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Spatial diversity of dry savanna woodlands

Assessing the spatial diversity of a dry savanna woodland stand in northern Namibia using neighbourhood-based measures

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Abstract. The dry woodland savannas of Namibia are of significant socio-economic importance. The paper tests the suitability of a number of diversity indicators developed for species poor systems in Europe in the woodland context. The indicators that were tested included the species specific mingling index, M_{Sp}, the measure of surround and the uniform angle index. The simple application of the methods permit relatively unschooled crews to conduct an enumeration in the field.The results show that the indicators do not only display current diversity status, but also reflect the ecological context of the individual species.

Introduction and background

The dry woodland savannas of northern Namibia are of significant socio-economic importance to many rural communities, providing a variety of timber and non-timber products. The woodland resources that are used range from building material and wood fuel to food, medicine and grazing (NFSP 1996). The quantities of the different products that are extracted are considerable. Ollikainen (1992) estimated for example, that firewood alone amounted to a total of 1.5 million cubic metres of wood during 1992. No quantity or value estimates of non-wood products are available for the Namibian dry woodland savannas, although these may be considerable.

The various woodland products differ in their importance to the various communities, and at different times. Although exact quantities were not indicated, Lee (1973) reported, for instance, that the intake of *Schinziophyton rautanenii* nuts could comprise up to 90% of the total food intake of some San communities. While this percentage will have changed in the meantime, Büschel (1999) indicated that the nuts still represent the staple diet of nomadic and sedentary San groups. The importance of the nuts increases particularly when agricultural crops are insufficient to meet normal requirements.

Other communities in the Kavango region of Namibia depend almost entirely on the production and sale of carvings for the tourism industry, although no studies seem to have been published in this regard. Some carvings are also produced in the Caprivi region, but the local population does not appear to depend as much on this form of income although no estimates are available.

The emphasis on different species for the carving industry is also shifting. In the early 1990s the industry in the Okavango region made use of *Pterocarpus angolensis* almost exclusively. Now, however, species like *Guibourtia coleosperma*, *Baikiaea plurijuga* and even *S. rautanenii* (despite its light weight) are being utilized extensively. This is primarily due to the overexploitation of *P. angolensis*.

Further woodland species, such as *Burkea africana* or *Terminalia sericea* serve mainly for poles or as firewood, although they support a caterpillar that also represents an important source of food (Leger 1997).

Spatial diversity and woodland structure

The word ''structure'' generally considers the composition of a population of trees in terms of specific characteristics. These may include tree age, size, species or sex (in the case of dioceous trees). Spatial structure, on the other hand looks at the arrangement of such characteristics in space. Spatial diversity refers to the arrangement of the characteristics in relation to each-other or in relation to a particular point on the ground.

The woodland savanna in northern Namibia is supported by coarse Aeolian sands with poor water holding capacity and nutrient status. The trees that occur here need to cope with highly variable precipitation and high evaporation rates. Frequent fires and exploitation further affect the environment. Taken in combination, trees and especially their seedling have to cope with a wide variety of conditions over a very short period of time and have adapted accordingly.

A number of the woodland species are frequently, though not exclusively, found in almost monospecific stands. This may be due to regeneration requirements, as in the case of *P. angolensis* (Graz 1996), the ability to compete, especially for water, as in the case of *B. plurijuga* (Mitlöhner 1997) or superior fire tolerance as in the case of *B. africana* (Rutherford 1981).

The monospecificity of stands of *S. rautanenii* and *T. sericea* have not been investigated. *T. sericiea*, however, is a pioneer that may quickly colonize open areas where it may actually form thickets (Shackleton 2001).

Büschel (1999) reported on the other hand that stands dominated by *S. rautanenii* were comprised of trees of different sizes and species in the Okavango region of Namibia. Similarly, Mitlöhner (1997) also described stands of mixed species, comprising of *P. angolensis*, *B. africana* and *B. plurijuga*, while observations near the study site also showed mixed stands (unpublished data).

In addition to being almost monospecific, trees within many stands often seem to be of similar size although not necessarily of similar age. Childes (1984) reported, for instance, that *B. plurijuga* stands were of variable age despite the equal size of the trees. Plants remain small for a number of years until environmental conditions are suitable for further development. This is probably also the case for *B. africana* and *S. rautanenii*, although nothing seems to have been documented.

The restriction of growth described by Childes for *B. plurijuga* is similar to the suffrutex development stage of *P. angolensis* reported by Vermeulen (1990). During this period seedlings from a number of years may accumulate in this developmental stage and develop together to the sapling stage when environmental conditions permit. In such cases the above ground parts are not of the same age as the roots. It is unclear if the differences in the ages of the roots will be reflected in the survival rate of the above ground parts of the trees.

It is also uncertain whether or not whole stands of any of the above species will die off and be replaced by others at a different location, or whether the existing regeneration is sufficient to replace those trees that have died.

The data pertaining to the structure of stands in northern Namibia currently available is superficial, despite its significant importance for management.

Spatial diversity, or a lack of spatial diversity, has important implications. Consider for instance the effect of exploitation on an even sized, monospecific stand; selection based on a minimum diameter may result in a local clear-felling (Von Breitenbach 1968 ■Au: Please approve the edit of the reference Von Breitenbach (1973) to Von Breitenbach (1968) to match with the reference list.■; Graz 1996). The resulting vegetation structure would be increasingly prone to fire that may cause further vegetation change, as well as subsequent erosion and nutrient loss (see Graz 1996).

Causes of mortality are not necessarily only of human origin, however. The different sizes of a number of species have, for example, their own degree of fire tolerance. This means that trees up to a particular size class may be removed from a stand by a sufficiently intense fire. Wilson and Witkowski (2003) found that the bark-thickness of *B. africana* increases with tree circumference between 0 and 400 mm. The thickness of the bark is the primary protector against the effect of fire on the cambium.

Fire tolerance may be overcome if the bark of trees is breached by animals (Yeaton 1988) or growth stresses (Graz 2003).

Studies relating to spatial aspects have in the past concentrated on the dispersion of plants using measures such as the nearest neighbour of Clark and Evans (1954) or point to plant distances after Pielou (1977) ■Au: Please approve the edit of the reference Pielou (1959) to Pielou (1977) to match with the reference list.■. More recently the uniform angle index (UAI) (Gadow 1999; Staupendahl 2001; Gadow et al. 2003) has been implemented to describe complex forest structures. The aggregation of tree attributes have only been addressed more recently by other measures, such as the "measure of surround" (Hui et al. 1998) or the spatial "mingling" (Gadow 1999).

The mingling measure is used to quantify the degree of interspersion or mingling of tree characteristics, as illustrated in Figure 1. Trees that are surrounded by others of similar characteristic are aggregated in terms of the characteristic, implying a lower degree of mingling of this characteristic. On the other hand, trees surrounded by others of dissimilar characteristic imply a higher degree of mingling. Mingling should not only be considered in terms of categorical data, such as species or sex, or whether a tree is alive or dead, but should be expanded to include any measure with which a tree might be described, including height or diameter.

Albert and Gadow (1998) reported on the use of these neighbourhood-based measures to assess the effect of selective thinning on the diversity of a beech stand in Germany. The authors had found the measures to be sensitive to small-scale differences and changes of woodland structure, and were able to provide more intuitively acceptable results than the segregation index of Pielou (1977, p. 227 ff).

This study aims to achieve two main objectives. The first objective is to assess the applicability of indicators that were developed and assessed in Europe to the Southern African context where little or no basic stand information is available for non-plantation areas. In addition, the study intends to generate information that will promote the understanding of the ecology of Namibia's woodland resources.

Description of the study area

The woodland area that was enumerated covers approximately 70 ha and is situated between 19°30′ E, 19°15′ S and 19°45′ E, 19°30′ S near the Kanovlei Forestry Research Station in the western Tsumkwe district of the Otjozondjupa region, northeastern Namibia.

The area is dominated by linear fossil dunes or sandy plains on calcareous deposition, similar to those in the adjoining Kavango region described by Graz (1999). The soils are Kalahari sands, classified as unconsolidated aeolian material by Coetzee (2001), with very poor water holding capacity and nutrient status, and subsequently a very low potential for any agricultural development (Department of Water Affairs 1991).

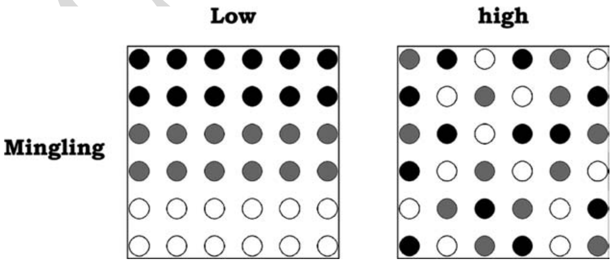

Figure 1. The mingling of black, grey and white 'trees' within two square stands (after Gadow,

The region is traversed by a system of *omuramba* (vegetated dry riverbed), with the soils classified as unconsolidated fluvial material (Coetzee 2001). These soils are shallower and have a heavier texture than the dunes (Department of Water Affairs 1971).

Precipitation is mostly in the form of thunderstorms amounting to an average rainfall of between 500 and 600 mm per year (Amakali 1992). However, the distribution of precipitation is highly variable and prominently positively skewed. Expected rainfall is therefore significantly lower than the long-term averages. Rain generally falls in the period September to May, with most rain occurring between December and March.

Average annual evaporation rates are between 2600 and 2800 mm (Crerar and Church 1988) resulting in an overall moisture deficit.

de Pauw and Coetzee (1999) have determined an approximate growing period of between 91 and 120 days, based on the relationship between available moisture, the amount of evapotranspiration and the average air temperature.

Although the general vegetation is described as tree savanna and woodland by Giess (1998), there is some significant variation in species and structural composition. The Directorate of Forestry identifies a number of dissimilar patches of forest or savanna (Chakanga 1995).

While the sandy planes and dunes are dominated by *Burkea africana*, various species of *Combretum*, *Pterocarpus angolensis*, *Schinziophyton rautanenii* and *Terminalia sericea*. Scattered patches of *Baikiaea plurijuga* also occur.

The lower lying omuramba vegetation is comprised primarily of *Acacia erioloba*, *Dichrostachys cinerea* and *Philenoptera nelsii*.

Nuts from the *S. rautanenii* trees within the stand are harvested by local communities to augment their food supply, and by the Directorate of Forestry to obtain material for the National Tree Seed Centre and for *ex situ* conservation of genetic material. Additionally the stand shows signs of periodic wood harvesting of *B. plurijuga* stems, as well as for firewood. Dry season fires are frequent (Graz 2003).

Material and methods

The interspersion of tree attributes

The original measure of mingling and its derivatives are based on the proportion of trees with dissimilar characteristics to those of a selected sample tree. The species mingling index M_i for a given sample tree, *i*, using *n* neighbours is, for example, obtained through:

$$M_i = \frac{1}{n}\sum_{j=1}^{n} m_{ij}, \tag{1}$$

where

$$m_{ij} = \begin{cases} 1, & \text{if the tree is of another species,} \\ 0, & \text{if the tree is of the same species.} \end{cases}$$

When four neighbours are used to determine M_i the index may obtain one of five possible values:

0/4 none of the neighbours are of a different species,
1/4 one of the neighbours is of a different species,
2/4 two of the neighbours are of a different species,
3/4 three of the neighbours are of a different species, and
4/4 all of the neighbours are of a different species.

The arithmetic mean (M_{Sp}) of the M_i values that were obtained for a particular species sp provides a measure of the degree of interspersion of the species in the area. M_{Sp} provides a value between 0 and 1.

Values close to 0 indicate that trees of the reference species sp occur in groups therefore implying a low degree of mingling and high degree of aggregation. High values of M_{Sp}, closer to 1, on the other hand, imply a high degree of mingling, i.e. trees of the reference species do not occur together.

As is the case when examining the distribution of data around a mean value, additional information may be extracted from the distribution of M_i values of individual species.

When the proportion that a species contributes to a stand is known, as assumed in the studies reported on by Lewandowski and Pommerening (1997) and Hui et al. (1998) a theoretical distribution of M_i values may be calculated based on the hypergeometric probability distribution. The distribution reflects the number of expected M_i values that would be obtained if all trees were interspersed randomly.

The hypergeometric distribution is used to determine the probability, P, that a number of trees of a particular species may occur in a given sample of n trees taken from a population of N trees containing k trees of the species of interest. The probability that x trees in the sample will be of the species of interest is then determined after Newmark (1997) as:

$$P = \frac{\binom{k}{x} \cdot \binom{N-k}{n-x}}{\binom{N}{n}} \quad \text{for } x = 0, 1, 2, \ldots, n,$$

which expands to:

$$P = \frac{\frac{k}{x(k-x)} \cdot \frac{(N-k)}{(n-x)(N-k-(n-x))}}{\frac{N}{n(N-n)}} \quad \text{for } x = 0, 1, 2, \ldots, n.$$

The resulting probability multiplied by the total number of samples that were taken provides the expected number of M_i values for that species. The observed and expected distributions of M_i values may then be compared with the application of standard statistical methods to test for significance of deviations from the theoretical (random) distribution.

Although no detailed data is available for any of the woodland areas in Namibia, and the extent of the woodland areas hampers the collection of such information, the sample size provided a suitable estimate of the species composition of the stand.

The simulation study reported on by Graz (2004) has shown that the mingling index is sensitive to the species composition of a stand. In a stand of trees interspersed randomly, for example the aggregation of a species, $1 - M_{\mathrm{Sp}}$, approximates the proportion that a species Sp contributes to the stand. This may be more intuitively understood if we consider each sample tree to provide an estimate of the proportion that its species contributes to the stand. Values of $1 - M_{\mathrm{Sp}}$ which are greater than the proportion contribution therefore indicate an overaggregation of the species, while lower values imply overdispersion within the stand. This relationship provides an important base from which the index may be interpreted.

This study investigated the interspersion of a number of tree characteristics. In addition to the mingling of species described above, the interspersion of tree dominance is quantified on the basis of diameter (T_{Sp}) and height (H_{Sp}) using the ‘‘measure of surround’’ described by Hui et al. (1998), and which is applied in a method analogous to that of the mingling index. More particularly:

$$(2) \qquad T_i = \frac{1}{n}\sum_{j=1}^{n} t_{ij},$$

where

$$t_{ij} = \begin{cases} 1, & \text{if the tree, } j, \text{ is thicker than the sample tree } i, \\ 0, & \text{otherwise.} \end{cases}$$

The species specific mean interspersion of tree diameter, T_{Sp}, is then the arithmetic mean of the values of T_i for that species.

Similarly, the interspersion of tree height, H_i, is obtained through:

$$(3) \qquad H_i = \frac{1}{n}\sum_{j=1}^{n} h_{ij},$$

where

$$h_{ij} = \begin{cases} 1, & \text{if the tree, } j, \text{ is higher than the sample tree } i, \\ 0, & \text{otherwise.} \end{cases}$$

The species specific interspersion of tree height, H_{Sp}, is then again determined as the mean of the values of H_i for the species.

An equivalent measure was used to quantify the interspersion of dead trees (D_{Sp}) by counting the number of dead neighbours for each sample tree.

Uniform angle index

The UAI was initially described by Gadow et al. (1998) and later by Staupendahl (2001) to provide a measure of the overall contagion of trees within a forest stand.

The index is obtained by identifying the n nearest neighbours of a sample tree. Starting with the closest neighbour and moving in a clockwise direction around the sample tree the angle, a_j, between two adjacent neighbours is determined in relation to the sample tree. The number of angles smaller than, or equal to, a given critical angle, a_0, are then counted, i.e.

$$W_i = \frac{1}{n}\sum_{j=1}^{n} w_{ij}, \tag{4}$$

■Au: Equations have been renumbered in order to appear sequentially, please check.■ where

$$w_{ij} = \begin{cases} 1, & \text{if } a_j \le a_0, \\ 0, & \text{otherwise.} \end{cases}$$

The critical angle (in degrees) is determined as:

$$a_0 = \frac{360^\circ}{\text{Number of neighbours}}. \tag{5}$$

Four neighbours would therefore be evaluated in terms of a 90° critical angle[1]. Since all of the indexes used to measure the interspersion of tree characteristics were based on four trees, the same neighbours could be used for the UAI.

A practical advantage of choosing $a_0 = 90^\circ$ is that two adjoining sides of a record book or clipboard may be used to determine whether or not an angle is greater than or less than the critical angle.

Effectively, the index describes the spatial distribution around a particular reference tree. If the species of the reference tree is noted we may obtain the mean value for either for the whole population or for a particular species of interest.

The mean value of the index is strongly correlated with the nearest neighbour index of dispersion of Clark and Evans (1954) that has long been used in ecological studies. Together with the number of trees in a stand, the UAI may be used to estimate the distribution of distances between a tree and its neighbours (Gadow et al. 2003).

This information is generally not available and comparison of observed index values are compared to the simulation results of Gadow et al. (1998) are used.

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[1] More recent studies have shown that this statement needs to be modified; a more suitable critical angle is 72° (see Gadow et al. 2003).

Sampling

The extent of the stand was recorded in the field using a Garmin Venture GPS. The track-log was stored for subsequent mapping. A regular sample grid of one geographic second was then superimposed on the stand amounting to a sample point approximately every 30 m at that latitude.

Sampling points were located using a standard GPS receiver. The accuracy of autonomous GPS readings was considered adequate for the purpose of the study. While a dense canopy reduces the reliability of a GPS reading within a stand (Dominy and Duncan 2001), many of the trees in the area had already shed their leaves and canopy interference was considered negligible after initial comparison of signal strengths in wooded and in open areas.

Since the enumeration coincided with the war in Iraq it is uncertain whether GPS readings were affected by selective availability on some days. It was felt, however, that this was acceptable.

At each sample point the closest tree with a dbh of 5 cm or more was identified to serve as reference tree. Although trees had, in a few cases, snapped off below breast height, such trees were nevertheless sampled, since they play a role in the interspersion of plants.

For each sample tree the four nearest neighbouring trees with a diameter of greater than 5 cm were determined and compared with the reference tree in terms of species, mortality, height and diameter, and the UAI was established.

Time was kept short by assigning two persons to each sampling team. While the enumerator collected the measures, a navigator moved to find the next sample point.

A total of 1121 sample points were assessed. The data was entered into a spreadsheet and the indexes were calculated for each species using cross tables.

Results and discussion

The species specific indexes are summarized in Table 1. The table also shows a surrogate species of ‘Dead’ created to record trees that were still standing but had been burnt beyond a stage where they might be identified. Also, species of the genus *Combretum* and *Comiphora* were lumped, as individual species could not readily be identified. The row marked ‘overall’ provides the each index as calculated over the entire data set.

The overall shows a contagion (W_i) greater than 0.6, here indicating a tendency towards non-random (clumped) dispersion of trees (after Gadow et al. 1998). The dispersion around trees of the individual species does not seem to diverge very much from the mean value of 0.665, if *Philenoptera nelsii* and *Securidaka longipedunculata* are discounted because of their very low overall occurrence. This is in line with general observations in the field.

The table shows that most of the species have a tendency to aggregate.

To compare the proportion of a given species within the stand and the value $1 - M_{\mathrm{Sp}}$ consider Table 2. The table omits those species with very few observations (less than 5% of the total). The final column in the table reflects the parameter M proposed by Graz (2004) to determine the degree of interspersion. The value of M is larger than 0 and less than or equal to 1. Values close to 0 indicates a very low degree of mingling, and 1 indicates a more random distribution of the species in the stand.

Table 2 shows that *B. plurijuga* has the highest degree of aggregation followed by *Terminalia sericea*.

More *T. sericea* seedlings survive in open areas, i.e. away from conspecific trees (Smith and Grant 1986) where it has the ability to form thickets (Shakelton 2001). This was evident in the field. *T. sericea* would colonize gaps in the canopy, thus causing the aggregation.

The dispersion of *B. plurijuga* is also shown in Figure 2. The figure shows that the species occurs in a very limited area. The accompanying graph shows the relative distribution of M_i values (bar) and the theoretical hypergeometric distribution. The graph shows a clear difference between the two, due to the clumping of the species, reflected by the low value of M (Table 2).

The cause of the aggregation of *B. plurijuga* is uncertain, since the trees had few larger neighbours as evidenced by the low value of T_{Sp} in Table 1. It is possible that the patch of *B. plurijuga* is a remnant of a larger stand that has been subject to high degrees of mortality. This possibility stems from reports by Von Breitenbach (1968) who suggested that the almost pure stands in the Caprivi region developed towards mixed stands as a result of fire.

The possibility is corroborated by the high degree of mortality (D_{Sp}) associated with the species (see Figure 3). The dead trees within the *B. plurijuga*

Table 1. Mean of the various indicators for each of the identified species.

Species of sample tree	N	P(Sp)	W_{Sp}	D_{Sp}	M_{Sp}	T_{Sp}	H_{Sp}
Burkea africana	116	0.103	0.688	0.226	0.751	0.323	0.332
Baikiaea plurijuga	194	0.173	0.665	0.116	0.653	0.249	0.256
Combretum species	214	0.191	0.657	0.148	0.697	0.484	0.479
Comiphora species	36	0.032	0.639	0.201	0.875	0.382	0.556
Ochna pulchra	26	0.023	0.635	0.087	0.962	0.567	0.673
Philenoptera nelsii	16	0.014	0.750	0.141	0.820	0.563	0.625
Pterocarpus angolensis	178	0.159	0.647	0.163	0.813	0.198	0.218
Schinziophyton rautanenii	75	0.067	0.653	0.137	0.875	0.243	0.300
Securidaka longipedunculata	2	0.002	0.625	0.125	0.962	0.375	0.625
Strychnos pungens	26	0.023	0.683	0.163	0.893	0.462	0.548
Terminalia sericea	96	0.086	0.641	0.130	0.781	0.565	0.602
Unidentifiable dead tree	142	0.127	0.701	0.285			
Overall	1121	1.0000	0.665	0.169	0.794	0.360	0.399

P(Sp) denotes the proportion that a species contributes to the stand as a whole. The species specific indicators are: W_{Sp} = mean UAI, D_{Sp} = mean mortality, M_{Sp} = mean mingling, T_{Sp} = mean diameter dominance, and H_{Sp} = mean height dominance. The overall values for each indicator was calculated using the entire data set.

Table 2. Comparing the proportion $P(\text{Sp})$ that a species contributes to the population with $(1 - M_{\text{Sp}})$.

Species of sample tree	N	$P(\text{Sp})$	M_{Sp}	$1 - M_{\text{Sp}}$	$M = \frac{P(p)}{1-M_{\text{Sp}}}$
Baikiaea plurijuga	116	0.103	0.653	0.347	0.298
Burkea africana	194	0.173	0.751	0.249	0.696
Combretum species	214	0.191	0.697	0.303	0.631
Pterocarpus angolensis	178	0.159	0.813	0.188	0.883
Schinziophyton rautanenii	75	0.067	0.875	0.125	0.627
Terminalia sericea	96	0.086	0.781	0.219	0.391
Unidentifiable dead tree	142	0.127		0.285*	0.447
Total	1121				

*Note that the value of D_{Sp} is used here (the mean proportion of dead neighbours), rather than the mingling index.

patch, shown in figure 3, are generally large trees. This is not evident from the indexes but supports the suggestion by Von Breitenbach cited above.

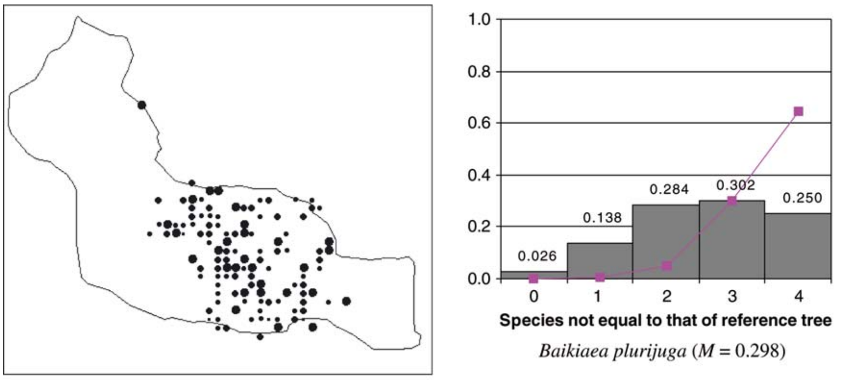
Actual tree mortality may be caused directly by repeated burning of the stem, as well as changes in the osmotic potential of the top-soil that is caused by the accumulation of ash in the upper soil layers (Mitlöhner pers. comm.)

In contrast to *B. plurijuga*, *P. angolensis* is interspersed almost randomly according to Table 2 and in Figure 2. As is evident in the figure, the observed distribution of M_i values (bars) follow the theoretical distribution much more closely than those of *B. plurijuga*. It must be noted, that *P. angolensis* occurs comparatively seldom within the *B. plurijuga* patch. This exclusion from the patch is more pronounced for *B. africana*. The reason or cause for this is not readily apparent. Outside this patch *B. africana* is more aggregated resulting in the lower value of M.

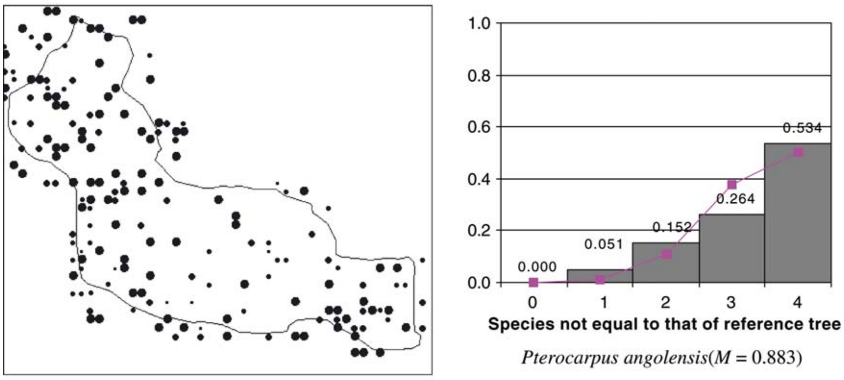
The random distribution of *P. angolensis* is probably a reflection of the regeneration requirements of the species. Vermeulen (1990) reports that *P. angolensis* is especially sensitive to competition in the seedling and establishment phases. The species therefore often regenerates in areas that have been cleared by human or other action. Other species would then establish themselves later.

The interspersion of trees of different size is reflected in the columns T_{Sp} (diameter specific) and H_{Sp} (height specific) in Table 1. Preliminary simulation results have shown that a random interspersion of tree sizes would result in an overall average of $T_{\text{Sp}} = 0.5$ and $H_{\text{Sp}} = 0.5$. The table shows, therefore, that size classes are not interspersed randomly.

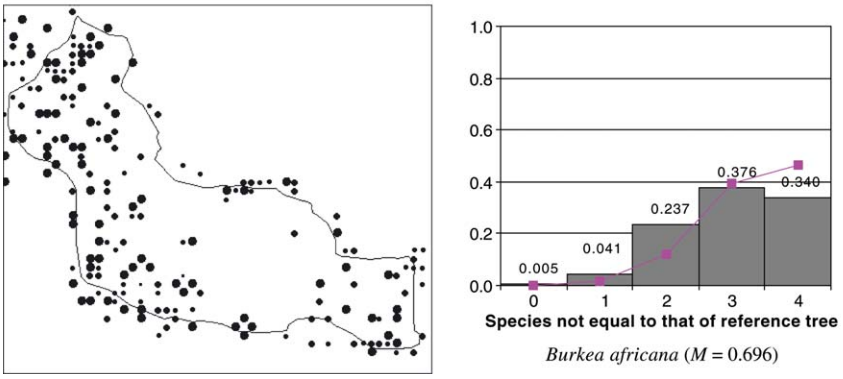
P. angolensis, *S. rautanenii* and *B. plurijuga* need to be highlighted. The low values of T_{Sp} and H_{Sp} for these species imply that few neighbouring trees are larger than the reference tree. This is supported by general observations in the field. The species therefore dominate in the area in which they occur. It also reflects the regeneration requirements of *P. angolensis* noted previously, but highlights the importance of further research into the demography of the other two species.



Baikiaea plurijuga ($M = 0.298$)



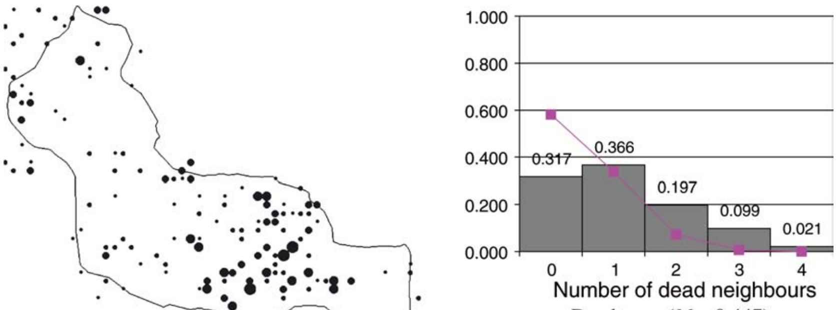
Pterocarpus angolensis($M = 0.883$)



Burkea africana ($M = 0.696$)

Figure 2. The dispersion of *Baikiaea plurijuga*, *Pterocarpus angolensis* and *Burkea africana*, within the study area. High values of M_i are shown in large circles and vice versa. The graphs depict the observed relative distribution of M_i values (bars), and the theoretical hypergeometric distribution (lines) of the values that would indicate a completely random interspersion of the species.

Table 1 also shows a similarity between the values of T_{Sp} and H_{Sp} of the individual species. Unpublished data shows a high degree of correlation between the dbh and height of *B. africana* ($r^2 = 0.8352$), as well as for *P. angolensis* ($r^2 = 0.7317$) for nearby stands.



Dead trees ($M = 0.447$)

CHANGE GRAPH

Figure 3. The aggregation of dead trees within the stand. The degree of interspersion is reflected by the size of the points, with a high degree of aggregation shown by larger points.

Differences between the two indexes are due to the number of species found in the stand, and the differences in their respective diameter – height relationships. A larger difference occurs for the *Comiphora* species, however, reflecting the squat form of the trees; a relatively thick-trunked but short tree.

Conclusions

In the past the applications of neighbourhood-based spatial measures were supported by detailed knowledge of the stands that were assessed, as noted above. This was not the case in this study, where only the extent of the stand was known. However, despite their simple application the indexes are able to provide information about the stands they describe, being able to reflect much of what is currently known about the individual tree species and their ecological circumstances.

The results have also highlighted gaps in our knowledge of the ecology of a few of the important trees, such as *Schinziophyton rautanenii*, *Baikiaea plurijuga*, and *Burkea africana*, as well as the various *Combretum* species that occur in the area. These include regeneration requirements and species succession, and highlights the need for further investigation.

The application of the measures described here has shown that they are easily applied in the field with relatively little training required, although the field crews will have to be able to identify the different tree species. This is particularly useful in view of the trend towards community based natural resource management in Namibia, where community members will have to assess their own resources. Since most of the rural community members are able to identify different plants in their vernaculars, species identification should not be a problem, despite sometimes limited literacy levels.

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