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Soil mixing and genesis as affected by tree uprooting in three temperate forests

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Summary

The purpose of this study was to identify general patterns of pedoturbation by tree uprooting in three different, forested landscapes and to quantify post-disturbance pedogenesis. Specifically, our study illustrates how the effects of 'tree-throw' on soils gradually become diminished over time by post-uprooting pedogenesis. We studied soil development within 46 pit-mounds in two regions of the Czech Republic, one on Haplic Cambisols and one on Entic Podzols. A third study site was in Michigan, USA, on Albic Podzols. Uprooting events were dated by using tree censuses, dendrochronology and radiometry. These dates provided information on several chronosequences of pedogenesis in the post-uprooting pits and mounds, dating back to 1816 AD (dendrochronological dating, Haplic Cambisols), 322 AD (median of calibration age, ^{14}C age = 1720 ± 35 BP, Entic Podzols) and 4077 BC (^{14}C age = 5260 ± 30 BP, Albic Podzols). Post-uprooting pedogenesis was most rapid in pits and slowest on mounds. Linear chronofunction models were the most applicable for pedogenesis, regardless of whether the soils were in pit or mound microsites. These models allowed us to estimate the time required for horizons in such disturbed sites to obtain the equivalent thicknesses of those in undisturbed sites. These ranged from 5 (O horizon in pits on the Haplic Cambisols) to > 16 000 years (E horizon on mounds on the Albic Podzols). On the Albic Podzols, development of eluvial and spodic horizon thicknesses suggested that pathways involving divergent pedogenesis may occur at these small and localized spatial scales.

Introduction

Tree uprooting is important in the evolution of some forest soils. In temperate, beech-dominated European forests, approximately one-third of all trees die as a result of uprooting, implying that, theoretically within 500–3000 years, every location in these forests is likely to be disturbed (Šamonil *et al*., 2010a, 2013). As a large tree topples, it tears up a lens of soil and leaves an irregularly shaped pit. The soil in the lens slowly detaches from the roots and subsides into an irregular mound, some of which falls and washes back into the pit (Figure 1). Tree uprooting ('tree-throw') interrupts the generally slow but progressive evolution of soils that involves mineral weathering, decomposition of organic matter, vertical segregation of their products into distinct horizons, and the resultant formation of organized soil profiles. Tree-throw disrupts this progression and is a regressive process (Johnson & Watson-Stegner, 1987). Tree uprooting mainly affects soil horizonation, as it mixes materials that were originally systematically stratified. The post-fall re-establishment of horizonation processes and profile differentiation is affected by the micro-topography that results from uprooting. The pits receive additional in-washed litter and minerals, and are the *loci* for additional percolating water, which usually facilitates horizon development and translocation. In contrast, mound soils are subject to reduced leaching, increased desiccation and runoff, and possibly accelerated erosion.

With few exceptions (Vassenev & Targulian, 1995), previous studies have focused on only a few pit-mound pairs at a single location. Our data come from multiple disturbance sites in three temperate forests in the Czech Republic and Michigan, USA. Our data also benefit from recent advances in tree-throw dating techniques (Šamonil *et al*., 2013). Our Michigan site includes the oldest reported uprooting features in the world, some more than 6000 years old, and our data for the Czech Republic include pit-mound pairs that are 1700 years or older (Šamonil *et al*., 2010a, 2013).

Our goal was to determine the patterns of mixing by tree uprooting, and the subsequent re-establishment of soil horizons and

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Figure 1 Tree-throw pit-mound created during the storm in Zofin on 18 January 2007.

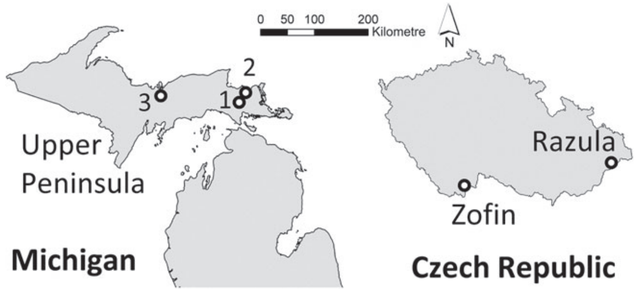

Figure 2 Location of the Razula and Zofin study areas in the Czech Republic and the research sites in Michigan, USA. For latitude and longitude see Table 1.

profiles, and to develop chronofunctions for these processes and to quantify rates of post-disturbance pedogenesis.

Materials and methods

Study sites

The study sites are at Zofin and Razula in the Czech Republic (CR), and at three locations in the eastern part of the Upper Peninsula of Michigan, USA (Figure 2 and Table 1). They are all at latitudes 45–50°N and span a gradient of soil leaching and weathering, with highly leached, weathered and acidic Albic Podzols on sandy glacial outwash in Michigan, intermediate Entic Podzols on granite at Zofin, and Haplic Cambisols (soil classification according to Michéli *et al*., 2007) on flysch at Razula. We avoided very shallow and extremely stony soils at Zofin and Razula (Hyperskeletic and Epileptic Cambisols and Podzols, and Leptosols). Soil textures become sandier from the Haplic Cambisols (Razula), through the Entic Podzols (Zofin) to the Albic Podzols (Michigan). This gradient was associated with increasing longevity of pit-mound micro-topographies (Šamonil *et al.,* 2009, 2013).

Tree uprooting is the most important disturbance factor in these forest ecosystems, although there are others, such as rare fires in Michigan and infrequent mammalian burrowing at all sites. The Michigan sites were located within managed forests that were last cut at least 40 years ago. The old-growth forest at Zofin has been under protection since 1838, and historical documents suggest it has never been cut. The old-growth forest at Razula has been under protection since 1933, and was affected by infrequent selective cutting and grazing before then (Table 1).

Dating

We selected tree-throw pit-mounds for potential dating by using stratified random techniques at both the Razula (in total 1562 pit-mounds studied in detail, Šamonil *et al*., 2009) and Zofin sites (1733 pit-mounds, Šamonil *et al*., 2014). In Michigan, tree-throw features were selected more subjectively (70 pit-mounds studied in detail, Šamonil *et al*., 2013). Dating techniques were adapted to expected different longevities of pit-mounds in individual localities (Šamonil *et al*., 2013). Dendrochronological dating was used at all sites, radiometric dating was not applied in Razula and tree census was not used in Michigan.

Tree-census data were used to establish the ages of the youngest (< 37 years) uprooting events in Zofin and Razula. This method involves repeated measurements (during the 1970s, 1990s and 2000s) of the dimensions of all trees with the diameter at breast height ≥ 10 cm within the reserves. We used ^{210}Pb (lead) dating (and also including ^{137}Cs (caesium) and ^{226}Ra (radium)) of soil material deposited within the tree-throw pits to date disturbance events younger than about 200 years. Dendrochronological dating was applied only to live trees, yielding a useful age range of about 400 years. Radiocarbon (^{14}C) dating was used for features older than 100 years. The age of the tree-throw events in Michigan was taken as the radiocarbon dates of buried wood or the pre-fall buried A horizons in the mound profiles (profile B in Figure 3 in Schaetzl, 1986; Šamonil *et al*., 2013). The various dating methods have different ranges of validity. Where these ranges overlapped, we cross-validated estimates of tree-throw ages (Šamonil *et al*., 2013). In total, we successfully dated 37 pit-mounds in Razula, 178 pit-mounds in Zofin and 14 pit-mounds in Michigan (Šamonil *et al*., 2009, 2013).

The dates that we report reflect various ages, relative to the disturbance events. Minimum ages of the events are reported by dendrochronological data for trees that had rooted on a dated pit-mound, or had recently grown in gaps formed during uprooting

Table 1 Overview of the physical and ecological conditions associated with each of the three study sites

Feature/locality	Razula	Zofin	Upper Peninsula
Parent material	Flysch	Granite	Outwash
Soil taxonomy	Haplic Cambisols	Entic Podzols	Albic Podzols
Location/latitude, longitude	49.36°N, 18.38°E	48.67°N, 14.70°E	46.32°N, 85.06°W 46.44°N, 84.82°W 46.37°N, 86.70°W
Average soil reaction (pH_{H2O}) in B horizon/dimensionless ± SD/n	5.1 ± 0.4/23	4.5 ± 0.2/14	5.1 ± 0.2/17
Cation exchange capacity in B horizon/mmol+/kg ± SD/n	130.77 ± 38.31/23	65.6 ± 17.9/14	40.9 ± 11.8/17
Soil texture fraction < 0.01 mm in B horizon/% ± SD/n	34.20 ± 11.6/23	2.5 ± 1.7/14	0.2 ± 0.8/17
Soil texture fraction < 0.002 mm in B horizon/% ± SD/n	12.7 ± 5.9/23	0.25 ± 0.59/14	0.1 ± 0.4/17
Forest type	Fir-beech forest	(Spruce)-fir-beech forest	Hardwoods
Main tree species	*Fagus sylvatica* L., *Abies alba* Mill.	*Fagus sylvatica* L., *Picea abies* (L.) Karsten, *Abies alba* Mill.	*Acer saccharum* Marsh., *A. pensylvanicum* L., *A. rubrum* L., *Quercus rubra* L., *Tsuga canadensis* (L.) Carr., *Pinus* spp.
Range of altitudinal gradient / m a.s.l.	600–812	730–837	215–270
Mean annual precipitation / mm	1057	900	800
Average seasonal maximum of snow cover depth / cm	75–100	75–100	Circa 100
Mean average temperature / °C	5.0–6.0	4.3	5.1
Maximal observed pit-mound longevity / year	220	1688	6089

events, and some data from tree-censuses, as well as ^{210}Pb- and ^{14}C-dates from the sedimentation funnel within the tree-throw pit. Real (best actual) age estimates of disturbance events were obtained by complete tree-census data and by coring trees that grew in the vicinity of pit-mounds but had germinated before the disturbance event. Release in radial growth of these trees was used to establish the date of the uprooting event. Finally, radiocarbon dates of remnants of uprooted trunks in mounds provided maximum ages (see details in Šamonil *et al*., 2009, 2013).

Soil selection and characterization

We selected only the most precisely dated pit-mounds for this study (14 pit-mounds in both Razula and Michigan; 18 pit-mounds in Zofin). The 46 sites were described and sampled in 1.5-m deep and 0.6-m wide trenches along the axes of the pit-mound pairs (profile A in Figure 3). The soil horizonation across the face of the trenches was carefully sketched (Table 2). We sampled by horizons in the trench and at fixed depths in the pit and mound, and also in an adjacent undisturbed reference pedon at depths of 5, 15, 30, 50 and 100 cm. About 700 samples (Figures 4–6) were analysed for the main processes in soils: transformation and translocation of organic compounds (such as humification); weathering and leaching processes (mineral formation and alteration, clay illuviation); and oxidation-reduction processes (Šamonil *et al*., 2010b), and complemented and verified the morphological survey. Within

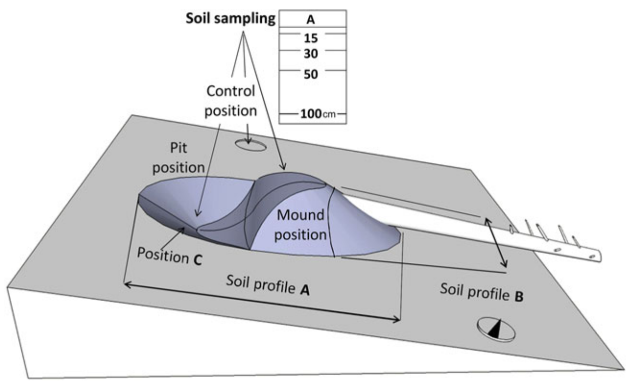

Figure 3 A schematic pit-mound pair and uprooted tree trunk, with positions of sampled profiles on pit, mound and undisturbed control sites.

this study we refer to some characteristics of the sorption complex, including exchangeable Ca^{2+}, Mg^{2+}, K^+, Na^+, exchangeable acidity (Al + H) and effective cation exchange capacity (CEC). These were all analysed according to Gillman & Sumpter (1986; $BaCl_2$-compulsive exchange procedure, native pH).

Development of soil chronofunctions

We quantified pedogenesis in the pits and mounds in terms of the thicknesses of newly-formed horizons as compared with the

Table 2 Soil horizons used

Group of horizons		Description of individual horizons
Terrestrial upper **organic horizons**	O	**L** = litter organic horizon
		F = fermented organic horizon
		H = humification organic horizon
Uppermost **mineral soil horizons** enriched with organic matter	A	A**m** = mollic horizon
		A**u** = umbric horizon
Eluvial horizons	E	E**p** = eluvial (= Albic) podzolic horizon
Metamorphic and illuvial horizons	B	B**v** = cambic horizon
		B**vs**, Bs = spodic horizon without illuviation process; Bs = lower spodic horizon in Albic Podzols; Bvs = sole spodic horizon in Entic Podzols
		B**h** = spodic horizon of organic substances illuviation
		B**hs** = spodic horizon of illuviation of complexes of sesquioxides and organic substances
		Bs**m**, Bhs**m** = ortstein horizon
		Bt = argic horizon
		Bx = fragipan (like) horizon
		B**w** = weakly developed B horizon in terms of soil colour or soil structure
Substratum horizons	C	**C** = substratum (unconsolidated) horizon, without features of pedogenesis, physically weathered bedrock is accepted
	R	**R** = bedrock, unweathered rock

Additional symbols	Description	Example
()	Weakly obvious horizon or properties	(E), B(h)s, (Bv)C, A(Ep)
AE, AB, BC	Transitional horizon	BvsC, ABv1, ABvs, BC
1, 2, 3 …	Order of separated zones of one horizon	C1, C2, C3, 1BC, 2BC, 3BC
f	Burried (= fossil) undisturbed horizon	fA
g	Hydromorphic properties	BvgC

Organic horizons based on Klinka *et al.* (1997) and mineral horizons on World Reference Base and Czech taxonomies (Michéli *et al.,* 2007; Němeček *et al.,* 2011).

equivalent horizons in the reference pedons. Intensity of horizon development in terms of colour and chemical evolution were noted but not quantified in this study. We modelled the relationships between horizon thickness and the age of the disturbance event, which was taken as the new $\text{time}_{\text{zero}}$ for soil formation. We applied generalized linear models (GLMs) and linear models with generalized least squares (GLS), using R software (http://www.R-project.org/). Horizon thicknesses were represented by mean values across individual pit-mound transects. Characterizing horizon thickness as medians, $Q_{0.8}$ values and linear mixed-effects models (computed on original data with individual mounds as a random effect) all gave similar responses.

Chronosequence data were fitted to linear, quadratic and hyperbolic statistical models and evaluated for goodness of fit. Linear and quadratic models have been widely applied (Schaetzl *et al.*, 1994), but there have been limited applications of the hyperbolic model, $y = x/(b + ax)$. When both a and b are positive the function increases for positive values of x (age), with an initial slope of $1/b$ and a horizontal asymptote of $1/a$. The development of several soil properties appears to be hyperbolic (Schaetzl & Anderson, 2005). Because non-positive values of response are not allowed in this parametrization, hyperbolic models could only be used with chronosequences where zero means do not occur.

The homoscedasticity of residuals from linear models was tested with the Breusch-Pagan test (Breusch & Pagan, 1979), and if significant ($\alpha = 0.05$) the model was re-fitted using generalized least squares (GLS). Because the complexity of soil development gave greater variance in horizon thicknesses at older sites, two models with variances taken as fixed and power functions of age were compared with Akaike's information criterion (AIC) adjusted for small sample size (AICc):

$$\text{AICc} = \text{AIC} + 2k\,(k + 1)\,/\,(n - k - 1)\,, \qquad (1)$$

where k is the number of model parameters and n is the sample size (Akaike, 1974). Only models significant at $\alpha = 0.05$ were accepted. Quadratic models had to be significantly better than the corresponding linear model to be accepted. As another measure of goodness of fit, a generalization of the coefficient of determination R^2 (Nagelkerke, 1991) was computed.

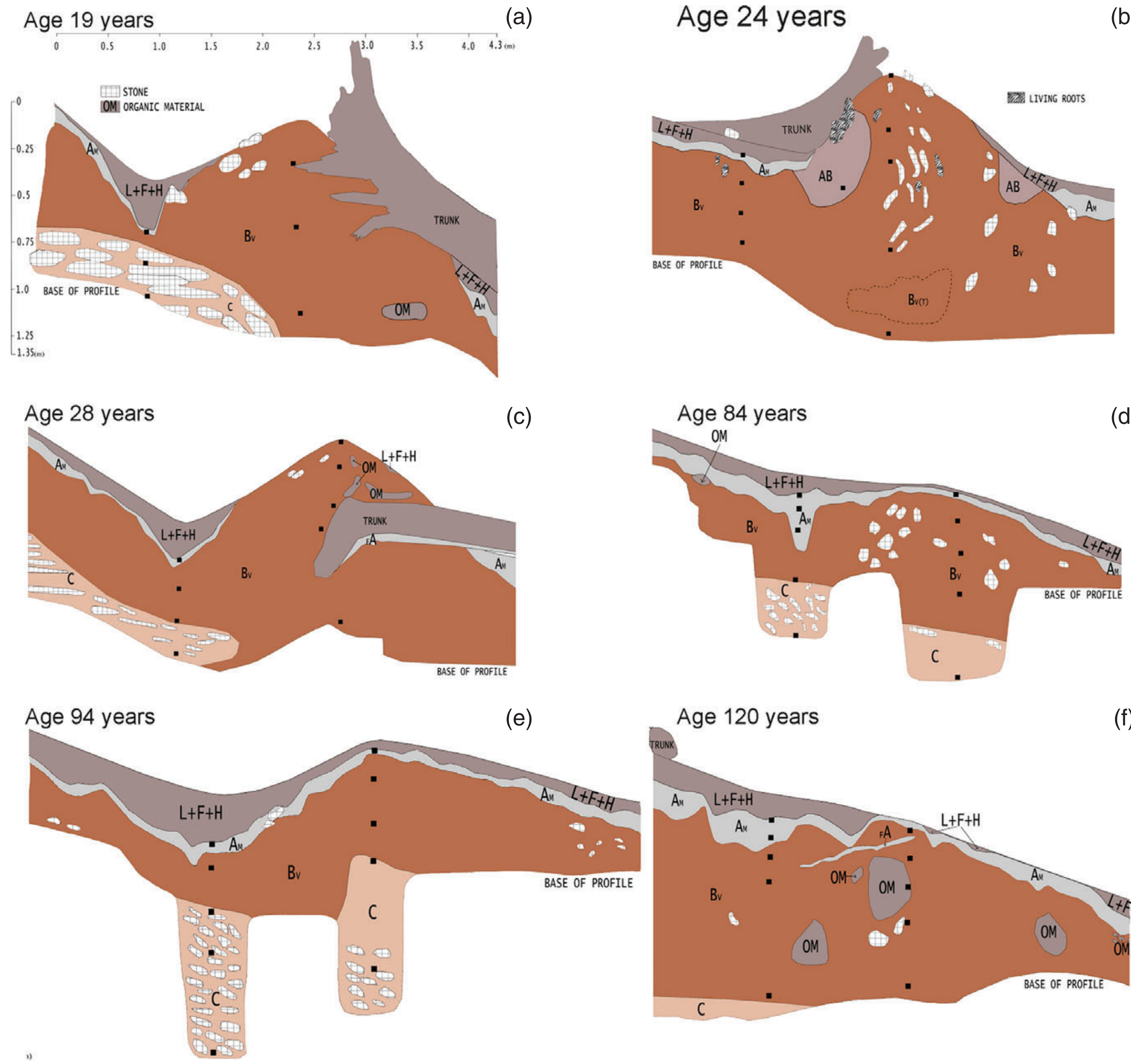

Figure 4 Soil horizonation in selected pit-mound pairs (a–f) in Haplic Cambisols at Razula. Black squares are sampled locations. For horizon codes, see Table 2. Ages are derived from tree census and dendrochronology.

Results

Soil morphology

Soil morphology and laboratory analyses confirmed that weathering and leaching processes were tracing podzolization at Zofin and Michigan and brunification at Razula. However, evidence of clay translocation, melanizing complexation or hydromorphic processes were also observed in disturbed and control undisturbed microsites, particularly at Razula.

Because they lack E horizons and have little B horizon variability, soil morphologies in pit-mounds on Haplic Cambisols (Figure 4) were simpler and less informative than those in the Entic Podzols (Figure 5). This was especially so for the complex and clearly defined horizonation of the Albic Podzols (Figure 6) (see also Figure S1). The more diffuse boundaries in the Haplic Cambisols also made precise distinctions and depth measurements more difficult. At our sites, profile morphologies (horizon sequences, thicknesses and transitions) within pits and mounds always differed from those at control sites.

Elongate solitary rocks in the disturbed soils often come to rest vertically (Figures 4b,f, 5c,e–g), with many slumping back to the horizontal only after the pit becomes in-filled. In the more lithic

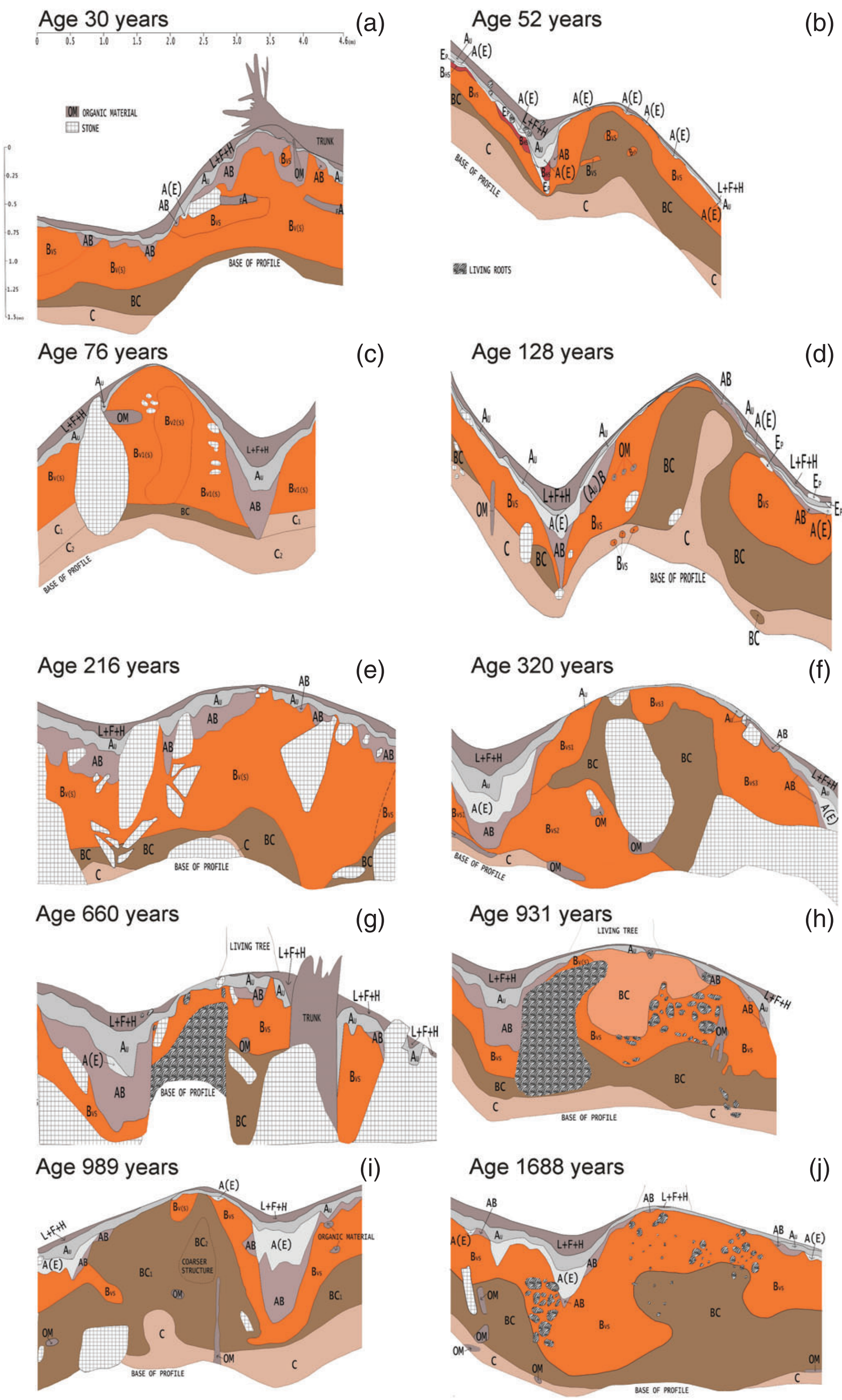

Figure 5 Soil horizonation in selected pit-mounds (a–j) in Entic Podzols at Zofin. For details, see Figure 4 and Table 2. Ages are derived from tree census, dendrochronology and radiometry data.

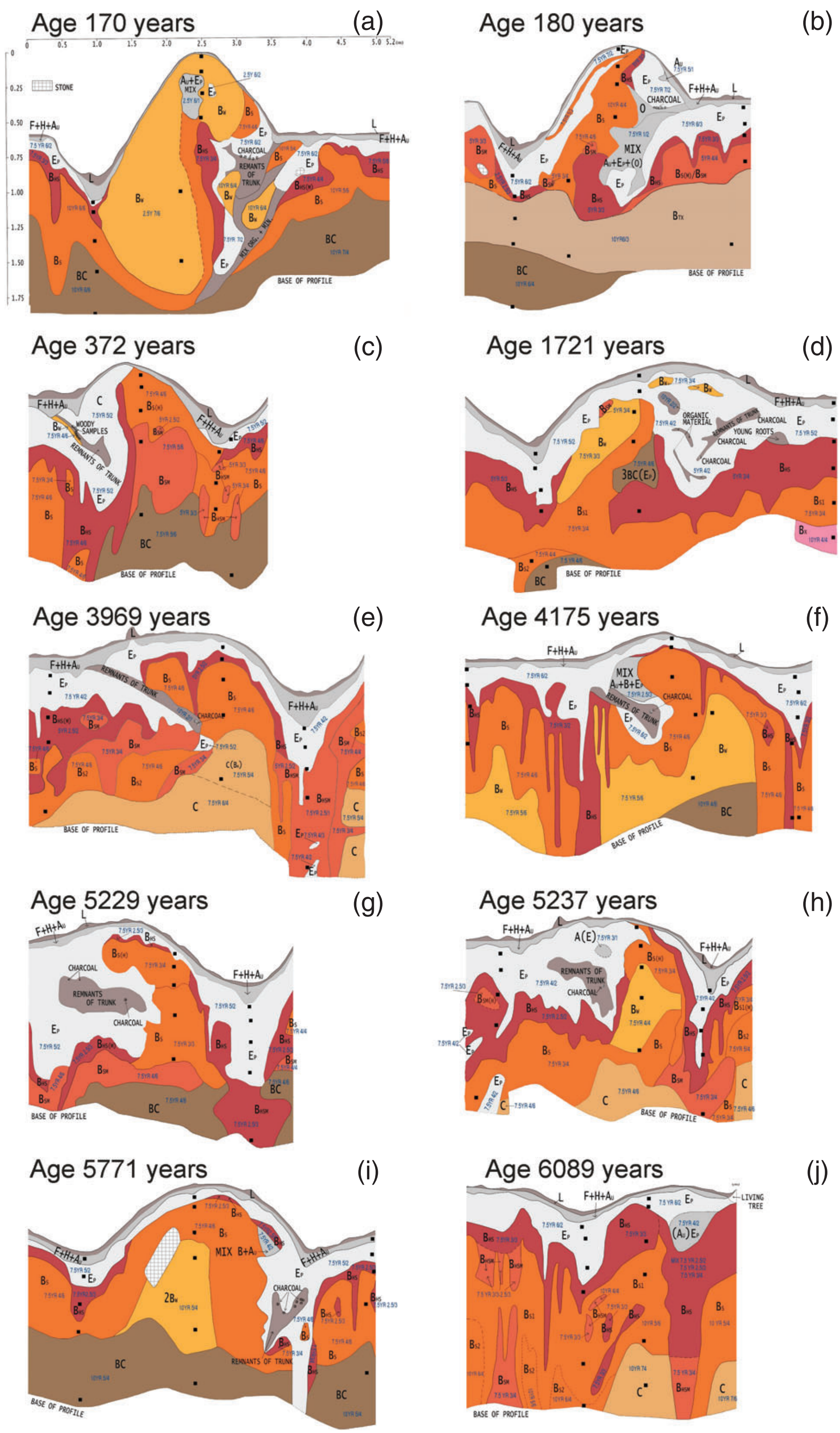

Figure 6 Soil horizonation in pit-mounds (a–j) in Albic Podzols in Michigan site. For details, see Figure 4 and Table 2. Ages are derived from dendrochronology and radiometry data.

soils at Zofin and Razula, we often observed signs of bedrock excavation by uprooting where the bottoms of the tree-throw pits reach the R horizon (Figures 4a,c,e, 5e–g). In mounds, E, B and C horizon remnants were also often vertical, particularly in sites on gentle slopes (Figure 6a–c). In mounds on steeper slopes, horizon fragments were tilted, vertical or over-turned (see Figure 5a,b). Where horizons were over-turned intact (Schaetzl, 1986), they indicate rotation of the lens about a hinge close (usually < 2 m) to the uprooted tree. The horizons usually retained their original sequence, but were upturned or inverted. Various soil properties such as orientation of cutans and size of soil aggregate structure, helped to identify upturned horizons, particularly in Haplic Cambisols.

The deposition of uprooted material increases the solum thickness on mounds because it overlies the original soil. Such soil deepening was clearest in Haplic Cambisols, where mixed upturned cambic horizons were barely distinguishable from the undisturbed B and BC horizons beneath (Figure 4a–c). Below some mounds we observed buried soil horizons that appear to date from earlier disturbances (Figure 6a,j).

The O and A horizons were thicker in the pits and thinner on mounds in all three regions (Figures 4–6), especially in the Haplic Cambisols (Figure 4a–f, 'funnel-like' forms). Increasing thicknesses of A horizons were also observed at the mound edges, and attributed to erosion and sedimentation during mound deterioration.

New O and A horizons in pits were clearly distinguishable at all sites, even the youngest, indicating the rapidity of pedogenesis there. The effects of runoff water flowing into pits and associated erosion/sedimentation on pedogenesis differed between sites. In the Albic Podzols, the organic matter that accumulated in the pit O horizons led to the rapid acidification and eluviation of the upper part of the mineral soil below, forming exceptionally thick E horizon tongues below the pit centre (Figure 6a–j). Consequently, CEC, exchangeable cation contents (particularly Ca, Mg and K) and base saturation were small in the upper mineral horizons of pit soils. These processes have had a rapid impact on the soils in the pits, especially in Michigan, largely because of the small surface area and rapid permeability of the sandy Michigan soils.

Litter also accumulated in the pits on the finer-textured Haplic Cambisols (Figure 4a–f) but the larger clay content and base status of the flysch parent material inhibited leaching and facilitated the melanizing complexing of humus on clay minerals, thus forming thick A, but no E, horizons. The finer textures and better base status also promoted more active assemblages of soil fauna, and consequent mixing of litter into the mineral soil. This also contributes to the formation of A horizons, with larger CEC values and nutrient contents in the Haplic Cambisols than in the thick O horizons of the Podzols.

Pit soils in the Entic Podzols were morphologically intermediate between Albic Podzols and Haplic Cambisols and had thick A horizons but also thin E horizons (Figure 5b,f,g,i,j). Thus all of the pits were sites of organic matter accumulation, but the impacts were mainly governed by texture and base status. Inflow of water into the pits, coupled with poor permeabilities in the fine-textured Haplic Cambisols, often led to the formation of hydromorphic properties in BvgC horizons (Table 2), but this was not observed in the sandier soils.

Material from pre-disturbance lower subsoils (BC and C horizons) was commonly excavated and incorporated into the mounds. In older mounds this material had developed into Bs or Bw horizons (Figures 4d, 5b–d,f,h,j, 6a,c–i, 7b). Although Bhs horizons usually had Munsell colours of 5YR–7.5YR 3/3 and darker (Schaetzl & Anderson, 2005), Bs horizons were lighter and yellower (7.5YR 4/6, 10YR 4/6, 4/4 and 5/6), and substratum horizons were even lighter. This process was morphologically less obvious in flysch parent materials, on soils with deep B horizons and where trees had shallow root systems and uprooting pits. Post-disturbance pedogenic horizonation was readily observed within this originally subsoil material because of the absence of noticeable pre-disturbance horizons.

Some morphologic features and pedogenic processes were specifically associated with particular localities. In Michigan, soil below uprooted trunk fragments was frequently more eluviated than adjacent undisturbed soil. Some decayed trunks left hemi-cylindrical traces of E and Bhs horizons in the underlying soil (Figure 6g,h). Buried A and E horizon materials under mounds without the trunk present left more planar traces. Hemi-cylindrical traces were distinguished by digging transects orthogonal to the direction of tree fall (Figure 2, profile B). The presence and shape of E and Bhs horizons indicate relatively rapid post-disturbance pedogenesis in the soils beneath the uprooted tree. Fallen trunks, which were sometimes charred, gradually decomposed and became a source of organic acids, which may assist in the podzolization process. We refer to the E and Bhs horizons buried beneath the mound as 'covert Podzols' (Figures 6c–i, 7a,c).

The non-charred remains of trunks were not observed in mounds older than about 375 years. The older ^{14}C dates reported here and in Šamonil *et al.* (2013) were based on charcoal found at the contact with the buried soil, below the mound, *sensu* Schaetzl (1986). In the oldest mounds, the little charcoal that remained was fragile. However, the thickness of the underground zone of the E horizon in these older mounds was substantial (Figures 6g, 7a). In the finer-textured soils of the Czech Republic, woody materials remained for only a few decades after the uprooting event (Figure 4c). According to Šamonil *et al.* (2009) the oldest existing uprooted trunks in the Czech beech-dominated old-growth forests were 50–60 years old (calculated in Razula).

Chronofunctions of soil development

Of the many chronofunction models tested for the development of soil horizon thickness, the linear model was most often the best fit (at $\alpha = 0.05$, Table 3). Although the quadratic model was often equally statistically significant, the addition of the quadratic component often did not contribute any additional significance.

In a number of cases, the chronofunction model for horizon thicknesses in pit soils did not intersect at the origin, but was

Figure 7 Pit-mound profiles. (a) Albic Podzol pit-mound profile dated 3217 BC (median of calibration age, ^{14}C age = 4480 ± 35 BP. Note the strongly developed covert E horizon in the buried soil beneath the mound and the strong new E and Bhs horizons in the pit, and the thin, new E and Bhs horizons in the mound. (b) Incipient spodic horizonation in a mound dated 1882 AD on an Entic Podzol at Žofín uplifted substratum material (dendrochronological dating). (c) Complete profile of a pit-mound pair on Albic Podzols in Michigan dated to 1957 BC (median of calibration age, ^{14}C age = 3600 ± 30 BP). Note the thick E and B horizons in the pit, and thinner horizons in the mound. This site also shows a good example of a buried soil beneath the mound. (d) Organo-mineral sedimentation funnel in a pit in an Entic Podzol in Žofín dated to 1844 AD (dendrochronological).

Table 3 Soil chronofunctions tested with Akaike information criterion (AICc), coefficient of determination (R^2) and *P*-values

			Linear model			Quadratic model			Hyperbolic model		
Locality, soils	Horizon	Microsite	AIC	R^2	*P*	AIC	R^2	*P*	AIC	R^2	*P*
Razula, Haplic Cambisols	O	Pit	172	0.20	0.074	175	0.20	0.211	**164**	**0.46**	**0.034**
	O	Mound	**138**	**0.71**	**< 0.001**	145	0.60	0.002	–	–	–
	Am	Pit	**167**	**0.53**	**< 0.001**	170	0.53	0.005	**168**	**0.55**	**0.016**
	Am	Mound	**128**	**0.90**	**< 0.001**	129	0.91	< 0.001	–	–	–
Zofin, Entic Podzols	O	Pit	178	0.09	0.215	177	0.26	0.101	–	–	–
	O	Mound	**156**	**0.31**	**0.016**	159	0.32	0.052	–	–	–
	Au	Pit	213	0.13	0.142	**204**	**0.54**	**0.003**	**200**	**0.41**	**0.004**
	Au	Mound	202	0.06	0.332	205	0.06	0.635	–	–	–
	Bvs	Mound	**133**	**0.81**	**< 0.001**	**129**	**0.91**	**< 0.001**	–	–	–
Michigan, Albic Podzols	O	Pit	134	0.22	0.089	137	0.26	0.188	–	–	–
	O	Mound	116	0.21	0.103	**115**	**0.44**	**0.043**	**111**	**0.40**	**0.024**
	Au	Pit	98	0.04	0.513	99	0.19	0.322	97	0.14	0.119
	Au	Mound	92	0.20	0.103	93	0.30	0.138	**80**	**0.43**	**0.031**
	Ep	Pit	**170**	**0.42**	**0.013**	169	0.54	0.014	–	–	–
	Ep	Mound	**145**	**0.42**	**0.013**	146	0.51	0.020	–	–	–
	Bhs	Pit	**179**	**0.35**	**0.013**	181	0.40	0.061	171	0.34	0.056
	Bhs	Mound	**132**	**0.51**	**0.002**	134	0.57	0.004	–	–	–

Statistically significant models ($\alpha = 0.05$) are in bold; bold for quadratic models only where the quadratic component added additional significance; dash – hyperbolic model could not be fitted because of zero values in the response variable; for horizon codes see Table 2.

markedly positive at $time_{zero}$ (Figures 8d, 10d, 10f). This finding suggests that the initial development of the given horizon was non-linear; horizons began to form quickly after the disturbance event and the rate of development slowed with time. Alternatively, some soil characteristics associated with the pit soils, as in the B horizon, were not completely re-set by the disturbance event.

In contrast, the extrapolated chronofunction model for several mounds showed negative intercepts at $time_{zero}$ (Figures 8c, 10e). This suggests that the onset of pedogenic horizonation was delayed, with for instance some acidification required before chelation, or the formation of a loose Bs horizon before the development of a Bhs. (Franzmeier & Whiteside, 1963). No one chronofunction model worked best for both pit and mound soils at any site, with various models best for similar horizons in different microsites, and others for different horizons at one type of microsite.

Mathematical models were not statistically significant at $\alpha = 0.05$ for some O and A horizons in both pits and mounds (Table 3), mostly in Entic Podzols, as these have O and A horizons of variable thicknesses, even in the reference profiles (Šamonil *et al.,* 2011). Local variability of O and A horizons within pits and mounds was common and did not increase with time. Instead, increased variation with time was observed in the successfully-modelled E and Bhs horizons on Albic Podzols (Figure 10), the chronofunctions of which required widening confidence intervals with time.

All of the best-fit chronofunctions exhibited positive slopes, indicative of progressive increasing soil horizon and profile thicknesses after uprooting for soils in both pits and mounds, which suggests that pedogenic processes are not easily reversible. This trend was especially apparent in the Albic Podzols (Figure 10a–f). Mineral horizon thinning occurred in Entic Podzols, but only rarely, and not at all in Haplic Cambisols and Albic Podzols (Figures 8–10).

Chronofunctions indicated that Michigan Albic Podzol E and Bhs horizons thickened faster in pits than on mounds (Figure 10c–f). Differences in E horizon development between mounds and pits, as indicated by thickness, was only just significant ($P = 0.08$). Increasing pedogenic differences between soil development in pits and in mounds over time show that uprooting and the subsequent micro-topography affected the rates of pedogenesis at a pedon-to-pedon scale. We did not observe similar trends at the Czech sites, the chronofunctions of which suggested ambiguous or convergent trajectories of pedogenic development in pits and mounds (Figures 8, 9).

Rates of pedogenesis

We used the chronofunctions to estimate how long it would take for horizon thicknesses in pit and mound microsites to match those in the adjacent reference pedons (Figures 8–10). Pedogenic development in pits was considerably faster than on mounds. The O horizons in pits on Haplic Cambisols reached the average reference pedon thickness after only 5 years, whereas on mounds an equivalent thickness was achieved after about 150 years (Figure 8a,b). The more rapid thickening in pits is because in these micro-topographic low areas litter can accumulate as it washes or is blown in. Litter in pits also decays more slowly because of cooler and moister conditions and thicker snow cover.

Similarly, A horizons in Haplic Cambisol pits were as thick as in undisturbed reference pedons after only 75 years (Figure 8d). On mounds the equivalent development period was about 160 years

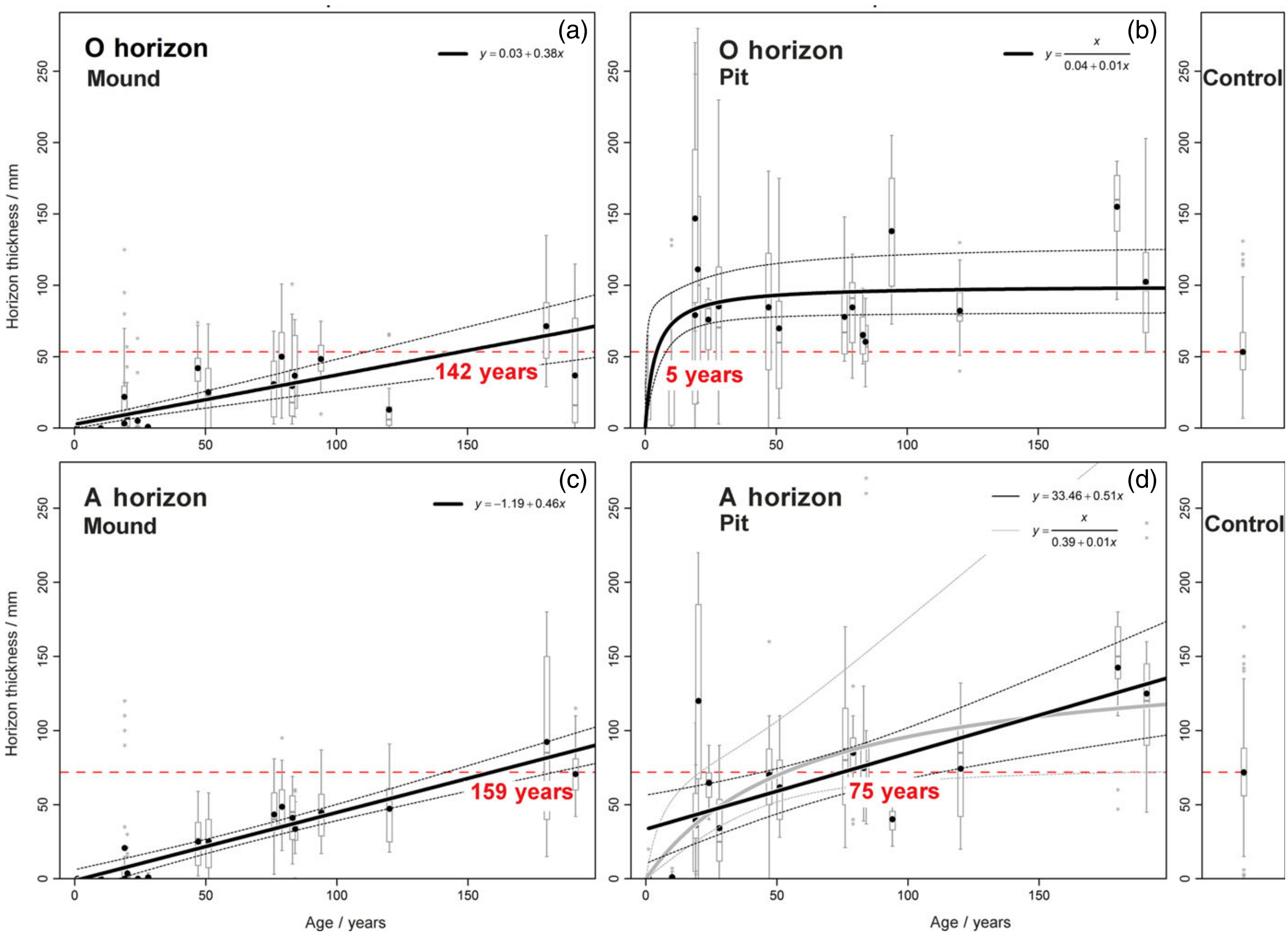

Figure 8 Boxplots of O (a,b) and A (c,d) horizon thickness chronofunctions on Haplic Cambisols at Razula, with the middle 50% in box, whiskers extending over the remainder of the data range and outliers as stars. Means are represented by circles; medians by thick lines. Each boxplot represents one pit or mound; the means for the aggregated reference pedons are red dashed lines. Where the chronofunction is statistically significant, the best model is a solid black line with the 95% confidence intervals as dashed lines; the second best is solid grey. The best model equation uses AICc for evaluation. The red dashed line is the corresponding mean thickness in undisturbed reference profiles, with the time required for the best model to match them shown in red.

(Figure 8c). The A horizon thickness was connected most closely with age ($R^2 = 0.9$) on Haplic Cambisol mounds. The A horizon development on Albic Podzols was the slowest and on mounds it reached the same thickness as on undisturbed positions after about 240 years (Figure 10b). On Entic Podzols, modelling of A horizon thickness was successful only for the pit soils, where it reached the value of the control pedons after about 45 years (Figure 9a).

The chronofunctions for both pit and mound sites confirmed that development of E and B horizons was slower than for O or A horizons. On Entic Podzols, the B horizons in mounds had reached the average thickness of the undisturbed pedons after about 590 years (Figure 9b). The Bhs horizons in mounds (as well as the O and E horizons) in the Albic Podzols (Michigan site) never reached the thicknesses observed in the reference pedons throughout the entire > 6000-year chronosequence. In these soils the chronofunction model for E and Bhs horizons on mounds extrapolated to reference pedon thicknesses after more than 16 500 and more than 12 700 years, respectively (Figure 10c,e). These data reflect not only the slower development of mound soils in general, but also the fact that Bhs horizons take thousands of years to form, even in undisturbed soils. In contrast, the corresponding E and Bhs horizons in the pits were extrapolated to the reference soil thicknesses after only about 4500 and 3000 years, respectively (Figure 10d,f). Although the chronofunctions indicated an initial lag in Bhs development, it was then faster than for the E horizons in both pits and mounds.

Discussion

Pedogenesis on tree-throw pit-mounds

Morphological features of soils have long been a valuable source of information about the effects of uprooting on pedogenesis (Schaetzl, 1986, 1990; Bormann *et al.*, 1995). With only a few exceptions (Vassenev & Targulian, 1995), the earlier studies

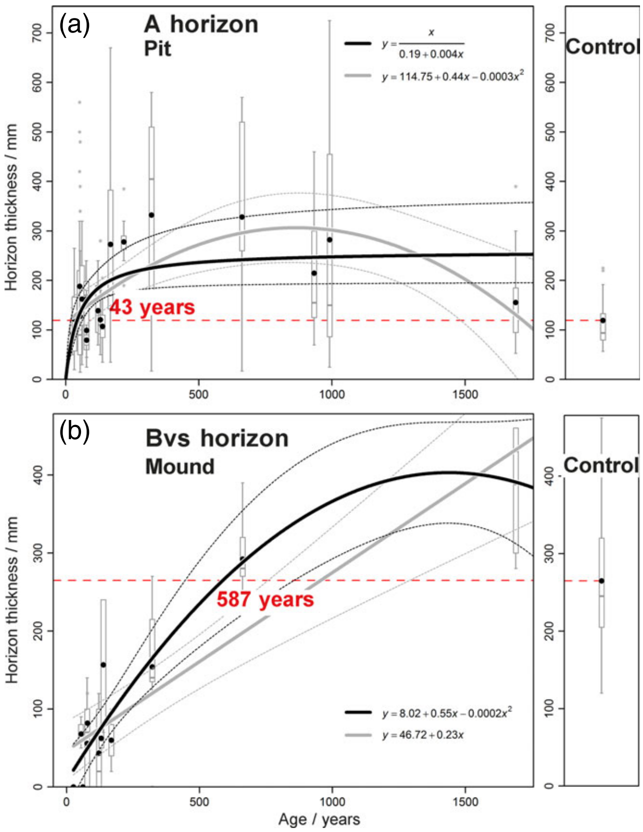

Figure 9 Boxplots of A (a) and Bvs (b) horizon thickness chronofunctions for pits and mounds on Entic Podzols at the Zofin site. For details see Figure 8 and Table 2.

focused on single sites, and few compared the effects of uprooting on and pedogenesis between different regions. These limited data suggest that it is difficult to generalize about the effects of pedoturbation on pedogenesis. Our own earlier studies suggest that conclusions based on Albic Podzols are not readily transferable to regions with different pedogenic regimes (Šamonil *et al*., 2010a,2010b).

Most of the earlier studies lack precise dates for the uprooting events (Veneman *et al*., 1984; Bormann *et al.,* 1995). Many also assume linear rates of post-uprooting pedogenesis. Although often satisfactory, the automatic assumption of linearity for soil development can be misleading (Schaetzl *et al*., 1994). Linear models may underestimate regressive elements in pedogenesis (Johnson *et al*., 1990) and fail to account for the general complexity of pedogenesis.

However, earlier studies within the Albic Podzol region of Michigan have shown that rapid soil development occurs in pits, but that pedogenesis is slower on mounds (Schaetzl, 1990; Šamonil *et al*., 2010a). Four thousand to 10 000 years are required for the development of a spodic (roughly comparable to a Bhs) horizon on level ground in the USA and Canada (see Franzmeier & Whiteside, 1963; Barrett & Schaetzl, 1992). Our results show how variable estimates of these rates become when micro-topographic effects are factored in. Uprooting microsites within a given landscape not only have widely varying rates of pedogenesis, but also different time$_{zero}$. Pit-mound pairs can occur within a metre or two of each other, cumulatively leading to much small-scale spatial variability. Uprooting micro-topography both resets the pedogenic clock and mediates rates of post-disturbance pedogenesis (Phillips, 2013).

Albic Podzols in pits show rapid development, probably driven by large infiltration rates, resulting from deep snow, and because of the increased amounts of organic acids, because of the deeper thicker litter. Corresponding mound soils develop more slowly, again affected by the micro-topographic shape and form that sheds both water and litter, and because the micro-topographic upper components freeze in winter, leading to runoff in spring, and they therefore lose some water and litter (Schaetzl, 1990).

At most of our sites in Michigan and Zofin, unlike those studied by Veneman *et al.* (1984), pit-mound features > 500 years old do not have soil profile stratigraphy (horizon thicknesses and proportions) corresponding to those in undisturbed reference pedons. Our data from Michigan agree more with Bormann *et al.* (1995), who observed slow development of E horizons on tree-throw mounds in Alaska. They observed 1.1-cm thick E horizons after 150 years and 2.1-cm thick E horizons after 350 years. According to Bormann *et al.* (1995), the Bhs horizon was thicker (2.1 cm at 150 years and 3.8 cm at 350 years). The slower initial development of the mound Bhs horizon than of the E horizon in our results may be related to the deposition of loose pre-disturbance Bs, Bw, BC or C horizon materials, which only later qualify as Bhs.

We usually observed increasing soil horizon thicknesses with time at all sites, pointing to progressive soil development (Johnson *et al*., 1990). Examples of thinning of soil horizons over time in our results were rare. Some authors (see Vassenev & Targulian, 1995; Šamonil *et al*., 2010a,b) have speculated from limited soil data about the possibilities of regressive development and suggest that pit O and A horizons may eventually become thinner as the uprooting micro-topography gradually becomes levelled, thus eliminating the special pedogenic conditions in the pits. This idea was not generally supported by our chronofunctions.

We also note that if the lower boundary of the E (or any) horizon in a formerly disturbed or undisturbed microsite extends below the depth of rooting the probability of rejuvenation of these horizons through new uprooting is very small. Vassenev & Targulian (1995) concluded that soil horizon thicknesses will never approximate those of undisturbed control sites in large pit-mounds.

'Tonguing' of E and B horizons is a common morphologic feature below tree-throw pits (Figures 6, 7). Schaetzl (1990) described deep E and B horizon tongues in a tree-throw pit dated by ^{14}C to be 2010 ± 70 BP. Similar tongues had developed in tree-throw pits that were only 1000 years old. At our sites, we observed that tonguing markedly increases with time, leading to an increase in the variability of horizon thicknesses and boundary irregularities between microsites and with time. Increased horizon thickness variability with time was also described by Barrett & Schaetzl (1993) on undisturbed Albic Podzol sites, all at least 4000 years old.

Divergence increased between pits and mounds in the rates and degree of podzolization, as shown by the modelled horizon

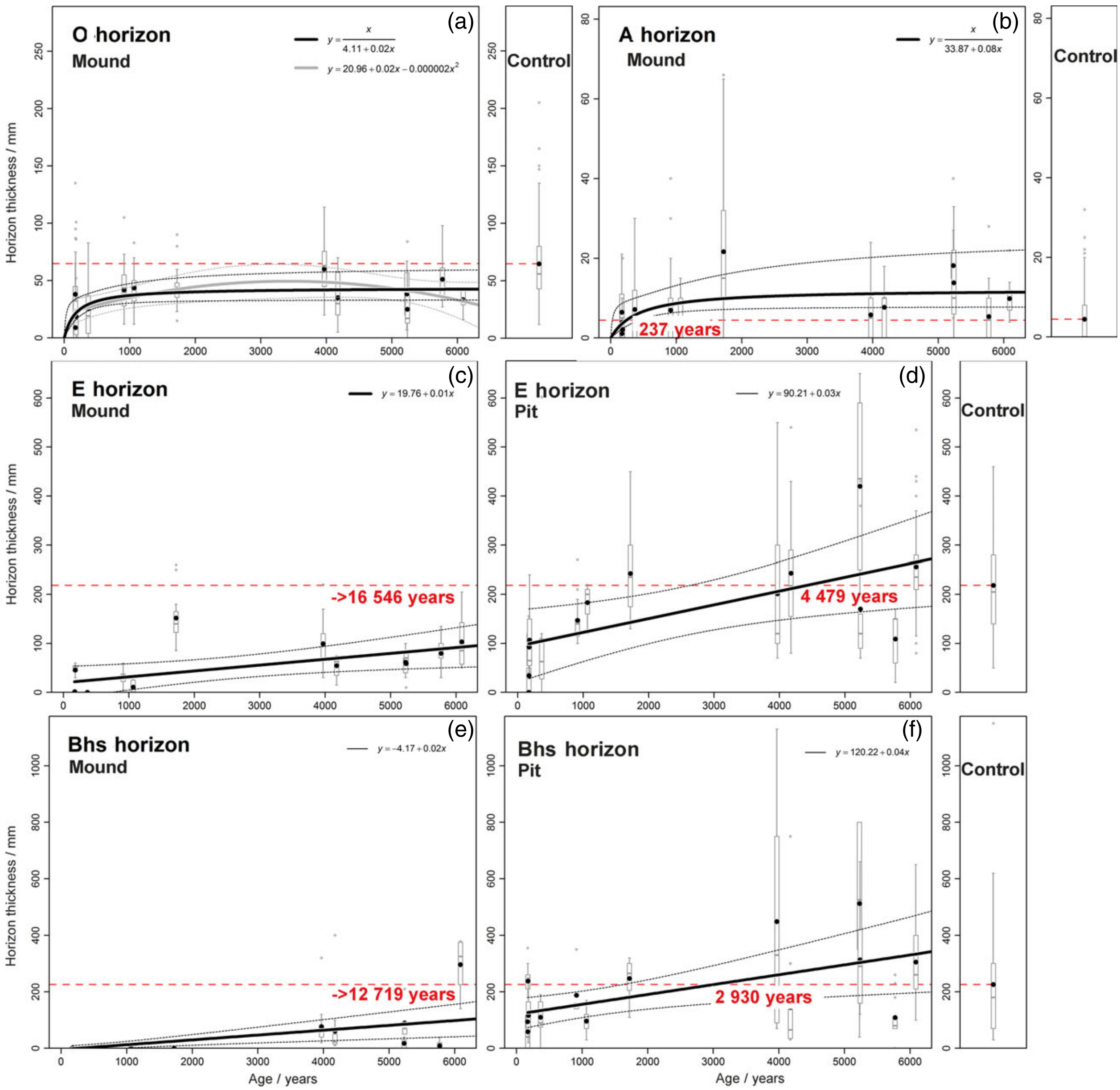

Figure 10 Boxplots of O (a), A (b), E (c,d) and Bhs (e,f) horizon thickness chronofunctions in Albic Podzols on the Michigan sites. For details see Figure 8 and Table 2.

thickness chronofunctions. This mediation of soil evolution by micro-topography (Phillips, 2001) should be confirmed by soil chemical characteristics (Myster & Malahy, 2008). This divergent development only operates at the spatial scale of tree-throw micro-topography (Lepš & Rejmánek, 1991).

Vassenev & Targulian (1995) observed rapid disintegration of the remains of the pre-uprooting illuvial (B) horizon in mounds. The rapid increase in the thickness of the new spodic horizon in mounds on our Entic Podzols, may relate to the disintegration of pre-uprooting soil structures. However, this contradicts Schaetzl's (1990) finding of slower weathering and formation of spodic horizons on Albic Podzol mounds. As noted earlier, our results may be obscured by difficulties in the differentiation of newly formed from pre-disturbance B horizons in mounds.

Our 'covert podzols' merit further attention, perhaps in relation to 'basket' or 'egg cup' podzols (Bloomfield, 1953; Schaetzl, 1990). The gradual decomposition of uprooted, and sometimes burnt, trunks, which are a source of organic acids for podzolization, may explain the larger proportion of C in illuvial horizons developed after disturbances in mountain podzolic soils in Alaska (Kramer *et al*., 2004). It may also be connected to the surprisingly large concentrations of C in mineral soils on tree-throw mounds (Liechty *et al*., 1997). Even charcoal is not entirely stable in soils; estimates place mean residence times at 3000–12 000 years (Preston &

Schmidt, 2006). Different forms of pyrogenic carbon originating during the fire event can also be the source of organic acids in the podzolization process (Haumaier & Zech, 1995; Preston & Schmidt, 2006) and thus it can facilitate the development of the buried soil. In addition to large localized variation in chelating capacity, podzolization processes can be locally intensified with extra percolation water. The sandy soil textures and deep snow cover at the Michigan site facilitate deep percolation and accelerate pedogenesis (Schaetzl & Isard, 1996). It appears that this effect can also penetrate into and through even a thick tree-throw mound (Figure 6).

The lack of significance of the regression models for five of the chronofunctions does not necessarily imply that these profiles have developed chaotically. Post-disturbance pedogenic development may be too complex for the models (Walker *et al*., 2010). The lack of significance for the Zofin model may be related to the exceptionally large local pedodiversity and soil variability (Šamonil *et al*., 2011, 2014). Pedodiversity and the formation of non-linear networks can limit the applicability of chronofunctions (Walker *et al*., 2010; Phillips, 2015).

Extrapolations from findings on the impact of tree-throw on soils from the pit-mound scale to stands and landscapes are difficult and may conclude that the overall effect of uprooting is to rejuvenate soils of the whole landscape, although in a piecemeal fashion, and thus inhibit soil formation from achieving some sort of terminal stage (Bormann *et al*., 1995). This interpretation is complicated by the non-random occurrences of new disturbances, which are least probable in pits (Šebková *et al*., 2012). Soils in pits may develop to such a point, and so rapidly, that future disturbances cannot obliterate them, because the bottoms of the horizons extend below the depth of rooting. Thus, post-disturbance lower subsoil development in pits may be irreversible.

As well as effects on horizon development, uprooting also affects soil thickness by the lateral transfer of soil and regolith material from pit to mound, obscuring the link between soil depth and topography (Gabet & Mudd, 2010). In lithic soils, weathering and pedogenesis can be locally stimulated and mineral nutrients replenished by the excavation and subsequent weathering of fresh bedrock (Phillips *et al*., 2005).

Methodological issues

Several studies have documented the thick accumulation of organic matter in tree-throw pits and the rapid pedogenesis that it facilitates (Schaetzl, 1990; Šamonil *et al*., 2010a). However, few have paid equal attention to the newly formed soils in mounds. By studying the generally slower and divergent soil development in mounds, a more complete picture emerges of the pedogenic effects of uprooting and the consequent pit-mound topography.

However, the assessment of soil development in mounds is difficult because mound soil materials have a history of previous pedogenesis. Therefore, sampling mound tops must take into account the pedoturbation process and origin of soil material. Our recommendation is to study soil morphology within entire mounds and to sample where post-disturbance pedogenesis is most visible (uplifted substratum material), even if this is not the mound summit.

We dated material from sediments in the narrow funnels in the pits of very old tree-throws on Entic Podzols. The intersection of the funnel with the organically poor BC and C horizons in some profiles made the application of ^{210}Pb and ^{14}C dating easier, especially on the pit face opposite the mound (position C in Figure 3). However, there is still a possibility of contamination by extraneous material. In sandy sediments, the measuring of magnetic susceptibility may facilitate the location of a transition zone between disturbed soils and underlying soil material not affected by tree-throw.

Supporting Information

The following supporting information is available in the online version of this article:

Figure S1. Albic Podzol pit-mound profile older than 5200 years. Note the thick E and B horizons in the pit, the thin, new E and Bhs horizons in the mound, and the covert E horizon in the buried soil beneath the mound.

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