Structural indices for plant metapopulation studies: An example using a *Vaccinium vitis-idaea* L. metapopulation

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Two new index types, called structural indices, are introduced for plant metapopulation studies. The first index employs minimum-eigenvalue eigenvectors of the covariance matrix of ln-transformed population parameters. The second approximates constant 1 by a linear combination of log-transformed parameters. Indices are illustrated on biomass data of aboveground fractions in a *Vaccinium vitis-idaea* L. metapopulation from South Karelia. Maximum stable structural indices are proportions of leaves and stems. These indices have a lower variability than the biomass parameters but may have a higher sensitivity to the ecological conditions in a habitat.

Key words: allocations, biomass, constant regression, eigenvalue analysis, morphology, slenderness index.

Abbreviations: SI — structural index, MSI — multiplicative SI; LSI — logarithmic SI; CRLSI — constant-regression-based LSI; EVLSI — eigenvector-based LSI.

Introduction

Among the characteristics of a plant population, a particular value is vested in those remaining invariant in different ecological conditions and random environmental fluctuations. These features can be interpreted within the metapopulation concept (Hanski, 1989, Hanski & Gilpin, 1991, 1997). In this paper the metapopulation means a set of relatively isolated local populations. It forms a bridge between the local and regional levels of plant population studies (Gotelli, 1991).

Studying metapopulation morphology, the invariant characteristics can be topological and metrical. The first are, e.g. architectural parameters which describe plant branching patterns, the arrangement of shoot and root systems, etc. (Hallé, 1974, Wilson & Archer, 1979, Remphrey *et al.*, 1983, Room, 1983, Callaghan *et al.*, 1990). Architecture determines a general set of features delineating the shape, and geometrical and external structure of a plant (Ross, 1981, Anderssen, 1984).

The second type of invariants includes, among others, various allometric indices that express the interrelations of the morphometric parameters of a specimen, the change in the proportions of its various parts as a consequence of the growth or evolution (Hyxley & Teissier, 1936, Raup & Michelson, 1965). Allometry describes how the linear measurements and angles of a specimen's body with a specific architecture can change. There is no clear distinction between topological and metrical characteristics.

The present paper introduces, for the purposes of metapopulation study, a new class of indices called structural indices, solving by this the problem of finding out all the invariant generalized proportions between population parameters. We define a structural index (SI) as a non-trivial function of measurable variables, with an approximately constant value in a variety of environments, or in the metapopulation. SI can be considered either as a formula (expression) defining the value of the corresponding characteristics, or it can be the numeric value of this expression. In the present paper, both meanings are used interchangeably.

In practice SIs can be used in many ways depending on the objective of the study. First, the coefficients of the linear form of SI indicate a stable statistical relationship between the population parameters, thus reflecting some basic process or equilibrium conditions in the population. Second, SI may be rather sensitive to ecological changes in the environment of the population. We illustrate the use of SIs on a *Vaccinium vitis-idaea* L. metapopulation. As a result we establish all the stable proportions between the eight biomass parameters of the aboveground fractions of cowberry and study their dependence on the habitat, the year, and shoot density.

Construction of structural indices

General principles

Construction of SI means forming, from measured parameters, a new numerical characteristics that expresses a certain proportion that is constant (invariant) in various environments within the metapopulation. Multiplicative structural indices (MSI) are constructed by elementary algebraic operations – multiplication, division and exponentiation of the measured parameters. A simple example of an MSI is the ratio

$$\text{Leaf mass / Stem mass.} \tag{1}$$

This ratio depends on the architecture of plants in the population but the total mass of shoots does not significantly influence it, assuming that the denominator and numerator depend approximately proportionally on the total mass. For this reason, the SI (1) is in many cases considerably more stable than the measured variables ‘Leaf mass, and ‘Stem mass’.

By taking logarithms and rearranging the terms thereafter, we can transform any positive MSI into logarithmic structural index (LSI) defined as a relatively constant linear combination of ln-transformed parameters $\ln(x_i)$:

$$\Sigma c_i \ln(x_i) + c_0 \tag{2}$$

As in the case of MSI, the measurement units of the component variables do not influence LSIs except the arbitrary additive constant c_0. This implies that the variance of LSI does not involve the units of component variables. Hence, one can legitimately compare different LSIs on the basis of their variance to find the most constant one. There is no restriction on combining various original parameters with different biological or physical meaning in a single LSI.

Construction of logarithmic structural indices by the eigenvalue method

We propose two methods for finding the theoretically most stable LSIs. The first method is based on the fact that if the variables are strongly correlated, some eigenvalues of the data covariance matrix are close to zero (Rao, 1973). This implies that the data scatter ellipsoid can be approximated by a plane which defines a nearly constant linear form.

In terms of the algebraic eigenvalue analysis, suppose we have found eigenvector $v = (v_1,...,v_p)$ of the empirical covariance matrix of ln-transformed population parameters $\ln(x_i)$ and vector v is normed as

$$\Sigma (v_i)^2 = 1. \tag{3}$$

Then the linear combination

$$\Sigma v_i \ln(x_i) \tag{4}$$

is eigenvector-based LSI (shortly EVLSI), assumed that eigenvalue σ^2 corresponding to eigenvector v is relatively small (minimal, for example). Since the variance of LSI (4) equals to σ^2, EVLSI has a small variance compared to all the possible normed linear combinations of logarithmic variables $\ln(x_i)$.

Note that several multivariate statistical techniques, such as principal component analysis and factor analysis, widely used in vegetation science for ordination purposes (e.g. Kent & Coker, 1992, Jongman *et al.*, 1995), focus on the most variable linear combinations of the measured variables. Considering our objective, we are on the contrary interested in the most stable linear combinations.

In real data, several (say k) small eigenvalues may exist. This means that k independent LSIs exist for the same set of data variables. Mathematically, the k LSIs define a k-dimensional subspace in the space of all variables. In this subspace, any normed vector defines an LSI. The freedom in choosing this vector may be used to optimize LSI in some way. We have applied this approach to the two-dimensional subspace of two best EVLSIs. The corresponding EVLSI $E^{\#}$ has a maximal sensitivity to the habitat factor.

As a rule, optimal EVLSIs and their MSI analogues do not have a simple interpretation. Fortunately, in many cases, particularly in *Vaccinium vitis-idaea* biomass data, a slight change in the LSI coefficients produces rather good SIs that benefit from both clear interpretation and almost optimal (minimal) variance. We have called the SIs of this type modified SIs and denote them by M.

Construction of logarithmic structural indices by the constant regression method

The second construction of LSIs is based on constant regression analysis (Möls, 1985, 1986). In this analysis, a given numeric non-zero constant (usually 1) is approximated by a linear combination of ln-transformed variables:

$$1 \approx \sum c_i \ln(x_i). \qquad (5)$$

Coefficients c_i can be fitted by ordinary least squares routine. Note that in a standard regression-analysis setup, the left-side term in (5) is a random variable, while regressors $\ln(x_i)$ are fixed and do not have measurement errors (Seber, 1977). In the constant regression analysis, on the contrary, the regressors are considered as random variables, and the left-side term is a positive constant. We call the LSI (5) a constant-regression-based LSI (shortly CRLSI).

In accordance with its definition, LSI must be as constant as possible. However, the variance of an LSI depends on the norming of coefficients c_i and is therefore not an inappropriate measure of constancy. This is especially important when comparing CRLSIs with EVLSIs. In general, a correct way to compare different LSIs is to compare their relative variances defined as

$$\text{relative variance of LSI} = (\text{variance of LSI})/ \sum c_i^2. \qquad (6)$$

LSIs with smaller relative variance are preferred. EVLSIs always have a minimum relative variance and, in particular, a smaller relative variance than the analogous CRLSIs.

Material and methods

Area

The *Vaccinium vitis-idaea* data were gleaned in the Kivach Nature Reserve (33°55' E, 62°40' N), South Karelia, Russia. Long but relatively mild winters and short cool summers are typical of the area. The period with daily mean temperatures of +5° C and above lasts for about 145-155 days. Precipitation is 200-250 mm over the summer period and 550-600 mm over the whole year. The duration of the snow cover is 165-175 days, and its mean thickness is 30-45 cm (Agroclimatic handbook of Karelian A.S.S.R., 1959). Biogeographically the territory lies in the middle taiga subzone in the Zaonezhsky region (Cinzerling, 1934).

Sampling methods and data

Vaccinium vitis-idaea is found in nearly all the habitats of the nature reserve considered here as a metapopulation. Study populations (called also sample plots) were situated in the south-eastern part of the territory, on a fluvioglacial undulating plain. The tree layer consists mainly of *Pinus sylvestris* L. or *Pinus sylvestris* mixed with *Picea abies* (L.) Karst.

Sample plots Nos. 1-8 were all situated on an alluvial sandy podzol, plot No.9 lay on peaty soil and plot No.10 on a clayey loam podzol (Table 1). The configuration of sample plots corresponded to the natural boundaries of

Table 1. Main characteristics of the sample plots. A – age (years), H – height (m), D – density, C% – *Vaccinium vitis-idaea* projective cover (%).

Forest type and topography	Tree stand			C %	Study years
	A	H	D		
1. *Cladina-Calluna-Vaccinium*-type pinewood on a flat plain	35	10.0	0.5	27	1977
2. *Pleurozium-Calluna-Vaccinium*-type pinewood on a slope of northerly exposition of 2-3°	42	14.5	0.6	20	1977
3. *Cladina-Vaccinium-Calluna*-type pinewood on a flat plain	65	17.5	0.6	12	1977
4. *Pleurozium-Vaccinium*-type pinewood on a flat plain	130	23.0	0.6	35	1976-1978
5. *Pleurozium-Vaccinium*-type pinewood on a flat plain	130	23.0	0.6	36	1976-1978
6. *Pleurozium-Myrtillus-Vaccinium*-type pinewood on a flat plain	132	27.0	0.6	29	1977
7. *Pleurozium-Vaccinium*-type pinewood on the gently undulating foot of an esker	137	21.5	0.7	24	1977
8. *Pleurozium-Vaccinium*-type pinewood on a slope of southerly exposition of 3-4°	142	24.0	0.8	41	1977
9. *Sphagnum-Ledum*-type pinewood on the edge of a raised pine bog	140	24.0	0.8	15	1976-1978
10. *Polytrichum*-type mixed pine-spruce forest on the flat bottom of a hollow	176	21.0	1.0	32	1976-1978

Vaccinium vitis-idaea populations; therefore their sizes were unequal, from 0.5 to 2.0 ha. Sample plots Nos. 4, 5, 9 and 10 were studied during three consecutive years (1976-1978), while all others only in 1977.

In each sample plot a random set of at least 80 quadrates (subplots) of size 0.25×0.25 m was laid out. The aboveground parts of each separate ramet of *Vaccinium vitis-idaea* were cut at the soil surface at the end of September and weighed in their fresh condition. Four fractions were separated from the shoots: leaves and stems of the current year increment (*cl* and *cs*, respectively), leaves and stem parts of previous years (*ol* and *os*, respectively). The sum of the current year increments (*c*), the sum of the older parts of shoots (*o*), and also the total biomass of leaves (*l*) and stems (*s*) were calculated from these data for each subplot and thereafter ln-transformed. Moreover, the number of shoots in each subplot was counted at the time of weighing. As a result, a ten-dimensional multivariate data set was formed (Table 2).

Table 2. Variables measured in subplots of *Vaccinium vitis-idaea* populations.

Variable	Denotation	Comments
Biomass of current-year leaves	*cl*	ln of weight
Biomass of current-year stem parts	*cs*	ln of weight
Biomass of older leaves	*ol*	ln of weight
Biomass of older stem parts	*os*	ln of weight
Biomass of all current-year parts	*c*	from *cl* and *cs*
Biomass of all older parts	*o*	from *ol* and *os*
Leaf biomass	*l*	from *cl* and *ol*
Stem biomass	*s*	from *cs* and *os*
Total biomass of aboveground parts	*b*	from *c* and *o*
Number of shoots in subplot		counted

Data processing

All the quadrates having some biomass fraction equal to zero, and also those with significantly outlying values having a Studentized residual for the constant regression model $1 = \alpha_1 cl + \alpha_2 cs + \alpha_3 ol + \alpha_4 os$ greater than 2.6, were filtered out from the data. After this revision records of 1416 subplots remain in the data.

Data processing was mainly realized by the SAS procedures SAS/PRINCOMP and SAS/GLM (SAS Institute Inc., 1996). Various LSIs for different sets of mathematically independent biomass variables were studied using both the eigenvalue method and the constant regression method. Additionally, the two best EVLSIs for the full set of independent variables {*cl*, *cs*, *ol*, *os*} were combined, with the help of GLM/MANOVA/CANONICAL option, into a single 'combined' LSI $E^{\#}$ having the highest F-value in respect to the factor 'population' (or 'habitat', or 'plot'). Modified LSIs were established where appropriate.

The sensitivity of LSIs relatively to ecological factors was evaluated by F-statistic, calculated from ANOVA with the LSI as the dependent variable and populations (sample plots) as the levels of a fixed-type factor 'Plot'.

The EVLSIs were also calculated after the influence of shoot density on the biomass fractions had been eliminated (for the CRLSIs this modification is not applicable).

Results

Optimal logarithmic structural indices for the Vaccinium vitis-idaea L. metapopulation

The most useful and interesting LSIs for different sets of population parameters (variables) are given in Table 3. Here we argue that Table 3 exhausts all the optimal or suboptimal LSIs. We proceed with EVLSIs only, the argumentation for CRLSIs is similar.

Let us first look at EVLSIs constructed from the variables *cl* and *cs*. The relative variance of $E_{cl,cs}$ based solely on these variables is 0.0652 (Table 3). If we include additional variables *ol* and *os*, the variance of LSI will decrease, as it should, but only to 0.0595 (cf. $E_{cl,cs,ol,os}$ in Table 3). Analogically, inclusion of *o* will reduce the variance only from 0.0652 to 0.0622 (cf. $E_{cl,cs,o}$). Those indices exhaust all the possible refinements of $E_{cl,cs}$ since the simultaneous inclusion of mathematically interdependent variables (e.g. the triplet *ol*, *os* and *o*) would not be correct. Consequently, $E_{cl,cs}$ cannot be significantly improved by expanding its base set of variables.

Table 3. Optimal LSIs for the *Vaccinium vitis-idaea* metapopulation. E and R stand for EVLSI and CRLSI, respectively. M denotes modified versions of these indices (see text). $E^{\#}$ is the F-maximizing (in respect to factor 'Plot') linear combination of the two best EVLSIs. Subscripts refer to biomass variables used in the LSI. Relative variance is calculated across all subplots and years using Formula (6).

LSI	Expression for calculation	Relative variance
$E_{cl,cs,ol,os}$	$0.651cl - 0.718cs - 0.211ol + 0.129os$	0.0595
$E^{\#}_{cl,cs,ol,os}$	$0.375cl - 0.442cs + 0.549ol - 0.602os$	0.1119
$R_{cl,cs,ol,os}$	$0.551cl - 0.737cs + 0.116ol - 0.074os$	0.0681
$E_{cl,cs,o}$	$0.675cl - 0.730cs - 0.106o$	0.0622
$E_{cl,cs}$	$0.623cl - 0.783cs$	0.0652
$R_{cl,cs}$	$0.628cl - 0.785cs$	0.0708
$M_{cl,cs}$	$0.707cl - 0.707cs$	0.0827
$E_{l,s}$	$0.685l - 0.729s$	0.0618
$R_{l,s}$	$0.912l - 0.774s$	0.0808
$M_{l,s}$	$0.707l - 0.707s$	0.0634

Starting next with parameters *ol* and *os*, we get new EVLSIs $E_{ol,os}$ and $E_{c,ol,os}$. Indices of this series have a relative variance over 0.1 and are in that way inferior to $E_{cl,cs}$. For this reason they are not presented in Table 3. The same is true for the sets of variables $\{cl, os\}$, $\{ol, cs\}$, $\{cl, ol\}$, and $\{cs, os\}$.

The last pair of parameters appropriate for constructing LSI is $\{l, s\}$, a combination to which no other variables can be supplemented because of mutual mathematical dependence. The corresponding LSI $E_{l,s}$ is at least as good as $E_{cl,cs}$ (Table 3).

From the preceding results we see that if LSI contains variables *cl* and *cs*, or, alternatively, variables *l* and *s*, all other mathematically independent variables do not significantly contribute to the constancy of LSI. Less stable are LSIs based on *ol* and *os* only.

As seen from Table 3, the optimal non-logarithmic (or MSI) version of $E_{cl,cs,ol,os}$ based on old and new leaves and stems is

$$MSI_{cl,cs,ol,os} = (os^{0.129}\, cl^{0.651})/(ol^{0.211}\, cs^{0.718}). \qquad (7)$$

This MSI can be modified as follows:

$$MSI_{cl,cs,ol,os} = (os^{0.0}\, cl^{0.7071})/(ol^{0.0}\, cs^{0.7071}) = (cl/cs)^{0.7071}, \qquad (8)$$

where the exponents ±0.7071 relate to the norming condition (3): $0.7071^2 + (-0.7071)^2 = 1$. In Table 3, the logarithmic (LSI) version of this modified index is denoted by $M_{cl,cs}$. It expresses essentially the ratio of 'Mass of the current-year leaves' to 'Mass of the current-year stems'; $M_{cl,cs}$ serves also as a modified version for some other LSIs, in particular for $E_{cl,cs}$ and $E_{cl,cs,o}$.

From the above results we can see that the theoretically most stable proportions in *Vaccinium vitis-idaea* aboveground fractions are 'Mass of the current-year leaves' /' Mass of the current-year stems' and 'Mass of all leaves'/'Mass of all stems'.

Dependence of logarithmic structural indices on habitat

The *Vaccinium vitis-idaea* metapopulation data have been partitioned by discrete factors 'Plot' (population or habitat) with 10 levels, 'Year' with 3 levels, and the continuous factor 'Density of shoots'. A total of 18 combinations of the two discrete factors are presented in the data. These factors describe the environmental heterogeneity of subplots studied.

To evaluate the influence of habitat on population parameters, LSIs in Table 3 were calculated for each subplot, and the resulting LSI values were subsequently analysed by ANOVA. The effect of year was eliminated by considering only the measurements made in 1977. The mean values of different LSIs for all the studied populations are given in Table 4. Table 5 summarises results from one-way ANOVA with fixed-type factor 'Plot' for 'Year' = 1977 data subarray. All indices, as well as the original variables, depend significantly on the habitat ('Plot') of the *Vaccinium vitis-idaea* population.

Here a question arises: how sensitive are LSIs when used for distinguishing habitats? Measuring the ecological sensitivity of an LSI by F-statistic, it follows from Table 5 that some LSIs are more sensitive to the habitat

Table 4. The mean values of some LSIs in 1977. N is the number of subplots in a sample plot. Standard error is ±0.03 for the plot mean values and ±0.01 for the total mean values

Sample plot	N	$E_{cl,cs,ol,os}$	$E^{\#}_{cl,cs,ol,os}$	$E_{l,s}$	$R_{l,s}$	$M_{l,s}$
1	90	0.76	0.72	0.44	0.75	0.49
2	86	0.71	0.40	0.20	0.45	0.25
3	89	0.74	0.92	0.58	0.83	0.61
4	97	0.76	0.96	0.64	1.03	0.70
5	92	0.80	1.01	0.67	1.05	0.73
6	89	0.68	0.76	0.49	0.75	0.53
7	91	0.85	0.91	0.59	0.89	0.63
8	90	0.82	0.80	0.47	0.89	0.55
9	74	0.75	0.82	0.54	0.72	0.56
10	86	0.68	0.68	0.46	0.78	0.52
All	884	0.76	0.80	0.51	0.82	0.56

Table 5. Main statistics of ln-transformed biomass variables and LSIs for the 1977 data: results of one-way ANOVA with factor 'Plot'. Residual variance has 874 degrees of freedom. F-statistic for the null hypothesis 'Plot has no effect' measures the sensitivity of the variable or LSI to differences in habitats. Number of shoots in subplot is not eliminated.

Variable or LSI	Mean value	Residual variance	F
o	1.386	0.804	18.3
ol	0.895	0.891	18.1
os	0.375	0.811	18.9
c	0.886	0.642	17.0
cl	0.632	0.748	17.0
cs	0.675	0.477	15.6
l	1.507	0.696	17.9
s	0.715	0.603	18.6
b	1.893	0.638	17.9
$E_{cl,cs,ol,os}$	0.756	0.052	5.5
$E^{\#}_{cl,cs,ol,os}$	0.801	0.077	35.7
$E_{cl,cs,o}$	0.773	0.051	11.1
$E_{cl,cs}$	0.923	0.053	13.6
$E_{l,s}$	0.511	0.041	38.3
$R_{cl,cs,ol,os}$	0.922	0.050	19.3
$R_{cl,cs}$	0.926	0.053	13.7
$R_{l,s}$	0.821	0.084	31.4
$M_{cl,cs}$	0.925	0.069	15.6
$M_{l,s}$	0.560	0.043	37.2

factor 'Plot' than any of the observed biomass variables. Indices $E_{l,s}$ and $M_{l,s}$ are particularly sensitive. Combined index $E^{\#}_{cl,cs,ol,os}$ also has a high sensitivity but this is because it has been especially designed for detecting differences in habitats.

Consequently, the *Vaccinium vitis-idaea* leaves-and-stem data do not enable the LSIs which eliminate the influence of the environment.

Dependence of logarithmic structural indices on year

Dependence of LSIs on year was tested in plots 4, 5, 9, and 10 where observations were carried out during all three years (Table 1). Results of ANOVA for this data subarray with factors 'Year' and 'Plot' are given in Table 6. A significant interaction between 'Year' and 'Plot' shows that yearly fluctuations in different habitats are not exactly synchronous.

Table 6. The least squares means* and P-values of some LSIs. Superscripts ^{7} and ^{8} mark significant differences from years 1977 and 1978, respectively.

LSI	Least squares means			P-values of effects	
	1996	1997	1998	'Year'	'Plot×Year'
$E_{cl,cs,ol,os}$	0.74	0.75	0.72	0.3191	0.0039
$E^{\#}_{cl,cs,ol,os}$	$1.00^{7,8}$	0.87	0.88	0.0000	0.0000
$E_{l,s}$	$0.69^{7,8}$	0.58	0.55	0.0000	0.0000
$R_{l,s}$	$1.04^{7,8}$	0.91	0.85	0.0000	0.0000
$M_{l,s}$	$0.74^{7,8}$	0.63	0.59	0.0000	0.0000

* *The least squares means* is a specific term in statistics. It refers to mean values calculated by using linear models in analysis of variance.

Dependence of logarithmic structural indices on shoot density

The influence of shoot density on the proportions of different biomass fractions was evaluated in two ways. First, the coefficients of an LSI in Table 3 were compared with those calculated after the shoot density was eliminated by partialling out the variable 'Number of shoots in the subplot' in the SAS/PRINCOMP procedure. As a result, we can conclude that the coefficients of EVLSIs for *Vaccinium vitis-idaea* aboveground biomass fractions do not practically depend on the density of shoots. For example, $E_{cl,cs,ol,os}$ (Table 3) changes, after the elimination of shoot density, to

$$E_{cl,cs,ol,os} = 0.643cl - 0.726cs - 0.215ol + 0.120os\,, \quad (9)$$

and its variance changes only from 0.0595 to 0.0592. The angle between the vectors of coefficients is 0.86 degrees. The angles for indices $E_{cl,cs,o}$, $E_{cl,cs}$, and $E_{l,s}$ are 1.34, 0.25 and 0.16 degrees, respectively, the variances being practically equal.

The shoot density effect was also evaluated by ANOVA with explanatory variables 'Plot' (random factor), 'Year', and 'Number of shoots in subplot'. This analysis has demonstrated that, in addition to other factors, LSIs also depend on shoot density but the dependence is extremely weak (the determination coefficient R^2 is less than 0.03). Table 7 represents some details of the related analysis. Figure 1 graphically illustrates the dependence of $E_{l,s}$ on the number of shoots in subplot.

Table 7. F-statistics related with the null hypothesis 'Density of shoots has no effect' (4 and 4111 degrees of freedom, the effect of habitat and year.eliminated) for the basic parameters and for LSIs with a low F value.

Variable	F	Variable	F
cl	909	$E_{cl,cs,ol,os}$	5.23
cs	762	$E_{l,s}$	4.04
ol	736	$R_{cl,cs,ol,os}$	12.28
os	728	$M_{l,s}$	15.2

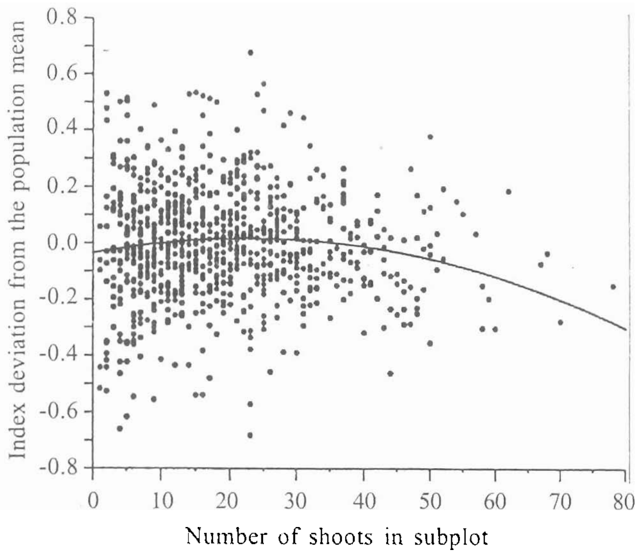

Fig. 1. Scatter plot and the second-order regression line of index $E_{l,s}$ as depending on the shoot density

Interpretation of logarithmic structural indices

The slenderness indices

In accordance with its definition, index $M_{l,s}$ (Table 3) characterizes the mass of leaves integrated with a unit mass of stems. Therefore this index will be called 'the slenderness index', its low value meaning more slender ramets in the population. Besides $M_{l,s}$, the slenderness of shoots can also be expressed by indices $E_{l,s}$ and $R_{l,s}$ which were constructed from the same biomass variables l and s.

A comparison of all the ten sample plots (Table 4) has demonstrated that plots 4 and 5 have high $M_{l,s}$ values (about 0.7), plots 1, 3, 6, 7, 8, 9, and 10 have medium index values (about 0.5 - 0.6), and plot 2 has a very low index 0.25. The Bonferroni-corrected comparison test has shown that plots 4 and 5 are significantly ($p < 0.01$) distinct from the other plots, and so is plot 2. A similar pattern of differences between plots has been demonstrated by indices $E_{cl,cs}$, $M_{cl,cs}$ and $R_{cl,cs}$ expressing the proportion of new leaves and new stems.

Figure 2 visualizes the dependence of $M_{l,s}$ on sample plots even more dynamically. The index distribution in plots 1 and 2 is clearly left-shifted while in plots 4 and 5 it is right-shifted. Sorting the plots by median (i.e. index value corresponding to the y-axis value of 0.5) groups the plots as {2}, {1}, {3, 6, 7, 8, 9, 10}, and {4, 5}. This ordering method is not influenced by suspect extreme index values in some subplots. Consequently, it is more 'robust' than the ordering achieved by using mean values. In the case of $M_{l,s}$, both orderings coincide.

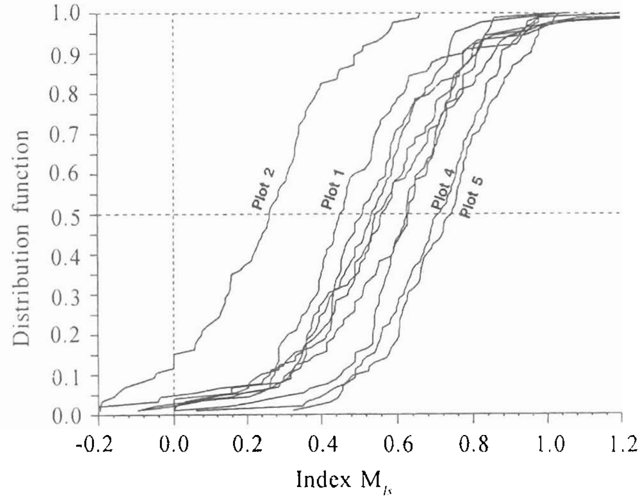

Fig. 2. Cumulative distribution functions of slenderness index $M_{l,s}$ for sample plots

It can be conjectured that the slenderness indices discovered in *Vaccinium vitis-idaea* aboveground biomass data are related to light conditions in the habitat. On plot 2, and also on plot 1, the tree stand was young and closed (Table 1), with low light incidence on undergrowth as compared to other plots. As a result, the ratio of *Vaccinium vitis-idaea* leaf to stem biomass was relatively low. On the other hand, plots 4 and 5, where the field and bottom layers received more light, have the highest index values. The same tendency can be followed in Figure 1 where the subplots with a high shoot density have, on average, a lower index value.

The main invariant

The most stable LSI, with respect to factors 'Year', 'Plot', 'Year×Plot', and 'Shoot density', is index $E_{cl,cs,ol,os}$ which has a low F-statistic value (or high P-value) for all these factors (cf. Tables 5, 6, and 7). Motivated by this, we call $E_{cl,cs,ol,os}$ 'The main invariant'.

To reveal the meaning of $E_{cl,cs,ol,os}$, we write its expression (cf. Table 3) in the following form:

$$E_{cl,cs,ol,os} = (0.651cl - 0.718cs) + (0.129os - 0.211ol). \quad (10)$$

As in the slenderness index, the dominating term here is $0.651cl - 0.718cs$ which can be interpreted as a specific proportion of new leaves and new stems. In some subplots however, a downfall of leaves may essentially decrease this term and, hence, the whole index. Assuming that the downfall of new leaves is correlated with the downfall of older leaves, the variability of the index can be reduced adding a compensation term, $0.129os - 0.211ol$, that increases in the case of leaf downfall. From the above discussion we see that $E_{cl,cs,ol,os}$ can be interpreted as the slenderness index corrected against an increased downfall of leaves.

Discussion

SIs are metrical invariants but express a structural relationship more general than allometric relationships. Allometry mainly describes changes in specimens' shape and size during the growth or evolution, while SIs describe constancy in the variability of sample units, e.g. in subplots. Allometry, at least in its initial sense (Hyxley & Teissier, 1936), is purely morphometric, whereas SIs describe morphometric parameters together with variables such as the 'Number of shoots' or 'Biomass of last-year leaves'. Allometry deals, as a rule, with a relatively small number of variables while SIs tend to take into account as many variables as possible. Moreover, in allometry independent and dependent parameters should be fixed before data processing, while for SIs all parameters are considered as functionally equivalent.

The two statistical methods proposed in this paper for constructing optimal structural indices have performed well in the case of *Vaccinium vitis-idaea* data. They provide clear insight into the multivariate structure of the measured parameters. This encourages us to recommend these methods for studying other populations and data sets as well.

For a plant ecologist, it may be difficult to decide which method to prefer. One might favour CRLSIs due to their easy construction by a simple multiple regression analysis routine, and because of a better scale with a fixed standard value (equal to 1). On the other hand, EVLSIs may seem more natural for those experienced in principal component analysis. CRLSIs have a larger relative variance than EVLSIs but, at least for *Vaccinium vitis-idaea* aboveground biomass data, both methods give similar results. Nevertheless, they are not directly comparable since the coefficients of CRLSI are not normed.

In accordance with the general definition, every LSI characterizes some specific structural relationship between population parameters that is held approximately constant throughout the whole metapopulation. In the case of EVLSIs, the exact meaning of this is that LSI has a minimal variance over the whole metapopulation, and possibly over time. Analogously, CRLSI is closest to the constant 1 across all populations. This invariance is a mathematical formulation of a natural requirement that LSI must characterize a metapopulation as a whole. The existence of SIs for a given set of variables in a given metapopulation, although established by mathematical means, should be regarded as a biological phenomenon. Table 3 shows that the studied *Vaccinium vitis-idaea* metapopulation enables rather good LSIs for aboveground biomass parameters.

It is obvious and important that an SI of a plant population can have (if ever) a nearly constant value only within a given range of living conditions. The aim of conditioning the SI definition to a certain ecological range is to link the variety of populations regarded as a metapopulation with the same SI. Outside this specific range, even the most stable SI may change significantly.

On the other hand, SI having a low variability within the metapopulation may exhibit clear and statistically significant differences between populations. In particular, *Vaccinium vitis-idaea* leaf-and-stem data do not enable LSIs that are free from the influence of the habitat. On the contrary, LSIs for the studied metapopulation have even a higher statistical sensitivity to environmental conditions than the original parameters. Low variability (residual variance) within ecologically homogeneous habitats but a clear response to differences in habitats play the key role here. It must be noted, however, that other mathematical methods apply more directly for building indices with maximal ecological sensitivity (e.g. canonical analysis in SAS GLM, and the discriminant analysis). With some limitations, the first method mentioned is realized in constructing $E^*_{cl,cs,ol,os}$.

Statistical analysis of nine biomass parameters in the *Vaccinium vitis-idaea* metapopulation has demonstrated that, among all the possible two-parameter or multi-parameter functions, the SIs 'Mass of all leaves'/ 'Mass of all stems' and 'Mass of the last-year leaves'/ 'Mass of the last-year stems' are close to the theoretically most stable indices for this metapopulation. In particular, these simple indices are considerably more stable than the original aboveground biomass parameters (cf. Residual variance in Table 5). This fact may be interpreted as an evidence that a *Vaccinium vitis-idaea* ramet, independent of its habitat, has on average a constant proportion of leaves attached to stems.

Proportions between the biomass of old leaves' and stems' are less stable probably due to the damage to overwintering leaves. Although the snow cover during all the years of the experiment was deep enough (24 - 49 cm) to prevent frost damages, on May 3, 1976 when the sample areas were almost free from snow, the temperature fell to -8.9° C. On May 6, 1978 the temperature was -7.1° C. Such frost can damage and cause the downfall of overwintered leaves, while stems are more resistant. The amount of lost leaves can greatly differ not only in detached populations but also within the same population due to differences in the microenvironment (Raatikainen & Vänninen, 1988). The increased variability of the proportion of old leaves can also explain the significant effect of factor 'Year' on indices $E_{l,s}$, $R_{l,s}$, and $M_{l,s}$ (Table 6).

Vaccinium vitis-idaea is a half-shadow species (Landolt, 1977, Frank *et al.*, 1988) and adjusts itself to shading with the allocation of more resources to stems and, consequently, with the elongation of the stem like shadow-intolerant species (Pickett & Kempf, 1980, Bloom *et al.*, 1985). Changes of the allocation pattern in the metapopulation subunits also cause changes in LSIs. If the constant in (5) equals 1, coefficients c_i will ensure that CRLSI has on average a value close to 1. Those populations having a significantly lower or, on the contrary, a significantly higher index value must be considered as non-typical for the given metapopulation, while in 'normal' populations CRLSI is slightly less than 1. Close to normal are, for instance, populations 1, 3, and 6 – 10 (Table 4). Populations 4 and 5, growing in the best conditions for *Vaccinium vitis-idaea*, have non-typically high index values, while plot 1 has a minimal index value.

Significant dependence of LSIs on time could be explained by weather conditions. The current-year biomass values are influenced by the weather in the growth period of *Vaccinium vitis-idaea* shoots, while for the old parts of ramets, winter and early spring are crucial, as Havas (1966) and Raatikainen and Vänninen (1988) have demonstrated. The vegetation periods during the study years were rather different. June 1977 was very poor in precipitation compared to 1976. Intensive apical growth of stems began one week earlier in 1977 (on June, 6 and June, 14, respectively) and lasted 2-3 weeks longer than in the previous year (up to July, 17–25). In 1978, May and the first half of July were very dry. Intensive growth started on June, 14–21 and lasted until August, 1–9 (Paal & Paal 1989).

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СТРУКТУРНЫЕ ИНДЕКСЫ ДЛЯ ИССЛЕДОВАНИЯ МЕТАПОПУЛЯЦИЙ НА ПРИМЕРЕ МЕТАПОПУЛЯЦИИ *VACCINIUM VITIS-IDAEA* L.

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Резюме

Для исследования метапопуляций растений предлагаются два индекса нового типа, названные структурными индексами. Первый из них базируется на использовании собственных векторов ковариационной матрицы логарифмически трансформированных параметров популяции. Индексы второго типа аппроксимируют, в смысле наименьших квадратов, константу 1, используя линейную комбинацию логарифмически трансформированных параметров. Применение структурных индексов продемонстрировано на данных биомассы надземных фракций популяций брусники, собранных из разных биотопов в южной Карелии (Россия). Самые стабильные структурные индексы характеризуют пропорции биомассы листьев и стеблей. С одной стороны, эти индексы варьируют значительно меньше, чем исходные данные биомассы, с другой стороны, они являются более чувствительными относительно экологических условий местообитания.

Ключевые слова: аллокация, биомасса, константная регрессия, анализ собственных значений, морфология