Acta Societatis Botanicorum Poloniae
Journal homepage: pbsociety.org.pl/journals/index.php/asbp
ORIGINAL RESEARCH PAPER Received: 2012.03.01 Accepted: 2013.01.18 Published electronically: 2013.03.05 Acta Soc Bot Pol 82(1):5–11 DOI: 10.5586/asbp.2013.003

Spatial variability more influential than soil pH and land relief on thermophilous vegetation in overgrown coppice oak forests

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Abstract

The overgrown coppice oak forests that cover the southern slopes beneath the foothills of the Sudetes (Silesia, Central Europe) are considered to be Euro-Siberian steppic woods with a *Quercus* sp. habitat (91I0): a priority habitat in the European Union, according to the Natura 2000 system. In subcontinental parts of Central Europe, thermophilous oak forest vegetation is found extrazonally; its presence, in the study site, is related to previous coppice management. In this paper we explore the differentiation of the vegetation caused both by land-relief derived variables (potential heat load, slope inclination and exposition, soil depth) and soil pH, as well as spatial processes. The data on the vegetation were collected from 117 regularly arranged sampling plots, located in three mountain ranges. The vegetation consisted of a mixture of species considered as typical for different habitats (mesophilous forests, acidophilous forests, thermophilous oak forests, grassland, thermophilous fringes and mesophilous mantle) and was relatively rich in species. Many of the species found were rare and are protected in Poland. The results of the bioindication, on the basis of Ellenberg indicator values, suggest the pH gradient to be the most important, followed by the insolation/moisture gradient, to the differentiation of the studied vegetation. The thermophilous oak forests seem to occupy the niche between acidophilous and mesophilous forest. However the decomposition of spatial variation, assessed on the basis of semivariance values of the vegetation similarity coefficient (frequency index), emphasizes a strong differentiation of vegetation between sites and mountain ranges.

The results of canonical correspondence analysis, performed on a spatially stratified sub-set of the data, revealed a stronger effect caused by spatial variation (32.7% of explained species variation) than environmental variables, such as soil pH and potential heat load (13.1%). Since the shared variation was low (1.8%), it showed a strong influence of spatial processes, revealing the effect of the local species pool.

Keywords: Euro-Siberian steppic woods, species pool, potential heat load, soil reaction, thermophilous oak forests, traditional forest management, variation partitioning, 91I0 habitat

Introduction

Intense management activities in Central European forests culminated 100–300 years ago, as a result of the growing demand for firewood, fodder, construction supplies and other specific purposes, e.g. oak bark for tanning [1]. Many of these forest management approaches can be seen as disturbances that were beneficial for species richness [2]. For instance, the presence of thermophilous oak forest in subcontinental parts of Central Europe could be considered to be a result of traditional forest management. In the lowlands of Poland, the presence of this forest type is mostly connected with former pasturing of cattle in the forest [3], while in areas of the Czech Republic and Slovakia some stands of thermophilous oak forest developed as a result of coppicing [4,5].

It is known that traditional coppicing systems could considerably affect forest ground vegetation, being beneficial for light-demanding species, and cessation of this system led to a decrease in biodiversity [6–8]. However, this significant change in the European forests has been greatly overlooked [9], and most of the studies in this field are geographically limited to lowland woodlands in north-western Europe [5].

In Poland, coppicing was applied quite frequently in the first half of the 20th century in the region of Silesia (south-west Poland), where a small number of oak forests of coppice origin have persisted until now [10]. They usually occur in dispersed patches on the southern slopes of hills on acid bedrock. Some of these forests differ from other tree stands by specific, species-rich vegetation consisting of numerous light-demanding and thermophilous species, and are classified as thermophilous oak forest [11,12]. The historical coppicing in Silesia is not only a

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Handling Editor: Beata Zagórska-Marek

local issue, since the phenomenon of an extrazonal occurrence of thermophilous vegetation on the northern limit of its range has troubled botanists for almost a century [13–15], and its ecology is still poorly known [16]. Moreover, the vegetation is considered to be Euro-Siberian steppic woods with *Quercus* spp. habitat (91I0): a priority habitat in the European Union according to the Natura 2000 system, and a thermophilous form of acidophilous oak forests (habitat 9190 according to Natura 2000). Because coppicing is almost unknown in Poland, there have been no comprehensive studies devoted strictly to the vegetation ecology of forests previously managed in this way. Some descriptions of vegetation could be derived from regional phytosociological studies also performed, among others, in coppiced stands [11,12,17,18]. Unfortunately, it is known that preferential sampling used in phytosociological studies, when focusing on vegetation classification, could give a biased pattern of species composition and biodiversity [19–21]. Although the spatial differentiation is potentially a significant factor shaping community structure [22], it was not considered in previous studies.

In this paper we present the results of an examination of the vegetation of overgrown (not cut since the end of World War II) oak forests of coppice origin, which cover slopes with a southern exposure in the submontane area of Silesia (south-west Poland, Central Europe). Firstly, we were interested in the beta diversity: the results of a previous case study [23] suggested an ecotone character for thermophilous oak forests. In this study, we explored the relationship of thermophilous forests with other types of vegetation, using ordination techniques and data collected in non-preferential sampling. Secondly, in such a hilly landscape, it is highly probable that land relief has influenced vegetation [24], and we therefore tested the effect of land relief-derived variables (exposition, slope inclination, potential head load, soil depth) on the studied vegetation. This data set was completed by measurements of soil pH, also known to influence the studied vegetation [23]. In these two analyses, mentioned above, we also assessed the effect of spatial variability.

Material and methods

Study area

The study was performed at eight sites, located in three mountain ranges (Fig. 1) in the northern foothills of the Sudetes (Silesia, Poland, Central Europe):

(***i***) Kaczawskie Mts foothills, three sites, 61 sampling plots in total. The geological setting consisted of green schists (metamorphic basalt rocks).

(***ii***) Wałbrzyskie Mts foothills, four sites, 47 sampling plots in total. The geological setting consisted of phyllite (metamorphic rocks).

(***iii***) Ślęża Massif, Mt. Radunia, one site, reserve "Radunia", nine sampling plots. The geological setting consisted of serpentinite (metamorphic rocks).

The average annual temperature in the Sudety foothills is about 7.0°C. The average annual precipitation is about 800 mm, with the maximum in summer [11].

The studied tree stands cover the bases of the slopes, mid-slopes and summit plateaus of hills at altitudes of 300–580 m a.s.l. The slopes are often intersected by gorges eroded by water. Rapid folds of slopes are also present, from the south to north direction. This land relief means that convex, sunny sites are located close to shady, moist habitats. The soils are shallow, acidic, with a high content of coarse fragments, and the forest floor receives a high amount of light [12,23].

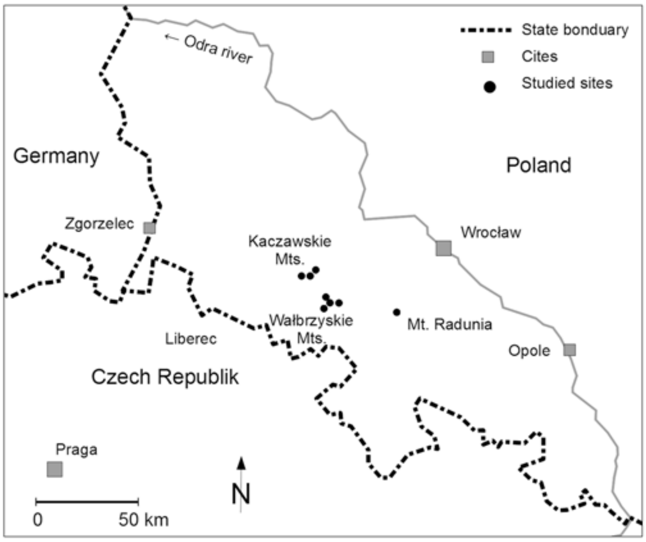

Fig. 1 Location of study sites.

The stands had ages varying from 80 up to 118 years, and were single layer stands dominated by sessile oak [*Quercus petraea* (Matt.) Lieb.]. The sites have been continuously forested since at least 1748. The coppice origin of the stands was confirmed by forest documentation of the State Forest Holding districts: Jawor, Miękinia and Wałbrzych. The exception was the Radunia reserve; however at this site, the presence of a cluster of stems coming from one stump undoubtedly confirms this kind of past management. The stands were managed for tanbark production in 14–20 years rotation periods. In some of the stands, single stemmed trees (standards) were also present, as a result of attempts undertaken before World War II at conversion into coppice with standards. The cessation of coppice management in Silesia began at the end of the 19th century and, after World War II, coppicing was no longer applied. The low productivity of the studied stands has resulted in some of them persisting as non-converted into high forests, or with conversion restricted to singling multi-stem individuals [25].

The vegetation was classified as follows: Central European acidophilous oak forest, *Calamagrostio arundinaceae-Quercetum* (Hartm. 1934) Scam. Et Pass. 1959; submontane acidophilous oak forest, *Luzulo luzuloidis-Quercetum* Hiltzer 1932, including its thermophilous form *L.-Q. genistetosum tinctoriae*; and submontane thermophilous oak forest with the wild service tree [*Sorbus torminalis* (L.) Crantz] *Sorbo torminalis-Quercetum* Svoboda ex Blažková 1962. In the gorges, ravine forest with limes and sycamores (*Tilio platyphyllis-Acerion pseudoplatani* Klika 1955) occurred [11,12,17].

Vegetation recording

The field survey was performed in two stages. Initially, in the field, a GPS receiver was used to delineate the extent of habitats defined as "forest of sessile oak of coppice origin placed on the convex part of slopes with, generally, southern exposure". Then, on the topographic maps, the locations of sampling plots were established along the transects parallel to the slope. The concave forms of relief (gorges), covered by ravine forests, were not sampled. The centers of circular sampling plots with an area of 250 m^2 were located at intervals of 50 or 100 m, depending on the slope length. The size of plot was chosen according to the method of Chytrý and Otypková [26]. Finally, the centers of the plots were found in the field with the use of a GPS receiver. All species of vascular plants were recorded in the sampling plots, and their cover was visually assessed, using the Braun-Blanquet cover-abundance scale (r, +, 1, 2, 3, 4, 5). The nomenclature of vascular plants was according to Mirek et al. [27]. The slope inclination and direction, as well as soil depth, were measured on each plot.

Analytical methods

We used detrended correspondence analysis (DCA) to find a general pattern of vegetation that extracts the main gradients in species composition. The bioindication of environmental conditions was performed on the basis of Ellenberg's indicator values (*EIV*) [28], as an aid during interpretation of the ordination diagram [29]. The average values of the Ellenberg's indicator values were calculated for light (*EIV L*), soil reaction (*EIV R*), moisture (*EIV M*) and nitrogen (*EIV N*) using Juice software [30].

To explore the structure of the species composition, six groups of species were distinguished: (***i***) thermophilous oak forests (species considered to be characteristic of *Quercetalia pubescenti-petraeae* order, six species), (***ii***) mesophilous and eutrophic broadleaved forests (order *Fagetalia sylvaticae*, 38 species), (***iii***) acidophilous oak forest and coniferous forests (classes *Quercetea robori-petraeae* and *Vaccinio-Piceetea*, 12 species), (***iv***) mesophilous mantles (class *Rhamno-Prunetea*, species from *Berberidion alliance* excluded, six species), (***v***) thermophilous fringes (class *Trifolio-Geranietea sanguinei*, six species), and (***vi***) grassland species (classes *Festuco-Brometea* and *Molinio-Arrhenatheretea*, 24 species). The affinity of plant species to classes of plant communities was checked using a guidebook to the vegetation of Poland [31].

To obtain a more detailed view of the changes in species composition at a spatial scale, a variogram was computed [32]. The variogram decomposed the spatial variability of the observed traits among distance classes [33]. In this study, we analyzed the variability of indices of floristic similarity between plots at different spatial scales. The matrix of distances was created on the basis of GPS measurements and the similarities of vegetation were computed with the frequency index [34]. The frequency index gave similar results to other qualitative similarity indices (e.g. Jaccard, Sørensen) and was convenient to use in further computation of semivariograms. The applied distance class corresponded to the levels of spatial organization of the sampling plots: transects (50–300 m), sites (200–1000 m), mountain ranges (300–7000 m), and the entire region (20–45 km). The ranges overlapped due to differences in the length of transects and site areas, as well as mountain ranges. In the case of Mt. Radunia, data for the site were the same as for the mountain range. Thus, the extent of the "mountain range" level started from 300 m (the distance between the most distant plots at the Radunia site).

The effect of environmental and spatial variables on vegetation was analyzed by canonical correspondence analysis (CCA). Being aware of pseudo replication, for the purpose of this analysis a subset of 56 plots (seven plots per site) was

Tab. 1 List of vascular plant species.

No.	Species	Frequency of occurrence (%)	Median value of non-zero cover (%)
1	*Quercus petraea*	100	3
2	*Calamagrostis arundinacea*	86.3	2
3	*Convallaria majalis*	86.3	+
4	*Hieracium murorum*	81.2	+
5	*Poa nemoralis*	79.5	1
6	*Galium schultesii*	77.8	+
7	*Festuca ovina*	55.6	1
8	*Hieracium sabaudum*	53.8	+
9	*Acer pseudoplatanus*	53	+
10	*Tilia cordata*	52.1	+
11	*Rosa canina*	51.3	+
12	*Silene nutans*	51.3	+
13	*Veronica officinalis*	51.3	+
14	*Viola reichenbachiana*	51.3	+
15	*Carpinus betulus*	48.7	2
16	*Vaccinium myrtillus*	47	+
17	*Sorbus aucuparia*	45.3	+
18	*Deschampsia flexuosa*	43.6	2
19	*Cerasus avium*	42.7	r
20	*Melampyrum pratense*	41	+
21	*Impatiens parviflora*	40.2	+
22	*Sedum maximum*	40.2	+
23	*Digitalis grandiflora*	39.3	+
24	*Polygonatum odoratum*	38.5	+
25	*Solidago virgaurea*	37.6	+
26	*Campanula persicifolia*	36.8	+
27	*Moehringia trinervia*	36.8	+
28	*Acer platanoides*	35.9	+
29	*Crataegus monogyna*	33.3	+
30	*Fraxinus excelsior*	33.3	+
31	*Ficaria verna*	32.5	+
32	*Rubus* sp.	32.5	+
33	*Vincetoxicum hirundinaria*	32.5	+
34	*Lathyrus niger*	31.6	+
35	*Pinus sylvestris*	29.1	1
36	*Brachypodium sylvaticum*	29.1	+
37	*Luzula luzuloides*	27.4	+
38	*Melica nutans*	27.4	+
39	*Hedera helix*	26.5	+
40	*Genista tinctoria*	25.6	+
41	*Galium aparine*	23.9	+
42	*Cephalanthera longifolia*	23.1	+
43	*Fragaria vesca*	22.2	+
44	*Galium odoratum*	22.2	+
45	*Melampyrum nemorosum*	21.4	+
46	*Hypericum perforatum*	21.4	r
47	*Prunus spinosa*	20.5	+
48	*Veronica chamaedrys*	20.5	+
49	*Lathyrus vernus*	18.8	+
50	*Adoxa moschatellina*	17.1	+
51	*Galeopsis tetrahit*	17.1	+
52	*Galium mollugo*	17.1	+
53	*Galium rotundifolium*	17.1	+
54	*Corylus avellana*	16.2	2
55	*Betula pendula*	16.2	+
56	*Mercurialis perennis*	16.2	+
57	*Urtica dioica*	16.2	+
58	*Alliaria petiolata*	15.4	+

Tab. 1 *(continued)*

No.	Species	Frequency of occurrence (%)	Median value of non-zero cover (%)
59	*Asarum europaeum*	15.4	+
60	*Galeopsis pubescens*	15.4	+
61	*Sorbus torminalis*	15.4	+
62	*Euphorbia cyparissias*	14.5	+
63	*Festuca rubra*	14.5	r
64	*Linaria vulgaris*	14.5	r
65	*Fagus sylvatica*	13.7	+
66	*Brachypodium pinnatum*	12.8	1
67	*Festuca gigantea*	12.8	+
68	*Geranium robertianum*	12.8	+
69	*Hepatica nobilis*	12.8	r
70	*Luzula campestris*	11.1	+
71	*Anemone nemorosa*	10.3	+
72	*Mycelis muralis*	10.3	+
73	*Picea abies*	10.3	r
74	*Populus tremula*	10.3	r
75	*Anthoxanthum odoratum*	9.4	+
76	*Astragalus glycyphyllos*	9.4	+
77	*Calystegia sepium*	9.4	+
78	*Hieracium laevigatum*	9.4	+
79	*Polygonatum multiflorum*	9.4	+
80	*Trifolium montanum*	9.4	+
81	*Luzula multiflora*	8.5	+
82	*Melittis melissophyllum*	7.7	+
83	*Cornus mas*	7.7	r
84	*Platanthera bifolia*	7.7	r
85	*Dryopteris dilatata*	6.8	+
86	*Juniperus communis*	6.8	r
87	*Sambucus nigra*	6.8	r
88	*Senecio ovatus*	6.8	r
89	*Galeobdolon luteum*	11.1	1
90	*Agrimonia eupatoria*	6	+
91	*Anthriscus sylvestris*	6	+
92	*Genista germanica*	6	+
93	*Pimpinella saxifraga*	6	+
94	*Poa pratensis*	6	+
95	*Achillea millefolium*	6	r
96	*Mentha arvensis*	6	r
97	*Crataegus laevigata*	5.1	1
98	*Carex muricata*	5.1	+
99	*Daphne mezereum*	5.1	+
100	*Pulmonaria obscura*	5.1	+
101	*Myrrhis odorata*	5.1	r
102	*Pyrus communis*	5.1	r
103	*Scrophularia nodosa*	5.1	r
104	*Athyrium filix-femina*	4.3	2
105	*Dryopteris filix-mas*	4.3	+
106	*Frangula alnus*	4.3	+
107	*Poa annua*	4.3	+
108	*Stellaria graminea*	4.3	+
109	*Carex montana*	3.4	+
110	*Hieracium pilosella*	3.4	+
111	*Pseudotsuga menziesii*	3.4	+
112	*Stachys sylvatica*	3.4	+
113	*Aegopodium podagraria*	3.4	r
114	*Ajuga reptans*	3.4	r
115	*Campanula trachelium*	3.4	r
116	*Lilium martagon*	3.4	r

randomly selected by a stratified-random method. In those plots, the soil pH was measured in KCl solution for dry soil samples: three samples per plot were taken and the results were averaged. The potential heat load (HL) was calculated from the slope, aspect and latitude, according to formula number 3 proposed in [35]. The soil depth was also measured by driving in a steel rod. The spatial relationships were defined by nine variables generated from the third order polynomial function of the geographical coordinates of latitude (*Lat*) and longitude (*Lon*) for each plot [33,36]. In order to avoid artificial increases in the explained variation, only variables, which significantly affected species composition, were incorporated into analyses (forward selection, $\alpha = 0.05$). The selection procedures were applied separately for environmental and spatial variables. Then, the variation was partialling out as proposed [36]. The significance of environmental variables was tested using the Monte Carlo method with 999 permutations. The conditional effect of variables was calculated as a lambda-A value, that is, the increase in the sum of all canonical eigenvalues of the ordination, when the variable is added to the already included environmental variables [37].

Only species that occurred on more than three plots were included in the ordination analyses (DCA and CCA).

Results

Altogether, 191 plant species were found, within 117 sampling plots. The list of all species, together with the frequency and the median value of non-zero cover, is presented in Tab. 1, while all records are stored in Polish Vegetation Database [38]. Among the species found, 77 (almost 40%) occurred in fewer than three plots, whereas 35 (18%) occurred in more than one-third of all plots. The number of species per plot varied five-fold from 11 up to 54, with an average of 28 species per plot. The cover of forest floor species (layer c) also varied considerably from 10% up to 90%, with an average of 61%. Of these species, 14 are protected in Poland.

The sum of eigenvalues in unconstrained ordination (DCA) was 2.31: the first axis explained 8.3% of total species variance, while the second explained 6.6%. Generally, the first axis could be considered as reflecting vegetation variability in a pH gradient (Fig. 2). It highlighted the difference between mesophilous and acidophilous forest vegetation. Species characteristic of thermophilous oak forests were placed exactly between the two first groups. The species considered as characteristic of thermophilous mantle, as well as of grass-dominated vegetation, were also concentrated in the center of the diagram (Fig. 2).

The values of semivariance (Fig. 3) were the lowest at the spatial scales of transect and site, when only plots belonging to the same sites were compared. This indicates that differences between plots from the same site, even those placed in different parts of the slope (slope base, mid-slope or summit plateau), were relatively small. The values of semivariance increased rapidly at a spatial scale above 3 km when only plots belonging to different sites were compared; this highlights the differentiation of vegetation between sites. Then, at a distance above 7 km, the semivariance somewhat decreased as a result of "averaging" the vegetation of the two compared mountain ranges: Kaczawskie and Wałbrzyskie. The next rapid increase of semivariance occurred at distances above 20 km, when the plots from Radunia were compared with plots from the two previously mentioned mountain ranges.

Tab. 1 *(continued)*

No.	Species	Frequency of occurrence (%)	Median value of non-zero cover (%)
117	*Maianthemum bifolium*	3.4	r
118	*Polygonatum verticilatum*	3.4	r
119	*Polypodium vulgare*	3.4	r
120	*Larix decidua*	2.6	1
121	*Arrhenatherum elatius*	2.6	+
122	*Calluna vulgaris*	2.6	+
123	*Carex vulpina*	2.6	+
124	*Centaurea jacea*	2.6	+
125	*Coronilla varia*	2.6	+
126	*Glechoma hederacea*	2.6	+
127	*Hypericum montanum*	2.6	+
128	*Melica uniflora*	2.6	+
129	*Populus × canadensis*	2.6	+
130	*Silene vulgaris*	2.6	+
131	*Stellaria holostea*	2.6	+
132	*Tilia platyphyllos*	2.6	+
133	*Trifolium rubens*	2.6	+
134	*Viola canina*	2.6	+
135	*Viscaria vulgaris*	18.8	+
136	*Acer campestre*	2.6	r
137	*Betonica officinalis*	2.6	r
138	*Epilobium montanum*	2.6	r
139	*Melandrium album*	2.6	r
140	*Vicia cracca*	2.6	r
141	*Prenanthes purpurea*	1.7	1
142	*Astrantia major*	1.7	+
143	*Carex vesicaria*	1.7	+
144	*Dactylis polygama*	1.7	+
145	*Erigeron annuus*	1.7	+
146	*Geum urbanum*	1.7	+
147	*Juncus articulatus*	1.7	+
148	*Mentha arvensis*	1.7	+
149	*Monotropa hypophegea*	1.7	+
150	*Rumex acetosella*	1.7	+
151	*Sanicula europaea*	1.7	+
152	*Arabis glabra*	1.7	r
153	*Cornus sanguinea*	1.7	r
154	*Galium verum*	1.7	r
155	*Phyteuma spicatum*	1.7	r
156	*Primula elatior*	1.7	r
157	*Taraxacum sect. Ruderalia*	1.7	r
158	*Thymus pulegioides*	1.7	r
159	*Berteroa incana*	0.9	1
160	*Molinia arundinacea*	0.9	1
161	*Acinos arvensis*	0.9	+
162	*Allium vineale*	0.9	+
163	*Centaurea scabiosa*	0.9	+
164	*Elymus repens*	0.9	+
165	*Holcus lanatus*	0.9	+
166	*Myosotis stricta*	0.9	+
167	*Poa trivialis*	0.9	+
168	*Senecio viscosus*	0.9	+
169	*Trientalis europaea*	0.9	+
170	*Alyssum alyssoides*	0.9	r
171	*Arctium minus*	0.9	r
172	*Asplenium septentrionale*	0.9	r
173	*Balota nigra*	0.9	r
174	*Campanula patula*	0.9	r

The procedure of stepwise selection in constrained analyses (CCA) revealed that the significant conditional effects on vegetation structure were soil pH and HL. The conditional effect of pH (lambda-A = 0.08) was more influential than that of HL (lambda-A = 0.06). The significant spatial variables, deriving from geographical coordinates, were: Lon^2, *Lat*, $Lon \times Lat^2$. The environmental and geographical variables explained in total 47.4% of total variability of species composition. The spatial variables were significant alone ($P < 0.001$) and explained about 32.7% of species composition variability. The environmental variables, however significant ($P < 0.001$), explained far less variation: 13.1%. The amount of variation shared by those two groups was only 1.6%.

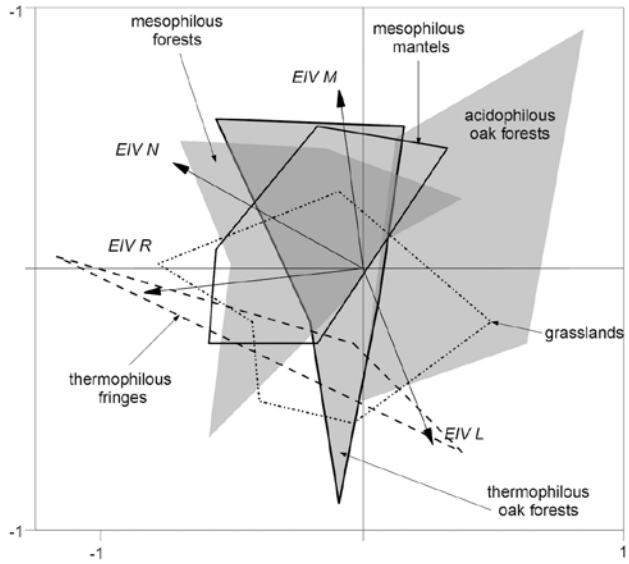

Fig. 2 The DCA ordination plot of species. The areas marked by grey colour or black lines show the distribution of the scores for characteristic species within a given species group. The arrows show the position of *EIV*. The species scores of plants that were not considered as characteristic for distinct groups, are not shown.

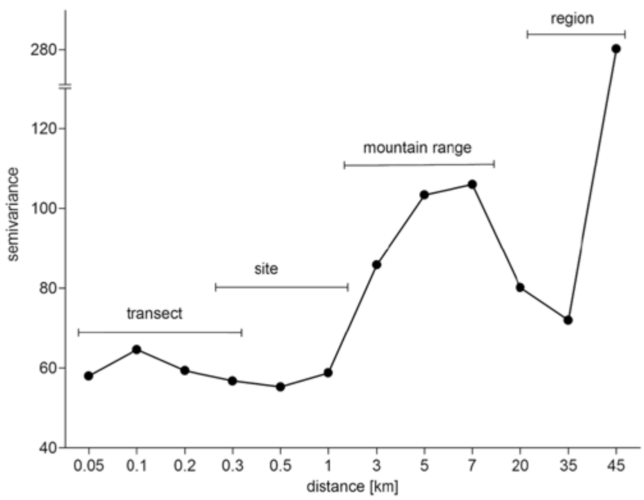

Fig. 3 Variogram of frequency index. The lines show the spatial extent of different levels of organisation (transect, site, mountain range, region). Note the semi-logarithmic scale on the horizontal and the break on the vertical axis.

Tab. 1 *(continued)*

No.	Species	Frequency of occurrence (%)	Median value of non-zero cover (%)
175	*Carex sylvatica*	0.9	r
176	*Crepis biennis*	0.9	r
177	*Fragaria moschata*	0.9	r
178	*Hypochoeris radicata*	0.9	r
179	*Lapsana communis*	0.9	r
180	*Lathyrus sylvestris*	0.9	r
181	*Lotus corniculatus*	0.9	r
182	*Lysimachia vulgaris*	0.9	r
183	*Milium effusum*	0.9	r
184	*Paris quadrifolia*	0.9	r
185	*Pteridium aquilium*	0.9	r
186	*Rumex acetosa*	0.9	r
187	*Rumex crispus*	0.9	r
188	*Senecio jacobaea*	0.9	r
189	*Solidaster luteus*	0.9	r
190	*Urtica urens*	0.9	r
191	*Vicia cassubica*	0.9	r

Nomenclature according to Mirek et al. [27], with the exception of *Solidaster luteum* (ornamental taxa). Species are sorted according to the frequency of their occurrence (in total 117 sampling plots) and the median value of non-zero cover.

Discussion

The mixture of species in the studied vegetation was fairly unusual, especially the high proportion of species typical of non-forest habitats. However, this is typical for thermophilous oak forests in Poland which occur there extrazonally [3,31]. In this study, the coexistence of species with a relatively high demand for light and fertility can be convincingly explained by previous coppice management at the mesic sites. The promotion of oak leads to the elimination of other tree species with a more closed canopy, and allows the establishment of light-demanding herbaceous species on the forest floor [4,5,10].

In the areas south of the Sudetes and Carpathians, the thermophilous oak forests are considered as a peculiar vegetation type that occupies a niche between the acidophilous oak forests and mesophilous forest [4]. The results of this investigation show a similar pattern of species ordination, where the themophilous oak forest species were placed between mesic and acidophilous species. However, the niche is probably only temporary, since succession processes have been observed after cessation of coppicing [6,7,9]. This could lead to a succession from species-rich to a typical mesic forest [5]. Unfortunately, to the authors' knowledge, there have been no long-term observations or manipulative experiments in this type of forest that can be used to verify the hypothesis of the origin and dynamics of the examined vegetation. There are several reasons explaining why this vegetation has persisted until now, more than half a century after the cessation of coppicing. Among these, apart from the existence of man-created tree stand structures, are also: specific land relief creating refuges for different ecological groups of plant species, edaphically limited dryness related to shallow, structural soils, and heavy browsing of tree saplings by ungulates [23]. Putting aside the working hypothesis on the origin and dynamics of the vegetation, these forests are undoubtedly important from the point of view of nature protection, at the scale of both region as well as the entire state, since 7% of the recorded species are protected.

It was initially hypothesized that the vegetation is under the prevailing effect of light or heat gradients [23]. The land relief could also be supposed to cause a strong difference between plots placed along the transects, as was shown in deep valleys [24]. However, the results revealed that soil pH was the most important environmental gradient. It should be highlighted that this effect occurred in a relatively limited gradient of HL, since the study was restricted to the convex sections of slopes, with generally southern expositions. Nevertheless, the effect of spatial variation was also very strong on niche-conditioned variability of the vegetation. The differentiation of vegetation between sites and mountain ranges was more pronounced than intra-site differentiation caused by land relief (Fig. 3). Because the percentage of variability shared by the environmental and spatial variables was relatively low (less than 2%), we can assume that the between-sites and between-ranges variability was not caused exclusively by differences in pH and/or HL between those particular units. Since the last remnants of stands of coppice origin occur in detached patches, the local process could thus have strongly shaped species composition. This could be summarized as an effect of the regional species pool (in the sense of Zobel [39]). We were not able to distinguish which kind of processes were crucial: these could be a limitation of the distribution of some species [40], together with individual site history, as well as the landscape context of the location of each studied site in term of both its contemporary [41] or/and historical pattern [42].

Conclusions

The studied tree stands supported a relatively high number of vascular plants on the forest floor, many of which are protected. These plant species can be considered as typical for different kinds of habitats. However, such a mixture, as well as species richness, could be convincingly explained by historical forest management and specific land relief. The species considered as diagnostic for thermophilous oak forests occupy a niche between acidophilous oak forests and mesophilous forests. The species composition is under the effect of soil pH and HL, but those environmental variables are less influential than the spatial variation of the examined vegetation.

Acknowledgments

Thanks are due to two anonymous reviewers for their comments, especially for critical review of the species list. The study was supported by funding from the University of Wrocław.

Authors' contributions

The following declarations about authors' contributions to the research have been made: concept of the study: THS; field work: MS, THS; writing – MS, THS.

References

1. Bürgi M. Habitat alterations caused by long-term changes in forest use in northeastern Switzerland. In: Kirby KJ, Watkins C, editors. The ecological history of European forest. Oxford: CAB International; 1998. p. 203–211.
2. Wohlgemuth T, Bürgi M, Scheidegger C, Schütz M. Dominance reduction of species through disturbance – a proposed management principle for central European forests. For Ecol Manage. 2002;166(1–3):1–15. http://dx.doi.org/10.1016/S0378-1127(01)00662-4
3. Jakubowska-Gabara J. Decline of *Potentillo albae-Quercetum* Libb. 1933 phytocoenoses in Poland. Vegetatio. 1996;124(1):45–59. http://dx.doi.org/10.1007/BF00045143
4. Roleček J. Vegetation types of dry-mesic oak forests in Slovakia. Preslia. 2005;77(3):241–261.
5. Hédl R, Kopecký M, Komárek J. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Divers Distrib. 2010;16(2):267–276. http://dx.doi.org/10.1111/j.1472-4642.2010.00637.x
6. Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A, et al. Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. J Appl Ecol. 2004;41(6):1065–1079. http://dx.doi.org/10.1111/j.0021-8901.2004.00960.x
7. Müller SW, Rusterholz HP, Baur B. Effects of forestry practices on relict plant species on limestone cliffs in the northern Swiss Jura mountains. For Ecol Manage. 2006;237(1–3):227–236. http://dx.doi.org/10.1016/j.foreco.2006.09.048
8. van Calster H, Baeten L, Verheyen K, De Keersmaeker L, Dekeyser S, Rogister JE, et al. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. For Ecol Manage. 2008;256(4):519–528. http://dx.doi.org/10.1016/j.foreco.2008.04.042
9. Baeten L, Bauwens B, De Schrijver A, De Keersmaeker L, van Calster H, Vandekerkhove K, et al. Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. Appl Veg Sci. 2009;12(2):187–197. http://dx.doi.org/10.1111/j.1654-109X.2009.01013.x
10. Szymura TH. Tradycyjna gospodarka odroślowa w Europie Środkowej i jej wpływ na różnorodność biologiczną. Sylwan. 2010;154(8):545–551.
11. Kwiatkowski P. Zbiorowiska leśne Pogórza Złotoryjskiego. Fragm Flor Geobot Polonica. 2001;8:178–218.
12. Kwiatkowski P. Podgórska ciepłolubna dąbrowa brekiniowa *Sorbo torminalis-Quercetum* na Pogórzu Złotoryjskim. Fragm Flor Geobot Polonica. 2003;10:175–193.
13. Paczoski J. Dąbrowy Białowieży. Przegląd Leśniczy. 1926;11:517–529.
14. Domin K. The plant associations of the valley of Radotin. Preslia. 1928;7:3–68.
15. Klika J. Geobotanicki studie rostlinných společenstev Velké Hory u Karlštejna. Rozpr České Akad Věd. 1928;37(12):1–42.
16. Ellenberg HH. Vegetation ecology of central Europe. 4th ed. Cambridge: Cambridge University Press; 2009.
17. Szczęśniak E. Szata roślinna północno-zachodniej części Pogórza Wałbrzyskiego. II. Zbiorowiska leśne. Acta Uni Wrat Prace Bot. 1999;73:83–113.
18. Berdowski W, Panek E. Roślinność rezerwatu "Góra Radunia" w województwie wrocławskim. Parki Narodowe i Rezerwaty Przyrody. 1999;18(2):3–13.
19. Holeksa J, Woźniak G. Biased vegetation patterns and detection of vegetation changes using phytosociological databases. A case study in the forests of the Babia Góra National Park (the West Carpathians, Poland). Phytocoenologia. 2005;35(1):1–18. http://dx.doi.org/10.1127/0340-269X/2005/0035-0001
20. Hédl R. Is sampling subjectivity a distorting factor in surveys for vegetation diversity? Folia Geobot. 2007;42(2):191–198. http://dx.doi.org/10.1007/BF02893885
21. Michalcová D, Lvončík S, Chytrý M, Hájek O. Bias in vegetation databases? A comparison of stratified-random and preferential sampling. J Veg Sci. 2011;22(2):281–291. http://dx.doi.org/10.1111/j.1654-1103.2010.01249.x
22. Hubbell SP. The unified neutral theory of biodiversity and biogeography. Princeton NJ: Princeton University Press; 2001.
23. Szymura TH, Szymura M. Soil properties and light availability determine species richness and vegetation diversity in an overgrown coppice oak stand. Polish J Ecol. 2011;59(3):523–533.
24. Zelný D, Chytrý M. Environmental control of the vegetation pattern in deep river valleys of the Bohemian Massif. Preslia. 2007;79:205–222.
25. Szymura TH. How does recent vegetation reflect previous systems of forest management? Polish J Ecol. 2012;60(4):859–862.
26. Chytrý M, Otýpková Z. Plot sizes used for phytosociological sampling of European vegetation. J Veg Sci. 2003;14(4):563–570. http://dx.doi.org/10.1111/j.1654-1103.2003.tb02183.x
27. Mirek Z, Piękoś-Mirkowa H, Zając A, Zając M. Flowering plants and pteridophytes of Poland a checklist. In: Mirek Z, editor. Biodiversity of Poland. Cracow: W. Szafer Institute of Botany, Polish Academy of Sciences; 2002. (vol 1).
28. Ellenberg H, Weber HE, Düll R, Werner W, Paulißen D. Zeigerwerte der Pflanzen in Mitteleuropa. Scr Geobot. 1992;18:1–258.
29. Persson S. Ecological indicator values as an aid in the interpretation of ordination diagrams. J Ecol. 1981;69(1):71. http://dx.doi.org/10.2307/2259816
30. Tichý L. Juice (version 6.4.59). Brno: Masaryk University; 2007.
31. Matuszkiewicz W. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Warszawa: Polish Scientific Publishers PWN; 2006.
32. Isaaks EH, Srivastava RM. An introduction to applied geostatistics. Oxford: Oxford University Press; 1989.
33. Legendre P, Legendre LFJ. Numerical ecology. 2nd ed. Amsterdam: Elsevier; 1998.
34. Tichý L. New similarity indices for the assignment of relevés to the vegetation units of an existing phytosociological classification. Plant Ecol. 2005;179(1):67–72. http://dx.doi.org/10.1007/s11258-004-5798-8
35. McCune B, Keon D. Equations for potential annual direct incident radiation and heat load. J Veg Sci. 2002;13(4):603–606. http://dx.doi.org/10.1111/j.1654-1103.2002.tb02087.x
36. Borcard D, Legendre P, Drapeau P. Partialling out the spatial component of ecological variation. Ecology. 1992;73(3):1045. http://dx.doi.org/10.2307/1940179
37. ter Braak CJF, Prentice IC. A theory of gradient analysis. Adv Ecol Res. 2004;34:235–282.
38. Kącki Z, Śliwiński M. The Polish Vegetation Database: structure, resources and development. Acta Soc Bot Pol. 2012;81(2):75–79. http://dx.doi.org/10.5586/asbp.2012.014
39. Zobel M. The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? Trends Ecol Evol. 1997;12(7):266–269. http://dx.doi.org/10.1016/S0169-5347(97)01096-3
40. Ehrlen J, Eriksson O. Dispersal limitation and patch occupancy in forest herbs. Ecology. 2000;81(6):1667. http://dx.doi.org/10.2307/177315
41. Vondrák J, Prach K. Occurrence of heliophilous species on isolated rocky outcrops in a forested landscape: relict species or recent arrivals. Preslia. 2006;78:115–121.
42. Honnay O, Jacquemyn H, Bossuyt B, Hermy M. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytol. 2005;166(3):723–736. http://dx.doi.org/10.1111/j.1469-8137.2005.01352.x