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# The main causes of the variation in the soil aggregate proportion and stability along gradient of natural forests in the outer Western Carpathians, Czech Republic

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ABSTRACT

In soils, the proportion and stability of aggregates tends to differ with local relief and/or plant cover. In this study, we assess the dependence of forest soil aggregation on physical, physicochemical and (bio)chemical properties in a) topsoil and subsurface horizons, and b) between reference soil groups, altitudes and natural vegetation, in the Outer Western Carpathians (Czech Republic). Relationships between soil properties were modelled using multiple logistic regression, while impacts of habitat divisions were assessed through discriminant analysis. Overall, soil properties impacted aggregate stability indices more ($R^2$ 0.40–0.57) than aggregate proportion ($R^2$ 0.12–0.58) with diameter $< 3$ mm. Aggregate stability in topsoil was mainly influenced by clay content, total organic carbon, microbial biomass carbon, base saturation and activity of the enzymes acid phosphomonoesterase and urease. In deeper horizons, the influence of biogenic activity was reduced, with aggregation controlled mainly by sorption processes such as pH, base saturation and catalase activity. Bulk density was most affected by biogenic components in topsoil, which indirectly influenced porosity, total organic carbon and acid phosphomonoesterase activity. Water-holding capacity and porosity, closely linked to aggregate structure, better predicted macroaggregation than microaggregation. Thus, in natural forests, soil aggregation is most correlated with distribution of soil properties. Aggregate proportion differed markedly between broadleaved and coniferous forests, while aggregate stability differed most between marginal forest-steppe conditions and temperate forests from floodplains to mountains. Importantly, the results strongly support the main hypothesis that vegetation (forest community) has a stronger influence on soil aggregation than natural factors such as soil type or altitude. In contrast, presence of natural forest accounted for 59.9–71.9 % of soil aggregate proportion (SAP) in topsoil or subsurface horizons, and 54.0–75.0 % of aggregate stability (AS), Altitude affected 63.3–85.4 % of SAP and 53.9–64.6 % of AS, and soil group 57.3–81.3 % of SAP and 51.8–71.3 % of AS. These patterns reflect strong ecosystem gradients, with mixed and broadleaved forests supporting deeper, more stable aggregation than coniferous or marginal forest-steppe. Our findings highlight the fact that soil microbial activity and enzymatic functions, enhanced by species-rich vegetation, are the drivers of carbon sequestration and soil structure resilience, and that mixed forests promote aggregation across horizons, increasing carbon retention and ecosystem adaptability under changing habitat conditions.

## 1. Introduction

Soil aggregates are clusters of solid particles connected during soil-forming processes into structural elements. Soil structure is important indicator of soil quality and ecosystem function (Kibblewhite et al., 2007). The aggregation from soil structural elements is explored through variously shaped fractions influencing soil porosity and through aggregated particle stability suggesting soil physical property resistance (Mason et al., 2011). While soil aggregation is not presently considered a terrestrial ecosystem indicator, it is used as an indicator of ecosystem function and thus has potential for i) assessing natural vegetation cover, and ii) for use in sustainable landscape management proposals (Bronick

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and Lal 2005).

Formation of aggregates begins when primary finer soil particles, created through the progressive breakup of rock or organic residues during seasonal and chemical fluctuations, bind together into colloidal particles with larger active surfaces. The active colloidial surface has a predominantly negative charge from residual energy remaining after breakup and this can bind to cations (Mason and Moore 1982), thereby initiating aggregation (Six et al., 1998). The cation binding process is driven by the concentration of free hydrogen ions ($H^+$), manifesting as soil acidity (pH). Soil $H^+$ activity occurs through autoprotolysis or reactions of acids (Ross et al., 2008), with high $H^+$ concentrations displacing alkaline cations, binding anions and stimulating soil particle disintegration (Cosby et al., 2001). Conversely, low $H^+$ concentrations enable alkaline cation binding on soil particle surfaces, leading to condensation into high-molecular complexes.

The impact of soil pH on aggregation processes will vary depending on the concentration of organic matter in the soil and/or the presence of mineral colloids and bound polyvalent cations (Bronick and Lal 2005). Soil organic matter (SOM) is an important source of carbon, the main binder in aggregates. In chemically neutral soils, aggregates will be formed through particle bonding by exchangeable calcium and magnesium ions ($Ca^{2+}$ and $Mg^{2+}$), while in acidic or organically poor soils, aggregation depends on the presence of ferric and aluminium ions ($Fe^{3+}$ and $Al^{3+}$); in both cases, however, the resulting microaggregates are combined into macroaggregates through the addition of carbon in SOM (Barral et al., 1998; Six et al., 2002; Wuddivira and Camps-Roach 2007).

The combination of aggregates takes place through cementation or association, with the cementation process differing with mineral grain size and association depending closely on pH (Tobiášová et al., 2018). In coarse-grained soils, cementation takes place through the formation of an organic covering layer around the mineral grains, while in fine-grained soils, it is based on adsorption between mineral and organic colloids (Kleber et al., 2007). In contrast, association is based on condensation of organic molecules around charged (hydro)oxides, with a higher SOM content increasing aggregate stability directly under independence on inner conditions at various soil groups (Six et al., 2004). Stable organically-connected macroaggregates affect ecosystem functions more effectively in fertile soils (Jakšík et al., 2015).

This relationship between aggregation and soil properties ultimately dictates functioning of the soil-forming ecosystem, with aggregation, hydrostatic properties and nutrient supply supporting soil biological activity, water infiltration, hydraulic conductivity, aeration and nutrient availability (Patra et al., 2019; Nikodem et al., 2021; Pirmoradian et al., 2005). According to Wang et al., (2017), this influence of soil properties on aggregate formation, and subsequent changes in the soil environment caused by the permanent presence of aggregates, is suggestive of soil development self-regulation, which leads to increased soil resistance against external degradative influences, measured as aggregate stability (Saygin et al., 2012).

Plants contribute to soil aggregation through accumulation of SOM and intensification of chemical disintegration of rock/minerals through acid exudates (Blum et al., 2002). Furthermore, macroaggregate formation is predominantly driven by the activity of soil organisms, including plant root systems and fungal dynamics, and biochemical decomposition of organic residues (Coleman et al., 2018). Unless there is some disruption to inner-soil conditions, it is the feedback between plants and SOM that maintains the self-regulating development of soil macroaggregate formation. Such disruptions may include the natural temporary interruptions of seasonal vegetation dormancy, or permanent interruptions caused by the destruction of local plant communities (Kibblewhite et al., 2007), whether through fire, for example, or anthropogenic land management.

Aggregate stability will differ along relief, soil and plant community gradients. Differences in relief have significant impacts on soil development in geologically homogeneous environments (Zhang et al., 2021), with less stable aggregates forming on steep slopes and more stable aggregates on gentle slopes, especially where SOM accumulates (Canton et al., 2009). On the other hand, formation of stable aggregates in the topsoil of gentle slopes may be restricted under wet conditions through soil particle leaching (Amézketa 1999). The decline in soil $Ca^{2+}$ content caused by this leaching (or acidification) strongly supresses soil aggregation and, as a result, acidic soils are predominantly characterised by less stable microaggregates. Even in acidic soils, however, any increase in plant SOM can temporarily support the formation of more stable aggregates (Pirmoradian et al., 2005).

In this study, we investigate assumption that relationships between forest soil physical and (bio)chemical properties and aggregate proportion and stability are influenced more by site conditions than by natural natural plant conditions. Structurally, forests unite the most difficult terrestrial biomes on the planet (Olson et al., 2001). Unlike cultivated agricultural soils, forest soils tend naturally to have much higher rates of aggregation, with naturally annual increases in SOM input enhancing feedback dynamics with physical and chemical soil properties (Jakšík et al., 2015). The most resistant macroaggregates are formed through the annual forest growth dynamics of root systems and their associated microbial activity, which temporarily retain soil environmental features from the time of their formation. Subsequent mark influence of macroaggregates on soil structure reinforces the self-regulation of soil properties. Increasing correlations with biochemical properties suggest natural character of the ecosystem (Hishi et al., 2014). However, the relief affects aggregate stability more than SOM at hotspots under trees (Tomášová et al., 2024). Owing to joint effect between relief and plant community, the assessment of aggregation relationships is based on comparison of soil properties correlations distributed along natural conditions or along ecosystem types.

## 2. Material and methods

### 2.1. Geographical framework

Sampling for soil properties took place in natural forested biomes of the Outer Western Carpathians (OWC), Czech Republic (48.622–49.963 N, 15.983–18.853E; 150–1324 m a.s.l.; 12,114 km$^2$). Most of the Czech Republic lies on the Bohemian Massif (84.6 %), with part (15.4 %) including the Western Carpathians. At the border between these two geographic blocks, transitional temperate-zone forest biomes developed which have formed a key corridor for species migrations between northern and southern Europe since the end of the last ice age (Pokorný et al., 2015). Central-European biomes were distinguished along climate and water-influenced bedrock, which then condition mature forest stand structure (Neuhäuslová et al., 1997). The climatic properties of mean temperature and annual precipitation were obtained for the period 1961–1990 before global warming impacts became obvious for biome polygons overlayed onto the 1 × 1 km grid of the Czech Hydrometeorological Institute Database (Vondráková et al., 2013). Data on bedrock type in each polygon were obtained from the Czech Biogeographical Division database (Culek and Grulich 2009).

The biomes were distinguished as i) zonobiomes (conditioned strictly by climate properties at middle altitudes), ii) pedobiomes (conditioned by soil conditions, independent of climate) and iii) orobiomes (conditioned by high altitude) (Walter and Breckle 2002). Altitude data for each biome was obtained from the 10 × 10 m digital elevation model provided in the Geographical Database of the Czech Office for Surveying, Mapping and Cadastre (Samec et al., 2018). Terrestrial biomes, defined globally by Olson et al., (2001), were typified for the CR according to studies by (i) Míchal (1983), who identified dominant temperate mixed forest zonobiome and mountain taiga orobiome, (ii) Jeník and Sekyra (1995), who defined high-mountain tundra, (iii) Klimo et al., (2008), who distinguished floodplain forests, and (iv) Chytrý (2012), who distinguished forest-steppe and temperate conifer forests. At present, the Czech Republic supports six forest biome types, with 87.3 % of forested land comprising temperate mixed forest, 8.5 %

floodplain forest, 2.5 % forest-steppe, 1.2 % temperate conifer forest, 0.4 % mountain taiga and less than 0.1 % high-mountain tundra.

Carpathian forests were investigated at small selections of four natural stands corresponding with structure of each biome covering > 0.01 % (Kasmerchak et al., 2019). The selection was carried out among natural forests with continuous area > 1 ha or among supra-regionally important reserves, where the most widespread forest-steppe and mixed forest zonobiomes are protected over 3.14 % of the OWC area, the floodplain forest pedobiome over almost 3.1 %, while the least widespread orobiome of mountain taiga over 88.7 % (Simon 2004). In the OWC, the temperate mixed forest biome was distinguished as oak- and beech-forests in respect to natural variability of tree composition changing with altitude. Our selection of the natural forests was concentrated to localities with monitoring of forest types or ecosystem functions according to the principle of comparability among discontinuously occurring similar site conditions (McGloin et al., 2018). The monitoring of forest types focused on comparisons between specific forest areas, with localities included in the ecosystem function monitoring expanded to encompass the full altitudinal range of Central European forests (Krejza et al., 2021; Fig. 1). The monitoring in natural forests was established by Mendel University in Brno, while forest ecosystem functions are observed by Czech Academy of Sciences (Klimo et al., 2008; Acosta et al., 2017). Each selected forest stand was sampled from a single soil pit located to central part of the optimally grown plant community (Kučera et al., 2011).

### 2.2. Soil condition characteristics

Each soil-pit site was characterised by i) altitude zone, using the elevation model of Voženílek (2000), ii) reference soil group, according to the WRB-ISSS-ISRIC (Schad et al., 2014), and iii) surface and subsurface soil horizon organo-mineral properties (Kasmerchak et al., 2019). Soil properties were separated into independent variables (predictors) including granularity, hydrophysical, physicochemical and (bio)chemical properties and dependent aggregation variables (Table 1).

#### 2.2.1. Soil aggregation predictors

Soil properties were selected with respect to complex soil group characteristics, including natural plant community signs (Bauer et al., 2017). The grain particles were characterised as sand (0.1–2.0 mm), loam (0.05–0.1 mm), silt (0.002–0.05 mm) and clay (< 0.002 mm) granulometrically (Franciškovic-Bilinski et al., 2003). Soil hydrophysical properties were measured as mechanical bulk density ($D_d$), specific density ($D_s$) and hydrostatic water-holding capacity, porosity and aeration gravimetrically from a 100 $cm^3$ undisturbed soil core sample (Berger and Hager 2000). Physicochemical properties have included pH($H_2O$), assessed acidimetrically from a 1:2.5 soil/water suspension, and base saturation (BS), assessed via the ratio between base cation content and total exchangeable cation concentration at 0.1 M $BaCl_2$ (Cools and de Vos 2020). (Bio)chemical analysis focused on indicators of plant nutrient availability in SOM (Lehmann and Kleber 2015). Biochemical indicators were characterised through microbial carbon ($C_{mic}$), total organic carbon ($C_{org}$) and total nitrogen ($N_{tot}$) content, and enzyme activities of acid phosphomonoesterase (APMEA), urease and catalase (Rao et al., 2000). In this case, carbon and nitrogen content indicates total SOM availability, and enzyme activity is indicative of growth-limiting nutrient availability, with APMEA responsible for phosphorus availability and urease for nitrogen availability from organic matter in the presence of catalase. Content of $C_{mic}$, $C_{org}$ and $N_{tot}$ were measured spectrophotometrically according to Vance et al., (1987), APMEA according to Rejšek (1991), urease activity via

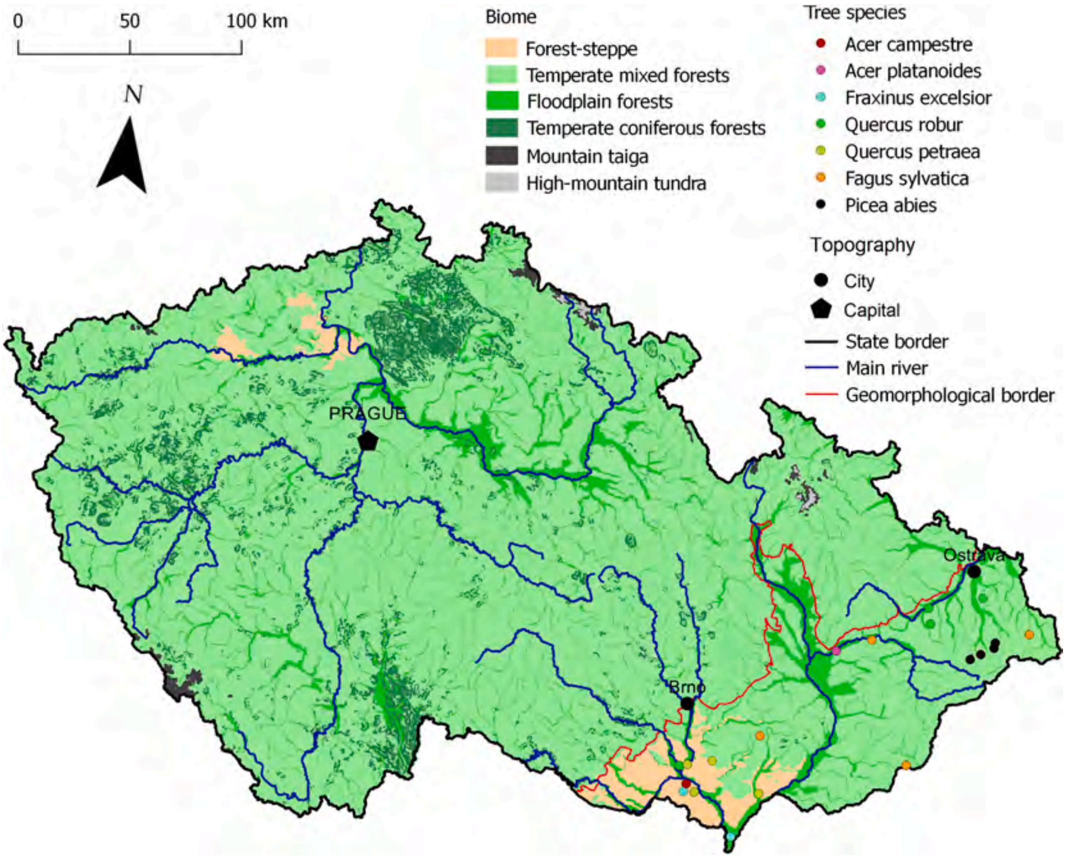


**Fig. 1.** Forest biome distribution in the Czech Republic divided between the Bohemian Massif in the west and the Outer Western Carpathians in the east with dominant tree species localisation in natural forests selected for the assessment of soil aggregation.

**Table 1**
Division of the measured soil properties into sets according to physical, physicochemical or chemical character.

| Set | Subset | Variable | Reference |
|---|---|---|---|
| Physical | Aggregation | Aggregate proportion | Kasmerchak et al. (2019) |
| | | Aggregate stability (WSI) | Nimmo and Perkins (2002) |
| | Granular | Grain size | Franciškovic-Bilinski et al. (2003) |
| | Mechanical | Bulk density ($D_d$) | Berger and Hager (2000) |
| | | Specific density ($D_s$) | Kučera et al. (2011) |
| | Hydrostatic | Water-holding capacity (WHC) | Spacik et al. (2023) |
| | | Porosity (P) | Kučera et al. (2011) |
| | | Aeration (A) | Kučera et al. (2011) |
| Physico-chemical | Soil acidity | pH($H_2O$) | Cools and de Vos (2020) |
| | Sorption | Base saturation (BS) | Kučera et al. (2011) |
| | | Cation exchange capacity (CEC) | Cools and de Vos (2020) |
| (Bio) chemical | Organic matter | Microbial carbon ($C_{mic}$) | Vance et al. (1987) |
| | | Total organic carbon ($C_{org}$) | Cools and de Vos (2020) |
| | | Total nitrogen ($N_{tot}$) | Cools and de Vos (2020) |
| | Enzyme activity | Acid phosphomonoesterase activity (APMEA) | Rejšek (1991) |
| | | Urease activity (UA) | Kandeler and Gerber (1988) |
| | | Catalase activity (CA) | Beck (1971) |

comparative incubation according to Kandeler and Gerber (1988), and catalase activity volumetrically according to Beck (1971).

### 2.2.2. Soil aggregate behaviour

Soil aggregation was assessed through fractionation and stability indexation on quantitative samples taken from each soil horizon. In each case, volume proportions of the soil aggregate fraction were measured using a Mastersizer 3000 laser particle size analyser (Malvern Panalytical, UK) with the connected Hydro LV dispersion unit (MIE optical model with 1.55 refractive index (quartz) and 0.1 adsorption). Dried samples were poured into the device under 2000 rpm stable water circulation until shading reached 2–4 %. Particle size distribution measurements, lasting 2 min each, were then repeated 18 times or until the circulation time exceeded 180 min, after which the measurements were extended to 10 min intervals. After reaching 180 min circulation, complete aggregate dispersion was achieved by adding 10 ml of 50 g/l $(NaPO_3)_6$ followed by ultrasonication for 240 s (Kasmerchak et al., 2019). The aggregate fractions were classified as microaggregates (≤250 μm) or macroaggregates (>250 μm), with microaggregates further divided into very fine (<2 μm), fine (2–16 μm), medium (16–50 μm) and coarse (50–250 μm) fractions.

Aggregate stability was assessed using the wet sieving procedure outlined in Nimmo and Perkins (2002). Briefly, soil samples were first disrupted for 3 min at a frequency of 35 cycles per min and a vertical amplitude of 1.3 cm. The remaining aggregates were then sieved into their separate fractions under the same disruption frequency and amplitude in a 2 g/l $(NaPO_3)_6$ solution until total disaggregation. The disaggregated particles were then dried at 105 °C and used for calculation of water stability index (WSI), based on the ratio between water-stable ($m_W$) and decaying particles ($m_D$):

$$WSI = \frac{m_W}{m_W + m_D} \tag{1}$$

where $m_W$ represents weight of aggregates dispersed in distilled water, while $m_D$ is weight of aggregates dispersed in the $(NaPO_3)_6$ solution.

## 2.3. Statistical modelling

Effects of forest soil properties on aggregation were statistically assessed through verification of the assumption about normality of the compared quantities, linearity in relationships between predictors and aggregate proportion and through verification of the variously divided habitat effects on relationships between soil properties. Normality and linear relationships between soil property predictors and aggregate proportion in each fraction were evaluated through exploratory data analysis. Generalised effects of soil properties on aggregate proportion were assessed through multiple logistic regression, while the effect of natural conditions on distribution of related soil properties and aggregation was assessed through discriminant analysis (DA).

Simple linear relationships were obtained using a linear correlation matrix, with significant Pearson coefficients (R) set at $p < 0.05$. Assumptions for multiple relationships were obtained from vector matches between corresponding z-transformed predictors and aggregation properties using principal component analysis (PCA), with matches taken from eigen value axes covering > 50 % of variance (Webster 2001). The number of significant eigen values was then used to limit factor analysis predictor sets, with soil properties potentially influencing aggregation selected through factor load, factor load power being derived through matches with vector occurrence on eigen value axes. Interpretation of sets as biogenic, sorption or weathering components was based on the most effective predictors indicating soil-forming processes (Lisetskii et al., 2015). Component scores confirmed the discriminability of biome types at different distances.

Non-linear effects of soil properties on aggregate proportion were compared, without respect to normal distribution, via logistic regression (LR) with the determination index $(R^2) > 0.5$, Akaike information criterion, residual normality, logit linearity, independence and multicollinearity applied on potentially correlating properties and cumulated predictor effects. Multiple non-linear regressions were optimised for dependent aggregation variables ($Y$) standardised into intervals (0; 1), as:

$$Y = \frac{e^{\sum_{k=1}^{q} b_q . x_q + c}}{1 + e^{\sum_{k=1}^{q} b_q . x_q + c}} \tag{2}$$

where $x$ is the standardised soil property, $b$ is function direction, $c$ is the intercept and $q$ is the number of soil properties Logistic parameters were extended with confidence interval from product between standard error and critical value of normal distribution ($z_{p/2} = 1.96$). The residual normality of the LR was checked using the Kolmogorov–Smirnov test, logit linearity using the Breusch–Pagan test for homoscedasticity, predictor independence using the Wald test and multicollinearity using the variation inflation factor (Ferrari and Cribari-Neto, 2004).

Habitat effects on distribution of related soil properties and aggregation were assessed through evaluation of biomes, altitudinal zones and soil groups by calculating the least square difference between canonical functions (CFSD) of predictors ($Z_{pred}$) and aggregation ($Z_{agg}$) after optimisation through DA:

$$CFSD = \left(\overline{Z}_{pred} - \overline{Z}_{agg}\right)^2 \tag{3}$$

These values were taken as averages of standardised classification coefficients of natural condition types ($Z_i$) in particular forest stands:

$$Z_i = \sum_{k=1}^{q} a_q . x_{iq} \tag{4}$$

where $i$ is the number of forest stands sampled; $a$ is the discriminant vector parameter obtained as a ratio of differences between standardised variables ($\overline{x}_j - \overline{x}_{j+1}$) and the covariance matrix, where $j$ is the number of natural conditions classified. Reliability of the canonical function was assessed via separability from the proportion of well-classified natural condition types (Guisan and Zimmermann 2000).

## 3. Results

### 3.1. Forest biome compounds

The most common Central-European temperate mixed forests cover around 68.6 % of the Outer Western Carpathians due to 19 % of floodplain forest and 12.4 % of forest-steppe (Table 2). Carpathian biomes tend to occur at lower altitudes than average in the Czech Republic, while marginal conifer forests are located higher than average. Furthermore, Carpathian biomes tend to occur under warmer conditions, while floodplain, mixed and mountain forests grow under wetter conditions than in other parts of the CR.

Mixed forests were sampled despite having relatively low coverage, a wide altitudinal distribution and four soil groups. Likewise, floodplain forests and forest-steppe were sampled separately, despite occurring in the same altitudinal zone and having partially overlapping soil groups. While Luvisols occur commonly under forest-steppe, floodplain and mixed forest, Fluvisols were typical for floodplain forest only and Cambisols and Stagnosols for mixed forest only. Mountain forests only occurred at high altitudes where Podzols prevailed (Table 3).

### 3.2. Exploratory soil data analysis

Silt, $D_d$, water holding capacity, porosity, aeration, base saturation and catalase activity distribution values for topsoil were all normally distributed, as were loam, silt, $D_d$, water holding capacity, porosity, aeration, physical chemistry, $N_{tot}$ and acid phosphatase activity in subsurface horizons.

In the most common biomes, topsoil generally had the highest soil property values. In subsoil, maximums for sand and silt grain fractions and phosphatase activity tended to occur in mixed forest, while maximums for hydrophysical and physicochemical properties occurred in forest-steppe. In contrast, lowest values for both normally and non-normally distributed properties were found in all habitats (Table 4).

Very fine, medium and coarse aggregate fractions were normally distributed in topsoil, as were macroaggregates in the subsurface horizons. Aside from the fine particle fraction, WSI was normally distributed in all topsoil fractions. Highest aggregate fraction values tended to be found in the most common biomes, as were maximum physicochemical properties, while lowest values tended to be found in the subsoil horizons of less widespread biomes, alongside aggregate fraction maximums. Highest topsoil WSI values were concentrated in zonobiomes, generally in subsurface soil horizons between floodplain and mixed forest, while lowest WSI values were recorded most often in mountain conifer forests (Table 5).

**Table 3**
Altitude zonality and soil group proportions (%) in sampled Carpathian forest biomes.

| Site component | Unit | Floodplain forests | Forest-steppe | Temperate mixed forests | Mountain taiga |
|---|---|---|---|---|---|
| Altitude zone | Lowland | 25.0 | 75.0 | – | – |
| | Upland | 75.0 | 25.0 | 50.0 | – |
| | Highland | – | – | 37.5 | – |
| | Mountain | – | – | 12.5 | 100.0 |
| Soil group | Fluvisols | 75.0 | – | – | – |
| | Luvisols | 25.0 | 50.0 | 37.5 | – |
| | Cambisols | – | 50.0 | 25.0 | 25.0 |
| | Podzols | – | – | 12.5 | 75.0 |
| | Stagnosols | – | – | 25.0 | – |

Soil properties affected aggregate size in topsoil horizons more than in subsurface horizons, with sand, silt, bulk density, water-holding capacity, physical chemistry and carbon affecting the proportion of macroaggregates the most, and loam, clay and porosity having a less significant effect. The influence of sand, silt, BS and $C_{mic}$ overcame to subsurface horizons. Similarly, hydrophysical and physicochemical properties, $C_{mic}$ and catalase activity also affected finer aggregates (Table 6). Other aggregate fractions displayed linear effects from soil properties only rarely. Most fractions in topsoil were influenced by $D_d$, pH and $C_{mic}$, while subsurface horizons were mainly affected by silt and pH. While sand, clay, porosity and carbon had a direct effect on macroaggregates, loam, silt, $D_d$, $D_s$ and physicochemical properties displayed indirect effects.

More than 50 % of variance in soil properties was regulated through three components. The most significant biogenic component covered 35.7 % of variance in topsoil horizons, based on correlations between $D_d$, clay and carbon content and phosphatase activity, and 23.3 % based on correlations between pH, aeration and catalase activity in subsurface horizons. The sorption component covered 20.2 % in topsoil, based on correlations between soil BS and catalase activity, and 21.7 % in subsurface horizons based on correlations between base saturation, $D_s$ and APMEA. The substrate component, consisting of the correlation between

**Table 2**
Terrestrial biome typification generalised along Bohemian Massif and Carpathians in the Czech Republic (CR).

| Characteristics | Zonality | Pedobiome | | Zonobiome | | Orobiome | |
|---|---|---|---|---|---|---|---|
| | Biome | Floodplain forests | Temperate coniferous forests | Forest-steppe | Temperate mixed forests | Mountain taiga | High-mountain tundra |
| Proportion (%) | CR | 8.49 | 1.20 | 2.49 | 87.34 | 0.42 | 0.07 |
| | Bohemian | 6.60 | 1.42 | 0.70 | 90.72 | 0.49 | 0.08 |
| | Carpathian | 18.97 | 0.00 | 12.40 | 68.61 | 0.02 | – |
| Altitude (m a.s.l.) | CR | 392.02 ± 164.71 | 379.32 ± 130.83 | 206.51 ± 51.73 | 470.24 ± 174.96 | 1117.97 ± 103.41 | 1274.11 ± 119.58 |
| | Bohemian | 410.12 ± 165.03 | 396.20 ± 105.83 | 222.88 ± 73.24 | 479.38 ± 170.94 | 1116.32 ± 103.85 | 1274.11 ± 119.58 |
| | Carpathian | 286.51 ± 119.16 | 379.47 ± 56.61 | 197.65 ± 29.49 | 372.09 ± 164.80 | 1194.84 ± 27.26 | – |
| Temperature (°C) | CR | 7.26 ± 0.98 | 7.02 ± 1.55 | 8.70 ± 0.56 | 7.05 ± 1.04 | 3.59 ± 0.55 | 2.82 ± 0.43 |
| | Bohemian | 7.17 ± 0.96 | 7.33 ± 0.48 | 8.10 ± 0.43 | 7.04 ± 0.93 | 3.58 ± 0.56 | 2.82 ± 0.43 |
| | Carpathian | 7.75 ± 1.08 | 8.14 ± 0.42 | 9.05 ± 0.25 | 7.55 ± 0.95 | 3.67 ± 0.49 | – |
| Precipitation (mm) | CR | 698.08 ± 112.28 | 654.27 ± 158.11 | 508.46 ± 26.40 | 704.87 ± 120.23 | 1068.34 ± 96.62 | 1069.42 ± 56.44 |
| | Bohemian | 695.52 ± 107.41 | 683.41 ± 78.93 | 513.95 ± 19.39 | 704.11 ± 107.15 | 1065.04 ± 94.10 | 1069.42 ± 56.44 |
| | Carpathian | 701.05 ± 140.61 | 607.67 ± 61.42 | 506.39 ± 30.56 | 729.93 ± 142.54 | 1222.23 ± 105.22 | – |

**Table 4**

Soil (hydro)physical and chemical properties in Carpathian forest biomes on territory of the Czech Republic. Grain fractions of sand [0.1–2.0 mm], loam [0.05–0.1 mm], silt [0.01–0.05 mm] and clay [< 0.002 mm] (%); $D_d$ – bulk density (g/cm$^3$); $D_s$ – specific density (g/cm$^3$); WHC – water-holding capacity (%); P – soil porosity (%); A – soil aeration (%); BS – base saturation (%); $C_{org}$ – organic carbon (%); $C_{mic}$ –microbial carbon (%); $N_{tot}$ – total nitrogen (%); APMEA – acid phosphomonoesterase activity (µg/hour); UA – urease activity (µg/hour); CA – catalase activity (µg/hour); $A_1$ – skewness test criterion; $E_1$ – elevation test criterion (**bold** significant disrupted distribution).

| Soil horizon | Property | Floodplain forests | Forest-steppe | Temperate mixed forests | Mountain taiga | E1 | A1 |
|---|---|---|---|---|---|---|---|
| Top-soil | Sand | 25.1 ± 16.9 | 34.4 ± 24.3 | 17.3 ± 8.6 | 44.1 ± 16.1 | 0.51 | **1.98** |
| | Loam | 10.7 ± 2.5 | 16.4 ± 6.3 | 16.4 ± 7.0 | 13.8 ± 4.0 | 0.95 | **2.84** |
| | Silt | 37.5 ± 10.5 | 36.0 ± 14.4 | 42.2 ± 9.1 | 29.4 ± 8.9 | −0.29 | 0.09 |
| | Clay | 9.2 ± 6.9 | 3.5 ± 4.7 | 8.1 ± 8.2 | 2.6 ± 3.3 | **6.63** | **4.54** |
| | $D_d$ | 1.02 ± 0.29 | 0.92 ± 0.08 | 0.98 ± 0.39 | 1.00 ± 0.34 | 0.45 | 0.96 |
| | $D_s$ | 2.38 ± 0.12 | 2.35 ± 0.1 | 2.21 ± 0.35 | 2.29 ± 0.15 | **4.99** | **4.09** |
| | WHC | 43.58 ± 8.54 | 34.53 ± 6.60 | 39.56 ± 13.20 | 39.65 ± 14.36 | 1.43 | 1.10 |
| | P | 57.53 ± 10.48 | 60.62 ± 2.84 | 56.09 ± 15.12 | 56.85 ± 12.59 | 0.50 | 0.78 |
| | A | 39.21 ± 12.02 | 51.18 ± 10.46 | 43.46 ± 20.35 | 29.83 ± 16.48 | 0.13 | 0.00 |
| | pH | 5.28 ± 0.62 | 6.3 ± 1.25 | 4.51 ± 1.10 | 3.62 ± 0.26 | −0.16 | **2.20** |
| | BS | 66.83 ± 38.4 | 85.49 ± 27.32 | 44.96 ± 28.19 | 14.1 ± 7.46 | 1.75 | 1.06 |
| | $C_{org}$ | 7.94 ± 4.65 | 7.74 ± 3.77 | 7.88 ± 8.16 | 6.01 ± 3.42 | **8.22** | **4.76** |
| | $C_{mic}$ | 949 ± 801 | 335 ± 123 | 1379 ± 1672 | 1933 ± 2335 | **7.96** | **5.71** |
| | $N_{tot}$ | 0.40 ± 0.19 | 0.53 ± 0.12 | 0.56 ± 0.50 | 0.31 ± 0.18 | **5.70** | **4.35** |
| | APMEA | 231.5 ± 139.5 | 194.1 ± 166.12 | 213.68 ± 148.62 | 184.66 ± 64.18 | **2.28** | **2.80** |
| | UA | 134.37 ± 95.65 | 169.83 ± 9.25 | 97.58 ± 87.3 | 53.7 ± 40.2 | 1.07 | **2.48** |
| | CA | 24.67 ± 16.51 | 82.4 ± 10.7 | 41.17 ± 32.65 | 12.95 ± 11.94 | 1.16 | 1.43 |
| Subsurface | Sand | 25.6 ± 19.9 | 38.4 ± 37.2 | 15.7 ± 7.1 | 45.2 ± 18.4 | 1.37 | **2.42** |
| | Loam | 10.2 ± 9.2 | 15.0 ± 8.9 | 15.8 ± 5.1 | 13.2 ± 2.2 | −0.03 | 0.93 |
| | Silt | 32.7 ± 14.5 | 33.8 ± 22.6 | 43.6 ± 7.8 | 29.3 ± 11.4 | 0.01 | 1.10 |
| | Clay | 14.2 ± 10.8 | 3.6 ± 4.8 | 7.7 ± 5.9 | 1.6 ± 1.1 | 1.12 | **3.07** |
| | $D_d$ | 1.32 ± 0.26 | 1.02 ± 0.30 | 1.32 ± 0.24 | 1.13 ± 0.06 | 0.62 | 0.88 |
| | $D_s$ | 2.50 ± 0.12 | 2.33 ± 0.16 | 2.38 ± 0.35 | 2.38 ± 0.13 | **9.98** | **5.06** |
| | WHC | 36.61 ± 7.72 | 29.78 ± 7.43 | 33.57 ± 3.4 | 36.50 ± 8.49 | 1.28 | 0.46 |
| | P | 47.34 ± 7.84 | 56.44 ± 11.32 | 43.96 ± 8.97 | 52.72 ± 1.00 | 0.85 | 0.96 |
| | A | 30.44 ± 20.79 | 47.54 ± 8.37 | 32.57 ± 19.04 | 30.64 ± 16.9 | 0.47 | 1.66 |
| | pH | 6.21 ± 1.40 | 6.38 ± 1.44 | 4.59 ± 1.26 | 3.98 ± 0.38 | 0.89 | 1.61 |
| | BS | 59.08 ± 41.96 | 82.18 ± 32.97 | 44.1 ± 29.58 | 13.7 ± 9.31 | 1.69 | 0.92 |
| | $C_{org}$ | 5.56 ± 6.87 | 2.58 ± 0.63 | 2.23 ± 1.98 | 3.00 ± 1.79 | **14.99** | **6.66** |
| | $C_{mic}$ | 518 ± 382 | 93 ± 49 | 509 ± 726 | 1098 ± 1171 | **6.99** | **5.17** |
| | $N_{tot}$ | 0.24 ± 0.14 | 0.24 ± 0.13 | 0.13 ± 0.11 | 0.18 ± 0.12 | 0.66 | 1.34 |
| | APMEA | 80.99 ± 40.69 | 70.37 ± 45.07 | 101.38 ± 67.97 | 89.64 ± 57.39 | 1.61 | 1.84 |
| | UA | 43.49 ± 47.51 | 81.31 ± 75.09 | 39.51 ± 44.43 | 22.52 ± 20.62 | −0.36 | **2.62** |
| | CA | 14.80 ± 14.00 | 48.52 ± 25.72 | 11.11 ± 13.17 | 6.41 ± 6.17 | **2.33** | **3.27** |

**Table 5**

Soil aggregate fractions and water stability indexes (WSI) in Carpathian forest biomes on territory of the Czech Republic. $A_1$ – skewness test criterion; $E_1$ – elevation test criterion (**bold** significant disrupted distribution).

| Soil horizon | Behavior | Fraction | Floodplain forests | Forest-steppe | Temperate mixed forests | Mountain taiga | E1 | A1 |
|---|---|---|---|---|---|---|---|---|
| Top-soil | Aggregates | < 2 µm | 27.56 ± 35.53 | 20.8 ± 19.07 | 5.02 ± 10.83 | 2.44 ± 4.05 | **6.90** | **5.23** |
| | | 2–16 µm | 19.58 ± 9.22 | 33.77 ± 7.96 | 26.01 ± 10.07 | 17.01 ± 5.67 | 0.05 | 0.14 |
| | | 16–50 µm | 20.51 ± 11.03 | 23.82 ± 6.58 | 30.66 ± 10.05 | 24.31 ± 6.52 | 0.76 | 0.55 |
| | | 50–250 µm | 26.51 ± 19.9 | 18.88 ± 7.55 | 31.58 ± 13.73 | 41.93 ± 4.13 | 0.70 | 0.25 |
| | | > 250 µm | 18.43 ± 5.58 | 18.24 ± 6.86 | 17.5 ± 12.79 | 34.31 ± 17.97 | **4.44** | **3.60** |
| | Index | $WSI_{vf}$ | 0.17 ± 0.1 | 0.08 ± 0.08 | 0.19 ± 0.06 | 0.11 ± 0.10 | 1.39 | 1.34 |
| | | $WSI_f$ | 0.42 ± 0.12 | 0.36 ± 0.07 | 0.34 ± 0.06 | 0.27 ± 0.06 | **2.33** | **2.07** |
| | | $WSI_{me}$ | 0.53 ± 0.15 | 0.50 ± 0.06 | 0.45 ± 0.07 | 0.35 ± 0.10 | 0.02 | 0.07 |
| | | $WSI_c$ | 0.66 ± 0.15 | 0.67 ± 0.06 | 0.59 ± 0.09 | 0.51 ± 0.07 | 0.53 | 0.97 |
| | | $WSI_m$ | 0.77 ± 0.12 | 0.88 ± 0.08 | 0.79 ± 0.14 | 0.71 ± 0.09 | 1.11 | 0.30 |
| Subsurface | Aggregates | < 2 µm | 26.76 ± 11.96 | 3.10 ± 1.44 | 8.11 ± 8.45 | 1.20 ± 0.34 | 2.69 | **3.48** |
| | | 2–16 µm | 32.65 ± 2.82 | 37.64 ± 7.19 | 33.64 ± 3.44 | 18.60 ± 4.23 | 0.24 | 1.38 |
| | | 16–50 µm | 22.31 ± 10.88 | 28.38 ± 2.67 | 31.52 ± 5.52 | 31.74 ± 6.40 | −0.35 | 1.02 |
| | | 50–250 µm | 14.12 ± 4.15 | 27.23 ± 6.60 | 24.08 ± 9.07 | 40.39 ± 6.71 | 0.60 | 0.45 |
| | | > 250 µm | 10.33 ± 8.62 | 10.99 ± 6.09 | 8.30 ± 8.63 | 23.95 ± 8.50 | 0.13 | 1.92 |
| | Index | $WSI_{vf}$ | 0.10 ± 0.10 | 0.21 ± 0.07 | 0.17 ± 0.08 | 0.13 ± 0.03 | 0.88 | 0.17 |
| | | $WSI_f$ | 0.41 ± 0.07 | 0.35 ± 0.02 | 0.36 ± 0.06 | 0.28 ± 0.01 | 0.36 | 1.22 |
| | | $WSI_{me}$ | 0.56 ± 0.04 | 0.49 ± 0.04 | 0.50 ± 0.06 | 0.34 ± 0.03 | 0.31 | 1.15 |
| | | $WSI_c$ | 0.70 ± 0.03 | 0.60 ± 0.03 | 0.63 ± 0.08 | 0.56 ± 0.05 | 0.23 | 0.84 |
| | | $WSI_m$ | 0.73 ± 0.08 | 0.74 ± 0.15 | 0.79 ± 0.15 | 0.75 ± 0.03 | −0.18 | 1.62 |

sand and silt content, covered just 12.4 % of variance in topsoil and 10.5 % in subsurface horizons (Fig. 2; Supplement 1). The component scores reflected the similarities between soil groups within particular forest stands, regardless of their relative distance. Soils under zonal mixed forests were most similar to floodplain forests. Forest-steppe soils contrasted with taiga soils, while they were most similar to floodplain soils

**Table 6**

Linear correlations between aggregate particles and (hydro)physical and chemical soil properties along top and subsurface horizons (for definitions of variables, see Table 4). Pearson coefficients significant at $p < 0.05$ are **bold**, moderately significant coeffients are normal and insignificant coefficients are grey.

| Horizon | Top-soil | | | | | Subsurface | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Variable | < 2 µm | 2–16 µm | 16–50 µm | 50–250 µm | > 250 µm | < 2 µm | 2–16 µm | 16–50 µm | 50–250 µm | > 250 µm |
| Sand | 0.00 | −0.07 | −0.37 | 0.08 | **0.41** | −0.03 | **−0.46** | −0.38 | 0.38 | **0.55** |
| Loam | 0.08 | 0.01 | 0.06 | −0.01 | −0.20 | −0.08 | 0.17 | −0.02 | 0.05 | −0.04 |
| Silt | −0.05 | 0.10 | **0.42** | −0.09 | **−0.43** | −0.14 | 0.38 | **0.54** | −0.26 | **−0.49** |
| Clay | −0.28 | −0.05 | 0.15 | 0.28 | 0.11 | **0.46** | 0.25 | −0.26 | −0.42 | −0.33 |
| $D_d$ | 0.18 | **0.40** | 0.02 | −0.35 | **−0.46** | **0.48** | 0.18 | −0.08 | **−0.50** | −0.14 |
| $D_s$ | 0.21 | 0.26 | −0.05 | −0.27 | **−0.44** | 0.33 | 0.15 | −0.19 | −0.26 | −0.34 |
| WHC | −0.03 | **−0.49** | −0.10 | 0.20 | **0.50** | 0.10 | −0.24 | 0.21 | −0.08 | 0.18 |
| P | −0.13 | −0.38 | −0.04 | 0.32 | 0.38 | −0.33 | −0.11 | −0.05 | 0.41 | −0.09 |
| A | 0.35 | −0.07 | −0.23 | −0.14 | 0.06 | −0.13 | 0.17 | −0.08 | 0.10 | −0.13 |
| pH | **0.45** | 0.34 | −0.21 | **−0.40** | **−0.41** | 0.27 | **0.58** | −0.42 | −0.36 | −0.10 |
| BS | 0.13 | **0.41** | −0.05 | −0.19 | **−0.41** | 0.16 | **0.59** | −0.17 | −0.31 | −0.41 |
| $C_{org}$ | −0.02 | −0.24 | −0.19 | 0.23 | **0.44** | 0.09 | 0.07 | −0.30 | −0.06 | 0.32 |
| $C_{mic}$ | −0.11 | **−0.41** | −0.12 | 0.36 | **0.42** | −0.11 | −0.43 | 0.05 | 0.26 | **0.57** |
| $N_{tot}$ | −0.14 | −0.06 | −0.10 | 0.20 | 0.31 | −0.12 | 0.21 | −0.04 | −0.02 | 0.33 |
| APMEA | −0.13 | −0.16 | −0.02 | 0.22 | 0.29 | −0.17 | −0.23 | 0.14 | 0.18 | 0.20 |
| UA | 0.00 | 0.18 | −0.13 | 0.03 | −0.15 | −0.08 | 0.34 | −0.13 | −0.03 | 0.15 |
| CA | −0.03 | **0.41** | −0.05 | −0.08 | −0.09 | −0.14 | **0.55** | −0.13 | −0.07 | −0.03 |

parallely with temperate mixed forests (Fig. 3).

Alternating principal component effects with increasing soil depth devided the correlations for predictors and aggregation. Biogenic component affected bulk density the most and indirectly carbon content, porosity and APMEA in topsoil, whereas its effect was limited to urease and catalase activity only in the subsurface horizons. Urease and catalase activity were strongly dependent on the sorption component as well as pH and BS in the topsoil. Sorption component was more pronounced in subsurface horizons, where it directly or indirectly affected most soil properties. Soil aggregate proportion was influenced equally by both main components. WSI was dependent more on soil properties directed by sorption component (Fig. 4).

PCA confirmed the effects of BS on aggregation in topsoil horizons; $D_d$ on fine aggregation; and water-holding capacity, phosphatase activity and $C_{mic}$ on coarse aggregation. Subsurface fine aggregates were affected most by clay, silt, $D_d$, pH, water-holding capacity and BS. Very fine aggregate WSI in topsoil was influenced most by APMEA and $C_{mic}$, while the coarser aggregate indices were influenced most by BS, $D_d$ and $D_s$. In contrast, very fine to medium aggregate WSIs were affected predominantly by catalase and urease activity, silt content and physicochemical properties, while coarser aggregate WSIs were mainly influenced by clay and silt content, $D_d$, water-holding capacity, physical chemistry and urease activity.

### *3.3. Generalised effects of soil properties on aggregation*

Soil aggregation predictors were unified from the most significant components through sand, silt and clay content, $D_d$, BS, $C_{org}$, $C_{mic}$, APMEA and catalase activity in topsoil horizons, and through sand and silt content, $D_s$, aeration, physical chemistry and phosphatase and catalase activity in subsurface horizons. Soil aggregates showed a significantly stronger dependence on non-linear combinations of physical and chemical properties than linear correlations with individual properties, with non-linear effects of selected potentially correlating properties on aggregate size varying between 1 and 39 % and the unified effect varying between 12 and 58 %. In contrast, predictor selection effect on WSI varied between 6 and 24 %, while the unified effect varied between 40 and 57 %. While chemical properties influenced aggregate size more in subsurface horizons than topsoil, WSI was more affected in topsoil than subsurface horizons, with the non-linear effect of soil properties being stronger on WSI than aggregate size (Table 7). Finally, soil properties had strongest influence on water stability in coarse aggregates ($R^2 > 0.57$) and least on fine aggregates ($R^2 \leq 0.40$); however, the fine aggregate index was affected more than other fractions in subsurface horizons ($R^2 \leq 0.45$), with macroaggregates affected via edge significance.

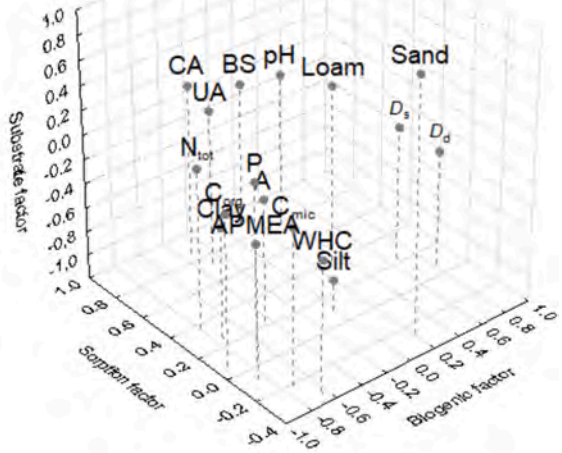
Logit linearity and predictor independence were generally maintained, but residual normality was affected for all aggregate sizes in topsoils. On average, the proportions of sand and silt ensured that multicollinearity remained mid-level. Uncorrelated clay, $D_d$, $D_s$, aeration, pH, base saturation, $C_{mic}$ and APMEA only occurred in subsurface horizons, while CA occurred in topsoil horizons and had an average positive impact on multicollinearity. In contrast, the higher multicollinearity of $C_{org}$ values increased the average multicollinearity in non-linear models (Supplement 2).

Soil predictors had an uneven influence on aggregation. Overall, non-linear function parameters tended to follow similar directions in subsurface horizons. Proportions of medium subsurface microaggregates and macroaggregates were the most significantly affected through phosphatase activity. The medium aggregate proportion was also markedly affected by silt and pH, while the macroaggregate proportion depended more on BS and catalase activity, but less on sand content, $C_{org}$ and pH. Topsoil WSIs depended consistently on sand and clay contents, $D_d$, base saturation and enzyme activities. The sand, $C_{org}$ and APMEA parameters influenced WSI at very fine aggregates. Topsoil chemical properties appeared to influence WSI in medium microaggregates and macroaggregates in the same direction, with strictly positive effects of chemical properties concentrated on medium to coarse microaggregates and positive effects of physical properties on fine to medium microaggregates. In contrast, subsurface horizons were characterised by similar effects of physical properties on the proportions of coarse microaggregate and macroaggregates, with an indirect influence on the edge stability of very fine microaggregates and macroaggregates. Aside from coarse microaggregates, strictly negative effects of granularity tended to occur more often in subsurface horizons. Physicochemical properties tended to influence the proportion of medium to coarse microaggregates in similar directions, but with a positive effect on fine to coarse aggregate stability. While enzyme activity showed a similar influence on fine to medium aggregates, the influence on medium to coarse aggregate stability was strictly negative (Supplement 3).

### *3.4. Common distribution between soil properties and aggregation*

Differences between discriminant functions for soil properties and aggregates increased from divisions along biomes, altitude zones to soil groups. Aggregate size corresponded more with topsoil horizon discriminant functions than WSI, while division of indices in subsurface horizons reflected soil properties more. Overall, difference values between discriminant functions corresponded with mean separability (Table 8). Forest biomes influenced 59.9–71.9 % of soil aggregate

**a) top-soil horizons**



**b) subsurface horizons**

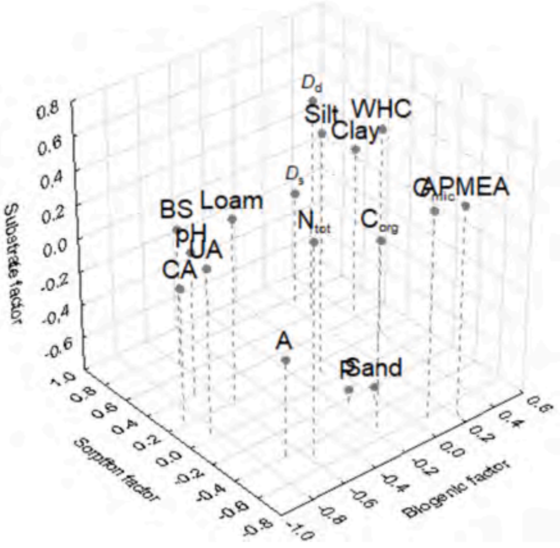


**Fig. 2.** Effects of factor loads on soil properties indicating biogenic, sorption and substrate component of aggregation in top and subsurface horizons (for definitions of variables, see Table 4).

proportion in topsoil and subsurface horizons, but 54.0–75.0 % of WSI; altitude influenced 63.3–85.4 % of aggregate proportion, but 53.9–64.6 % of WSI; and soil group separated 57.3–81.3 % of aggregate representation, but 51.8–71.3 % of WSI. On the other hand, subsurface soil properties were completely distributed along altitudinal zones and soil groups, though they did not achieve the same correspondence with aggregate distribution as biomes (Fig. 5).

Similarities between the distribution of soil predictors and aggregation in forest biomes were conditioned by similar discriminant function parameters. The function parameters along other types of natural condition divisions were contrast often. Consistently proportional chemical parameters, topsoil granularity parameters and all correlating subsurface physical properties confirmed similarities between floodplain and temperate forests. Overall, topsoil aggregate proportions were similar in floodplain and temperate forests, while subsurface aggregates were similar in forest-steppe and temperate forest. In contrast, topsoil aggregate stability was similar in floodplain, temperate and mountain forests, while subsurface aggregate stability was similar between forest-steppe and temperate forest only (Supplement 4).

## 4. Discussion

We found that temperate forest communities partitioned soil aggregation more strongly than altitude zones or soil groups through correlations with granularity, organic matter content, physical chemistry and biochemistry. The statistically significant influence of soil properties formed under living systems suggests that soil aggregation could act as a complex indicator of ecosystem status.

### 4.1. *Soil survey design limitations*

Soil behaviour was evaluated through multivariate analysis after partitioning the input data into predictors and receptors (Ferrari and Cribari-Neto 2004). Dependences determined multivariately, were closer than simple correlations alone. Linear correlations characterised 11–24 % of variance between soil properties and fine microaggregates, and 1–32 % of variance with macroaggregates, while multiple logistic regressions described 12–58 % of variance with microaggregates and 28–57 % with macroaggregates. While aggregation was more affected by sand, silt, bulk density, water-holding capacity, base saturation and $C_{org}$ in topsoil horizons, closest dependences of soil aggregation were conditioned through the influence of physicochemical properties and enzyme activity. High multicollinearity of sand, silt and $C_{org}$ data suggested overestimated effect on aggregation. On the other hand, soil BS had an uniform influence on aggregate proportion and stability in both topsoil and subsurface horizons, confirming it as a useful indicator of soil behaviour. Indeed, use of soil fertility assessed through BS has already been shown to increase the reliability of soil acidification and water retention models (Bauer et al., 2017). Soil effects based on enzyme activity were classed under the two most significant biogenic and sorption components. Acid phosphomonoesterase activity with clay content, $C_{org}$ and bulk density represented the biogenic component. Catalase activity with BS represented the sorption component. Less significant substrate component was based predominantly on effects by particle fractions of sand and silt.

The partitioning of soil data into predictors and aggregation receptors also enabled simulation of soil behaviour through standard global approaches (Webster 2001). In this study, predictors were defined through (hydro)physical, physicochemical and (bio)chemical properties, including bulk density, water-holding capacity, porosity and aeration; note, however, these can also be defined through soil aggregation (Kibblewhite et al., 2007). For example, while our results showed soil $D_d$ as strongly associated with microaggregation, water holding capacity was more strongly related to macroaggregation. While mechanical soil properties are not normally related to aggregation in coarse-grained soils, macropores, and even major micropores, occur in the spaces between aggregated particles (Menon et al., 2020), with macropores ($\geq$0.08 mm) arising most frequently as cavities between stone contacts or through soil biota activity. Unclear soil pore formation suggests either deviations in global model accuracy or their elimination through self-regulating functions (Forman and Godron 1986). On the other hand, soil porosity is an elementary indicator of soil structure and, as such, is a simpler means of deriving soil aggregation (Rabot et al., 2018). Similarly, water holding capacity, which is strongly dependent on presence of micropores, clay content and/or $C_{org}$, can be derived from the proportions of soil aggregates. As water holding capacity is also a soil group indicator, however, its use as a compound ecosystem assessment predictor is simpler than through aggregation (Chersich 2018).

Principal components of soil aggregation confirmed correlations between grain composition and SOM, with decomposition of organic

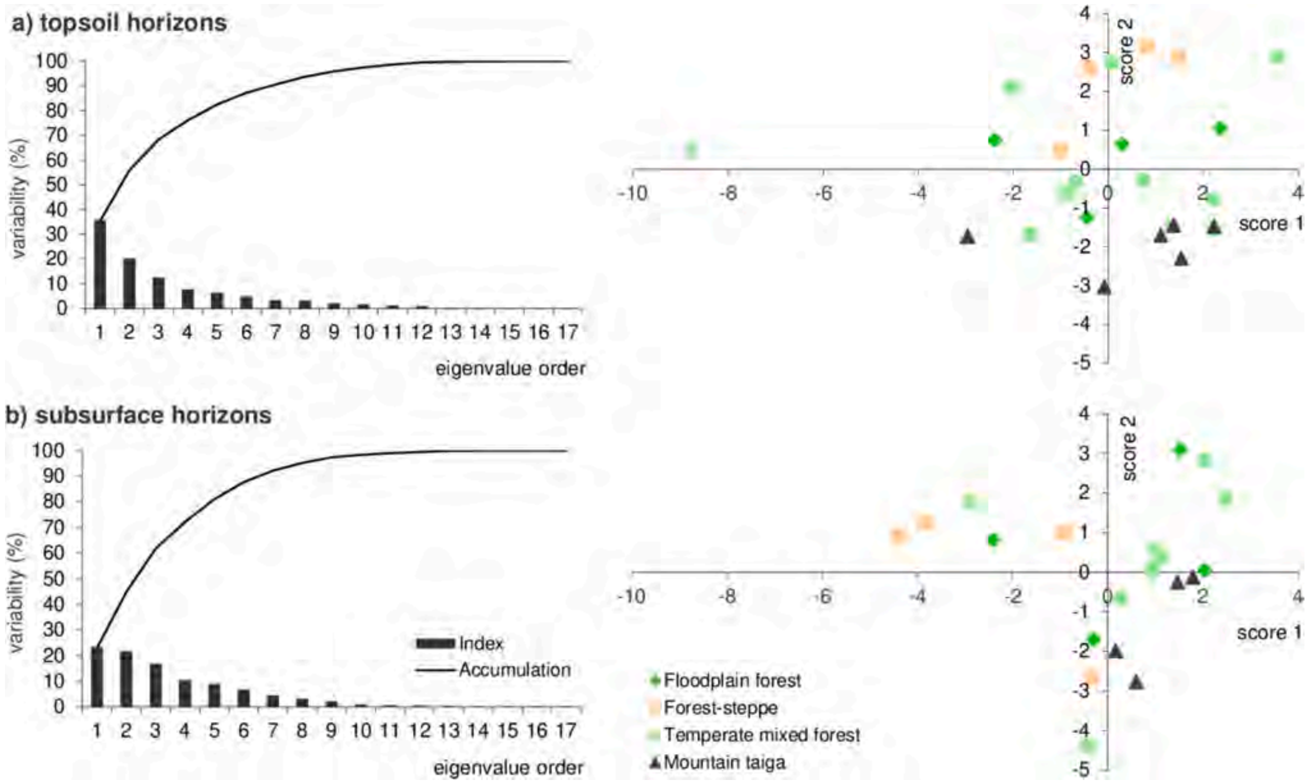


**Fig. 3.** Principal component eigenvalues with cumulative variability (left) and scores (right) from soil properties between top and subsurface horizons in the Carpathian forest biomes.

residues responsible for soil-forming microprocesses and differential processes, while soil properties related to biogenic components were responsible for cementation and/or association microprocesses. Likewise, negative correlations between grain-size and $C_{org}$ corresponded with mineral grain cementation in soil microaggregates, while positive correlations were related to increased proportion of organic matter associations in soil macroaggregates. Our modelled soil aggregate fraction estimations confirmed pH as a releaser enabling the breakup of organic macromolecules (Nimmo and Perkins 2002). Soil acidity accounted around 22 % of aggregation conditions under the sorption component. The most important driver within the sorption component was catalase activity, which impacted aerobic soil organic matter decomposition processes by interfering with BS development through preservation of organic colloids (Ross et al., 2008). At the same time, organically bound carbon content, together with clay and phosphatase activity within the biogenic component, were the dominant plant community factors affecting soil aggregation.

Though our single soil survey did not allow observation of local modes towards aggregate formation and stabilisation, the PCA revealed generally widespread modes of soil aggregation through correlations between BS and biochemical properties, and $C_{org}$ with coarser aggregates. However, both sand, silt and $C_{org}$ content and enzyme activity obtained in the single survey were affected by multicollinearity, which overestimated the effect on coarser aggregates in subsurface horizons. As coarse grain fractions tend to be less variable over time due to gradual release during rock weathering, their effect on aggregate distribution is mainly limited to less stable microaggregates (Tobiášová et al., 2018). Similarly, the higher multicollinearity of $C_{org}$ rarely affects the stability of very fine aggregates. Overall, a higher content of coarse grain fractions or $C_{org}$ distinguished aggregation in Cambisols and Podzols, as opposed to Fluvisols and zonal Luvisols. Consequently, the significantly lower multicollinearity of $C_{mic}$ and the predominantly medium multicollinearity of enzyme activity supported dominance of the biogenic component in soil aggregation (Alaboz, 2020).

### 4.2. Forest environmental effects on soil aggregation

Our results showed a clustering of similar soil aggregates along temperate forest types that differed according to altitude or soil group. The significance of soil aggregation was limited by the soil-forming environment. In effect, spatial divisions of weathered mantle relief or soil groups create localised conditions for differential soil aggregation, to which vegetation then adapts (Lisetskii et al., 2015). Nonetheless, soil separability could have been increased through the inclusion of other relief features or soil typification. Under the same climatic conditions, bedrock type will have a strong influence on weathering rate, which influences organic matter decomposition more than vegetation. Favourable relief without any abrupt downslope movements and depth of associated soil particle occurrence, preserved against weather fluctuations, affects aggregate stability (Shedayi et al., 2016).

Slope movements, weather fluctuations and rock weathering rates all infer selection on transported particles, resulting in differing granularity and soil aggregation (Zaleski et al., 2006; Mazurek et al., 2018). These habitat effects on soil aggregation are changeable due to vegetation growth, which accumulates humus in soil (Chersich 2018). Surface humus accumulation is concentrated into cold and acidic conditions, where coarser granularity of soil-forming substrates supports occurrence of coniferous forests (Ding et al., 2017). The more demanding broadleaved tree-species were able to adapt topsoil horizons for successful regeneration due to humus concentrating alkaline substances from soil to stabilise organic matter (Tobiášová et al., 2018). Natural differences in the demands of conifer and broadleaved tree-species on sites have highlighted transients among topsoil properties in different forest types. In our study, aggregate correlations suggested a territorial relationship between floodplain and mixed forest/forest-steppe, while aggregate stability was dependent on soil properties likewise in wide gradient from floodplain to mountain forest out of edge conditions at forest-steppe.

The component scores confirmed that forest-steppe soils in the Outer Western Carpathians provided marginal conditions for forest growth.

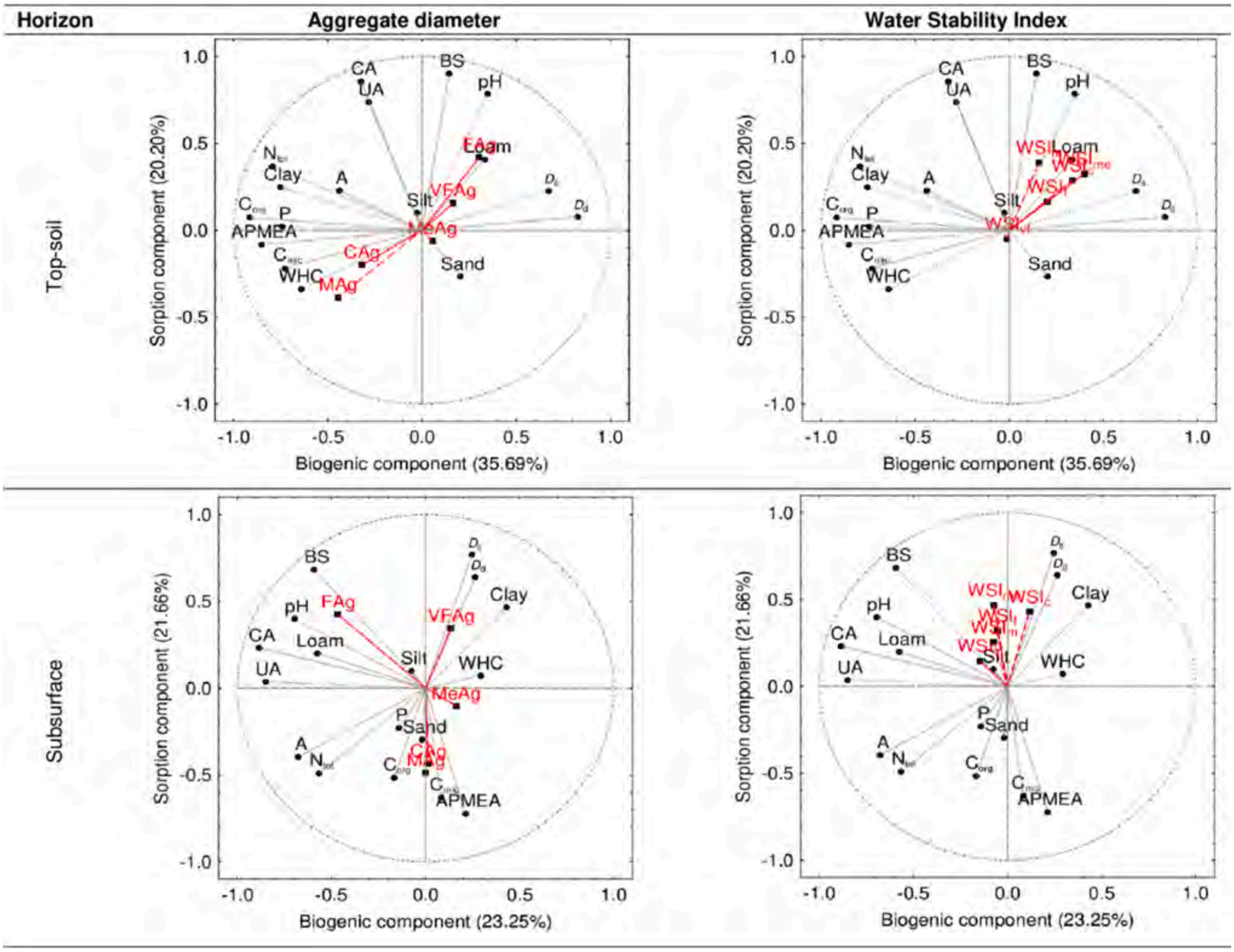


**Fig. 4.** Component vectors comparing relationships between soil physical and (bio)chemical properties and aggregate behaviour in top and subsurface horizons (for definitions of variables, see Table 4).

**Table 7**

Composite logistic model attributes for aggregate size and water stability indices estimations. Determination indices explaining more than 50 % of total variability or significant test criterions are **bold**.

| Parameter | Behaviour | Horizon | < 2 μm | 2–16 μm | 16–50 μm | 50–250 μm | > 250 μm |
|---|---|---|---|---|---|---|---|
| $R^2$ | Aggregate size | Top-soil | 0.12 | 0.44 | 0.44 | 0.47 | 0.28 |
| | | Subsurface | 0.37 | 0.49 | **0.58** | 0.29 | **0.57** |
| | Water stability index | Top-soil | **0.52** | 0.40 | **0.54** | **0.57** | **0.50** |
| | | Subsurface | 0.46 | 0.45 | 0.41 | 0.41 | 0.40 |
| AIC | Aggregate size | Top-soil | 77.25 | 32.89 | 78.01 | 79.74 | 88.35 |
| | | Subsurface | 49.09 | 61.37 | 58.40 | 71.11 | 48.30 |
| | Water stability index | Top-soil | 64.03 | 85.52 | 74.49 | 75.70 | 76.88 |
| | | Subsurface | 68.67 | 63.61 | 67.69 | 67.34 | 69.91 |
| Residual normality | Aggregate size | Top-soil | **0.41** | **0.40** | **0.40** | **0.45** | **0.45** |
| | | Subsurface | **0.49** | 0.43 | 0.29 | 0.39 | **0.51** |
| | Water stability index | Top-soil | **0.42** | **0.40** | **0.40** | **0.40** | **0.40** |
| | | Subsurface | 0.34 | **0.56** | 0.41 | 0.40 | 0.33 |
| Linearity | Aggregate size | Top-soil | 4.65 | **18.16** | 9.96 | 8.88 | 8.40 |
| | | Subsurface | 9.08 | 7.57 | 3.03 | 2.17 | 5.80 |
| | Water stability index | Top-soil | 11.20 | 6.56 | 11.65 | 10.96 | 13.36 |
| | | Subsurface | 7.58 | 4.26 | 6.19 | 4.32 | 4.94 |
| Independence | Aggregate size | Top-soil | 0.02 | 2.80 | 0.19 | 0.02 | 2.70 |
| | | Subsurface | 0.22 | **5.80** | 0.42 | 1.50 | 1.80 |
| | Water stability index | Top-soil | **3.90** | 0.13 | 3.70 | **3.90** | **5.00** |
| | | Subsurface | 0.83 | 3.00 | 1.20 | 0.37 | 1.00 |
| Multicolinearity | Aggregate size | Top-soil | 6.65 | 6.69 | 6.87 | 6.89 | 6.68 |
| | | Subsurface | 6.00 | 5.63 | 6.03 | 6.00 | 6.77 |
| | Water stability index | Top-soil | 7.32 | 6.59 | 6.38 | 6.36 | 6.25 |
| | | Subsurface | 6.11 | 6.03 | 5.98 | 5.92 | 5.94 |

**Table 8**
Comparison of separabilities between soil properties (variables) and aggregate behavior and canonical function square differences (CFSD) in forest habitat divisions.

| Soil horizon | Division | Unit | Variables | Aggregates | WSI |
|---|---|---|---|---|---|
| Top-soil | Biomes | Floodplain forest | 100.00 | 50.00 | 25.00 |
| | | Forest-steppe | 100.00 | 50.00 | 50.00 |
| | | Temperate mixed forest | 90.91 | 72.73 | 90.91 |
| | | Mountain taiga | 100.00 | 66.67 | 50.00 |
| | | CFSD | – | 289.91 | 340.02 |
| | Altitudes | Lowlands | 100.00 | 75.00 | 25.00 |
| | | Uplands | 100.00 | 70.00 | 70.00 |
| | | Highlands | 100.00 | 33.33 | 33.33 |
| | | Mountains | 100.00 | 75.00 | 87.50 |
| | | CFSD | – | 402.84 | 425.56 |
| | Soil groups | Fluvisols | 100.00 | 66.67 | 33.33 |
| | | Stagnosols | 100.00 | 75.00 | 50.00 |
| | | Luvisols | 100.00 | 33.33 | 50.00 |
| | | Cambisols | 100.00 | 40.00 | 40.00 |
| | | Podzols | 100.00 | 71.43 | 85.71 |
| | | CFSD | – | 2087.49 | 2252.85 |
| Subsurface | Biomes | Floodplain forest | 50.00 | 75.00 | 100.00 |
| | | Forest-steppe | 100.00 | 50.00 | 50.00 |
| | | Temperate mixed forest | 87.50 | 62.50 | 50.00 |
| | | Mountain taiga | 75.00 | 100.00 | 100.00 |
| | | CFSD | – | 462.26 | 332.78 |
| | Altitudes | Lowlands | 75.00 | 75.00 | 50.00 |
| | | Uplands | 100.00 | 100.00 | 75.00 |
| | | Highlands | 100.00 | 66.67 | 33.33 |
| | | Mountains | 80.00 | 100.00 | 100.00 |
| | | CFSD | – | 1933.53 | 850.78 |
| | Soil groups | Fluvisols | 66.67 | 100.00 | 100.00 |
| | | Stagnosols | 50.00 | 100.00 | 50.00 |
| | | Luvisols | 83.33 | 66.67 | 66.67 |
| | | Cambisols | 80.00 | 40.00 | 40.00 |
| | | Podzols | 75.00 | 100.00 | 100.00 |
| | | CFSD | – | 564.15 | 369.78 |

Forest-steppes were opposite to mountain taiga under upper tree limit. Conversely, floodplain soils were more similar to those found in zonal mixed forests, despite being located close to forest-steppe at low altitudes (Klimo et al., 2008). These contrasts in component scores were most evident in topsoils, whereas contrasts in subsurface horizons appeared more clearly defined according to soil acidity. The contrasts in topsoil scores suggest consequences for plant community differentiation in terms of soil aggregation. Soil exchangeable cations contribute to site fertility by mediating connections between microbial saccharides and clay, forming firmer, more stable aggregates than dead organic matter alone (Chenu and Stotzky, 2002). Under these conditions, soil biota actively organise clay particles and dead organic matter, thereby accelerating aggregation (Tisdall et al., 1997). In contrast, subsurface soil properties separated conditions for less stable aggregation under similarly acidic spruce, mountain beech and forest-steppe oak forests from more stable aggregation in fertile floodplains, forest steppe and upland mixed forest. The differences between forest soil horizons distinguished the effects of biota on soil aggregation in the surface layers from the effects of mineral particles and dead organic matter in the deeper layers (Wuddivira and Camps-Roach, 2007). While biota effects differed between forest communities, and were lower in subsurface soil horizons, their effect remained higher than that of the bedrock. The most effective biogenic component within soil property correlations included aggregated particle composition and biochemical activity. The phosphatase activity and $C_{mic}$ content differed between forest communities by way of main factors genesis toward soil aggregation. APMEA decreases most with soil depth, where vegetation effects become inhibited, while it decreases least with altitude, where vegetation becomes more homogeneous until conifers dominate. In contrast, more diverse vegetation indicates an increase in soil biochemical activity, which in turn has the greatest effect on aggregation (Gu et al., 2020). Mixed forests, that provide suitable conditions for species-rich ground flora, improve soil due to aggregation in more horizons simultaneously. The deeper soil aggregation subsequently supports ecosystem adaptability during environmental changes through longer retention of carbon substances from dead organic matter decomposition (Feng et al., 2024).

According to Basset et al. (2023), changes in infiltration rates are mechanistically governed by the dynamics of soil structure, which mediates the interactions between soil water and vegetation. An increase in aggregate size (MWD $>$ 3 mm) and a higher proportion of water-stable aggregates (WSA $>$ 70 %) promote the formation of macropores that substantially facilitate preferential water flow, thereby enhancing water availability for plants (Nawaz et al., 2013; Huang and Hartemink, 2020). This effect is further amplified by the accumulation of soil organic carbon (SOC $>$ 1.5 %), which supports aggregation and the permanent development of pore networks (Nyamadzawo et al., 2007; Jemai et al., 2012). Conversely, high bulk density and structural degradation, often resulting from intensive tillage or compaction, restrict infiltration, leading to greater surface runoff and potential vegetation stress (Sastre et al., 2018). These findings confirm that the relationship between soil–water–vegetation processes and observed infiltration patterns is dynamic: changes in soil management directly influence structure, which regulates soil hydraulic properties and, in turn, feeds back to vegetation processes through altered water availability (Noellemeyer et al., 2008).

Such dynamics are also evident when comparing different ecosystems. According to Gajić et al. (2010), a higher content of soil organic matter (SOM) in forest soils—particularly within the 0–30 cm soil horizon—contributes to improved soil aggregate stability compared to grassland and agriculturally managed soils. This assertion is consistent with earlier findings (Tisdal and Oades, 1982), which emphasize that the structural complexity of forest ecosystems—such as well-developed root systems and fungal hyphae—enhances the formation and stabilization of soil aggregates. In broadleaved forests, the high quality of litter, rich in labile carbon and nutrients, promotes microbial activity and SOM formation, subsequently increasing the proportion of water-stable aggregates ($>$0.25 mm) and enhancing the weighted mean weight diameter (wMWD) of aggregates. In contrast, soils subjected to long-term tillage or maintained as grasslands typically exhibit lower SOM content and significantly reduced proportions of agronomically valuable aggregates (0.25–10 mm), along with higher proportions of coarse clods ($>$10 mm) and unstable microaggregates ($<$0.25 mm). These observations suggest that forest systems—particularly broadleaved ones—support favorable soil structure due to higher litter quality and sustained microbial activity, in contrast to coniferous forests, which generally produce litter with a greater proportion of recalcitrant compounds. This may result in a slower turnover of SOM and reduced aggregate stability. This perspective is further supported by the findings of Chen et al. (2022), who demonstrated that broadleaved forests, due to higher-quality litter and more active microbial communities, provide more favorable conditions for long-term stabilization of SOC than coniferous forests. In coniferous systems, the predominance of recalcitrant compounds in litter may lead to slower SOC turnover and a lower contribution of microbial necromass to the formation of stable carbon forms (Averill and Waring, 2018; Chen et al., 2021).

## 5. Conclusion

The aggregate proportion and stability both were divided at forest soils inside temperate zone significantly along plant communities. Forest communities affected soil aggregate stability more than proportion of aggregates through granularity, bulk density, pH, base saturation, organic matter and activities of acid phosphomonoesterase and catalase. Chemical properties of organic matter including enzymatic activity

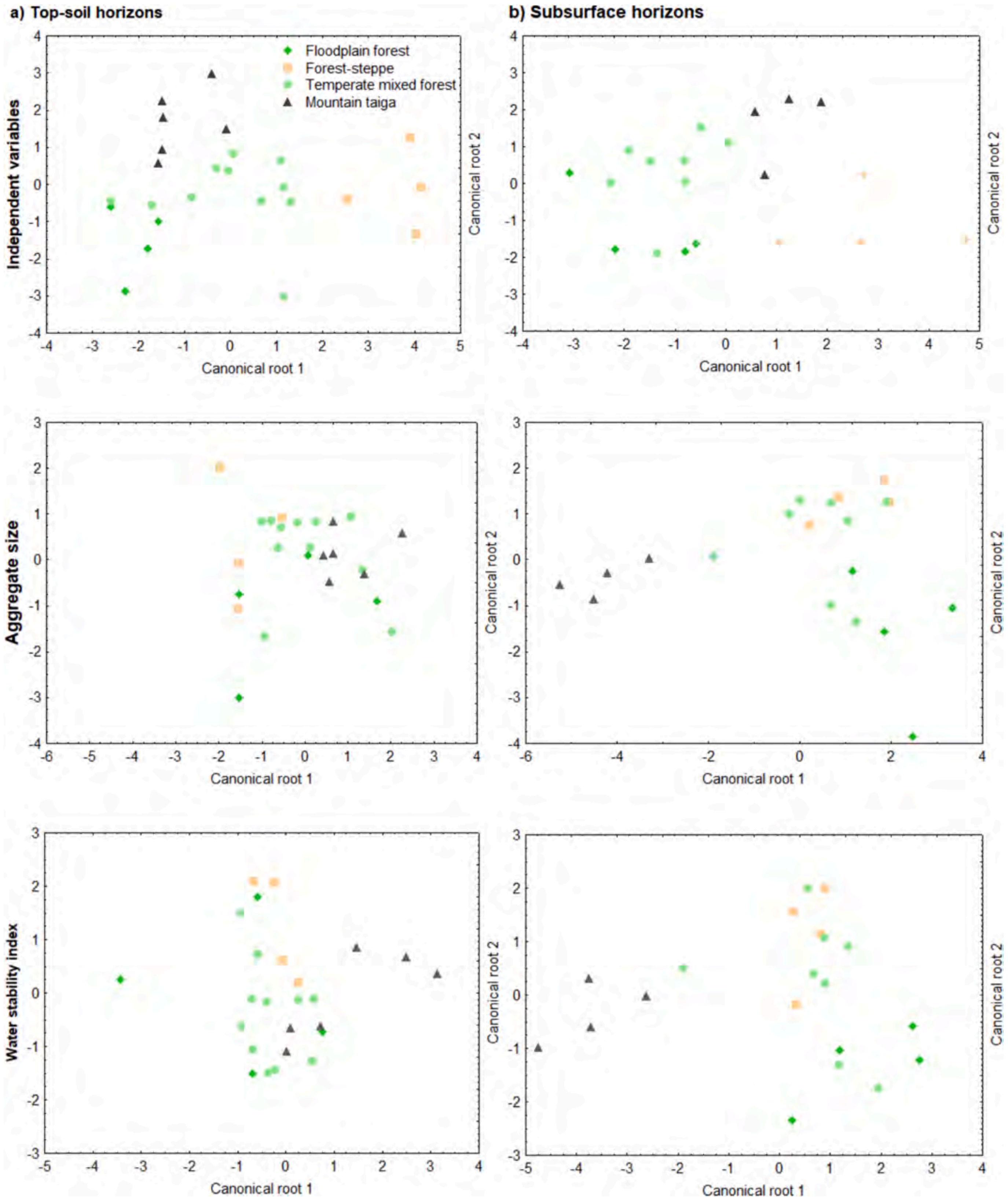


**Fig. 5.** Discriminant analysis of forest biome effects on soil property value distribution and on aggregate behaviour.

separated soil aggregation the most. The soil aggregate proportion was differed strongly between broadleaved and conifer forests, while aggregate stability differed between i) edge conditions in forest-steppes, and ii) floodplain, mixed to mountain forests. Due to connection with forest division, the correlations of soil aggregates with biochemical properties suggested role in assessment of plant community naturalness or in assessment of ecosystem stability.

Our findings are partly limited by the uneven representation of biomes and soil groups, as mountain Podzols and floodplain Fluvisols were less represented compared to broadleaved and mixed forests. The smaller sample size in certain communities increases model variability, which limits extrapolation beyond the studied area; however, consistent relationships between soil aggregate proportion and stability, biochemical properties, and forest type confirm the robustness of the main conclusions.

## CRediT authorship contribution statement

**Gabriela Tomášová:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Pavel Samec:** Writing – original draft, Visualization, Supervision, Methodology, Data curation, Conceptualization. **Lenka Pavlů:** Validation, Resources, Conceptualization. **Ladislav Holík:** Resources, Data curation.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2025.117543.

## Data availability

The data that has been used is confidential.

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