Topographic attributes and ecological indicator values in assessing the ground-floor vegetation patterns

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Abstract. The paper discusses the question whether geographical information systems (GIS) and digital elevation models (DEM) are useful tools for studying correlations between topographic attributes of a given area, and vascular flora requirements reflected by ecological indicator values (EIVs). The model object was a 4-km-long gorge section of the Sopot river valley (80.5 ha), the Central Roztocze Highlands, South-East Poland. Species lists for 40 ca. 200-m-long and 100-350-m-wide sections, according to the river course, separately for the left and right riverbanks, were made. The analysis of the area was based on a 3-meter resolution DEM. We applied primary topographic attributes: slope, and planar, vertical, and total curvatures and also secondary topographic attributes: solar radiation (SRAD) and topographic wetness index (TWI), as well as other terrain characters: denivelation, total, flat and upslope area of each section. Using the multivariate analyses, we analysed relationships between weighted averages of EIVs for each species and topographic attributes.

The GIS and DEM became useful tools for the detection of patterns of species with different habitat requirements. The species number correlated positively with the total and flat area of a section and the TWI, while the denivelation, mean slope and upslope area had a reverse vector. Among the most frequent and abundant herb species, we found several spatial patterns of distribution, namely those of: *Maianthemum bifolium, Carex remota, C. acutiformis, Filipendula ulmaria, Dryopteris filix-mas*, and *Urtica dioica*. The rarest species represented *Ajuga genevensis, Scorzonera humilis*, and *Stachys palustris* patterns.

Key words: digital elevation models, forest vegetation, geographical information systems, multivariate ordination analysis, riparian vegetation, spatial patterns, solar radiation, topographic wetness index

1. Introduction

One of the main static characteristics of ecosystems is topography. Topography, both elevation and latitude, determines physical and biological processes occurring within landscape. Terrain features have a major impact on movements of flowing and precipitation waters carrying chemical and biological substances and on the supply of solar radiation on the ground surface (Wilson & Gallant 2000; Kraak & Ormeling 2003; Urbański 2012). Solar radiation powers micrometeorological processes and correlates with air and soil temperature and moisture, sensible heat flux, and evapotranspiration and, thus, shapes vegetation composition and function (Moore *et al.* 1991; Franklin 1995; Kumar *et al.* 1997; Dorner *et al.* 2002; Sarr *et al.* 2005; Fitterer *et al.* 2012).

Terrain parameters are the basis for the development of research methods and techniques referred to as terrain analysis. A basic dataset is provided by the topographic map, which can have an analogous or digital form; owing to visualisation of the three-dimensional image of the surface area, the latter form offers ample opportunities for modelling hydrological, geomorphological, and biological phenomena and processes at different spatial scales: from global phenomena and processes occurring around the Earth, through the regional and landscape level, to those that occur at a micro- and nanoscale, i.e. in local sites or single patches of plant communities. In natural sciences research, the raster form of the model the Digital Elevation Model (DEM) or, less frequently, the Digital Terrain Model (DTM) are used (Moore et al. 1991; Tappeiner et al. 1998; Pfeffer et al. 2003; Feldmeyer-Christe et al. 2007; Kopecký & Čižkova

2010; Mendas 2010; Fitterer *et al.* 2012; Czarnecka & Chabudziński 2014; Czarnecka *et al.* 2015). Two groups of topographic attributes calculated from the DEM (Wilson & Gallant 2000; Kraak & Ormeling 2003; Evans *et al.* 2014): primary topographic attributes – slope, aspect, planar (or contour), vertical (or profile), and total curvature; and secondary topographic attributes – solar radiation (SRAD) and topographic wetness index (TWI) provide the basis of analytical procedures.

The approach using plants as indicators or predictors of the environment quality has widely developed since the first attempt made by Ellenberg (1974), who defined 'indicator values' reflecting the realised optima for species of Central Europe expressed as ordinal numbers. The system of ecological indicator values (EIVs) provides a very valuable tool for habitat calibration and, in spite of many critical comments and limitations (cf. Diekmann 2003 and literature cited therein), it is still applied for modelling plant distribution at various spatial scales in different regions of Europe (Ertsen et al. 1998; Wamelink et al. 1998, 2002; van Dobben et al. 1999; Schaffers & Sýkora 2000; Wilson et al. 2001; Gégout 2003; Lawesson et al. 2003; Seidling 2005; Bergès et al. 2006; Petřik & Wild 2006; Feldmeyer-Christe et al. 2007; Seidling & Fischer 2008; Crosti et al. 2010; Angiolini et al. 2011; Balkovič et al. 2012).

Over the last decades, the EIV system was widely used, together with the DEMs and multivariate ordination analyses (MOAs), to study relationships between topographic characters and ecological features of different landscapes, including species occurrence and vegetation diversity (Lyon & Sagers 1998; Tappeiner *et al.* 1998; van Dobben *et al.* 1999; Wilson *et al.* 2001; Pfeffer *et al.* 2003; Seidling 2005; Bergès *et al.* 2006; Petřik & Wild 2006; Jolley *et al.* 2010; Angiolini *et al.* 2011; Czarnecka & Chabudziński 2011, 2014; Czarnecka *et al.* 2015).

In the present paper, we would like to propose a procedural algorithm in modelling the spatial patterns of ground-floor vegetation based on the example of a small-scale, almost totally forested river valley. The goal of the research was to demonstrate how vegetation patterns reflect differentiation of topographic attributes of the valley. In particular, we tried to find correlations between morphological characters of the river valley and local vascular flora and its requirements expressed as EIVs, using the GIS, DEM and MOAs. Finally, we discussed the usefulness of the DEM for studying relationships between topographic and ecological attributes of vegetation landscape.

2. Material and methods

2.1. Study area

The study area was a ca. 4-km-long gorge section of the Sopot river (IV rank river), crossing the escarpment zone of the Central Roztocze Highlands, South-East Poland (Fig. 1). A characteristic feature of the river gorge is a large slope of the riverbed, a large depression of the valley bottom, and presence of numerous rock faults and springs, all of which give the valley a mountainous character. The valley was formed of the Cretaceous gaizes and marls, lithotamnic limestones, and detrital marls, covered by Pleistocene and Holocene alluvial sands, sandy-clay deluvia, and peats, on which



Fig. 1. The course of the Sopot river against the background of the Roztocze region and the studied valley section. The DEM done with a resolution of 3 m, vertical exaggeration = 3.

Explanations: L1-L20 - left-side sections of the valley, R1-R20 - right-side sections of the valley

different types of soils evolved (Czarnecka & Janiec 2001, 2002; Janiec & Czarnecka 2001). The study area (80.5 ha) is wooded in 99.5% and only slightly transformed by human impact. The main character of the vegetation landscape of steep slopes is created by the upland mixed fir forest Abietetum polonicum (Dziub. 1928) BR. Bl. et Vlieg. 1939, which covers the study area in 46.1%. The share of other forest communities is as follows: riverside ash-alder forest Fraxino-Alnetum W.Mat. 1952 (21.2%), bog alder forest Ribeso nigri-Alnetum Sol.-Górn. (1975)1987 (14.2%), oak-pine mixed forest Querco roboris-Pinetum (W.Mat. 1981) J.Mat. 1988 (7.0%), moist mixed coniferous forest Querco-Piceetum (W.Mat. 1952) W.Mat. et Polak. 1955 (5.7%), pine forests - suboceanic Leucobryo-Pinetum W.Mat. (1962)1973 and subcontinental Peucedano-Pinetum W.Mat. (1962)1973 (3.2% together), secondary pine communities (0.8%). The remaining area (0.5%) is covered by sedge and meadow vegetation (Czarnecka et al. 2015). The most valuable gorge part of the valley had been preserved since 1958 in a landscape reserve called 'Czartowe Pole' ('The Devil's Field'). The reserve was also included into the Natura 2000 network within both types of protected sites: Special Protected Area (PLB 060012) and Special Area of Conservation (PLH 060018).

2.2. Field and laboratory studies

The main materials comprised species lists for each ca. 200-m-long, 100-350-m-wide section, according to the river valley course, separately for the left and right riverbanks (Fig. 1). The frequency and abundance of each vascular plant species (pteridophytes and spermatophytes, except for shrubs and trees) in the groundfloor vegetation were established using a simplified, combined scale, where: 1 - means sporadic species (single individuals or small, scarce clumps of plants); 2 - rare and non-abundant species (bigger clumps or patches of plants, covering <10% of the section area); 3 - frequent and abundant species (10-50% of the section area); 4 - common and very abundant species (>50% of the section area). To estimate the real habitat conditions in the study area and the ecological scale of particular plant species, we also used other field materials: phytosociological relevés in different types of plant communities (60 in total) and soil pits (27 in total; 140 samples of mineral and organic formations) distributed proportionally to the community area, and the diversity of the identified communities. Using commonly accepted methods, soil dispersion (=granulometry) and soil types, as well as basic physico-chemical properties of soil formations, namely the content of organic matter/ organic carbon, active acidity, calcium carbonate, basic nutrients - Ca, K, Na, Mg, Fe, P, and N in the form of ammonia and nitrate, were determined (Czarnecka et al.

2001, 2015; Czarnecka & Janiec 2001; B. Czarnecka, unpbl. data).

The EIVs for the Polish vascular flora (Zarzycki *et al.* 2002) which were established on the theoretical and methodological basis of the original Ellenberg system (Ellenberg 1974; Ellenberg *et al.* 1992) describe the Polish populations of plants against the background of local climatic and edaphic conditions, which might be slightly different than those throughout Central Europe. The EIVs used in the present study were additionally calibrated based on measured environmental variables found during field and laboratory studies.

From the group of climatic factors (i.e. C - continentality, L-light, and T-temperature), we elaborated only the L value ranging from 1 (deep shade) to 5 (full light). The C and T values were deliberately not taken into account, as their value is constant in such a small area. We took into account 5 indicator values from the group of edaphic factors describing the most typical habitat conditions of the species. Two of them, soil moisture -W, and soil/water acidity (pH) -R, are common indicators for Ellenberg's and Zarzycki's system, although different in the number of degrees. In our case, the W value shows a moisture scale from very dry habitats (degree 1) to wet (degree 5) and aquatic ones (degree 6), while the R value indicates the amplitude of habitat acidity from highly acidic soils, pH <4 (degree 1) to alkaline soils, pH > 7 (degree 5).

The last three ecological indicators, namely Tr, D and H, are new in comparison with Ellenberg's system. The trophy value (Tr) was elaborated for vascular plants of Poland by Zarzycki et al. (2002) instead of 'Stickstoffzahl (N-Zahl)' = 'nitrogen figure' (N) by Ellenberg (1974, 1992). This value indicates the content of different nutrients, particularly N, K, Mg, Ca, and P making habitats differently fertile and ranging from extremely poor (extremely oligotrophic - grade 1) to very rich (extremely fertile - grade 5). The D value points to a different character of soil dispersion: 1-rock crevices, 2 - rock debris, 3 - sands, 4 - clay and dusty deposits, 5 - clays and loams. The H value indicates humus and/or organic matter content in soil; grade 1 denotes soil poor in organic matter, 2 - mineral-humic soil, and 3 – soil rich in organic matter.

Vascular plants nomenclature followed Mirek *et. al.* (2002) and plant communities were distinguished after Matuszkiewicz (2008).

2.3. Terrain attributes datasets

The analysis of the area was based on the DEM and its derivatives, and was conducted in basic fields, i.e. 200-m-long sections, for which floristic mapping was done: 40 sections in total (Fig. 1). Spatial data were obtained from topographic maps at the 1:10 000 scale by successive digitization of contour lines, elevation points, valley edges and their height. The Topo to Raster tool of the ArcGIS 10.1 (Hutchinson 1989) was used to generate the DEM with a resolution of 3 m (Hengl 2006). Based on the DEM, two groups of topographic attributes were calculated (Wilson & Gallant 2000; Kraak & Ormeling 2003; Evans *et al.* 2014): primary – slope, planar, vertical, and total curvature; and secondary – the solar radiation (SRAD) and topographic wetness index (TWI). Apart from the above-listed primary and secondary attributes, the next terrain characters were taken into account: the denivelation, total area of a given section, flat area (i.e. $\leq 2^{\circ}$ of terrain slope), and upslope area (>2° of terrain slope).

For calculation of terrain attributes, we used tools available in the ArcToolbox of the ArcGIS 10.1 program and the Spatial Analyst extension. The raster of slope was expressed in degrees and was calculated using the Slope tool, which fits a plane to the z-values of a 3×3 cell neighbourhood around the processing or centre cell. The slope value of this plane is calculated using the average maximum technique (Burrough & McDonell 1998). The rasters with curvatures were calculated on default settings of the Curvature tool. The SRAD was calculated for the vegetation season (April-October) with the Solar radiation tool, which calculates insolation across a landscape or for specific locations, based on methods from the hemispherical viewshed algorithm (Fu & Rich 2002). For the TWI, we used a script from the ESRI website (ESRI 2003) which calculates the TWI that is a function of the natural logarithm of the ratio of local upslope contributing area and slope (Beven & Kirkby 1979).

Subsequently, each of the topographic attributes was analysed for each section using the Zonal Statistics tool. With its assistance, statistics was calculated for each zone defined by a zone dataset (in our case, these were particular sections of the valley), based on values from other datasets (slope, planar, vertical and total curvature, SRAD, and TWI). The mean and sum values of the primary and secondary topographic attributes were taken into account.

2.4. Statistical analysis

The mean value of a specific EIV in each valley section was calculated using a modified formula for the weighted average (Czarnecka & Chabudziński 2011):

$$W_{A} = \frac{\sum_{i=1}^{n} (A_{i}^{2} \times I_{i})}{\sum_{i=1}^{n} A_{i}^{2}}$$

where: W_A – weighted average,

 A_i – abundance of cover of the i-th species in a given section of the valley,

 I_i – ecological indicator value for the i-th species,

n – number of species in the section.

In the next step, we calculated correlations of topographic attributes of the valleys, species richness, and the EIVs for all species in each section. According to the suggestions of some authors (Ertsen *et al.* 1998; Seidling 2005; Bergès *et al.* 2006) we analysed the EIVs only for one vegetation layer, i.e. ground-floor vegetation (pteridophytes and spermatophytes, except for the shrub and tree species). Because majority of the values of the topographic attributes did not have a normal distribution (the Shapiro-Wilk test), Spearman's rank correlation coefficients (r) were calculated between the number of species and the mean value for a specific EIV in each section and topographic attributes of the valley. All statistics were calculated using Statistica PL, version 9.0.

To analyse the relationships between weighted averages for a particular EIV of ground flora and topographic attributes of the valley, we used multivariate ordination methods in Canoco version 4.5 (ter Braak & Šmilauer 2002; Lepš & Šmilauer 2003). In order to test the proposed algorithm, we analysed relationships for two groups of species: (1) the most frequent species, i.e. occurring in $\geq 50\%$ sections and having the greatest frequency and abundance in the valley habitats; (2) the rarest species, i.e. occurring in only 1-2 sections; grade 1 in the 4-grade scale used for the assessment of species abundance (nomenclature after Mirek et al. 2002; see Appendix 1). According to the length of the gradient from a preliminary Detrended Canonical Analysis (DCA), a linear model was used the Redundancy Detrended Analysis (RDA). To find the minimum number of statistically significant variables, we used a manual procedure with 499 Monte Carlo significance permutation tests (MCT) and forward selection of species-topographic attributes. The eigenvalues and percentages of floristic and topographic variance explained by the first four axes were calculated. The pattern obtained from the classification was transferred onto a graph with sample groups marked in the RDA.

3. Results

3.1. Topographic attributes vs. spatial patterns of common species

We found 239 herb plant species (spermatophytes and pteridophytes) in the ground-floor vegetation of the study area. For the most frequent 48 herb species (Appendix 1), the RDA analysis revealed distinct differentiation of ecological species groups associated with the topographic attributes and EIVs (Table 1, Fig. 2). Each group (spatial pattern) received a name of the species with the longest vector. The pattern of *Maianthemum bifolium* (full species names are given in Appendix 1), apart from the 'flag' species, comprises the species regarded as elements of mixed coniferous forests,

Table 1. Results of the Monte Carlo permutation tests and forward selection for relations between common and rare species, topographic attributes and ecological indicator values in the Sopot river valley. Significance level: $*0.01 < P \le 0.05$, $**0.0001 < P \le 0.01$

Variable	Common species		Rare species	
	ΛA	F ratio	ΛA	F ratio
No. of species	0.09	4.77**	0.04	1.86*
SRAD_mean	0.03	2.09**		
CT_mean	0.02	1.60*		
Н	0.21	10.08**		
W	0.05	3.15**		
Tr	0.04	2.63**		
L	0.08	4.39**	0.08	3.95**
D			0.13	5.71*

Explanations: see Fig. 2

particularly *Abietetum polonicum* (e.g. *Circaea alpina*, *Carex digitata*, *Oxalis acetosella*). They were correlated with the total area of a given section, TWI_sum, and SRAD_sum. Species of the *Carex remota* pattern (elements of ash-alder forests *Fraxino-Alnetum – Mentha aquatica*, *Eupatorium cannabinum*, *Senecio nemorensis*,

and others), were most highly correlated with the flat area and number of species in the section and TWI_mean, and significantly more weakly correlated with the mean and sum CV. *Ranunculus repens* was related to this group of species, although its vector was considerably shorter. In general, both the above-mentioned species groups were negatively correlated with axis 1.

The other two species groups were negatively correlated with axis 2. Deschampsia caespitosa and Epilobium palustre were related to the basic species of the Carex acutiformis pattern, i.e. components of bog alder forests Ribeso nigri-Alnetum (also Carex elongata, Galium palustre, Polygonum hydropiper, Crepis paludosa, and others), and Phalaris arundinacea held an intermediate place between the patterns for riparian and alder forests. Soil dispersion (D value) seemed to be the most important factor for species representing the latter distribution pattern. Two other EIVs, namely H and W, which indicate the share of species with requirements for high humus content and moisture, described to a comparable degree species representing the Filipendula ulmaria pattern, which comprised Mysosotis palustris and Poa trivialis as well. These three taxa were also correlated with vectors of other EIVs: most strongly with L, and more weakly with R and Tr.



Fig. 2. Spatial patterns for the most frequent 48 species occurring in the Sopot river valley. Each spatial pattern received a name of the 'flag' species (bold), i.e., a species with the longest vector. For full species names see Appendix 1. Eigenvalues: Axis 1 - 26.64, Axis 2 - 12.21, Axis 3 - 6.17, Axis 4 - 4.26 Explanations: TA-total area, FA-flat area, UAupslope area, DN-denivelation, SL mean-mean slope. CP mean-mean planar curvature. CP sum - sum planar curvature, CV_mean-mean vertical curvature, CV sum-sum vertical curvature, CT mean-mean total curvature, CT sum-sum total curvature, SRAD_mean - mean solar radiation, SRAD sum - sum solar radiation, TWI mean mean topographic wetness index, TWI_sum-sum topographic wetness index. Ecological indicator values for: light - L, moisture - W, trophy - Tr, acidity - R, soil dispersion - D, organic matter/ humus content - H

Another two groups can be distinguished among species that were positively correlated with axis 1. The first one, defined as the Dryopteris filix-mas pattern (apart from this species also Mycelis muralis, Galeobdolon luteum, and Stellaria nemorum), representing species typical for deciduous broad-leaved forests of the Querco-Fagetea Br.-Bl. et Vlieg. 1937 class, seemed to be most highly correlated with terrain denivelation and upslope area of a given section. The final species group with a non-homogeneous ecological affinity, defined as the Urtica dioica pattern (including Aegopodium podagraria, Impatiens noli-tangere, Chrysosplenium alternifolium, Moehringia trinervia), indicated somewhat disturbed habitats and/or habitats with an increased content of nitrogen compounds. Such topographic attributes as the SRAD mean, CT mean, CT sum, CP mean, and CP sum had no significant impact on spatial patterns of the most frequent and abundant species.

The test of significance of all canonical axes explained 75.1% of the variables (F ratio = 2.588; P<0.01). The sum value of the MCT showed that axis 1 explained 26.6% of all the variables analysed for 48 common species (F ratio = 6.525; P<0.01). Forward selection of species-topographic relationships showed 7 statistically significant variables (Table 1).

3.2. Topographic attributes vs. spatial patterns of rare species

The differentiation in the spatial patterns of ground flora of the studied valley included spatial patterns of

26 rare species (Fig. 3, Appendix 1). The largest group comprised thermophilous species - the Ajuga genevensis pattern (e.g. Selinum carvifolia, Trifolium repens, *Pimpinella saxifraga*) positively correlated with axis 1 and vector L, and more weakly correlated with the CV_ sum, CT mean and CT sum. This group also included Malva neglecta and Galium verum. The species of the Scorzonera humilis pattern (also Sedum maximum and Lycopodium clavatum) represent pine communities Leucobryo-Pinetum and Peucedano-Pinetum, following the direction of vectors of common species from the Maianthemum bifolium pattern (Fig. 2). Two other slope species: Peucedanum oreoselinum and Equisetum *hyemale* were related to this pattern. Species from the Stachys palustris pattern occurring at the valley bottom (also Hypericum tetrapterum, Listera ovata, Veronica montana) were correlated with axis 2 and followed the DN and FA vectors. The TWI mean followed the vector of species number, while the TWI sum followed the SRAD sum vector. Both TWI values and SRAD sum were not statistically significant (P>0.05) for rare species studied and for that reason they were not placed on the graph (Fig. 3). The centre of the diagram comprises rare species from different habitats, i.e. Lilium martagon, Hedera helix, Ophioglossum vulgatum, and others.

The cumulative percentage of rare species and topographic variance explained by the first two RDA axes was 66.8%. They were statistically significant (F ratio = 5.349, P<0.05, and F = 1.724, P<0.001, for the first





Explanations: see Fig. 2

and second axis, respectively). Three variables were statistically significant for the patterns of the rare species: number of species and two of the EIVs - L and D (Table 1).

4. Discussion

Topographic information explains only a certain proportion of vegetation in a cultural landscape (Tappeiner *et al.* 1998) but it may be very useful in natural or semi-natural forested areas such as the studied river valley (Czarnecka *et al.* 2001; Janiec & Czarnecka 2001; Czarnecka & Janiec 2002). Topography shapes and constrains vegetation patterns in several ways, creating a range of environmental conditions that favour different plant communities and ecosystem processes. Topography, in conjunction with geomorphic processes, also creates stable vegetation boundaries and vegetation-free areas throughout landscape. Finally, elevation gradients impose directionality to which ecological and physical processes respond in shaping landscape patterns (Dorner *et al.* 2002).

Elevation gradients (denivelations) determine soil variables, vegetation production levels, and patterns of species disturbance (Franklin 1995; Lyon & Sagers 1998; Dorner *et al.* 2002; Pfeffer *et al.* 2003; Fitterer *et al.* 2012). The terrain denivelation of the Sopot river valley expressed as the incision into the substratum (mean = 20 m, max = 27 m) significantly negatively influenced the EIVs for ground-floor vegetation: L, W, Tr, R, D, and H (Czarnecka *et al.* 2015). That attribute was not significant for species richness and ecological variety of the flora in the gorge section of the other river valley, the Szum river, similar in a mountainous character but incised in a bedrock for maximum 15 m (Czarnecka & Chabudziński 2014).

The width of the floodplain terrace seems to be of great importance for the species richness because of the presence of rich hygrophilous and nitrophilous vegetation, i.e. riverside carrs and bog alder forests. Their occurrence is promoted, from the riverbed side, by sedimentation of heavier and, hence, more nutrientrich mineral formations: loams, clayey sands, heavy and silty clays. The flat area of a given valley section proved to be a determining factor for species representing the Carex remota pattern, whose frequency and abundance were the greatest in various forms of riverside carrs Fraxino-Alnetum. Despite opposite vectors, species comprised in the Urtica dioica pattern are frequent components of riparian communities (Impatiens noli-tangere, Chrysosplenium alternifolium), likewise Ranunculus repens or Galium aparine. In turn, at the slope side and in the side valleys in the left riverbank, i.e. at the sites fed with waters of numerous springs and effluents, there are proper conditions

for formation of the rich low peat beds (cf. Czarnecka et al. 2015). These habitat conditions are associated with the Carex acutiformis pattern comprising species from boggy valleys (e.g. C. acutiformis, C. elongata, Galium palustre, Solanum dulcamara), and also with Cardamine amara, a crenophyte, indicating the importance of spring waters in feeding bog alder forests Ribeso nigri-Alnetum (Czarnecka & Janiec 2002). The vector for the D, following the direction of the vectors of the aforementioned species, should be regarded in relation to the granulometric composition of formations underlying peat layers (Czarnecka & Janiec 2001). Rare species of the Stachys palustris pattern are also associated with differently moist habitats in the valley bottom (Czarnecka & Janiec 2002; B. Czarnecka, unpbl. data). The placement of the Filipendula ulmaria pattern species, the components of macroforb communities, in the system of the two first RDA axes and the direction of their vectors following that for light, acidity and trophy, indicate that they are remnants of open, fertile, wet meadows and rushes, undergoing succession towards forest communities for over 40 years (Fijałkowski 1973; Czarnecka et al. 2001; Czarnecka & Janiec 2002).

In the case of common species, significant negative correlations were found for the mean slope in the individual valley sections and all of the studied EIVs: L, W, Tr, R, D, and H. The correlations were usually higher for the right riverbank which is characterized by southern aspect and its derivatives (Czarnecka et al. 2015). The upslope area influenced the decrease in the share of species with higher requirements for light, humidity, heavier soil formations, and humus content. Greater slopes, higher insolation, and lower humidity offered less favourable conditions for accumulation of organic matter and humification thereof. Soils in such conditions are more acidic and poorer podzolics overgrown with different coniferous forests, first of all upland mixed fir forest Abietetum polonicum (Czarnecka et al. 2001; Janiec & Czarnecka 2001; Czarnecka & Janiec 2002, 2006). Many species from the Maianthemum bifolium pattern are associated with this community, e.g. Circaea alpina, C. lutetiana, Paris quadrifolia, and Equisetum sylvaticum, which 'enter' lower slope parts from the neighbouring riparian forests and are characteristic for the fertile forms of fir forest Abietetum polonicum circaeetosum (after Matuszkiewicz 1977; see also Czarnecka et al. 2001). These patches of fir forest are also the main habitat for broad-leaved forest species (Dryopteris filix-mas pattern). Festuca gigantea is a deciduous forest species, which was not included in any of the distinguished patterns and whose vector follows the course of vectors for total curvature. In turn, Maianthemum bifolium, Carex digitata, Dryopteris carthusiana, or D. dilatata are components of groundfloor vegetation of poorer patches of fir forest Abietetum

polonicum typicum (Matuszkiewicz 1977; Czarnecka et al. 2001). Vaccinium myrtillus included in this pattern is a common component of pine and mixed forests, whereas Lycopodium annotinum is mainly a component of ground-floor vegetation of moist mixed forest with spruce Querco-Piceetum, which forms a narrow belt at the foot of the slopes at the site of transition from mineral to organic soils (Czarnecka & Janiec 2002, 2006), hence the close neighbourhood of Lycopodium annotinum with species representing the Carex remota pattern. In turn, rare species of the Scorzonera humilis pattern are associated with patches of dry pine forests, particularly Peucedano-Pinetum, and oak-pine mixed forest Querco roboris-Pinetum (Czarnecka et al. 2001; Czarnecka & Janiec 2002).

A positive influence of vertical curvatures on the species number and the increase in species with higher requirements for light was noted for the right-side bank of the study earlier (Czarnecka et al. 2015). In contrast, the total curvatures (particularly the CT sum) influenced significantly the decrease in the share of species with higher L, H, W, and D values which indicates that the slopes of the valley are dominated by convex rather than concave forms. Negative correlations between the planar curvature and the Tr and R values were also found. This implies that the planar curvature of the contour lines has more 'ridges' (promoting divergence of flowing waters) than 'valleys' which promotes convergence of flowing waters (cf. Wilson & Gallant 2000; Kraak & Ormeling 2003; Urbański 2012; Evans et al. 2014). This situation, locally together with narrow terrace and water velocity (i.e. in a 'strict' gorge section of the studied valley), reduces the repository role of the river, and leads to reduction of nutrient content and soil reaction (Werner & Zedler 2002; Francis et al. 2008; Jolley et al. 2010).

In earlier studies in the gorge sections of the river valleys crossing the escarpment zone of the Roztocze Highlands, we confirmed that the SRAD and TWI values were significantly correlated with the number of species and diversity of ground-floor vegetation (Czarnecka & Chabudziński 2011, 2014; Czarnecka et al. 2015). The SRAD is highly variable from place to place due to changing slope and aspect (Kumar et al. 1997; Pfeffer et al. 2003; Fitterer et al. 2012). In this study, we found that vectors for the SRAD sum and TWI sum were strongly correlated with the Maianthemum bifolium pattern comprising the species of different coniferous forests (Carex digitata, Oxalis acetosella, Dryopteris carthusiana, D. dilatata, and others). Simultaneously, the SRAD sum seems to be much more important for the species of the *Carex remota* pattern (that is, for riverside carr species), while the TWI sum - for the Dryopteris filix mas pattern (broad-leaved forest species). Among rare species, the Ajuga genevensis pattern exhibited the highest L value and it was correlated with the mean value of solar radiation as well as with both total and vertical curvatures. The TWI values had no influence on this ecological group of species. They were components of non-forest thermophilous community of intermediate character between meadow of the *Molinio-Arrhenatheretea* R.Tx. 1937 class and outskirt community of the *Trifolio-Geranietea sanguinei* Th. Müller 1962 class connected with leached brown soil (Czarnecka & Janiec 2002) occurring on the most 'sunny' and dry slope of the right riverbank (Czarnecka *et al.* 2015).

Soil moisture is commonly recognized as one of the most important determinants of vegetation composition, productivity and distribution patterns (Ertsen et al. 1998; Tappeiner et al. 1998; Schaffers & Sýkora 2000; Wamelink et al. 2002; Lawesson et al. 2003; Cousins & Lindborg 2004; Grabs et al. 2009; Crosti et al. 2010; Jolley et al. 2010; Moelsund et al. 2013). However, exact measurement of water regime is very difficult. For this reason, the TWI derived from DEMs is commonly used in analyses of relationships between abiotic and biotic environmental characters. The TWI correlates well with soil attributes such as horizon depth, groundwater table, silt and organic matter contents, and thereby provides a good indicator of habitat productivity (Moore et al. 1991; Franklin 1995; Sørensen et al. 2006; Grabs et al. 2009; Kopecký & Čižkova 2010; Fitterer et al. 2012). In our research, the TWI, particularly its mean value, was significantly positively correlated with the species abundance and the studied EIVs: L, W, Tr, R, D, H. The RDA analysis showed that the TWI mean vector was placed between the vectors for species from the Carex remota and C. acutiformis patterns, i.e. inhabiting moist and wet habitats, respectively, while the TWI sum vector was placed between the patters of Majanthemum bifolium (species of mixed coniferous forests) and Dryopteris filix-mas (species of broad-lived forests). As a rule, the TWI was more important for the ground flora on the right (more 'sunny') than the left (more 'shiny') riverbank, with the exception of the Tr value (Czarnecka et al. 2015).

Biological indication can be defined as making use of specific reactions of organisms to their environment (Diekmann 2003). The EIVs for Central European flora (Ellenberg 1974; Ellenberg *et al.* 1992) are widely used in vegetation assessment, both to estimate soil variables from floristic data and to predict vegetation composition from given soil properties (Ertsen *et al.* 1998; van Dobben *et al.* 1999; Schaffers & Sýkora 2000; Wilson *et al.* 2001; Wamelink *et al.* 2002; Gégout 2003; Lawesson *et al.* 2003; Seidling 2005; Bergès *et al.* 2006; Petřik & Wild 2006; Feldmeyer-Christe *et al.* 2007; Crosti *et al.* 2010; Angiolini *et al.* 2011; Balkovič *et al.* 2012). The wide success of Ellenberg's system is probably associated with the fact that for a majority of species autecology and life history in general do not differ considerably throughout Europe (Lawesson *et al.* 2003), at least in nemoral and boreal regions (Godefroid & Dana 2007; Seidling & Fischer 2008).

While ecological indicators from the group of climatic factors, particularly the C and T values, are of greater importance on macroscale, e.g. in the studies of spatial distribution of different types of vegetation, the other ones, namely L, W, N, and R, are the main factors responsible for structuring communities and determining species assemblages on microscale, e.g. in a given community. Among the EIVs, the R seems to be the most frequent subject of studies (Ertsen et al. 1998; Lyon & Sagers 1998; Wamelink et al. 1998, 2002; van Dobben et al. 1999; Schaffers & Sýkora 2000; Wilson et al. 2001; Lawesson et al. 2003; Seidling & Fischer 2008; Crosti et al. 2010; Jolley et al. 2010; Balkovič et al. 2012; Czarnecka & Chabudziński 2014; Czarnecka et al. 2015). However, some authors found during field measurements that pH values for some ecological groups of species were different than those expected from Ellenberg's scale, which strongly limits the use of the R values and requires re-calibration (Ertsen et al. 1998; Wamelink et al. 1998, 2002; Schaffers & Sýkora 2000; Lawesson et al. 2003; Feldmeyer-Christe et al. 2007). The recognised influence of soil acidity and calcium content on species occurrence (Schaffers & Sýkora 2000) may also apply to the study area due to the presence of Ca-rich formations of various origins and age influencing approximately a nine-fold differentiation of water mineralisation (Janiec & Czarnecka 2001; Czarnecka & Janiec 2002).

Apart from the chemical composition of the formations, topography affects soil pH which 'cooperates' with soil moisture. The moisture regime also correlates with organic matter/humus content, or widely with the soil nutrient regime, particularly nitrogen supply (Wilson *et al.* 2001; Seidling & Fischer 2008). According to Ellenberg *et al.* (1992), the 'nitrogen figure' (N) may be interpreted as an indicator of general nutrient status and that is why, it is widely used in habitat calibration (Ertsen et al. 1998; Wamelink et al. 1998; van Dobben et al. 1999; Schaffers & Sýkora 2000; Gégout et al. 2003; Bergès et al. 2006). Schaffers & Sýkora (2000) even stressed that Ellenberg's N-values are strongly correlated with biomass production, suggesting that they could be replaced by 'productivity values'. In the present study, we analysed the influence of topographic attributes on values of two other indicators describing requirements of the ground-floor vegetation - H and Tr values, the latter elaborated for Polish vascular flora instead of the N value (Zarzycki et al. 2002). The section area and the mean TWI may be important for the rise of the Tr and H values, while denivelation, upslope area, mean slope, mean planar curvature, and mean SRAD influence negatively the two indicators, with some exceptions for the left-side sections (Czarnecka et al. 2015). To confirm the relationships between moisture regime and humus content and trophy value, the placement of vectors for these EIVs should be shown as well as vectors for species representing two spatial patterns: Carex acutiformis (bog alder forests) and Filipendula ulmaria (wet meadows).

5. Conclusions

Our study provides evidence for response of the species richness and diversity of the ground-floor vegetation to topographic attributes of a forested river valley. We also proved that the EIV system, which had been widely applied for modelling plant distribution on large spatial scales, i.e. on the global, regional, and landscape levels, may be used on a micro- and nanoscale, even to single patches of plant communities. It has to be stressed that GIS and DEM became useful tools for detection of patterns of species with different requirements for habitat resources, and distribution of their ecological groups in correlation with primary and secondary topographic attributes along river valleys as well as other landscapes characterized by varied topography, especially in highland and mountain regions.

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Appendix 1. List of 239 species recorded in the Sopot river valley (nomenclature after Mirek *et al.* 2002). Ecological groups were named according to the optimum of species occurrence in riverine landscapes of the study area. Species inhabiting forest and non-forest communities, are ordered along water gradient of a given vegetation type. Species included in the category 'ruderals' occur in the sites transformed by human activity, e.g., touristic paths, roads, forest outskirts, forest cuttings, etc.

Explanations: 1 - bog alder forests, 2 - ash-alder forests, 3 - deciduous forests, 4 - mixed coniferous forests, 5 - mixed fir forests, 6 - coniferous forests, 7 - pine forests, 8 - springs, 9 - waters and watersides, 10 - rushes, 11 - transitional peatbogs, 12 - meadows, 13 - dry grasslands, 14 - rocks, 15 - ruderals

Most frequent species (48): Aegopodium podagraria L., Aeg pod, 2; Athyrium filix-femina (L.) Roth, Ath fil, 2; Caltha palustris L., Cal pal, 1; Cardamine amara L., Car ama, 8; Carex acutiformis Ehrah., Car acu, 1; Carex digitata L., Car dig, 5; Carex elongata L., Car elo, 1; Carex remota L., Car rem, 2; Chrysosplenium alternifolium L., Chr alt, 2; Circaea alpina L., Cir alp, 2; Circaea lutetiana L., Cir lut, 2; Cirsium oleraceum (L.) Scop., Cir ole, 2; Crepis paludosa (L.) Moench, Cre pal, 1; Deschampsia caespitosa (L.) P. Beauv., Des cae, 1; Dryopteris carthusiana (Vill.) H. P. Fuchs, Dry car, 4; Dryopteris dilatata (Hoffin.) A. Gray, Dry dil, 4; Dryopteris filix-mas (L.) Schott, , Dry fil, 2; Epilobium palustre L., Epi pal, 1; Equisetum sylvaticum L., Equ syl, 2; Eupatorium cannabinum L., Eup can, 2; Festuca gigantea (L.) VilL., Fes gig, 2; Filipendula ulmaria (L.) Maxim., Fil ulm, 1; Galeobdolon luteum Huds., Gal lut, 2; Galium aparine L., Gal apa, 2; Galium palustre L., Gal pal, 1; Impatiens noli-tangere L., Imp nol, 2; Luzula pilosa (L.) Willd., Luz pil, 5; Lycopodium annotinum L., Lyc ann, 4; Lysimachia vulgaris L., Lys vul, 1; Maianthemum bifolium (L.) F. W. Schmidt, Mai bif, 5; Mentha aquatica L., Men aqu, 1; Moehringia trinervia (L.) Clairv., Moe tri, 3; Mycelis muralis (L.) Dumort, Myc mur, 5; Myosotis palustris (L.) L. emend Rchb., Myo pal, 1; Oxalis acetosella L., Oxa ace, 5; Paris quadrifolia L., Par qua, 3; Phalaris arundinacea L., Pha aru, 1; Poa trivialis L., Poa tri, 12; Polygonum hydropiper L., Pol hyd, 9; Polypodium vulgare L., Pol vul, 5; Ranunculus repens L., Ran rep, 2; Senecio nemorensis agg., Sen nem, 2; Solanum dulcamara L., Sol dul, 1; Stellaria nemorum L., Ste nem, 2; Trientalis europaea L., Tri eur, 4; Urtica dioica L., Urt dio, 2; Vaccinium myrtillus L., Vac myr, 6; Valeriana simplicifolia (Rchb.) Kabath , Val sim, 1.

Less frequent species (165): Achillea millefolium L. s. s., Ach mil, 13; Actaea spicata L., Act spi, 3; Adoxa moschatellina L., Ado mos, 2; Agrimonia eupatoria L., Agr eup, 13; Agropyron caninum (L.) P. Beauv., Agr can, 2; Agrostis capillaris L., Agr cap, 12; Agrostis gigantea Roth, Agr gig, 15; Agrostis stolonifera L., Agr sto, 12; Ajuga reptans L., Aju rep, 2; Alchemilla monticola Opiz, Alc mon, 12; Alopecurus pratensis L., Alo pra, 12; Anemone nemorosa L., Ane nem, 3; Angelica sylvestris L., Ang syl, 1; Anthoxanthum odoratum L. s. s., Ant odo, 12; Asarum europaeum L., Asa eur, 3; Asplenium trichomanes L., Asp tri, 14; Berula erecta (Huds.) Coville, Ber ere, 10; Bidens tripartita L., Bid tri, 9; Brachypodium sylvaticum (Huds.) P. Beauv., Bra syl, 2; Briza media L., Bri med, 12; Bromus inermis Leyss., Bro ine, 13; Calamagrostis arundinacea (L.) Roth, Cal aru, 7; Calamagrostis canescens (Weber) Roth, Cal can, 1; Calamagrostis epigejos (L.) Roth, Cal epi, 15; Calamagrostis villosa (Chaix) J. F. Gmel., Cal vil, 4; Calla palustris L., Cll pal, 1; Calluna vulgaris (L.) Hull, Cal vul, 7; Campanula patula L. s. s., Cam pat, 12; Campanula trachelium L., Cam tra, 3; Cardamine impatiens L., Car imp, 2; Cardamine pratensis L. s. s., Car pra, 12; Carex brizoides L., Car bri, 2; Carex canescens L., Car can, 11; Carex echinata Murray, Car ech, 11; Carex gracilis Curtis, Car gra, 10; Carex hirta L., Car hir, 12; Carex nigra Reichard, Car nig, 11; Carex pairae F. W. Schultz, Car pai, 13; Carex pallescens L., Car pal, 12; Carex pilosa Scop., Car pil, 4; Carex rostrata Stokes, Car ros, 10; Carex sylvatica Huds., Car syl, 3; Carum carvi L., Car car, 13; Centaurea jacea L., Cen jac, 12; Chaerophyllum aromaticum L., Cha aro, 2; Chaerophyllum hirsutum L., Cha hir, 2; Chaerophyllum temulum L., Cha tem, 2; Chamaenerion angustifolium (L.) Scop., Cha ang, 15; Chelidonium majus L., Che maj, 15; Cirsium arvense (L.) Scop., Cir arv, 15; Cirsium palustre (L.) Scop., Cir pal, 1; Comarum palustre L., Com pal, 11; Convallaria majalis L., Con maj, 7; Convolvulus arvensis L., Con arv, 15; Cruciata glabra (L.) Eherend., Cru gla, 4; Cynosurus cristatus L., Cyn cri, 12; Dactylis glomerata L., Dac glo, 12; Dactylorhiza maculata (L.) Soó, Dac mac, 1; Dactylorhiza majalis (Rchb.) Hunt & Summerh., Dac maj, 12; Danthonia decumbens DC., Dan dec, 7; Daphne mezereum L., Dap mez, 3; Deschampsia flexuosa (L.) Trin., Des fle, 7; Epilobium hirsutum L., Epi hir, 15; Epilobium montanum L., Epi mon, 15; Epipactis palustris (L.) Crantz, Epi pal, 12; Equisetum arvense L., Equ arv, 12; Equisetum fluviatile L., Equ flu, 10; Equisetum palustre L., Equ pal, 12; Equisetum pratense Ehrh., Equ pra, 2; Eriophorum angustifolium Honck., Eri ang, 11; Euphorbia amygdaloides L., Eup amy, 3; Euphorbia cyparissias L., Eup cyp, 13; Festuca ovina L. s. s., Fes ovi, 7; Fragaria vesca L., Fra ves, 4; Galeopsis pubescens Besser, Gal pub, 15; Galeopsis tetrahit L., Gal tet, 15; Galium mollugo L. s. s., Gal mol, 12; Galium odoratum (L.) Scop., Gal odo, 3; Galium schultesii Vest, Gal sch, 3; Geranium robertianum L., Ger rob, 3; Geum rivale L., Geu riv, 1; Geum urbanum L., Geu urb, 12; Glechoma hederacea L., Gle hed, 12; Glyceria maxima (Hartm.) Holmb., Gly max, 10; Glyceria plicata Fr., Gly pli, 10; Gymnocarpium dryopteris (L.) Newman, Gym dry, 5; Hepatica nobilis Schreb., Hep nob, 3; Heracleum sphondylium L. s. s., Her sph, 12; Hieracium lachenalii C. C. Gmel., Hie lac, 4; Hieracium murorum L., Hie mur, 4; Hieracium pilosella L., Hie pil, 13; Holcus lanatus L., Hol lan, 12; Humulus lupulus L., Hum lup, 2; Huperzia selago (L.) Bernh. ex Schrank & Mart., Hup sel, 4; Hypericum maculatum Crantz, Hyp mac, 12; Hypericum perforatum L., Hyp per, 13; Iris pseudacorus L., Iri pse, 1; Juncus effusus L., Jun eff, 1; Knautia arvensis (L.) J. M. Coult., Kna arv, 13; Lamium album L., Lam alb, 15; Lamium maculatum L., Lam mac, 15; Lapsana communis L. s. s., Lap com, 15; Lathyrus pratensis L., Lat pra, 12; Lemna minor L., Lem min, 9; Lemna trisulca L., Lem tri, 9; Leucanthemum vulgare Lam., Leu vul, 12; Luzula multiflora (Retz.) Lej., Luz mul, 13; Lychnis flos-cuculi L., Lyc flo, 12; Lycopus europaeus L., Lyc eur, 1; Lysimachia nummularia L., Lys num, 12; Lysimachia thyrsiflora L., Lys thy, 1; Lythrum salicaria L., Lyt sal, 12; Medicago falcata L., Med fal, 13; Melampyrum pratense L., Mel pra, 7; Melica nutans L., Mel nut, 3; Mentha longifolia (L.) L., Men lon, 2; Menyanthes trifoliata L., Men tri, 11; Mercurialis perennis L., Mer per, 2; Millium effusum L., Mil eff, 3; Petasites albus (L.) Gaertn., Pet alb, 2; Peucedanum palustre (L.) Moench.), Peu pal, 1; Phegopteris connectilis (Michx.) Watt, Phe con, 2; Phragmites australis (Cav.) Trin. ex Steud., Phr aus, 1; Plantago media L., Pla med, 12; Poa annua L., Poa ann, 15; Poa palustris L., Poa pal, 1; Poa pratensis L. s. s., Poa pra, 12; Polygonatum odoratum (Mill.) Druce, Pol odo, 7; Prunella vulgaris L., Pru vul, 12; Pteridium aquilinum (L.) Kuhn, Pte aqu, 7; Pulmonaria obscura Dumort., Pul obs, 2; Ranunculus acris L. s. s., Ran acr, 12; Rubus idaeus L., Rub ida, 15; Rubus saxatilis L., Rub sax, 7; Rumex acetosa L., Rum ace, 12; Rumex acetosella L., Rum ace, 7; Rumex aquaticus L., Rum aqu, 10; Rumex crispus L., Rum cri, 12; Rumex hydrolapathum Huds., Rum

hyd, 1; Rumex obtusifolius L., Rum obt, 15; Rumex sanguineus L., Rum san, 2; Salvia verticillata L., Sal ver, 13; Sanicula europaea L., San eur, 3; Saponaria officinalis L., Sap off, 15; Scirpus sylvaticus L., Sci syl, 12; Scrophularia nodosa L., Scr nod, 2; Scutellaria galericulata L., Scu gal, 1; Solidago virgaurea L. s. s., Sol vir, 6; Stachys sylvatica L., Sta syl, 2; Stellaria graminea L., Ste gra, 12; Stellaria media (L.) Vill., Ste med, 15; Stellaria palustris Retz., Ste pal, 11; Stellaria uliginosa Murray, Ste uli, 1; Taraxacum officinale F. H. Wigg, Tar off, 12; Thelypteris palustris Schott, The pal, 1; Trifolium alpestre L., Tri alp, 13; Trifolium pratense L., Tri pra, 12; Vaccinium vitis-idaea L., Vac vit, 7; Veronica beccabunga L., Ver bec, 9; Veronica chamaedrys L. s. s., Ver cha, 12; Veronica officinalis L., Ver off, 7; Vinca minor L., Vin min, 2; Viola palustris L., Vio pal, 1; Viola reichenbachiana Jord. ex Boreau, Vio rei, 3; Viola riviniana Rchb., Vio riv, 3.

Rare species (26): Ajuga genevensis L., Aju gen, 13; Cicuta virosa L., Cic vir, 1; Circaea intermedia Ehrh., Cir int, 2; Coronilla varia L., Cor var, 13; Equisetum hyemale L., Equ hye, 2; Galium verum L. s. s., Gal ver, 13; Hedera helix L., Hed hel, 2; Hypericum tetrapterum Fr., Hyp tet, 12; Lilium martagon L., Lil mar, 3; Listera ovata (L.) R. Br., Lis ova, 2; Lycopodium clavatum L., Lyc cla, 7; Malva neglecta Wallr., Mal neg, 15; Ophioglossum vulgatum L., Oph vul, 12; Peucedanum oreosolinum (L.) Moench, Peu ore, 7; Pimpinella saxifraga L., Pim sax, 13; Plantago lanceolata L., Pla lan, 12; Polygala vulgaris L. s. s., Plg vul, 13; Polygonatum verticillatum (L.) All., Pol ver, 3; Scorzonera humilis L., Sco hum, 7; Scrophularia umbrosa Dumort., Scr umb, 10; Sedum maximum (L.) Hoffm., Sed max, 7; Selinum carvifolia (L.) L., Sel car, 12; Stachys palustris L., Sta pal, 12; Trifolium repens L., Tri rep, 12; Veronica montana L., Ver mon, 2; Vicia cracca L., Vic cra, 13