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Converse pathways of soil evolution caused by tree uprooting: A synthesis from three regions with varying soil formation processes

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ABSTRACT

Post-disturbance pedogenetic pathways were characterized in three landscapes representing different degrees of weathering and leaching. Tree uprooting has been the main form of disturbance in all three landscapes. We hypothesized that the pedogenetic effect of trees due to uprooting is mainly governed by the regional degree of pedogenesis, which in turn affects soil and landscape evolution.

The three regions were characterized by a chronosequence of treethrow pit-mound pairs, from fresh to almost leveled forms. Two sequences originated from the Czech Republic, one on Haplic Cambisols and one on Entic Podzols. The third and the oldest chronosequence, in Michigan, USA, was on Albic Podzols (dating back to 4080 BCE). We analyzed 38 chemical and physical soil properties for 700 samples from 42 pit-mound pairs in these regions. Ordination and regression techniques allowed us to evaluate the effect of sample depth, microsite (pit, mound, and undisturbed control position), and age of the soils formed after uprooting.

Depth was the most significant variable in all regions ($p < 0.001$), followed by microsite location, and then age (time since disturbance). The significance of these variables decreased with increasing weathering and leaching intensity. The results suggest that intense pedogenesis, as at the Michigan site, decreases the polygenetic impacts of uprooting on soil development pathways. On Haplic Cambisols, disturbances increased the local variability of pedogenic processes by changing melanization and hydromorphic processes, as well as by mineral alteration. Conversely, on Albic Podzols, we found comparative chemical uniformity in post-uprooting pedogenesis between microsites, despite rapid podzolization in pits and slower podzolization on mounds. The general chemical convergence of pedogenesis in these landscapes towards vertically-dominated podzolization may limit divergence of pedogenic pathways after a disturbance. The formation and translocation of labile organic matter-sesquioxide complexes in the uppermost podzolic horizons in Entic Podzolś was a key threshold, in that it changed the pedochemical, ecological and biogeomorphic role of the treethrow features in the soil and landscape evolution. Although treethrow pits were accumulation sites for soil elements in Haplic Cambisols and Entic Podzols, they were microsites of intense leaching and elemental loss in Albic Podzols.

1. Introduction

Tree uprooting is the most evident and significant biogeomorphic disturbance agent in many forest soils (Fig. 1, Schaetzl et al., 1989; Phillips and Marion, 2006; Pawlik et al., 2016a). For example, in temperate, central European, primeval forests approximately 30% of all trees die as a result of uprooting, and theoretically, within 500–3000 years every site in such forests is likely to be disturbed by uprooting (e.g., Skvorcova et al., 1983). So-called rotation periods, showing how often an area equivalent to an entire area is disturbed (Pickett and White, 1985), are comparable or even shorter in other temperate or boreal forests (review by Šamonil et al., 2010a).

From a general theoretical perspective, biomechanical soil disturbances are an important source of the kind of local, transient changes that are usually associated with deterministic chaos. A self-organizing, chaotic, and unpredictable mode of soil behavior may be a substantial component of the usually-assumed non-chaotic mode (Walker et al., 2010; Phillips, 2013c). Both chaotic and non-chaotic modes contribute soil evolution on all scales, but their individual effects are little known. Focusing on non-chaotic soil behavior in experiments,

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Fig. 1. An extremely large, complex root plate formed by uprooting on Entic Podzols during the Kyrill storm in Zofin, Czech Republic, in 2007. Tape represents 1 m. Photo by Pavel Šamonil.

mathematical models and interpretations can result in simplifications or even false results in soil and biogeomorphic studies (see Peckham, 2009). The predominance of a self-organizing component in the evolution of a soil landscape leading to divergent evolution is the most evident such example (Phillips, 1993), which represents a converse direction and an important alternative to the traditionally-assumed convergent evolution (see Phillips, 2001). Although differences in initial conditions and local perturbations are gradually smoothed in convergent evolution, leading to decreased soil spatial variability, differences nonetheless persist and can even increase, producing a more variable soil cover; this is one example of divergent soil evolution. In any case, when pedogenesis is dynamically unstable and chaotic, the effects of small disturbances such as those associated with pedologic influences of individual trees become exaggerated over time (Phillips, 2000, 2013a, 2013b; Toomanian et al., 2006; Milan et al., 2009; Borujeni et al., 2010; Phillips and Van Dyke, 2016). Using pedomorphology data, Šamonil et al. (2015) found possible divergent soil evolution after tree uprooting in Albic Podzols, wheres other soil units expressed different post-disturbance evolutionary pathways. These findings suggest a regionally-specific role of tree uprooting in pedogenesis, although the direction of post-uprooting erosion-sedimentation processes and the specifics of microclimate within treethrow pits and mounds seem to be universal (the mound is generally drier, has a higher radiation balance and a wider amplitude of temperature with comparison to the pit, see Beatty and Stone, 1986). However, such pedomorphic results only minimally inform us about complex soil formation processes, and need to be validated by pedochemical analyses. Datasets from different soil regions can fundamentally help improve still-unsupported theoretical derivations regarding the switching of soil behavior modes on pedon scales, the role of deterministic chaos, and the directions of post-disturbance evolutionary trajectories in soils.

Most of the case studies on uprooting so far have focused on Spodosols, and most of the research has been on single sites in the US, Canada and Russia (Skvorcova and Ulanova, 1977; Schaetzl, 1990; Small et al., 1990; Bormann et al., 1995; Kramer et al., 2004). Only few such studies are truly comparative, using pedochemical data from different soil regions (Skvorcova et al., 1983; Vassenev and Targulian, 1995). Nonetheless, these studies suffer from a relatively low amount of data and inaccurate (or lack of) dating of uprooting events. These geographical and methodological limitations fundamentally reduce our ability to study post-disturbance pedogenetical pathways and do little to help derive conceptual generalities regarding the effect of uprooting disturbances on pedogenesis and eco-evolution dynamics (Corenblit et al., 2011; Pawlik et al., 2016b). Here, we focus on this still unsolved issue and compare the pedogenetic impacts of uprooting on dated chronosequences from multiple landscapes.

Our primary hypothesis is that trees do not affect pedogenesis through uprooting in a universal way, but rather various or even opposing post-disturbance evolutionary trajectories can arise, depending on the intensity of regional soil evolution processes. This hypothetically causes regionally-specific feedbacks in the tree-soil coevolution system (see Šamonil et al., 2014). The specific purposes of this study are to evaluate the effects of sample depth, microsite (pit, mound, and undisturbed control position), and age of soils since tree uprooting in three different soil regions. Using these data, we aim to build a general conceptual model of post-uprooting pedogenetical pathways. This model is made possible by existing tree uprooting research performed in three soil regions, where since 2006 (regions of Haplic Cambisols, Entic Podzols and Albic Podzols) we precisely dated a number of uprooting events (Šamonil et al., 2009, 2013), studied the formation of the forest floor on treethrow microsites (Šamonil et al., 2008a, 2008b), and assessed pedomorphic (Šamonil et al., 2015), biogemorphic (Šamonil et al., 2016; Phillips et al., 2017), and limited pedochemical processes (standard laboratory extract methods used solely on Haplic Cambisols by Šamonil et al., 2010b in studies of post-uprooting pedogenesiswere deepen using voltammetry of microparticles and diffuse reflectance spectroscopy by Tejnecký et al. (2015). These modern methods allowed us to develop a much deeper understanding of composition of mixed chemical extracts of Al, Fe, Si, and Mn).

2. Materials and methods

2.1. Study sites

Our three soil regions are in the Czech Republic (CR)–the Razula and Zofin forest reserves–and the Upper Peninsula of Michigan, USA (Fig. 2 and Table 1). The regions all have humid climates, and together they roughly span a gradient of texture and intensity of pedogenesis (see von Zezscheitz et al., 1973), with (1) strongly weathered, leached and acidic Albic Podzols on pure sandy outwash in Michigan (2) intermediate severity of podzolization, including clay destruction, on acidic Entic Podzols on loamy sand granite residuum at Zofin, and (3) clay formation without its destruction on Haplic Cambisols (Michéli et al., 2007) on loam or clay-loam flysch residuum at Razula (Fig. 3; Table 1) Precipitation decreases along this gradient. Mean slope inclination ranges from 8° (Zofin) to 19° (Razula). All forests are

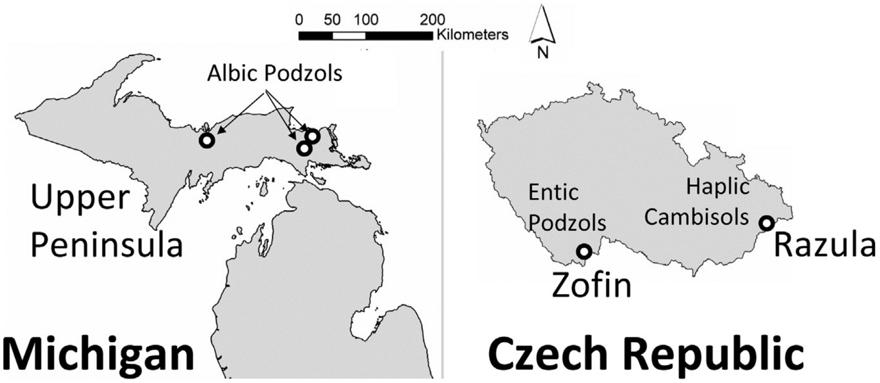

Fig. 2. Locations of the three study sites. For details see Table 1.

dominated by broadleaf species, specifically by *Fagus sylvatica* in both Czech sites and *Acer* spp. in Michigan (Table 1, Šamonil et al., 2011, 2016).

We examined soils within treethrow pits and on mounds at sites that represented the most typical soils of the region, avoiding wet (soil having hydromorphic properties or even stagnic, gleyic or histic horizons) and stony sites (classified according to Michéli et al., 2007 as Leptosols or Hyperskeletic, Leptic and Lithic Lower Soil Units of the other soils units). The gradient in clay content was associated with increasing activity of erosion and slope processes, and therefore with decreasing longevity of treethrow pit-mound pairs (Šamonil et al., 2015; Table 1).

Tree uprooting has been common in the recent past at all three study sites (Šamonil et al., 2011, 2016; Phillips et al., 2017). Other disturbance agents, such as fire in Michigan and mammalian burrowing (wild boar or woodchuck) are uncommon but worthy of mention here. Data were collected in Michigan in managed forests that were last selectively cut at least 40 years ago. The core zone of Zofin reserve has never been cut and has been under protection since 1838. The old-growth forest at Razula has been under protection since 1933, but was affected by infrequent selective cutting and grazing prior to that time (Table 1). We selected these sites as representative of the natural picture of local post-disturbance pedogenesis.

2.2. Dating of uprooting events

In total, 1562 (Razula) and 1733 (Zofin) pit-mound pairs were studied in terms of their dimensions, morphology, degree of trunk decay (where applicable), and organic horizon characteristics (Šamonil et al., 2009, 2014). Subsets of these were selected for dating using stratified random techniques. In Michigan, we used a more subjective technique for selection of 70 pit-mound sites to study and date. We applied our self-named "cross dating" procedure to establish the ages of the uprooting events. This method integrates dendrochronological, tree census and radiometric (isotopes ^{137}Cs, ^{210}Pb, ^{226}Ra, ^{14}C) techniques to establish the ages of pit-mound pairs, and hence, the age of the treethrow event. In all, we dated 178 treethrow pit-mound pairs in Zofin, 37 in Razula, and 14 in Michigan. Dating techniques as well as the results are described in detail by Šamonil et al. (2009, 2013).

2.3. Soil selection and characterization

Soil data were collected for 14 of the most precisely dated pit-mound pairs of different age in each region (42 total). These sites represent three rough chronosequences, one on Haplic Cambisols (from 1988 to 1816 CE), one on Entic Podzols (from 1979 to circa 320 CE), and one on Albic Podzols (from 1842 CE to circa 4080 BCE). The morphology of the soils in all of the 42 uprooting features were described from ca 1.5 m deep and 0.6 m wide trenches along the axis of the pit-mound pair (profile A in Fig. 4; Šamonil et al., 2015). Although treethrow pit–mounds were oriented in a multitude of directions, relative to slope inclination, downslope orientation predominated. The control profiles occurred on the same landscape position as did the relevant disturbed profiles. The selected control areas did not express footprints of former disturbance (although we assumed that the control profiles could have been disturbed in deep past). We sampled all soil horizons at depths of 5, 15, 30, 50, and 100 cm directly in excavated trenches, in addition to other horizons occurring between these depths

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

Feature/locality	Razula	Zofin	Upper Peninsula
Soil taxonomy (WRB 2007)	Haplic Cambisols	Entic Podzols	Albic Podzols
Parent material	Flysch	Granite	Outwash
Location (Lat., Long.) (°)	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-H_2O) in B horizon ± 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)	130.7 ± 38.3 (23)	65.6 ± 17.9 (14)	40.9 ± 11.8 (17)
Soil texture fraction < 0.01 mm in B horizon (%) ± SD (n)	34.2 ± 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, Abies alba*	*Fagus sylvatica, Picea abies, Abies alba*	*Acer saccharum, A. pensylvanicum, A. rubrum, Quercus rubra, Tsuga canadensis, 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) (Šamonil et al., 2013)	220	1690	6183

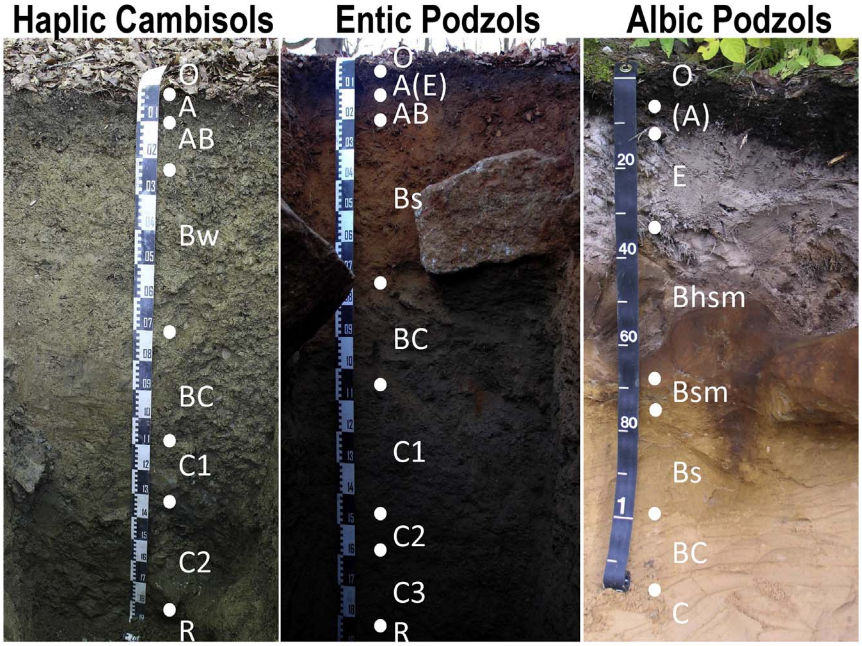

Fig. 3. Typical (control) soil profiles at each of the three study sites. Descriptions of upper organic horizons were made according to Klinka et al. (1997). Mineral horizons were described according to Němeček et al. (2011) and Michéli et al. (2007).

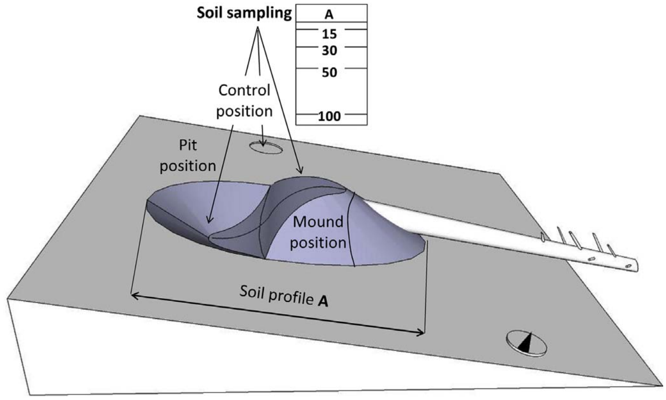

Fig. 4. A schematic treethrow pit-mound pair still with uprooted trunk, with locations of sampled profiles on microsites – pit, mound, and undisturbed control.

in their specific position in the trench, across the three microsites (pit, mound, undisturbed reference pedon). In total, 700 soil samples were sampled and analyzed for standard chemical and physical characteristics. We chose these analyses to characterize the dominant pedogenic processes in these soils: transformation and translocation of organic compounds (humification, melanization etc.); weathering and leaching processes (formation and alteration of minerals, clay illuviation, podzolization, etc.); and oxidation-reduction processes.

All soil samples were analyzed according to the procedures outlined in Zbíral (2002, 2003) and Zbíral et al. (2004): exchange soil reaction (pH-KCl) – 0.2 M KCl; active soil reaction (pH-H_2O); color quotient (Q4/6) – calculated using the equation Q4/6 = E465/E665, where E465 and E665 are the extinctions (0.05 M $Na_4P_2O_7$ extract) at wavelengths 465 and 665 nm (Chen et al., 1977); total organic C (Cox) – spectrophotometric approach after oxidation by $H_2SO_4 + K_2Cr_2O_7$ according to ISO (1995); C content in total humic substances (C–THS), and separately in humic acids (C–HA) and in fulvic acids (C–FA) – all in $Na_4P_2O_7$; total N content according to Kjeldahl (Bremner, 1996); exchangeable Ca^{2+}, Mg^{2+}, K^+, Na^+, exchangeable acidity (Al + H) and effective cation exchange capacity (CEC) – all according to Gillman (Gillman and Sumpter, 1986; $BaCl_2$-compulsive exchange procedure, native pH); and particle-size distribution according to Casagrande (Bernhardt, 1994). Concentrations of elements in the various liquid extracts were measured using an atomic absorption spectrophotometer (GBC 932 AB Plus) and with a Specol 221 UV/VIS spectrophotometer.

The contents of crystalline, amorphous and labile Fe, Al, Mn and Si forms were determined for all samples by simple extraction methods. Although the extracted forms of Fe and Al can be classified into these three forms (Courchesne and Turmel, 2008), for Mn and Si, this division is less clear (Guest et al., 2002).

i. The contents of reactive-exchangeable and weakly organics bond forms (Fe_k, Al_k, Mn_k, Si_k) were determined by using 0.5 M KCl (37.27 g l^{-1}) (1:10, *v*/*w*), according to Drábek et al. (2003, 2005).
ii. The contents of sum of exchangeable, organic and particularly amorphous forms and organic complexes (Fe_{ox}, Al_{ox}, Mn_{ox}, Si_{ox}) were determined with acid ammonium oxalate, according to Courchesne and Turmel (2008), with 0.2 M of ammonium oxalate at pH 3 (at a ratio of 0.25:10, *w*/*v*).
iii. The contents of sum of exchangeable, organic, amorphous and mainly crystalline forms (Fe_d, Al_d, Mn_d, Si_d) were determined by extraction with a dithionite–citrate solution (DC) (McKeague et al., 1971) at a ratio of 0.5:25 (*w*/*v*), according to Courchesne and Turmel (2008).

Tejnecký et al. (2015) examined in detail the mineralogy of these extracts using voltammetry of microparticles and diffuse reflectance spectroscopy and Šamonil et al. (2010b) published local pedochemical data regarding uprooted Cambisols. The data from Zofin and Michigan, as well as summary syntheses and the conceptual model, have not been published previously.

2.4. *Data analysis*

Using soil data from the 42 treethrow sites we assessed the importance of three characteristics on soil development: (i) depth, (ii) age (after disturbance by tree uprooting), and (iii) microsite location (pit, mound, undisturbed, i.e. control position), using a set of redundancy analyses (RDA), separately for each region. Because the age of the soils sampled at the currently undisturbed (control) microsites is unknown, and soils here are always older than those on the pit-mound pair itself, only the data from pits and mounds were used when examining the effects of age. This approach resulted in two kinds of analyses (with and without data from controls).

In each RDA, one of these three characteristics was used as explanatory variable; the remaining two (or one) were included as covariates. In addition, the effect of age, together with its interactions with both sampling depth and microsite, were analyzed with the net effect of these two variables partialled out. We did not include control profiles in these calculations, as explained above. Response (dependent) variables in all RDAs were the 32 measured physical and chemical soil properties. The explained variation was computed using permutationally adjusted R^2 (Peres-Neto et al., 2006) based on 10,000 permutations. To avoid possible problems with autocorrelation of data from the same microsite and within a pit–mound pair, we used a three-level hierarchical block randomization scheme, respecting the autocorrelation resulting from sampling design (Manly, 2006). Microsite blocks containing data from individual pits or mounds (or controls) were nested in pit–mound blocks and randomizations were only allowed to occur within each level of hierarchy. This permutation scheme ensured that potential autocorrelation affected also null distributions of test statistics derived from the randomized data which prevented the occurrence of falsely significant results (particularly in age-related analyses).

We also studied the relationship between individual soil properties and the three variables used in the RDA (depth, age and microsite). Using generalized linear models (GLM) with gaussian and gamma distributions, we started with a full model including all three explanatory variables and all their interactions. Two variants were fitted, with sampling depth added as either a linear or quadratic term. The model was then reduced by backwards selection, dropping non-significant terms ($\alpha = 0.05$) with the highest p values one at a time, until only significant terms remained. The structure of the residuals from this analysis was then inspected, and from the models that were satisfactory in this respect, the final one was chosen using AIC. As in the case of RDA, the autocorrelation within microsites on individual pit–mound pairs had to be taken into account, and the significance of individual terms was tested using the same randomization scheme as described above. All analyses were performed in R (R Core Team, 2015).

3. Results and discussion

3.1. Soil forming processes and differences between soil regions

Data from chemical and physical laboratory analyses confirmed that weathering and leaching processes are following traditional podzolization pathways at the Zofin and Michigan sites (Table 2, Figs. 3, 5). According to the fulvate-complex theory of podzolization (McKeague et al., 1978; Buurman, 1984; Lundström et al., 2000; Buurman and Jongmans, 2005) unsaturated organo-metallic complexes are formed in litter on the forest floor (O and A horizons) and subsequently mobilized and precipitated in the B (spodic) horizon upon saturation of organic molecules through metal complexation (see forms of Fe, Al and C in Fig. 5). In such soils, high acidities often lead to clay destruction as well (Schaetzl and Thompson, 2015). Alternatively, in the finer-textured soils at the Razula site, secondary (clay) mineral formation pathways are also operating (Table 2, Tejnecký et al., 2015). As expected, terrain pedomorphology (see Šamonil et al., 2015) as well as soil analyses showed evidence of clay translocation at the Razula, as argillans on peds and as clay-enriched B horizons. Melanization and hydromorphic (redox) processes were also observed in disturbed and control undisturbed microsites as well, particularly in Razula. These processes were supported by occurrence of cambic Bwg horizon with stagnic properties in some pits (e.g. Table 2), unimodal development of total organic carbon within the pit (Fig. 5), direction of C and Mn forms to the pit (Fig. 7) as well as by former findings of Šamonil et al. (Šamonil et al., 2010b, 2015) and Tejnecký et al. (2015).

Contrary to our expectations, active as well as exchangeable soil reactions were both higher in the Albic Podzols (range of pH-H_2O = 4.1–6.3) than the Entic Podzols (range of pH-H_2O = 3.6–5.0, see also Table 1). This difference can be partly elucidated by significantly higher cation exchange capacities (up to 250 mmol$^+$/kg) and organic matter contents in the Entic Podzols. The higher CEC in Entic Podzols was naturally accompanied by increased exchangeable acidities, as well as H^+ concentrations. Higher amounts of organic matter frequently support soil acidification and some of this effect can be also due to the different vegetation covers of the three forest ecosystems.

Although CEC and pH were mutually positively correlated in the Cambisols at Razula, similar correlations were negative for Podzols. The negative correlations may have been caused by the formation of organo-mineral complexes between soil organic matter and short-range order Al and Fe phases (Fe_{ox}, Al_{ox}, see Grand and Lavkulich, 2013). Organo-mineral complexes, together with organic compounds, represented the main components of cation exchange capacity on Entic and Albic Podzols. Therefore amount of carbon, and its forms and complexes were strongly correlated with CEC (Figs. 6, 7, Table 2, see Grand and Lavkulich, 2013). Although complexation of organic matter with metallic compounds can also have significant podzolization potential in Cambisols (Titeux et al., 2002), it was only minimally present in our profiles, through the translocation of organic carbon (Cox), and specially fulvic acids (C-FA), in older treethrow pits. Cation exchange capacities were probably preferentially driven by clay contents (Table 1, Šamonil et al., 2010b), although the role of organic matter cannot be considered negligible (e.g. Gruba and Mulder, 2015) in the Haplic Cambisols (Fig. 5-7).

Contents of amorphous and crystalline forms of Fe and Al and their organic complexes were significantly lower in B horizons of Albic Podzols than in Haplic Cambisols, and particularly in Entic Podzols – despite the intense podzolization at the Michigan site (Table 2, Fig. 3, Šamonil et al., 2015; Schaetzl et al., 2015; Schaetzl and Rothstein, 2016). This relationship can be attributed to significantly lower concentrations of Al and Fe in the quartz-rich outwash parent materials in Michigan. Contents of **organic C** and its specific forms (C-HA, C-FA) were the highest on Entic Podzols (Table 2, Fig. 5). The results of laboratory analyses show that Albic Podzols on outwash had significantly lower buffer potential and relatively low amounts of fulvic acids, but, obviously, in sufficient amounts to initiate illuviation of labile organic matter-sesquioxide complexes. A similar observation was made by Stützer (1999) in shallow podzolic soils in mountain areas. Relatively low buffering capacity of soil on outwash is reflected in relatively rapid post-disturbance pedogenesis, as observed by Schaetzl (1986) and Šamonil et al. (2015) (see review by Lundström et al., 2000).

3.2. Role of sample depth in soil data

Sample depth was the most important variable with respect to post-disturbance soil development ($p < 0.001$, Table 3); it was more significant than either age or microsite. Sample depth explained nearly 13% of the variability on Haplic Cambisols, and 14.9% on Entic Podzols. In the most podzolized region, on Albic Podzols, depth explained only 6.0% of the data variability. This lower proportion reflected the age-dependent deepening of unimodal (or bimodal) concentrations of the fractions of C, Al, Fe and Si from eluviation and illiviation of labile organo-mineral complexes (Fig. 5). These components reached their maximal concentrations in the mid-B horizon (Bhs, Bhsm, Fig. 5). Higher concentrations of amorphous and crystalline Fe in the uppermost horizons (Fe_{ox}, Fe_d in Fig. 5) within disturbed microsites on Albic Podzols showed repeated mobilization of these complexes after their former immobilization in pre-disturbance spodic horizons. Tanskanen and Ilvesniemi (2004) observed such re-precipitation of metallic complexes in soils disturbed by plowing. Tree uprooting has obviously had similar effects in these forested landscapes.

The **unimodal shapes of concentrations** of many soil properties in profiles resulted in their orthogonal relationship to sample depth and hence, the lack of linear statistical fit (Fig. 6). On the other hand, for the Haplic Cambisols the extensive sorption of C on particles of the clay-

Table 2
Examples of soil chemical and physical properties for disturbed and adjacent undisturbed soil profiles in the three soil regions.

Soil unit (locality)	Microsite and age (years)	Soil horizon	Sample depth (cm)	pH-KCl	Nt (%)	Cox (%)	C-HA/FA	Q4/6	CEC (mmol$^+$/kg)	Al + H (mmol$^+$/kg)	Ca^{2+} (mmol$^+$/kg)	Mg^{2+} (mmol$^+$/kg)	K$^+$ (mmol$^+$/kg)	Al$_k$ mg/kg
Haplic Cambisols (Razula)	Control	A	5	3.85	0.49	4.73	0.91	6.22	180.0	36.0	148.0	20.8	5.0	107.6
		AB	15	3.53	0.30	2.75	0.79	8.10	168.0	80.0	77.6	13.5	1.8	554.1
		Bw	30	3.67	0.22	2.13	1.25	7.59	165.0	40.0	126.0	19.0	2.7	441.9
		Bw	50	3.68	0.12	1.85	1.07	7.37	174.0	72.0	89.2	16.2	2.5	558.5
		(B)C	100	3.85	0.11	1.10	1.00	5.16	178.0	20.0	168.0	14.5	3.0	136.9
	Pit (192)	A	5	3.92	0.43	5.00	1.32	6.59	191.0	42.0	163.0	16.7	4.7	79.7
		AB	15	3.96	0.38	4.25	1.10	7.37	187.0	34.0	169.0	14.8	2.8	51.7
		Bw	30	4.10	0.34	3.83	1.00	6.01	178.0	22.0	175.0	15.1	2.7	32.2
		Bw(g)	50	4.69	0.21	3.23	1.07	6.49	183.0	24.0	167.0	18.7	3.6	97.3
		C	80	3.89	0.11	0.98	1.83	5.19	201.0	0.0	261.0	19.3	5.0	0.0
	Mound (192)	A	5	3.63	0.26	3.23	2.05	6.82	179.0	68.0	88.8	20.6	8.4	468.8
		AB	15	3.59	0.20	2.10	4.20	5.97	220.0	72.0	163.0	23.1	6.2	541.1
		Bw	30	3.67	0.13	1.60	4.78	5.72	245.0	36.0	259.0	27.6	5.6	222.1
		Bw	50	3.76	0.12	1.48	4.00	5.57	221.0	28.0	246.0	27.6	4.4	150.9
		C	100	3.56	0.12	1.43	1.22	5.82	193.0	60.0	135.0	29.8	4.1	471.6
Entic Podzols (Zofin)	Control	A	3	3.04	1.00	14.38	1.89	8.21	177.0	26.5	72.0	7.9	4.1	242.4
		A(E)	9	3.04	0.44	7.50	1.22	7.04	94.1	26.5	21.4	5.6	0.9	495.0
		(A)B	15	3.49	0.30	5.72	0.50	10.29	75.2	25.5	10.9	3.8	0.3	775.1
		Bs	30	3.96	0.14	3.32	0.35	9.94	43.6	13.8	9.8	4.5	0.9	500.1
		BC	50	4.22	0.10	1.08	0.38	9.38	41.6	4.6	6.0	2.7	0.3	198.3
		C	100	4.10	0.06	0.65	0.56	9.74	20.0	2.0	6.7	3.0	0.6	174.8
	Pit (991)	A	5	3.09	0.94	10.77	1.07	8.28	103.0	33.7	16.6	7.0	3.0	609.4
		A	15	3.40	0.74	10.29	0.95	8.30	107.0	33.7	15.0	5.4	1.9	751.0
		A(E)	30	3.42	0.64	8.95	0.81	7.49	84.5	30.6	9.8	4.3	0.9	741.7
		AB	50	3.78	0.22	4.38	0.60	8.15	62.9	20.9	7.7	3.7	1.0	684.1
		C	100	4.19	0.10	0.99	0.50	7.69	29.4	5.1	7.5	3.4	1.1	224.4
	Mound (991)	A	3	3.50	0.60	8.75	1.05	8.75	96.4	25.0	16.2	5.4	3.2	544.3
		Bs	15	4.05	0.18	1.83	0.44	8.44	32.2	10.7	5.8	3.0	1.0	384.8
		BC	30	4.28	0.11	1.59	0.33	9.24	34.5	6.6	7.8	3.1	0.8	215.5
		BC	50	4.31	0.07	0.55	0.43	6.57	23.1	4.6	6.6	3.2	1.0	174.1
		(B)C	100	4.35	0.05	0.55	0.39	7.56	17.7	4.6	5.5	3.1	1.0	146.3
		C	120	4.30	0.08	0.70	0.89	7.11	9.1	2.6	5.1	3.1	1.1	149.8
Albic Podzols (Michigan)	Control	E	5	3.43	0.04	0.63	1.20	4.53	29.0	10.0	8.8	3.6	0.5	18.1
		E	15	3.74	0.02	0.43	0.04	4.09	23.2	6.8	5.8	2.4	0.1	17.8
		Bhs	30	3.95	0.12	1.73	0.32	8.18	53.7	39.4	9.8	3.4	1.8	241.4
		Bhs	50	4.03	0.10	1.59	0.35	7.50	44.0	33.9	9.4	3.3	0.8	193.1
		Bs	100	4.74	0.04	0.24	0.10	6.50	29.9	6.8	6.4	2.6	0.7	16.2
	Pit (3969)	AE	5	3.71	0.04	1.15	1.38	4.01	23.4	6.6	7.2	3.2	0.9	11.5
		E	15	3.67	0.03	0.41	0.50	4.03	17.4	6.6	1.6	1.6	1.0	16.3
		E	30	3.63	0.03	0.34	0.57	4.14	44.5	7.6	2.4	1.8	0.9	31.1
		Bhs(m)	50	4.11	0.07	1.14	0.31	7.69	44.9	31.0	6.0	2.5	1.0	135.1
		Bhs(m)	100	4.30	0.05	0.88	0.37	8.11	41.7	28.6	3.0	1.8	0.9	108.5
	Mound (3969)	A(E)	5	3.50	0.05	0.70	1.03	4.80	29.4	15.2	2.6	1.2	0.8	34.5
		Bhs	15	3.99	0.07	1.25	0.46	8.34	55.8	37.2	10.2	3.0	0.8	165.6
		Bs	30	4.54	0.04	0.52	0.50	7.44	29.5	13.8	8.2	2.9	0.5	50.3
		Bs	50	4.60	0.03	0.71	0.40	6.39	27.4	11.6	8.2	3.1	0.6	39.1
		B(C)	100	4.81	0.02	0.19	0.78	7.11	16.1	4.6	6.0	3.0	0.6	12.4

(continued on next page)

Table 2 *(continued)*

Soil unit (locality)	Fe_k mg/kg	Mn_k mg/kg	Al_{ox} mg/kg	Fe_{ox} mg/kg	Mn_{ox} mg/kg	Si_{ox} mg/kg	Al_d mg/kg	Fe_d mg/kg	Mn_d mg/kg	Si_d mg/kg	Fraction 2–0.1 mm (%)	Fraction 0.1–0.05 mm (%)	Fraction 0.05–0.01 mm (%)	Fraction < 0.01 mm (%)
Haplic Cambisols (Razula)	1.8	537.0	2553	4364	1801	172	3083	20,377	1830	820	45.0	15.0	24.0	16.0
	1.7	346.7	2829	4668	1529	163	3156	20,702	1564	765	42.0	15.0	24.0	19.0
	0.5	184.0	2556	4260	1556	196	3017	22,177	1581	934	23.0	11.0	21.5	34.5
	0.3	121.0	2552	4000	1391	191	3016	22,017	1398	947	22.0	10.0	22.0	46.0
	0.0	116.9	1881	4212	1366	217	2618	21,082	1429	878	18.0	8.0	23.5	50.5
	19.9	699.8	1956	4292	1456	148	2374	17,967	1516	841	64.0	12.0	17.0	7.0
	2.0	471.4	1986	3482	1433	162	2488	17,172	1545	825	45.0	16.0	25.0	14.0
	4.9	470.5	1951	3678	1426	134	2550	17,537	1556	745	47.0	13.5	22.5	17.0
	0.5	242.7	1745	3024	1194	149	2315	18,582	1230	843	37.0	14.5	24.5	24.0
	0.3	85.4	918	1958	2627	249	990	10,012	2704	616	47.0	13.0	20.5	19.5
	3.0	248.8	2169	3146	863	159	2563	18,762	897	854	46.0	10.0	18.0	26.0
	0.2	101.1	2106	3589	634	178	2541	23,292	652	1132	34.0	9.0	18.0	36.0
	0.3	93.4	1628	3194	640	209	2096	22,637	656	1208	34.0	11.0	17.0	38.0
	0.0	128.6	1452	2916	724	185	1950	20,617	771	1056	40.0	11.0	16.0	33.0
	0.7	131.8	2030	3024	1897	187	2457	22,182	1867	1152	48.0	8.0	13.0	31.0
Entic Podzols (Zofin)	152.8	6.4	2400	5045	12	32	2565	8967	0	850	92.5	3.5	4.0	0.0
	139.8	1.6	3117	8331	10	152	2395	16,278	8	1400	78.0	14.0	6.0	2.0
	102.6	2.1	12,256	28,135	43	700	10,430	39,346	63	1500	72.0	16.5	9.5	2.0
	15.6	0.5	19,140	16,785	43	2072	14,460	24,937	46	2000	85.0	8.0	6.0	1.0
	2.1	0.3	14,004	2791	29	3500	7810	9739	28	2450	90.0	5.0	5.0	0.0
	0.3	0.8	6478	1332	99	1568	3905	12,001	105	1550	92.5	3.5	4.0	0.0
	322.9	6.8	3908	9928	20	128	2860	14,587	25	950	78.0	15.0	7.0	0.0
	186.2	19.6	6147	12,741	48	252	5090	20,959	66	1650	78.0	14.0	8.0	0.0
	118.8	8.1	6354	12,980	34	192	5295	23,536	69	1650	72.0	16.5	11.5	0.0
	49.2	2.9	9694	16,324	43	524	8100	26,448	78	1400	78.0	7.0	12.5	2.5
	2.2	1.3	6216	2668	102	916	4480	8533	89	950	82.5	13.5	4.0	0.0
	107.4	42.0	6416	7871	86	352	5420	16,246	118	1050	74.0	16.5	9.5	0.0
	10.1	4.1	13,214	14,462	85	1392	9720	23,096	101	2200	74.0	5.5	8.0	2.5
	2.0	1.0	16,983	5526	66	3496	10,195	13,230	75	2200	85.0	6.0	9.0	2.7
	0.7	0.5	10,769	3233	67	2524	5720	10,540	73	1900	84.5	7.5	8.0	0.0
	0.4	0.8	6424	1747	67	1428	3230	8207	76	1900	91.0	5.0	4.0	0.0
	0.3	0.8	4074	1199	105	860	2375	8722	120	1700	81.0	10.0	9.0	0.0
Albic Podzols (Michigan)	2.5	0.1	108	90	2	0	65	1647	13	50	78.0	14.0	5.5	2.5
	2.0	0.0	85	123	1	0	115	1681	14	0	90.0	5.0	5.0	0.0
	36.1	0.6	5077	6075	8	544	3930	8024	19	500	84.0	12.0	4.0	0.0
	21.8	0.6	3426	3824	9	160	2945	5646	23	200	82.5	14.0	3.5	0.0
	3.0	0.1	2104	832	10	596	1865	1444	21	250	93.0	4.5	2.5	0.0
	1.9	0.4	51	71	3	60	75	1254	19	0	84.0	12.5	3.5	0.0
	2.0	0.0	62	69	2	76	280	1429	16	0	83.5	14.0	2.5	0.0
	4.7	0.1	93	146	3	44	205	1649	12	0	83.5	13.0	3.5	0.0
	20.8	1.6	3518	3915	22	428	2835	5046	30	0	82.5	15.0	2.5	0.0
	9.2	0.5	2822	1640	7	184	2025	2063	12	0	79.0	18.0	3.0	0.0
	5.0	0.1	149	111	2	32	175	1471	17	0	73.0	19.0	7.0	1.0
	25.9	0.7	3012	2918	8	264	2620	4359	20	50	79.5	16.0	4.5	0.0
	3.5	0.6	3566	1178	15	856	2335	2100	25	300	80.0	16.5	3.5	0.0
	1.7	0.3	3690	1641	11	976	2290	2813	24	50	78.0	17.0	4.0	1.0
	1.2	0.5	1579	459	16	556	540	1159	25	0	80.0	17.5	2.5	0.0

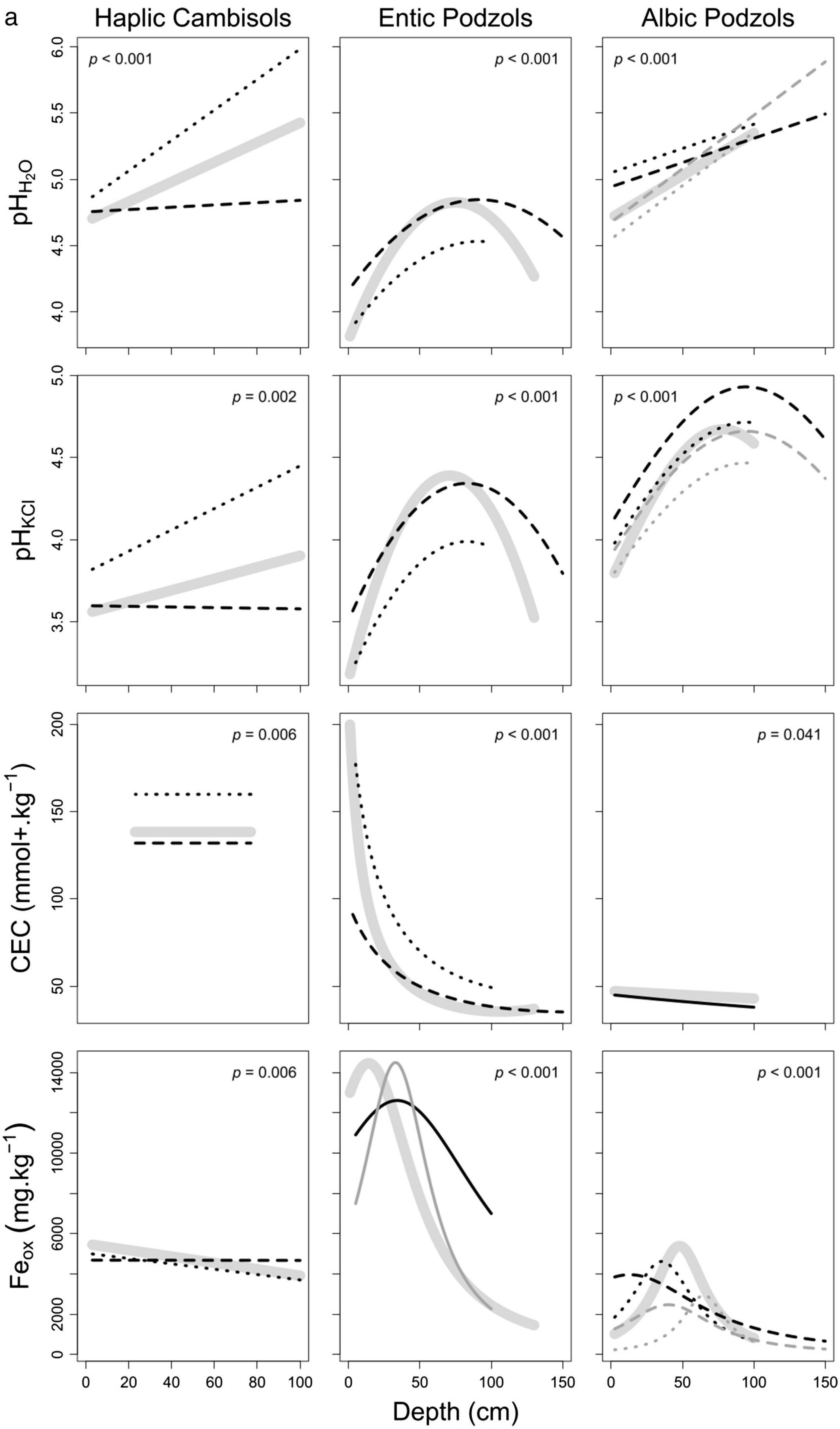

Fig. 5. Significant models of the selected soil properties, in relation to the sample depth, microsite and age. Ages of young and old pits or mounds correspond to the youngest and oldest dated uprooting events within each soil unit (19 and 250 years on Haplic Cambisols, 32 and 1690 on Entic Podzols and 168 and 6089 years on Albic Podzols, respectively).

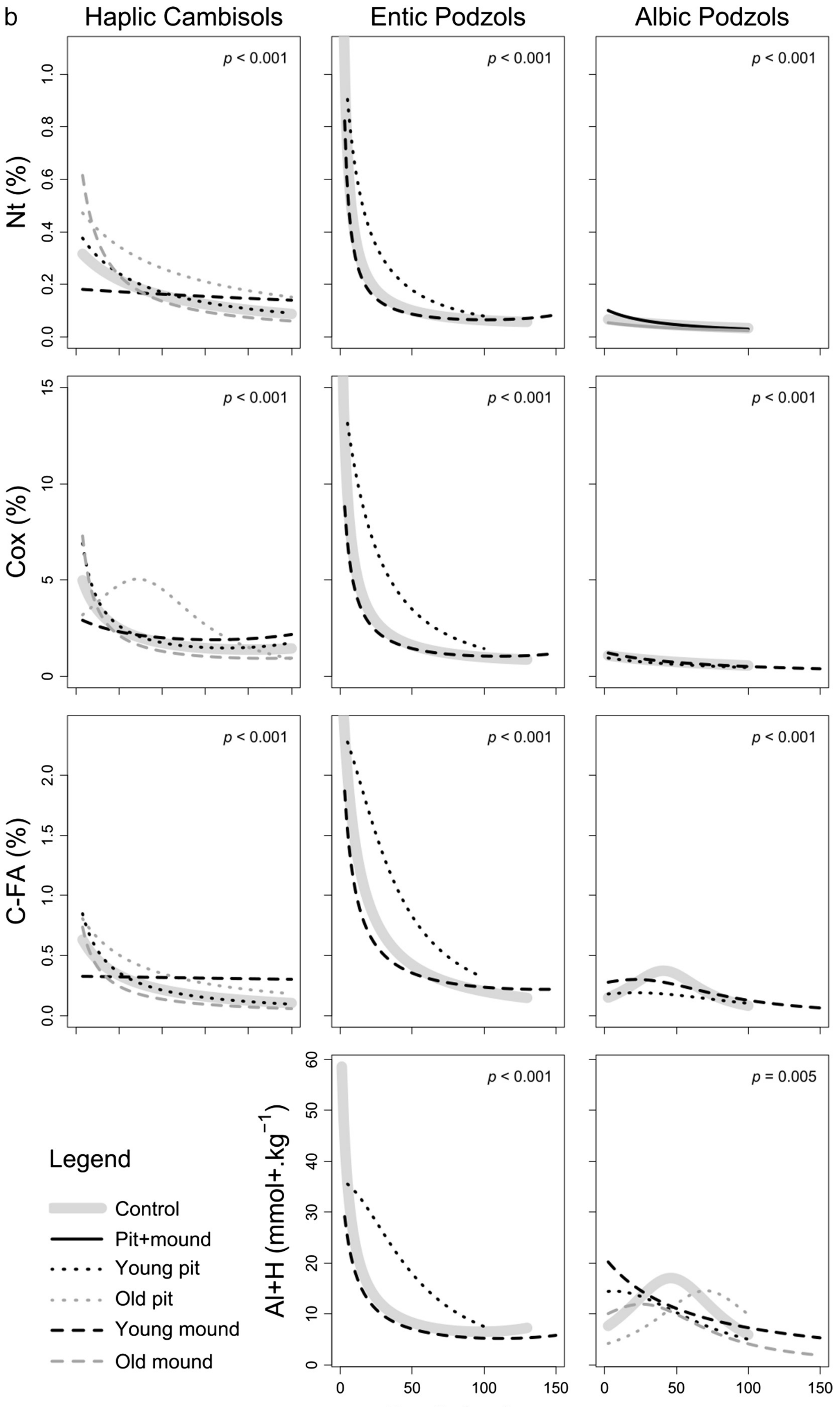

Fig. 5. (*continued*)

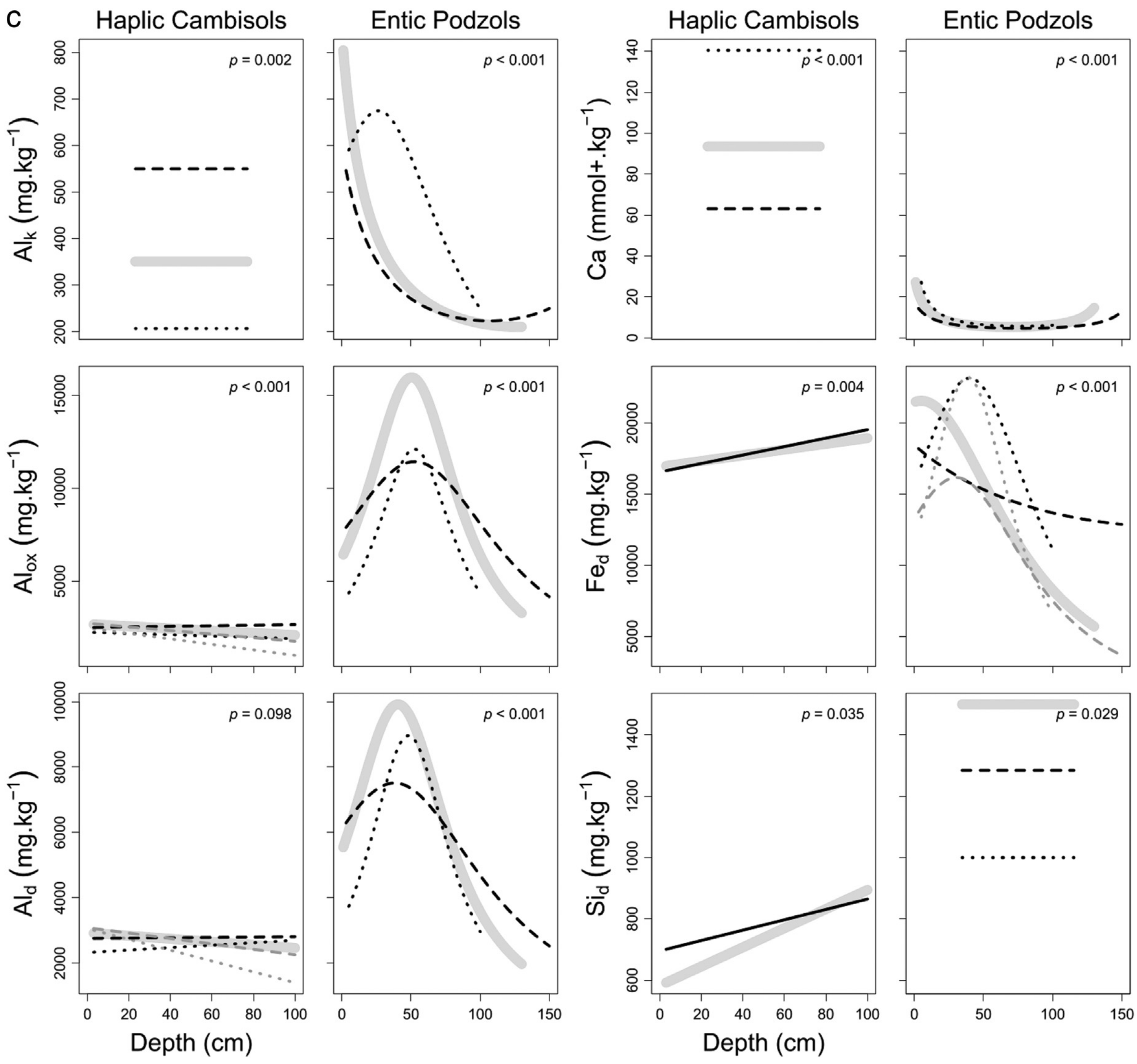

Fig. 5. (*continued*)

rich soil matrix led to a sharp decrease of C with depth, as well as connected N concentrations, usually along **exponential decay trajectories**. Increases with depth also occurred for crystalline Fe (Fe_d) in the Haplic Cambisols, which was unlike soils in both regions of Podzols. The highest concentrations of Fe_d in medial soil horizons of Podzols illustrated the pedogenic origin of this fraction, rather than geogenic. This predominance was even more visible in Al forms (Fig. 5-7).

Clay contents, soil reaction (pH-H_2O, pH-KCl), and Si_{ox} concentrations belonged in the category of soil properties that had similar relationships with sample depth in all three studied regions. All of these properties increased with depth. Although all these properties are affected by pedogenesis, their increasing values with depth indicates (especially in case of Si_{ox}) the significant role of bedrock in their constitution (e.g. appearance of weathered claystones on flysch at Razula reserve and weathered granite at Zofin).

3.3. Evolutionary trajectories, and the general role of microsite and age in pedogenesis

We can assume that the microsite and its interaction with time since the disturbance event can be viewed as one possible alternative within the soil development pathway system, i.e. it may be a factor of soil nonlinearity or polygenesis (Johnson and Watson-Stegner, 1987). Each microsite potentially presents a specific developmental trajectory in soils below, because the site changes the local microclimate (Beatty and Stone, 1986), flora (von Oheimb et al., 2007) and hydrology (Schaetzl, 1990), as well as characteristics of the forest floor.

Statistically, the significance of microsite decreased with increasing degree of podzolization (Table 3). The largest proportion of data variation by microsite was explained on Haplic Cambisols (7.3%, $p < 0.001$), less so on Entic Podzols (4.8%, $p < 0.001$), and least on Albic Podzols (2.1%, $p = 0.076$). Moreover, in soil regions without strong illuviation of organic matter-sesquioxide complexes (Haplic Cambisols and Entic Podzols), an additional 3–4% of the data variability was explained by interactions of microsite with depth, or even with age (Haplic Cambisols, 2.3%, $p = 0.045$).

The age of treethrow features was particularly important as an explanatory variable on Haplic Cambisols, where it obtained statistical significance in interactions with the depth and microsite (Table 3). In the Albic Podzol region, age was significant only in its interaction with depth. Age exceeded the level of statistical significance in all calculations on Entic Podzols as well (Table 3). The low significance of the age variable on Entic Podzols could be connected with the high local soil variability (Šamonil et al., 2011) and diversity (Šamonil et al., 2014), i.e., there exists a relatively high importance of the local soil environment.

Evaluation of post-disturbance pedogenet pathways requires simultaneous considering of the effect of microsite, time and depth. Our data (Table 3, Fig. 5a,b, 7) generally clearly show that soils in post-disturbance microsites are pedochemically closer to undisturbed (control) soils at the Michigan site, where soil weathering and leaching were the most intense. In other words, although neoformation of podzolic E and Bhs horizons here is extremely rapid in pits and much slower on mounds (e.g. Al + H in Fig. 5, Table 2, Šamonil et al., 2015), its pedochemical properties are nearly the same in all microsites. We speculate that the pedogenic impact of pit and mound microtopography is reduced by predominance of vertical podzolization and by the limitation of lateral processes in the extremely poor, acidic and permeable parent materials of Michigan. In the sandy parent materials at the Michigan site, there is no evidence of lateral podzolization (Sommer et al., 2001; see also Schaetzl et al., 2015).

Alternatively, soils in the Cambisol region (Razula) were the most variable after disturbance, with respect to soil chemistry and physics data (Table 3, Figs. 5, 7). The secondary (clay) mineral formation (Tables 1, 2, Tejnecký et al., 2015), which are key pedogenetical process in Cambisols (e.g. Schaetzl and Thompson, 2015), was here supplemented by strong melanization connected with bioturbation by soil fauna (Šamonil et al., 2008a, 2008b), clay illuviation, clay mineral alteration (Tejnecký et al., 2015) and hydromorphic processes (Schaetzl, 1990). This finding can be associated with the decreasing number of statistically significant models of individual soil properties with increasing severity of podzolization in regions (Fig. 5). Although we report on 27 valid statistical models for Haplic Cambisols, we found only 23 such models on Entic Podzols using the same technique, and only 15 models on Albic Podzols.

3.4. Equivocal pedogenetical role of disturbed microsites

Although microclimatic differences across microsites seem to be universal, i.e., mounds are often drier and warmer than pit microsites in the same landscape (Beatty and Stone, 1986; Schaetzl, 1990), our data suggest that – the role of treethrow microsites as a factor of the soil polygenesis, was more equivocal. Of the 38 evaluated soil properties, only amorphous and crystalline forms of manganese and aluminum (Mn_{ox}, Mn_d, Al_{ox}, Al_d) always had maximal concentrations in treethrow pits, probably due to redoximorphic processes for manganese and accumulation of organic matter and associated organically-bound Al and poorly crystalline aluminosilicates (Fiedler and Kalbitz, 2003). In Albic Podzols, the formation of thick E horizons, indicative of extreme podzolization, acidification, and nutrient loss (the lowest amounts of Ca^{2+}, Mg^{2+}, and K^+, and high exchangeable acidities) were most commonly observed in pits. This finding agrees with those of others, who described this process in detail (Bormann et al., 1995; Cremeans and Kalisz, 1988; Schaetzl, 1990; Schaetzl and Follmer, 1990; Kabrick et al., 1997). Alternatively, accumulation of nutrients, as well as higher CEC and pH values, occurred within pit soils on Haplic Cambisols and Entic Podzols. This key difference in the pedogenetic role of treethrow mounds and pits is likely due to the high buffer capacities of the clay minerals in Haplic Cambisols (see also Šamonil et al., 2010b) and the lowered importance of translocation of organic matter-sesquioxide complexes in Entic Podzols. In this region, we sometimes found weak E horizons in some very old treethrow pits (Šamonil et al., 2015) but generally these soils still did not exhibit pedomorphic formation of eluvial E and illuvial Bhs horiozons. Our results suggest that the start of eluviation of labile organic matter-sesquioxide complexes from the upper mineral horizons is a key threshold point in the development of soils in pits, representing a transition in post-uprooting microsites from accumulation to leaching. Prior to this point, pedogenetic development on treethrow sites is similar to that on Cambisols, even in soils with spodic properties. In a humid climate such as in our study, this point can be reached on poor rock in less time. On bedrock with the higher buffering power, it probably takes longer.

3.5. Evolution of undisturbed soils

Soils on microtopographically flat (control) sites were generally intermediate in character between pit and mound sites. However, such soils are also considerably older, and hence often have higher amounts of clay, crystalline and amorphous forms of Al, Si and partially also Fe and Mn. Such forms of metals may require hundreds or thousands of years to develop (e.g. Arduino et al., 1984; Pai et al., 2004). Hence, they are correlated with control positions because of the greater age of these soils. Unfortunately, the longevity of undisturbed formation of control profiles is not exactly known and can be only estimated. If we assume that many sites have rotation periods of 900–1400 years (Šamonil et al., 2009, 2013), then each site within the studied forest landscapes has theoretically been disturbed circa 8 times during the Holocene. Nevertheless, the duration of the rotation period does not exclude possibility of, locally much longer time periods between disturbances (cf. Šamonil et al., 2013). Instead, the rotation period provides only information about mean disturbance dynamics. Some sites will be frequently disturbed but others will remain undisturbed for thousands of years. Evaluation of age and denudation rates in undisturbed profiles is challenge for future research.

3.6. Pedomorphology versus pedochemistry

Šamonil et al. (2015) observed increasing differences in E horizon thicknesses over time between pit and mound sites. They hypothesized that this finding was due to divergent pedomorphic soil evolution, initiated by uprooting. Our current results are not in contradiction with these former findings. Instead, our current data on soil chemistry provide a more complete picture of soil formation and suggest that, in terms of soil chemistry, similar soil formation processes operate across all the microsites (Fig. 8).

3.7. Effect of long-term development of soil landscape

Long-term changes in soils could also influence current post-disturbance pedogenetical pathways. Some soil and landscape studies in northern Michigan revealed postglacial non-linear soil formation, at least in parts of the landscape (see Johnson et al., 1990). In the Albic Podzol region, clay-enriched lower horizons with argillic properties were repeatedly noted in soils that have spodic horizons in the upper profile (Šamonil et al., 2015). This horizon sequence generally is taken to imply that podzolization is preceded by clay illuviation (see bisequal soils in Schaetzl, 1996; Bockheim, 2003; Schaetzl and Thompson, 2015). Based on our results from these three regions with soils of varying textures, we can generally derive expected changes in post-uprooting pedogenesis due to movement in regional soil evolution. The long-term sequencing of lessivage on region scale followed by podzolization will lead to qualitative flattening and homogenization of post-disturbance soil evolutionary trajectories at local scales. In other words, the assumed convergence of soil chemistry on a landscape scale towards vertically-dominated podzolization locally causes convergence of post-disturbance pedogenetical pathways.

3.8. Feedbacks from soil disturbance to forest development

Changes in soil development, as impacted by tree uprooting, have strong effects on forest regeneration. The affinity of woody species to mound microsites has long been known (see Nakashizuka, 1989; Palmer et al., 2000; von Oheimb et al., 2007; Simon et al., 2011; Šebková et al., 2012; Šamonil et al., 2016). This affinity is presumably due to the usually unfavorable microclimate of pit sites. The wetter and colder character of pit is likely an advantage for organisms only in dry and arid regions. Pits are also sites of higher seed predation by small mammals (e.g. Simon et al., 2011), and juvenile plants by fungal pathogens (e.g. Šamonil et al., 2008b). Most importantly, organic matter accumulation within pits can

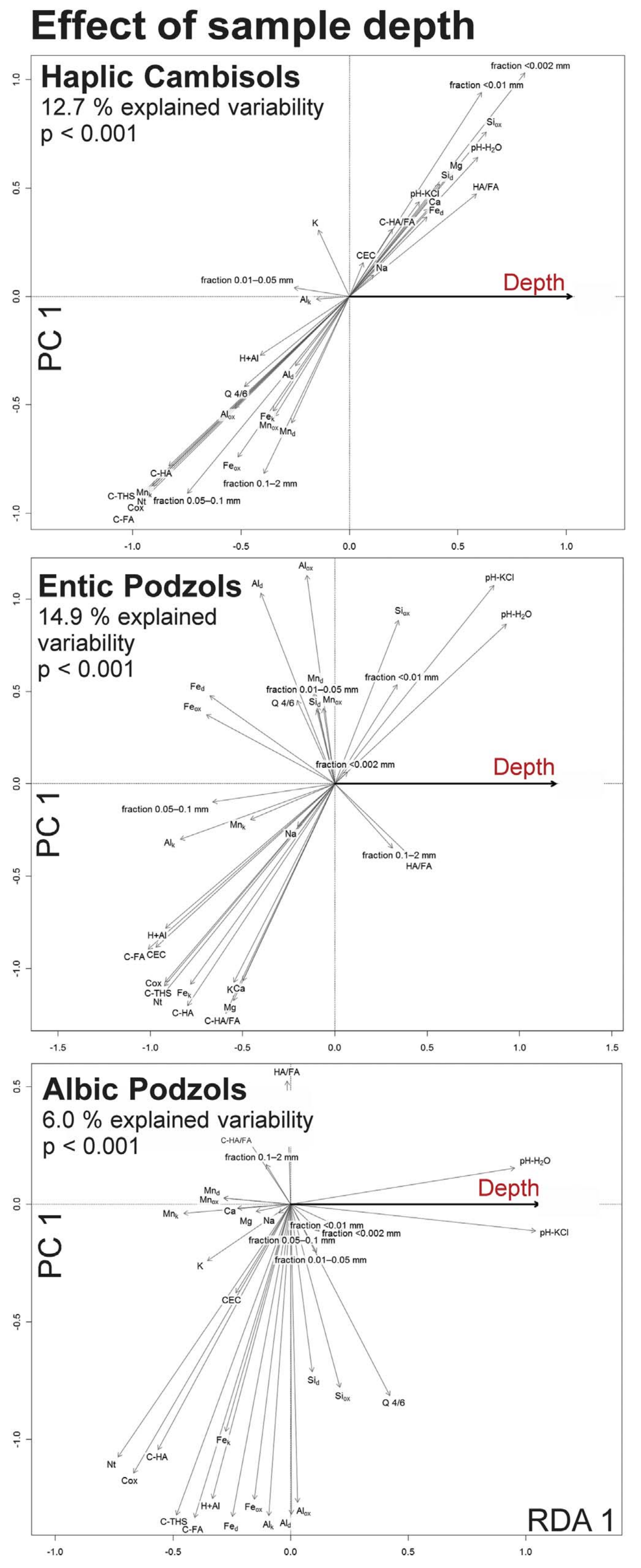

Fig. 6. Redundancy analyses showing the effects of depth on soil development after treethrow disturbances. For details see Materials and Methods.

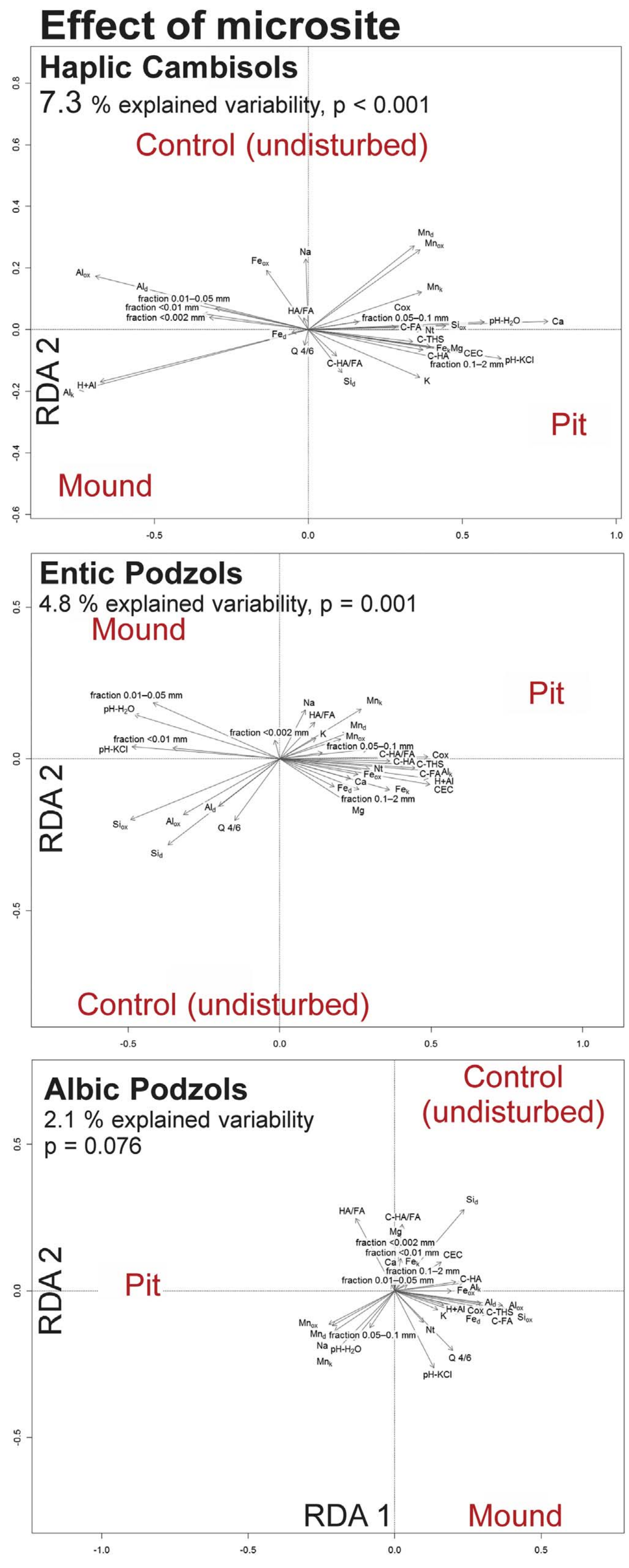

Fig. 7. Redundancy analyses showing effect of microsite (pit, mound, undisturbed control) on soil development.

be thick, which inhibits the successful germination of seedlings (Beatty and Stone, 1986; Šamonil et al., 2008a, 2008b). This divergence can be even more significant after leaching and acidification of pit soils becomes enhanced in the post-disturbance years. The decreasing probability of successful establishment of plants within pits can, in turn, alter the spatial pattern of trees within the forested landscape (Szwagrzyk and Czerwczak, 1993; Janík et al., 2016) and hence, the spatial distribution of additional uprooting disturbances (Šamonil et al., 2014).

Table 3
Results of ordination analyses. Statistically significant results are in bold and marked with asterisks (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). For details about settings of analyses, see Section 2.4.

Site	Variable	Explained data variability (%)	P value	
Haplic Cambisols (Razula)	**depth**	**12.7**	**< 0.001**	***
	microsite	**7.3**	**< 0.001**	***
	age	2.7	0.397	
	age × microsite	**2.3**	**0.045**	*
	age × depth	**1.1**	**0.004**	**
	depth × microsite	**4.0**	**< 0.001**	***
Entic Podzols (Zofin)	**depth**	**14.9**	**< 0.001**	***
	microsite	**4.8**	**0.001**	***
	age	0.9	0.912	
	age × microsite	0.5	0.793	
	age × depth	0.3	0.405	
	depth × microsite	**3.0**	**< 0.001**	***
Albic Podzols (Michigan)	**depth**	**6.0**	**< 0.001**	***
	microsite	2.1	0.076	
	age	3.7	0.117	
	age × microsite	0.6	0.873	
	age × depth	**1.1**	**0.020**	*
	depth × microsite	0.8	0.058	

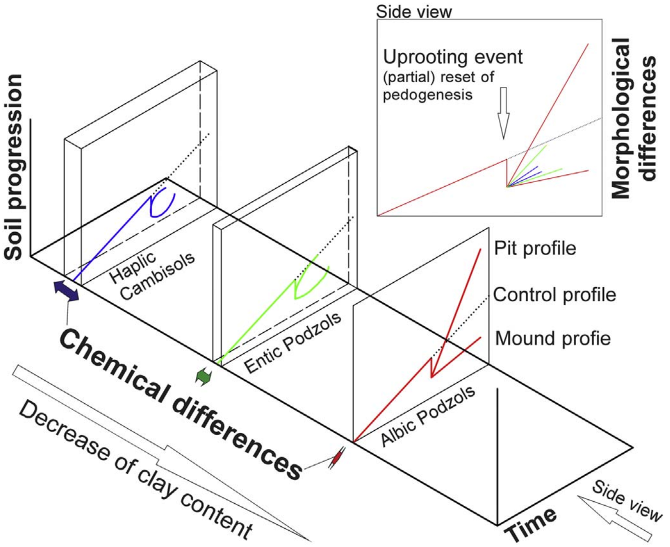

Fig. 8. Conceptual model of post-disturbance soil formation (red, green, and blue lines, respectively) in the three soil regions, on Haplic Cambisols, Entic Podzols, and Albic Podzols. Although morphological data point to non-linear pedogenesis, chemical differences suggest post-disturbance, polygenetic soil formation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our results also suggest that the self-reinforcing pedologic influences of trees (SRPIT) model (Phillips and Marion, 2004; Phillips, 2008) needs refinement. The SRPIT model treats all former tree sites as a single microsite, without distinguishing between pits and mounds, or stump decay sites. Our results suggest that pedogenetic feedbacks cause rejuvenation on mounds, but progressive leaching in pits.

4. Conclusions

Post-uprooting pedogenetical pathways were compared between treethrow pits, mounds and undisturbed control profiles in three regions with different soil textures and intensities of weathering and leaching. Sample depth was the most significant variable in all three regions ($p < 0.001$) followed by microsite, and finally age since disturbance. Increasing contents of coarse fractions in soils and increasing intensity of podzolization caused chemical homogenization of post-uprooting pedogenetical pathways between the microsites. Results suggest that, in more highly developed soils, responses to disturbance may be more limited than in less-developed soils, which may decrease the polygenetic effects of uprooting. Convergent or divergent development can differ according to what soil property one is concerned with, or even broad classes of properties (e.g., soil morphology vs. soil chemistry).

The start of eluviation of labile organic matter-sesquioxide complexes from the upper mineral horizons is a key threshold in the pedogenesis in pits, representing a transition in post-uprooting microsites from accumulation to leaching. An occurrence of such threshold point can cause a type of mode switching of soil behavior. For centuries, disturbance can result in divergence; eventually, however, a threshold is approached, and a convergent mode is encountered across the landscape.

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