

The significance of different indices for stand structure and diversity in forests

Markus Neumann^{*}, Franz Starlinger

Forstliche Bundesversuchsanstalt Wien, A 1131 Vienna, Austria

Abstract

Data from the so-called Level II Plots which were established within the frame of the Pan-European Programme for Intensive and Continuous Monitoring of Forest Ecosystems were used to quantify stand structure and species diversity by means of different indices. The calculations presented are based on species composition, spatial pattern as well as diameter and height distribution.

The data assessed are suitable to calculate different measures of structural diversity, if a mapping of the stands is carried out. A comparison of the different indices by means of correlation analysis shows that there exist only few and weak correlations between species diversity of different vegetation layers, and between plant species diversity and diversity of stand structure, while among all the indices of stand structure a correlation exists. More complex indices of stand diversity perform quite well in characterising the specific situation. Mountain forests are compared with forests from lower elevations. They show a tendency towards irregular stand structures.

No correlation between the naturalness of tree species composition and the calculated diversity indices can be found within the sample. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Biodiversity; Species diversity; Stand structure; Naturalness; Mountain forests

1. Introduction

Diversity has become a more and more popular topic within the discussion of sustainability in the last decade, though the maintenance of diversity of forest ecosystems is required since many years (Swindel et al., 1984; Schuler, 1998), especially stressed in the Rio declaration and renewed by the Lisbon conference in 1998. Although the term diversity is widely used, no comprehensive definition exists (Hurlbert, 1971; Kaennel, 1998). Generally it is the variety and

variability among organisms, defined by number and frequency of different items organised at many levels, ranging hierarchical from genes across species to ecosystems (Smitinand, 1995). Species diversity is the best known, but by far not the only level of diversity (Turner, 1995). Within forestry genetic diversity and structural diversity are also important facets. Methods applied in assessing different types of diversity are as manifold as the ways of calculating measures of diversity. Moreover, any diversity determination is relative to its area basis (Myers et al., 1995). Under central European growing conditions, structural diversity obtains a comparatively higher importance, as tree species diversity is rather low, especially in mountain forests. Also for characterisation of stand structure, many methods have been

^{*} Corresponding author. Tel.: +43-1-87838-1329;
fax: +43-1-87838-1250.

E-mail address: markus.neumann@fbva.bmlf.gv.at (M. Neumann).

applied, based on the spatial distribution of trees (horizontal or vertical), on diameter distributions, or on other indicators used since a long time (Wenk et al., 1990).

In order to gain a better understanding of the effects of air pollution and other stress factors on forests, within ICP Forests (International Cooperative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests) the “Pan-European programme for Intensive Monitoring of Forest Ecosystems” has been implemented. The common activities are clustered into several surveys, i.e. crown condition assessment, soil survey, soil solution analysis, foliar analysis, increment measurement, deposition measurement, meteorological measurements, and ground vegetation assessment. A mapping of the stands has been carried out in Austria, additionally. In this

context, nearly 900 permanent observation plots have been installed in the European Union and in several non-EU countries according to harmonised methods. In Austria, 20 plots were installed (Neumann, 1996). The plots (Table 1) were selected to represent “the most important forest species and most widespread growing conditions” (UN/ECE, 1998). Approximately one half of the Austrian plots can be classified as mountain forests.

Within ICP Forests biodiversity is a matter of concern. First, possible effects of air pollution and other stress factors on species diversity at the monitoring plots have to be regarded (Bobbink et al., 1998). Second, interference could exist between stand structure or structural diversity, respectively, and the processes to be monitored. Moreover, this network, consisting of several hundreds of monitoring plots all

Table 1
Elevation, mean stand age, annual precipitation, mean temperature and species richness of four vegetation layers for all plots^a

Plot number	Plot name	Elevation (m a.s.l.)	Mean age	Annual precipitation (mm)	Mean temperature (°C)	RI of tree layer	RI of tree species regenerating	RI of vascular plants	RI of bryophytes and lichens
1	Sauerbrunn	390	93	754	9.0	3 (Qp)	12	48	5
2	Unterpullendorf	290	77	630	9.6	3 (Qp, Qc)	12	76	6
3	Brückl	930	56	923	7.0	2 (Pa, Ld)	6	52	11
4	Greifenburg	1190	63	1141	7.7	5 (Pa)	2	9	16
5	Fresach	720	113	1002	8.0	2 (Ps, Pa)	5	21	12
6	Pöggstall	860	98	862	5.3	3 (Pa)	4	44	11
7	Grimmenstein	500	78	884	7.5	8 (Fs)	7	20	8
8	Dobersberg	630	107	713	6.7	4 (Pa, Fs)	6	17	9
9	Klausen-Leopoldsdorf	510	58	804	8.2	2 (Fs)	3	20	3
10	Hochburg	460	108	1005	8.1	2 (Pa)	4	14	10
11	Mondsee	860	135	1521	8.1	2 (Pa)	6	20	7
12	Lungötz	920	138	1378	5.0	2 (Pa, Aa)	3	8	20
13	Leutschach	670	101	1117	8.4	9 (Pa, Aa, Fs)	9	30	2
14	Niklasdorf	960	127	771	7.9	2 (Pa, Ld)	7	51	6
15	Mürzzuschlag	715	51	933	6.0	5 (Pa)	4	59	30
16	Murau	1540	104	918	5.0	2 (Pa, Ld)	2	11	26
17	Jochberg	1050	75	1358	5.7	1 (Pa)	3	69	13
18	Ehrwald	1020	133	1250	5.8	3 (Pa, Ld)	5	72	8
19	Zillertal	1490	163	1272	6.2	2 (Pa)	1	4	18
20	Hochhädrich	1320	118	2020	7.1	4 (Pa, Aa)	5	17	14
203_1	Hauersteig 1	350	99	850	8.3	4 (Pa)	No data		
203_2	Hauersteig 2	350	99			2 (Pa)	11	41	3
203_3	Hauersteig 3	350	99			2 (Pa)	10	38	0
203_4	Hauersteig 4	350	99			2 (Pa)	9	41	2
703_88	Arnoldstein 1988	660	21	1290	7.7	1 (Pa)	No data		
703_98	Arnoldstein 1998	660	31			1 (Pa)	No data		

^a Tree species which are dominant or subdominant on the plots: *Picea abies* (Pa), *Pinus sylvestris* (Ps), *Larix decidua* (Ld), *Abies alba* (Aa), *Fagus sylvatica* (Fs), *Quercus petraea* group (Qp), *Quercus cerris* (Qc).

over Europe where the data are assessed according to standardised methods, offers an excellent opportunity to use it as a basis for diversity assessments.

As the Austrian monitoring plots represent a big part of the ecological variability that occurs within Europe, covering a wide altitude range and including conifer as well as broadleaf forests from a variety of geological units, they seem to be highly appropriate for use in pilot studies. The present study should give contributions to the following questions.

- In how far are the data available within the programme of ICP Forests suited to calculate measures of diversity?
- Are there correlations between the different measures of diversity? Is there a correlation among species diversity of different vegetation layers and between species diversity and structural diversity? To what extent the varying measures of diversity are redundant? Are they differing in their predicative power?

Moreover, questions of general ecological relevance can be examined.

- Are differences in diversity on stand level recognisable at the studied plots which could be explained by the ecological background, e.g. by altitude or by the naturalness of the forest community?

While there are several studies which are comparing indices of species diversity (e.g. Magnussen and Boyle, 1995; Köhl and Zingg, 1996; Franc, 1998) or stand structure (e.g. Payandeh, 1970; Gleichmar and Gerold, 1998) or both (Eckmüllner, 1999) focussing on methodology, only few studies exist which compare different indices over a wide range of ecological conditions. Few studies exist on the relationship between stand structure and species diversity as well (Pitkanen, 1997).

2. Data and methods

2.1. Study area

In Austria, the permanent observation plots have been installed in 1995 (Neumann, 1996). Selection and installation of the plots was done according to

harmonised methods (UN/ECE, 1998). Younger stands at earlier development stages were excluded, and the plots were preferably established in homogenous stands. The 20 plots are managed in a “traditional” way by the owners without any restriction. Unmanaged reserves were not included. As access to the plots had to be possible all over the year, plots at an elevation above 1600 m are not represented. Information on stand history is scarce, the majority of the stands originated from natural regeneration. The plots comprise each an area of 0.25 ha. They are rectangular, but their shape had to be modified individually in order to fulfil the criteria of homogeneity.

The 20 monitoring plots are well distributed over Austria (Fig. 1), covering nearly the whole vertical range and corresponding site conditions and including the most common tree species and forest communities (Table 1), from lowland deciduous forests with oak (*Quercus* spp.) or beech (*Fagus sylvatica*), to montane broadleaf-conifer stands with spruce (*Picea abies*), silver-fir (*Abies alba*), and beech to conifer dominated stands with spruce, larch (*Larix decidua*), and pine (*Pinus sylvestris*).

Results from five plots of long-term yield experiments located at two sites were included to provide possibilities for comparison. These plots situated at lower elevations were established by planting and are intensively managed (Rössler, 1997; Neumann, 1997).

2.2. Sampling methods

Data to be assessed are defined in the ICP Forests Manual (UN/ECE, 1998), the assessments are either mandatory or optional. The data used here were assessed within the periodic increment measurements on the plots and within the ground vegetation assessment.

In the course of the installation of the plots the coordinates of each tree (above a calliper limit of 5 cm) on the plots and in a surrounding buffer zone were measured, the crown projection area and the tree species was determined. Within the frame of increment assessment, diameter, tree height, and crown length were measured.

The ground vegetation assessment was carried out within the plot on one larger sub-plot with 225 or 400 m² as well as on 10 small sub-plots with 4 m² each (Starlinger, 1998). Results from these small sub-plots

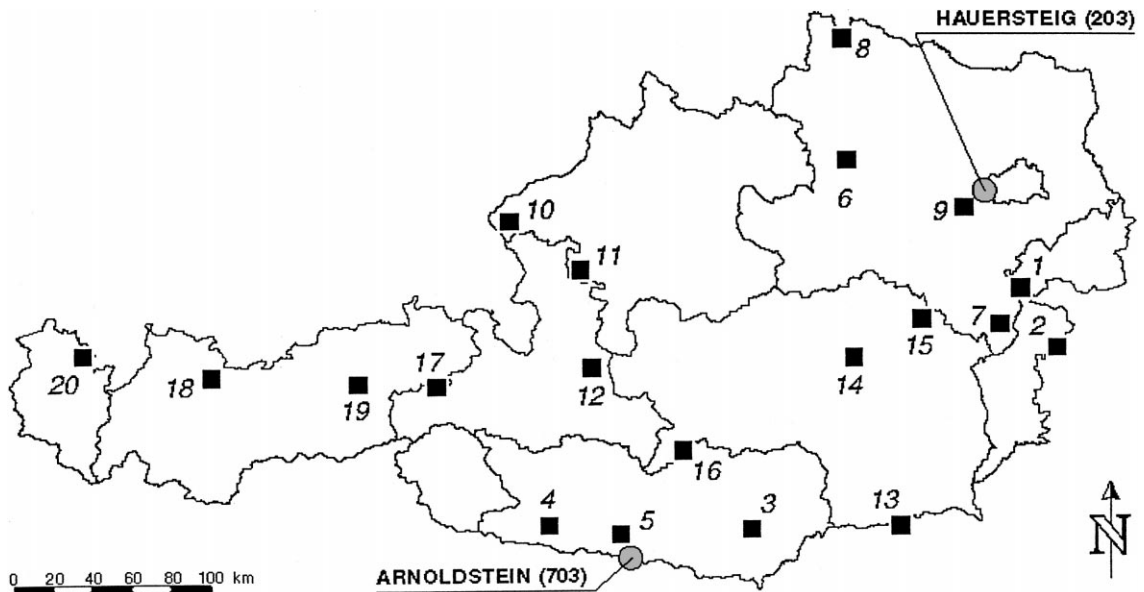


Fig. 1. Location of the 20 permanent observation plots and the two experimental sites.

are not presented here. Each species was quantified by the differentiated cover-abundance scale of Westhoff and van der Maarel (1978), species were stratified into tree layer, tree regeneration (i.e. below 5 m), vascular plants (i.e. shrub and herb layer) and ground layer (bryophytes and lichens).

The data set from the five experimental plots are identical, but ground vegetation assessment was carried out only at “Hauersteig”.

2.3. Computed indices

With the data available, 11 measures for both species and structural diversity were calculated for each plot or sample (Table 2). All the indices refer to within-sample or plot diversity (i.e. alpha diversity; Whittaker, 1977). Trees within the buffer zone were included into the calculation of the Clark–Evans Index (CE) and the Gadow Index (GI) to avoid the border effect.

Indices for species diversity, like the Shannon Index (SH) or the Simpson Index (SI), integrate both species number and the relative abundance of the different species, while by calculating Evenness (E) the influence of species number is removed by standardisation. The relative abundance of each species can be calculated by stem number, basal area, coverage volume, or

total biomass. The cover-abundance data from ground vegetation assessment were transformed into cover percentages per species, while for tree layer the proportions of both basal area and stem number of total plot area were applied.

The indices for spatial distribution or horizontal structure compare a hypothetical distribution with the real situation. The Pielou Index (PI) tests the spatial distribution of trees by the average minimum distance from random points to the nearest tree. For the calculation of PI we choose a systematic grid with a distance of 3 m, resulting in about 230 sample points per plot, according to their shape, disregarding sample points at the borderline. As its calculation is based on neighbourhood pattern, it describes stand microstructure. High values (greater than 1) indicate a clustered horizontal distribution, while values below 1 characterise a regular distribution; in stands with random distribution, the index should be around 1. The same classification is valid for the Cox Index (CI). The CI is the ratio of variance to mean stem number on sub-plots which should be 1 if trees are randomly distributed. Depending on the size of the sub-plots, CI is suitable to describe stand structure on different scales. For the calculation of CI the plots were divided into sub-plots of 100 m² resulting in 21–25 sub-plots according to the different shapes of the plots.

Table 2

Applied diversity measures and formulas

Species-richness: $RI = N$	N is the number of species
Shannon Index of diversity (Shannon, 1948): $SH = \sum_i^N (-\log_2 \pi_i) \pi_i$	π_i is the relative abundance of the i th species, this can be calculated by proportion of number, coverage or basal area; instead of \log_2 also \ln or \log_{10} is used
Simpson Index of diversity (Simpson, 1949): $SI = \sum_i^N (1 - \pi_i) \pi_i$	π_i is the relative abundance of the i th species, this can be calculated by proportion of number, coverage or basal area
Evenness (Lloyd and Ghelardi, 1964; Magurran, 1988): $E = SH / \log_2 N$	N is the number of species
Pielou Index of nonrandomness (Pielou, 1959): $PI = \frac{n}{A} \frac{1}{k} \sum_i^k r_i^2$	n is stem number per plot, A is the plot area, k the number of sample points and r_i is the minimum distance from sample point to nearest tree
Cox Index of clumping (Strand, 1953; Cox, 1971): $CI = \frac{s_x^2}{\bar{x}}$	s_x^2 is the variance and \bar{x} is the mean stem number on sub-plots
Clark–Evans Index of aggregation (Clark and Evans, 1954): $CE = \frac{1}{n} \sum_i^n r_i 2\sqrt{\rho}$	r_i is the distance from one tree to his next neighbour and ρ is density of tree per square meter
Gadow Index of neighbourhood pattern (Gadow et al., 1998): $GI = \frac{1}{n} \sum_i^n \frac{1}{4} \sum_1^4 z_i$	z_i is 1 if angle less or equal 90° and z_i is 0 if angle greater 90°
Vertical evenness: $VE = \sum_i^4 (-\log \pi_i) \frac{\pi_i}{\log 4}$	π_i is the relative crown area of all trees in the i th height layer
Complexity Index (Holdridge, 1967): $HC = H BA n N$	H is the top-height, BA the basal area, n the stem number and N the number of species
Stand Diversity Index (Jaehne and Dohrenbusch, 1997): SD	Combines the variation of species \times dbh \times distance \times crown

The Clark–Evans Index (CE) tests the distance between nearest neighbours. The values are restricted to the range between 0 and 2.15 and indicate clustered distribution with values below 1, while complete regular hexagonal distribution results in the highest index of 2.15. Therefore, low values of PI or CI indicate regular distribution and should be correlated with high values of CE.

The Gadow Index (GI) as proposed by Gadow et al. (1998) classifies the horizontal structure by the mean heading angle to the four next trees. Values below 0.5 indicate regularity while values greater 0.6 should characterise clumped stands.

While there are many more than the four indices described above to measure horizontal structure, there are only few for vertical structure (Pretzsch, 1996; Ferris-Kaan et al., 1998). The first index of Pretzsch as a measure of vertical species diversity is a combination of Shannon indices after stratification into three layers. The latter takes the cover per layer into account but needs special field assessments and was not

applicable to the data available. Therefore as an index to characterise the vertical distribution of coverage within a stand we calculated a new index of Vertical Evenness (VE): The trees were stratified into four layers (limits at 80, 50, and 20% of maximum height on the plot), their crown projection area was calculated, and the Shannon formula was applied to the resulting proportions. Furthermore, the result was standardised by the four layers according to the Evenness formula. Low values of VE characterise single-storied stands, while the theoretical maximum of 1 would result for vertical equally distributed trees. A similar approach has recently been proposed by Weber (1999).

All of the indices described above concentrate on single elements of diversity. Jaehne and Dohrenbusch (1997) proposed the Stand Diversity Index (SD) as a new measure by integrating main elements of diversity combining measures for the variation of species composition, diameter, tree distance and crown dimension into one single figure. According

to their work, stands with an SD higher than 9 are very diverse, and stands below 4 have to be regarded as monotonous. While the methods described by Jaehne and Dohrenbusch (1997) are field oriented and contain some subjective elements, we adapted it slightly to make it workable for data processing based on the existing assessments.

The Complexity Index (HC) by Holdridge (1967) on the other hand is not based on measures of diversity or variation but on traditional measures of stand description: Multiplying number of tree species by stem number, dominant height, and basal area, this index is determined strongly by number of species and measures of growth performance but contains no information on spatial distribution nor accounts for within stand variation. We use a calliper limit of 5 cm instead of 10 cm as proposed by Holdridge and take into account the whole plot area instead of 0.1 ha.

To quantify the variation of diameter distribution the standard deviation in relation to mean diameter was calculated. As this simple measure performs quite well no other measures for tree size diversity (see Buongiorno et al., 1994; Fuldner, 1995) were calculated. Furthermore, the Segregation Index by Pielou (1961) as well as skewness and excess of diameter distribution were calculated, but no essential results were obtained, and therefore, they are not presented here. Most of the indices briefly described here can be found in textbooks of ecology or forestry (Pielou, 1975; Magurran, 1988; Wenk et al., 1990).

A further method of stand classification is the “hemeroby” as a measure for the influence of human utilisation on ecosystems (Jalas, 1955; Sukopp, 1969, 1972). Recently the hemeroby of Austrian forest ecosystems was assessed by Grabherr et al. (1998) who developed methods for a quantification of the

expert judgements on which the different criteria of hemeroby are based. The methods can be found by Grabherr et al. (1998); here only one criterion, i.e. the “naturalness of tree species composition”, will be used. This naturalness is derived from a comparison of the present tree species composition with the composition of the potential natural forest community. The hemeroby is rated using an ordinal scale that ranges between artificial (1) and natural (9).

The correlation analyses (Spearman’s rho) were calculated with SPSS, version 7.0. Only the data from the 20 monitoring plots (ICP Forests) were used for the correlation analyses.

3. Results

3.1. Species diversity

In Table 1 the values of Species-Richness (RI) of tree layer, tree regeneration, vascular plants (herb and shrub layer, including tree species regenerating), and of the ground layer (bryophytes and lichens) are shown. On the monitoring plots, we determined more than 70 species of vascular plants on some plots and up to 30 species of bryophytes or lichens. Usually RI of vascular plants is higher than RI of bryophytes and lichens. Four plots (Lungötz (12), Greifenburg (4), Zillertal (19), and Murau (16)) have few species of vascular plants (i.e. not more than 11 species), but are rich in bryophytes and lichens. These spruce dominated sites are situated on siliceous bedrock in the montane and lower subalpine altitudinal zones.

All the correlations between indices of species diversity for the tree layer by SH or SI are highly significant at 0.01 level (Table 3). Applying the

Table 3
Correlation coefficients (Spearman’s rho) between different indices of species diversity in tree layer

	SH (basal area)	SH (stem number)	SI (basal area)	SI (stem number)	E (evenness)	SH trees on vegetation plot
SH (basal area)	1.000					
SH (stem number)	0.876**	1.000				
SI (basal area)	0.973**	0.804**	1.000			
SI (stem number)	0.907**	0.970**	0.864**	1.000		
Evenness	0.807**	0.774**	0.842**	0.865**	1.000	
SH tree layer on vegetation plot (cover)	0.939**	0.760**	0.912**	0.781**	0.660**	1.000

** Correlation is significant at the 0.01 level (2-tailed).

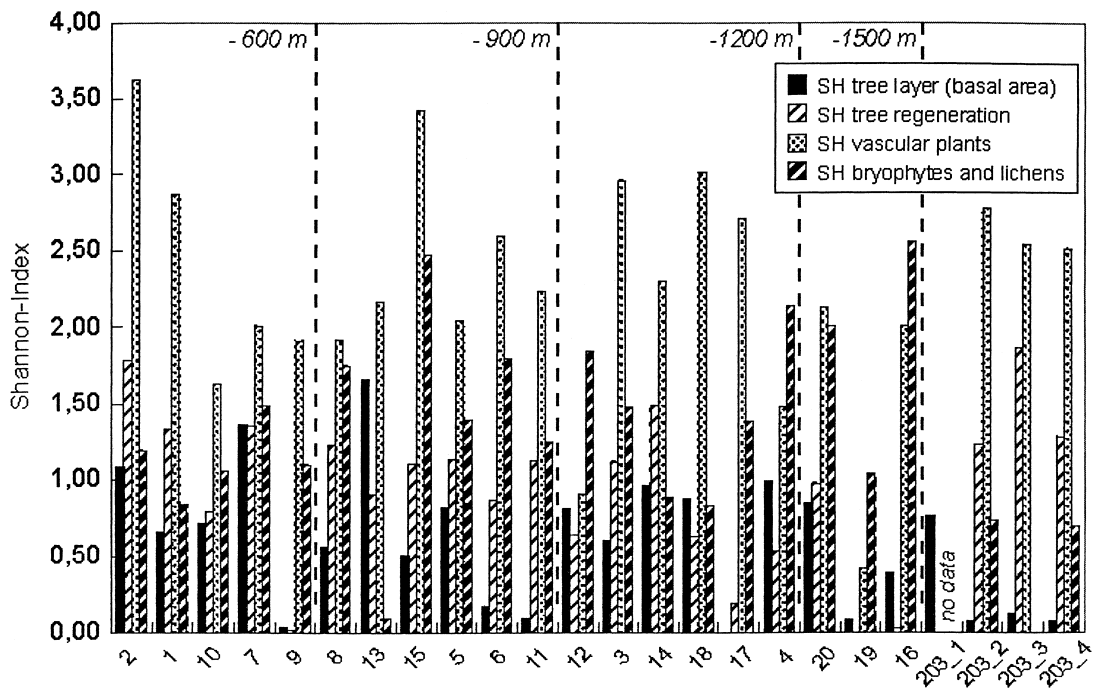


Fig. 2. Shannon indices of tree layer (basal area), tree regeneration, vascular plants (herb and shrub layer), bryophytes/lichens (ground layer) for the 20 permanent observation plots, ordered by increasing elevation, and for the experimental site at Hauersteig. Plot number cf. Table 1.

formulae to number or basal area based species proportions makes no essential difference as is shown by the highly significant correlations. Even SH calculated for tree species on the ground vegetation sub-plots (225/400 m²) is correlated significantly with all other indices of species diversity. Evenness is correlated higher with SI than with SH.

SH indices based on basal area or cover, respectively, for the species diversity of four vegetation layers (Fig. 2) differ between the plots but even more between the different layers. Highest values are found in the herb and shrub layer (vascular plants), but in some cases the diversity of bryophytes and lichens is as high or even higher (plots at Lungötz (12), Greifenburg (4), Hochhädrich (20), Zillertal (19) and Murau (16)). The diversity of tree species in the regeneration layer is generally higher than the diversity of the tree layer. An exception to this rule makes the plots at Ehrwald (18), Greifenburg (4), Zillertal (19), and Murau (16) which are situated at 1000–1550 m altitude, and the plot at Leutschach (13), at 670 m altitude, where the diversity of the tree layer is extremely high. Diversity of the tree layer is low on three

experimental plots (203) and at Klausen-Leopoldsdorf (9), Pöggstall (6), Mondsee (11), and Jochberg (17).

Bivariate correlation analyses of SH for the four assessed layers exhibited a weak but significant positive correlation between diversity of vascular plants and trees in the regeneration layer (Table 4). Between the other layers, no correlation was found.

SH of tree species in regeneration layer showed a highly significant decrease with elevation. Between elevation and the other vegetation layers no significant correlation was found. However, as opposed to the other layers, SH of ground layer (bryophytes/lichens) shows a tendency to increase with elevation.

3.2. Structural diversity

The indices of stand structure behave similarly for all tested plots. This is pointed out by a comparison of PI versus CI (Fig. 3) which also includes the findings for the experimental plots. The classification into regular or irregular distribution is almost identical, only differences in detail exist. The intensively managed experimental plots are all to be classified as

Table 4
Correlation coefficients (Spearman's rho) between indices of diversity for different vegetation layers

SH	Elevation	Vascular plants	Bryophytes and lichens	Regenerating tree species	Tree layer
Elevation	1.000				
Vascular plants	-0.208	1.000			
Bryophytes and lichens	0.327	-0.166	1.000		
Regenerating tree species	-0.569**	0.473*	-0.128	1.000	
Tree layer	-0.153	0.088	-0.277	0.414	1.000

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

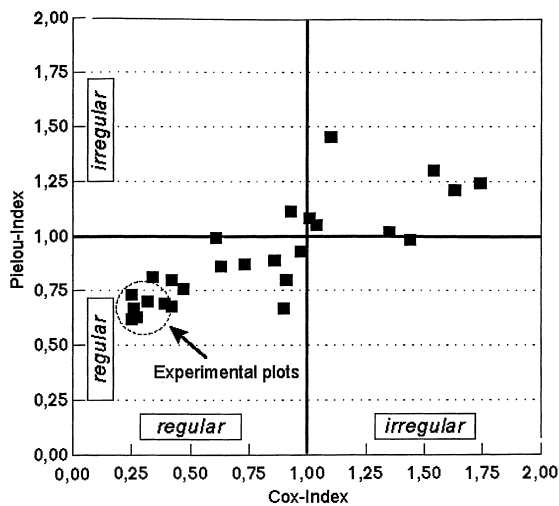


Fig. 3. Comparison of Cox Index as a measure of macrostructure versus Pielou Index as a measure of microstructure.

regular. Stands with contrary classification may exist but are not contained in our sample. Disregarding the two beech stands in Grimmenstein (7) and Klausen-Leopoldsdorf (9), a tendency of increasing clustering or clumping with elevation is evident. This is reflected by the highly significant increase of PI with elevation (Table 5), whereas with CI no significant correlation was found.

At our stands, the GI performs only partially well, the more regular plots were detected, but the clumped situation as indicated by CI and PI cannot be replicated by the GI.

The plots at Sauerbrunn (1), Pöggstall (6), Mondsee (11), and three of the experimental plots have values of VE below 0.25 (Fig. 4), indicating single-storied stands, while the multi-storied stands in Leutschach (13), Fresach (5), and Greifenburg (4) are characterised by values above 0.75.

Table 5
Correlation coefficients (Spearman's rho) between different indices of structural diversity and combined indices

	Elevation	S.D. dbh	VE	CE	CI	PI	GI	HC	SD
Elevation	1.000								
S.D. dbh	0.299	1.000							
VE	0.525*	0.911**	1.000						
CE	-0.533*	-0.716**	-0.660**	1.000					
CI	0.337	0.693**	0.556*	-0.834**	1.000				
PI	0.657**	0.669**	0.659**	-0.932**	0.783**	1.000			
GI	0.516*	0.715**	0.719**	-0.781**	0.662**	0.801**	1.000		
HC	0.223	0.590**	0.471*	-0.436	0.348	0.431	0.259	1.000	
SD	-0.135	0.505**	0.464*	-0.337	0.392	0.272	0.208	0.460*	1.000

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

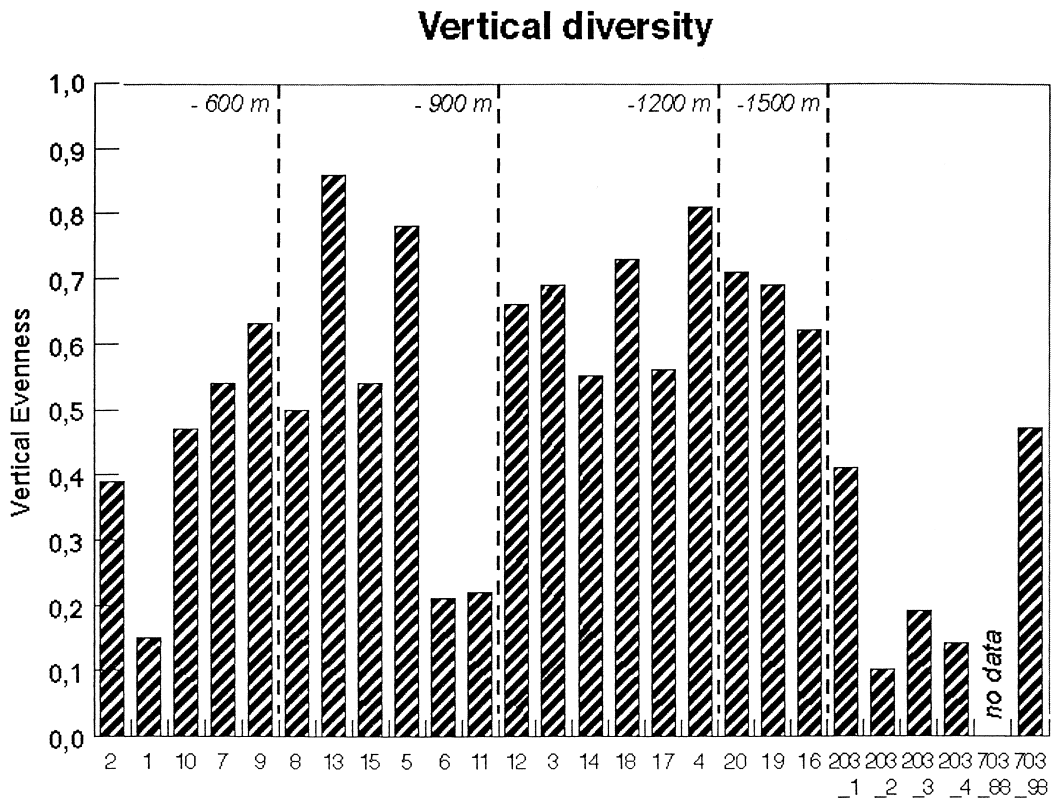


Fig. 4. Vertical evenness for the 20 permanent observation plots, ordered by increasing elevation, and for the experimental sites at Hauersteig and Arnoldstein. Plot number cf. Table 1.

While correlations between the indices of species diversity are scarce, there are many relationships between the indices describing structural diversity (Table 5). The correlation between all indices describing horizontal structure is quite high: between PI and CI the correlation coefficient amounts to about 0.8, between PI and CE to about -0.9 and finally to -0.8

between CI and CE. The fact that our measure of VE is significantly correlated with all indices for horizontal structure is remarkable, but not astonishing: The standard deviation of diameter distribution, a well-known traditional parameter in forest yield research, behaves in the same way. This simple measure of dimensional diversity is highly significantly correlated

Table 6

Correlation coefficients (Spearman's rho) between different indices of structure and species diversity

	S.D. dbh	VE	CE	CI	PI	GI	HC	SD
SI tree layer (basal area)	0.244	0.328	-0.154	0.132	0.036	0.119	-0.062	0.660**
SH tree layer (basal area)	0.302	0.373	-0.235	0.211	0.128	0.122	0.064	0.756**
Evenness	0.239	0.282	-0.210	0.153	0.146	0.275	-0.009	0.599**
SH regenerating trees	-0.422	-0.415	0.364	-0.352	-0.416	-0.410	-0.088	0.362
SH bryophytes and lichens	0.032	0.002	-0.145	0.206	0.308	0.195	0.236	0.048
SH vascular plants	-0.451^*	-0.287	0.417	-0.505^*	-0.436	-0.252	-0.334	0.072
SH tree layer on vegetation plot (cover)	0.210	0.307	-0.121	0.133	0.006	-0.031	0.005	0.690**

* Correlation is significant at the 0.05 level (2-tailed).

** Correlation is significant at the 0.01 level (2-tailed).

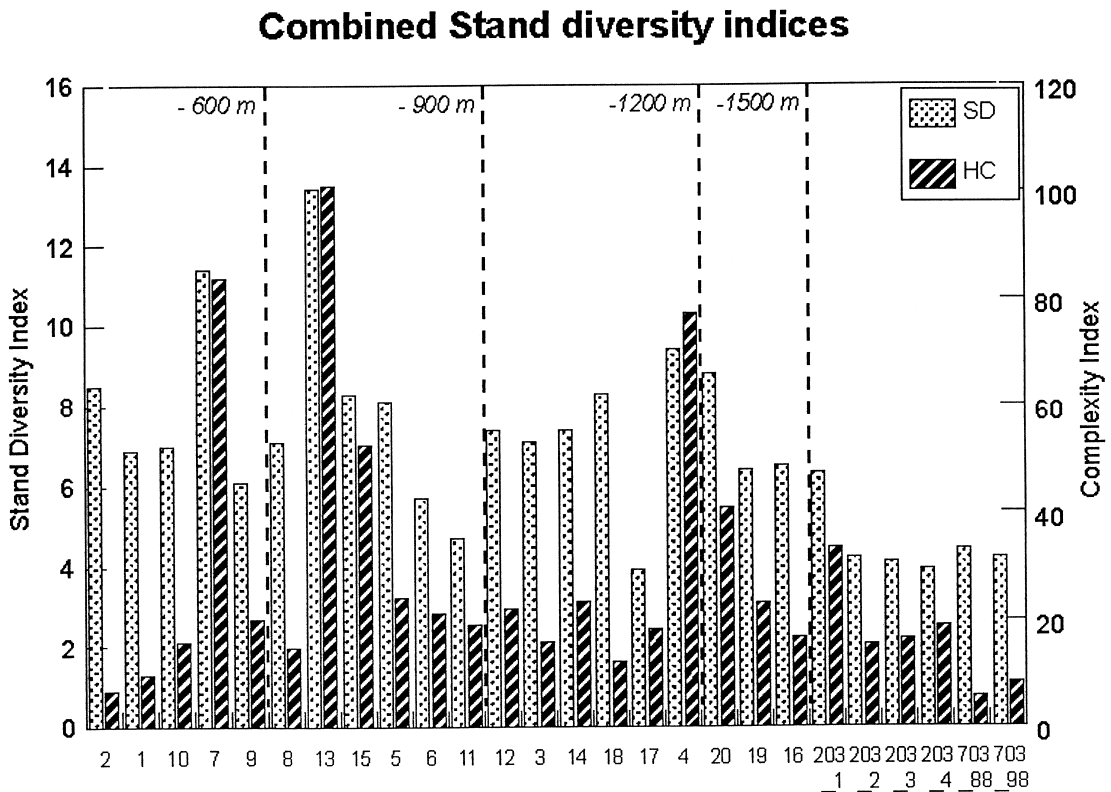


Fig. 5. Combined indices of Stand Diversity and Stand Complexity for the 20 permanent observation plots, ordered by increasing elevation, and for the experimental sites at Hauerstein and Arnoldstein. Plot number cf. Table 1.

with all other indices of structural diversity, and it is correlated with SH of vascular plants, a measure of species diversity, too (Table 6).

3.3. Combined indices

The three stands with highest HC at Grimmenstein (7), Leutschach (13), and Greifenburg (4) are also characterised by the highest values of SD (Fig. 5). However, when comparing the less complex (HC) with the less diverse stands (SD) the relationship is less evident for these. But over all 20 plots, the correlation is significant at the 0.05 level (Table 5). With both HC and SD no correlation was found with the indices describing horizontal structure. On the other hand weak positive correlations with vertical structure (VE) were significant at the 0.05 level. With both combined indices no correlation with elevation was found (Table 5 and Fig. 5).

3.4. Correlation between structural diversity and species diversity

The scatterplot in Fig. 6 exemplifies for SH and PI that there is no correlation between stand structure and tree species diversity. The relationships of species and structural diversity in detail are shown in Table 6. The indices for horizontal structure (CE, CI, PI and GI) are more or less uncorrelated with species diversity, only between CI and diversity of vascular plants there is a weak negative correlation. SH of vascular plants is negatively correlated with the standard deviation of diameters, too. The HC is not correlated with species diversity, while the SD is correlated significantly with both SI and SH for tree layer, Evenness, and SH for tree cover on the vegetation plots.

Concerning the “naturalness of tree species composition” (Figs. 7 and 8) the frequency distribution of the 20 plots is quite similar to findings for Austrian

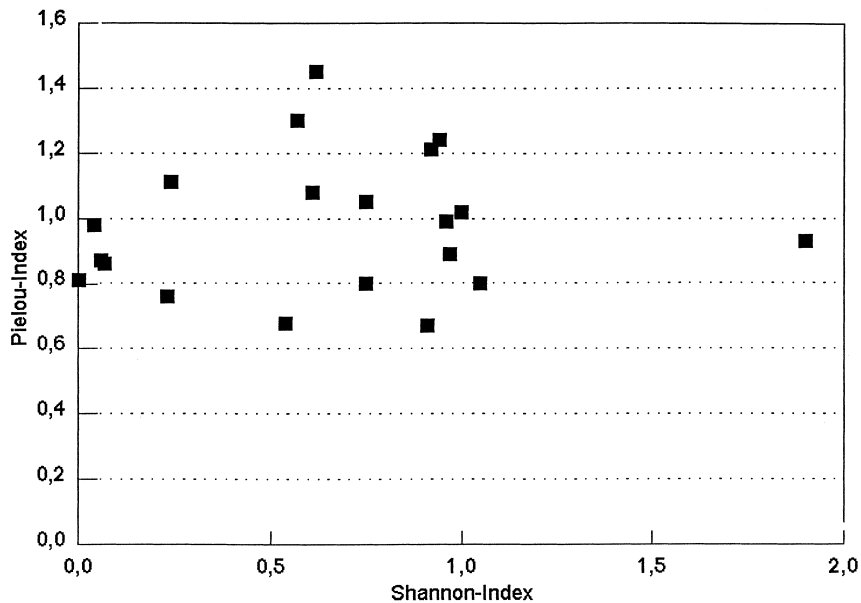


Fig. 6. Scatter-plot of Shannon indices of tree layers as a measure of species diversity versus Pielou indices as a measure of horizontal microstructure.

forests as a whole (Grabherr et al., 1998). Here, five plots were classified as semi-natural or natural (Grimenstein (7), Klausen-Leopoldsdorf (9), Greifenburg (4), Zillertal (19), and Murau(16)). The experimental plots and two monitoring plots (Hochburg (10) and

Mondsee(11)) have been assessed as artificial. Species diversity in tree layer, both determined with SH (Fig. 7) and with SI (not shown), is uncorrelated with naturalness of tree species composition. The diversity of vascular plants of ground vegetation is

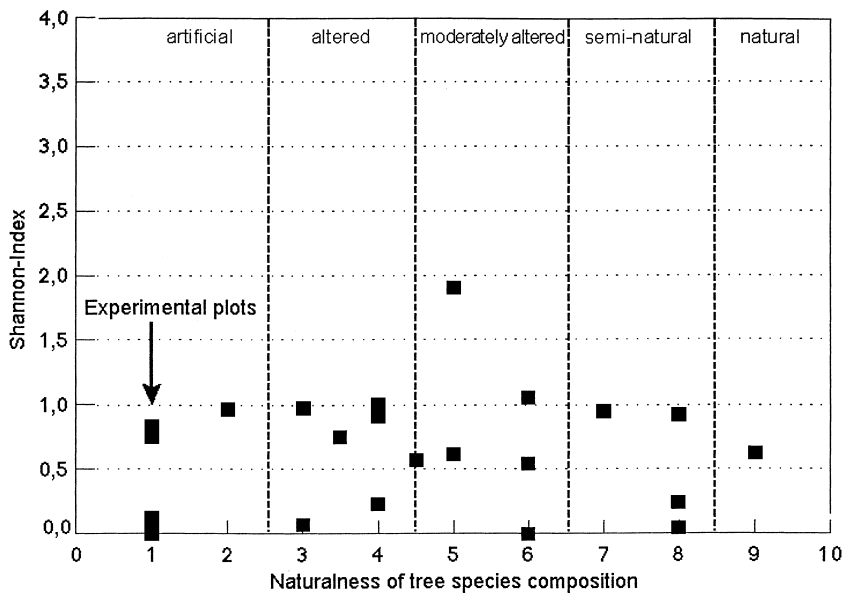


Fig. 7. Diversity of tree layer (Shannon indices) compared with naturalness of tree species composition.

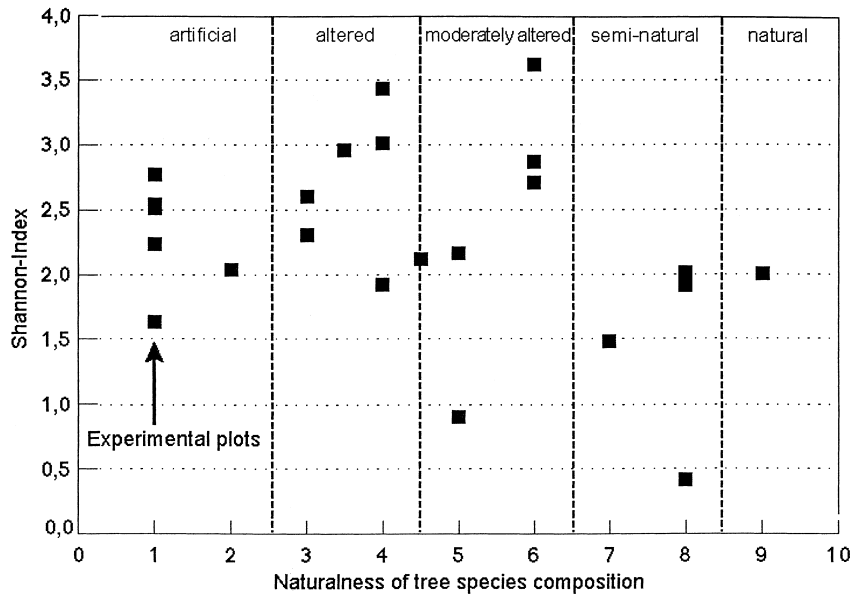


Fig. 8. Diversity of vascular plants in herb and shrub layer (Shannon indices) compared with naturalness of tree species composition.

not correlated with naturalness of tree species composition, either (Fig. 8). With respect to the relationship between naturalness and stand diversity (SD; not shown) no correlation was found.

4. Discussion

4.1. Species diversity

In our sample, there is only weak evidence for the influence of stand structure (Table 6) or elevation (Table 4) on species diversity. As species diversity is influenced also by soil fertility, succession stage, or tree species composition, a reduction of variability by stratification (e.g. by soil type, tree species, stand age) should be necessary in order to work out correlations of species diversity with a single influencing factor. This was not possible with our restricted number of plots. However, if such investigations will be extended to the whole network of ICP Forests, better results are to be expected.

In our study, a decrease of the diversity of tree species in regeneration layer with increasing elevation was highly significant (Table 4). This is backed by the fact that the highest species numbers (RI) of 10–12

(Table 1) occurred at low elevations (Unterpullendorf (2), Hauersteig (203), Sauerbrunn (1)). The composition of the tree layer on the one hand is influenced by forest management, and on the other hand interspecific competition can result in a strong reduction of species number within a forest stand. Compared to it, in the regeneration layer of a stand species can also be found of which adult trees are occurring somewhere in the surrounding area only. Therefore, the regeneration layer is less influenced by forest management and by competitive exclusion than the tree layer. For this reason the decrease of the diversity of regenerating tree species with elevation can be explained by the low number of tree species occurring in the montane and subalpine zones, compared to tree species which are bound to lower altitudes. At higher altitudes, spruce dominates in regeneration throughout.

Low species diversity in the tree layer is attributable to the influence of forest management on the experimental plots and on the monitoring plots at Pöggstall (6), Mondsee (11), and Jochberg (17) which are dominated by spruce, but it is to be regarded natural on the beech dominated site of Klausen-Leopoldsdorf (9).

While all the indices of species diversity for the tree layer are highly significantly correlated (Table 3),

there are no correlations or only weak relationships between the diversity indices of the different layers (Table 4). It is an important question in conservation biology whether there are taxonomic groups which, because of strong correlations, can serve as surrogates for diversity of other less well-known groups or for overall species diversity (Ehrlich and Norton, 1996). Missing correlations, in our data, between bryophyte and vascular plant diversity can be interpreted as the consequence of contrasting ecological demands of the respective groups. Whereas bryophytes are strongly dependent on moisture, for the growth of vascular plants light is more important. Therefore, it seems more promising to explain the diversity of both groups by site and stand characters. However, if correlations between bryophyte and vascular plant diversity could not be found, this does not mean that there are no correlations with other taxonomic groups. As an example, Usher and Keiller (1998) in British farm woodlands found a relationship between species richness of moths (Macrolepidoptera) and herbaceous plant species richness. In this case a functional relationship is evident, as the larvae of the moths are feeding on plants. Generally, the assessment of diversity allows a description of the analysed element only, inference to the diversity of other elements of the ecosystem needs caution.

The efficiency of the Shannon and Simpson formulae to characterise diversity is discussed controversially in the literature: SH should be preferred as it is more sensitive than SI where there are changes in species richness (Magnussen and Boyle, 1995; Köhl and Zingg, 1996), on the other hand the existence of rare species does not modify SH (Franc, 1998). According to our findings, there is no big difference (cf. the high correlation between both indices) when they are applied to the tree layer.

If indices of species diversity are used as a surrogate for ecosystem stability or sustainability (Sterba, 1998), high importance is attributed to them. Quite often, high species diversity is regarded to be natural; this opinion cannot be supported generally by our findings, as no correlation between naturalness and species diversity could be observed (Figs. 7 and 8). Moreover, some of the most diverse of our plots owe their diversity to human influence. For instance, the mixed oak-stand at Unterpullendorf (2), with *Quercus cerris* and *Q. petraea*, most probably, due

to former utilisation as a forest pasture, is a substitute community for an oak-hornbeam forest community which typically is less rich in species and less diverse (Schume and Starlinger, 1996). However, in several studies dealing with organisms that are bound to decaying wood, i.e. saproxylic beetles (Ammer and Schubert, 1999; Martikainen et al., 1999) and fungi (Lindblad, 1998; Sippola and Renvall, 1999), a strong connection of species diversity and richness to naturalness and occurrence in old-growth forests, respectively, was found.

Nevertheless, species diversity is a useful tool in plant ecology and forestry to compare effects of different methods of site preparation (Swindel et al., 1984; Harrington and Edwards, 1996) or effects of timber harvest (Kammesheidt, 1996) in respect to species composition. But the question whether diversity is a desirable good per se remains.

4.2. Structural diversity

Structural diversity is a matter of concern within forestry since a long time, as regular distribution provides maximal space and optimal growing conditions for each individual, while a clustered distribution causes increment loss (Pretzsch, 1995). Nowadays, the orientation to yield maximal increment is more and more supplemented or even substituted by the wish to establish or maintain stands with highest stability or protective effects. This is valid especially for mountain forests where the demand for protective functions is high, in particular. Indices of structural diversity are used to select “best” silvicultural treatments by means of modelling (Pretzsch, 1996) and to decide upon protective functions (Bürki, 1981). Although the generally very diverse structure of virgin forests is evident, the conclusion that therefore diverse forests are better qualified to fulfil the desired functions remains questionable.

Three of the applied indices for structural diversity (CE, CI, PI) perform generally well, and no preference can be given to anyone of them (Table 5 and Fig. 3). In other studies, the most frequently employed index is CE, but Payandeh (1970) pointed out some drawbacks of this measure and recommended both the PI and CI in his profound comparison of different indices. On the other side, the aggregation index (CE) was preferred by Gleichmar and Gerold (1998). A combina-

tion of PI and CI (like in Fig. 3) seems to provide both information on micro- and macrostructure. Both CE and PI are describing microstructure by focussing on the distances between single trees or sample points to trees, respectively. CI, on the other hand, describes the macrostructure by comparing the number of stems between sub-samples; thus the smaller the area of the sub-plots is chosen the closer together the results between CI and the others are to be expected (Upton and Fingleton, 1988). It is remarkable that both by CI and by PI the classification into regular and irregular distribution is almost identical (Fig. 3), the use of a systematic grid instead of randomly distributed points is not changing the PI essentially. A situation with regular macrostructural distribution and irregular microstructure is imaginable theoretically only, while the reverse situation with regularly distributed but clustered trees is typical for higher mountain regions. The index of neighbourhood pattern (GI) may be used in special cases to distinguish between more regular stands (or afforestations).

Stands at elevations above 900 m, i.e. mountain forests, show a tendency towards more complex structures which is reflected by the correlations of PI, CE, GI, and VE with elevation (Table 5 and Fig. 3). The more regular stands at lower elevations partly are caused by forest management, as the proportion of even-aged intensively managed spruce stands (e.g. Hochburg (10), Pöggstall (6)) is highest there. All of the experimental plots (203, 703) fall into this category.

Care must be taken in avoiding border effects, and the fact that all measures of structural diversity are greatly affected by sample size should be taken into account, especially when comparing results from different sources (Eckmüllner, 1999).

Both the recently proposed Stand Diversity Index by Jaehne and Dohrenbusch (1997) as well as the Complexity Index by Holdridge (1967) provide plausible results. The advantage of HC is the simple data base needed, while SD needs more detailed assessments, but it seems to be more sensitive, and it exhibits a strong correlation with species diversity of tree layer (Table 6).

Although the correlations between stand structure and species diversity are weak (Table 6), it is remarkable that there is a decrease of vascular plant diversity (SH) with increasing structural diversity, as measured by CI and by standard deviation of DBH. With our

data, it could not be examined whether there is a correlation of more complex stand structure with a lower permeability to light. Even crown projection from the stand mapping data could not be used, as the tree species are differing in crown density, thus the crown of a larch being much more translucent than the crown of a beech.

5. Conclusions

Data assessed within the ICP Forests programme of intensive forest monitoring are suitable to derive indices for stand structure and species diversity, if tree localisation and crown dimension is recorded. In many countries these data are available, and with this European-wide harmonised data set, there is an excellent basis to advance the state of the art in the field of diversity assessments. Data from aerial photography may enhance the data base wherever available.

It was shown by many correlations between structural indices as well as between indices of species diversity that the methods of calculation is not so important, if the same element or layer of a forest stand is analysed. On the other hand, the missing correlation between most indices of species diversity of different layers points at the great importance of the selection of analysed elements. It becomes evident that sites poor in vascular plants are often rich in bryophytes or lichens; therefore, it is crucial to know whether these have been included in ground vegetation assessment or not when comparing results from different surveys. In forest communities with low diversity of vascular plants it might depend on the assessment of bryophytes and lichens that effects of air pollution and other stress factors on the forest ecosystem can be found in the course of the ground vegetation assessment.

The structure of mountain forests, i.e. forest at altitudes higher than 900 m, predominantly can be described as more complex, i.e. clumped or clustered and multi-storied. However, limits between mountain and lowland forests are poorly defined. Typical sub-alpine forests, i.e. from elevations above 1600 m were not included in our data. Diversity of tree species in the regeneration layer is decreasing with elevation. At the highest altitudes spruce is dominating in the regeneration layer.

With the calculated indices, no correlation is found between diversity and the naturalness of tree species composition.

The importance of indices is growing as they are used increasingly to compare alternatives and to control management decisions. The more they are used the more important is our lack of knowledge. Our knowledge has to be improved especially with respect to the question how reliable the index concerned is. Should they characterise the situation only, or will they be used to decide upon management strategies in respect to naturalness, ecosystem stability, or sustainability? In any case the selection of the elements to be analysed is the most crucial point.

Acknowledgements

The data assessment on the intensive monitoring plots was co-financed by the European Commission within the European Union Scheme on the Protection of Forests against Air Pollution. We thank Prof. Dr. H. Bugmann and two anonymous reviewers for valuable comments on the first version of the present paper.

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