

Herb Layer Diversity and Phytoindicative Evaluation of Habitat Conditions of Forest Permanent Plots in Poland¹

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Abstract

The influence of climatic and pollution gradients was determined on species richness, species diversity, and values of phytoindicators of the herb layer in pine and mixed pine forest communities in Poland. Geographical longitude was used as a synthetic measure of geographical position. Ellenberg's indices were used as synthetic measures of habitat differentiation, calculated as weighed averages: L (light index), T (temperature index), K (continentality index), F (moisture index), R (reaction index), N (nitrogen index). Richness and diversity variables were used: razem (total number of species), gatB (number of shrub species), gatC (number of herb layer species), diver (Shannon's diversity index $H = -\sum p \log p$), simps (Simpson's index $S = \sum p^2$), beta ($\beta = [1 - \text{simps}] / [1 - \text{gatC}]$). Additional dependent variables included the proportion of number and cover of different Raunkiaer's life forms as well as shares of number and cover of species of different leaf anatomy and different syntaxonomic character. By using Ellenberg's indices the vegetation on consecutive sample plots was not strongly differentiated. All sites on the climatic transect occurred on dry, strongly acidic or acidic soil, with low nitrogen content. Values for the index of continentality "K" reflected clearly the climatic differentiation from west to east. The number of herb layer species depended on the geographical longitude (correlation coefficient 0.851) for pine and mixed forests together, 0.840 for pine forests only, and 0.926 for mixed forests only. All diversity indices were also strongly correlated with the longitude. Generally, the share of the number of chamaephytes and therophytes was positively correlated with the longitude. In pine forests there was also a general tendency for the number of scleromorphic species to decrease (and mesomorphic species to increase) in the west-east direction. Meadow species also generally tended to increase in the west-east direction. For all the plots taken together the cover of meadow species is correlated with the longitude (correlation coefficient 0.881), 0.905 for pine forests only, and 0.910 for mixed forests.

Introduction

Species richness and species diversity are some of the most important structural features of forest communities. They are influenced by a range of factors such as large-scale geography and habitat (Cowling 1990, Day and others 1988, Grime 1979, Jurko 1985, Prusinkiewicz 1970). Other important factors are the history of vegetation development in the Holocene (Huntley 1993) and the history of use (Law and Morton 1993) to interpopulational and successional interactions (Dollar and others 1992, Trevin and others 1993). The role of the different factors changes in relation to the scale of the phenomenon considered.

In analyses on a scale larger than the region, overall geographical factors, including macroclimatic differentiation, are most important. Macroclimatic differentiation consists of many elements, including mean annual temperature, total precipitation, moisture deficit, the amplitude of annual temperatures, the degree of continentality of the climate and the length of the growing season. These elements are mutually interlinked and are dependent on geographical location. It is for this reason also that many studies consider the link between structural features of the flora and vegetation and geographical location, treating the latter as a synthetic indicator of macroclimatic differentiation.

This paper defines the relationships between geographical location (which determines macroclimatic differentiation and reflects the history of development of the vegetation), habitat conditions (Ellenberg 1974), and selected characteristics of the species richness and diversity of the ground cover in two narrowly-defined types of forest community, namely, within typical pine forests and within mixed

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forests. The subjects of analysis are 17 study areas lying along a west-east gradient of continentality (Breymer, 1996).

Methods

The species diversity of the herb layer and the phytoindicators of habitat conditions were obtained from phytosociological records of all species occurring on 400 m² in each of the 17 plots. The majority of the records were taken in May 1995. A detailed description of the methodology and of the characterization of the vegetation cover is given in a separate study (Roo-Zielinska and Solon 1996).

Defined on the basis of information contained in each of the 17 phytosociological records were values for basic indices of diversity, namely: (a) the number of species of vascular plants; (b) the Shannon Index (Shannon and Weaver 1949), $H = -\sum p \log p$; (c) the Simpson Index (Simpson 1949), $S = \sum (p^2)$; (d) the beta index (Simpson 1949) $\beta = [1 - \text{simps}] / [1 - \text{gatC}]$; and (e) the index of evenness $HH_{\max}$ in the form $HH_{\max} = H / \log(n)$ (where p_i is the share of a species in the total cover of vascular plants in the ground cover layer; n = total number of species in a record). The number and proportion in cover of species representing different Raunkiaer life forms, types of leaf permanence, and types of anatomical structure also were calculated. Detailed characteristics of species were taken from Ellenberg (1974). The phytosociological structure of the ground cover layer was also described by using the list of characteristic species from Matuszkiewicz (1981).

The analytical method of indicative numbers from Ellenberg (1974) was used to assess habitat-climatic conditions (insolation "L" and the degree of continentality "K"), as well as habitat-edaphic conditions (the moisture "F" and acidity "R" of soils, as well as their nitrogen content "N"). All the phytoindicative analyses were done on the floristic composition of the ground layer, which reacts most vigorously to changes in abiotic conditions, and in which anthropogenic influences become visible most quickly. The index of insolation "L" indicates the relative strength of insolation (from 1: species requiring full shade; to 10: plant species requiring full light). The index of continentality "K" describes the resistance of a species to the frequency and length of occurrence of dry periods in the growing season, as well as to the length of the pre-frost period (from 1: the most marked features of an Atlantic climate; to 10: the most marked continental features). The index of humidity "F" expresses the ecological reaction of species in relation to the humidity of the substrate in the growing season (from 1: those requiring extremely dry soils; to 12: aquatic plants that are mostly completely submerged in water). The index of soil reaction "R" expresses biologically the acidity of the substrate experienced by plants (from 1: species requiring very highly acid soil [$\text{pH} < 3.5$]; to 10: those requiring neutral or basic soils [$\text{pH} > 6.5$]). The nitrogen index "N" expresses the ecological reaction of species to the content of nitrogen in the soil (from 1: species only occurring in soils poor in nitrogen; to 10: species only in soils very rich in nitrogen, such as those intensively fertilized). The mean values of phytoindicators were calculated twice for each of the phytosociological records — the first value was obtained only on the basis of the number of species of defined divisions of habitat requirements while the second (weighted mean) also included species cover. The method of Ellenberg and its various applications have often been discussed in the literature. It is useful in both the presentation of the spatial differentiation of current habitat conditions (Kostrowicki and Wojcik 1971, Roo-Zielinska 1982, 1994) and very well-suited to the dynamic expression of phenomena (Roo-Zielinska 1993, Roo-Zielinska and Solon 1990, 1994).

The relationships between geographical location and the values of phytoindicators (independent variables) and indices of diversity, as well as the proportions of species representative of different ecological groups (dependent variables) were defined on the basis of correlation and regression analyses for three groups of sites: for all 17 sites on the west-east transect; only for the 9 pine forest sites on the west-east transect; and only for the 8 mixed forest sites on the west-east

transect. The Stepwise Variable Selection procedure was used in the choice of the independent variables of strongest influence on changes in species diversity.

Results

The number of species and species diversity of the vascular plants in the ground layer increased in the west to east direction within both pine forests and mixed forests, with the value of the Shannon Index changing from 1.87 to 5.20, the value of the Beta Index within the range 0.82 to 0.99 and the value of the Simpson Index varying between 0.35 and 0.03. A similar range of variability was observed in the index of uniformity (HHmax), which varied from 0.71 to 0.96. The relationships between indices of richness and diversity and longitude were regularly statistically-significant. For all the indices analyzed the absolute correlation coefficients were above 0.74 (table 1). The correlations between all the indices of richness and diversity and the Ellenberg indices were considerably weaker when all areas were considered together. All of them (except the number of lichens) were correlated with the coefficient of continentality (table 2). In all three groups the relationships between the value for the index of species richness of the ground layer and the independent variables (longitude and phytoindicators) are best described by a straight line relationship $gatC = (a * dlugeo) + (b * fito)$, in which gatC is the number of species of the ground layer; dlugeo the geographical longitude; fito the phytoindicative indices denoting: the mean index for light requirements (L) for all species (in the case of all 17 areas considered together or for pine forest only) or the mean index for moisture requirements (F) also calculated for all species only in the mixed forests (fig. 1). Another situation arises in the case of the variability of values for the Shannon Index. In all three groups of sites, the relationships between the value of the Index and the independent variables is best described by a straight line with longitude as the dependent variable. However, the modifying influence of local habitat factors is minimal and not statistically significant (fig. 2).

Variability was low in the proportion of different life forms across the gradient. Within mixed forests a strong positive correlation was found between the relative cover of chamaephytes and geophytes in the overall cover and the longitude. A similar, but weaker, relationship was also observed in the case of joint analysis of all transect sites (table 1), while differences in habitat conditions exerted a weaker influence on the number of different life forms (table 2).

Geographical variability in the proportion of species of different leaf longevity was not apparent. Only in the case of the number and cover proportion of species with green wintering leaves showed a clear correlation with longitude (table 1). This relationship is best described by an exponential equation or regression the form $Y = \exp(a + bX)$, albeit with the parameters of the line not differing significantly between all the analyzed blocks (fig. 3).

Clear geographic variability was found in the proportion of species of different anatomical types. Positive correlations were found between the quantitative shares of meso- and hygromorphic species and longitude, while inverse correlations characterized the relationship between the quantitative shares of scleromorphic species and longitude (table 1). This latter relationship was best expressed by an exponential regression (fig. 4).

Species characteristics of the class *Vaccinio-Piceetea* were the main components of the ground cover layer of the areas studied. Their shares in the total number of species varied from 20 to 50 percent, but they always constituted the dominant group. The cover of this group varied from 21 to 74 percent of total cover.

The composition of the ground cover of the studied areas also included other groups of species of which the most important were those characteristic (Matuszkiewicz 1981) for the classes *Molinio-Arrhenatheretea*, *Sedo-Scleranthetea*, *Nardo-Callunetea*, *Quercus-Fagetea*, *Trifolio-Geranietea*, *Festuco-Brometea* and *Epilobietea*.

The geographical variation in the numbers of species of differing syntaxonomic affiliation was different for different groups. Statistically significant correlation

relationships between longitude and the amount of a particular group were more numerous and stronger in the case of areal representation than in the case of quantitative representation (*table 1*). The clearest relationship was observed in relation to the cover proportion of species characteristic of the classes *Molinio-Arrhenatheretea* and *Vaccinio-Piceetea*. This relationship was best expressed by the straight line relationship of the form $Y=p_1+p_2X$ (*fig. 5*).

Table 1 — Statistically significant correlations between geographical longitude (independent variable) and diversity indices and shares of different species groups.¹

	All plots on transect		Pine forests on transect		Mixed forest on transect	
Number of plots	17		9		8	
all vascular species	0.8422***		0.8506***		0.9246***	
shrub species	0.7903***		0.8528***		0.9267***	
herb layer						
vascular species	0.8509***		0.8396***		0.9260***	
beta index	0.8978***		0.9241***		0.8823***	
Simpson's index	-0.8812***		-0.9156***		-0.8977***	
Shannon's index	0.9058***		0.9186***		0.9502***	
HHmax	0.8733***		0.9004***		0.8686***	
	by species cover	by species number	by species cover	by species number	by species cover	by species number
Herbaceous						
Chamaephytes	0.6047*	0.5013*			0.7919*	
Geophytes	0.5209*				0.8212*	
Terophytes		0.6911**	0.6953*	0.8363**		
evergreen species	-0.7409***		-0.9099***	-0.7489*		
overwintering						
green species	0.7261***	0.8363***	0.7834*	0.8484**	0.8208*	0.8439**
summergreen species		-0.6691**				-0.7871*
helo- and higrormorphic		0.7528***		0.8571**		
mesomorphic species		0.5902*		0.7621*		
scleromorphic species		-0.7856***		-0.8918**		
EP	0.5165*				0.8619**	
MA	0.8813***	-0.6079**	0.9046***		0.9096**	
NC		0.7567***		0.7525*		0.8430**
QF				0.7297*	0.7328*	-0.7466*
TG	0.6815**			-0.7324*	0.8246*	
VP	-0.6542**		-0.7900*			

1* = $p < 0.05$

** = $p < 0.01$

*** = $p < 0.001$

Table 2 — Statistically significant correlations between phytoindicative characteristics (independent variables) and species richness of C layer.¹

	All plots on transect		Pine forests on transect		Mixed forest on transect	
Number of plots	17		9		8	
	by species cover	by species number	by species cover	by species number	by species cover	by species number
L	-0.5277*	-0.5277*				
K	0.5702*	0.5563*				
F					0.7770*	
R	0.5682*	0.5682*	0.7073*	0.7073*		

¹* = $p < 0.05$

** = $p < 0.01$

*** = $p < 0.001$

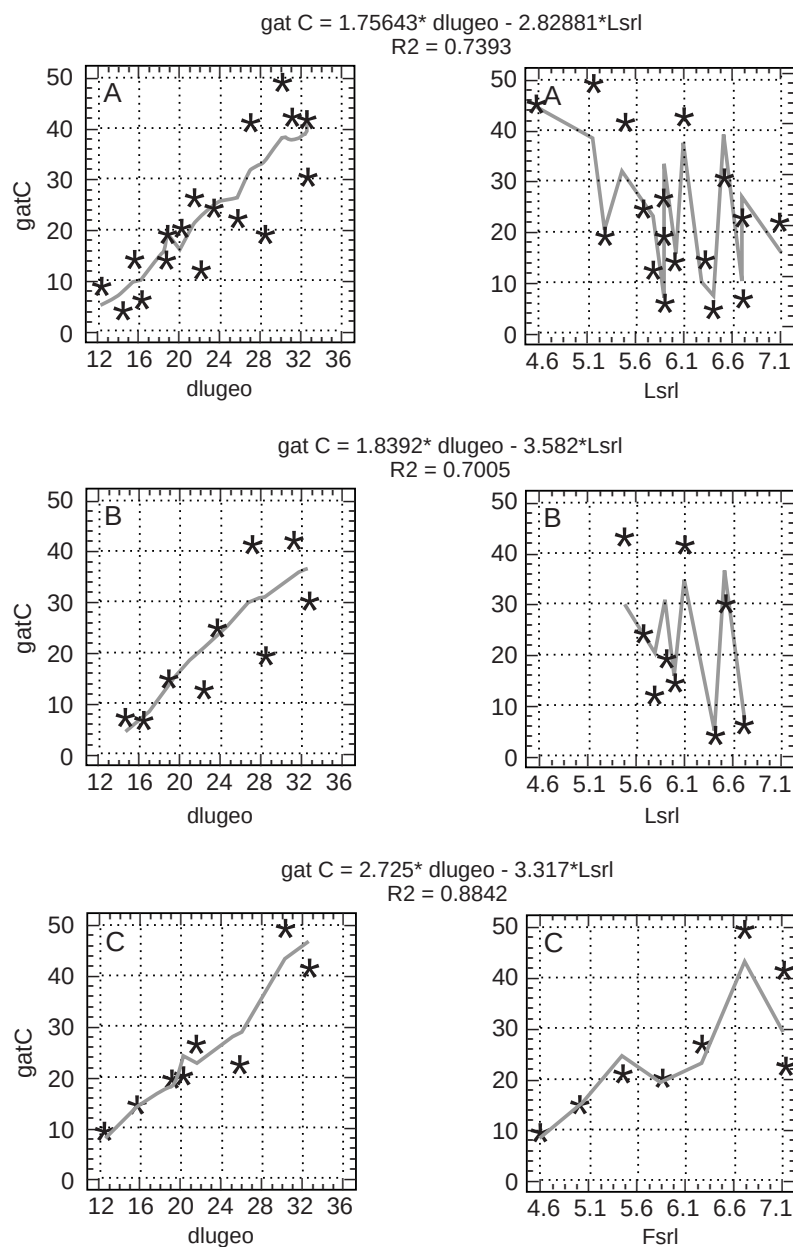


Figure 1 — Regression lines for the relationship between the number of species of the herb layer (y axis) and geographical longitude and phytoindicative indices (x axis). (A) All plots on the west-east transect; (B) pine forests on the transect; (C) mixed forests on the transect. Key: dlugeo = longitude; gat C = number of species; Lsrl = mean index for light requirements; and Fsrl = mean index for moisture requirement.

Figure 2 — Regression lines for Shannon index (y axis) on geographical longitude (x axis) according to the linear model $Y=p_1+p_2X$. (A) All plots on the west-east transect; (B) pine forests on the transect; (C) mixed forests on the transect. Dluggeo = longitude; gat C = number of species; Lsrl = mean index for light requirements; and FsrI = mean index for moisture requirement.

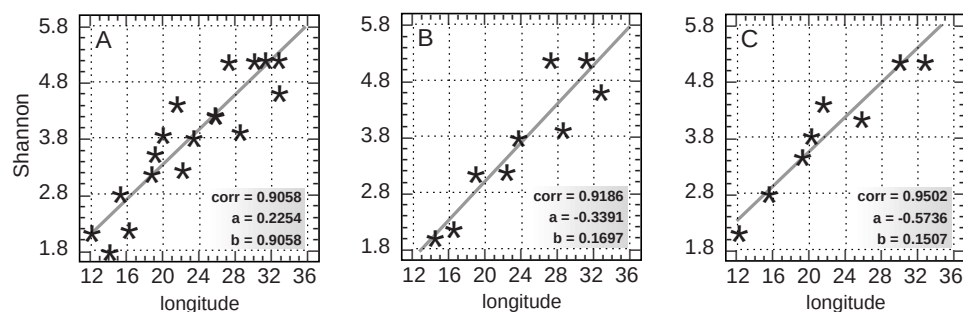


Figure 3 — Regression lines for the share in cover of overwintering green species (y axis) on geographical longitude (x axis) according to the model $Y=\exp(p_1+p_2X)$. (A) All plots on the west-east transect; (B) pine forests on the transect; (C) mixed forests on the transect.

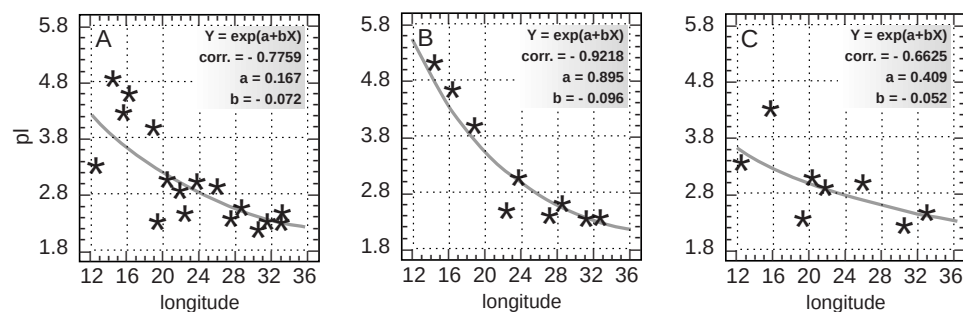


Figure 4 — Regression lines for the share of scleromorphic species (y axis) on geographical longitude (x axis) according to the model $Y=\exp(p_1+p_2X)$. (A) All plots on the west-east transect; (B) pine forests on the transect; (C) mixed forests on the transect.

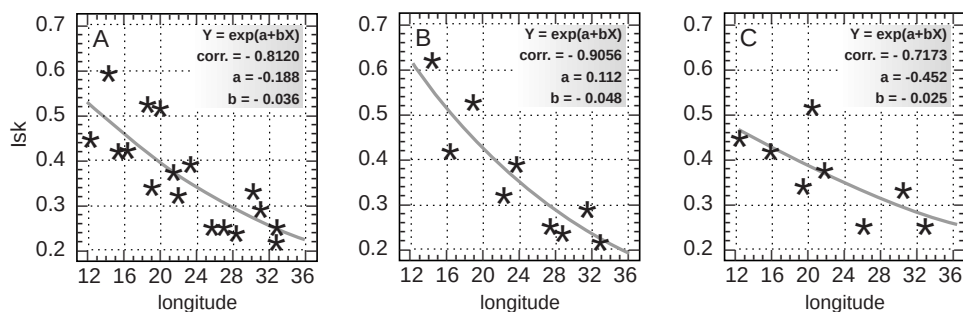
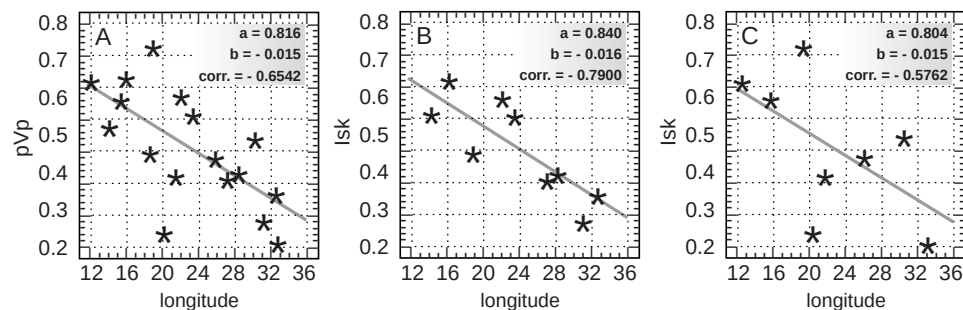


Figure 5 — Regression lines for the proportion of cover of characteristic species of the Vaccinio-Piceetea class (y axis) on geographical longitude (x axis) according to the model $Y=p_1+p_2X$. (A) All plots on the west-east transect; (B) pine forests on the transect; (C) mixed forests on the transect.



Results and Conclusions

The transect on the 52° north latitude between 12 and 33° longitude east in Poland had varying ground cover in sites with pine forest and mixed forest. From west to east we observed an increase in the total number of vascular plant species per unit area as well as in the species richness of vascular plants in both the shrub and the herb layer. However, the number of species of lichens is not correlated with longitude but is entirely determined by local habitat conditions and the degree of maturity of the phytocoenosis. An increase was also calculated in values of the Shannon diversity index and the beta index; and a simultaneous fall was found in the value of the Simpson Index. In addition, increases were determined for the value of the index of evenness HH_{max} , which attests generally to changes in the dominance structure from species poor to species rich; the number cover of species with green wintering leaves (with a simultaneous fall in the cover of evergreen species); the number of mesomorphic species (and a fall in the number of scleromorphic species); and the proportion of meadow species in the overall cover.

The results clearly confirm the assumption that within a single narrowly-defined type of forest habitat, longitude is the main factor influencing the species richness and diversity of the herb layer, as well as its ecological and phytosociological structure. In spite of this finding, the relationships obtained should be treated as first approximations of a general model linking the structural characteristics of the community with environmental conditions. According to Baker (1990), differences in species richness may only be explained on the basis of a multi-factor model; thus, with any hypothesis linking species diversity with only one factor, this has limited significance.

In the case of forest communities, the number of species in the ground layer is shaped not only under the influence of edaphic and geographic conditions, but is also dependent on the age, character, and structure of the tree stand. In particular, the character of the herb layer is often determined by the amount of solar energy reaching the forest floor (Specht and others 1990, Specht and others 1991, Specht and Specht 1993). Specht and Specht (1989b) showed that the influence of the light infiltration through the crown is different for different ecological groups of the herb layer. In particular, increased shading is associated with a linear decrease in the number of sclerophilous species. Also, the amount, time, and spatial variability of the litter fall may affect the heterogeneity and richness of the herb layer (Smith 1987). Other factors having a great influence on the richness and ecological character of the ground cover layer is the dynamic stage and level of anthropogenic impact on the forest community. It has been shown many times that mature forest communities and/or those little modified from the natural state are characterized by considerably lower proportions of annual and biennial plants when compared with early developmental stages or phytocoenoses subject to strong anthropogenic impacts (Dodge and others 1983, Dollar and others 1992, Kirby 1988, 1990, Trabaud and Lepart 1980, Trevin and others 1993, Vankat and Carson 1991). On the other hand, under moderate anthropogenic pressure overall species richness may increase (Grime 1979, Reader and others 1991).

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