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Distance and T-square sampling for spatial measures of tree diversity

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ABSTRACT

Distance sampling and its statistically improved variant, T-square sampling, are important sampling methods in plant ecology. They have often been applied in the context of plant density estimations and are comparatively easy to implement, since they intuitively follow the nearest-neighbour principle and thus do not require the layout of sample plots. Previous research studying distance sampling suggested that T-square sampling may also lead to an improved estimation of spatial tree diversity indices. We simulated distance and T-square sampling in six large fully mapped forest areas for seven tree diversity indices of which some competed for the same diversity aspect, i.e. *tree location* (dispersion), *tree species* and *tree size diversity*. Our results demonstrated that both distance and T-square sampling are indeed robust methods for sampling spatial measures of tree diversity. The sample size required for a sampling error of 10% does not exceed 20% of the total number of trees in a sampling area. T-square sampling has the ability to adapt to different spatial patterns of tree locations and this ability is key to the way the method controls estimation bias. The sample size required for species mingling and size differentiation clearly depends on the underlying spatial tree pattern in the sampling area. With most diversity indices, sample size reductions between 0.06% and 40% could be achieved by the application of T-square sampling compared to traditional distance sampling. All other conditions being equal, we could identify the uniform angle index, the species mingling index and the size differentiation index as those diversity indices achieving lower sampling error values than their competitors. For tree density estimations the Diggle and Byth estimators performed best. Based on our results, T-square sampling can be considered a robust sampling method for spatial tree diversity indices that is easy to apply in the field.

1. Introduction

With ongoing climate change the monitoring of biodiversity is crucial to identifying the right time for counteracting the loss of species and diversity in forest ecosystems (Banks-Leite et al., 2020). In this context, spatial tree diversity indices are important, because they can be measured with comparatively little effort and can act as surrogate measures of biodiversity (Pommerening and Grabarnik, 2019).

Non-spatial and spatial tree diversity indices do not necessarily need to be measured by mapping an entire plant population but can be collected on a sample basis which can considerably reduce the monitoring effort. The most common approach in forestry has been to combine tree diversity sampling with existing forest inventories. This strategy makes sense, because it requires little additional effort even if additional trees or tree variables need to be measured. In most cases, however, it is possible to simply use existing forest inventory data and to compute tree diversity indices from them without making any changes to the inventory protocols (Sterba, 2008; Motz et al., 2010).

Another strategy is to apply specialised sampling methods with the sole objective to sample measures of tree diversity. For this strategy, straightforward methods are often preferred that can be applied rapidly and with comparative ease. In plant ecology, distance methods are particularly popular for their ease of application. They are also known as plot-less sampling methods (Krebs, 1999; Diggle, 2014), because there is no need to lay out sample plots, which saves time and effort. The term plot-less sampling method is also often applied to angle count sampling (Bitterlich, 1984). Distance sampling includes a variety of different methods including line/strip transect sampling, point transect sampling,

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ordered distance and point quarter methods. Distance sampling has traditionally been used to estimate population density, i.e. the number of individuals per unit area, and to determine whether a spatial plant pattern is random, clustered or regular (Krebs, 1999). The focus of this study is on nearest-neighbour distance sampling. In plant ecology, typically two different kinds of distances are considered, distances (1) between sample points and nearest plants, and (2) between plants and their nearest neighbour plant. We have considered both types of distances in this study and extended the method to include a comparatively new possibility of using distance methods for the sampling of spatial tree diversity indices. This purpose has first been proposed by Füldner (1996) and Pommerening and Lewandowski (1996), and a modification of the distance method for sampling spatial diversity indices has been published by Hui and Albert (2004).

A well-known draw-back of distance methods is the fact that this type of sampling favours isolated individuals, i.e. plants surrounded by more empty space than the average individual (Diggle, 2014). In the context of forest ecosystems, isolated individuals are usually trees that are larger than the average tree and the empty space surrounding them is, in ecological terms, often considered their specific “growing space”, which they use to draw resources from. The preference of such trees in sampling can lead to biased estimations, as they are assigned a larger inclusion probability than smaller and less isolated trees (Pielou, 1977; Krebs, 1999).

Besag and Gleaves (1973) proposed the T-square procedure for alleviating the problem related to the preferential selection of isolated individuals. This is a variant of the distance method introducing a constraint for the selection of plants nearest to a sample point as detailed in Section 2.2. The constraint ensures that isolated plants do not have a larger inclusion probability than other plants. In the past, the T-square method has been applied to estimating population density and to testing spatial plant patterns for complete spatial randomness (CSR). To our knowledge, T-square sampling has so far never been explored for estimating spatial diversity indices. T-square and other distance-based methods for sampling spatial point patterns have recently been considered as a tool for surveying refugee camps and other unplanned human settlements (Bostoen et al., 2007; Diggle, 2014).

Spatial diversity indices usually indicate three different aspects of plant diversity, i.e. *location diversity* (dispersion), *species diversity* and *size diversity* (Pommerening and Grabarnik, 2019). Several competing indices have been proposed for each of these three aspects. For practical and scientific reasons, it is interesting to learn how such competing indices perform in terms of sampling error relative to one another. The sampling performance of competing tree diversity indices helps understand how they interact with specific sampling designs and provides decision support in practical sampling applications in terms of which index to prefer from a list of competitors (Pommerening and Stoyan, 2008; Torquato, 2002).

Based on the known benefit of T-square sampling in terms of mitigating the bias arising from the preference of isolated individuals in density estimations, our hypothesis was that this method is also likely to improve the estimation of spatial diversity indices. Accordingly, the objective of this study was to quantitatively examine the potential of T-square distance sampling for estimating spatial tree diversity indices in relation to the traditional distance sampling method carried out without bias control. We were particularly interested to learn (1) what factors drive the performance of the two methods, and (2) whether the performance differs between competing diversity indices. Finally, (3) we intended to find out whether T-square distance sampling can be considered a robust sampling method that produces reliable estimates across different spatial patterns and diversity indices.

2. Materials and methods

2.1. Spatial tree diversity indices

We selected seven different plant diversity indices measuring the diversity of plant location, plant species and plant size diversity (Table 1) in such a way that at least two of them compete with each other in terms of quantifying the same diversity aspect. The indices selected are often considered in the monitoring of tree diversity (Motz et al., 2010).

The *aggregation index* of Clark and Evans (1954) is one of the earliest diversity indices quantifying the spatial pattern of plant dispersion. The index is very efficient and popular and is known to perform best in statistical tests for complete spatial randomness (CSR; Corral-Rivas et al., 2006). Observed mean first-neighbour distance, $\bar{r}^{(1)}$, is divided by the mean distance of a plant pattern where the plant locations are completely random, $\mathbf{E}r^{(1)}$, which requires information on population density (Eq. 1 in Table 1). Usually, the interpretation of R' values is as follows: $R' > 1$, if the pattern has a tendency to regularity (also termed overdispersal), $R' = 1$, if it is completely random and $R' < 1$, if there is clustering in a pattern (also termed underdispersal). In a practical sampling context, the index components $\bar{r}^{(1)}$ and population density N are estimated as explained in Section 2.3.

Like the aggregation index by Clark and Evans (1954), the *uniform angle index* (Eq. 2) describes the spatial pattern of plant locations, i.e. the dispersion of the k nearest neighbours around a subject plant. However, this index is based on angles between neighbouring plants. The uniform angle index gives the proportion of angles between neighbouring plants (either in clockwise or anti-clockwise direction) that are smaller than a reference angle $\alpha_0 = \frac{360^\circ}{k+1}$. For $k = 4$ neighbours $\alpha_0 = 72^\circ$ (80 gon), which is expected for regular point patterns. Small values of W_i near 0 indicate that the plants in the vicinity of reference plant i are regularly dispersed (=overdispersed), whereas large values of W_i near 1 point to a clustered arrangement (=underdispersal) of the k neighbours of a subject plant (Aguirre et al., 2003).

Corral Rivas (2006) introduced the *mean directional index* (Eq. 3) as an alternative to the uniform angle index and the aggregation index by Clark and Evans (1954). This index is based on the directions of the lines that point from the subject plant to its nearest neighbours. More precisely, the mean directional index is the length of the sum of k unit vectors pointing from the sample plant to its nearest neighbours. The index takes large values in the case of clustering (=underdispersal) and small ones in the case of regular (overdispersed) plant patterns. Under the conditions of a Poisson process the expected value of the mean directional index, $\mathbf{E}R$, takes the value of 1.799 for $k = 4$ neighbours (Illian et al., 2008). Similar indices are used to describe animal movements and angular dispersion in plant neighbourhood models (Richards et al., 2010; Dale and Fortin, 2014).

Gadow (1993) defined *spatial species mingling* as the mean heterospecific fraction of plants among the k nearest neighbours of a subject plant i (Eq. 4 in Table 1). Due to the discrete nature of outcomes for a given k, there are only $k+1$ possible values M_i can take, i.e. $0/k$, $1/k$, …, k/k, where the number in the numerator denotes the number of neighbours with a species different from that of plant i. All index values lie between 0 and 1.

Hui et al. (2008) and Hui et al. (2011) proposed the *species richness-weighted mingling index* $M_i^{'}$ (Eq. 5 in Table 1) as an extension of the original mingling index by Gadow (1993) by merging the concept of species mingling with the concept of species richness. Accordingly, each M_i (from Eq. 4) is multiplied by the species richness s_i among the k nearest neighbours. Wang et al. (2021) amended the index definition by introducing term c (see Eq. 5 in Table 1) to ensure that the maximum number of species that are theoretically possible in a group of $k+1$ plants is limited by the number of species present in a population or by the number of nearest neighbours, k. Both the species segregation and

Table 1
Definitions of the spatial plant diversity indices used in this study.

Eq.	Name	Diversity of	Formula	Variable definitions
(1)	Aggregation index (Clark and Evans, 1954)	Location	$R' = \frac{\bar{r}^{(1)}}{\mathbf{E}r^{(1)}}$	$\bar{r}^{(1)}$– observed mean arithmetic distance between sample tree i and its first nearest neighbour; $\mathbf{E}r^{(1)} = 1/(2 \times \sqrt{N})$ with N – tree density.
(2)	Uniform angle index (Aguirre et al., 2003)	Location	$W_i = \frac{1}{k}\sum_{j=1}^{k} \mathbf{1}(\alpha_j < \alpha_0)$	α_j are the angles between neighbouring trees in (anti-)clockwise direction;$\alpha_0 = \frac{360^{\circ}}{k+1}$
(3)	Mean directional index (Corral-Rivas, 2006)	Location	$R_i = \sqrt{\left(\sum_{j=1}^{k}\cos\,\alpha_{ij}\right)^2 + \left(\sum_{j=1}^{k}\sin\,\alpha_{ij}\right)^2}$	α_{ij} is the angle pointing away from reference tree i to neighbours j and a reference bearing (e.g. due north).
(4)	Species mingling (Gadow, 1993)	Species	$M_i = \frac{1}{k}\sum_{j=1}^{k} \mathbf{1}\left(\text{species}_i \neq \text{species}_j\right)$	$\mathbf{1}(A) = 1$, if A is true, otherwise $\mathbf{1}(A) = 0$
(5)	Weighted species mingling (Hui et al., 2011)	Species	$M_i' = \frac{1}{k \times c}\sum_{j=1}^{k} \mathbf{1}\left(\text{species}_i \neq \text{species}_j\right) \times s_i$	s_i– species richness among the k nearest neighbours of tree i; $c = \min(S, k+1)$, where S – total species richness (either in the total population or at a specific sample point)
(6)	Size differentiation (Gadow, 1993)	Size	$T_i = 1 - \frac{1}{k}\sum_{j=1}^{k} \frac{\min(m_i, m_j)}{\max(m_i, m_j)}$	m_i– size of subject tree i, m_j – size of neighbour j
(7)	Size dominance (Aguirre et al., 2003)	Size	$U_i = \frac{1}{k}\sum_{j=1}^{k} \mathbf{1}(\mathrm{m}_i > \mathrm{m}_j)$	See previous definitions

the richness-weighted mingling index are less dependent on overall population species richness than the original mingling index. Values of M_i' are generally smaller and take a larger range of different values than those of M_i.

Gadow (1993) defined *size differentiation* (Eq. 6 in Table 1) as the mean ratio of smaller and larger plant sizes of the k nearest neighbours subtracted from one. Size differentiation produces continuous results between 0 and 1 and T_i increases with increasing average size difference between neighbouring plants.

The *size dominance index* (Eq. 7 in Table 1) was introduced by Hui et al. (1998) and later refined by Aguirre et al. (2003). The index gives the proportion of the k nearest neighbours dominated by subject plant i. The index draws on similarities with the construction of the mingling index, thus transforming a continuous variable into a binary one and in analogy to the species mingling index also produces only $k+1$ possible U_i values.

For each of these indices and each sampling replication, the means were estimated by pooling the index values of all sample trees using the general estimator introduced as Eq. (8) in Section 2.3. We used stem diameter (measured at 1.3 m above ground level) as a measure of tree size for m in Eqs. (6) and (7). All diversity indices were estimated for $k = 4$ nearest neighbours, the most commonly used value of k in the literature (Aguirre et al., 2003; Pommerening and Grabarnik, 2019), except for the aggregation index by Clark and Evans (1954) which only requires the consideration of the first nearest tree neighbour.

2.2. Sampling methods

Two nearest-neighbour distance methods were used in our simulations, i.e. traditional distance and T-square sampling. Both of them are not limited to trees or plants in general, but can be applied in a wide range of contexts. We based both methods on systematic grids of sample points with a random starting point and random inclination where the sample points were the locations of grid points. Systematic sampling is known for its efficiency in field measurements, but also for reducing overall variance compared to simple random sampling (Motz et al., 2010). First, we applied traditional distance sampling where the tree nearest to each sample point was selected as sample tree P according to Euclidean distance (Fig. 1).

As an alternative, T-square sampling (Besag and Gleaves, 1973;

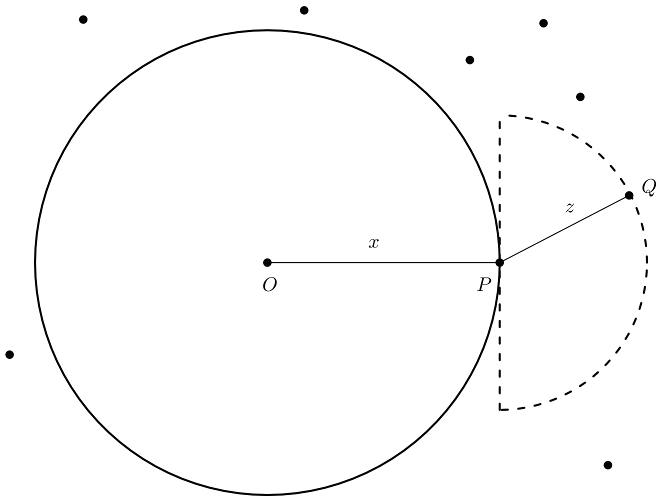

Fig. 1. Schematic view of a T-square sample with trees represented by point locations: P is the nearest Euclidean tree neighbour of sample point O and Q is the T-square nearest tree neighbour of sample tree P. The angle OPQ must be at least 90° so that P is constrained to be in the hemisphere to the right of the vertical dashed straight line. Distance x is measured from sample point O to its nearest tree neighbour P whilst z, the T-square distance, is measured from sample tree P to its nearest T-square neighbour (Krebs, 1999; Diggle, 2014).

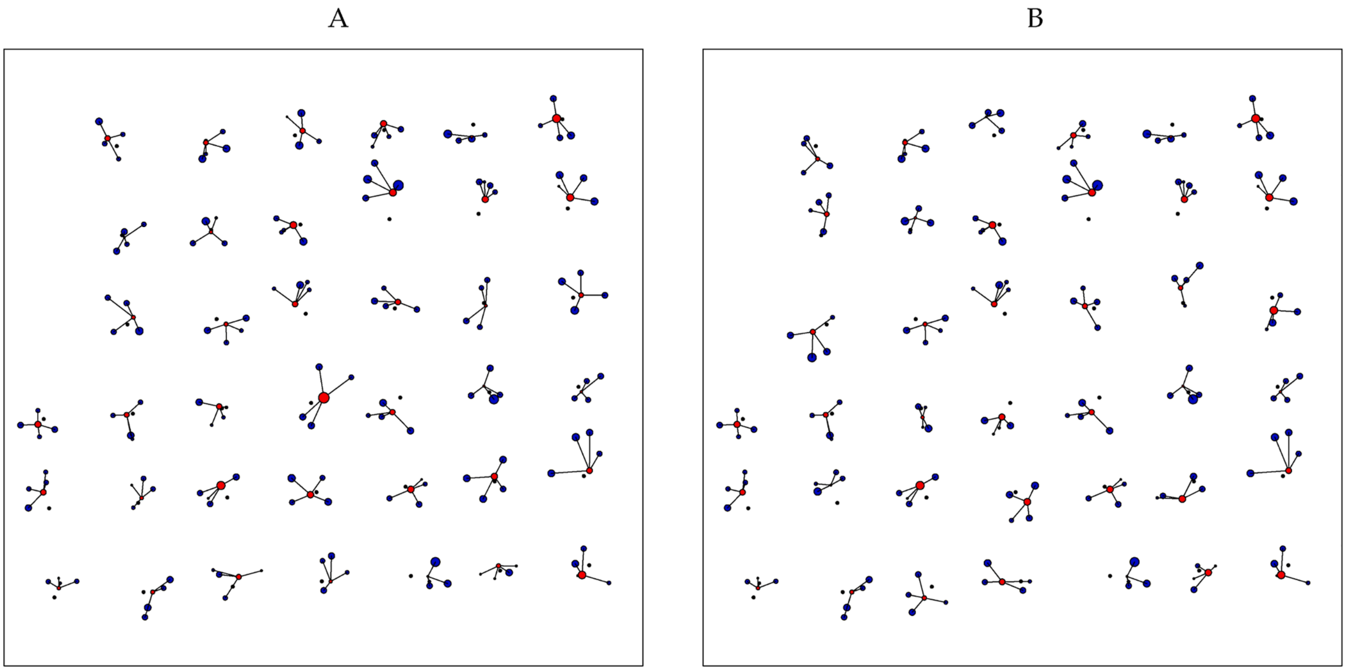

Fig. 2. Sampling area Rosalia (Austria), 170 × 164 m. A: Replication of a sampling simulation of the traditional distance sampling method. B: Replication of a sampling simulation of the T-square sampling method. Sample size $n = 39$. Black: Sample points. Red: Sample trees. Blue: $k = 4$ nearest neighbours for calculating the tree diversity indices of Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Krebs, 1999; Diggle, 2014; Zhang et al., 2022) was applied. With T-square sampling, the selection of the nearest Euclidean neighbour of a sample point *O*, i.e. sample tree *P*, has to satisfy the T-square criterion: The angle formed by points *OPQ* must be at least 90° (Fig. 1). Here *Q* is the nearest Euclidean neighbour of the potential sample tree *P*. If this condition is not met, the next closest Euclidean tree neighbour of sample point *O* is considered until one is found that satisfies the angular constraint. In the context of the traditional distance sampling method, the unconstrained distance between the sample tree and its first Euclidean neighbour is denoted $r_i^{(1)}$, and z_i, also referred to as T-square distance, is the constrained distance of T-square sampling. If the first nearest neighbour of a sample point happens to satisfy the T-square criterion, $z_i = r_i^{(1)}$.

Once sample trees *P* were identified using both traditional distance sampling and T-square sampling, the four nearest Euclidean neighbours of each sample tree were determined in a second step and the diversity indices of Section 2.1 were calculated. With both sampling methods, the principle of selecting these neighbours of sample trees was the same, i.e. no further constraint was applied.

2.3. *Sampling simulations*

Sample sizes included 5, 10, 20, 30, …, 140, 150 sample trees and each of the 16 sample sizes was independently replicated 10,000 times. Each replication was based on a different grid of sample points with a different random starting point and grid inclination. Also, in each replication, the same sample points were used for both sampling methods, traditional distance and T-square sampling (Fig. 2), for more effective comparison. A minimum distance of 10 m between sample points and sampling area boundary was ensured in all simulations to reduce biased estimations due to spatial edge effects to a minimum.

Following sampling and index calculation based on the selected sample trees, mean indices were calculated across all sample trees for all diversity indices but the aggregation index by Clark and Evans (1954), i.e. the sample tree arithmetic means of these indices constitute the estimators:

$$\widehat{Y} = \frac{1}{n}\sum\nolimits_{i=1}^{n} y_i \tag{8}$$

Here, n is the number of sample trees, i.e. the sample size in absolute terms. For better comparison and generalisation we later divided n by the total number of trees in the sampling area and calculated a percentage sample size. y_i is an arbitrary individual-tree spatial diversity index and $\widehat{Y}$ is the population estimator. For each diversity index of Table 1, $\widehat{Y}$ is estimated 10,000 times for each of the 16 sample sizes for both sampling methods.

The estimation of the aggregation index by Clark and Evans (1954) proceeded in two steps. First, for each sample point, point-to-tree and inter-tree distances were recorded. These were required for two purposes, (1) for estimating the mean of distance, $r_i^{(1)}$ or z_i, between sample trees and their first Euclidean neighbour (Fig. 1) as required by (Eq. 1 in Table 1) and (2) for estimating population density, $\widehat{N}$, which is also required by (Eq. 1 in Table 1). At each sample point, $r_i^{(1)}$ and z_i were recorded and the arithmetic mean, $\bar{r}^{(1)}$, was calculated for each sampling replication using Eq. (8). Following this, population density was estimated for each sampling replication. Population density can be estimated in at least three different ways; for more estimators see Zhang et al. (2022). For the traditional distance sampling method we studied two estimators. Köhler (1951) suggested the estimator

$$\widehat{N}^{(\mathrm{K})} = \frac{n^2}{\left(\sum_{i=1}^{n}\frac{r_i^{(2)}+r_i^{(3)}}{2}\right)^2} \tag{9}$$

In Köhler's estimator, $r_i^{(2)}$ and $r_i^{(3)}$ are the distances between sample tree i and its second and third Euclidean nearest neighbour, respectively. As an alternative, Diggle (1975) suggested estimator

$$\widehat{N}^{(\mathrm{D})} = \sqrt{\frac{n}{\pi\sum_{i=1}^{n}x_i^2} \times \frac{n}{\pi\sum_{i=1}^{n}\left(r_i^{(1)}\right)^2}} \tag{10}$$

Here, x_i is the distance between sample point and sample tree i and $r_i^{(1)}$ is the distance between sample tree i and its first Euclidean nearest neighbour. We computed both estimators as part of simulating the traditional distance method and analysed their performances.

For T-square sampling, Byth (1982) showed that the most robust estimator of population density was

$$\widehat{N}^{(\mathrm{B})} = \frac{n^2}{2\sum_{i=1}^{n} x_i \times \sqrt{2} \times \sum_{i=1}^{n} z_i} \tag{11}$$

In Eq. (11), all notations are as before and z_i is the aforementioned T-square distance of sample tree i (see Fig. 1). We applied Eq. (11) only as part of the T-square sampling simulations.

For evaluating the simulation results and as an expression of sampling error we quantified *relative RMSE* defined as

$$\mathrm{rRMSE} = \frac{\sqrt{\frac{1}{m-1}\sum_{i=1}^{m}\left(\widehat{Y}_i - \widehat{Y}\right)^2 + \left(\frac{1}{m}\sum_{i=1}^{m}\left(\widehat{Y}_i - \widehat{Y}\right)\right)^2}}{\widehat{Y}}, \tag{12}$$

where $\widehat{Y}_i$ is the ith estimated diversity index per replication (Eq. 8), $\widehat{Y}$ is the corresponding observed index estimated as the mean of all trees in the total sampling area, $m = 10,000$ is the number of simulated sampling replications. In addition, we also calculated the relative bias as

$$\mathrm{rBias} = \frac{\sum_{i=1}^{m}\left(\widehat{Y}_i - \widehat{Y}\right)}{m\widehat{Y}}. \tag{13}$$

For better clarity of trends, both rRMSE and rBias were modelled using a power function (Eq. (14); O'Regan and Arvanitis, 1966), where both characteristics of Eqs. (12) and (13) are represented by symbol E:

$$\mathrm{E} = \alpha_0 \times n^{\alpha_1} \tag{14}$$

Symbol n denotes sample size, α_0 and α_1 are model parameters. This model function was also applied for calculating the *critical sample size* required for rRMSE = 10%, see Sections 3.3 and 3.4. We used our own R code (R Development Core Team, 2023) and the R `spatstat` package (Baddeley et al., 2016) in these calculations.

2.4. Study data

We carried out sampling simulations in large, fully mapped tree sampling areas that provided a high diversity of different spatial patterns (Table 2).

The size of the sampling areas ranges from 1 ha (Tazigou) to 2.8 ha (Rosalia) and, related to size, the absolute number of trees, N, has a minimum of 269 trees at Clocaenog and a maximum of 2383 trees at Hirschlacke. Species richness is highest at Knysna (S = 20 species) and lowest at Hirschlacke (S = 5 species). The range of stem diameters is wide and similar in all six plots. It is lowest at Knysna and largest at Rosalia. The aggregation index by Clark and Evans (1954) indicated that Clocaenog, Hirschlacke, Knysna and Pen yr Allt Ganol have spatial tree location patterns that are close to complete spatial randomness. The trees at Rosalia are overdispersed (regular tree location pattern), whilst at Tazigou there is underdispersion (clustered tree location pattern). The values of the aggregation index were related to the mean distance between subject tree and first nearest neighbour, $\bar{r}$. Highest species mingling exists at Knysna ($\bar{M} = 0.82$) and lowest at Hirschlacke ($\bar{M} = 0.18$). Stem-diameter differentiation is highest at Pen yr Allt Ganol ($\bar{T} = 0.48$) and lowest at Rosalia ($\bar{T} = 0.30$).

2.4.1. Clocaenog forest area (Wales, UK)

Clocaenog Forest lies on the southern side of the Denbigh moors, a relatively high dissected plateau rising to between 300 m and 500 m asl. The forest area (Tyfiant Coed plot 6 at 53° 04′ 56.79″ N, 003° 27′ 09.28″ W) included in this study is situated at an altitude of 350 m asl. The underlying solid geology is Silurian made up of slates, shales and grits. The soil is generally fine textured and often quite stony. Podzolic brown earth predominates where site drainage is sufficient. The climate is relatively harsh with cool temperatures and high rainfall. Rainfall is in excess of 1300 mm. The site was planted with Japanese larch (*Larix kaempferi* (LAMB.) CARR.) and lodgepole pine (*Pinus contorta* DOUGL. ex LOUD.) in 1932. Sitka and Norway spruce (*Picea sitchensis* (BONG.) CARR. and *Picea abies* L. KARST., respectively) colonized the forest area from adjacent stands in the late 1990s. Clocaenog forest area has size 98 × 107 m and was surveyed in 2004.

2.4.2. Hirschlacke forest area (Austria)

The Hirschlacke forest area (48.64 N, 13.96 E) is situated in the northwestern corner of Austria, near the borders to the Czech Republic in the North and to Germany in the West at an elevation of 750 m asl. The main soil type is a gleyic cambisol. The mean annual temperature is 6.7 °C and the mean annual precipitation has been recorded as 1146 mm. When Hirschlacke was established as a research forest in 1977, the trees were 120 years old and dominated by Norway spruce. The forest also includes smaller proportions of silver fir (*Abies alba* MILL.) and beech (*Fagus sylvatica* L.). After 1977, the Hirschlacke forest area was treated by a combination of local, individual-based crown thinnings and target diameter harvesting (Reininger, 2000) for achieving a transformation to a complex-structured forest. After 40 years of treatment and observation, the Hirschlacke forest area is approaching a structure reminiscent of that which is typical of single-tree selection systems (Sterba, 2004). For the sampling simulation study, a 153 × 166 m large rectangular subplot and the data of the 2017 survey were used.

2.4.3. Knysna forest area (South Africa)

The Knysna forest area is part of the southernmost patches of the Afromontane forest in South Africa located south of the mountains between Humansdorp and Mossel Bay. Established in the Diepwalle State Forest in 1937, the Knysna forest area represents the largest indigenous forest complex in South Africa. The forest has been taken out of forest management in 1954 and is located to the north of the southern coastal town of Knysna (at about 33° 57′S, 23° 11′E). The forest area involves 25 different species, the most frequent ones include ironwood (*Olea capensis* L. subsp. *macrocarpa*), kamassi (*Gonioma kamassi* E. MEY.) and real yellowwood (*Podocarpus latifolius* (THUNB.) R. BR. EX MIRB.). The study

Table 2

Area, number of trees, N, global species richness, S, minimum stem diameter, $d_{\min}$, maximum stem diameter, $d_{\max}$, aggregation index, $\bar{R}'$, species mingling, $\bar{M}$, stem-diameter differentiation, $\bar{T}$, and mean distance between subject tree and first nearest neighbour, $\bar{r}$, in the six plots. The spatial indices were calculated from all trees in the sampling area without spatial edge correction as recommended for large tree populations by Pommerening and Stoyan (2006).

Sampling area	Area [ha]	Number of trees,N	S	$d_{\min}$ [cm]	$d_{\max}$ [cm]	$\bar{R}'$	$\bar{M}$	$\bar{T}$	$\bar{r}$
Clocaenog	1.05	269	11	5.1	77.2	1.065	0.544	0.409	3.323
Hirschlacke	2.54	2383	5	5.0	77.2	0.957	0.179	0.374	1.562
Knysna	1.46	803	20	5.5	66.7	0.936	0.823	0.421	1.997
Pen yr Allt Ganol	1.06	1190	11	1.9	65.0	0.999	0.599	0.477	1.492
Rosalia	2.79	1048	7	10.0	85.0	1.208	0.450	0.304	3.115
Tazigou	1.00	1040	12	1.0	66.0	0.765	0.591	0.450	1.186

area is situated at 517 m asl and the average annual maximum temperature for the region is 19.2 °C whilst the average minimum is 11.1 °C. The mean annual precipitation may vary between 700 and 1230 mm (Gadow et al., 2016). A large sub-plot of size 130 × 120 m measured in 1972 was included in this study.

2.4.4. Pen yr Allt Ganol forest area (Wales, UK)

Pen yr Allt Ganol (53° 06′ 25.60″ N, 003° 48′ 59.15″ W) is situated in Gwydyr Forest at an elevation of 230 m asl near the village of Betws y Coed (Snowdonia National Park, North Wales, UK). The main soil type is brown earth. Annual rainfall is in excess of 1200 mm. The mature stand consists of an overstorey formed by Scots pine (*Pinus sylvestris* L.) and Sitka spruce and was planted in 1931. Underneath the main canopy there is a rich understorey of mainly native broadleaved species; birch (*Betula* spp.) trees hold the largest proportion among them. Although originally managed the forest has been largely left to natural development for the last 20–30 years. The Pen yr Allt Ganol forest area has a size of 104 × 102 m and the data of the 2001 survey were used in this study (Pommerening and Uria-Diez, 2017).

2.4.5. Rosalia forest area (Austria)

The Rosalia forest area (48.72 N, 16.17 E) is situated at 620 m asl in the Rosalia Mountains in the eastern part of Austria at the northern border between the federal states Lower Austria and Burgenland. The area is part of the university forest of the University of Natural Resources and Life Sciences, BOKU, and includes a mixture of mainly Norway spruce, Scots pine, European larch (*Larix decidua* Mill.) and beech. The main soil type is a podsolic cambisol. Mean annual temperature is 9.5 °C and mean annual precipitation has been recorded as 750 mm. Before 1980 the forest area was managed as part of an agricultural estate with irregular, selective single-tree harvests which gradually gave rise to complex forest structure. Later on the ownership changed and the forest structure was simplified (Sterba, 2004). When the monitoring data were analysed in 1997, the forest was 98 years old with only a small cohort of young trees. For the simulation study, a 170 × 164 m large rectangular sub-plot and the data of the 1997 survey were used.

2.4.6. Tazigou forest area (China)

Tazigou Experimental Forest Farm (43°05′–43°40′ N, 129°56′–131°04′ E) is located in Jilin Province, China. This area of secondary forest is situated on Laoyeling Mountain of the Changbai Mountain range. The elevation ranges from 300 m to 1200 m asl with annual rainfall ranging from 500 mm to 600 mm. The average annual temperature is 3.9 °C. The area has predominantly dark brown soil (humic cambisols) with a high natural fertility. The main tree species include Mongolian oak (*Quercus mongolica* Fisch. ex Ledeb.), Asian white birch (*Betula platyphylla* Sukaczev), Korean pine (*Pinus koraiensis* Siebold & Zucc.), Ussuri popular (*Populus ussuriensis* Komarov), and Amur lime (*Tilia amurensis* Rupr.). The fully mapped 100 × 100 m plot included in this research is plot a at Tazigou as surveyed in 2013 (Wang et al., 2021).

3. Results

3.1. Sampling design performance by diversity indices

A crucial element of the aggregation index by Clark and Evans (1954; Eq. 1 in Table 1), $\widehat{R}'$, accounting for tree location diversity is the tree density estimation (Eqs. (9)–(11). The estimator proposed by Köhler (1951; Eq. 9) has proved to be inappropriate in most inventory areas due to a considerable bias (Figs. S1-S5). The only exception was the estimator's performance at Tazigou (Fig. S6). Here rBias and rRMSE were considerably lower throughout the sample size range than in all other sampling areas. This was most likely related to the clustered dispersion of tree locations at Tazigou (Table 2). The most robust density estimator in nearly all six sampling areas was that proposed by Diggle (1975; Eq. 10) using both the distance between sample point and sample tree and the distance between sample tree and the first neighbour (as part of the traditional distance method). Only at Rosalia (Fig. S5), where the aggregation index indicated regular tree locations (Table 2), the T-square sampling density estimator proposed by Byth (1982; Eq. (11) apparently performed better than Diggle's estimator. The T-square sampling estimator performed best (with lowest rRMSE and rBias values) at Rosalia and worst at Tazigou. These sampling areas represent patterns with the most regular and most clustered tree locations, respectively, of all six sampling areas (Table 2).

Both the mean directional index (Eq. 3 in Table 1), $\widehat{R}$, and the uniform angle (Eq. 2 in Table 1), $\widehat{W}$, can be considered robust alternatives to the aggregation index: In all six sampling areas the rRMSE curves quickly fell below a value of 0.2 and kept decreasing whereas the corresponding curves of the aggregation index decreased much less with increasing sample size (Figs. S1-S6). The results also show that the uniform angle index outperformed the mean directional index in all sampling areas, i.e. the associated rRMSE curves were markedly lower than those related to the mean directional index. Since both indices do not require tree density estimations, the differences in the rBias and rRMSE curves of the two sampling designs were small. The T-square sampling method, however, appears to have improved the results of both indices in most sampling areas (Figs. S1-S6).

In most sampling areas, species mingling (Eq. 4 in Table 1), $\widehat{M}$, showed a more consistent performance than the weighted species mingling index (Eq. 5 in Table 1), $\widehat{M}'$. Due to its composite structure involving Eq. (4) and local species richness, most estimations of $\widehat{M}'$ were associated with a comparatively large and even with an increasing bias. An exception was the Hirschlacke sampling area, where it was the estimation of the traditional species mingling index,$\widehat{M}$, which led to a large bias. The T-square sampling estimator was often able to lower rRMSE and rBias of $\widehat{M}$ compared to traditional distance sampling, e.g. at Clocaenog (Fig. S1), Hirschlacke (Fig. S2), Rosalia (Fig. S5) and Tazigou (Fig. S6), however, the difference was comparatively small.

When it comes to size inequality, stem-diameter differentiation, $\widehat{T}$, usually showed a better performance than diameter dominance, $\widehat{U}$, with the exception of the Hirschlacke sampling area (Fig. S2), where the corresponding rRMSE curves were quite similar. Apart from the Clocaenog sampling area (Fig. S1), in all other five study areas T-square sampling resulted in slightly lower rRMSE curves for both competing indices compared to traditional distance sampling (Figs. S2-S6).

3.2. Differences in the sample trees selected in the two inventory designs

When considering the percentage of sample trees that differed between T-square and traditional distance sampling, ΔT, at any site and sample size, it is evident that this percentage can differ substantially between sampling areas (Fig. 3A). The highest number of $\Delta T = 36.7\%$ was achieved at Rosalia and the lowest at Tazigou ($\Delta T = 23.7\%$). In all other sampling areas, ΔT was approximately 30%. Apart from very low sample sizes, this percentage was comparatively constant across sample sizes with only a slight increase (Clocaenog, Tazigou) or decrease (Knysna, Pen yr Allt Ganol).

Intercept a of the linear relationship $\Delta T = a + b \times n$ indicates the average percentage of sample trees that differ at any site between T-square and traditional distance sampling. Apparently, there was a strong correlation between aggregation index $\widehat{R}'$ and intercept a (Fig. 3B). This suggests that T-square sampling responds to and interacts with the spatial pattern of tree locations. ΔT is apparently very high in sampling areas with regular tree location patterns (Rosalia) and quite low in areas with clustered tree location patterns (Tazigou). In the other four study areas, the aggregation index has values around 1.0 (Table 2; Fig. 3B), i.e. the tree location patterns are close to complete spatial randomness. Apparently ΔT for such patterns is approximately 30%.

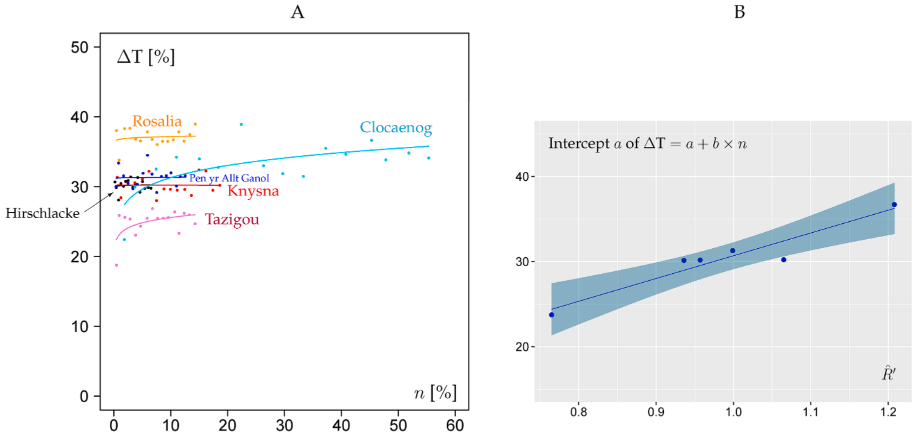

Fig. 3. A: Percentage of sample trees that differ between traditional distance sampling and T-square sampling, ΔT, in the six sampling areas dependent on sample size. Each data point is a mean of 10,000 replications. The trend curves were modelled using Eq. (14). n – sample size in percent of the total number of trees in the sampling area. B: The linear relationship between the intercept a in $\Delta T = a + b \times n$ and the aggregation index, R', along with the corresponding 95%-confidence intervals. The coefficient of determination $\widetilde{R}^2$ was 0.91.

3.3. Dependence of critical sample size for rRMSE = 10% on spatial species and size patterns

Interestingly, our analyses revealed that the sample size required for rRMSE = 10% in species mingling, $\widehat{M}$ (Eq. 4), and size differentiation, $\widehat{T}$ (Eq. 6), depends on how far removed the observed spatial species and size pattern of a sampling area is from the state of independent (random) species or size attributes, i.e. from a situation where any of these two attributes have no spatial correlation. We explored this relationship with the underlying spatial pattern using the species and the size segregation indices (Pommerening and Grabarnik, 2019, p. 132 and 141; Fig. 4). These indices are based on ratios where $\widehat{M}$ and $\widehat{T}$ are divided by the corresponding expected values accounting for random species and size dispersion.

It turned out that the sample size required for rRMSE = 10% was usually not larger than 5 % when species and size segregation indices are near 0, i.e. when species and size attributes are independent (randomly dispersed). The larger the values of these segregation indices get the more there is a trend for the same species or the same sizes to be arranged in clusters and, as a consequence, the more the required sample size increases. In most cases, this increase happened exponentially, i.e. after a region of moderate increase the sample size would suddenly markedly increase. Only for size differentiation and traditional distance sampling a linear increase could be discerned (Fig. 4B). The different scales on the ordinates indicate that species mingling generally requires a much larger sample size than size differentiation.

3.4. Critical sample size for rRMSE = 10%

When calculating the sample size required for achieving rRMSE = 10%, it was obvious that the corresponding sample size required was comparatively low (Fig. 5). Across all indices and both sampling methods a sample size of $n = 20\%$ was sufficient in all sampling areas, often, however, much smaller numbers apply. Aggregation index (Eq. 1 in Table 1) and species mingling (Eq. 4 in Table 1) were often among those indices that required larger sample sizes whilst uniform angle index (Eq. 2 in Table 1), mean directional index (Eq. 3 in Table 1) and differentiation index (Eq. 6 in Table 1) could be estimated accurately from smaller sample sizes. For all indices whose data points were situated below the 1: 1 line in the graphs of Fig. 5 it follows that the use of T-square sampling leads to lower sample sizes compared to the application of traditional distance sampling.

This involved the majority of indices in all sampling areas. Domi-

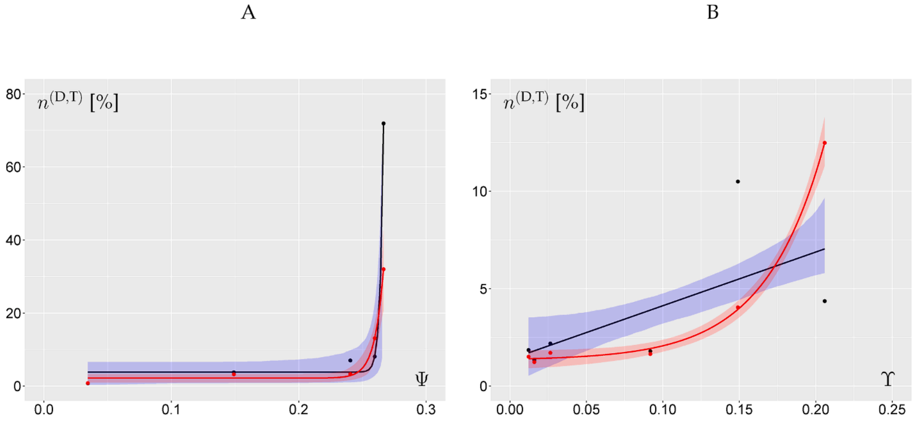

Fig. 4. Critical sample size, $n^{(\mathrm{D,T})}$, required in traditional distance sampling and T-square sampling for achieving rRMSE = 10% (Eq. 12) calculated from Eq. (14) as $n = \sqrt[a_1]{\frac{a_0}{10}}$ over the species segregation index (A), $\Psi = 1 - \frac{M}{\mathbf{E}M}$, and the size segregation index (B), $\Upsilon = 1 - \frac{T}{\mathbf{E}T}$ (Pommerening and Grabarnik, 2019, p. 132 and 141). $\mathbf{E}M$ is expected species mingling, $\mathbf{E}T$ is expected size differentiation. Black, blue – traditional distance sampling, red – T-square sampling. The trend curves were modelled using functions $n^{(\mathrm{D,T})} = a_0 + e^{a_1 + a_2 \times \Psi}$ and $n^{(\mathrm{D,T})} = a_0 + e^{a_1 + a_2 \times \Upsilon}$ along with the 95%-envelopes derived from the residuals through bootstrapping. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

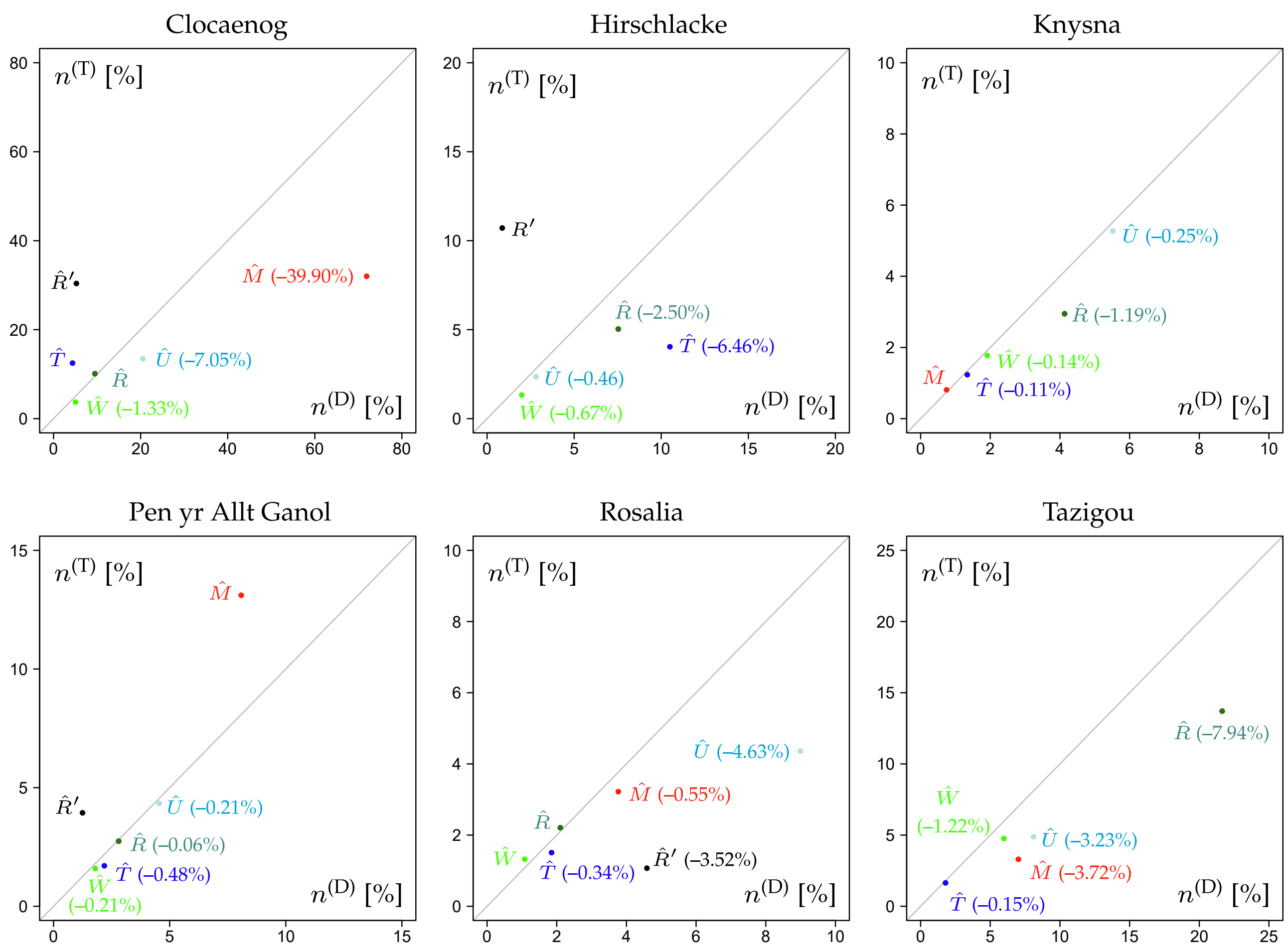

Fig. 5. Critical sample size, $n^{(T)}$, required in T-square sampling for achieving rRMSE = 10% (Eq. 12) over the same critical sample size, $n^{(D)}$, required by traditional distance sampling and calculated from Eq. (14) as $n = \sqrt[\alpha_1]{\frac{\alpha_0}{10}}$. Sample size n is expressed in percent of the total number of trees in the sampling area. The tree diversity indices follow the notation of Table 1. For those indices where T-square sampling led to smaller values of rRMSE (Eq. 12) compared to traditional distance sampling, the reduction in sample size, n, is given in brackets. Indices for which the critical sample size exceeded 100% were excluded from the graphs.

nance index $\hat{U}$ (Eq. 7 in Table 1) benefitted from T-square sampling in all sampling areas. The largest percentage gain that could be achieved through the application of T-square sampling was a 40% reduction in sample size ($\hat{M}$ at Clocaenog), followed by 8% for $\hat{R}$ at Tazigou and 7% for $\hat{U}$ at Clocaenog. Our results indicated that T-square sampling can be considered a robust option that does not lead to any catastrophically bad consequences in the estimation of any of the seven diversity indices in any of the six sampling areas.

4. Discussion

Distance sampling and its modification, i.e. T-square sampling (Besag and Gleaves, 1973), play an important role in plant ecology (Krebs, 1999; Newton, 2007). More recently T-square sampling has been proposed for surveying refugee camps and other human settlements (Bostoen et al., 2007; Diggle, 2014) and it is likely that there are many more interesting applications. Spatial tree diversity indices have in the past performed remarkably well in studies involving distance sampling (Pommerening and Lewandowski, 1996; Pommerening, 1997; Kint et al., 2004) and this good performance suggested that T-square sampling may lead to further improvements whilst at the same time reducing the potential bias arising from the preferential selection of isolated individuals to a minimum.

Our results confirmed that T-square sampling has indeed a major influence on the estimation of population density. We found that the estimators suggested by Diggle (1975; Eq. 10) for traditional distance sampling and the estimator put forward by Byth (1982; Eq. 11) for T-square sampling are very reliable across different spatial patterns, whereas the forestry estimator proposed by Köhler (1951; Eq. 9) cannot be recommended for its unpredictable behaviour. In addition, the results shown in Fig. 3A suggest that T-square sampling is particularly effective in forests with regular (overdispersed) tree patterns, since ΔT is highest here and the corresponding density estimations are most accurate at the same time.

Comparing the sampling performance of competing diversity indices in terms of traditional distance and T-square sampling was one objective of our study. The aggregation index by Clark and Evans (1954; Eq. 1 in Table 1) requires population density as input and additionally uses the distance between sample tree and first nearest neighbour. As such the aggregation index is a *composite index* similar to the weighted species mingling index (Eq. 5 in Table 1). The estimation of composite tree diversity indices is often associated with larger sampling errors than that of simple indices (Pommerening and Sterba, 2024). This was also confirmed in our study (Figs. S1-S6). It was interesting to see that the indices competing with the aggregation index, i.e. the uniform angle index (Eq. 2 in Table 1) and the mean directional index (Eq. 3 in Table 1), which generally do not involve population density estimations, can often be estimated from samples with a much lower sample size than that required for the aggregation index. This means that these two indices are robust alternatives to the aggregation index. Here again the uniform angle index outperformed the mean directional index, i.e. the associated rRMSE curves were markedly lower than those related to the mean directional index. In a similar way, the traditional species mingling index (Eq. 4 in Table 1) should be preferred in distance sampling to the weighted species mingling index (Eq. 5 in Table 1). In terms of size diversity, the size differentiation index (Eq. 6 in Table 1) largely outperformed the size dominance index (Eq. 7 in Table 1) in our distance sampling simulations. This sampling performance provides strategic information useful for sampling planning. However, sampling performance should not be confused with an index' general ability to indicate spatial diversity patterns or with its statistical power.

We were able to show that T-square sampling flexibly responds to the spatial pattern of tree locations in sampling areas (Fig. 3). As our discussion of different density estimators in Section 2.3 has shown, inter-tree distances play a crucial role in density estimations and these depend on the spatial pattern of tree locations. In regular (overdispersed) patterns, T-square sampling selects approximately 10% more sample trees that differ from those selected in traditional distance sampling (ΔT) compared to the situation of complete spatial randomness. In such patterns, the interaction between tree and sample point locations apparently leads to a large number of angles *OPQ* (see Section 2.2) that are smaller than 90°. In clustered (underdispersed) patterns, T-square sampling selects approximately 10% less sample trees that differ from those selected in traditional distance sampling (ΔT) compared to the situation of complete spatial randomess. Here, the interaction between tree and sample point locations apparently leads to a large number of angles *OPQ* (see Section 2.2) that are larger than 90°. The different percentages of differing sample trees, ΔT, are part of an interesting self-adaptation strategy of T-square sampling. As an alternative to T-square sampling for spatial diversity indices, Hui and Albert (2004) proposed a sampling design where the four nearest Euclidean tree neighbours of each sample point are considered sample trees and for each of these four the corresponding tree diversity indices are determined so that there are four index results per sample point.

An important result of our study was finding evidence for the fact that the critical sample size for species mingling and size differentiation clearly depends on the degree to which trees of the same species or of the same size are arranged in spatial clusters (Fig. 4). Such segregation patterns are, in fact usually the more interesting cases rather than situations where both attributes are more or less randomly dispersed. However, when such clusters occur, the sample size required for rRMSE = 10% increases and, after passing a certain tipping point, sample size can dramatically increase. This illustrates how spatial forest structure interacts with sampling designs: The sampling error itself is also an expression of tree diversity and the more diverse a forest gets the larger the sample size has to be in order to achieve a certain sampling error (Pommerening and Stoyan, 2008).

In a forestry context, it may be of interest to know how baseline forestry characteristics such as basal area per hectare, *G*, and quadratic mean diameter, d_g, can be estimated in T-square sampling in addition to spatial measures of tree diversity. Since the estimation of tree density (number of trees per hectare, *N*) can be relied on when using either the Diggle or the Byth estimators (Eqs. 10 or 11), the quadratic mean diameter, d_g, can be estimated by simply calculating this characteristic according to forest mensuration textbooks. Previous simulation studies have, however, shown that it is best to measure the stem diameters not only of the sample trees but also for the four nearest neighbours, i.e. five diameter measurements per sample point, and to calculate d_g based on these measurements (Pommerening, 1997). *G* can then be retrieved through the well-known relationship

$$\widehat{G} = \frac{\widehat{N} \times \pi \times \widehat{d}_g^2}{4} \tag{15}$$

Our results have demonstrated that T-square sampling makes a small contribution to either decreasing the sample size (for a fixed rRMSE) or increasing the accuracy of distance sampling (for a fixed sample size). In other words, traditional distance sampling is a good method for estimating most diversity indices and leads to only a small bias if any so that there is not much room for T-square sampling to make improvements. This performance of T-square sampling also implies that the preference of isolated individuals in distance sampling is apparently a minor issue in our context, which is of little consequence to spatial diversity indices unless they include measures of tree density. On the other hand, T-square sampling did actually improve the estimation performance of most spatial diversity indices in all our six sampling areas and never contributed to extremely bad estimations. In many situations, sample size reductions between 0.06% and 40% could be achieved by the application of T-square sampling (Fig. 5). As such our initial hypothesis is largely true. Therefore, T-square sampling can be considered a robust sampling method for spatial tree diversity indices.

5. Conclusions

Both traditional distance and T-square sampling are robust methods for sampling spatial measures of tree diversity that deliver reliable results when sampling no more than 20% of all trees in a sampling area. The estimators of distance sampling in conjunction with systematic grids of sample points particularly benefit from spreading the sample trees evenly across the whole sampling area and thus provide a good coverage of the forest (Pommerening, 1997; Kint et al., 2004). T-square sampling has the ability to adapt to different spatial patterns of tree locations. With most spatial patterns, T-square sampling is able to decrease sample size or increase accuracy of traditional distance sampling and has the added benefit of an in-built bias control. We could also show that rRMSE of species mingling and size differentiation clearly depends on the underlying spatial pattern. When applying distance sampling, the uniform angle index (Eq. 2 in Table 1), the species mingling index (Eq. 4 in Table 1) and the size differentiation index (Eq. 6 in Table 1) can be recommended, because in terms of rRMSE and rBias they performed better across different spatial patterns than their competitors. For tree density estimations the Diggle and Byth estimators (Eqs. 10 and 11) can be relied on.

6. Data accessibility statement

The data will be made available on request. R scripts can be obtained from AP.

7. Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors did not use any AI or AI-assisted technologies.

CRediT authorship contribution statement

Arne Pommerening: Conceptualization, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Hubert Sterba:** Data curation, Methodology, Writing – review & editing. **Bianca N.I. Eskelson:** Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.111995.

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