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Toposequences of Forest Soil Properties Between Differently Elevated Igneous and Sedimentary Mountain Ranges

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ABSTRACT

Soil properties are significantly, but unevenly, conditioned by the landscape relief and/or bedrock. Here, we compare forest soil properties along toposequences between differently elevated areas of denuded Variscan mountain ranges and the alpine-fold Carpathians in the Czech Republic (Central Europe). Correlating soil properties were selected by multivariate analysis of granularity, physicochemical and chemical variables. Toposequences were defined from the selected soil properties through principal component analysis and vector overlays with relief and bedrock types. The relief or bedrock effects were compared by nonparametric tests of soil horizon properties between average values at the toposequences and weighted averages of the penetrating geological subdivision types. Eleven forest soil toposequence types were distinguished along wetland, lowland and highland conditions. Particular toposequences were characterised by different grain fractions, C_{org}, Al_2O_3 and P_2O_5 between soil horizons. The soil-forming effect of relief appeared to be more pronounced in flat areas, with marked transitions between rocks; on the other hand, the bedrock effect was more pronounced in geologically less structured fold areas. The different relief or bedrock effects on soil-forming conditions suggest specification of soil body assessment during terrestrial ecosystem classification.

1 | Introduction

Soils occur in an organised manner within the landscape. The soil occurrence can be mapped as either a toposequence of structural features, or as a series (catena) of soil-forming processes between edge conditions in an altitudinally differentiated area (Hall 1983). Toposequence soil characteristics based on the definition of soil-forming conditions tend to precede catena assessment, which requires knowledge about processes toward soil differentiation from original rocks. Associations between landscape divisions and soil properties have suggested that the more divided part has a greater influence on the soil toposequence than the less divided part (Phillips and Marion 2007). Variability between landscape divisions and toposequences also shapes interfaces between ecosystems, where significant differences in bioproduction are found (Augusto et al. 2000; Vesterdal and Raulund-Rasmussen 1998; Pavlů et al. 2007).

Soil-forming conditions consist of variable environmental properties. Climate, rocks and living forms create a medium for factors in soil development (Yaalon 1975). Climate influences soil development the most through hydrotermic regime in landscape, which is seen during evaporation and temperature cycles. Rocks subsequently provide weathering products and landforms. Living forms

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[Correction added on 12 December 2025, after first online publication: The copyright line was changed.]

Summary

- Mountain systems precondition soils through relief and bedrock types despite similar climate.
- Differences between soil horizons indicate geological effects on toposequences.
- Bedrock more influenced soils in rocky uniform areas, while relief along differently weathering rocks.
- Soil toposequences provided pattern for a robust ecosystem classification.

precondition soil forming by organic matter and by extracellulary active metabolites (Nannipieri et al. 2003). Soil development is controlled through instability of external conditions due to actions of physical, chemical and biological processes (Huggett 1976). Already, Jenny (1941, 1961) proposed to understand soil-forming conditions as functions of climatogenic, rock-forming (especially erosional-sedimentation), topographic and biological processes in time. Huggett (1998) concluded that the variability of environmental properties, together with non-linear relationships between soil and surrounding landscape, transforms soil development into system evolution.

Soil toposequence reflects influences of erosional-sedimentation processes on landscape development in catchments downslope. The genesis of a soil toposequence begins with the weathering of rocks, which releases particles moving under gravitational influence or redistribution resulting in soil body differentiation (Khomo et al. 2011). While erosion begins along ridges under gravitational influence, redistribution counteracts gravity via the activity of living organisms or through water ingress. Eroded rock particles are gradually deposited in the lower parts of the slopes, where they are intensively transformed into soils. Soil formation on this deposited hillwash begins with the leaching of fine (clay) particles and turbidity. Erosional-sedimentation processes lead to grain size differentiation as well as to differential hydromorphisation (Brown et al. 2004).

Inner-soil grain differentiation develops both with profile depth and between bodies from ridge to valley. Development of soil grain composition is driven by deposit stratification, weathering, surface or lateral transport, through bioturbidity and/or through displacement (Chittleborough 1992). Common origin of soils and weathered rocks at catena is characterized by concordance, grain differentiation, clay leaching (eluviation) and by hydromorphisms (Phillips and Marion 2007). Clay content increasing from surface to subsoil is the most common sign of soil body development in the world (Paton et al. 1995). At the same time, leached soils are deeper as they occur predominantly on the lower halves of slopes, where the accumulation of weathered particles is concentrated. Nevertheless, soil development velocity is generally faster, where easily weathered bedrock and steeper relief occur, both of which accelerate mass redistribution (Khomo et al. 2013). Accumulation of fine particles on the lower slopes helps hydromorfisation by limiting permeability, and is a final characteristic of hydrologically connected soil development in catena (Khomo et al. 2011).

The mapping of the common soil and weathered rock development is based on diagnostic features or through process classification. Soil toposequence development is assessed through topographically geological relationships (Brown et al. 2004). Geological relationships within a toposequence are investigated through overlays of pedo-geomorphic, pedo-lithographic and litho-geographic features (Newell Price et al. 1997). Thanks to overlays among occurrences of soil groups, rocks and landforms, the soil-regolith units, soil-geomorphic units as well as soil-bedrock-landform units were characterised. Soil-regolith units are intervals of variable soil properties within a common weathering mantle that condition ecosystem diversity (Phillips and Marion 2007). More derived soil-geomorphic units may be characterised as similar hydrically influenced soil bodies within catchments. The level of water influence on soil is considered as an effect of landscape forming through weathering and erosion. The soil-geomorphic units are indicated by grain differentiation and mineral composition of soil-forming substrates (Zinck et al. 2016). Finally, the most complex soil-bedrock-landform classification characterises common occurrence of soils and rocks within every relief type based on intervals of physical, chemical and mineralogical properties in solid bodies (Teixeira et al. 2019). Soil-bedrock-landforms distinguish markedly developed soils from slightly developed bodies on various quick-weathering bedrock. The advantage of their comprehensive characteristics is an indication of the terrestrial ecosystem type (Villela et al. 2013).

The present study was focused on the verification of the presumption that differently elevated mountain systems have divided occurrences of soil toposequences. Differently folded adjacent mountains provide various soil-forming conditions despite the same climatic zone. Soil development differentiation under a uniform climate is caused through antagonistic relief or bedrock effects (Zinck et al. 2016). Various rocks suggest differentiation of soil properties, while mass movements downslope limit these differences. On the other hand, the differences among soil bodies on the same rocks depend only on relief (Samec et al. 2019). Soil toposequences are mapped through either transect generalization between ridges and valleys, or through statistical modeling (Birkeland 1999). The geological effects were assessed in the present study through a comparison of statistically defined soil toposequences between denuded and neoid fold mountains. The differences in soil toposequences are most likely to occur along hillwashes or wetlands, which have developed most during Quaternary environmental changes (Catt 1992). Quaternary alternations between sedimentation and erosion caused the division of surface substrates ranging from relic (pre-Quaternary) to Pleistocene, Holocene and hillside (Maher 1998). Pre-Quaternary sediments formed bodies of relic autochthonous soils. The Quaternary sediments formed allochthonous soils. Similarity between soils and bedrock remained greatest at autochthonous soils, while it was suppressed in allochthonous soils (Bhattacharyya et al. 1993). On the other hand, the allochthonous character of hillwash has differentiated soil toposequences mainly in altitudinally more broken mountains.

2 | Material and Methods

2.1 | Toposequence Framework

The soil toposequences for this study were based on 17,013 pits excavated during routine forest surveys in the Bohemian Massif (Czech Republic) and were compared with previous

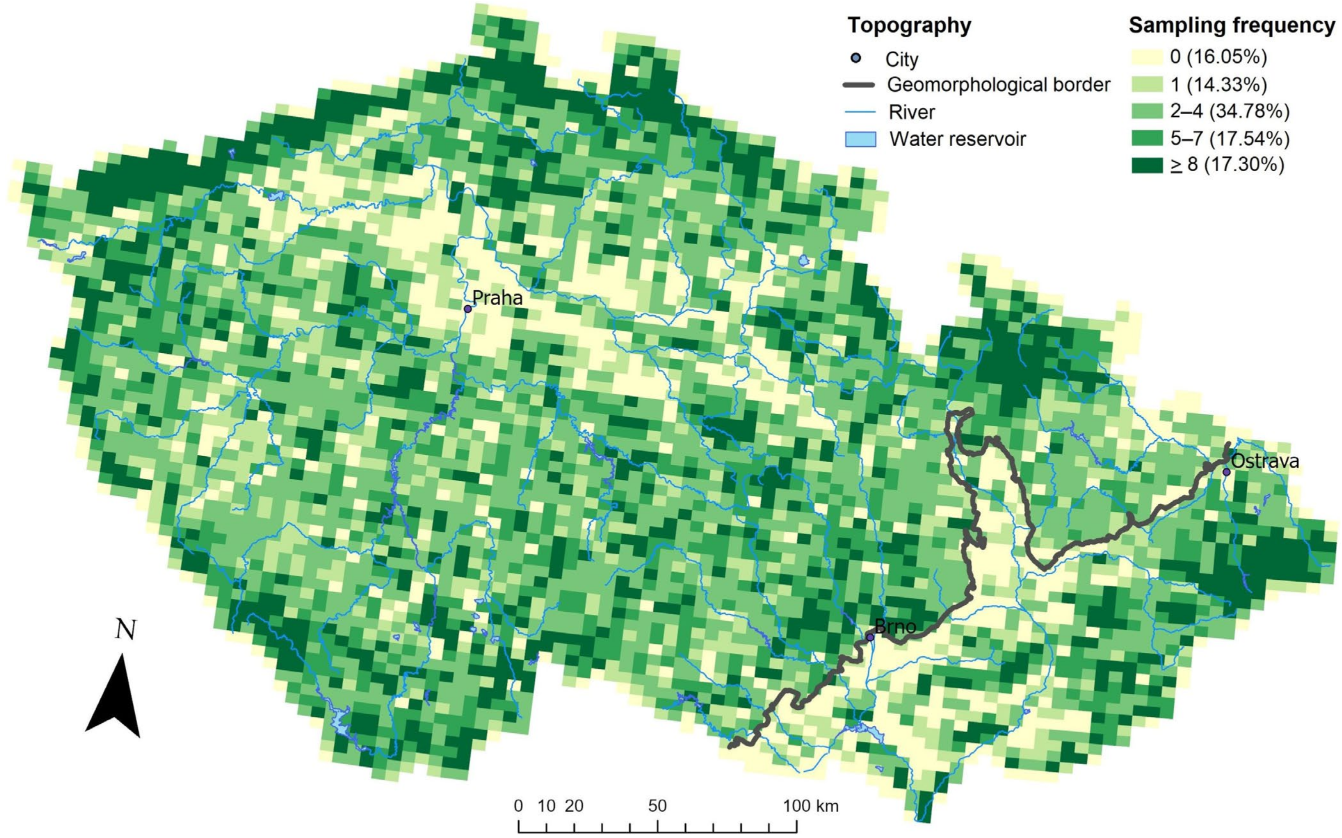


FIGURE 1 | Distribution of forest soil pits generalised to state base map grid in the Czech Republic.

classification in the Outer Western Carpathians (OWC) (Samec et al. 2019). The Carpathian forests were totally represented by 10 soil toposequence types from floodplains (2 types) to hilly-countries (5 types) and highlands (3 types). Present-day forests in the Bohemian Massif range on the territory of the CR have been preserved on 23,750 km^2 (35.6%), while Carpathian forests cover only 3150 km^2 (26.0%).

The Bohemian Massif is a remnant of the Variscan mountains in Central Europe, which was secondarily dissected along tectonic faults during the Saxon phase of Alpian folding and then denuded again during the Quaternary period, while the OWCs are Alpian mountains on the site of the Paratethys sea basin (Yegorova and Starostenko 2002). The Variscan folding connected metamorphic bodies from previous Perigondwanian microcontinents and penetrated them with intrusive rocks (Finger et al. 2007). The following Mesozoic denudation was then altered by shallow-water sedimentation, first along the Carpathian Foredeep and culminating in the Bohemian Cretaceous basin (Čech 2011). The retreat of the sea at the end of the Mesozoic era was followed by the formation of lake basins; however, the folding of the Alpine-Carpathian arc on the one hand awakened volcanic activity and on the other divided the former Variscan massifs contrasting with Mesozoic basins by altitude (Ulrych and Pivec 1997).

2.2 | Data

Data obtained from the soil pits included granularity, physicochemical sorption and pH, and nutrient contents in topsoil (TSH < 15 cm) and subsoil (SSH ≥ 15 cm) horizons from a database administered by the Czech Forestry Institute (Pecháček et al. 2023). The database was composed of surveys on forest type (6594 pits), forest nutrition (3153 pits) and from the national inventory (7266 pits) (Figure 1). The forest type surveys proceeded periodically during updates of forest management plans with an irregularly composed pit system. The forest nutrition survey was concentrated in areas under significant acidifying load in a grid 500 · 500 m, while the national inventory covered the whole CR regularly by grid 2 · 2 km. Irregularly distributed soil pits as well as regularly 500 · 500 m gridded pits were sampled both in TSH and in SSH. The national inventory provided soil data either from TSH of humic soils (5250 pits), or from SSH of mineral profiles (2016 pits).

Soil group classification was carried out according to WRB-ISSS-ISRIC (Schad et al. 2014). The soil pits included 15 reference groups, of which the most common were Cambisols (70.4%), Stagnosols (10.3%), Leptosols (4.1%), Retisols (3.1%), Luvisols (2.9%) and Fluvisols (2.6%). The other soil groups contained totally 6.6% including Podzols (2.3%) or Histosols (1.4%), which were preserved almost solely in forests. Grain-size composition was obtained sedimentographically according to USDA criteria (Burt 2004). Soil sorption was obtained through concentrations of exchangeable cations (Al^{3+}, H^+, Ca^{2+}, Mg^{2+}, K^+ and Na^+) on active colloid surfaces. The sum of exchangeable ion concentrations defined cation exchange capacity (CEC) and ratio between base cations and CEC subsequently defined base saturation (BS) (Cools and de Vos 2020). Soil acidity was determined acidometrically as active pH (H_2O) and potential pH (KCl). Organic carbon (C_{org}) and total nitrogen (N_t) contents were obtained through infra-red spectrometry after dry combustion, while (pseudo-)total contents of mineral substances (Fe, Al, Mn, Ca, Mg, K and P) through atomic-absorption spectrometry after extraction in aqua regia during nutrition surveys or in 20% HCl during typification surveys (Čechmánková et al. 2021; Neudertová Hellebrandová et al. 2024). The comparability between mineral substance extractions was verified through modes of soil data aggregation (Neudertová Hellebrandová et al. 2024).

Evaluation of soil toposequences was based on statistical detection of property edge values from soil pits and on the proportion of relief and bedrock types. Relief and bedrock were characterised among soil pits by intersection with polygonal biome classification of the CR (Culek and Grulich 2009). Czech relief types are generally represented by plateaus (27.4%), hillycountries (52.0%), highlands (2.6%) and by mountain altitudes (only 2.6%), while the Bohemian Massif mainly comprises plains (16.4%), broken plateaus (36.7%) and hillycountries (10.1%), with present-day forest covering namely broken plateaus (28.1%), slopes (15.0%) and highlands (12.4%). However, Czech relief was formed from 60.7% in sediments, almost 27.1% in metamorphites, 9.9% in intrusive rocks and 2.2% in volcanoclastics (Figure 2). The Bohemian Massif was predominantly made up of acid metamorphites (24.3%), loesses (11.6%) and greywackes (10.1%), with forests mostly found on acid metamorphites (29.6%), greywackes (12.5%), granites (9.0%) and acid waterlogged sediments (7.7%).

2.3 | Statistical Analysis of Soil Toposequences

The soil toposequence statistical characteristics were carried out through multivariate selection and classification of soil properties. Multivariate selection was designed for finding a subset of the most correlated soil properties using the dimensionality reduction effect. Dimensionality reduction was achieved through a series of principal component analyses (PCA), factor analyses (FA) and cluster analyses (CLU). PCA was used both in the selection of correlated properties and in toposequence classification. Selective PCA sorted properties from the subsets with identical units, whose latent vectors were in a common quadrant of the component weights that were not significantly skewed in the direction of a single vector. The number of component weights required was determined by Cattell index graph from the number of influential factors that included > 90% of the total variance (Thalib et al. 1999).

The maximum number of factors included for determining the optimal number of component weights was used to determine conditions for applying FA. However, soil properties that did not reach a significance of $p > 0.60$ were excluded from FA. Similar properties from the same subset were eliminated only on the variable with a higher absolute value of factor loading. FA results were verified by CLU using Euclidean metrics. The collateral use of simple linkage and Ward's approach checking robust relationships among selected soil properties has clarified: (1) that all subset compositions of soil properties were preserved; (2) that each subset was represented at least by one property; (3) that properties from one subset corresponding with another subset were preferred; (4) that different properties were excluded (Samec 2020).

Toposequences from correlated properties selections were resolved at point field of soil pits along boundaries of distinct component score (CS) quadrants. The CSs were calculated between orthogonal weights containing > 50% of total variance (Dempster et al. 2013). Soil toposequence characteristics were derived through a comparison of differentiation between soil properties edge values or between prevailing relief and bedrock types (Samec et al. 2019). Relief or bedrock effects were compared though Wald-Wolfowitz non-parametric tests between arithmetic averages of soil properties in each toposequence and weighted averages of penetrating relief or bedrock types at $p < 0.05$. The divergent scale of soil pit toposequences was simply displayed as the most dominant type in grid with cell area 18 km^2 at Czech 1:10,000 base map (SALSC 2019). Subsequent comparison with OWC was conducted through discussion.

3 | Results

3.1 | Principal Component Analysis

The most common assessed forest soils in the Bohemian Massif were Dystric Cambisols (22.8%), Haplic Cambisols (17.3%), Umbric Cambisols (7.6%), Haplic Podzols (6.6%), Entic Podzols (4.2%) and Dystric Stagnosols (4.0%). More than 32% of soil pits included units of just 1%–4% proportion, and almost 14% of the pits consisted of units represented by less than 1%. Relief was most frequently sampled in broken plateaus (27.2%), slopes (15.4%) and in highlands (12.0%). The most frequently sampled bedrock types were acid metamorphites (31.6%), acid plutonites (10.1%), greywackes (8.3%) and acid waterlogged sediments (7.7%). More than half of the soil pits were located in dominant relief types (54.3%) and also in prevailing bedrock (55.8%).

Potentially correlated soil properties consisted of sand, silt and clay grain fractions, pH, base saturation, organically bound carbon and pseudo-total Al_2O_3, CaO and MgO contents. PCA indicated significant correlations among C_{org}, N_t, Fe_2O_3, Al_2O_3, MnO, CaO and P_2O_5 in top-soil horizons, but only among Al_2O_3, MnO and CaO in subsurface horizons. The closest correlations were estimated between sand and fine silt contents, pH, BS, C_{org}, Al_2O_3 and CaO. The loam fraction usually correlated with chemical properties lowly except with pH, N_t and MgO. Nevertheless, pH and MgO were more different between top and subsurface horizons than N_t or P_2O_5. Increasing vertical differences among soil properties resulted in an increasing number of component weights between TSH and SSH. While TSHs included seven weights representing the majority of the variance, the SSHs needed eight weights to achieve equally high variance (Figure 3). The increasing number of component weights kept the distribution of soil property latent vectors at the quadrant majority; consequently, the most frequent toposequences had similar component score intervals over 50% of the variance. Only C_{org}, which remained near vector zero, occurred more closely to fine grain fractions in TSH, while remaining relatively similar to outlying sand content in SSH (Figure 4).

3.2 | Soil Toposequence Classification

The Czech Republic was divided into 11 forest soil toposequences. Toposequences were delineated along edge values of granularity or physicochemical properties from wetland, lowland dusted and

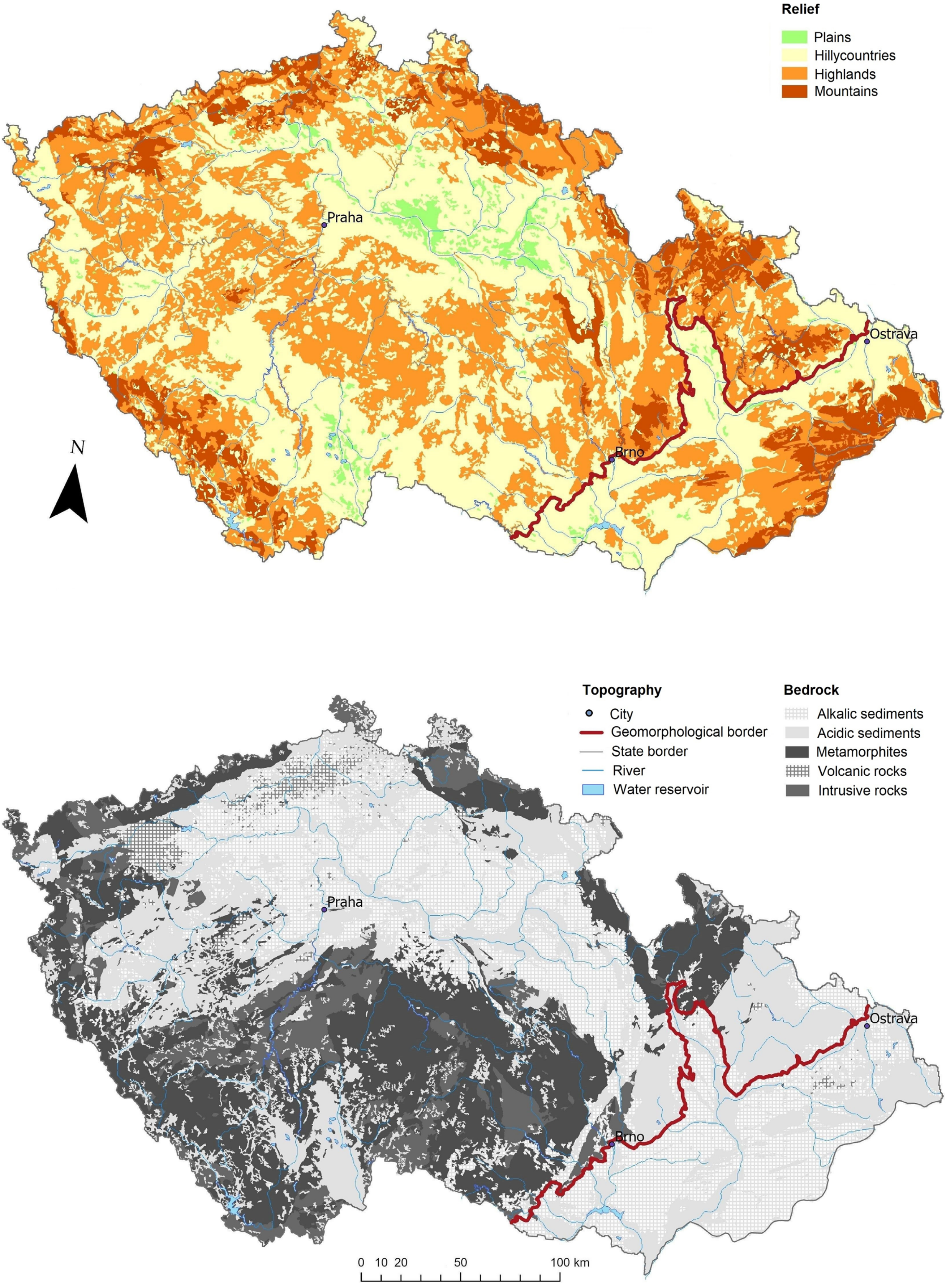


FIGURE 2 | Typification of relief (above) and bedrock (below) separated along geomorphological border between the Bohemian Massif (west part) and the Outer Western Carpathians (east part) in the Czech Republic.

incline to steep slopes in the Carpathians. The wetland toposequences included 3.3% of forest soils, lowland toposequences included 3.2%, while incline sequences included 93.4%. The most common coarse-grain slopes included 26.5% from forests and poor slopes almost 24.0%. The Bohemian Massif was characterised only by seven forest soil toposequences. The toposequences from the Bohemian Massif were divided between low-lying fluvial (0.15%), relic (0.35%) and luvic (0.34%) characterised by a unique representation of soil groups, and between higher-lying coarse-grain (28.8%), poor (27.6%), nutrient-medium (22.3%) and nutrient-rich (20.5%) slopes characterised by edge SSH properties (Figures 4 and 5). Coarse-grain slopes were delineated by granularity, while poor, nutrient-medium and rich slopes were distinguished by BS.

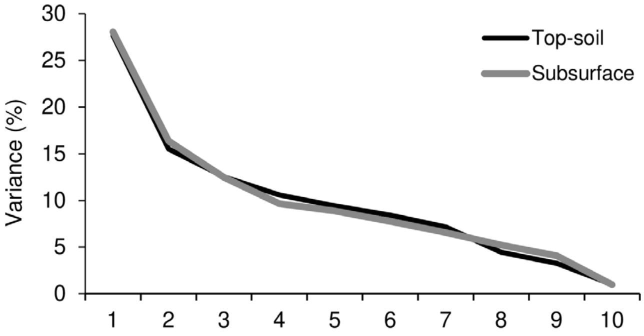


FIGURE 3 | The variance comprising dominant component scores of top and subsurface forest soil horizons.

Forests in the Bohemian Massif were distinguished from OWC by the occurrence of relic soil and nutrient-rich slopes without waterlogged depressions, loess hillcountries, proluvia and flysch range (Figure 6).

Soil toposequences are in the territory of Bohemian Massif characterized by unique combinations of prevailing relief and bedrock types and soil groups. Relief, bedrock and soil combinations corresponded with unique soil horizon property intervals. The toposequences were most clearly divided by the differing proportions of soil groups. Cambisols, Stagnosols and Fluvisols were found in all toposequences, but the toposequences were divided thanks to their varying proportions or presence of rarely occurring soils. Only Cambisols exceeded 18% in each toposequence. The proportion of codominant Fluvisols and Stagnosols fluctuated between 0.1%–15.4% and 1.6%–19.2%., respectively. Soil toposequences were generally divided into two groups: the first comprising fluvial landforms, relic sites and nutrient-poor slopes with Cambisols covering ≤40% of forest area, and a second group comprising luvic hillycountry, coarse-grain slopes, nutrient-medium and nutrient-rich slopes with Cambisol occurrences covering >40% of forest area in each sequence. Fluvial landforms differ from the other toposequences by occurrence of Gleysols covering more than 30% of the forest area. On the contrary, relic sites were predominantly covered by Leptosols. Luvic hillycountries were predominantly covered by associations of Cambisols and Leptosols; coarse-grain slopes by Cambisols and Podzols; and nutrient-medium slopes mainly with Cambisols

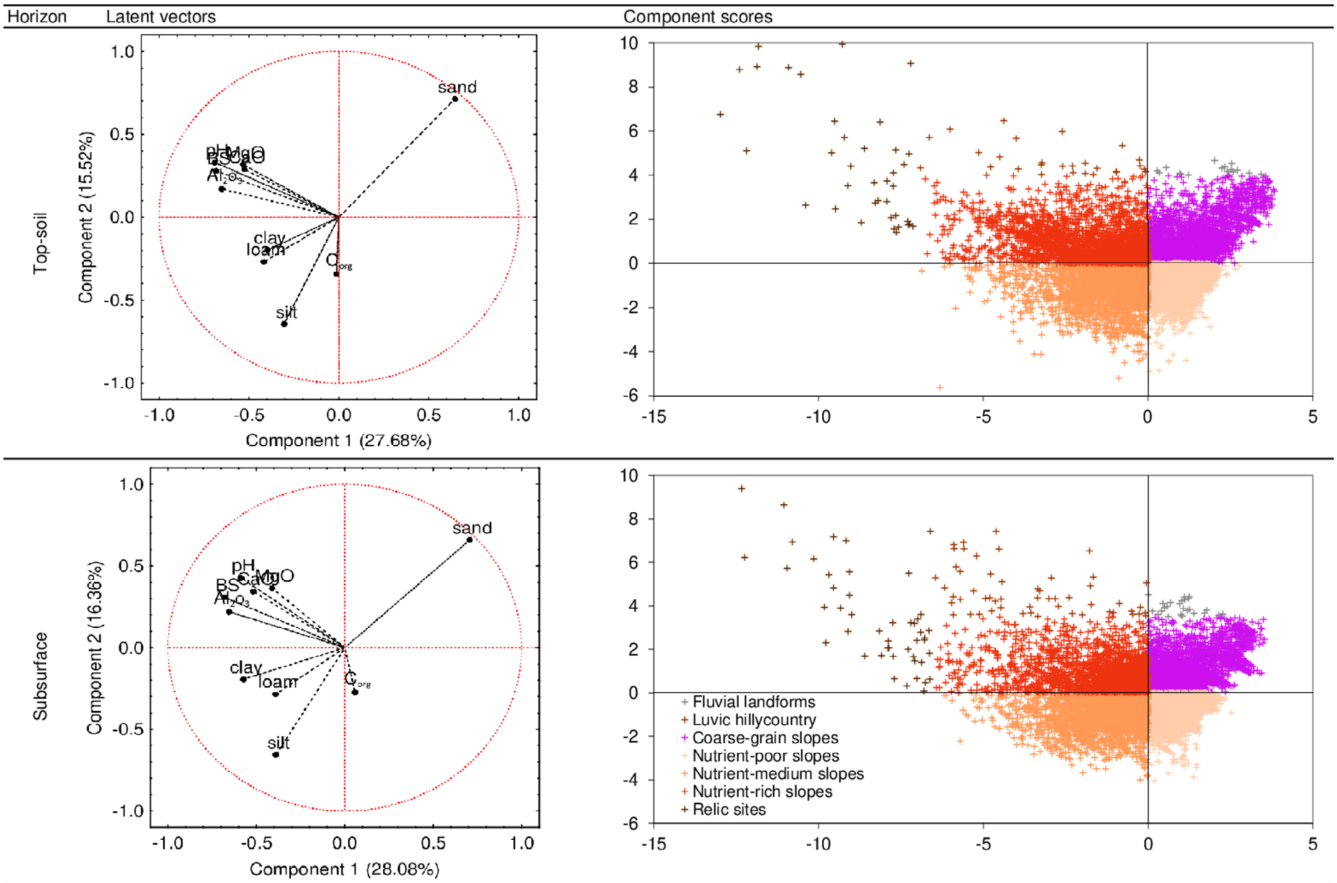
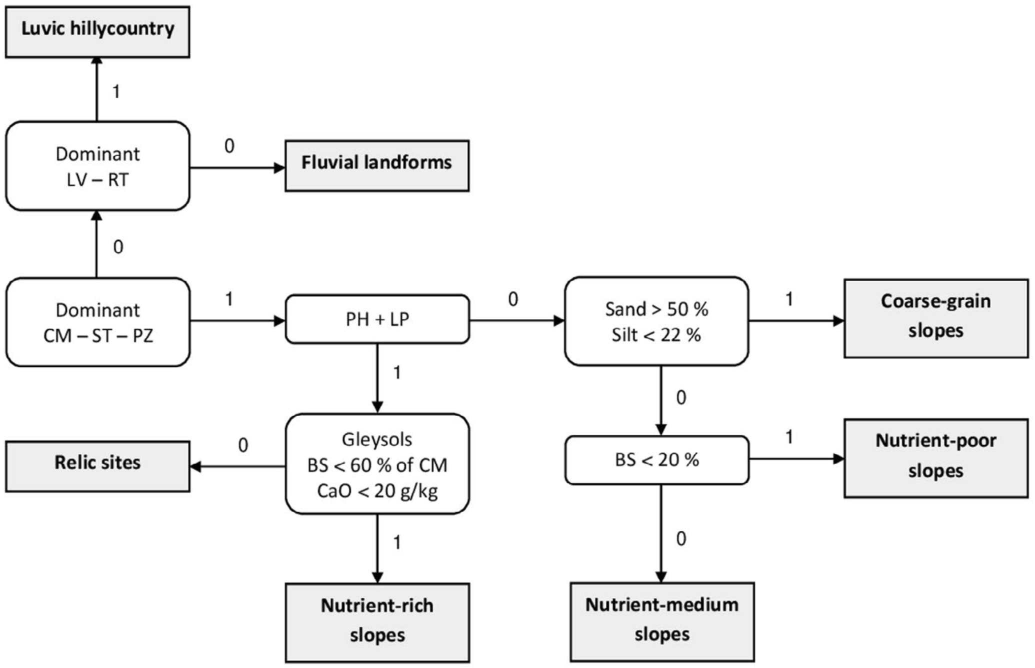


FIGURE 4 | Principal component analyses from properties of top and subsurface forest soil horizons.

a) Bohemian Massif



b) Western Carpathians

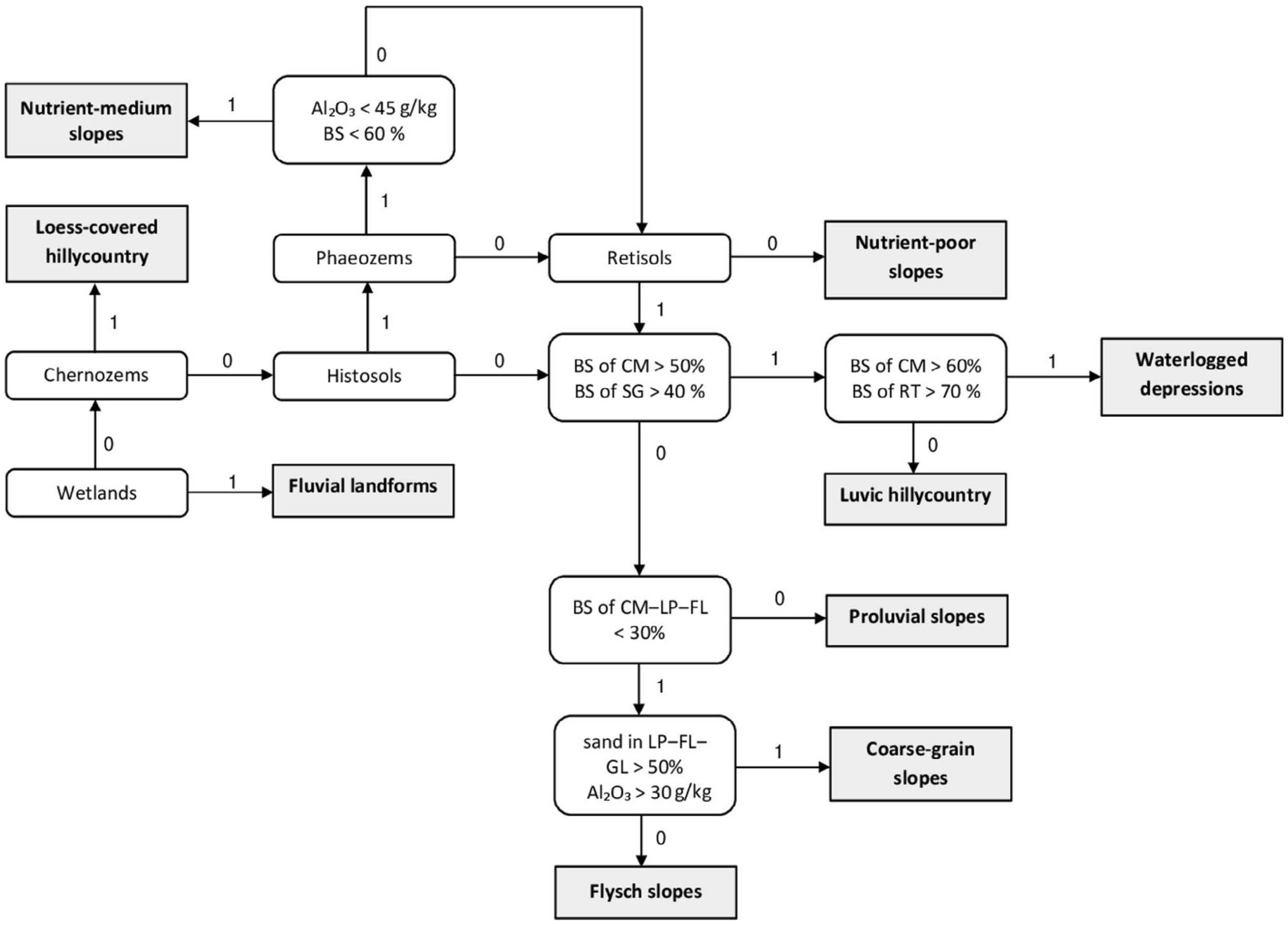
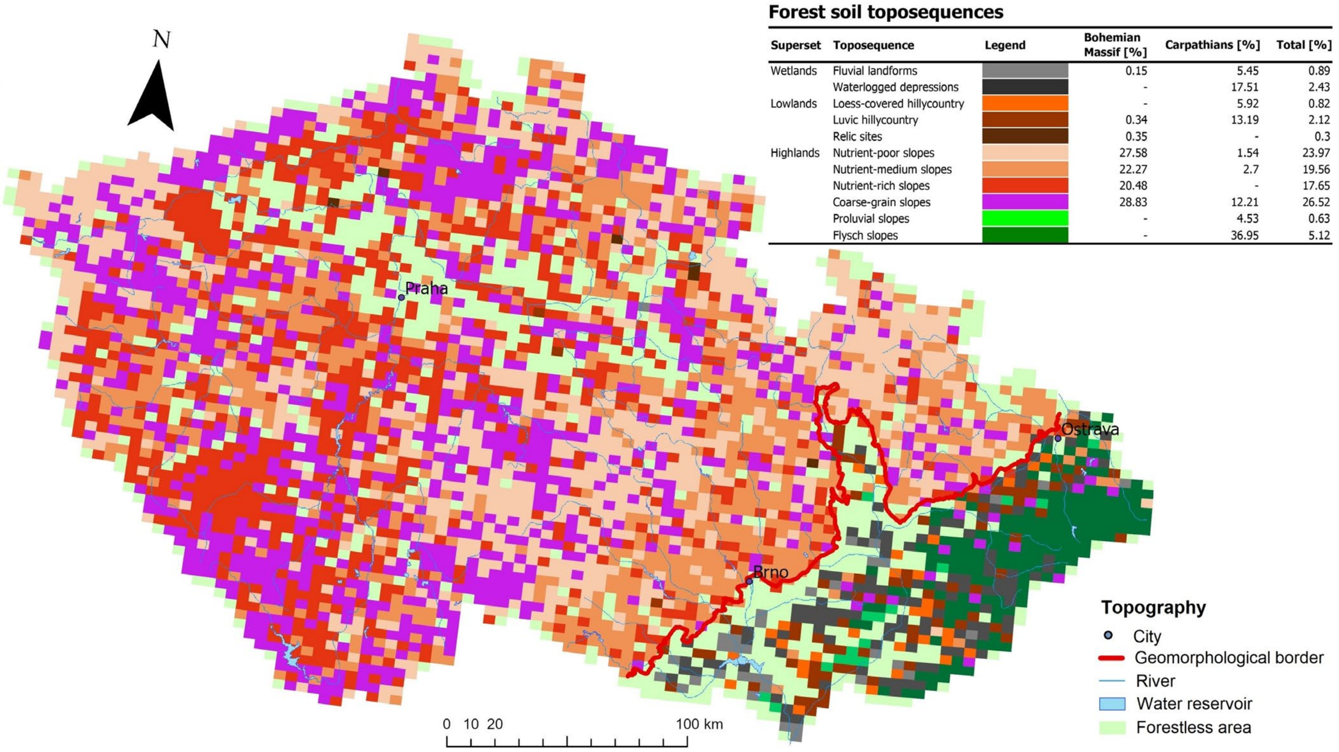


FIGURE 5 | Legend on next page.

FIGURE 5 | Classification chart of forest soil toposequences through soil group properties in the Bohemian Massif (a) compared with the Outer Western Carpathians (b). 1—Agreement; 0—Disagreement.



Forest soil toposequences

Superset	Toposequence	Legend	Bohemian Massif [%]	Carpathians [%]	Total [%]
Wetlands	Fluvial landforms	▨	0.15	5.45	0.89
	Waterlogged depressions	⬛	-	17.51	2.43
Lowlands	Loess-covered hillycountry	🟧	-	5.92	0.82
	Luvic hillycountry	🟫	0.34	13.19	2.12
	Relic sites	🟫	0.35	-	0.3
Highlands	Nutrient-poor slopes	🟧	27.58	1.54	23.97
	Nutrient-medium slopes	🟧	22.27	2.7	19.56
	Nutrient-rich slopes	🟥	20.48	-	17.65
	Coarse-grain slopes	🟪	28.83	12.21	26.52
	Proluvial slopes	🟩	-	4.53	0.63
	Flysch slopes	🟩	-	36.95	5.12

FIGURE 6 | Forest soil toposequence generalisation to dominant types in base map grid of the Czech Republic divided along the Bohemian Massif (west part) and the Outer Western Carpathians (east part).

and Stagnosols. In contrast, nutrient-poor slopes were characterized by the lowest Cambisol proportion < 30% in comparison with incline toposequences and by Stagnosol and Podzol associations covering < 13% of forests subsequently. The most common Cambisols covering > 60% in nutrient-rich slopes were followed by less than 13% of Leptosols and Stagnosols (Table 1).

The division of soil toposequences into two groups based on Cambisol dominance corresponded with edge differences in soil horizon properties. The soil horizon properties differed either vertically between TSH and SSH, or between toposequences. Clay and C_{org} contents differed markedly between soil horizons, but only insignificantly between toposequences. In return, contents of sand and silt, pH, base saturation and pseudo-total nutrients indicated some toposequences (Table 2). Fluvial landforms were characterised by the highest sand content > 80% and by the lowest contents of silt < 4%, clay < 1.8% and also C_{org}. On the other hand, the lowest sand content under the highest clay content, pH and BS, occurred in relic sites, while the highest C_{org} contents were concentrated between poor and nutrient-medium slopes. High sand content between 50% and 80% indicated both luvic hillycountries and coarse-grain slopes. The highest silt contents occurred between oppositely fertile slopes including relic sites. Similarly, lowest values of physicochemical pH and BS occurred in series from coarse-grain to nutrient-medium slopes. Highest contents of pseudo-total mineral nutrients indicated luvic hillycountries and relic sites, while the lowest contents indicated fluvial landforms as well as coarse-grain and poor slopes.

3.3 | Relief and Bedrock Contributions

Relief influenced means of soil properties in toposequences more than bedrock. The differences in soil property values among particular relief types were the most evident in subsurface horizons. Relief exerted the most obvious influence on fluvial landforms, which were linked to plain relief by almost 58%. On the other hand, broken plateaus and slopes provided prevailing conditions for most toposequences. Terrain depressions were only associated with the occurrence of luvic hillycountries and hillycountry altitudes were unique only for relic sites. Highland altitudes formed conditions for toposequence composition from nutrient-poor to nutrient-medium slopes (Table 3). The bedrock effect was less than the relief effect due to the marked presence of metamorphic rocks in most toposequences. Particular toposequences were influenced by waterlogged sediments, limestones and granites only between 8% and 30% (Table 4). The bedrock effect was more evident through the distribution of top-soil horizon properties, while relief tended to have a more significant effect on distributions of pH, base saturation C_{org}, Al_2O_3 and MgO in subsurface horizons. Bedrock influenced only BS, C_{org} and basic nutrients in the subsurface horizons. The bedrock effect was reflected only in the distribution of physicochemical

TABLE 1 | Reference soil group representation in toposequences of grain and chemical properties in the Bohemian Massif (%).

Toposequence	Histosols	Leptosols	Fluvisols	Luvisols	Cambisols	Podzols	Stagnosols	Gleysols	Others
Fluvial landforms	—	—	15.38	—	**23.08**	7.69	19.23	**30.77**	3.85
Luvic hillycountry	3.45	**39.66**	3.45	—	**44.83**	1.72	1.72	3.45	1.72
Relic sites	—	**57.63**	1.69	3.39	18.64	—	3.39	—	15.25
Coarse-grain slopes	0.31	1.14	0.31	0.12	**50.45**	27.59	1.57	1.86	0.61
Nutrient-medium slopes	2.53	1.53	0.82	4.67	**51.76**	4.49	15.28	3.72	6.97
Nutrient-poor slopes	**1.41**	**0.70**	**0.11**	**0.02**	**32.05**	**5.71**	**6.63**	**1.13**	**0.32**
Nutrient-rich slopes	0.29	6.46	4.10	1.18	**67.17**	3.16	6.80	5.22	2.67

Note: The sum of the most frequent soil groups covering > 50% of the toposequence was highlighted **bold**.

properties and of CaO values in the top-soil horizons, while the relief effect was limited to pH and BS in the top horizons (Table 5).

4 | Discussion

A flat area may be covered by fewer forest soil toposequences than neoid fold areas. Soil toposequence characteristics on the denuded territory of the Bohemian Massif were mostly based on soil group proportion and on soil properties, followed by relief effects preliminary to bedrock. Forest soil toposequences in the neoid Outer Western Carpathians were mostly influenced by soil properties and subsequently by bedrock rather than by relief. Regional differences in relief or bedrock effects were caused due to: (1) different geotectonic structures; (2) hillwash; and (3) weathering (Costantini et al. 2007; Khomo et al. 2013; Samec et al. 2019).

Relief and bedrock effects have linked soil with the landscape evolution to irreplaceable differentiation in needs toward restoration of managed ecosystems (Zinck et al. 2016).

4.1 | Soil Toposequence Differentiation

Soil property distribution was more pronounced in flat relief than in broken relief due to a close link between rock structure and geomorphology. The denuded Bohemian Massif is divided into areas differing significantly in origin, rocks and also in weathering (Chytrý 2012). The most contrasting systems are broken volcanic mountains since the Tertiary period, rock cities from Mesozoic sandstones, river basins and mountain plateaus. Volcanic mountains differ most relative to rock cities in nutrient content. Riverine basins, understandably, differ most from Variscan mountains through mean altitude (Pavlů et al. 2007). Though the Outer Western Carpathians are mostly built of acid sediments, the Outer-Carpathian relief is characterised by higher elevation between valleys and mountain peaks than the Variscan mountains (Culek 2007). Furthermore, the relief effect on Carpathian soils increased from flat forelands to broken flysch range. However, the influence of the Carpathian bedrock was slightly more pronounced due to homogenising hillwash effects (Samec et al. 2019).

Hillwashes are formed as surface soil sediments through gravitational movements, bioturbidity or by frost heave. The most widespread gravitational movements of earth masses dissect toposquences in a peculiar manner downslope and along contour lines. Gravitational division of soils in the Bohemian Massif has wiped out differences between distinct rock transitions, while in the Carpathians it mainly moderated slope gradients in a geologically more similar environment (Horáček et al. 2018). Though slope gradient moderation during soil development is accompanied by a gradual decrease in soil thickness below the peak, and an accompanying increase in the foothill, the toposequences tend to be more similar along the contour. The relief slope is reflected in the soil toposequence by skeletal rectification, while toposequence similarity is indicated by the redistribution of organic matter and skeleton after windfalls (Román-Sánchez and Šamonil 2022). The direction of hillwash similarity corresponded with alternating effects of the components of the geological environment between differently evolving geotectonic areas. Relief affected soil properties more in the Bohemian Massif. Rocks affected soil properties the most between fertile Carpathian foredeep and predominantly acidic flysch range. On the other hand, it is likely that irregularly spaced soil pits from routine forest surveys have only captured approximate directions of hillwash similarity. Hillwash properties were indicated indirectly by differences in grain size, C_{org}, CaO and P_2O_5 between soil group horizons (Dempster et al. 2013).

4.2 | Role of Geological Environment

The geological environment divided soil toposequences most clearly into waterlogged and water-unaffected. Low relief

TABLE 2 | Intervals of grain and chemical properties consisted of soil acidity (pH), base saturation (BS) and pseudo-total substance contents in forest soil toposequences.

Horizon	Toposequence	Sand (%)	Silt (%)	Clay (%)	pH (KCl)	BS (%)	C_{org} (%)	Al_2O_3 (g/kg)	CaO (g/kg)	MgO (g/kg)
Top-soil	Fluvial landforms	90.6 ± 6.03	4.0 ± 3.4	0.8 ± 0.8	4.3 ± 0.5	51.5 ± 31.9	1.1 ± 1.5	13.1 ± 13.3	2.4 ± 2.6	4.3 ± 7.8
	Luvic hillycountry	68.6 ± 12.9	11.5 ± 7.4	3.0 ± 3.1	5.4 ± 1.2	77.8 ± 24.2	3.8 ± 2.2	58.1 ± 32.5	33.5 ± 36.0	16.0 ± 14.8
	Relic sites	26.1 ± 17.9	28.5 ± 13.2	6.9 ± 6.6	6.4 ± 0.9	87.9 ± 21.1	4.7 ± 3.1	51.6 ± 32.9	116.6 ± 131.3	49.9 ± 62.2
	Coarse-grain slopes	55.6 ± 12.8	19.8 ± 7.6	2.5 ± 1.2	3.4 ± 0.4	17.3 ± 12.8	3.4 ± 2.3	21.7 ± 12.1	1.5 ± 1.4	3.5 ± 2.8
	Nutrient-poor slopes	39.6 ± 7.2	28.9 ± 6.8	3.3 ± 1.2	3.3 ± 0.2	13.6 ± 9.2	5.9 ± 4.2	15.2 ± 10.9	1.1 ± 1.5	2.2 ± 2.2
	Nutrient-medium slopes	23.8 ± 10.1	33.2 ± 10.3	4.6 ± 3.4	3.8 ± 0.6	32.9 ± 20.0	5.0 ± 4.4	31.8 ± 13.0	3.7 ± 3.8	5.3 ± 2.9
	Nutrient-rich slopes	38.6 ± 9.9	25.1 ± 7.9	3.9 ± 2.7	4.3 ± 0.9	52.3 ± 31.6	3.9 ± 2.4	41.2 ± 15.9	7.8 ± 9.5	8.8 ± 6.2
Sub-surface	Fluvial landforms	88.8 ± 4.7	3.9 ± 2.2	1.8 ± 1.8	5.4 ± 0.6	74.7 ± 27.2	0.4 ± 0.3	15.6 ± 17.4	1.9 ± 1.4	3.4 ± 4.6
	Luvic hillycountry	59.1 ± 16.0	15.0 ± 9.1	5.8 ± 5.9	5.8 ± 1.2	78.6 ± 26.1	1.7 ± 2.3	61.9 ± 35.8	46.1 ± 52.6	43.3 ± 54.8
	Relic sites	14.8 ± 14.0	26.2 ± 10.2	21.1 ± 13.6	6.7 ± 0.7	93.0 ± 12.6	1.7 ± 3.7	62.3 ± 32.4	124.2 ± 100.4	39.1 ± 115.3
	Coarse-grain slopes	61.5 ± 12.4	15.6 ± 6.8	3.1 ± 1.8	3.9 ± 0.4	20.0 ± 15.2	1.2 ± 1.7	25.9 ± 17.1	1.4 ± 2.5	4.3 ± 4.5
	Nutrient-poor slopes	41.6 ± 7.8	26.8 ± 5.5	4.1 ± 1.9	3.6 ± 0.3	12.3 ± 8.9	2.8 ± 4.4	16.9 ± 11.7	0.9 ± 1.3	2.4 ± 2.3
	Nutrient-medium slopes	23.4 ± 10.4	31.7 ± 9.7	8.6 ± 6.2	4.0 ± 0.6	34.3 ± 20.8	1.8 ± 4.8	40.9 ± 16.3	3.3 ± 3.9	6.5 ± 3.9
	Nutrient-rich slopes	39.0 ± 12.4	21.9 ± 7.9	6.5 ± 5.4	4.6 ± 0.9	52.0 ± 27.9	1.2 ± 1.8	53.8 ± 22.8	7.8 ± 11.8	11.0 ± 9.1

TABLE 3 | Representation of typified relief in forest soil toposequences of the Bohemian Massif (%).

Toposequence	**Depressions**	**Waterlogged plateaus**	**Plains**	**Valleys**	**Broken plateaus**	**Slopes**	**Hilly-countries**	**Rocky uplands**	**Highlands**	**Others**
Fluvial landforms	7.69	11.54	**57.69**	3.85	3.85	3.85	7.69	3.85	—	—
Luvic hillycountry	**13.79**	1.72	3.45	12.07	**37.93**	1.72	10.34	1.72	13.79	3.45
Relic sites	5.08	—	**15.25**	5.08	**18.64**	11.86	**28.81**	1.69	3.39	10.17
Coarse-grain slopes	6.10	0.65	11.18	5.47	**24.91**	**15.57**	**12.89**	3.00	10.83	2.73
Nutrient-poor slopes	7.10	0.13	5.33	6.33	**23.88**	**22.03**	10.28	1.00	**13.41**	3.30
Nutrien-medium slopes	9.42	0.24	9.24	7.86	**35.81**	**10.13**	8.02	0.95	**12.11**	3.35
Nutrient-rich slopes	7.98	0.43	6.97	9.99	**25.74**	**12.42**	**12.57**	0.60	11.82	8.26

Note: The sum of the most frequent relief types covering > 50% of the toposequence was highlighted in **bold**.

TABLE 4 | Bedrock representation in forest soil toposequences of the Bohemian Massif (%).

Toposequence	**Waterlogged sediments**	**Gravel-sands**	**Sandstones**	**Graywackes**	**Marls**	**Lime-stones**	**Granites**	**Volcanites**	**Meta-morphites**	**Others**
Fluvial landforms	**29.92**	**26.92**	3.85	—	7.69	—	3.85	—	11.54	19.23
Luvic hillycountry	**15.52**	1.72	5.17	1.72	3.45	**12.07**	1.72	8.62	**24.14**	25.86
Relic sites	5.08	**11.86**	1.69	1.69	**27.12**	**13.56**	—	10.17	5.08	23.73
Coarse-grain slopes	6.92	5.20	9.98	5.65	0.86	0.04	**14.67**	0.84	**37.80**	18.05
Nutrient-poor slopes	6.99	1.28	5.16	6.35	0.53	0.06	**12.77**	0.64	**49.45**	16.76
Nutrien-medium slopes	**11.03**	2.69	4.33	**15.28**	2.40	1.03	4.51	2.59	**26.84**	29.30
Nutrient-rich slopes	**8.03**	3.24	2.21	**7.26**	3.64	2.04	6.51	**7.00**	**33.11**	26.94

Note: The sum of the most frequent bedrocks covering > 50% of the toposequence was highlighted in **bold**.

TABLE 5 | Statistically significant differences (**bold**) between properties of forest soil toposequences and penetrating relief or bedrock types.

Structure	Horizon	Sand	Silt	Clay	pH	BS	C_{org}	Al_2O_3	CaO	MgO
Terrain	Top-soil	1.11	0.00	0.56	**2.23**	**2.23**	1.67	1.11	1.11	1.11
	Subsurface	1.67	1.67	1.11	**2.23**	**2.23**	**2.23**	**2.23**	1.11	**2.23**
	Total	1.11	1.67	1.11	1.67	1.11	1.67	**3.34**	**2.78**	**2.23**
Bedrock	Top-soil	1.11	1.11	1.67	**2.23**	**2.78**	1.67	0.56	**2.23**	0.00
	Subsurface	1.67	1.11	1.67	0.56	**2.23**	**2.23**	1.67	**2.23**	**2.23**
	Total	1.67	1.67	1.11	1.67	**3.34**	1.67	**2.23**	1.67	1.67

has conditioned the occurrence of waterlogged depressions only in the Carpathians, while fluvial landforms were distinguishable throughout the CR by means of soil groups or their chemical properties. Nevertheless, soil properties remained in more than 50% of the locations connected with flat relief in fluvial landforms, relic sites and luvic hillycountries. Lower water-unaffected toposequences were delineated along soil groups, while higher sequences were defined primarily by grain size or BS in subsurface horizons. The soil group effect was distributed along Cambisols covering $\leq 40\%$ or $> 40\%$ of the sequence (Khomo et al. 2013). Fluvial landforms included $> 57\%$ plain relief, $> 30\%$ Gleysols or soils sandy more than from 80%. Surrounding luvic hillycountries were characterised by highly fertile Leptosol and Cambisol associations. On the other hand, scattered relic sites distinguished by a predominance of Leptosols with the lowest sand content and the highest clay and nutrient levels and highest pH and base saturation (Kruckeberg 2013). The most widespread coarse-grained slopes were characterised by the common occurrence of Cambisols and Podzols with the lowest BS and with sand content $> 50\%$. Similar nutrient-poor slopes were typified by low nutrient contents at the highest C_{org} content, but differed in Cambisol proportion $< 30\%$, which were replaced by an association of Stagnosols with Podzols. In contrast, an association of Cambisols and Stagnosols with higher C_{org} contents was characteristic for nutrient-medium slopes (Pavlů et al. 2007), while nutrient-rich slopes were unprecedented by Cambisol occurrence exceeding 60% of the area and by subdominance of Leptosols and Stagnosols (Burns and Tonkin 1982).

The larger area of the Bohemian Massif and the smaller number of soil toposequences, meant that the most spread toposequences were characterised using properties mainly from Variscan areas. Different toposequence characteristics between the Bohemian Massif and Carpathians were due to both bedrock effects increasing from west to east and variable Al_2O_3 or P_2O_5 contents between soil horizons (Oppong Sarkodie et al. 2024). Lower Al_2O_3 content and the presence of Phaeozems differed Carpathian nutrient-medium slopes from the occurrences in the Bohemian Massif. Vertically distinct P_2O_5 content between soil horizons predetermined the occurrence of loess-covered hillycountries specifically in the Carpathians. Low phosphorus content specified nutrient-poor slopes (Samec et al. 2019). On the other hand, the low bedrock effect was mainly due to the extensive occurrence of metamorphites, which intruded into most of the toposequences. At the same time, waterlogged sediments, limestones and granites retained their influence on 30% of the area covered by forest soils.

The dominant relationship between granites or metamorphites and Cambisols has homogenised the proportion of soil toposequence in the Bohemian Massif compared to neoid fold areas. Toposequence homogeneity was conditioned by gentle slopes with low soil redistribution in cratonised reliefs (Khomo et al. 2013). In general, soil occurrence on gentle slopes is distributed between ridges covered by coarse-grain soils and hillslopes enriched by clay particles (Brown et al. 2004). On the other hand, the Cambisol dominance in the flysch range was related to slope movements, which accelerated the development of age-limited soil bodies (Costantini et al. 2007).

4.3 | Toposequence Applicability for Landscape Ecology

Soil toposequences can occur at unique compositions inside each geotectonical system. The unique occurrence of soil toposequences was caused by a change in only one soil-forming condition, although the other conditions were similar among adjacent geotectonical units. The variability in the soil-forming conditions suggested that the ecosystem classification mode could also be unique in each variously folded mountain range (Villela et al. 2013).

Really used classifications of soil-forming conditions focus on soil group occurrence estimation in the landscape. The indirect estimation of soil groups requires an equilibrium state at soil-forming processes. Because the equilibrium state with minimum intensity of soil-forming processes does not come naturally, the soil group modeling is limited to the estimation of probable occurrence in a space with permanent conditions (Paton et al. 1995). The probable occurrence of soil groups under permanent environmental conditions was classified as a forest soil association (Phillips and Marion 2007). Soil associations are inner-heterogeneous bodies consisting of matrices (with a proportion $> 70\%$) and facets (with a proposition $\leq 30\%$) of simultaneously evolving soils (Sedláček et al. 2009). Czechia is covered by 55 soil association types, from which 53 are covered by forests. Two associations occur outside forestland strictly and, conversely, six associations occur near-to-entirely under forests (Macků and Homolová 2007). Soil association definition indicated in general that the Bohemian Massif and the Outer Western Carpathians differ only by facets, while matrices occur similarly at both penetrating geotectonic systems.

Direct classifications of soil properties, contrarily, suggested that geotectonic systems penetrating the CR were covered by markedly different soils. Previous classifications of soil resistance against acidification through comparison of physicochemical properties with acid deposition and bedrock mineral reservoir have delineated the Carpathians as more resistant due to higher base saturation and proportion of deciduous forests (Purdon et al. 2004). Soil resistance against acidification was in the Bohemian Massif detected only apart in volcanic mountains and in karstic areas. The proposed soil toposequences also have distinguished geotectonic systems in the CR, but smaller rock outcrops were united along soil acidity. Soil acidity at both direct classifications delineated variously adaptable plant communities (Macků et al. 2006). The toposequences using differences between top and subsurface horizons specify approaches for ecosystem restoration after disruption with the presumption that soil develops slower than variable effects from the external environment (Zinck et al. 2016). Disfavourable topsoil horizon properties appear to be restorable through reintroduction of native tree species bounding base cations. Suitable topsoil horizons on acidic rocks can be protected through natural regeneration of native tree species (Vesterdal and Raulund-Rasmussen 1998).

5 | Conclusions

Variously folded mountains provide an environment for unique soil toposequence composition. Differences in soil toposequence proportions were caused by alternating relief or bedrock types, while chemical properties of single toposequences were affected the most by soil groups. The relief was more applicable in areas divided by differently weathered rocks. In contrast, bedrock was more applicable in rocky uniform areas. The influence of relief or bedrock on toposequences tended to be differentiated by soil granularity, base saturation, C_{org}, Al_2O_3, CaO and P_2O_5. The effects of differently formed relief types were indicated horizontally by variable physicochemical properties and by CaO content, while bedrock effects were indicated by vertically different contents of grain fractions, C_{org}, Al_2O_3 and P_2O_5 between soil horizons. The differences between soil horizons suggested toposequence effects on the occurrence of plant communities.

Author Contributions

Pavel Samec: conceptualization, methodology, formal analysis, writing – original draft. **Matěj Horáček:** conceptualization, methodology, visualization, writing – review and editing. **Jan Pecháček:** data curation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from Ministry of Agriculture of the Czech Republic. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the author(s) with the permission of Ministry of Agriculture of the Czech Republic.

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