elongation of mounds downslope over time, and their decreasing longevity with increasing slope, seems likely to develop, and has been observed in clay–loam textured Cambisols (Šamonil et al., 2008, 2009).

The random distribution of the pit–mound features at our study sites may be partially explained by their great longevity, which leads to an exceptionally wide spectrum of microtopographic features of different ages across the landscape. As a result, the footprints of unrelated uprooting events of varying ages are intermixed in a complex spatial pattern. On some landscapes, pit–mound features are clustered (e.g. Skvorcova et al., 1983). For example, on granite in central European temperate forests Šamonil et al. (2014) reported a clustered distribution

of pit–mound features; they were even more clustered in areas of podzolized soils. Such clustered distributions are probably associated with gap-phase treefalls (e.g. White et al., 1985; Runkle, 1990). More regular distributions (cf. Kabrick et al., 1997) of pit–mound features are observed across shorter distances, because of the "rewriting" of former microtopographic features by more recent soil disturbances, i.e. uprooting of trees that have established on former pit or mound sites. These types of treethrow features are usually only visible in the subsurface, not as microtopography (Šamonil et al., 2015).

The positive co-occurrence of trees and mounds occurs across a wide variety of bedrock types (Lyford and MacLean, 1966; Cremeans and Kalisz, 1988; Šamonil et al., 2009; Šebková et al., 2012). The affinity of trees to mounds in our sites was likely influenced by one or more of the following factors: (i) their microclimatic uniqueness (see below), (ii) thin O horizons, which facilitate seedling establishment, (iii) the higher availability of nutrient rich spodic horizons within the mounds, due to the overturning of the soil profile during uprooting (Schaetzl, 1986), and (iv) minimal erosion of mounds due to their sandy textures. We consider points (i) and (ii) to be universal. Because of the convex shape of the mounds, they are generally warmer and drier in summer, but with greater temperature amplitudes (Beatty and Stone, 1986; Peterson and Cambell, 1993; Clinton and Baker, 2000). Mounds also shed litter, leading to thin O horizons (Šamonil et al., 2008), which may possibly facilitate germination. Then, the higher solar irradiation and higher nutrient contents of the mineral soils in the mounds, with fewer fungal pathogens and lowered competition, likely leads to great seedling success rates. For example, Simon et al. (2011) found lower densities of seeds of *Fagus sylvatica* on mounds as compared with pits, but the mortality rate was so high in pits that it eventually led to a near absence of regeneration there.

Points (iii) and (iv) are a function of the local geologic substrate and soils, explaining why the relationship between trees and mounds was strongly positive in Michigan, in contrast to some other regions. In areas of fine-textured soils, fresh pit–mound pairs are occasionally
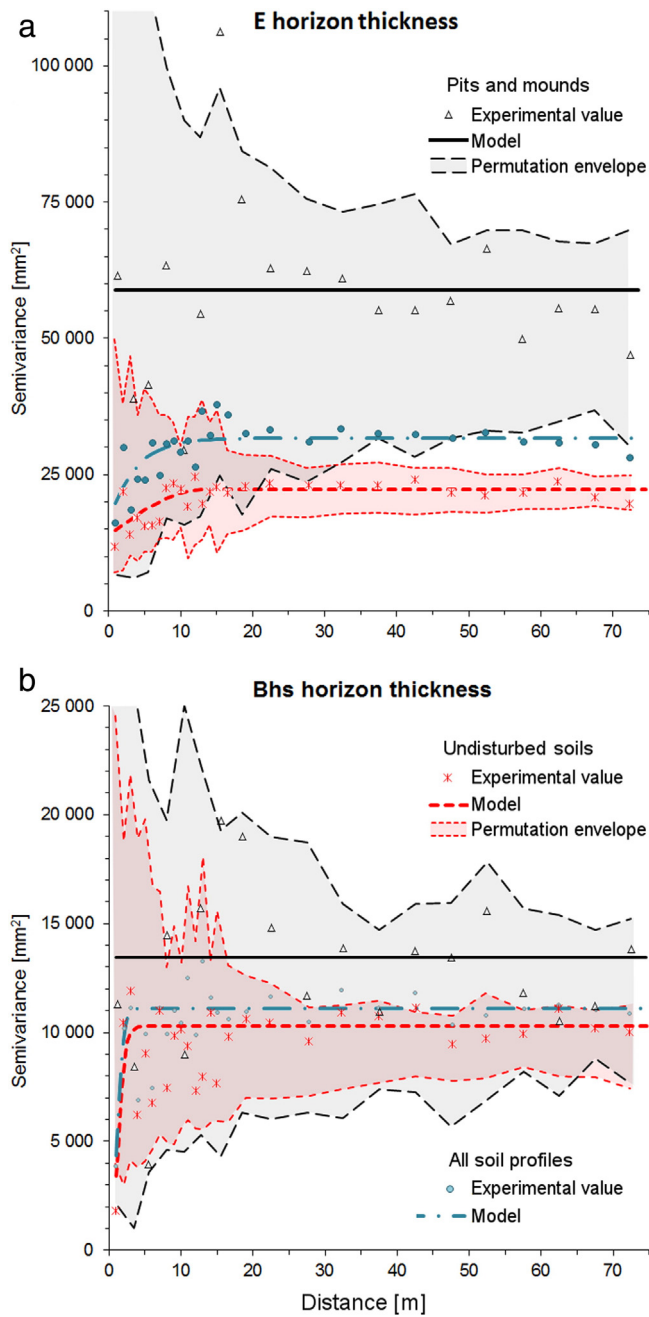
a

E horizon thickness

Pits and mounds
△ Experimental value
— Model
-- Permutation envelope

b

Bhs horizon thickness

Undisturbed soils
✳ Experimental value
--- Model
⋯ Permutation envelope

All soil profiles
● Experimental value
-·- Model

Fig. 5. Square-rooted semivariograms (values on the y-axis are in mm) for E and Bhs horizon thicknesses at the Munising site. Disturbed positions of soil profiles within treethrow pits and mounds are in black, undisturbed positions are in red, and all positions together are in green. Dashed lines indicate confidence envelopes for variograms, using 99 permutations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

sites of intensive erosion, whereas older, more stable mounds are better suited for successful tree regeneration (Šebková et al., 2012). Additionally, in finer-textured soils leaching in pits is less intense, retaining nutrients that might leach to great depths in sandier soils. In such soils, nutrients released during the decay of accumulated organic matter from mounds or other nearby sites is, instead, adsorbed onto the clay fraction within the pit soils (Šamonil et al., 2010a, 2015). Therefore, pit microsites have higher concentrations of nutrients, when compared to mounds (Šamonil et al., 2010a). At the Michigan sites, however, sandy pits are deeply leached and comparatively nutrient poor.

Some tree species can, through biomechanical effects such as uprooting, influence their environment to the point that they benefit from their
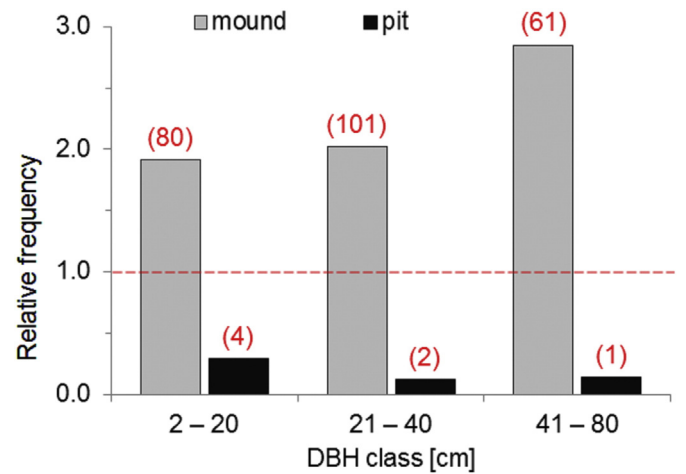

Fig. 6. The occurrence of trees (separately for different DBH classes) on treethrow mounds and pits. The occurrence is expressed as relative frequency in relation to the proportion of pit and mound features within the plot. The null hypothesis, i.e. proportion of trees on individual microsites is adequate to the areal proportion of these microsites, is shown as a dashed line. Occupation of microsites was statistically significant on p-values <0.001 (Chi square test). Red labels represent the frequencies of trees in each category.

affinities for disturbed microsites; this has been referred to as ecosystem engineering (Verboom and Pate, 2013). We did not find any woody species that had particular affinities for pits, but the majority of the woody species (particularly *A. saccharum*, *P. serotina*) did have clear affinities for mounds. Collins and Pickett (1982) have already described the affinity of *A. saccharum* and *P. serotina* to mounds. Zeide (1981) reported on an especially strong relationship between *B. alleghaniensis* regeneration and treethrow mounds. We also observed a positive relationship between birch species and mound microsites.

Uprooting events have significantly increased the spatial variability in soil horizon types and thicknesses at the study sites. A mathematical model by Finke et al. (2014), for loess soils in Belgium, showed similar results. In Michigan, sill values of disturbed pedons exceeded the sill in undisturbed profiles, by about 70% (Fig. 5). Some of the very oldest pit–mound pairs now occur as level (reference) sites, adding to the
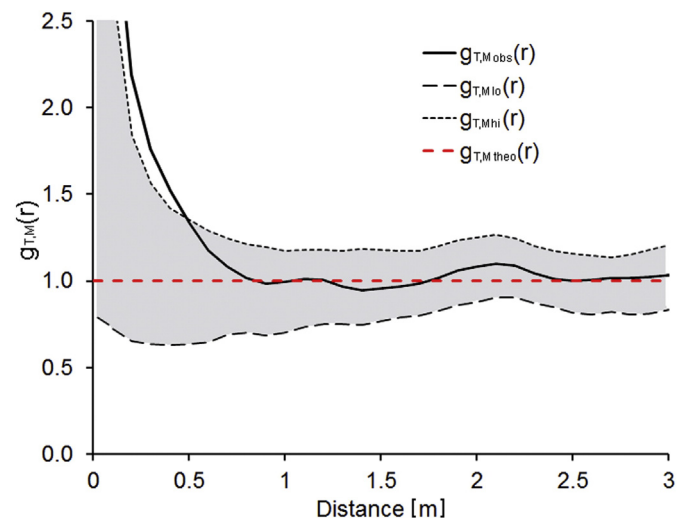

Fig. 7. Spatial relationship between *Acer saccharum* trees and treethrow mounds at the Munising site. We used the cross-type pair correlation functions $g_{T,M}(r)$. $g_{T,M\,obs}(r)$ — observed function, $g_{T,M\,theo}(r)$ — theoretical value of the independence of components hypothesis. $g_{T,M\,lo}(r)$, $g_{T,M\,hi}(r)$ — the lower and upper pointwise envelopes resulting from 199 simulations obtained by random shifts of sub-patterns (trees, mounds), independently of each other. If the value of g $g_{T,M\,obs}(r)$ is larger than the value of the $g_{T,M\,hi}(r)$ then the *Acer saccharum* trees and mounds are positively associated. If the value of $g_{T,M\,obs}(r)$ is smaller than value of the $g_{T,M\,lo}(r)$ the trees and mounds are negatively associated. In the gray zone, we cannot reject the independence of components hypothesis.

spatial complexity of the otherwise level land surface (confirmed by terrain microphotography as well as by soil morphology in excavations, Šamonil et al., 2015).

Modern forest management practices, removing trees before they can fall, or the cutting of uprooted trees, as in many cases the rootwad settles back into the pit after trunk withdrawal, acts to limit intensity of treethrow disturbances (Roering et al., 2010) and therefore, slows the development of additional spatial variability in soils. Decreased soil variability is often accompanied by a loss of biodiversity (Šamonil et al., 2008; von Oheimb et al., 2007; Nachtergale et al., 2002). Our results suggested that the ranges of spatial autocorrelation are shorter in the deeper Bhs horizons than in the E horizons, which correspond with results of Šamonil et al. (2011) from a naturally disturbed central European beech-dominated forest (see also Kabrick et al., 1997). These findings can be explained by assuming that a longer time period is necessary for rejuvenation of deeper horizons, after pedogenesis is reset by the disturbance event. In managed forests, where soil disturbances are less common, surficial processes and pedogenesis work to even-out the spatial variability in soils, as microtopography is less pronounced. Greater spatial continuity in deeper horizons, as revealed Borůvka et al. (2007) in mountain spruce and beech managed forests in the Czech Republic, was attributed to the fact that organic horizons are more susceptible to external impacts, whereas B horizons are more influenced by regional factors (forest type, forest stand age and geomorphology) in regions where geometry of bedrock weathering fronts is not exceptionally complex.

The impact of tree uprooting on pedogenesis at the stand and landscape scale has usually been resolved by extrapolations of results from the finer (treethrow pit-mound) scales (e.g., Brown and Martel, 1981; Skvorcova et al., 1983; Burns et al., 1984; Bormann et al., 1995). Researchers using this approach have often concluded that uprooting simply causes rejuvenation of soils in the landscape, or that it inhibits soil genesis from progressing to some sort of terminal stage. Although this conclusion may be true at the local (pit–mound) scale, it ignores other spin-offs of the process, such as the rapid and seemingly irreversible, post-disturbance soil development in deep pits (Schaetzl, 1990; Šamonil et al., 2010b, 2015), and the non-random occurrences of new disturbances (which are the least probable in pits; Šebková et al., 2012). Indeed, strongly developed soil morphologies in pits in northern Michigan may quickly develop to such a point that future disturbances cannot obliterate them, because the bottoms of the horizons extend below the depth of rooting. Therefore the resulting effect of tree uprooting dynamics on soil formation at coarser scales could be even vastly different from the oft-referenced rejuvenation that occurs on fine spatial scales.

5. Conclusions

Using highly detailed sampling from areas considerably larger than has been used in previous studies, we mapped and characterized over 1000 pit and mound features across an area of 2.8 ha. Our current study has followed previous studies in this area (Šamonil et al., 2013, 2015) where exceptional longevity of treethrow pit–mounds and specific post-disturbance pedogenesis within these forms were revealed. It therefore enhances our current knowledge, mainly with respect to spatial relationships between ecosystem components, soil, treethrow features and trees. The observed lack of runoff on mainly gentle slopes on sandy sediment/soils, coupled with the fact that trees here appear to not fall preferentially downslope, leads us to conclude that uprooting here does not play a major role in mass movement of sediment, as it commonly does in areas of steeper slope (Norman et al., 1995). The great longevity of the pit–mound forms here also has led to spatial randomness, perhaps because most sites on the forest floor are subject to uprooting over the several thousands of years timespan necessary to obliterate the microtopography. The success of forest plants, both their germination and survival, is not, however, random; trees establish much more successfully on mounds, as has been reported for other forests (Schaetzl et al., 1989a; Šebková et al., 2012). We observed almost

no successful tree regeneration in pits. The result of this interaction was generally a random distribution of trees at the study sites. Thus, the impact of such long-lived and dense (17% of the surface) microtopography on the forest ecosystem is impressive, both ecologically and spatially.

Lastly, the persistence of this microtopography has had a pronounced impact on soil genesis and spatial variability. Soils develop rapidly in pits, possibly due to the increased litter accumulation and water infiltration found to occur there (Schaetzl, 1990; Šamonil et al., 2013). In the older pits, soils may develop to a point that uprooting cannot disturb them, as large roots fail to penetrate into the lower solum. Thus, microtopography here has led to increased spatial variability in the soils, at spatial scales from few meters to the stand scale. Spatial autocorrelation data showed that uprooting increased sills for all evaluated horizons and shortened the ranges for E and Bhs horizon thicknesses. The effect of treethrow dynamics on soil characteristics was greatest and statistically most significant for E horizon thicknesses, where the range was shortened from 13 m to 10 m, whereas the maximal level of semivariance (sill) increased by 42%.

Overall, our study sites represent a type of temporal end member along a continuum of forest soil disturbance; the frequency of uprooting may not be greater here than elsewhere, but the sandy textures, gentle slopes and thick littler probably facilitate the persistence of the resulting microtopography (treethrow pit–mounds longevity was studied by Šamonil et al., 2013). As a result, its long-term influence on the soils and the forest ecosystem is large and long-lasting.

Appendix A. Overview of the soil data collection methods at the Munising site: (i) regular (10-m square grid within the main 1-ha square plot) and schematic sampling (eight 0.05-ha plots) — black crosses, and (ii) random sampling (throughout the study plot, 100 soil profiles within 1-ha plot and 3 profiles within each circle) — red crosses.
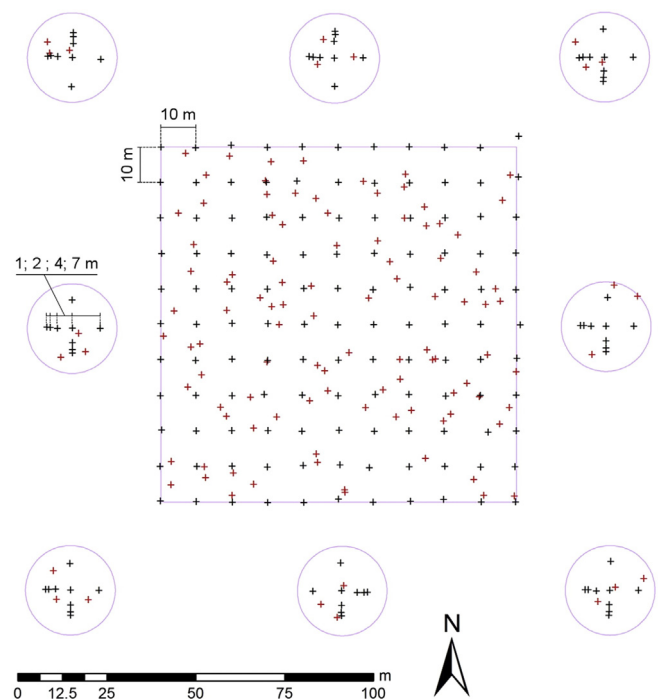
Appendix B. General elevations, locations of pit–mound features and tree locations and sizes at the Munising site
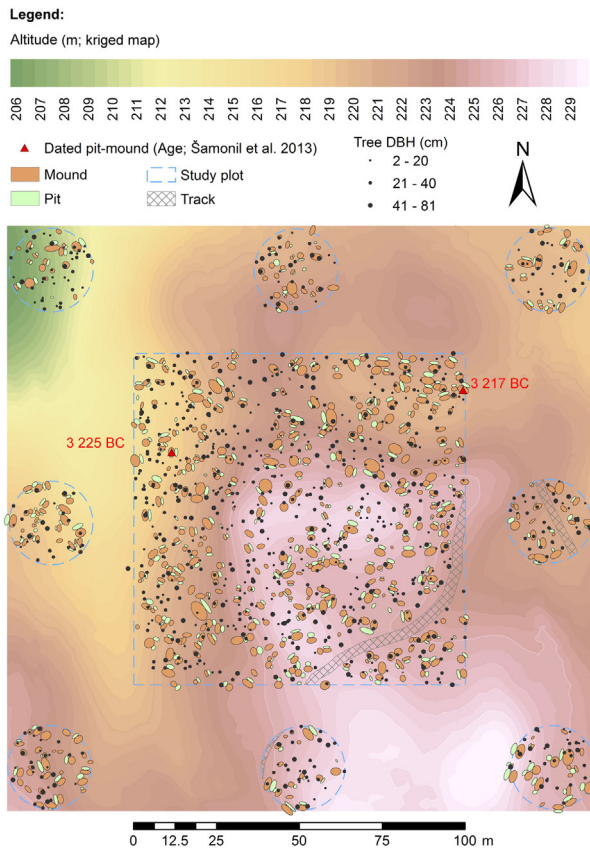
Appendix C. General elevations and locations of pit–mound features at the Strongs site
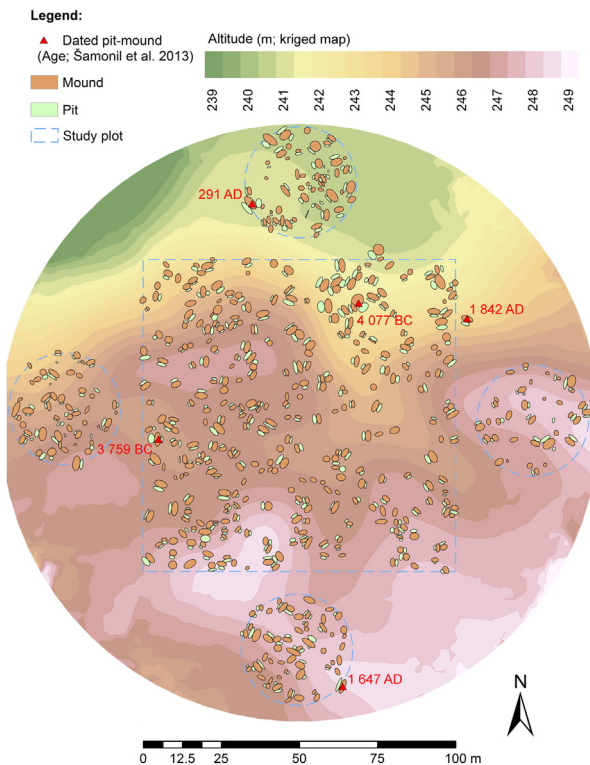
References

Anonymous, 1995. ISOIDIS 14235. Soil Quality. Determination of Organic Carbon in Soil by Sulfochromic Oxidation. International Organization for Standardization, Berlin, Vienna, and Zurich.

Baddeley, A., 2008. Analysing spatial point patterns in R. CSIRO, Australia.

Beatty, S.W., Stone, E.L., 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16, 539–548.

Bernhardt, C., 1994. Particle Size Analysis — Classification and Sedimentation Methods. Springer, London.

Bormann, B.T., Spaltenstein, H., McCleellan, M.H., Ugolini, F.C., Cromack Jr., K., Nay, S.M., 1995. Rapid soil development after windthrow disturbance in pristine forests. J. Ecol. 83, 747–757.

Borůvka, L., Mládková, L., Penížek, V., Drábek, O., Vašát, R., 2007. Forest soil acidification assessment using principal component analysis and geostatistics. Geoderma 140, 374–382.

Bremner, J.M., 1996. Nitrogen-total. In: Sparks, et al. (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods. Number 5 in Soil Science Society of America Book Series. Soil Science Society of America, Inc. and American Society of Agronomy, Madison, Wisconsin, pp. 1085–1121.

Brown, J.L., Martel, Y., 1981. Intérêt des Chablis dans l'étude des paléosols. Géog. Phys. Quatern. 35, 87–92.

Burns, S.F., Tonkin, P.J., Campbell, A.S., Delroy, N.D., 1984. A study of effects of episodic forest windthrow on the genesis of high country yellow-brown earths and related podzolised soils. N. Z. Soil News 32, 210.

Buurman, P. (Ed.), 1984. PodzolsVan Nostrand Reinhold Soil Science Series. Van Nostrand Reinhold Company, New York, USA.

Buurman, P., Jongmans, A.G., 2005. Podzolisation and soil organic matter dynamics. Geoderma 125, 71–83.

Chen, Y., Senesi, N., Schnitzer, M., 1977. Information provided on humic substances by E4/E6 ratios. Soil Sci. Soc. Am. J. 41, 352–358.

Clinton, B.D., Baker, C.R., 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. For. Ecol. Manag. 126, 51–60.

Collins, B.S., Pickett, S.T.A., 1982. Vegetation composition and relation to environment in an Allegheny hardwoods forest. Am. Midl. Nat. 108, 117–123.

Courchesne, F., Turmel, M.C., 2008. Extractable Al, Fe, Mn and Si. In: Carter, M.R., Gregorich, E.G. (Eds.), Soil Sampling and Methods of Analysis, second ed. Canadian Society of Soil Science. CRC Press, pp. 307–315.

Cremeans, D.W., Kalisz, P.J., 1988. Distribution and characteristics of windthrow microtopography on the Cumberland plateau of Kentucky. Soil Sci. Soc. Am. J. 52, 816–821.

Drábek, O., Borůvka, L., Mládková, L., Kočárek, M., 2003. Possible method of luminiumspeciation in forest soils. J. Inorg. Biochem. 97, 8–15.

Drábek, O., Mládková, L, Borůvka, L, Száková, J., Nikodem, A., Němeček, K., 2005. Comparison of water-soluble and exchangeable forms of Al in acid forest soils. J. Inorg. Biochem. 99, 1788–1795.

FAO, 2014. World reference base for soil resources. World Soil Resour. Rep. 106, 1–181.

Finke, P.A., Vanwalleghem, T., Opolot, E., Poesen, J., Deckers, J., 2014. Estimating the effect of tree uprooting on variation of soil horizon depth by confronting pedogenetic simulations to measurements in a Belgian loess area. J. Geophys. Res. Earth Surf. 118, 2124–2139.

Gabet, J.E., Mudd, S.M., 2010. Bedrock erosion by root fracture and treethrow: a coupled biogeomorphic model to explore the humped soil production function and the persistence of hillslope soils. J. Geophys. Res. 115 (F04005), 1–14.

Gillman, G.P., Sumpter, M.E., 1986. Modification of the compulsive exchange method for measuring exchange characteristics of soils. Aust. J. Soil Res. 17, 61–66.

Kabrick, J.M., Clayton, M.K., McBratney, A.B., McSweeney, K., 1997. Cradle-knoll patterns and characteristics on drumlins in northeastern Wisconsin. Soil Sci. Soc. Am. J. 61, 595–603.

Karpachevskiy, L.O., Cholopova, L.B., Prosvirina, A.P., 1980. O dinamike stroenija pocvennogo pokrova v lesnych biogeocenozach. Pochvovedenie 5, 40–49 (in Russian).

Kononova, M.M., Bel'chikova, N.P., 1961. Uskorennye metody opredeleniya sostava gumusa. Pochvovedeniye 10, 75–87 (in Russian).

Lark, R.M., 2000. A comparison of some robust of the variogram for use in soil survey. Eur. J. Soil Sci. 51, 137–157.

Lõhmus, P., Turja, K., Lõhmus, A., 2010. Lichen communities on treefall mounds depend more on root/plate than stand characteristics. For. Ecol. Manag. 260, 1754–1761.

Lyford, W.H., MacLean, D.W., 1966. Mound and pit relation to soil disturbance and tree distribution in New Brunswick, Canada. Harv. For. Pap. 15, 1–18.

McKeague, J.A., Day, J.H., 1966. Dithionite and oxalate-extractable Fe and Al as aids indifferentiating variol classes of soil. Can. J. Soil Sci. 45, 13–22.

McKeague, J.A., Brydon, J.E., Miles, N.M., 1971. Differentiation of forms of extractable ion and aluminum in soils. Soil Sci. Soc. Am. Proc. 35, 33–38.

Nachtergale, L., Ghekiere, K., De Schrijver, A., Muys, B., Luyssaert, S., Lust, N., 2002. Earthworm biomass and species diversity in windthrow sites of a temperate lowland forest. Pedobiologia 46, 440–451.

Norman, S.A., Schaetzl, R.J., Small, T.W., 1995. Effects of slope angle on mass movement by tree uprooting. Geomorphology 14, 19–27.

Pawlik, Ł., 2013. The role of trees in the geomorphic system of forested hillslopes – a review. Earth Sci. Rev. 126, 250–265.

Peterson, C.J., Cambell, J.E., 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. Bull. Torr. Bot. Club 120, 451–460.

Phillips, J.D., 2001. Divergent evolution and the spatial structure of soil landscape variability. Catena 43, 101–113.

Phillips, J.D., 2010. The convenient fiction of steady-state soil thickness. Geoderma 156, 389–398.

Putz, F.E., 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64, 1069–1074.

Ripley, B.D., 1988. Statistical Inference for Spatial Processes. Cambridge University Press.

Roering, J.J., Marshall, J., Booth, A.M., Mort, M., Jin, Q., 2010. Evidence for biotic controls on topography and soil production. Earth Planet. Sci. Lett. 298, 183–190.

Runkle, J.R., 1990. Gap dynamics in an Ohio Acer-Fagus forest and speculations on the geography of disturbance. Can. J. For. Res. 20, 632–641.

Šamonil, P., Šebková, B., Douda, J., Vrška, T., 2008. Role of position within the windthrow in forest floor chemistry in the flysch zone of the Carpathians. Can. J. For. Res. 38, 1646–1660.

Šamonil, P., Antolík, L., Svoboda, M., Adam, D., 2009. Dynamics of windthrow events in a natural fir–beech forest in the Carpathian mountains. For. Ecol. Manag. 257, 1148–1156.

Šamonil, P., Král, K., Hort, L., 2010a. The role of tree uprooting in soil formation: a critical literature review. Geoderma 157, 65–79.

Šamonil, P., Tejnecký, V., Borůvka, L., Šebková, B., Janík, D., Šebek, O., 2010b. The role of tree uprooting in Cambisol development. Geoderma 159, 83–98.

Šamonil, P., Valtera, M., Bek, S., Šebková, B., Vrška, T., Houška, J., 2011. Soil variability through spatial scales in a permanently disturbed natural spruce–fir–beech forest. Eur. J. For. Res. 130, 1075–1091.

Šamonil, P., Schaetzl, R.J., Valtera, M., Goliáš, V., Baldrian, P., Vašíčková, I., Adam, D., Janík, D., Hort, L., 2013. Crossdating of disturbances by tree uprooting: can treethrow microtopography persist for 6000 years? For. Ecol. Manag. 307, 123–135.

Šamonil, P., Vašíčková, I., Daněk, P., Janík, D., Adam, D., 2014. Disturbances can control fine-scale pedodiversity in old-growth forest: is the soil evolution theory disturbed as well? Biogeosciences 11, 5889–5905.

Šamonil, P., Daněk, P., Schaetzl, R.J., Vašíčková, I., Valtera, M., 2015. Soil mixing and genesis as affected by tree uprooting in three temperate forests. Eur. J. Soil Sci. 66, 598–603.

Schaetzl, R.J., 1986. Complete soil profile inversion by tree uprooting. Phys. Geogr. 7, 181–189.

Schaetzl, R.J., 1990. Effects of treethrow microtopography on the characteristics and genesis of spodosols, Michigan, USA. Catena 17, 111–126.

Schaetzl, R.J., Follmer, L.R., 1990. Longevity of threethrow microtopography: implications for mass wasting. Geomorphology 3, 113–123.

Schaetzl, R.J., Harris, W., 2011. Spodosols. In: Huang, P.M., Li, Y., Sumner, M.E. (Eds.), Handbook of Soil Sciences, second ed. CRC Press, New York, pp. 33–127.

Schaetzl, R.J., Isard, S.A., 1996. Regional-scale relationships between climate and strength of podzolization in the Great Lakes region, North America. Catena 28, 47–69.

Schaetzl, R.J., Thompson, M.L., 2015. Soil Genesis and Geomorphology. Cambridge University Press, New York, USA.

Schaetzl, R.I., Burns, S.F., Johnson, D.L., Small, T.W., 1989a. Tree uprooting: review of impacts on forest ecology. Vegetatio 79, 165–176.

Schaetzl, R.J., Johnson, D.L., Burns, S.F., Small, T.W., 1989b. Tree uprooting: review of terminology, process, and environment implications. Can. J. For. Res. 19, 1–11.

Schaetzl, R.J., Burns, S.F., Small, T.W., Johnson, D.L., 1990. Tree uprooting: review of types and patterns of soil disturbance. Phys. Geogr. 11, 277–291.

Schaetzl, R.J., Luehmann, M.D., Rothstein, D., 2015. Pulses of podzolization: the importance of spring snowmelt, summer storms, and fall rains on spodosol development. Soil Sci. Soc. Am. J. 79, 117–131.

Šebková, B., Šamonil, P., Valtera, M., Adam, D., Janík, D., 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. For. Ecol. Manag. 280, 9–19.

Shubayeva, V.I., Karpachevskiy, L.O., 1983. Soil–windfall complexes and pedogenesis in the Siberian stone pine forests of the maritime territory. Pochvovedeniye 9, 96–103.

Simon, A., Gratzer, G., Sieghardt, M., 2011. The influence of windthrow microsites on tree regeneration and establishment in an old growth mountain forest. For. Ecol. Manag. 262, 1289–1297.

Skvorcova, E.B., Ulanova, N.G., Basevic, V.F., 1983. Ekologiceskaja rol Vetrovalov. Lesnaja Promyslennost, Moskva.

Small, T.W., Schaetzl, R.J., Brixie, J.M., 1990. Redistribution and mixing of soil gravels by tree uprooting. Prof. Geogr. 42, 445–457.

Sommer, M., Halm, D., Geisinger, C., et al., 2001. Lateral podzolization in a sandstone catchment. Geoderma 103, 231–247.

Soil Survey Staff, 2014. Keys to Soil Taxonomy. Natural Resources Conservation Service (372 pp.).

Stoyan, D., Stoyan, H., 1994. Fractals, Random Shapes and Point Fields: Methods of Geometrical Statistics. John Wiley & Sons, Chichester, UK.

Tejnecký, V., Šamonil, P., Matys, G.T., Vašát, R., Ash, C., Drahota, P., Šebek, O., Němeček, K., Drábek, O., 2015. Transformation of iron forms during soil formation after tree uprooting in a natural beech-dominated forest. Catena 132, 12–20.

Ulanova, N., 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manag. 135, 155–167.

Valtera, M., Šamonil, P., Boublík, K., 2013. Soil variability in naturally disturbed Norway spruce forests in the Carpathians: bridging spatial scales. For. Ecol. Manag. 310, 134–146.

Valtera, M., Šamonil, P., Svoboda, M., Janda, P., 2015. Effects of topography and forest dynamics on soil variability in natural *Picea abies* mountain forests. Plant Soil 392, 57–69.

Vassenev, I.I., Targulian, V.O., 1995. Windtrhrow and Taiga Pedogenesis (Regimes, Processes, Morphogenesis of Soil Successions). Nauka, Moskva.

Verboom, W.H., Pate, J.S., 2013. Geoderma 211–2, 154–183.

von Oheimb, G., Friedel, A., Bertsch, A., Härdtle, W., 2007. The effects of windthrow on plant species richness in a central European beech forest. Plant Ecol. 191, 47–65.

Webster, R., Oliver, M.A., 2007. Geostatistics for Environmental Scientists. second ed. John Wiley & 537 Sons, Ltd., Chinchester, UK.

White, P.S., MacKenzie, M.D., Busing, R.T., 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. Can. J. For. Res. 15, 233–240.

Zbíral, J., 2002. Analýza půd I. Ústřední kontrolní a zkušební ústav zemědělský, Brno.

Zbíral, J., 2003. Analýza půd II. Ústřední kontrolní a zkušební ústav zemědělský, Brno.

Zbíral, J., Honsa, I., Malý, S., Čižmár, D., 2004. Analýza půd III. Ústřední kontrolní a zkušební ústav zemědělský, Brno.

Zeide, B., 1981. Method of mound dating. For. Sci. 27, 39–41.