

DIVERSITY PATTERN OF THE FOREST UNDERSTOREY VEGETATION IN RELATION TO SOME SITE CHARACTERISTICS

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Seloste

METSÄN PINTAKASVILLISUUDEN LAJIRUNSAUDEN SUHDE ERÄISIIN KASVUPAIKKAOTEKIÖIHIN

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A field data set representing boreal forest-floor vegetation in southern Finland was analyzed using a simultaneous equation model. The effect parameters were estimated by fitting the covariance structure implied by model specification to the sample covariance matrix. In order to describe the effects of the tree stand on the understorey vegetation, a sum variable "tree stand factor" was computed as a linear combination of the density characteristics of the tree stand by means of principal component analysis. In the model, some physical and chemical characteristics of the soil together with the tree stand factor were treated as predictors in such a way that the tree stand factor was specified to be dependent on the soil characteristics. Alpha diversity, measured as the total number of species per plot, was treated as a criterion variable. The study was undertaken with the aim to examine, whether and how the diversity pattern reflects the variation in the site characteristics.

The squared multiple correlation for the structural equation predicting the alpha diversity is 0.60 indicating that the predictors explain a considerable amount of variance in the criterion variable. The total calcium content of the soil and the mineralization rate of soil nitrogen (loss of ignition/amount of nitrogen) are the best predictors. Assuming that the incorporated soil characteristics are valid and adequate measures of the site fertility, the overall fertility has a marked independent effect on alpha diversity. On the other hand, alpha diversity appears to be essentially independent of the properties of the tree stand. Hence it is possible to use the alpha diversity as a practical tool of site classification.

In the statistical sense, the diversity pattern of boreal forest vegetation can be largely explained by edaphic variables. The model thus serves as a reasonable test of environmental hypotheses of diversity regulation. However, it seems likely that attempts to explain the diversity patterns with simple causal hypotheses are insufficient. The results obtained in this study together with observations in other situations suggest that diversity patterns appear to require more sophisticated and detailed hypotheses that take into account the complexity of organismic interactions with the environment.

1 INTRODUCTION

Patterns of species diversity are an important topic in theoretical and experimental ecology because they are determined by the basic evolutionary and ecological processes which govern the organization of an ecosystem (Pianka 1966). The concept of diversity itself is a difficult subject. Traditionally, di-

versity has two components: the number of species present (richness) and the evenness of distribution of numbers among species (Pielou 1969, Peet 1974, May 1975). MacArthur (1965) and Whittaker (1972) distinguish between "within" and "between" habitat diversity (alpha and beta diversity, the latter

being a measure of the rate of change along an environmental gradient). This study employs the alpha diversity, which is measured as the total number of plant species per plot. This is easily understood and not confounded by equitability (cf. Hurlbert 1971).

Conceptually, species diversity may be studied as the relationship of physical environmental factors to diversity or as the role of biotic processes (Ricklefs 1973). The physical environment determines the pattern of biotic interactions (see Werger & Maarel 1978). Biotic interaction induce patterns in resource partitioning which allows the coexistence of different species and is thus a proximate cause of observed species diversity. According to Richerson & Kwei-Lin Lum (1980), a complete explanation of diversity would link biotic processes and environmental variables to explain how patterns of immigration, extinction, speciation and competitive exclusion produce patterns of diversity (cf. MacArthur & Wilson 1967, Rosenzweig 1975). This study deals only with statis-

tical causal links of environment to diversity, but these relationships have implications for biotic interactions, too (cf. Tilman 1982).

The present study is based on spatial covariances between diversity, certain substantial physical and chemical factors and the properties of the tree stand. The covariance structure is analyzed by a simple simultaneous equation model (see e.g. Geraci 1976). The study was undertaken with the aim to examine how well the site factors explain the diversity pattern of the forest understorey vegetation. Theoretical implications of the findings are discussed.

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2. MATERIAL AND METHODS

2.1. Vegetation

The material consists of 106 sample plots, each 16×16 m in size, located in the districts of Lammi, Kuhmoinen and Mänttä, southern Finland (see Kuusipalo 1983). All of the sample plots represent closed forest stands on mineral soil. The material was collected in 1982. The coverage of different plant species was investigated in each sample plot. The phytosociology is explained in more detail by Kuusipalo (1983). Simple counts of the species present in each sample plot are used as a measure of alpha diversity.

2.2. Tree stand

The characteristics of the tree stand were measured in each sample plot. In this study, the total basal area (m²/ha) of the tree stand and the basal areas of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylves-*

tris L.) individuals are considered. Means and standard errors of these variables are given in Table 1. Basal area is a valid measure of the density of the tree stand (Bitterlich 1948). Both the density of the tree stand and the tree species composition affect the understorey vegetation considerably (cf. e.g. Cajander & Ilvessalo 1921, Sirén 1955). In comparison with spruce and pine, the densities of deciduous trees are very low in the study material. Practically, the low dominance of spruce implies a high dominance of pine (Kuusipalo 1983).

The tree stand characteristics are mutually connected. They form a complex of variables, the effects of which cannot be examined separately. Hence the covariance structure between the tree stand characteristics was analyzed using principal component analysis (PCA). The component scores for each observation (sample plot) were computed by using component loadings as weight coefficients. The original variables were then substituted

Table 1. Means and standard errors of the observed site characteristics.

Taulukko 1. Kasvuikäen tunnusten keskiarvot ja keskiarvot havaintoaineistossa.

Tree stand characteristics Puuston tunnuksot		Mean	Standard error
		Keskiarvo	Keskiarvhe
Total basal area Kokonaispohjapinta-ala	m ² /ha	29.8	0.7
Basal area of spruce Kuusen pohjapinta-ala	m ² /ha	19.7	1.2
Basal area of pine Männyn pohjapinta-ala	m ² /ha	8.7	1.1
Physical characteristics Fysikaaliset tunnuksot		Mean	Standard error
		Keskiarvo	Keskiarvhe
Relative proportion of soil particles below 0.06 mm, % Hienojen lajitteiden (< 0.06 mm) osuus, %		28.6	1.3
Dry weight of humus material, kg/ha Humuksen kuivapaino, kg/ha		31068	1144
Chemical characteristics (humus horizon) Kemialliset tunnuksot (humuskerros)		Mean	Standard error
		Keskiarvo	Keskiarvhe
Los of ignition/total nitrogen Hehikutushäviö/kokonaistyyppimäärä		67.8	1.1
Total content of calcium Kalsiumin kokonaismäärä	% dry humus	0.519	0.020
Total content of phosphorus Fosforin kokonaismäärä	% dry humus	0.102	0.002

by a new sum variable, which was formed as a linear combination of the original variables (Morrison 1976).

2.3. Soil

A set of soil samples was collected from each sample plot and analyzed in laboratory (for sampling procedure, see Tamminen 1982). Means and standard errors of the soil variables used in the present paper are given in Table 1. Mineral soil samples were sieved; all the material passing through a 0.06 mm sieve was included into the fine-grained fraction of the mineral soil. The relative proportion of soil particles below 0.06 mm is an

applicable variable for describing the properties of mineral soil since it correlates with e.g. field capacity and cation exchange capacity. The humus layer forms a major part of the rhizospheric horizon of the vascular plants and forms a substratum for terricolous bryophytes. In addition, it plays a decisive role in the nutritional cycles of a forest ecosystem (cf. Aaltonen 1940). The methods used in nutrient analyses are presented by Halonen & al. (1983). The C/N ratio is a commonly used index of mineralization rate of nitrogen (cf. Mengel & Kirkby 1979). In the present study, nitrogen availability was estimated by calculating the relation between organic fraction of the humus layer (loss of ignition) and total amount of nitrogen in the humus layer. Since the proportion of organic C in the humus layer is approximately constant, this index is roughly comparable with the C/N ratio. In addition to the nitrogen content, the total contents of calcium and phosphorus in the humus layer were incorporated in the model as measures of the nutrient status of the soil.

2.4. Model specification

It is assumed in the model specification that the distribution of the observed variables can be described, at least approximately, by the covariance matrix, so that information about parameters provided by moments of higher order may be ignored. In addition, it is assumed that the observed variables are, at least approximately, normally distributed. Consequently, the estimation of parameters is essentially that of fitting the covariance structure implied by the specification of parameter matrices to the sample covariance matrix (see Jöreskog 1973).

The normalities of the distributions of all incorporated variables were examined by calculating and testing the skewness and kurtosis statistics (Nie & al. 1975, p. 185). Transformations were used when needed. After that, the variables were standardized to zero mean and unit variance. The sample covariance matrix between variables was computed. The model is a simple recursive system, in which the measured characteristics of the soil and the sum variable of the tree stand characteristics, later called the tree

stand factor, are treated as predictors and the alpha diversity as a criterion variable. The soil characteristics are treated as exogenous independent (x) variables. The tree stand factor is treated as a determinative y-variable which is dependent on the x-variables, but has a specified effect on the alpha diversity (cf. Jöreskog & Sörbom 1981).

The model of diversity pattern can be expressed in matrix form as follows:

$$(1) \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} 0 & 0 \\ \beta_{21} & 0 \end{bmatrix} \begin{bmatrix} y_1 \\ y_2 \end{bmatrix} + \begin{bmatrix} \gamma_{11} & \gamma_{12} & \gamma_{13} & \gamma_{14} & \gamma_{15} \\ \gamma_{21} & \gamma_{22} & \gamma_{23} & \gamma_{24} & \gamma_{25} \end{bmatrix} \begin{bmatrix} x_1 \\ x_2 \\ x_3 \\ x_4 \\ x_5 \end{bmatrix} + \begin{bmatrix} \zeta_1 \\ \zeta_2 \end{bmatrix}$$

where y_1 is the tree stand factor, y_2 is the alpha diversity, x_1 is the relative proportion of soil particles below 0.06 mm, x_2 is the amount of humus material, x_3 is the ratio loss of ignition/N, x_4 is the content of calcium and x_5 is the content of phosphorus. The model involves three parameter matrices. **B** is sub-diagonal and its only non-zero element β_{21} represents the effect of the tree stand factor on the alpha diversity. The elements of Γ represent direct effects of exogenous (x) variables on endogenous (y) variables and ζ is a random vector of residual terms. In addition, a symmetric matrix Φ is involved, the elements of which represent correlations between the x-variables.

Consequently, the structural equations of the model (1) are

$$(2) y_1 = \gamma_{11}x_1 + \gamma_{12}x_2 + \gamma_{13}x_3 + \gamma_{14}x_4 + \gamma_{15}x_5 + \zeta_1$$

$$(3) y_2 = \beta_{21}y_1 + \gamma_{21}x_1 + \gamma_{22}x_2 + \gamma_{23}x_3 + \gamma_{24}x_4 + \gamma_{25}x_5 + \zeta_2$$

3. RESULTS

3.1. Tree stand factor

The computed principal component loadings for original variables representing the measured characteristics of the tree stand are presented in Table 2. The tree stand factor is calculated as a linear combination of the total

Unlike (2), equation (3) is not a true regression equation since the residual term ζ_2 is not uncorrelated with y_1 .

It can be seen from the model specification, that there are both direct and indirect effects of the x-variables on y_2 . The sums of direct and indirect effects are called total effects. For example, the direct effect of x_1 on y_2 is γ_{21} and the indirect effect of x_1 on y_2 via y_1 is $\gamma_{11}\beta_{21}$. The total effect of x_1 on y_2 is the sum of these effects.

2.5. Problem run

Maximum likelihood estimation of the model parameters was done with the program LISREL V (Jöreskog & Sörbom 1981). The method of maximum likelihood provides standard errors for the parameter estimates. The quotient of a parameter estimate and its standard error coincide with the t value to test whether the true parameter is zero. Parameters whose t values are larger than two in magnitude are normally judged to be different from zero (Jöreskog & Sörbom 1981). These parameters are denoted by a double asterisk (**). Parameters whose t values are larger than 1.5 in magnitude are considered nearly significant and denoted by an asterisk (*). The remaining parameters are considered weakly significant. LISREL V also provides squared multiple correlations for each structural equation. These can be interpreted as the proportion of variance explained by each equation. The coefficient of determination for the entire model is a measure of explanation power for several equations jointly (see Jöreskog & Sörbom 1981). These values are between zero and one, large values being associated with good models.

basal area of the tree stand and the basal areas of spruce and pine individuals in the stand. This latent variable is used in further comparisons instead of the original variables. It can be seen from the component loadings that high scores represent clearly spruce-dominated, dense forest stands, while low

Table 2. Principal component of the tree stand characteristics.

Taulukko 2. Puustotunnusten pääkomponenttimalli.

Correlation matrix – Korrelaatiomatriisi

	z_1	z_2	z_3	
Basal area – Pohjapinta-ala				
Pine – Mänty	z_1	1.000		
Spruce – Kuusi	z_2	-0.815	1.000	
Total – Koko puusto	z_3	-0.095	0.451	1.000

First principal component – Ensimmäinen pääkomponentti

Component loadings – Lataukset	z_1	z_2	z_3
λ_z	-0.861	0.992	0.409

scores represent pine-dominated and more open stands (cf. Kuusipalo 1983). Hence the high scores are also associated with a relatively low illumination level and with microclimatical and edaphical conditions typical of spruce stands (Aaltonen 1940, Sirén 1955, Kubin 1983).

The solution of the regression equation (2), in which the tree stand factor (y_1) is treated as a criterion variable and the soil characteristics (the x-variables) as predictors, is presented in Table 3. The squared multiple cor-

relation for this equation is 0.364 indicating a relatively low explanation power. It should be noted, that both the density of the stand and the tree species composition are dependent not only on the site fertility, but also on the age of the stand and on previous silvicultural treatments. In general, high component scores seem to be associated with high contents of nitrogen and calcium, thick layer of humus and high proportion of fine-grained particles in the soil.

3.2. Diversity pattern

The mean number of species for the whole study material is about 25, which represents the average species richness of the *Myrtillus* site type (e.g. Kujala 1961). The lowest number of species is 10, which approximately represents the species richness of the *Calluna* site type, while the maximum diversity (42) is encountered on a plot representing upland forest with rich grass-herb vegetation. The distribution of species richness is approximately normal (skewness = 0.220, kurtosis = -0.698).

The solution of the problem specified in model (1) is presented in Table 3. It can be

Table 3. Parameter estimates for the model of diversity pattern (1).

Taulukko 3. Diversiteettiä ennustavan mallin (1) parametrien estimaatit.

	B		Γ					ζ	r square
	y_1	y_2	x_1	x_2	x_3	x_4	x_5		
y_1	0.000		0.126*	0.195*	-0.479**	0.195**	-0.005	0.636**	0.364
y_2	0.076	0.000	0.134**	0.014	-282**	0.408**	-0.264**	0.405**	0.595
Total effects – Kokonaisvaikutukset									
y_2			x_1	x_2	x_3	x_4	x_5		
			0.143	0.029	-0.319	0.423	-0.265		
Φ									
	x_1	x_2	x_3	x_4	x_5				
x_1	1.000					Total coefficient of determination			
x_2	-0.132	1.000				Mallin kokonais selitysaste			
x_3	-0.168	0.290	1.000			R = 0.685			
x_4	0.240	-0.330	-0.516	1.000					
x_5	-0.059	0.572	-0.164	-0.124	1.000				

y_1 = Tree stand factor – Puustofaktori y_2 = Alpha diversity – Alfa-diversiteetti

x_1 = % soil fraction < 0.06 mm – Hienojen lajitteiden (< 0.06 mm) osuus

x_2 = Dry weight of humus – Humuksen kuivapaino x_3 = Loss of ignition/N – Hehkutushäviö/N

x_4 = Calcium content – Kalsiumpitoisuus x_5 = Phosphorus content – Fosforipitoisuus

seen from the squared multiple correlation for equation (3) that the model explains almost 60 per cent of variance in the alpha diversity indicating markedly strong relationships with the site characteristics. The effect β_{21} of the tree stand factor (y_1) on the alpha diversity (y_2) is weakly significant; neither are the total effects significantly different from the direct effects of the x-variables on y_2 (cf. Jöreskog & Sörbom 1981). Assuming that the tree stand factor describes the effects of tree stand properties on the understory vegetation accurately enough, the number of species appears to be essentially independent of shading and other environmental influences of tree canopy. It should, however, be noted that linear relationship may not thoroughly describe the behaviour of the diversity pattern in relation to the effects of the tree stand. Obviously, a low number of species may be encountered both under the severe shading of a very dense spruce canopy and in open pine stands which are mainly confined to dry, relatively unproductive forest sites. However, the soil variables evidently have a marked joint independent effect on the alpha diversity, which cannot be explained by indirect effects directly caused by the properties of the tree stand.

Among the physical characteristics of the soil, the amount of humus material (x_2) has no significant effect on the alpha diversity. This characteristic may be related to the properties of the tree stand: efficient litter production of spruce-dominated, dense tree stand affects strongly the accumulation of humus material (e.g. Kubin 1983). On the other hand, clear positive effect by the particle size distribution (x_1) indicates that the number of species is somewhat higher on soils with a relatively high proportion of soil particles below 0.06 mm. The forest soils in Finland are normally characterized by low proportion of fine-grained soil material (e.g. Aaltonen 1941). The most productive forest sites are largely confined to moraine soils with

relatively high proportion of this fraction (e.g. Viro 1947).

As far as the chemical properties of the soil are concerned, the model indicates strong causal relationships. The markedly strong positive effect of the calcium content (x_4) together with the negative effect of the ratio loss of ignition/N (x_3), the inverse of which can be regarded as an index of the mineralization rate of nitrogen, predict a considerable amount of variance in alpha diversity. These factors have been demonstrated to reflect the overall fertility of the site considerably well (e.g. Valmari 1921, Urvas & Erviö 1974). On the contrary, the content of phosphorus (x_5) has a relatively strong negative effect on alpha diversity. According to e.g. Valmari (1921), Viro (1951) and Urvas & Erviö (1974), there appears to be no positive correlation between the phosphorus content of the soil and forest site type. It has generally been assumed that even higher amounts of phosphorus are available for plants on barren forest sites since they are mainly confined to acid soils of granitic origin (cf. Valmari 1921, Mälkönen 1982). However, phosphorus is seldom a limiting resource in forest soils (cf. Mälkönen & al. 1980, see also Harper 1977, p. 337).

As can be seen from the Φ matrix of Table 3, there appears to be markedly high positive correlation between the amount of humus (x_2) and the content of phosphorus (x_5). In a thick layer of raw humus, a considerable proportion of total phosphorus is retained in dead plant material and is thus not available for exploitation by living plants (cf. Kaila 1956). The calcium content (x_4) appears to correlate strongly positively with the amount of nitrogen in organic humus material. According to e.g. Mälkönen (1982), calcium increases the mineralization rate of nitrogen. Generally, the mutual correlations among the x-variables are in accordance with previous forest soil studies carried out by e.g. Valmari (1921), Aaltonen (1941) etc.

4. DISCUSSION

The model accounts for a substantial proportion of variance in the alpha diversity. In the statistical sense, the diversity pattern of boreal forest vegetation can largely be explained by soil characteristics. However, it seems likely that attempts to explain the diversity patterns with simple causal hypotheses are inadequate (cf. Richerson & Kwei-lin Lum 1980). Some of the difficulties encountered in establishing causal mechanisms from spatial correlations are summarized by Grime (1965) and Harper (1977). One difficulty is the questionable measurability of relevant environmental factors. Some variables, e.g. mineral nutrient availability, cannot be measured reliably. On the other hand, many of the measurable variables correlating with vegetational variables are not true causes of the change; e.g., many correlations are due to the determination of environment by vegetation rather than the reciprocal relationships.

Estimation of the parameter matrices of a linear statistical model is essentially that of fitting the covariance structure implied by specification of the parameter matrices to a sample covariance matrix (see Jöreskog & Sörbom 1981). The main difficulties in this are encountered in calculating viable covariance estimates between the variables. Since the distributions of ecological variables are often skewed in opposite directions, peaked or even, and the covariance matrix would possibly not be positively definite, the analysis may lead to incorrect conclusions regarding the parameter values (Wainer & Thissen 1976). To quote Wainer & Thissen (1976), in such cases "a quick and easy approach is to assume normality and be on your merry way". In the present study, however, the normalities of the distributions were examined, although roughly, by means of skewness and kurtosis statistics.

A considerable source of error arises from the assumption of linearity of the causal relationships. Particularly when vegetational variables are considered, their responses to environmental influences are more complicated than can be described by covariance statistics (cf. Orlóci 1978, Austin 1980). If the environmental gradient is short, a linear hypothesis may, however, be plausible (Orlóci 1980). Structural equation model applied in the pre-

sent study constitutes a linear approximation of more complicated relationships, in which the deviations from linearity are included into the residual terms (cf. Jöreskog 1973, Jöreskog & Sörbom 1981).

With the above reservations, however, a multivariate linear approach provides information about mechanisms controlling the diversity patterns, which cannot be attained by means of detailed experimental studies or by a mere theoretical approach (cf. Richerson & Kwei-lin Lum 1980). According to Pianka's (1966) suggestion, appropriate observations on a limited scale are useful to help support or reject hypotheses regarding large scale features of diversity patterns.

Assuming that the contents of calcium and nitrogen and the relative proportion of fine-grained soil particles are valid and adequate measures of the site fertility (see Valmari 1921, Viro 1947 etc.), the overall fertility has a marked independent effect on alpha diversity. On the other hand, assuming that the density characteristics used in the present study describe the effect of the tree stand on understory vegetation reliably enough, alpha diversity appears to be essentially independent of the tree stand. Hence it is possible to use the alpha diversity as a criterion in practical site classification. The increase in species richness with increases in productivity is connected to the change in typical species composition of forest vegetation. Herb and grass species with a high intrinsic growth rate and, hence, a high demand of nutrients, are evidently more abundant on fertile forest sites. Less fertile sites are characteristically predominated by dwarf shrubs with economical use of mineral nutrients (cf. Bormann & Likens 1979). The more fertile the site is, the more exacting herb and grass species are able to survive. On the contrary, the number of less exacting species do not decrease correspondingly, as could be expected on the basis of the competitive exclusion principle (Hardin 1960).

According to Tilman's (1982) equilibrium theory of resource competition, each plant species has its specific optimal resource ratio which enables the species to dominate on such a microsite, the resource supply ratio of which corresponds to that of the species. He

suggested that plant community diversity should be maximal in moderately resource-poor habitats, and should decrease with either increases or decreases in resource richness. Communities with resource levels near the diversity peak should have many relatively co-dominant species, whereas more resource-rich, lower diversity communities should be dominated by a few species, with most of the species being rare. This situation results from the fact that the limiting resources of an environment are many and that species differ in their response to the combination of these resources. Enrichment with all of the limiting resources means that the biomass of the total community may increase but that all of the resources remain limiting. In the case of enrichment with all but one of the resources, the community would rapidly be driven towards dominance by the one species which is the superior competitor for the single limiting resource. An important point of the theory is that it is possible for numerous species to coexist in a spatially heterogeneous environment if the species differ in the proportion of nutrients that they require. For a given level of resource richness, increased spatial heterogeneity should lead to increased species richness, with the most marked effects in resource-poor habitats.

In the present study, it was not possible to determine environmental heterogeneity at the level of nutrient status. Some indirect conclusions may, however, be drawn. The forest floor is characterized by marked microtopographical heterogeneity. Different site patches form a mosaic of microsites, which are differentiated in terms of soil moisture, texture and structure and, hence, also in terms of nutrient status and nutrient availability (see Troedsson & Tamm 1969). On dry sites which are intrinsically poor in nutrients, too, the small-scale spatial variation is less steep than is the spatial variation on mesic sites. In other words, there exist no markedly productive microsites within dry forest sites, whereas within mesic forest sites, markedly less fertile microsites evidently occur. For example, in fertile herb and grass forests, dwarf shrubs such as *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L., as well as common forest mosses such as *Pleurozium schreberi* (Brid.) Mitt., are confined to higher microsites such as hummocks, stumps, stones etc. (cf. Kujala 1926).

On the other hand, herbs, grasses and more exacting mosses are confined mainly to lower microtopographical levels. This and still more fine-grained spatial variation may, at least partly, explain the fertility-dependent diversity pattern of forest vegetation.

The independent negative effect of the phosphorus content on species richness is surprisingly clear. Different plant species with different root formations tend to exploit soil volumes differently (Litav & Harper 1967, Ellern & al. 1970, etc.). As a result of root system differentiation, soil volumes are more completely occupied by species-rich vegetation than by species-poor vegetation. According to e.g. Mengel & Kirkby (1979), the mobility of phosphate ion is low; during a season of plant growth a phosphate ion is unlikely to move a greater distance than the diameter of a root hair. Steep depletion contours will therefore appear near to an absorbing root surface. The more completely the soil volumes are exploited by plant rootlets, the more efficiently the phosphate ions are removed from soil solution and utilized by plants. In contrast, the mobility of nitrates is high, depletion contours are less steep and the proximity of the root to the ions is less important (see also Harper 1977, p. 337). There is also a tendency towards higher primary production with the increase in species richness; herb and grass species with a high intrinsic growth rate are capable of utilizing the environmental resources more efficiently than are e.g. the dwarf shrubs. Consequently, a decline in soil phosphorus with an increase in species richness may even suggest that a greater amount of available phosphorus is retained in organic material, while the total quantity of phosphorus on a site remains unchanged (cf. Mengel & Kirkby 1979). Generally speaking, attempts to determine the site fertility simply by analyzing the nutrient contents of the soil are inadequate. In forest soil studies, much more attention has to be paid to interactions between organisms and the nutrient status of the soil (cf. Mälkönen 1974, Bormann & Likens 1979, Mengel & Kirkby 1979).

Forest growth is often limited by scarcity in nitrogen on similar sites; strong positive effects of the contents of calcium and nitrogen also imply that scarcity in them limit the occurrence of very many plant species. Only

a relatively few species with low mineral nutrient requirements, e.g. common forest dwarf shrubs and mosses, may survive on calcium- and nitrogen-poor sites. Hence, they are able to respond to the increase in available phosphorus independently of the variation in contents of calcium and nitrogen. On sites with limited supply of nitrogen and calcium but with a considerable supply of available phosphorus, they are capable of increasing their area at the expense of those species which require higher rate of calcium and nitrogen. On more fertile sites, rich grass and herb vegetation utilize soil phosphorus efficiently to a high biomass production. Consequently, the negative effect of phosphorus content on species richness may arise as a result of competitive exclusion induced by vigorous growth of a few species capable of utilizing the increase in phosphorus content indepen-

dently of the limitations in other nutrient resources.

The above interpretations are based on Tilman's (1982) theory that the resource supply ratio and the rate of small-scale spatial variation are major factors governing the occurrence and dominance of a given species and, hence also the diversity patterns. However, fitting a simple causal hypothesis to a sample covariance matrix is an insufficient approach to examine such a complex phenomena. Diversity patterns apparently require more sophisticated and detailed hypotheses that take into account the complexity of organismic interactions with the environment. Linear causal models such as presented in this study are only useful to the extent of reliability of the underlying hypotheses.

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SELOSTE

METSÄN PINTAKASVILLISUUDEN LAJIRUNSAUDEN SUHDE ERÄISIIN KASVUPAIKKATEKIJÖIHIN

Työ käsittelee metsän pintakasvillisuuden lajilukumääränä mitatun diveriteetin (alfa-diversiteetti) suhdetta eräisiin maaperän fysikaalisiin ja kemiallisiin tekijöihin sekä puuston rakenteessa ilmenevään vaihteluun. Aineisto käsittää samanpaikkaisesti suoritettua kasvillisuusanalyysit, puustomittaukset sekä maaperäanalyysit 106 metsikkönäytealalta Etelä-Suomesta. Aineiston pohjalta laskettiin tutkittujen muuttujien yhteisvaihtelua kuvaava otoskovarianssimatriisi, jonka kovarianssirakennetta tutkittiin ratkaisemalla diversiteetin riippuvuutta selittävästä muuttujista kuvaavan tilastollisen moniyhtälöllä parametreit.

Malli selittää lähes 60 prosenttia diversiteetin vaihtelusta tutkitussa aineistossa. Puuston puulajisuhteilla ja pohjapinta-alana arvioidulla tiheydellä ei havaittu olevan merkitsevää riippumatonta vaikutusta lajirunsauteen.

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teen. Parhaat selittäjät olivat humuskerroksen kalsiumpitoisuus sekä humuskerroksen orgaanisen aineksen suhde typen kokonaismäärään, joka kuvaa typen mobilisointiasustetta. Myös hienojen lajitteiden (< 0.06 mm) suhteellisella osuudella mineraalimaassa oli merkitsevä positiivinen vaikutus lajirunsauteen. Humuksen määrällä (kg/ha) ei ollut merkitsevää vaikutusta. Sen sijaan humuskerroksen fosforipitoisuudella oli selvä riippumaton negatiivinen vaikutus diversiteettiin.

Pintamaan typpi- ja kalsiumpitoisuuden sekä puuston kasvun välillä on useissa aikaisemmissa tutkimuksissa havaittu vallitsevan selvä riippuvuusuhde: mitä enemmän typpeä ja kalsiumia on maassa, sitä parempi on metsätuotteen. Samoin hienojen lajitteiden osuus mineraalimaassa kasvaa metsätuotteen parantuessa. Metsätuotteen ja maan fosforipitoisuuden välillä ei vastaavaa riippuvuutta ole. Näin ollen pintakasvillisuuden lajirunsaus

kuvastaa varsin hyvin maan tuottokykyä mitattua viljavuutta. Lajirunsautea on siten mahdollista käyttää apu-tunnusena arvioitaessa kasvupaikan boniteettia pintakasvillisuuden perusteella. Tällä saattaa olla merkitystä etenkin metsikön nuoremmassa kehitysvaiheissa, jolloin lajikoostumus ja runsausaste saattavat suuresti poiketa metsätuotteen pohjana olevista vanhan metsän kasvivyhdyskunnista.

Tulosten tarkastelussa pohdittiin resurssien tarjonnan suhteen sekä resurssien pienipiirteisen paikallisen vaihtelun merkitystä metsäkasvillisuuden diversiteettiä määrittävinä tekijöinä. Työssä esitetyn kaltaisten mallien suurin arvo on siinä, että niiden avulla voidaan laajaa aineistoon tukeutuen testata kokeellisten tutkimusten ja teoreettisten tarkastelujen pohjalta laadittuja hypoteeseja.