

Sampling measures of tree diversity

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ABSTRACT

The monitoring of tree diversity and forest structure is a key pre-requisite for understanding and managing forest ecosystems. This paper addresses the question whether and how tree diversity measures can be estimated as extensions of existing forest resource inventories. The sampling simulator CRANCOD was employed to compare the precision of angle count and fixed radius plot sampling with respect to nine representative diversity indices. The sampling methods were compared (a) in their overall precision in terms of estimating diversity indices and (b) in their ability to provide precise estimations for three different forest types independent of the spatial inventory scale, e.g. inventories at stand or enterprises level or national forest inventories. The results indicated that most of the spatially explicit indices are more precisely estimated by fixed radius plots. Interestingly the superiority of fixed radius plot sampling to angle count sampling increases significantly with increasing diameter differentiation of forests. However, basal area, basal area related diversity indices and Pielou's segregation index can be estimated by angle count sampling with at least the same precision as from fixed radius plots. This provides options for situations where discarding angle count sampling is not possible because permanent sampling designs are in place or the importance of forestry summary statistics exceeds that of tree diversity by far.

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1. Introduction

Increasing and maintaining biodiversity on earth is a very important objective of conservation (Hunter, 1999). To this end biodiversity indicators help to establish and to monitor levels of biodiversity in terrestrial and aquatic ecosystems. The number of these biodiversity indicators, however, is vast and they range from gene to landscape patterns depending on spatial scales. To simplify the monitoring of biodiversity surrogate measures have been proposed, which are closely correlated with direct measures of biodiversity, but are easier to measure. These surrogate measures include indices accounting for three basic tree diversity aspects (Gadow, 1999; Pommerening, 2002), i.e. *the diversity of tree locations*, *species diversity* and *the diversity of tree dimensions* (e.g. stem diameters, tree heights). The surrogate role is based on the observation that a large variety of forest structures and/or tree species generally also provides a large amount of habitats for different species (Aguirre et al., 2003; Fuller et al., 2004; Lexerod and Eid, 2006; Pommerening, 2002, 2006a; Shirley, 2004; Sterba and Zingg, 2006).

Tree diversity indices are also good quantitative descriptors of forest structures (Aguirre et al., 2003; Lexerod and Eid, 2006; Pommerening, 2002, 2006a; Sterba and Zingg, 2006), which is a key pre-requisite for understanding the interactions between patterns and processes in forest ecosystems. Diversity indices are also important input variables for the reconstruction of forest structures used in spatially explicit growth models and computer visualisations (Hasenauer, 2006; Pommerening, 2006a; Pommerening and Stoyan, 2008).

There are two different strategies of data collection, *mapping* and *sampling*. Mapping involves the full spatial enumeration of all trees within a large observation window (i.e. stem charts or stem maps), while in sampling only a sub-set of trees and their spatial relationships are measured, usually in very small replicated observation windows. Mapping is very common in ecological studies and the corresponding data allow the application of powerful statistics and detailed analyses of plant interactions (see for example Dale, 1999; Illian et al., 2008).

However, often summary characteristics for larger geographic entities, such as forest districts, forest enterprises, political regions and whole countries, are required for management and political decision making. In this context sampling methods are the only feasible option. Since the observation windows, i.e. the sample plots, used for this purpose are comparatively small, tree diversity and structural indices are naturally more suitable than other more sophisticated characteristics from spatial statistics (Pommerening

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Table 1
Overview of diversity indices used in the sampling simulation. The number n of nearest neighbours used in this study was $n = 4$.

Index	Variable definition
Shannon (SH(BA), SH(N))	
$H' = - \sum_{i=1}^s p_i \ln(p_i) \quad (1)$	p_i Relative frequency of species i either referring to basal area (BA) or to stem number (N)
Simpson (SIM(BA), SIM(N))	
$D = 1 - \sum_{i=1}^s p_i^2 \quad (2)$	p_i Relative frequency of species i either referring to basal area (BA) or to stem number (N)
Dominance (DOM)	
$U_i = \frac{1}{n} \sum_{j=1}^n 1(DBH_i > DBH_j) \quad (3)$	$1(A) = 1$ if A is true, otherwise $1(A) = 0$
DBH differentiation (TD)	
$TD_i = 1 - \frac{\min(DBH_i, DBH_j)}{\max(DBH_i, DBH_j)} \quad (4)$	j The first neighbour tree
Mean DBH differentiation (TDM)	
$TDM_i = 1 - \frac{1}{n} \sum_{j=1}^n \frac{\min(DBH_i, DBH_j)}{\max(DBH_i, DBH_j)} \quad (5)$	j 1... n neighbour trees
Aggregation index (R)	
$R = \frac{\bar{r}_{observed}}{E(r)} \quad (6)$	$\bar{r}_{observed}$ Arithmetic mean of distances between reference trees and neighbours $E(r) = 0.5 \cdot \sqrt{\frac{A}{N}}$ N : number of trees, A : area of observation window
Mean directional index (MDI)	
$R_i = \sqrt{\left(\sum_{j=1}^n \cos \alpha_{ij} \right)^2 + \left(\sum_{j=1}^n \sin \alpha_{ij} \right)^2} \quad (7)$	α_{ij} Angle between a line pointing away from the reference tree i to neighbours j and a reference bearing (e.g. to north)
Mingling (M)	
$M_i = \frac{1}{n} \sum_{j=1}^n 1(species_i \neq species_j) \quad (8)$	$1(A) = 1$ if A is true, otherwise $1(A) = 0$
Segregation index (S)	
$S = 1 - \frac{p_{ij}}{E(p_{ij})} \quad (9)$	p_{ij} Probability that reference tree i and its nearest neighbour j have different species

and Stoyan, 2008). This also offers the opportunity of combining the sampling of diversity measures with existing forest resource inventories (Sterba, 2008) and adds significant value to traditional forest inventory with a comparatively low additional effort. Also such a combination of inventory objectives clearly facilitates the ideas of multipurpose forestry based on sustainable principles (Pommerening and Murphy, 2004).

Although tree diversity measures and their potential for conservation management have been fully accepted, there are only few publications which are explicitly dealing with the question of sampling and the development of inventory designs. A number of them arrive quite ambiguous results. For example Merganič and Šmelko (2004) investigated different sample sizes for the classification of mixed forest stands into diversity classes. They found that with a sampling intensity of about 1.5% of the total stem number almost 90% of the stands were correctly classified. Another sampling simulation study by Kint et al. (2004) asserted that the necessary sample size for the evaluation of diversity indices is often greater than 20% of the total stem number. Therefore further research concerning this topic will be valuable.

The objective of this study is to identify which of the two sampling methods either angle count sampling or fixed radius plot sampling is most suitable to measure diversity indices across a wide

range of different species compositions and degrees of structural complexity under Central European conditions. Based on the data of large completely mapped forest stands a sampling simulator was used to compare different sampling methods and sizes, whereas sampling methods where chosen which are frequently used for forest resource inventories.

The sampling simulations and analyses were carried out in such a way that the results are transferable to forest resource inventories at various scales, from traditional stand-wise inventories to modern regional and national inventories. The results provide an answer to the question in what way, if at all, forest resource inventories and biodiversity monitoring match.

2. Materials and methods

2.1. Measures of tree diversity

Nine frequently used diversity indices were selected and their formulae are given in Table 1.

The Shannon index H' and Simpson index D are both non-spatially explicit measures of relative species composition in a forest (Shannon and Weaver, 1949; Simpson, 1949). In this study they are calculated for both basal area and stem number propor-

Table 2

Characterization of the selected stands used for the sampling simulations: number of trees per hectare (SPH), basal area (BA), arithmetic mean diameter (\overline{DBH}), standard deviation of DBH (s_{DBH}).

	Even-aged				Uneven-aged				Coppice	
	Pure		Mixed		Pure		Mixed		Mixed	
	1	2	3	4	5	6	7	8	9	10
Area [ha]	5.99	4.36	2.53	1.14	1.69	1.69	0.61	0.96	0.43	0.47
SPH [ha^{-1}]	380	562	385	865	387	536	820	522	2417	2176
BA [$m^2 ha^{-1}$]	16.7	29.8	38.0	48.3	13.8	32.2	44.5	35.2	16.0	35.1
\overline{DBH} [cm]	23.1	24.6	33.6	26.0	18.9	24.2	21.6	23.1	8.7	11.9
s_{DBH} [cm]	5.39	8.31	11.28	9.16	9.92	13.43	14.96	18.03	2.94	8.00

tions. H' (Eq. (1)) takes values between 0 for only one species and $\ln(Z)$ for Z species with equal relative proportions. The Simpson index (Eq. (2)) D can take values between 0 and 1 and is interpreted as the probability that two individual trees picked at random belong to different species.

Eq. (3) gives the dominance index according to Hui et al. (1998). This index is a spatially explicit measure of the diversity of tree dimensions. It takes values between 0 and 1 and gives the proportion of the four nearest neighbour trees that are smaller than the reference tree. U_i takes values >0.5 if the majority of nearest neighbours is larger than the reference tree and values <0.5 otherwise.

Alternatives to the dominance index are DBH differentiation (Eq. (4)) and mean DBH differentiation (Eq. (5)), which are also spatially explicit measures. Their index values range from 0 to 1 and are larger the larger the differences between the dimensions of the reference tree and the neighbours (Füldner, 1995; Pommerening, 2002). DBH differentiation uses one and mean DBH differentiation four nearest neighbours.

The aggregation index R (Eq. (6)) of Clark and Evans deals with the spatial arrangement of trees in a stand (Clark and Evans, 1965). R can take values between 0 and 2.1419, the interpretation of the values is usually as follows: $R > 1$ for patterns with a tendency to regularity and $R = 1$ in case of a completely random arrangement of tree positions, while $R < 1$ indicates clustering.

An alternative index representing the spatial arrangement of trees is the mean directional index (Corral-Rivas, 2006) with R_i values of 0 for a spatial arrangement in a square lattice and increasing values for more clustered patterns (Eq. (7)). The mean directional index uses $n = 4$ nearest neighbours.

The mingling index, another measure of species diversity (Eq. (8)), is defined as the proportion of the four nearest neighbours that differ from the reference tree in terms of tree species (Gadow, 1993). Values range between 0, for no intermingling and 1, when every neighbour belongs to a different species than the reference tree.

The segregation index S (Eq. (9)) by Pielou (1961) provides a spatially explicit measure for tree species diversity, which considers the ratio of the observed probability that the reference tree and its nearest neighbour belong to different species along with the same probability for completely randomly distributed or independent species attributes. S , which takes values between -1 and 1 , indicates spatially segregated tree species for $S > 0$, uncorrelated species patterns for $S = 0$ and spatially aggregated species for $S < 0$.

All diversity indices in Table 1 were used as population characteristics in this study, i.e. for the indices defined in Eqs. (3)–(5), (7) and (8) arithmetic means were calculated. As a population characteristic the mingling index (M) is for example computed as $\overline{M} = (1/N) \sum_{i=1}^N M_i$ with N = number of trees in a forest stand or a sample.

For further reading and examples of interpretation see Aguirre et al. (2003); Davies and Pommerening (2008); Kint et al. (2004); Kint (2005); Lexerod and Eid (2006); Merganič and Šmelko (2004), and Pommerening (2002, 2006a).

2.2. Mapped data

Spatially mapped data served as a basis for the sampling simulation. Data with a sufficiently large observation window (>1 ha) or a sufficiently large number of trees (at least 100 stems) were selected, based on Pommerening and Stoyan (2006) who found that under these conditions edge effects play a minor role. Using these criteria we selected mapped data from ten different forests as to provide a wide variety of different structures and species compositions. The data included mapped stands from Austria (experimental plots of the Institute for Forest Growth, BOKU-University, Vienna), Germany (data from STIPSI—A Sampling Simulator for Forest Stands and Forest Areas, FVA—The Forest Research Institute Baden Württemberg, 2005) and Switzerland (sample plots from WSL—Swiss Federal Institute for Forest, Snow and Landscape Research). The selected data were classified into forest types: (1) even-aged, (2) uneven-aged and (3) coppice stands, whereas even-aged and uneven-aged stands were subdivided into pure and mixed stands. This classification was made according to the major forest types of Central Europe. Note that even some of those stands that were classified as “pure” had more than one tree species present. However, in all “pure” stands the proportion of the main tree species exceeded 80% of the total stem number. Table 2 presents a short overview of the characteristics of the selected data.

The area of the observation windows varied between 0.43 and 5.99 ha, with a minimum of 380 and a maximum of 2417 stems per hectare. With a basal area between 13.8 and 48.3 $m^2 ha^{-1}$, a mean DBH (diameter at breast height, 1.30 m above forest floor) from 8.7 up to 33.6 cm and between one and ten different species the selected stands represent a large variety of characteristics. Further details of forest structure and tree diversity are provided in Fig. 1.

The aggregation index and the mean directional index both indicate a more or less random distribution of tree positions for the even-aged and uneven-aged stands, whereas the coppice stands show distinctive clusters of trees. Shannon and Simpson indices discriminate very well between pure and the mixed stands and the high species diversity of coppice stands is clearly indicated. Interestingly, the dominance index fails to discriminate between the five forest types. As expected, the DBH differentiation and the mean DBH differentiation give very similar results and clearly show a marked difference in the DBH differentiation for mixed stands when compared to pure stands and also generally higher differentiation values for the uneven-aged stands in comparison to even-aged stands. The low differentiation values for the coppice stands are also realistic when considering trees with multiple stems of similar size, which are typical of this forest type.

2.3. Sampling simulation

All sampling simulations were carried out with the CRANCOD program (Pommerening, 2006b). This software is able to simulate a variety of sampling designs based on:

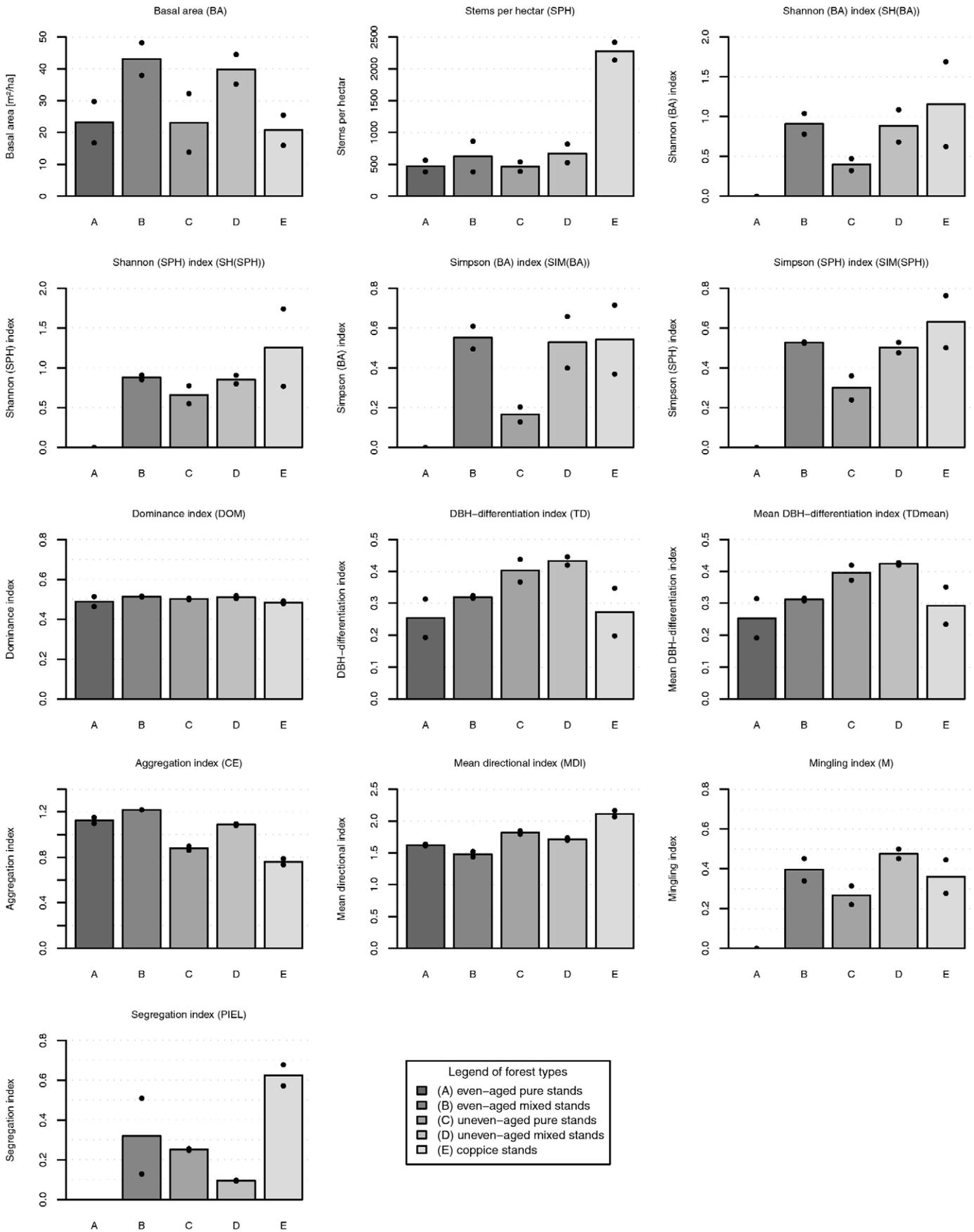


Fig. 1. Characterization of the sample sites by the corresponding tree diversity indices: bar plots show the arithmetic mean index value of the forest types, whereas points indicate the index values of single stands.

- Fixed radius plots or variable radius plots with a fixed number of sample trees using rectangular or circular sample plots.
- Bitterlich's (1984) angle count sampling, also referred to as variable radius plot sampling, relascope sampling and point sampling, with different basal area factors (BAF, basal area per hectare [$\text{m}^2 \text{ha}^{-1}$]) which each sample tree represents).

Samples are selected systematically with a random start and the spacing of the systematic grid can be modified by the user along with some other simulation parameters, e.g. the number of replications per sample size. For this study the angle count sampling method (AC) and sampling with circular fixed radius plots (FR) were chosen, as they are widely used in forest practice in many different European countries. For the angle count sampling a basal area factor of $4 \text{ m}^2 \text{ha}^{-1}$ was selected according to the recommendations of the Austrian National Forest Inventory for even- and uneven-aged high forest stands (Gabler and Schadauer, 2008). Using this BAF in high forest stands with tree dimensions common in this type of forest, angle count sample points include on average seven to eight trees. Translating this to coppice stand conditions with generally smaller tree diameters resulted in a BAF of $2 \text{ m}^2 \text{ha}^{-1}$.

To ensure the comparability of the two sampling methods the radius (r) of the circular fixed radius plots was calculated from the BAF, the basal area (BA) per hectare and the number of stems (SPH) per hectare for each stand according to Eq. (10), in order to obtain the same number of sample trees from both methods.

$$r = \sqrt{\frac{z \cdot 10,000}{\text{SPH} \cdot \pi}} \quad \text{with} \quad z = \frac{\text{BA}}{\text{BAF}} \quad (10)$$

Based on the average stand size of the study sites the initial grid spacing, i.e. the distance between sample plot centres, was set to 50 m. This grid spacing was then reduced by 5 m in successive simulation steps up to the point where no further reduction was possible, since small grid spacing values can cause sample plot overlaps. To avoid overlapping sample plots a minimum distance between the boundaries of the sample plots was set to 0.1 m. This minimum distance was also applied between sample plot boundaries and the boundaries of the study sites. Each simulation step was replicated 3000 times and the systematic grid was re-built in each of them from a randomly selected starting point and a random bearing. The results of the sampling simulations were then compared with those of the original mapped forests. For the estimation of spatial diversity indices from sampling all nearest neighbours of the sample trees were taken into account (Fig. 2) following the recommendation by Pommerening and Stoyan (2006). This is referred to as *plus-sampling* (Illian et al., 2008) and means that we considered also the off-plot nearest neighbours, which were not inside the sample plots.

In order to reduce any bias associated with the spatial results from the original mapped forests (edge bias) to a minimum the NN1-edge-correction method (Pommerening and Stoyan, 2006) was used. In addition to the nine tree diversity indices also the traditional forestry characteristics trees per hectare (SPH) and basal area (BA) were included in the sampling analysis.

The simulation process yielded index values for each replication (m_i), as well as detailed information on the number of simulated sample plots (sp), the bias and root mean square error (RMSE). As a result of the sampling simulation summary statistics were calculated for each index and sample size.

2.3.1. Statistics

Bias and RMSE comprehensively describe the accuracy for a given sampling design and sample size:

$$\text{Bias} = \hat{\theta} - \theta \quad (11)$$

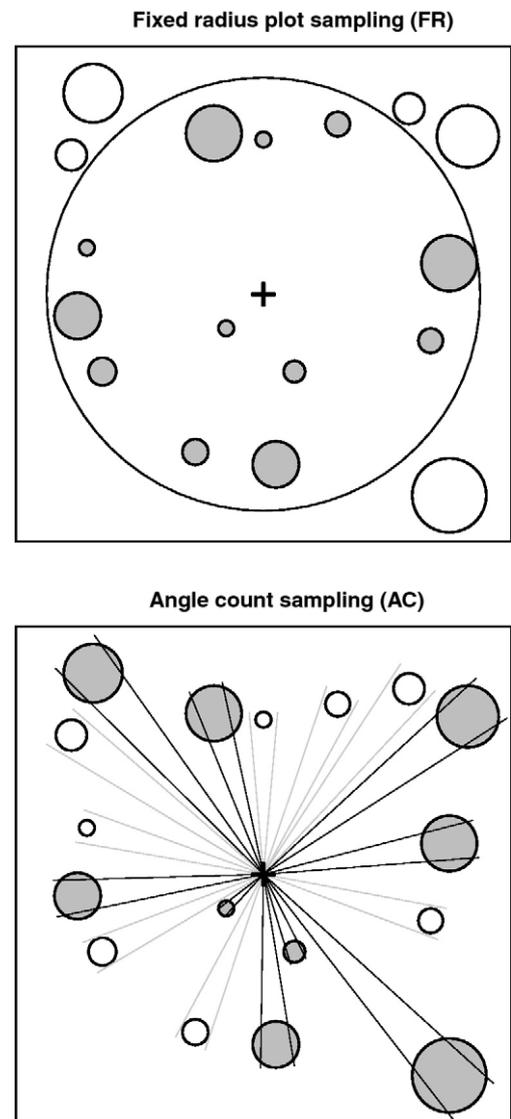


Fig. 2. Position of the sample trees (grey shaded) and their nearest neighbours (white) within and outside the sample plot area (plus sampling) for the fixed area plot sampling (upper) and for the angle count sampling method (lower).

$$\text{RMSE} = \sqrt{\frac{1}{m-1} \sum_{i=1}^m (\hat{\theta}_i - \theta)^2} \quad (12)$$

θ is the index value for the entire mapped population, $\hat{\theta}$ is the index value estimated from the m sampling replications, $\hat{\theta}_i$ is the index value estimated from sampling replication i , m is the total number of replications.

However, in this study a different approach was taken. Our principle objective was to describe the variation between sample plots within a stand as a population characteristic and thus to focus on precision rather than accuracy. Accuracy refers to the size of deviations from the true means, θ , whereas precision refers to the size of deviations from the mean, $\hat{\theta}$, obtained by the repeated application of the sampling procedure (Cochran, 1971). The concept of precision is related to efficiency: A sampling method is more efficient than another one, if a variable of interest can be estimated with a smaller sample size for a given precision (West, 2006). To estimate the necessary sample size for a given precision the standard deviation would be required. Therefore we derived the SD' as an equivalent to the standard deviation. Since the estimators for

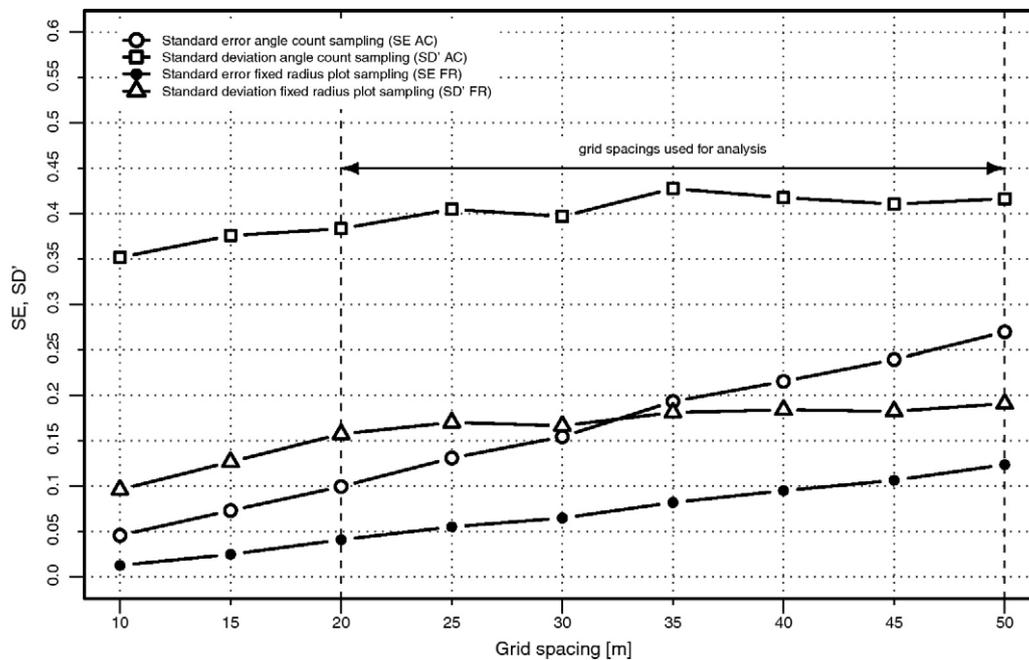


Fig. 3. Performance of standard error (*SE*) and standard deviation (*SD'*) for angle count sampling (*AC*) and fixed radius plot sampling (*FR*) with increasing grid spacing. Exemplary for the aggregation index (*CE*) in an uneven-aged mixed forest stand.

the true diversity indices are not the unweighted arithmetic means of the diversity indices as calculated for each fixed radius plot or angle count, we only could estimate an equivalent to the standard deviation (*SD'*). Which later on can be shown to be independent of sample size within a large range of grid spacings. *SD'* as a population characteristic for the variation between plots within forest stands is calculated according to Eqs. (13) and (14) from the output of the simulation process, namely the bias, the *RMSE*, the number of sample plots (*sp*, obtained by the repeated application of the sampling procedure), and the number of replications (*m*):

$$SE = \sqrt{\frac{(RMSE^2 - bias^2) \cdot m}{m - 1}} \quad (13)$$

$$SD' = SE \cdot \sqrt{sp} \quad (14)$$

In contrast to the *RMSE* and the standard error, the standard deviation *SD'* is within a certain range of grid spacing independent of the sample size and characterises the variation of the diversity indices within the investigated stands. Solving Eq. (14) for *sp* would then always give the necessary number of plots per stand for a wanted precision of the respective index.

2.3.2. Minimum grid spacing and population characteristic $\overline{SD'}$

Sampling grid spacing was the main variable determining the overall sample size, since the radius of the circular sample plots and the BAF were derived as described at the beginning of Section 2.3 and then fixed.

During the simulation process grid spacing was set to a high initial value, which corresponds to a small sample size, and then subsequently decreased to produce larger sample sizes. This process is limited by the requirement of non-overlapping sample plots for unbiased estimations.

With small grid spacing values it is also possible that one tree is selected as off-plot nearest neighbour of sample trees of more than one plot. This can lead to spatial autocorrelation effects (Bitterlich, 1968, 1984; Loetsch et al., 1973). To test if any autocorrelation effects occurred with decreasing grid spacing, the standard deviation (*SD'*) was plotted against the grid spacing. Fig. 3 shows the performance of *SD'* (Eq. (14)) with increasing grid spacing (i.e. with

decreasing sample size) using the aggregation index (Eq. (6) in Table 1) in an uneven-aged mixed stand as an example. Autocorrelation effects can be identified by a distinct decrease of *SD'*. *SD'* shows only a very moderate variation in the interval between 20 and 50 m, whereas a marked increase can be observed at grid spacings up to 20 m, which are most likely caused by autocorrelation effects. Thus same trend was found for all other indices. The grid spacing, where autocorrelation effects occurred for the first time, 20 m in this example, was used as a cut-off point to define minimum grid spacing.

Fig. 3 also shows the performance of *SE* (Eq. (13)) with increasing grid spacing. Contrary to *SD'*, *SE* is constantly increasing with increasing grid spacing for both sampling methods. Within a grid spacing of 20–50 m *SD'* obviously does not depend on the sample size. Therefore we decided to use only *SD'* values resulting from sampling grid spacings between 20 and 50 m for all further calculations. This is the sampling grid range, which ensures unbiased index estimations, because the sampling plots are spaced widely enough to avoid autocorrelation. We then calculated the population characteristic $\overline{SD'}$ as the quadratic mean of seven standard deviation values (Eq. (14)) between grid spacings of 20 and 50 m for each forest stand, tree diversity measure and sampling method. $\overline{SD'}$ is now a population characteristic, which is independent of the sample size.

Both strategies, avoiding autocorrelations and using $\overline{SD'}$ within a certain range of grid spacing, ensure that the results of this study can also be transferred to regional and national inventories, where autocorrelations typically do not occur because of grid spacings between 500 m and 3.5 km and where the dependence of sampling errors on sample size is different to that at stand level.

2.3.3. Testing the sampling methods

The sampling methods considered were compared in two different ways.

To study the precision of the sampling methods in estimating the different diversity indices for each forest type the ratio of the variances of the index values was compared. These ratios were calculated from variances obtained by squaring the $\overline{SD'}$ given in Fig. 4. The comparison of the variance ratios indicates the suitability of a sampling method for estimating an index with regard to a certain forest

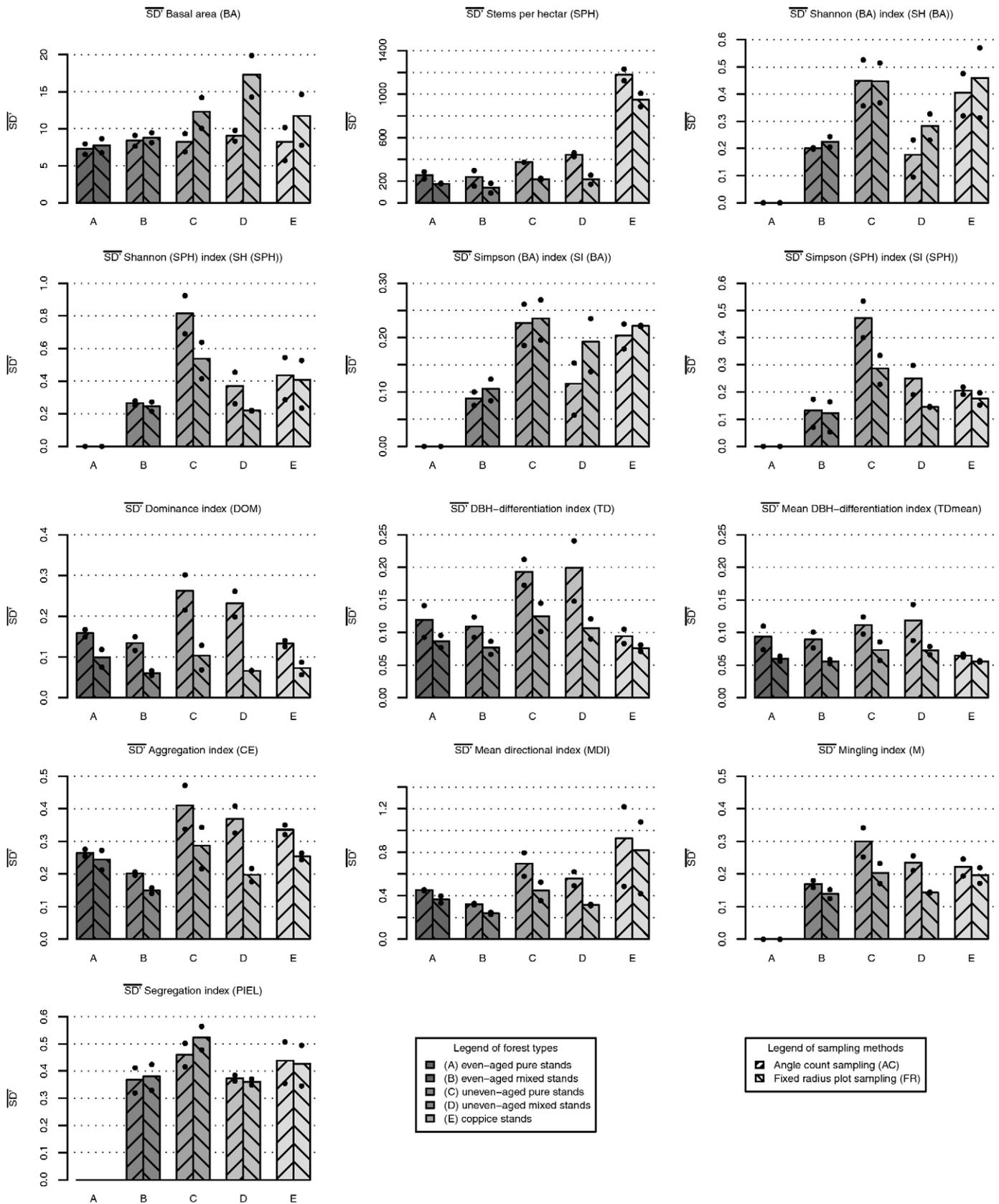


Fig. 4. Mean standard deviations, \overline{SD} , of the tree diversity indices calculated as quadratic mean of all standard deviations between 20 and 50 m grid spacing and obtained from the sampling methods in the five different forest types. Bar plots show the \overline{SD} values for each sampling method, index and forest type, whereas the points indicate the \overline{SD} values of the sampling methods associated with the two investigated stands per forest type.

Table 3
Variance ratios of the diversity indices for the ten forest stands used in this study. The values represent the variance ratio VAR_{AC}/VAR_{FR} .

	Even-aged				Uneven-aged				Coppice	
	Pure		Mixed		Pure		Mixed		Mixed	
	1	2	3	4	5	6	7	8	9	10
BA	0.937	0.846	0.886	0.925	0.470	0.432	0.242	0.339	0.539	0.483
SPH	1.528	2.710	2.911	2.746	2.744	3.155	3.249	6.189	1.612	1.493
SH (BA)	n.d.	n.d.	0.981	0.657	1.044	0.942	0.169	0.501	1.046	0.695
SH (SPH)	n.d.	n.d.	1.359	1.045	2.098	2.766	1.455	4.240	1.479	1.068
SIM (BA)	n.d.	n.d.	0.800	0.656	0.942	0.899	0.173	0.426	1.043	0.650
SIM (SPH)	n.d.	n.d.	1.796	1.114	2.555	3.089	1.741	4.111	1.587	1.227
DOM	1.595	4.927	5.109	4.472	5.496	9.926	8.801	15.603	2.069	6.185
TD	1.453	2.186	2.053	1.937	2.139	2.899	2.697	3.958	1.378	1.683
TDm	1.747	2.962	2.947	2.151	2.094	2.901	1.760	3.318	1.210	1.503
CE	1.023	1.432	1.715	1.947	1.889	2.440	2.257	5.363	1.732	1.759
MDI	1.315	1.779	2.071	1.618	2.289	2.670	2.353	4.048	1.349	1.277
M	n.d.	n.d.	1.628	1.397	2.163	2.183	2.202	3.146	1.278	1.256
PIEL (S)	n.d.	n.d.	0.942	0.943	0.791	0.757	1.211	0.958	1.053	1.057

BA: basal area per hectare; SPH: stems per hectare; CE: aggregation index by Clark and Evans; DOM: dominance; MDI: mean directional index; M: mingling; SH (BA): basal area based Shannon index; SH (SPH): SPH-based Shannon index; SIM (BA): BA-based Simpson index; SIM (SPH): SPH-based Simpson index; TD: differentiation; TDm: mean DBH differentiation; PIEL (S): segregation index by Pielou; n.d.: not defined in mono-species stands.

type: The larger the deviation of this ratio from 1, the more the sampling methods compared differ with regard to their precision.

In order to test, if generally one of the two sampling methods is more efficient, the following test has been performed: Assuming that the variance ratios in different forest types only deviate randomly from one, the probability for a variance ratio larger than 1 is the same as the probability for a variance ratio smaller than 1, namely 0.5. Given this, the probability that at least in k out of $s = 10$ stands (only $s = 8$ stands for the species diversity indices) the variance ratio is larger than 1, can be described by the binomial distribution, i.e. $P(\geq k, s) = \sum_{i=k}^s \binom{s}{i} \cdot 0.5^k \cdot 0.5^{s-k}$ with $s = 10$ and $s = 8$, respectively. If this probability is less than 0.05 the H_0 -hypothesis suggesting equal probability for larger variance of angle count sampling method (AC) compared to fixed radius plot sampling method (FR) will be rejected at the 5% significance level. The same test can be performed for $P(\leq k, s)$. If $P(\geq k, s) < 0.05$, the angle count sampling method leads to a significantly higher variance, while if $P(\leq k, s) < 0.05$, angle count sampling produces a significantly smaller variance. The results of these two tests are given in Table 4 and will be discussed in greater detail in the next section.

3. Results

The use of Eq. (10) ensures that the sample size in terms of the number of sample trees are equal for both sampling methods. The expected number of sample plots (sp) is a function of the square sampling grid, i.e. $sp = \sqrt{\text{area of the stand}[m^2]/\text{grid spacing}[m]^2}$. Fig. 4 provides an overview of the \overline{SD} values, which were obtained from the sampling simulations for the different diversity indices. The results give a first impression of the performance of the two sampling methods and indicate important differences. In most cases the \overline{SD} values for AC are larger than those for FR. Notable exceptions are basal area, the BA-based Shannon and Simpson indices and Pielou's segregation index. In many cases as expected \overline{SD} is larger for the two uneven-aged forest types than for the even-aged and the coppice types. However, in some cases such as basal area, the mingling index, DBH differentiation and diameter dominance, there is a trend that one sampling method leads to more uniform values of \overline{SD} across the different forest types than the other. Such an approximately even distribution of \overline{SD} is an important requirement for selecting a suitable sampling method.

With the mean standard deviations (\overline{SD}) given in Fig. 4 the variance ratios of Table 3 were calculated. These values indicate directly the ratios between the sample sizes of AC and FR necessary to achieve the same precision. For example the variance ratio of 0.242 for basal area per hectare (BA) and forest type number 7 means that for AC sampling a sampling intensity of only 24.2% of that of FR sampling is required to achieve a given precision. By contrast, for DBH differentiation (TD) 2.7 times the number of fixed radius plots are necessary to achieve the same precision with angle count sampling in the same forest type.

Generalizing over all forest types, for basal area and the basal area related species diversity indices (Shannon index and Simpson index), the variance between angle count plots is as expected about 30% less than the variance between the fixed radius plots within the stands. For stems per hectare the variance from angle count sampling is nearly 3 times as large as the within-stand variance incurred when using fixed radius plots. Interestingly, for the Pielou index the variances associated with both sampling methods are about the same, while for all the other spatially explicit diversity indices the variance obtained from angle count sampling is approximately twice the variance that results from using fixed radius plots. Strikingly large is the variance ratio between angle count sampling and fixed radius plot sampling for diameter dominance: The variance associated with angle count sampling is here on average nearly 6 times larger than that obtained from FR sampling.

Fig. 5 presents the correlations between the variance ratios VAR_{AC}/VAR_{FR} and DBH differentiation for the diversity indices used in this study. The variance ratio increases, i.e. the angle count sampling method is less efficient, with increasing DBH differentiation. This correlation is highly significant for the mean directional index and the DBH differentiation and significant for the aggregation and the mingling index. The relationship between variance ratios and diameter differentiation is much weaker for basal area, stems per hectare, the Shannon and the Simpson indices and for the segregation index.

We consider the correlation between the variance ratios and DBH differentiation as an important, new finding that merits more research in the future.

3.1. Overall comparison of the precision of the sampling methods

Table 4 presents the test results relating to the hypothesis, that both sampling methods produce the same variances for all diversity indices and forest types.

3.1.1. Forestry characteristics

The results of the forestry characteristics basal area and trees per hectare reflect the expectation that the angle count sampling method provides more precise estimations for BA and the fixed radius plot sampling method for SPH. Table 4 shows that this applies to all investigated stands. The differences in the precision of the two sampling methods are especially marked for uneven-aged and coppice stands.

3.1.2. Non-spatially explicit species diversity indices

As representatives of non-spatially explicit species diversity indices the sampling performance of Shannon and Simpson indices based on both relative BA and SPH frequencies was studied (Table 4). The SPH-based Shannon and Simpson indices are both clearly more precisely estimated ($pVAR_{AC} > VAR_{FR} = 0.004$) by means of the fixed radius plot sampling method. Not unexpectedly this is different for the BA-based Simpson and Shannon indices. The

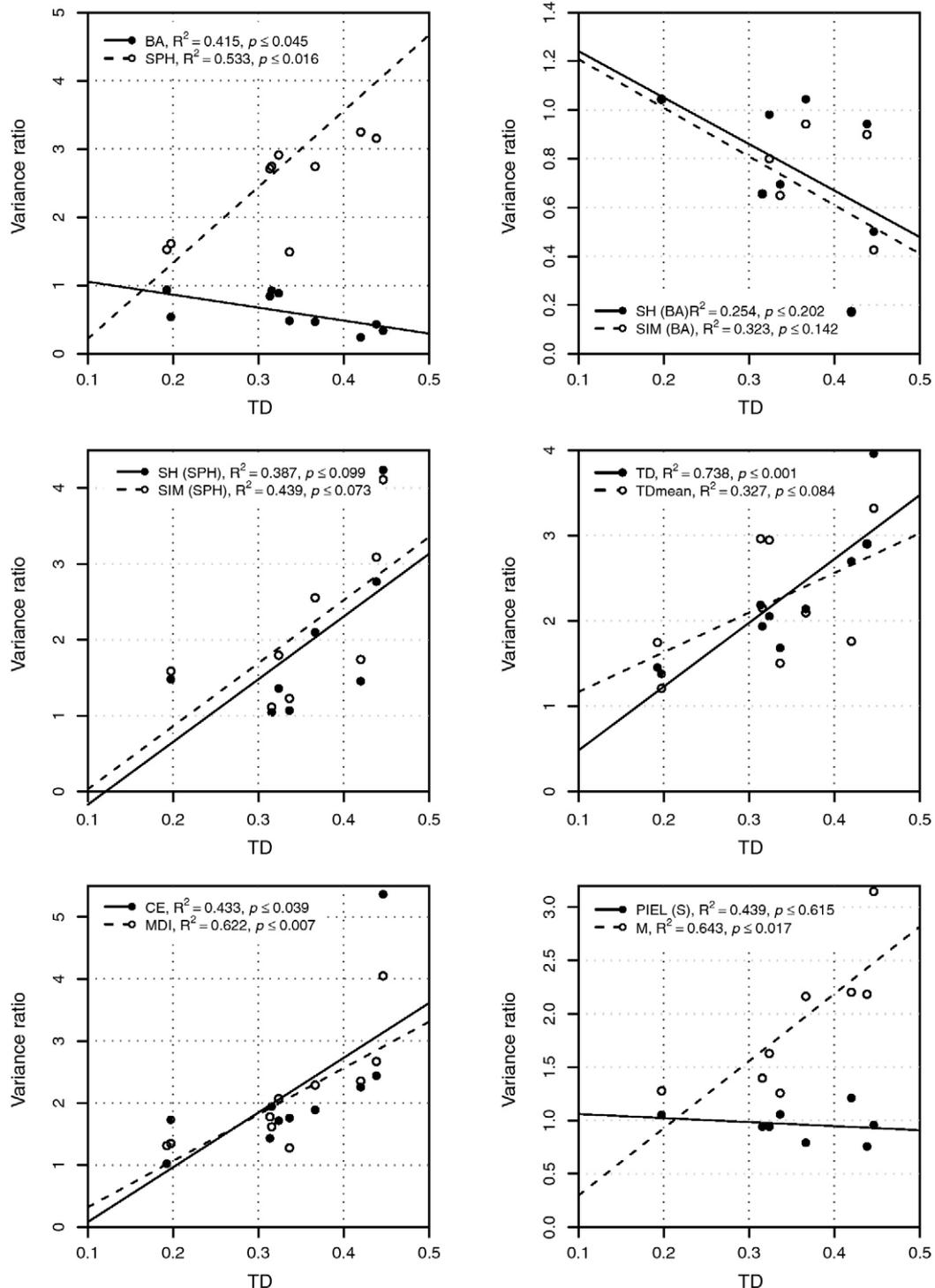


Fig. 5. Relationship between the variance ratio VAR_{AC}/VAR_{FR} of the investigated tree diversity indices and the DBH differentiation index (TD).

Table 4

Probabilities P for at least k out of $s=8, s=10$ stands, respectively, with a variance ratio larger than 1 based on the assumption (H_0 -hypothesis) that both cases ($VAR_{AC} > VAR_{FR}$ and $VAR_{FR} > VAR_{AC}$) are equally likely.

Variable	Number of stands observed, s	$VAR_{AC} > VAR_{FR}$		$VAR_{FR} > VAR_{AC}$	
		k	$P(\geq k, s)$	k	$P(\geq k, s)$
BA	10	0	1.000	10	0.001
SPH	10	10	0.001	0	1.000
SH (BA)	8	2	0.965	6	0.145
SH (SPH)	8	8	0.004	0	1.000
SIM (BA)	8	1	0.996	7	0.035
SIM (SPH)	8	8	0.004	0	1.000
DOM	10	10	0.001	0	1.000
TD	10	10	0.001	0	1.000
TDm	10	10	0.001	0	1.000
CE	10	10	0.001	0	1.000
MDI	10	10	0.001	0	1.000
M	8	8	0.004	0	1.000
PIEL (S)	8	3	0.855	5	0.363

BA: basal area per hectare; SPH: stems per hectare; CE: aggregation index by Clark and Evans; DOM: dominance; MDI: mean directional index; M: mingling; SH (BA): basal area based Shannon index; SH (SPH): SPH-based Shannon index; SIM (BA): BA-based Simpson index; SIM (SPH): SPH-based Simpson index; TD: differentiation; TDm: mean DBH differentiation; PIEL (S): segregation index by Pielou; n.d.: not defined in mono-species stands, k gives the number of stands where the H_0 was rejected.

BA-based Simpson index was significantly better estimated by the angle count sampling method with a probability of 0.035, while no clear statement can be made for the BA-based Shannon index.

3.1.2.1. Indices relating to the diversity of tree locations. For diversity indices in this group the superiority of the fixed area plot sampling method is highly significant ($pVAR_{AC} > VAR_{FR} = 0.001$) (Table 4). This means that the fixed radius plot sampling method is in each of the ten investigated stands the more precise method. The differences in the precision of the sampling methods are particularly interesting because of the greatly differing variance ratios (Table 3).

3.1.3. Spatially explicit species diversity indices

In this group the mingling index and Pielou's segregation index were compared. For the segregation index the p -values given in Table 4 considerably exceeded 0.05, i.e. none of the investigated sampling methods could be identified as the more precise one. However, for the mingling index the variance ratio associated with fixed radius plot sampling was highly significant ($pVAR_{AC} > VAR_{FR} = 0.004$), i.e. this method performed better than the angle count sampling method.

3.1.4. Impact of the grid spacing on the precision of the sampling methods

The results followed the expectation that summary characteristics are more precisely estimated with smaller grid spacing values and thus larger sample size until the grid spacing values are so small that autocorrelation effects occur.

4. Discussion

In this study the performance of angle count sampling method (AC) and fixed radius plot sampling method (FR) was analysed with regard to different diversity measures and forestry summary characteristics along a wide range of forest stands with different structural composition. The selected stands differ markedly in species composition and structural complexity and are representative of Central Europe. The diversity indices considered include measures of all three diversity aspects and are therefore a good representation of the vast range of tree diversity indices (see for

example: Pommerening, 2002; Staudhammer and LeMay, 2001; Sterba and Zingg, 2006).

Measures related to basal area, i.e. basal area per hectare and the BA related Shannon and Simpson indices, are more efficiently estimated using angle count sampling. In the group of spatially explicit diversity indices only the Pielou index can be sampled with the same efficiency using both sampling methods, AC and FR. This is an interesting finding suggesting that Pielou's segregation index is an obvious candidate for AC-based forest resource inventories, where the sampling design cannot easily be modified, e.g. the Austrian and German National Forest Inventories (Federal Ministry of Food, Agriculture and Consumer Protection, 2006; Gabler and Schadauer, 2008), or any inventory at forest district level, which is based on permanent sampling designs (Sterba, 2008).

Stems per hectare and all spatially explicit diversity indices other than the Pielou index are more efficiently estimated by fixed radius plot sampling. The superiority of FR to AC increases with increasing diameter differentiation. These results hold as long as the layout of the sampling grid avoids any bias as a result of edge effects or spatial autocorrelation between individual plots.

The superiority of FR to AC was already reported by Maltamo and Uuttera (1998) based on characteristics describing the species composition, number of tree layers and diameter distributions. However, the authors compared fixed radius plots with angle counts using $BAF = 2 \text{ m}^2 \text{ ha}^{-1}$ and $BAF = 1 \text{ m}^2 \text{ ha}^{-1}$ in a way that the radius of the sample plots was chosen large enough so that all angle count sample trees were included in the fixed radius plots. As a consequence the number of sample trees was largest for fixed radius plot sampling, less in the angle count samples with $BAF = 1 \text{ m}^2 \text{ ha}^{-1}$ and smallest in the angle count samples with $BAF = 2 \text{ m}^2 \text{ ha}^{-1}$. By contrast, in our design the number of sample trees was exactly the same with both sampling methods.

Schreuder et al. (1992) compared angle count sampling with fixed radius plot sampling in the same way as in our study, i.e. ensuring the same within plot sample size (see Eq. (10)). They found that angle count sampling was most efficient in describing stems per hectare, average d^2h (which is an approximation for mean tree volume) and sum of d^2h (as an approximation of volume per hectare by diameter class), except for the smallest DBH class, which included all trees with a diameter smaller than 45 cm. Our study, however, is only based on stands with mean diameters, which are smaller than this. Therefore our results are in agreement with the work by Schreuder et al. (1992) with regard to basal area and stem number precision. Since neither Schreuder et al. (1992) nor Maltamo and Uuttera (1998) investigated the performance of spatially explicit diversity indices in sampling, no direct comparisons with their results are possible.

We consider our finding, that the efficiency of AC decreases with decreasing DBH differentiation, as crucial. This allows calculating the number of excess angle count samples needed to achieve the same precision as with a given number of fixed radius plot samples with regard to a particular diversity index. The expected DBH differentiation can easily be estimated from a preparatory test survey and the number of excess angle count samples is a useful information for deciding, which sampling method to prefer. Since DBH differentiation is a spatially explicit measure of describing forest structure, this finding also emphasises that sampling and spatial statistics are closely related.

4.1. Advantages and disadvantages of combining forest resource inventories and tree diversity monitoring

When discussing the feasibility of combining forest resource inventories with tree diversity monitoring it is important to contrast the advantages with the possible trade-offs.

The outcomes of this study suggest that with a given sample size multipurpose forest resource inventories should either (a) use fixed radius plots and as a consequence potentially compromise the results of traditional forestry summary characteristics such as basal area or total volume, or (b) use angle count samples with potentially poorer results particularly for spatially explicit diversity indices. The newly discovered relationship between variance ratios and DBH differentiation (Fig. 5) provides a means of quantifying these trade-offs. Generally the loss in precision of quantitative information on forest structure or the loss in efficiency of sampling them is smaller, the smaller the DBH differentiation. Thus in forests with even-aged mono-specific stand management, which commonly show a comparatively low diameter differentiation, both sampling methods are equally efficient, while for uneven-aged, mixed species forests, a strategic decision is required, which information is more important, traditional forest summary statistics or information on tree diversity.

The study confirmed once again that angle count sampling is an efficient and precise method of estimating traditional forestry summary statistics, particularly basal area and volume. Our results, however, clearly indicated that in the majority of cases angle count sampling is significantly less suitable for tree diversity monitoring than fixed radius plot sampling. Maltamo and Uutera (1998) investigated the sampling of measures of forest structure by means of the angle count method. The results of their study revealed that the lack of precision incurred by angle count sampling can to some degree be compensated for by a significantly increased sample size compared to conventional forest inventories using the same sampling method for estimating current stand volume. This is consistent with our findings.

Kint et al. (2004) compared circular sample plot and distance methods with respect to estimating diversity indices. The distance method has often been suggested for sampling measures of forest structure and is very popular in ecology (see Fuldner (1995); Krebs (1999)). However, the distance method is a biased sampling method and was therefore not included in this study. Exciting recent work by Kleinn and Vičko (2006a,b) and Nothdurft et al. (2010) demonstrated that biased sampling methods such as distance or *k*-tree methods can be successfully corrected by methods of spatial statistics. Once again this stresses the close relationship between sampling and spatial statistics in forestry. These approaches may in the future widen the range of possible sampling methods and may also pave the way towards a successful combination of angle count based forest inventories with tree diversity monitoring.

As described in Section 2, an experimental design was developed in this study that allows making general statements, which are applicable to various levels of forest resource inventory. Over the last decades there has been a worldwide trend of discontinuing stand-wise inventories in favour of regional and national forest inventories, where large strata are the primary sampling and planning units rather than forest stands, e.g. see Gabler and Schadauer (2007); Lanz et al. (2010); Moravčík et al. (2010). The need to include biodiversity measures and the question of suitable sampling methods for them is, however, the same as for stand-wise inventories.

Some regional or national inventories are firmly based on the angle count method, e.g. the Austrian and German National Forest Inventories (Gschwantner et al., 2010; Polley et al., 2010). The results of this study have demonstrated the suitability of this sampling method for BA-based Shannon and Simpson index as well as for Pielou's segregation index. The concept of the mingling index is very similar to that of the segregation index, which suggests that an adaptation of the mingling index including expected values may also lead to a similarly good performance of the AC method.

Simultaneous monitoring of forestry and diversity summary characteristics clearly adds additional value to existing forest inventories on the expense of comparatively little additional costs (Sterba, 2008), as opposed to the considerable costs of setting up and of implementing separate biodiversity inventories. As a result valuable quantitative information on forest structure is gained and there is the possibility of monitoring changes in tree diversity. By contrast the costs can slightly increase as a result of using plus-sampling and there may initially be a need for amending the inventory protocol and for training field staff. However, these disadvantages are outweighed by a considerable gain.

It should also be noted that it is clearly beneficial to sample characteristics belonging to different aspects of forest ecosystems at the same sample points and at the same time so that the different pieces of information gathered can be related to each other. This would for example allow relating the dynamics of natural regeneration to changes in the main canopy but also relating the impact of biotic and abiotic disturbances to biodiversity. Measures of tree diversity are also very informative for modern silviculture using methods of near-natural forestry (Pommerening and Murphy, 2004) and they are also useful for modelling (Pommerening and Stoyan, 2008). This is an important synergy gain, which cannot be emphasised enough, since usually inventories in different forestry subject areas are designed and implemented separately.

5. Conclusions

The fixed radius plot sampling method has proved to be the most suitable sampling method for the majority of tree diversity indices particularly in uneven-aged forests. Only basal area based diversity indices and Pielou's segregation index are more precisely estimated by angle count sampling or this method leads at least not to worse results than fixed radius plot sampling. This applies particularly to even-aged forests.

Diameter differentiation has turned out to be a valuable measure for describing the trade-off between the precision of traditional forestry and of diversity summary characteristics.

The results of this study apply to various spatial inventory levels and represent the most important forest types in Central Europe. Further research is required with respect to different forest types in other parts of the world.

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