**The effect of ecological niche and spatial pattern on the diversity of oak forest vegetation**

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**Background:** Ecological niche and spatial processes are known to shape the species composition of plant communities. However, the relative importance of these factors can vary considerably from one habitat to another.

**Aims:** To determine the effect of environmental conditions and spatial processes on the species composition of forest vegetation, we studied a patchy system consisting of overgrown oak stands of coppice origin on slopes with a southern exposure in a diverse, submontane landscape.

**Methods:** Spatial patterns were surveyed with the principal coordinate analysis of neighbour matrices method, using a 'staggered' matrix to examine the effect of nested spatial scales. The variation partitioning procedure was applied to assess the relative influence of spatial and environmental components. Redundancy analysis was carried out to detect the effect of particular environmental variables.

**Results:** Vegetation composition was related to environmental variables (mostly water-holding capacity and Ca content), as well as spatial processes, such as dispersal limitation, at the large (ca. 15 km) and medium (ca. 3.5 km–1.0 km) scales, whereas at small scales (<1 km), these factors were not related to species composition.

**Conclusions:** The vegetation of the studied forests should be considered as a metacommunity, and the main drivers of species composition are species sorting and dispersal limitation.

**Keywords:** acidophilous oak forests; coppice management; edaphic drought; metacommunity; spatial processes; thermophilous oak forests

**Introduction**

The fundamental goal in vegetation ecology is to understand the forces that drive species distribution, especially with respect to environmental gradients and the maintenance of species diversity (Gilbert and Lechowicz 2004; Freestone and Inouye 2006). For a long time, the diversity of communities was explained by a focus on niche differentiation between their component species (Leibold and McPeek 2006). This approach is based on changes in communities across environmental gradients and considers the effect of local abiotic features on species interactions (Tilman 1982). As a result, deterministic species sorting along environmental gradients are identified. The niche perspective predicts that community composition is more homogeneous among sites that are characterised by similar environmental conditions (Leibold et al. 2004). However, species sorting may be also modified by spatial processes, such as dispersal limitation or the spatial mass effect (Hubbell 2001; Cottenie 2005). Moreover, Hubbell (2001) demonstrated that the effects of dispersal limitation, speciation and role of chance in time can produce patterns of species distribution similar to those found in nature, even assuming a lack of differences in environmental niches between species. It is assumed that similarity between communities decreases with increasing geographic distance and that this relationship is independent of environmental gradients (Hubbell 2001).

The development of theoretical knowledge on the effects of spatial processes coupled with new analytical techniques has stimulated a growing interest in the metacommunity theory (Leibold et al. 2004). A metacommunity is defined as a set of local communities linked by the dispersal of potentially interacting species (Leibold et al. 2004). The theory is based on four alternative paradigms that differ in terms of relative roles attributed to species sorting, mass-effect, neutral model and patch dynamics processes in community structures (Leibold at al. 2004; Cottenie 2005). Depending on the dominant processes, different types of metacommunities can be distinguished, for example, species sorting with limited dispersal metacommunity type, where pattern caused by deterministic species sorting along environmental gradients is altered by limited distribution of species (Cottenie 2005; Ng et al. 2009).

Field studies have shown that the relative role of environmental gradients and dispersal limitation have important impacts on competitive coexistence, response to fragmentation, alien species invasion and extinction rate. However, these two processes vary from region to region and change in their spatial scales and habitats (Chesson 2000; Mouquet and Loreau 2003; Davies et al. 2005; Gazol and Ibáñez 2010; Carranza et al. 2012; Newton et al. 2012). Therefore, understanding the spatial patterns of species diversity is fundamental for both...
community ecology and biological conservation (Freestone and Inouye 2006; Gazol and Ibáñez 2010).

Few studies have attempted to quantify the contribution of environmental heterogeneity (originating from resource gradients and disturbances), analysed against dispersal, to the species composition of vegetation in temperate forests (Gilbert and Lechowicz 2004; Karst et al. 2005; Gazol and Ibáñez 2010; Keith et al. 2011). Their results demonstrated the importance of both ecological niche and spatial processes on species composition; furthermore, it was also found that environmental variables that limit species distribution can differ across spatial scales (Gazol and Ibáñez 2010). In central Europe, numerous studies on the effects of environmental conditions on forest vegetation have been conducted, but they did not consider spatial processes and were also mostly focused on lowland, deep-soil forests (Härdtle et al. 2005; Hofmeister et al. 2009; Axmanova et al. 2011, but see also; Diwold et al. 2010; Keith et al. 2011).

The objective of this study was to determine the effect of variability in terms of environmental conditions and dispersal on the species composition of forest vegetation, analysed at multiple scales. We conducted our research in a patchy system of overgrown oak stands of coppice origin (uncut since the 1940s) located on slopes with southern exposure in a submontane landscape. Forest floor vegetation in such stands is characterised by the co-occurrence of species belonging to three different ecological groups, that is typical for thermophilous oak forests, mesic forests, and nutrient-poor forests on acidic soils. Such a mixture results in a relatively high species richness and high conservation value (Szymura 2010). The slopes were often intersected by water-eroded gorges or smoothly passed onto flatter areas with a deeper soil. Rapid changes of slope exposure from south to north were also present. Such land relief meant that convex, sunny sites were located in proximity to shady, moist habitats. The vegetation, according to the European Natura 2000 network, was classified as 9110 priority habitat – Euro-Siberian steppe woods with Quercus spp. and acidophilous oak forests (9190). At the studied sites, the steppic woods with oaks (9110 habitat), also called thermophilous oak forests, reach their northern limit of range in central Europe.

According to historical maps (Kriegskarte von Schlesien, Urmestischblatt and Messtischblatt), the study sites have been forested continuously since at least 1748. Most probably, the forests were exploited as fuel wood coppice (Szymura 2012) until about the 1830s, when they were turned to with a short-rotation coppice (ca. 14–20 years) for the production of high quality tanning bark. At the end of the nineteenth century, the production of oak bark became unprofitable and former coppice stands became gradually transformed into high forests, predominantly by applying the coppice-with-standards method. The conversion concentrated on the flatter areas where the expected productivity of stands was higher (Szymura 2012). After the Second World War, coppicing was discontinued and large areas remained unmanaged because of the low productivity of the sites. The age of stems at the time of the study was estimated at 78–105 years (Szymura 2012).

**Materials and methods**

**Study area**

The study was conducted at seven sites, located in the foothills of two mountain ranges (Kaczawskie Mts. – three sites; Walbrzyskie Mts. – four sites) in the Sudety Mts., Silesia, Poland (Figure 1). The geology consisted of green schists (metamorphic basalt rocks) and phyllite (metamorphic rocks). The mean annual temperature was about 7.0°C and the mean annual precipitation was ca. 800 mm, with the highest values recorded in summer.

The studied tree stands covered the bases of slopes, mid-slopes and summit plateaux of hills (elevations 300–580 m a.s.l.). The slopes were often intersected by water-eroded gorges or smoothly passed onto flatter areas with a deeper soil. Rapid changes of slope exposure from south to north were also present. Such land relief meant that convex, sunny sites were located in proximity to shady, moist habitats. The vegetation, according to the European Natura 2000 network, was classified as 9110 priority habitat – Euro-Siberian steppe woods with Quercus spp. and acidophilous oak forests (9190). At the studied sites, the steppic woods with oaks (9110 habitat), also called thermophilous oak forests, reach their northern limit of range in central Europe.

**Sampling design and field sampling procedure**

Sampling was made using nested spatial scales: plots within sites (PI, distances between plots ca. 50 m–1 km), sites within mountain ranges (S, distance between sites ca. 1.0–3.5 km), and finally the two mountain ranges (R, distance between ranges ca. 15 km). The field survey was carried out in two stages. Initially, in the field, a GPS receiver was used to delineate the extent of habitats defined as forest of sessile oak (Quercus petraea) of
coppice origin located on the convex part of slopes with generally southern exposure. The concave forms of relief (gorges) overgrown with ravine forests with sycamore (Acer pseudoplatanus) and lime (Tilia spp.) were excluded. The location of the sampling plots was randomly chosen and plot centres were determined in the field using a GPS receiver. To examine species composition at the scales of the study as a whole (R) and particular mountain ranges (S), we sampled seven sites (three in the Kaczawskie Mt. range and four in the Wałbrzyskie Mt. range). Seven sampling plots were established at each site (49 plots in total, Figure 1). This dataset was named A. Additional plots were established to obtain a better insight into the processes driving vegetation structure at the scale of plots within sites (Pl). These included four or five plots per site at three of the sampled sites (two in the Kaczawskie Mts. and one in the Wałbrzyskie Mts.). Data from the additional plots were incorporated into the data from dataset A. Dataset B, comprising 35 plots (12 and 11 per site, respectively), was used to analyse the vegetation composition individually in each of the three sites (Figure 1). The plots were circular, with an area of about 250 m² (8.92 m radius) and the plot size was chosen according to Chytrý and Otýpková (2003). In the sampling plots, the cover-abundance of all vascular plant species was recorded, using the Braun–Blanquet scale (+, 1, 2, 3, 4, 5). The nomenclature for vascular plants followed Mirek et al. (2002); all the data collected are stored in the Polish Vegetation Database (Kacki and Śliwiński 2012).

Environmental variables
Slope and aspect were determined for each plot, using a Suunto Tandem compass and clinometer, to estimate the potential heat load and to evaluate light availability. The percentage cover of rock outcrops and scree was assessed visually. Within each sampling plot, three points were set in the 0 (the magnetic north), 120 and 240° directions, at a distance of 5 m from the centre of the plot. At each of these points, a soil sample was taken for analysis, and soil depth (depth) was measured by driving a steel rod into the soil. The percentage of coarse fragments (CF), defined as mineral particles with a diameter >2 mm, was measured for each sample. A hemispherical photograph of the canopy was taken on a cloudy day from each of the three points per plot at 50 cm above the ground layer. The photographs were analysed by using the (WinScanopy 2003) software by Regent Instruments Inc. to evaluate under canopy light conditions. It was assumed that solar radiation, both diffuse and direct, available at the photographed point under the canopy, originated only from visible sky regions. The quantity of photosynthetically active blue sky radiation (PAR, 400–700 nm) in an open area was calculated on the basis of the geographical position, slope, solar constant and atmospheric transmittance. Subsequently, relative PPFD available under the canopy was calculated on the basis of visible sky regions (Rich 1989; WinScanopy 2003).

Soil moisture measurements, at the same points from where soil samples and photographs were taken, were made by using a portable time domain reflectometer...
(model LB-797, LAB-EL Elektronika Laboratoryjna, Poland) during a period of stable, warm weather without rain, in late August. Measurements were repeated three times around each point and then averaged to express the percentage of soil moisture. For all plots, the measurements were made during four subsequent days to obtain comparable results.

Each soil sample comprised five sub-samples of approximately 10–15 cm depth, or less on shallower soil, collected by a soil auger and then combined into one sample. The pH and concentration of nitrogen (N), available phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and organic carbon (C) were analysed in air-dried samples. The pH was measured in 1 M KCL (one part of soil:two parts of KCL). The concentration of N was determined using the Kjeldahl method. Potassium and P were extracted in calcium lactate, and their concentration was measured with spectrophotometry (P) or flame photometry (K) (Egnér et al. 1960). Calcium was extracted in acetic acid and Mg in CaCl2 before measurement, using atomic absorption spectrophotometry, on iCE™ 3500 spectrophotometer (Ostrowska et al. 1991). The concentration of C was determined by titration (Ostrowska et al. 1991). Soil texture was analysed with laser diffraction and the percentage of sand, silt and clay were calculated.

The potential heat load (HL) was calculated based on the slope inclination, aspect and latitude according to formula (3) in McCune and Keon (2002). The C:N ratio as a proxy for potential mineralisation rate (Janssen 1996) was calculated. The ratios of P:N and K:N were also calculated. The formula proposed by Jamagne et al. (1977) was used as a proxy for water holding capacity (WHC):

\[
WHC = \text{depth of the soil horizon} \times (100 - \text{coarse fragments} \%) 
\]

Statistical methods

Geographic distance, environmental heterogeneity and vegetation diversity across spatial scales. To show geographical distances across studied spatial scales, we calculated average geographical distances between sampling units for each of the spatial scales, that is the entire study region (R), sites within particular mountain ranges (S), and plots inside the particular sites (PI). To estimate environmental heterogeneity, we calculated standardised Euclidian distances between sampling units, while to obtain an estimate of vegetation diversity the average values of Bray–Curtis index were calculated. The calculation of vegetation dissimilarity was made on the basis of Hellinger-transformed plant species cover-abundance data. Both environmental heterogeneity and vegetation diversity values were calculated across all spatial scales.

Spatial variables and their correlations with species and environmental data. In the spatial model for R scale, we applied binary variables to identify each respective mountain range (1 – Kaczawskie, 0 – Walbrzychkie). We used the principal coordinate analysis of neighbour matrices (PCNM) (Borcard and Legendre 2002; Dray et al. 2006) to model spatial structures at the S and PI scales. The geographical coordinates of plots were used to compute PCNM, from which vectors that represented statistically significant positive spatial correlations were selected using Moran’s I values (Borcard and Legendre 2002; Borcard et al. 2004). The PCNM vectors were then used to construct a ‘staggered’ spatial matrix, where PCNM variables were arranged in blocks, with each block corresponding to sites in a given mountain range (S) or plots in given site (PI). Within these blocks, plots from another range or site were assigned a value of zero (Declerck et al. 2011).

Subsequently, the binary variables and vectors representing different spatial scales were used as explanatory variables in redundancy analysis (RDA) of species composition to examine their explanatory value in relation to vegetation structure observed on a given spatial scale. Correlations between the obtained site scores and species, on the one hand, and environmental variables, on the other, were also analysed to determine which species and which environmental resource distributions were associated with spatial structures on particular different scales. The significance of the correlations was tested with the Monte Carlo permutation method.

Variation partitioning and ordination of the vegetation. To decompose plant community composition into the environmental and spatial components, we applied the variation partitioning method (Borcard et al. 1992; Peres-Neto et al. 2006). Variation in terms of species composition was dissected into components explained by the environment and the three spatial scales (R, S and PI), as well as the fraction common to all these groups of variables. Only those environmental variables that were significantly related to species composition were incorporated into variation partitioning analyses. To identify these variables, we used the forward selection procedure, based on adjusted $R^2$ values (Blanchet et al. 2008).

The contribution of particular environmental variables to overall vegetation variability was analysed by using RDA. The influence of spatial structures was excluded from this analysis by taking variables describing spatial structures as conditional variables.

Analyses were carried out on data set A (49 plots) to construct a model for the entire vegetation. Sub-models were constructed to identify which environmental factors were related to vegetation composition at smaller spatial scales (S and PI). Data from data set A were used to construct two sub-models for vegetation in the particular mountain ranges. Data set B (35 plots) was used in three sub-models for vegetation at particular sites.

All computations were carried out by using ‘PCNM’, ‘vegan’ and ‘coin’ libraries in the R package (Oksanen et al. 2008; Hothorn et al. 2013). Before the analyses, the Hellinger transformation was applied to the species data. This procedure gives low weights to rare species (Legendre and
Gallagher 2001). Since the data remained noisy after transformation, only species that occurred in more than three plots (irrespective if excluded species had indicator values or not (Lawesson et al. 2000; Legendre and Gallagher 2001) were included in the variation partitioning and RDA analyses.

Results
Environmental variables and vegetation
The inclination of the plots differed considerably, from steep slopes to flat areas. Rocky outcrops and scree were present in numerous plots. Soils were shallow and coarse textured (49.1% coarse fraction), at an average depth of 15.3 cm, acidic (mean pH in KCL, 3.6), calcium-poor (mean Ca concentration, 171.9 mg dm$^{-3}$). Their water-holding capacity was low, and in summer, they retained a mean humidity of 9.5%. The potential heat load was high (mean HL, 0.9), as was the amount of light (PPFD) reaching the forest floor (mean, 22.1%) (Table 1). All environmental data are provided in supplementary material (Table S2).

We recorded 174 vascular plant species in total, 104 of which were present in more than three plots. The number of species per plot ranged from 11 to 52, with a mean of 29.5 species per plot. On the forest floor, the most common (>80% of plots) species were Convallaria majalis, Galium schultesii and Hieracium murorum (Table 2). The cover of forest floor vegetation varied from 10% to 90%, 62% on average. The highest values of cover were observed for graminoid species, Calamagrostis arundinacea and Poa nemoralis.

Table 1. Mean values, standard deviation and range of environmental traits for entire study region of sessile oak (Quercus petraea) forests of coppice origin on the southern slopes of the Kaczawskie Mts. and the Walbrzyskie Mts., Sudetes Mts., Poland.

| Variable     | Mean (±SD) | Range   |
|--------------|------------|---------|
| Depth (cm)   | 16.2 (6.8) | 6.0 – 34.0 |
| Outcrop (%)  | 4.9 (7.6)  | 0.00 – 35.0 |
| Slope (%)    | 17.9 (10.1)| 0.0 – 40.0 |
| HL           | 0.88 (0.05)| 0.71 – 0.94 |
| PPFD (%)     | 22.4 (4.2) | 12.6 – 35.0 |
| pH in KCL    | 3.58 (0.24)| 2.90 – 4.30 |
| N (%)        | 0.37 (0.17)| 0.10 – 0.88 |
| P (mg/100 g) | 1.68 (1.84)| 0.01 – 10.10 |
| K (mg/100 g) | 16.0 (7.2) | 4.5 – 35.2 |
| Mg (mg/100 g)| 11.1 (7.7) | 0.3 – 31.0 |
| Ca (mg/dm³)  | 172.6 (98.7)| 11.0 – 492.0 |
| C (%)        | 8.05 (5.40)| 2.52 – 31.30 |
| C:N          | 24.1 (17.5)| 6.2 – 119.5 |
| P:N          | 4.50 (4.51)| 0.04 – 20.90 |
| K:N          | 49.2 (32.7)| 10.4 – 248.9 |
| CF (%)       | 49.1 (15.4)| 14.4 – 75.6 |
| Sand (%)     | 48.8 (12.9)| 21.0 – 75.0 |
| Silt (%)     | 46.9 (11.8)| 23.0 – 72.0 |
| Clay (%)     | 4.3 (1.5)  | 1.00 – 8.00 |
| WHC (%)      | 887.8 (588.4)| 251.8 – 2855.0 |

Notes: HL, potential heat load; PPFD, photosynthetically active photon flux density; CF, soil coarse fragments; WHC, water holding capacity.

The average geographic distance between plots located at the same site was around 200 m, while the average geographic distance at the scale of entire study region was around 10 km (Figures 2–3). The average differences in environmental heterogeneity and the mean Bray–Curtis dissimilarity of vegetation calculated for each two plots within a site showed a tendency to increase with separation distance. The average environmental heterogeneity within a site was in some cases higher than that within the same mountain range (Figure 3).

Model of the vegetation for the entire study region
The results of ordination showed that models constructed on the basis of binary variables reflecting the division into two mountain ranges (R) as well as PCNM vectors reflecting the inter-site differentiation (S) significantly explained species composition. The model on the R scale returned $R^2_{\text{adj}} = 0.031$ ($P = 0.005$), whereas the S scale explained a fraction of variation which was twice that size ($R^2_{\text{adj}} = 0.069$, $P = 0.005$). By contrast, vectors reflecting spatial structures at the smallest, single-site scale (Pl) were not significantly related to vegetation composition ($R^2_{\text{adj}} = -0.008$, $P = 0.67$).

Numerous species were significantly correlated with the ordination axes of spatial structures on the R and S scales (Table 3; Figure 2; Supplementary data, Table S1). Some environmental variables were also correlated with the ordination axis representing the R and S scales. Among these variables, a distinctive pattern of base cation (Ca, Mg) concentration and soil pH was observed at the R scale, with higher values in the Kaczaskie Mountains (Table 3). At the S scale, correlations were observed with soil texture (silt, clay and sand), HL and C:N (Table 3, Figure 2). We did not observe any correlations between environmental variables and ordination axes at the Pl scale.

The fraction of variation in species composition which could be explained by environmental variables was higher ($R^2_{\text{adj}} = 0.14$, $P = 0.000$) when compared to those explained by spatial models (0.031 for R scale and 0.069 for S scale). The value of variation shared between space and environment was relatively low (0.01 for R scale and 0.02 for S scale; Figure 4).

The environmental factor with the largest correlation to species composition was WHC, followed by Ca, silt, HL and the P:N ratio (Table 4; unadjusted $R^2$ values, since the calculation of adjusted values is impossible in partial RDA (Oksanen et al. 2008)). The ordination produced three significant axes (Table 5, Figure 5). The first axis represents the combined effect of land-relief derived variables (HL, outcrop) and soil Ca (Table 5, Figure 5). The second axis mostly reflects the effect of WHC as well as the percentage of silt and was negatively correlated with Mg (Table 5, Figure 5). The third axis was not significantly correlated with any environmental variable (Table 5).

Sub-models of vegetation for ranges and sites
The two ordinations analysing the effect of environmental variables and spatial patterns for each individual mountain
range indicated the significance of both environmental and spatial structures at the S scale. The influence of spatial structures at the single-site scale (Pl) was insignificant, similar to the model for the entire study region (Figure 4). The fraction of variation explained by environmental variables in both mountain ranges was higher than the spatial component (Figure 4). In both mountain ranges, soil Ca concentration was significantly related to species

Table 2. List of 15 most frequent species (number of plots = 63) for entire study region of sessile oak (*Quercus petraea*) forests of coppice origin on the southern slopes of the Kaczawskie Mts. and the Wałbrzyskie Mts, Sudetes Mts, Poland.

| Species                  | Freq. (%) | C/A | Species                  | Freq. (%) | C/A |
|--------------------------|-----------|-----|--------------------------|-----------|-----|
| *Quercus petraea*        | 100       | 3   | *Acer pseudoplatanus*    | 57        | +   |
| *Convallaria majalis*    | 89        | +   | *Hieracium sabaudum*     | 57        | +   |
| *Galium schultesii*      | 83        | +   | *Festuca ovina*          | 54        | 1   |
| *Hieracium murorum*      | 83        | +   | *Carpinus betulus*       | 51        | +   |
| *Calamagrostis arundinacea* | 81    | 2   | *Cerasus avium*          | 51        | +   |
| *Poa nemoralis*          | 81        | 2   | *Silene nutans*          | 51        | +   |
| *Rosa canina*            | 60        | +   | *Sedum maximum*          | 49        | +   |
| *Tilia cordata*          | 59        | +   |                          |           |     |

Note: Percentage frequency of occurrence (Freq.) and modal value of non-zero cover-abundance (C/A) expressed on the Braun-Blanquet scale.
Table 3. List of environmental variables (Ca, pH, Mg, sand, silt, clay, HL, C:N) and the three species most strongly correlated with the ordination axes that modelled spatial structures at entire study region (R) and sites within mountain ranges (S) scales.

| Positive correlations | Negative correlations |
|-----------------------|-----------------------|
| **R spatial scale**   | **Z** | **P** | **Z** | **P** |
| Deschampsia flexuosa  | 4.996 | 0.000 | Sorbus terminalis | −4.094 | 0.000 |
| Impatiens parviflora  | 3.857 | 0.000 | Adoxa moschatellina | −3.670 | 0.000 |
| Corylus avellana      | 3.408 | 0.001 | Vaccinium myrtillus | −3.548 | 0.000 |
|                       |       |      | Ca              | −2.702 | 0.007 |
|                       |       |      | pH              | −2.281 | 0.023 |
|                       |       |      | Mg              | −2.258 | 0.024 |
|                       |       |      | Clay             | −2.008 | 0.045 |
| **S spatial scale RDA 1** |       |      | Vincetoxicum hirundinaria | −3.723 | 0.000 |
| Melampyrum pratense   | 5.061 | 0.000 | Calystegia sepium | −3.216 | 0.001 |
| Galium odoratum       | 3.783 | 0.000 | Alliaria petiolata | −2.778 | 0.005 |
| Luzula luzuloides     | 3.541 | 0.000 | HL               | −3.030 | 0.002 |
| Silt                  | 2.182 | 0.029 | Sand             | −2.275 | 0.023 |
|                       |       |      | Clay             | −2.925 | 0.002 |
| **S spatial scale RDA 2** |       |      | Hepatica nobilis | −2.746 | 0.006 |
| Hepadna exscapa       | 3.169 | 0.002 | Urtica dioica    | −2.731 | 0.006 |
| Vincetoxicum hirundinaria | 3.123 | 0.002 | Acer platanoides | −2.617 | 0.009 |
| Fagus sylvatica       | 3.088 | 0.002 | Veronica officinalis | −3.290 | 0.001 |
| Clay                  | 1.997 | 0.046 | C:N              | −2.817 | 0.006 |

Notes: Statistics (Z) and P values are shown. The negative values at the R scale indicate lower frequency of species occurrence or smaller values of environmental variables in the Wałbrzyskie Mt. range than in the Kaczawskie Mts (Sudetes Mts, Poland). All species correlated with the ordination axes are listed in supplementary materials. HL, potential heat load.

The effect of ecological niche and spatial pattern on the diversity of oak forest vegetation

The results indicated that species composition of vegetation in abandoned coppice oak forests on slopes with a southern exposure is shaped by environmental variables, as well as spatial patterns operating at the level of entire mountain ranges and inter-site scale. The environmental variables related to species composition represent different ecophysiological factors which interact and delimit the environmental species niche. These could be generally divided into three main groups: those connected with water (WHC, humidity, silt, clay), nutrients (Ca, P:N, Mg, C:N), and thermal conditions related to topography (HL, outcrop) and light availability (PPFD). Among environmental factors related to species, composition of vegetation moisture is considered to be one of the most important. Unfortunately, the exact measurement of its long-term influence is difficult (Kopecký and Čížková 2010). It is postulated that the susceptibility of plants to drought is more important than their tolerance to occasional periods of high soil moisture (Schaffers and Sýkora 2000). Therefore, incidental measurements of soil moisture in a period of summer drought can be used when modelling forest floor biomass productivity (Axmanova et al. 2011) or species distribution (Gilbert and Lechowicz 2004). Alternatively, soil water relations are modelled as a function of soil depth and texture (Schoenholtz et al. 2000; Bergès and Balandier 2010). In this study, the single most important factor related to vegetation composition was WHC, which was calculated as a function of soil depth and the coarse fraction of the soil. Values of WHC were correlated with measured soil moisture (Z = 2.671, P = 0.007, result for data set A, Monte Carlo permutation test); however, WHC was found to be related more to overall species composition than soil moisture values measured in the period of summer drought. Vegetation rich in drought tolerant and light demanding plant species, classified as thermophilous oak forest, is generally found at sites where the annual mean precipitation is below 650 mm (Chytrý 1997). Despite that the sites studied have mean annual precipitation of ca. 800 mm, it is possible for the
thin soil on solid rock to dry out completely (e.g. Ellenberg 2009; Bergès and Balandier 2010). Thus, localised edaphic drought creates a niche for thermophilous oak forest vegetation in the relatively humid and cool subcontinental central Europe.

The second important abiotic factor is soil Ca, which, along with pH, is widely recognised as a major factor related to species composition and species richness throughout central Europe (Chytrý et al. 2003; Ewald 2003; Hofmeister et al. 2009; Axmanová et al. 2011). Low pH soils usually have a poorer flora than Ca-rich soils (Schuster and Diekmann 2003). In this study, other nutrients, namely P and Mg, were related to species distribution. Phosphorus, an immobile element at low and high pH, is generally known as a factor limiting biomass production and species distribution in temperate forest ecosystems (Hofmeister et al. 2002; Axmanová et al. 2011). A problem of biological conservation, frequently appearing in thermophilous oak forests, is a phenomenon called ‘nitrogen time bomb’. In forests where coppicing or cattle pasturing is no longer applied, an increase of canopy cover and accumulation of organic matter is often

Figure 4. Venn diagrams of the adjusted $R^2$ values obtained from variation partitioning of factors influencing vegetation of sessile oak (*Quercus petreae*) forests of coppice origin on the southern slopes of the Kaczawskie Mts. and the Walbrzyskie Mts, Sudetes Mts, Poland. The grey circle represents the environmental component, the white circle with solid line represents the spatial component at the sites within mountain ranges (S) scale and the white circle with a dashed line represents the spatial component at the entire study region (R) scale. Only significant components are shown.
Table 4. The partial contribution of environmental variables to the distribution of species in sessile oak (*Quercus petreae*) forests of coppice origin on the southern slopes of the Kaczawskie Mts. and the Wałbrzyzkie Mts, Sudetes Mts, Poland.

| WHC | Ca | Silt | HL  | P:N | Mg | Outcrop | Clay | P | Moisture | PPFD | C:N | Conditional | Residual |
|-----|----|------|-----|-----|----|---------|------|---|----------|-------|-----|-------------|----------|
| Entire study region | | | | | | | | | | | | | |
| variability | 0.049 | 0.043 | 0.031 | 0.028 | 0.024 | 0.024 | 0.02 | 0.02 | | | 0.177 | 0.583 |
| F | 3.012 | 2.700 | 1.951 | 1.664 | 1.459 | 1.427 | 1.260 | 1.250 | | | | |
| P | 0.001 | 0.001 | 0.007 | 0.021 | 0.061 | 0.072 | 0.131 | 0.164 | | | | |
| Submodels: mountain ranges | | | | | | | | | | | | |
| Kaczawy | | | | | | | | | | | | |
| Variability | 0.108 | 0.080 | | | | | | | 0.078 | 0.072 | 0.099 | 0.563 |
| F | 2.855 | 2.143 | | | | | | | 2.090 | 1.924 | | |
| P | 0.001 | 0.004 | | | | | | | 0.003 | 0.009 | | |
| Wałbrzych | | | | | | | | | | | | |
| Variability | 0.105 | 0.037 | | | | | | | | | 0.059 | 0.362 | 0.638 |
| F | 3.635 | 1.307 | | | | | | | | | 2.018 | | |
| P | 0.006 | 0.140 | | | | | | | | | 0.006 | | |
| Submodels: individual sites | | | | | | | | | | | | |
| Site 1 | | | | | | | | | | | | |
| Variability | 0.260 | | | | | | | | | | | 0.739 |
| F | 1.758 | | | | | | | | | | | |
| P | 0.01 | | | | | | | | | | | |
| Site 2 | | | | | | | | | | | | |
| Variability | 0.295 | | | | | | | | | | | 0.498 |
| F | 2.380 | | | | | | | | | | | 1.641 |
| P | 0.014 | | | | | | | | | | | 0.042 |
| Site 3 | | | | | | | | | | | | |
| Variability | 0.343 | | | | | | | | | | | 0.426 |
| F | 3.223 | | | | | | | | | | | 2.171 |
| P | 0.001 | | | | | | | | | | | 0.027 |

Notes: Fractions of constrained variance (variability) and statistical significance (*P*) of environmental variables conditioned by spatial structures at entire study region (R) and sites within mountain ranges (S) scales are shown. The values of variance are calculated on the basis of unadjusted $R^2$ values. WHC, water holding capacity; HL, potential heat load; PPFD, photosynthetically active photon flux density.
Table 5. Values of interset correlations in redundancy analysis (RDA) of vegetation for entire study region of sessile oak (*Quercus petraea*) forests of coppice origin on the southern slopes of the Kaczawskie Mts. and the Walbrzyskie Mts, Sudetes Mts, Poland.

|               | RDA1 | RDA2 | RDA3 |
|---------------|------|------|------|
| Variation explained | 0.037 | 0.027 | 0.016 |
| F             | 4.465 | 3.310 | 1.910 |
| P             | 0.005 | 0.005 | 0.005 |
| Constraints   |      |      |      |
| WHC           | 0.236 |       | 0.675 |
| Ca            | 0.400 | −0.391 | −0.344 |
| Silt          | 0.348 | −0.182 | −0.093 |
| HL            | −0.406 | −0.302 | −0.162 |
| P:N           | 0.013 | −0.466 | 0.075 |
| Outcrop       | −0.399 | −0.119 | −0.083 |
| Clay          | 0.132 | 0.142 | −0.196 |

Notes: The effect of environmental variables was conditioned by variables describing spatial structures at entire study region (R) and sites within mountain ranges (S) scales. Values of statistically significant linear correlations are shown in bold. WHC, water holding capacity; HL, potential heat load.

Figure 5. The biplot of the redundancy analysis of vegetation for the entire region of sessile oak (*Quercus petraea*) forests of coppice origin on the southern slopes of the Kaczawskie Mts. and the Walbrzyskie Mts, Sudetes Mts, Poland. The larger panel shows species scores (arrows), the small left panel presents site scores (circles) and the scores for environmental variables (arrows). Only species with a value of goodness-of-fit above 0.95 are shown.

Note: Ace pla, *Acer platanoides* L.; Ado mos, *Adoxa moschatellina* L.; Agr eup, *Agrimonia eupatoria* L.; All pet, *Allaria petiolata* (M. Bieb.) Cavara & Grande; Ane nem, *Anemone nemorosa* L.; Asa eup, *Asarum europaeum* L.; Bra pin, *Brachypodium pinnatum* (L.) P. Beauv.; Cal aru, *Calamagrostis arundinacea* (L.) Roth; Cal sep, *Calystegia sepium* (L.) R. Br.; Cer av, *Cerasus avium* (L.) Moench; Con maj, *Convallaria majalis* L.; Cor ave, *Corylus avellana* L.; Cra lae, *Crataegus laevigata* (Poir.) DC.; Des fle, *Deschampsia flexuosa* (L.) Trin.; Fag syl, *Fagus sylvatica* L.; Fus gig, *Festuca gigantea* (L.) Vill.; Fus rub, *Festuca rubra* L. s. s.; Fra exc, *Fraxinus excelsior* L.; Gal apa, *Galium aparine* L.; Gal odo, *Galium odoratum* (L.) Scop.; Gal sch, *Galium schultesii* Vest; Imp par, *Impatiens parviflora* DC.; Lat nig, *Lathyrus niger* (L.) Bernh.; Lat ver, *Lathyrus vernus* (L.) Bernh.; Luz luz, *Luzula luzuloides* (Lam.) Dandy & Wilmott; Mel pra, *Melampyrum pratense* L.; Mel nut, *Melica nutans* L.; Mel mel, *Melittis melissophyllum* L.; Pin syl, *Pinus sylvestris* L.; Pol odo, *Polygonatum odoratum* (Mill.) Druce; Pul obs, *Pulmonaria obscura* Dumort.; Sor tor, *Sorbus torminalis* (L.) Crantz; Urt dio, *Urtica dioica* L.; Vac myr, *Vaccinium myrtillus* L.; Vin hir, *Vincetoxicum hirundinaria* Medik.
observed. Moreover, in all European forests a large amount of N is added via atmospheric deposition. The excessive input of N by organic matter accumulation and atmospheric deposition could lead to the expansion of nutrient-demanding, ruderal and invasive plant species. However, this expansion is restricted by light limitation caused by increased canopy cover in overgrown undisturbed coppice forests. If the canopy was opened to aid maintaining light-demanding plant species of the herbaceous layer, nitrophilous species could proliferate. However, P limitation may check the development of ruderal plants, thereby allowing the successful conservation of the target vegetation (Andrews et al. 2009; Verheyen et al. 2012; Kopecký et al. 2013; Vild et al. 2013). In the oak forests studied, the distribution of nutrient-demanding species (e.g., Galium aparine, Impatiens parviflora and Urtica dioica) was inversely related to soil Ca, Mg, as well as to the soil P:N ratio and positively related to N content or the C:N ratio (Figure 5). It suggests that the risk of a proliferation of nitrophilous species, following an eventual canopy opening, was rather unlikely.

Values of adjusted $R^2$ (Figure 3) are low, compared to mathematical models developed in other branches of ecology. However, this is a typical feature of plant community data, which commonly contain a lot of noise caused by stochastic events and measurement/observation errors. Moreover, ordination is only a simplification in a snapshot of the real relationship of organism with the environment. Therefore, low values of explained variation are quite common in vegetation analyses (Gauch 1982; Palmer 1993; McCune 1997).

Apart from variability relationship between species composition and environmental gradients, variables representing spatial structures were also weakly, but significantly related to species composition. A significant spatial component, after controlling for environmental components, can indicate neutral processes, such as dispersal limitation and/or local stochastic events. Spatial structures could also correspond to some unmeasured environmental variables (Legendre and Legendre 1998; Cottenie 2005; Declerck et al. 2011). However, since the study sites were chosen on the basis of sharing the same forest management history and the measured environmental traits describe fundamental environmental gradients (light, moisture, nutrients and pH), we can assume that the most important factors relating to the spatial structures are dispersal limitation and stochastic events. Topography, coupled with management history, resulted in a patchy distribution of habitats. It might have led to dispersal limitation of species typical to coppiced oak forests and subsequently to changes in species composition (Honnay et al. 2005; Carranza et al. 2012). Results of other studies have also shown that the number of light-demanding plant species in the submontane landscape of central Europe is limited mostly by their low dispersal (Vondrák and Prach 2006). Our results suggest that most species are able to disperse efficiently at the site scale, but their dispersal to other sites and mountain ranges is limited.

The pattern observed in this study, indicating both significant spatial structures and species sorting along environmental gradients, can result from variation of ecological niches of species coupled with high or low spatial dispersal (Cottenie 2005; Ng et al. 2009). As observed by Ng et al. (2009), assuming distance-dependent plant dispersal, efficient dispersal at short distances (small spatial scale) is more likely to occur than across long distances (large spatial scale). Therefore, the patterns obtained in this study (species sorting acting at all scales and the lack of significant spatial component at the smallest scale) indicate that the observed vegetation should be classified as species-sorting and limiting dispersal metacommunity type (Cottenie 2005; Ng et al. 2009). However, we cannot confirm it, because we did not study directly limitation of species distribution. The variation partitioning is an indirect method – the first step in analysing the metacommunity structure – and its use for assessment of distribution limitation can be biased (Gilbert and Bennett 2010). Although, it is possible to assess the limitation of dispersal of single species in a quantitative way, there is no method for whole metacommunity until now (Jacobson and Peres-Neto 2010). Moreover, the spatial distribution of plots was set up arbitrary; therefore, the scale used could not be optimal to the spatial processes examined in metacommunities studied (Wiens 1986).

Using the lessons from this study, applicable to the conservation of this vegetation type, the results suggest that attention should be paid not only to sites currently rich in light-demanding and drought-tolerant species but also other sites which could potentially be inhabited by these species. Studies in grassland metacommunities, representing species sorting – limited dispersal type, show that success in local conservation of the vegetation at particular sites, for example nature reserves, does not necessarily imply success on a regional scale. This could well be the case for the forests studied. The introduction of some target species, for example typical for thermophilous oak forest, in sites where they are absent and where soil conditions are appropriate could be applied and along with suitable management (e.g. canopy opening).

Conclusions
Edaphic drought creates niche for the thermophilous oak forests studied, whose composition is shaped both by environmental gradients and spatial processes, operating at different scales. The environmental variables operate at large, medium and small spatial scale, while the effect of spatial structures was not observed at the smallest scale. It suggests that in the surveyed metacommunity processes of species sorting with dispersal limitation at large and medium spatial scale are prevailing. Among the environmental factors, water holding capacity and soil calcium concentration were most strongly related to vegetation composition at all spatial scales. Our results suggest that successful conservation of this vegetation type requires paying attention to potential issues of dispersal limitation.
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Supplemental data
Supplemental data for this article can be accessed here.

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Tomasz Szymura’s main research activity concentrates on forest vegetation ecology and conservation biology. Magdalena Szymura’s interest include plant invasions, grassland vegetation and landscape ecology. Aurelia Macioł is a Ph.D. student who studies the biogeochemistry of aquatic ecosystems.

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The effect of ecological niche and spatial pattern on the diversity of oak forest vegetation

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