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Effect of Soil Diversity on Forest Plant Species Abundance: A Case Study from Central-European Highlands

Pavel Samec ^{1,2,*}, Jiří Volánek ¹ , Miloš Kučera ³ and Pavel Cudlín ²

¹ Department of Geology and Soil Science, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, CZ-613 00 Brno, Czech Republic; volanek@gmail.com

² Global Change Research Institute CAS, Belidla 986/4a, CZ-603 00 Brno, Czech Republic; cudlin.p@czechglobe.cz

³ Forest Management Institute Brandýs nad Labem, Nábřeží 1326, CZ-250 01 Brandýs nad Labem, Czech Republic; kucera.milos@uhul.cz

* Correspondence: samec.p@czechglobe.cz

Abstract: Plant distribution is most closely associated with the abiotic environment. The abiotic environment affects plant species' abundance unevenly. The asymmetry is further deviated by human interventions. Contrarily, soil properties preserve environmental influences from the anthropogenic perturbations. The study examined the supra-regional similarities of soil effects on plant species' abundance in temperate forests to determine: (i) spatial relationships between soil property and forest-plant diversity among geographical regions; (ii) whether the spatial dependencies among compared forest-diversity components are influenced by natural forest representation. The spatial dependence was assessed using geographically weighted regression (GWR) of soil properties and plant species abundance from forest stands among 91 biogeographical regions in the Czech Republic (Central Europe). Regional soil properties and plant species abundance were acquired from 7550 national forest inventory plots positioned in a 4 × 4 km grid. The effect of natural forests was assessed using linear regression between the sums of squared GWR residues and protected forest distribution in the regions. Total diversity of forest plants is significantly dependent on soil-group representation. The soil-group effect is more significant than that of bedrock bodies, most of all in biogeographical regions with protected forest representation >50%. Effects of soil chemical properties were not affected by protected forest distribution. Spatial dependency analysis separated biogeographical regions of optimal forest plant diversity from those where inadequate forest-ecosystem diversity should be increased alongside soil diversity.

Keywords: forest plant diversity; geodiversity; soil groups; soil chemical properties

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1. Introduction

Distribution of plants on Earth's surface is most closely associated with abiotic environment diversity (geodiversity) and most significantly conditions the diversity of other living forms. The relationship between terrestrial plants and geodiversity is not uniform but rather spatially differentiated along climatic transitions, soil properties and the intensity of human interventions [1]. While climate defines supra-regional differences in the relationships between geodiversity and plants, soil properties define local differences in ecosystem relationships [2]. Soil properties preserve geodiversity effects on plants, even though human interventions have disrupted ecosystem relationships. Nevertheless, positive soil diversity effects on the relationship tightness among general ecosystem-diversity components affected by human activities at a supra-regional level are not taken into account [3].

The total ecosystem diversity includes geo-, bio- and functional diversity. While biodiversity is formed by species abundance of life forms, functional diversity is the interconnection complexity of metabolic transfers among all ecosystem components [4]. Biodiversity varies along variously favourable site conditions. In ecosystems that rely

on solar radiation, biodiversity derives from the growth of plants. Environmental effects on plants systematize biodiversity through the diversification of food opportunities and habitats for animals. Terrestrial environment effects are limited by the continent size within which biodiversity is climate-controlled [5]. Biodiversity evolves through community isolation, landscape penetrability and habitat diversity. Continent biodiversity is directly proportional to the number of endemics resulting from a sufficiently long isolation period. Larger continents, therefore, provide greater environmental diversity with more unique sites of greater total ecosystem [6].

While the climate drives generalized trends in the progression of biodiversity on the greatest scale, in smaller areas many local effects apply. Altitudinal zonation divides the species composition of plant communities more significantly than horizontal climatic transitions [7]. Site-specific effects can completely reverse the trend of biodiversity progression [8]. The relationship between environmental diversity and biodiversity is either direct or indirect, depending on whether the progression of the ecosystem is predominantly influenced by climate or local characteristics [9]. The relationship proportionality between the environment and biodiversity is differentiated between areas affected by ice ages and not affected by Quaternary glaciation [1]. In areas without the direct effect of glaciation, low geodiversity is accompanied by high biodiversity and vice versa. In areas directly affected by environmental changes during glaciation, low geodiversity is accompanied by low biodiversity, and high geodiversity is accompanied by high biodiversity [10].

Different impacts of Quaternary climate changes amidst tropical-to-polar latitudes have differentiated the development coherence between plant-community diversity and geodiversity into declining proportionality between species abundance and environmental diversity [11]. The greatest plant diversity remained concentrated across humid tropics and subtropics, where it constitutes a response to the most significant transitions of environmental properties [5]. The mildest transitions between environmental properties and plant communities are found in the subpolar latitudes, where plant communities are also the most homogeneous in the largest areas [12]. The polar regions are not distinguished by any plant geoelements, yet the northern temperate zone border includes up to 80% of relevant geoelements. In contrast, the southern temperate boundaries include only 15.5% of plant genera due to dominant species overlap from different climatic regions. Tropical regions include up to 80% of genera found on the continent [13].

Biodiversity regulates productivity and protects the ecosystem from damage during climate change [14]. Productivity is modified by functionally substitutable organisms and by the selection of species in competition. Substitutability and selection increase community competition that supports ecosystem resilience to environmental change [15]. Biodiversity protects the ecosystem proportionally to the number of species that complementarily stabilize nutrient accessing while increasing the productivity [16]. Ecosystem resilience consists in the length, asynchronicity and individual species response form to environmental fluctuations. Effective protection is manifest by delaying productivity fluctuation effects [17]. Ecosystem resilience increase in spite of changes in the environment is achieved through asynchronous intraspecific response, differential species response rates and decreased competition. The intra- and interspecies response processes take place as a temporal substitutability of species, while the decrease in competition is controlled by substitutability in functional groups of organisms [18]. Due to these protective processes, changes in species composition have greater impacts on ecosystems than changes in the abiotic environment [19].

Although biodiversity shapes ecosystems through functional groups of organisms, its impact is not uniform due to the persisting dependence on the supra-regional to local properties of the abiotic environment. Such feedback between biodiversity and the abiotic environment complicate distinction among the causes of variability at ecosystem characteristics. The abiotic environment and repeated disturbances affect most ecosystem characteristics more than plant species' diversity [20]. Plant diversity is not as effective in increasing ecosystem diversity as dominant species that independently support nutrient

availability [21]. Supporting nutrient availability increases both biodiversity and ecosystem resilience [18]. Plants support nutrient accessibility by promoting their rhizosphere functions, which increases biodiversity by creating microbial niches, but also increases soil component diversity of geodiversity (pedodiversity).

In response, however, uneven local effects on pedodiversity development differentiate plant dependence on the abiotic environment proportionally to the extent of bedrock transformations during the Quaternary glaciation [22].

Uneven plant dependence on geodiversity is conditioned by geographical location and the extent of anthropogenic loading. Human activities affect all ecosystem components. Although local biodiversity is significantly declining due to human activities, species richness of biomes has declined little due to invasive-species introduction and transition-community formation in a fragmented landscape [5]. Biodiversity is globally used for evaluation of ecosystem health status since it controls key ecological processes [23–25]. However, replacing diverse transitions with ecosystems simplified by exploitation, crop cultivation or pollution has reduced the original diversity as a result of species extinction [26,27]. The effects of biodiversity loss on individual ecosystem characteristics differ together with varying nutrient availability [16]. The effect of nutrient availability on ecosystem diversity within the cultural landscape was an initial prerequisite of the study aim to assess the dependence of semi-natural plant-community diversity on soil diversity. Soil fertility differentiates the ways in which interactions between plants and bedrock develop [4,9,28]. On the other hand, the similarities between the environment and plant-community interactions suggest the importance of soil influences for biodiversity increase on a supra-regional scale [29]. Diversity was estimated in temperate forests, representing the most complex terrestrial ecosystems directly affected by Quaternary environmental changes [30]. Cultural landscape forests are communities in which the relationship between soil and plant diversity develops naturally, unless it is deviated by non-native tree species' afforestation or environmental change [31]. Such variations in the soil and plant diversity relationship caused by forest management indicate the impact of human activity on ecosystem integrity [32]. The dependence of forest diversity components was assessed in biogeographical regions, whose similarities suggest a supra-regional influence of local relationships [33].

2. Material and Methods

2.1. Investigated Area

The dependence of forest-plant species' diversity on soil properties was evaluated among Czech biogeographical regions (bioregions). The Czech Republic is a Central European country in the transient range of temperate climate (78,866 km², 115–1602 m n.m., 2.0–9.4 °C; 250–1470 mm) [34]. Potential forest cover of the Czech Republic exceeds 98%, and natural forest-less land occurs in alpine, rocky or peatland areas. Current forest cover is 34%. Natural representation of woody plants comprises European beech (*Fagus sylvatica*) (40%), oaks (*Quercus* sp.) (18%), Silver fir (*Abies alba*) (16%), Norway spruce (*Picea abies*) (15%) and Scots pine (*Pinus sylvestris*) (3%) [35], while actual composition is formed by 44% of Norway spruce, almost 10% of Scots pine, more than 10% of European beech and by 8% of oaks [36]. Approximately 16.7% of the Czech Republic was designated as Specially Protected Territory (SPT), out of which almost 60.5% is under forest cover [37].

Bioregions are basic territorial units used for individual division of biotic communities. The Czech Republic is divided into 91 bioregions appertained to 2 intervening provinces and 4 subprovinces [38]. The Central European province includes 71 bioregions in the Hercynian subprovince, 4 bioregions in the Polonian subprovince and 11 bioregions in the West Carpathian subprovince, while the Pannonian province includes 5 bioregions in a single North Pannonian subprovince (Figure 1). The Hercynian subprovince covers 84.7% of the Czech Republic territory and includes 83.3% of the SPTs. In contrast, the Polonian subprovince stretches over the smallest part of the Czech Republic with the total of 2.2% area cover and only 0.8% of protected areas. The West Carpathian subprovince

covers almost 9% of the Czech Republic and includes 14.9% of protected territories. The Pannonian province includes the remaining 4.1% of the Czech territory and 1% of the SPTs [39]. Within the Czech Republic, the Hercynian subprovince forest cover amounts to almost 35.9%, the West Carpathian to more than 37.8%, the Polonian to 12.4%, and the North Pannonian comprises a slightly smaller share of 12.3% [34].

Figure 1. Distribution of forest reserves, protected landscape areas (PLA) and national parks (NP) in the Czech Republic.

2.2. Data

Evaluated data consist of forest-division and forest-diversity component classifications. Forests were divided by overlapping biogeographical regions and SPTs. Forest-cover distribution was acquired from the geodatabase of regional forest development plans administered by the Forest Management Institute Brandýs nad Labem [40]. Bioregion distribution, including geodiversity components of relief and bedrock-type subpolygons, was adopted from the Unified Environmental Information System (UEIS) administered by the Ministry of the Environment of the Czech Republic [41]. Bedrock-geomorphological bodies (BGMBs), comprehensively capturing the altitudinal variability of the climate and the soil fertility, were derived by overlapping the types of relief and bedrock [42].

Czech SPTs are categorized into reserves and large-area units. While reserves predominantly include natural ecosystem remnants, large protected landscape areas and national parks integrate natural communities with seminatural for renaturalization purposes [43]. Polygons of specially protected territories were acquired from the UEIS geodatabase [44].

Unlike the forest-division systems, forest-diversity components were acquired from the National Forest Inventory (NFI) plot database surveyed in 2011–2015. Forest diversity was acquired from 7550 plots in a 4×4 km grid [45]. The grid size was set to capture site effect on temperate vegetation on a regional scale [46]. Inventory plot sites were simplified to BGMB and soil environment. The soil environment was characterized by group and chemical properties of the dominantly developed horizon. Soil groups were evaluated

according to the WRB-ISSS-ISRIC [47] and soil chemical properties according to the EMEP-LRTAP criteria [48]. Soil properties were determined as physico-chemical and budget-based. Physico-chemical properties were characterized by pH, determined by acidometry and by sorption properties: cation exchange capacity (CEC) and base saturation (BS) determined by ion-selective extraction. Substance budget determination addressed C_{org} , N_{tot} , Al_2O_3 , CaO , MgO and P_2O_5 , which are together with physical and physico-chemical soil properties most significantly differentiated in the Czech Republic [49].

Forest-plant communities were characterized by species abundance of the moss, herb, shrub and tree storeys [2]. The bryophyte composition was simplified to indicatively important species [50]. Vascular plants were defined using a system by Kubát et al. [51], with the exception of the tree-species characterization, which was simplified according to the Czech Forest Management Information Standard [40]. The NFI database includes records on 20 bryophyte indicator species, 815 herbaceous species, 139 species of shrubs and 62 woody species capable of reaching the tree layer.

2.3. Statistical Evaluation

The evaluation was divided into an assessment of soil effects and a comparison of management impact on forest plant communities. Soil effects were determined using global linear and geographically weighted regression (GWR) between soil diversity and forest plant species diversity (phytodiversity) at $p < 0.05$. Soil diversity (pedodiversity) was divided into soil-group diversity and diversity of chemical properties. Influence of pedodiversity components was compared with the geodiversity determined from the BGMB representation [42]. Diversity was estimated using the Shannon–Wiener (H') index, the calculation of which was adapted to the representation of polygons or to evaluated component numbers from inventory plots. The diversity of BGMBs as well as of the plant species' abundance in the particular forest stand storeys was determined using the equation:

$$H' = - \sum \left(\frac{A_n}{A} \right) \cdot \log_2 \left(\frac{A_n}{A} \right), \quad (1)$$

where A_n is the area of forest ecosystem component type in the bioregion and A is the area sum of the selected ecosystem component types in the bioregion [29]. Plant abundance was measured through H' -indices from percentual coverage of individual species in particular stand storey. Total forest phytodiversity (H'_{tfd}) was derived as the sum of plant species abundances in all stand storeys:

$$H'_{tfd} = H'_m + H'_h + H'_s + H'_t \quad (2)$$

where H'_m is the abundance of indicator bryophytes, H'_h is the grass-herbaceous storey species abundance, H'_s is the shrub storey species abundance and H'_t is the tree species abundance.

In contrast, the diversity of soil-group representations or intervals of chemical property values of dominantly developed soil horizons was determined by adjusting:

$$H'_f = - \sum \left(\frac{g_k}{g} \right) \cdot \log_2 \left(\frac{g_k}{g} \right), \quad (3)$$

where g_k is the interval value count of selected soil property in the bioregion and g is the number of intervals of the whole selected soil property classification range [49]. Similar to H'_{tfd} , soil-chemical diversity (H'_{sc}) was also determined by summing the interval diversities of the individual chemical properties (x):

$$H'_{sc} = \sum H'_x \quad (4)$$

Subsequently, the GWR was approximated either as a simple model for phytodiversity dependence on the BGMBs or soil groups, or as a multiple model with a linear combination of chemical property diversities:

$$Y_m = \beta_{m0} + \sum_{k=1}^q \beta_{mk} \cdot H'_{mk} + \epsilon_m \quad (5)$$

where Y_m is a dependent variable in the bioregion m , q is the number of independent variables, k is the independent variable order, H'_{mk} is the k -squared of independently variable diversity value of soil properties in the bioregion m , β_{m0} is the intercept parameter in the bioregion m , β_{mk} is the local k -squared independent variable coefficient and ϵ_m is a random error in the bioregion m [52]. Geographically weighted models were assessed using the Akaike Information Criterion (AIC) and determination indices (R^2). The $R^2 < 0.5$ indices demonstrated lowly significant regressions, while more significant $R^2 \geq 0.5$ were divided into five equally wide intervals [53].

Assessment of the forest management impact on the GWR size was based on managed and seminatural ecosystem differentiation. The GWR evaluation was performed using a linear regression of spatially weighted Residual Sum of Squares (RSS) dependence on the specially protected forest territory representation in bioregions. RSS showed the actual detected phytodiversity deviation from the model corresponding with geodiversity. The plant RSS dependence with protected territories confirmed the geodiversity influence on phytodiversity differing between natural and managed forests.

3. Results

Representation of specially protected forests (SPF) in the Czech Republic is directly proportional to the total forest cover of biogeographical subprovinces. Less than 30% of Czech forests are located in SPTs. The highest proportion of SPFs is found in the West Carpathian subprovince (45.8%). The lowest proportions of SPFs are found the Polonian (7.9%) and North Pannonian subprovinces (10.7%), while the largest Hercynian subprovince includes only 27.9% of SPFs.

The SPF representation has increased the correlations among ecosystem diversity components. The effects of managed forests on correlations were manifest by uneven differences between means and standard deviations (SD) with respect to the overall range of ecosystem properties. The distribution of values did not significantly affect the differences between the mean values and the SD. Area sizes of bedrock-geomorphological bodies in bioregions, soil group totals, soil cation exchange capacity, basic saturation, and the C_{org} , N_{tot} , CaO , MgO a P_2O_5 contents showed smaller averages than SD. On the contrary, the distribution of soil sorption and the herbaceous to shrub-storey covers of the inventory plots were significantly sloping; however, their averages and SD were balanced even at a wide range of values (Table 1).

The diversity of vascular forest plants was higher than the diversity of soil environment properties. Out of the total forest-plant diversity, the highest was among the herbal storey and the lowest among the mosses. Despite disrupted normality of the H' -indices, the shrub-storey species diversity was on average higher than that of the tree storey. The BGMB diversity and the soil-group representation resembled each other by almost identical H' -index ranges. Both groups of soil bodies showed higher diversity than individual soil chemical properties. Soil sorption was the most diversified out of all chemical properties. BS diversity was higher than CEC despite a similar range of H' -indices. The diversity of pH was lower than that of soil sorption; however, it was higher than that of mineral-content diversity. Moreover, the diversity of soil organic matter composition was higher than the diversity of mineral contents. Nutrient contents were more diversified than Al_2O_3 . The diversity of mineral contents decreased in the order of $MgO > P_2O_5 > CaO > Al_2O_3$.

The total forest phytodiversity was linearly conditioned the most by the BGMB diversity. Although the BGMB diversity in bioregions and the soil-group representation in inventory plots were similar, the diversity of soil chemical properties corresponded

more significantly with the soil-group diversity. Plant diversity was linearly less significantly dependent on the soil group representation, but more significantly dependent on soil chemical diversity. In descending order, the total forest plant diversity depended on $\text{pH} > \text{BS} > \text{CEC} > \text{CaO} > \text{P}_2\text{O}_5$. The dependence rate of total plant diversity or species diversity of individual forest ecosystem storeys on soil chemical properties differed due to the unevenness of the cover. The diversity of individual forest plant storeys depended most on the soil CaO content and less on pH, BS, CEC and N_{tot} . However, the species diversity of bryophytes depended most on the BGMBs. The forest herb and shrub species diversity reflected the BGMB and soil chemical property diversity to varying levels. While herbs were more dependent on the BGMB representation, shrubs were more dependent on pedochemical diversity (Table 2).

Table 1. Diversity intervals of compared forest ecosystem characteristics in biogeographical regions of the Czech Republic. BGMB—bedrock-geomorphological body; FSG—forest soil group; FSC—forest soil chemistry; CEC—cation exchange capacity; BS—base saturation; H' —Shannon–Wiener index; SD—standard deviation; E —elevation; A —skewness (bold significantly disrupted data normality at $p < 0.05$).

Diversity	Average $\pm$ SD	Min–Max	$H' \pm \text{SD}$	$H'_{\text{min}} - H'_{\text{max}}$	E	A
BGMB (km^2)	22.13 $\pm$ 43.49	0.00–506.91	2.56 $\pm$ 0.88	0.01–4.17	0.34	−0.72
FSG (n)	25 $\pm$ 43	1–409	2.50 $\pm$ 0.76	0.00–4.41	0.41	−0.26
FSC (1)	-	-	10.45 $\pm$ 2.40	0.00–15.31	2.81	−0.80
pH [$-\log c(\text{H}^+)$]	4.84 $\pm$ 0.86	4.11–7.57	1.07 $\pm$ 0.46	0.00–1.92	−0.12	−0.44
CEC (cmol^+/kg)	12.08 $\pm$ 12.27	2.70–421.10	1.38 $\pm$ 0.42	0.00–2.12	2.04	− 1.15
BS (%)	33.71 $\pm$ 33.73	7.40–99.95	1.66 $\pm$ 0.47	0.00–2.26	3.41	− 1.69
C_{org} (%)	2.02 $\pm$ 3.92	0.29–9.91	1.29 $\pm$ 0.53	0.00–2.36	−0.60	−0.24
N_{t} (%)	0.13 $\pm$ 0.16	0.03–0.32	1.41 $\pm$ 0.44	0.00–2.36	0.44	−0.45
Al_2O_3 (g/kg)	29.71 $\pm$ 17.98	8.35–81.07	0.53 $\pm$ 0.57	0.00–2.12	0.25	1.04
CaO (g/kg)	3.08 $\pm$ 17.89	0.13–87.70	0.80 $\pm$ 0.57	0.00–2.00	−0.89	0.28
MgO (g/kg)	5.71 $\pm$ 7.52	0.92–17.80	1.18 $\pm$ 0.61	0.00–2.28	−0.58	−0.29
P_2O_5 (g/kg)	0.75 $\pm$ 0.82	0.21–3.68	1.12 $\pm$ 0.40	0.00–2.25	0.93	−0.28
Tree (%)	44.17 $\pm$ 10.45	24.49–69.19	2.65 $\pm$ 0.71	1.14–4.06	−0.55	−0.22
Shrub (%)	18.43 $\pm$ 9.90	1.17–57.90	3.32 $\pm$ 0.63	0.59–4.31	2.90	− 1.13
Herb (%)	17.93 $\pm$ 7.41	4.69–37.61	4.54 $\pm$ 0.76	1.44–5.88	2.79	− 1.29
Moss (%)	21.04 $\pm$ 15.24	1.75–67.00	1.70 $\pm$ 0.82	0.00–3.03	−0.29	−0.74
Plant (%)	76.05 $\pm$ 28.35	47.75–100.00	12.20 $\pm$ 1.85	4.85–15.79	1.73	−0.93

Table 2. Linear correlations between compared Czech forest ecosystem diversity components (bold significant at $p < 0.05$). BGMB—bedrock-geomorphological body; FSG—forest soil group; FSC—forest soil chemistry; CEC—cation exchange capacity; BS—base saturation.

Component	Diversity	BGMB	FSG	FSC	pH	CEC	BS	C_{org}	N_{t}	Al_2O_3	CaO	MgO	P_2O_5
Abiotic	BGMB	-	0.29	0.18	−0.02	0.36	0.40	0.06	0.13	− 0.24	−0.05	0.05	0.40
	FSG	-	-	0.62	0.19	0.49	0.43	0.44	0.43	0.36	−0.03	0.56	0.14
Biotic	Tree	−0.18	−0.16	0.15	0.38	0.08	−0.12	−0.04	0.06	0.08	0.51	−0.13	−0.17
	Shrub	0.37	0.19	0.44	0.51	0.34	0.38	0.04	0.22	0.03	0.41	0.09	0.19
	Herb	0.48	0.09	0.27	0.33	0.27	0.31	0.08	0.22	−0.18	0.30	−0.09	0.19
	Moss	0.59	0.31	0.15	−0.08	0.21	0.43	0.05	0.03	−0.02	− 0.34	0.25	0.32
	Plant	0.52	0.18	0.38	0.42	0.35	0.40	0.05	0.20	−0.04	0.31	0.05	0.22

Geographically weighted regression confirmed global linear dependencies between forest ecosystem components with similar value variability. Spatial dependencies between the representation of polygons within bioregions and the recurrence of properties from inventory plots were differentiated. Due to the differences between bioregions, the total forest-plant-diversity dependence on the geodiversity components was closer than the dependence among particular soil-environment components. However, unlike the relationships found by global linear regression, spatial-plant diversity depended more on the soil group diversity than on

the BGMBs. Similarly, the dependence of plant diversity with soil chemical properties was significantly differentiated due to the bioregion dissimilarities (Table 3).

Geographical distribution of the diversity of forest-soil chemical properties simultaneously affects geodiversity and certain parts of phytodiversity. Soil-chemical diversity is most significantly related to the diversity of the forest moss and tree storeys. Seemingly similarly significant spatial dependencies are formed by soil-chemical properties with BGMBs and trees, and by soil groups and bryophytes. Soil-chemical properties influence the soil-group diversity the most. Similarly, the most important relationship between the soil and vegetation occurs between the soil-chemical properties and the bryophyte diversity. However, even similarly significant dependencies differed mostly by parameter opposite proportionalities. Soil-chemical diversity did not significantly determine the vascular-plant diversity distribution into the shrub storey. However, in contrast to the undergrowth storeys, the distribution of forest-tree diversity is significantly dependent on soil-chemical properties. Dependences of the BGMB and the tree-species diversity distribution differed in the parameters of soil pH, sorption properties and mineral contents. On the contrary, the soil group and the bryophyte-diversity dependences were similar due to the soil pH, CEC, BS, C_{org} , CaO and MgO parameters, and differed in N_{tot} , Al_2O_3 and P_2O_5 . Only the soil C_{org} content affected the components of ecosystem diversity, within similarly significant regressions, by the same proportion (Table 4).

Table 3. Geographically weighted regression among forest-geodiversity components and to total phytodiversity (TPD). BGMB—bedrock-geomorphological body; FSG—forest-soil group; FSC—forest-soil chemistry; A—parameter; A_0 —interception; ϵ —random error; w—weight; AQ—adaptive quartile; AIC—Akaike information criterion; R^2 —determination index.

X	Y	A	A_0	ϵ	w	AQ	AIC	R^2
BGMB	FSG	0.22 ± 0.06	1.95 ± 0.19	0.02 ± 0.69	51.49 ± 3.95	0.36	228	0.11 ± 0.04
	FSC	0.55 ± 0.78	9.13 ± 2.22	-0.06 ± 2.02	14.67 ± 2.46	0.08	467	0.28 ± 0.05
	TPD	1.14 ± 0.73	9.38 ± 2.00	0.00 ± 1.20	9.23 ± 2.09	0.05	363	0.59 ± 0.19
Soil group	FSC	2.04 ± 0.05	5.18 ± 0.10	-0.01 ± 1.87	72.38 ± 1.79	0.63	440	0.39 ± 0.01
	TPD	0.36 ± 0.86	11.10 ± 2.49	0.09 ± 1.14	6.31 ± 1.84	0.03	365	0.62 ± 0.18
Soil chemistry	TPD	0.34 ± 0.30	8.54 ± 3.70	0.02 ± 1.19	8.82 ± 1.97	0.04	364	0.59 ± 0.20

Table 4. Geographically weighted regression of soil chemical properties diversity with geodiversity components and forest phytodiversity (for detail explanatory of abbreviations see Table 3).

Formula	Attribute	BGMB	FSG	Tree	Shrub	Herb	Moss	Plant
Parameter	pH	-0.38 ± 0.21	-0.23 ± 0.07	0.40 ± 0.28	0.40 ± 0.12	0.14 ± 0.19	-0.19 ± 0.29	0.74 ± 0.37
	CEC	0.74 ± 0.11	0.37 ± 0.10	-0.04 ± 0.27	0.17 ± 0.06	0.19 ± 0.10	0.38 ± 0.48	0.65 ± 0.11
	BS	0.47 ± 0.07	0.43 ± 0.03	-0.21 ± 0.18	0.22 ± 0.04	0.33 ± 0.12	0.57 ± 0.38	0.91 ± 0.25
	C_{org}	-0.22 ± 0.27	0.47 ± 0.10	-0.09 ± 0.13	-0.32 ± 0.02	-0.20 ± 0.14	0.08 ± 0.45	-0.54 ± 0.51
	N_{tot}	0.17 ± 0.28	0.16 ± 0.11	0.04 ± 0.27	0.29 ± 0.09	0.26 ± 0.22	-0.15 ± 0.41	0.42 ± 0.70
	Al_2O_3	-0.05 ± 0.07	0.11 ± 0.08	0.18 ± 0.21	-0.14 ± 0.05	-0.33 ± 0.16	-0.18 ± 0.28	-0.47 ± 0.25
	CaO	-0.20 ± 0.04	-0.05 ± 0.03	0.40 ± 0.08	0.15 ± 0.01	0.17 ± 0.03	-0.54 ± 0.39	0.24 ± 0.19
	MgO	0.11 ± 0.15	0.42 ± 0.09	-0.19 ± 0.13	0.06 ± 0.09	-0.08 ± 0.24	0.16 ± 0.16	-0.03 ± 0.40
	P_2O_5	0.32 ± 0.08	-0.21 ± 0.12	-0.24 ± 0.07	0.06 ± 0.07	0.05 ± 0.17	0.44 ± 0.28	0.28 ± 0.36
	θ	1.20 ± 0.36	0.41 ± 0.11	2.78 ± 0.25	2.15 ± 0.10	3.58 ± 0.09	0.41 ± 0.36	8.96 ± 0.28
Characteristics	ϵ	0.00 ± 0.55	0.01 ± 0.42	0.00 ± 0.45	-0.01 ± 0.47	-0.02 ± 0.62	-0.01 ± 0.47	-0.04 ± 1.38
	w	53.24 ± 3.74	47.38 ± 4.17	38.74 ± 4.23	62.91 ± 3.11	53.11 ± 3.77	37.66 ± 4.13	55.57 ± 3.53
	AQ	0.38	0.32	0.24	0.48	0.37	0.24	0.40
	AIC	194	137	156	158	220	165	389
	R^2	0.58 ± 0.05	0.67 ± 0.02	0.57 ± 0.06	0.46 ± 0.06	0.42 ± 0.10	0.66 ± 0.08	0.45 ± 0.06

Pedodiversity affected forest diversity more than overall geodiversity. Natural forests retain a higher influence of soil groups. In contrast, the influence of the soil-chemical-diversity components is not increased in the SPTs. Natural environment changes the influence of geodiversity on phytodiversity only to a slight extent. Natural-forest represen-

tation separated the extent and proportion of the geo- and pedodiversity effects. While significant influence of pedodiversity on forest-plant diversity occurs mainly in bioregions with a higher proportion of protected territories, the influence of geodiversity on the diversity of forest plants is slightly higher in bioregions with a smaller proportion of protected territories (Table 5).

Smaller effect of soil-chemical diversity on forest plants has been interchanged by the soil-group representations, although the effect of a linear-chemical-diversity combination on soil-group diversity is more significant than the effect of BGMBs. Geographical dependence between the chemical properties and the forest-soil group diversity attained R^2 in the range of 0.63–0.70. The influence of soil-group diversity on forest-plant diversity attained the R^2 interval of 0.05–0.77. In the Czech Republic, soil-diversity-component dependencies are concentrated in two separate clusters of very high correlation in the west and medium-high correlation north of the Hercynian, North Pannonian and Carpathian subprovince boundary (Figure 2). Similarly, moderate correlations are concentrated in two clusters in the centre of the Hercynian subprovince and in the northeast of the Czech Republic. Very high correlation of pedodiversity includes 33.8% of forests, high correlation 9.1%, medium-high correlation less than 14.2%, most-extensive medium correlation almost 35.4% and moderate correlation only 7.5%. At the same time, the influence of pedodiversity on forest plant diversity is divided into a larger number of clusters separated by decreasing correlations. Very high correlations between pedo- and phytodiversity are found in the west, south and northeast of the Czech Republic. Clusters of significant correlations are segregated by low correlation comprising 43.9% of forests. Very high correlation includes less than 10.7% of forests, high correlation 9.9%, medium-high correlation 14.1%, medium correlation 8.6% and moderate correlation 12.8% (Figure 3). Significant spatial correlation agreement appeared in 11 bioregions in the Hercynian or West Carpathian subprovince. The area of identically evaluated GWRs is forested by better-than-average 40.7% and comprises a 51.9% share of protected forests.

Figure 2. Geographically weighted regression between forest-soil group and chemical-properties diversity in the Czech Republic.

Table 5. Linear regression of specially protected forest (SPF) representation effect on residual range from relationship between geo- and phytodiversity.

Geodiversity	R^2	F	p	SPF	Parameter
BGMB	0.01	0.53	0.47	0.00031	0.444
Soil group	0.01	1.33	0.25	−0.00065	0.591
Soil chemistry	0.00	0.02	0.89	−0.00005	0.502

Figure 3. Geographically weighted regression between forest-soil group and plant diversity in the Czech Republic.

4. Discussion

Diversity of the soil groups significantly affects the diversity of forest-plant species in temperate conditions. The influence of the soil groups' diversity is more significant than the influence of the bedrock-geomorphological bodies or the soil-chemical properties. Significant impact of pedodiversity on forest plants included more than half of the evaluated Central European forests. The impact of soil diversity is higher in specially protected forests and lower in managed forests. The impact of forest management on the pedo- and phytodiversity association foreshadow the effects on landscape biodiversity. Similarly, variability in the relationships among forest-diversity components affects the ways of evaluating properties of soil-environment indication, ecosystem functions and integrity [44].

Plant indication consists of a narrow range of environmental properties in plant species or community adaptation [54]. A comparison of global and localized statistical models pointed to differentiated relationships of forest plants with individual components of geodiversity. Whereas globally forest-plant diversity appeared to be downwardly dependent on the BGMBs, soil-chemical properties, and soil-group representation, the most significant spatially weighted dependence was due to the soil groups and the least

significant was due to the soil-chemical properties. Moreover, globally significant influences of the soil physicochemical properties and the CaO and P₂O₅ contents did not affect forest vegetation in individual bioregions equally. Diversity of the soil-chemical properties most affected the moss and the forest-tree diversity. Nevertheless, their dependencies were affected by species abundancy, but also by the distribution of identified species. Small numbers of species compensated for the spatial differences between bioregions, where the observed dependencies were incorrectly highlighted. On the other hand, the identified dependencies were optimal due to the preserved normal distribution of the species abundance.

Global and localized model differences follow the fact that vegetation in nutrient-poor areas is more strongly differentiated along rock-type transitions, while vegetation in nutrient-rich areas is more strongly differentiated with altitude [2,55,56]. In the Czech Republic, the variability of vegetation dependence on rock or relief type was reflected in the boundary between the Hercynian to Polonian subprovinces and in the North Pannonian to the West Carpathian subprovince regions. The Hercynian to Polonian subprovince area consists of old reliefs on nutrient-poorer bedrock with smaller differences in altitude. The area of the North Pannonian to West Carpathian subprovince is part of the younger alpine orogen with bigger altitude differences [38]. The Hercynian subprovince is characterized mainly by low correlations of forest plants, while the Pannonian–Carpathian subprovince is a transect of significant correlation transitions of forest ecosystem components.

The geographically weighted relationship of forest plants with the environment was closer than the relationship of soil-chemical properties with the soil-group representation. The relationship between forest plants and soil groups was broader than the relationships among soil properties. It reached both low and at the same time the most significant correlations out of the evaluated forest diversity properties. High GWRs of the plant and soil diversity comprised 34.7% of forests in the above-average forested regions. The high GWR concentrations were conditioned not only by the higher numbers of inventory plots enhancing the spatial correlation, but also by the higher proportion of protected territories [39,43,44]. Natural forests significantly maintain the soil-group relationships with plants but reduce the relief effects. Forest management disrupts natural relationships of soils with plants up to a point where they are replaced by more general geodiversity effects. However, the effects of soil-chemical properties on plants were not disrupted by the management. The disruption of relationships with soil groups forced plants to differentiate interactions with the soil-chemical properties along the BGMB boundaries. The effects of BGMBs coincide with the indicator plant species distribution both along the biogeographical subregion boundaries and along the transitions of soil-chemical properties.

The diversity of forest-soil chemical properties was most influenced by base saturation, organic matter content, MgO and P₂O₅. The soil carbon content formed equal relations with all the compared components of forest diversity. It evenly affected the plant diversity as well as mirrored the effects of the environment. Such equal proportionality in soil-carbon relationships is due to the plant and the atmosphere connection effects on the nutrient cycles [57]. At the same time, carbon increases forest diversity by supporting other soil properties along with all ecosystem functions [58]. Soil carbon improves physico-chemical sorption and nutrient availability. Its sorption efficiency and nutrient substrate formation increase ecosystem bioproduction and provide habitat for more biodiversity-enhancing organisms [59]. High GWR of pedodiversity components comprised more than 57.1% of the forest stands in the Czech Republic. The high soil GWR occurrences were not affected by large SPTs, which supports the assumption that soil-chemical diversity is unaffected by forestry management.

The soil-group representation has affected the diversity of forest-plant communities most out of the geodiversity components as a result of natural site protection. Yet again, the undisturbed effects of soil-chemical properties by forest management suggest that plants indicate the quality of individual environmental properties equally reliably in differently structured ecosystems. The correlation closeness was higher in bioregions with a higher

share of protected forests. The connection between protected forest cover and total forest cover in the Czech Republic is proportionally related to total SPT representation and biogeographical subprovince size [38]. The range of high correlations, on the one hand, adhered to the bioregion forest cover size, and on the other hand was defined along different GWRs between the pedo- and phytodiversity components. Due to the variable GWRs among the forest, diversity components were high correlations isolated into several distant clusters. The degree of dependence between the ecosystem components indicates the effectiveness of ecosystem functions in climate-change adaptation [43]. Similarly, the most influential soil-chemical properties included compounds determinable of forest-health deterioration [59].

The natural dependence closeness between the ecosystem diversity components is the result of ecological integrity [44]. Ecological integrity is the ability of an ecosystem to support a living community appropriate to site conditions on a regional scale [60]. The ecosystem integrity is formed by the species composition, structure and functional connections between species in the community. Promoting integrity consists of processes that increase the ecosystem diversity, in which new food opportunities arise. Ecosystem diversity is increased mainly by [4]. However, in addition to the disturbance recurrences, the degree of integrity is also indicated by the individual component sizes of ecosystem diversity [14]. The spatial dependence of forest-plant diversity on soil diversity indicates the integrity of the community with the bedrock. The correlations of the Central European forest diversity suggest distribution of their response to the variability of growth conditions along a gradient of soils with different fertility [49]. Soils of bedrock-derived fertility are less diversified and display lower resistance to changes in other environmental properties. Soils minerally unrelated to the bedrock are more diversified, though simplified species composition of managed forests reduced the adaptability of the ecosystem to the climate change. Forests with a composition corresponding with the soil diversity, on the other hand, appear to be adaptable.

5. Conclusions

Soil-group diversity affects the diversity of forest plants in temperate conditions more than the bedrock or soil-chemical properties. Plant diversity and soil-group dependence is significant in areas with an above-average forest cover and a share of protected territories >50%. Nevertheless, plant and soil-chemical property dependence was not affected by forest management. Spatial dependencies pointed to supra-regional overlaps of local relations between forest plants and soils, differentiating environment indication and ecosystem integrity. Environment indication was divided between nutrient-poor soils with low plant dependencies and more fertile soils with higher plant dependencies. Forest plants most distinctly reflect the diversification of soil base saturation and carbon, MgO and P₂O₅ contents. Spatial-dependency outstretches indicated ecological integrity, which can be consolidated by increasing forest plant diversity in agreement with geodiversity.

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