



1 **Spatial diversity of dry savanna woodlands**
2 *Assessing the spatial diversity of a dry savanna woodland*
3 *stand in northern Namibia using neighbourhood-based*
4 *measures*

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10 **Key words:** Ecology, Mingling index, Namibia, Spatial diversity, Spatial structure, Uniform angle
11 index, Woodland savanna

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

19

20 **Introduction and background**

21 The dry woodland savannas of northern Namibia are of significant socio-
22 economic importance to many rural communities, providing a variety of tim-
23 ber and non-timber products. The woodland resources that are used range
24 from building material and wood fuel to food, medicine and grazing (NFSP
25 1996). The quantities of the different products that are extracted are consid-
26 erable. Ollikainen (1992) estimated for example, that firewood alone amounted
27 to a total of 1.5 million cubic metres of wood during 1992. No quantity or
28 value estimates of non-wood products are available for the Namibian dry
29 woodland savannas, although these may be considerable.

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

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

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

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

52 **Spatial diversity and woodland structure**

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

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

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

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

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

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

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

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

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

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

107 Causes of mortality are not necessarily only of human origin, however. The
108 different sizes of a number of species have, for example, their own degree of fire
109 tolerance. This means that trees up to a particular size class may be removed
110 from a stand by a sufficiently intense fire. Wilson and Witkowski (2003) found
111 that the bark-thickness of *B. africana* increases with tree circumference between
112 0 and 400 mm. The thickness of the bark is the primary protector against the
113 effect of fire on the cambium.

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

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

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

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

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

145 Description of the study area

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

150 The area is dominated by linear fossil dunes or sandy plains on calcareous
 151 deposition, similar to those in the adjoining Kavango region described by Graz
 152 (1999). The soils are Kalahari sands, classified as unconsolidated aeolian
 153 material by Coetzee (2001), with very poor water holding capacity and nutrient
 154 status, and subsequently a very low potential for any agricultural development
 155 (Department of Water Affairs 1991).

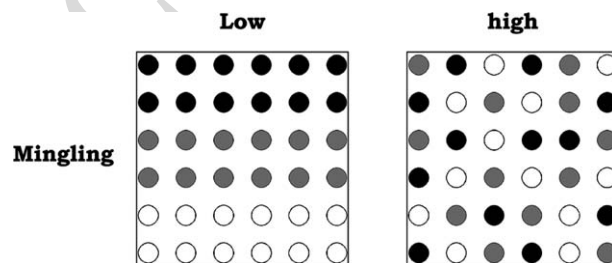


Figure 1. The mingling of black, grey and white 'trees' within two square stands (after Gadow,

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

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

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

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

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

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

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

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

186 **Material and methods**

187 *The interspersions of tree attributes*

188 The original measure of mingling and its derivatives are based on the pro-
 189 portion of trees with dissimilar characteristics to those of a selected sample
 190 tree. The species mingling index M_i for a given sample tree, i , using n neigh-
 191 bours is, for example, obtained through:

$$(1) \quad M_i = \frac{1}{n} \sum_{j=1}^n m_{ij},$$

193 where

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

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

197 0/4 none of the neighbours are of a different species,

198 1/4 one of the neighbours is of a different species,

199 2/4 two of the neighbours are of a different species,

200 3/4 three of the neighbours are of a different species, and

201 4/4 all of the neighbours are of a different species.

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

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

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

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

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

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

224 which expands to:

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

226 The resulting probability multiplied by the total number of samples that
227 were taken provides the expected number of M_i values for that species. The

228 observed and expected distributions of M_i values may then be compared with
 229 the application of standard statistical methods to test for significance of
 230 deviations from the theoretical (random) distribution.

231 Although no detailed data is available for any of the woodland areas in
 232 Namibia, and the extent of the woodland areas hampers the collection of such
 233 information, the sample size provided a suitable estimate of the species com-
 234 position of the stand.

235 The simulation study reported on by Graz (2004) has shown that the ming-
 236 gling index is sensitive to the species composition of a stand. In a stand of trees
 237 interspersed randomly, for example the aggregation of a species, $1 - M_{Sp}$,
 238 approximates the proportion that a species Sp contributes to the stand. This
 239 may be more intuitively understood if we consider each sample tree to provide
 240 an estimate of the proportion that its species contributes to the stand. Values of
 241 $1 - M_{Sp}$ which are greater than the proportion contribution therefore indicate
 242 an overaggregation of the species, while lower values imply overdispersion
 243 within the stand. This relationship provides an important base from which the
 244 index may be interpreted.

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

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

251 where

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

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

255 Similarly, the interspersions of tree height, H_i , is obtained through:

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

257 where

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

259 The species specific interspersions of tree height, H_{Sp} , is then again deter-
 260 mined as the mean of the values of H_i for the species.

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

263 *Uniform angle index*

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

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

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

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

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

276 The critical angle (in degrees) is determined as:

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

278 Four neighbours would therefore be evaluated in terms of a 90° critical
279 angle¹. Since all of the indexes used to measure the interspersion of tree
280 characteristics were based on four trees, the same neighbours could be used for
281 the UAI.

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

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

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

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

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

297 *Sampling*

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

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

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

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

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

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

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

323 **Results and discussion**

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

330 The overall shows a contagion (W_i) greater than 0.6, here indicating a ten-
 331 dency towards non-random (clumped) dispersion of trees (after Gadow et al.
 332 1998). The dispersion around trees of the individual species does not seem to
 333 diverge very much from the mean value of 0.665, if *Philenoptera nelsii* and
 334 *Securidaka longipedunculata* are discounted because of their very low overall
 335 occurrence. This is in line with general observations in the field.

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

337 To compare the proportion of a given species within the stand and the value
 338 $1 - M_{Sp}$ consider Table 2. The table omits those species with very few
 339 observations (less than 5% of the total). The final column in the table reflects
 340 the parameter M proposed by Graz (2004) to determine the degree of inter-
 341 spersion. The value of M is larger than 0 and less than or equal to 1. Values
 342 close to 0 indicates a very low degree of mingling, and 1 indicates a more
 343 random distribution of the species in the stand.

344 Table 2 shows that *B. plurijuga* has the highest degree of aggregation fol-
 345 lowed by *Terminalia sericea*.

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

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

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

361 The possibility is corroborated by the high degree of mortality (D_{Sp}) asso-
 362 ciated 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}
<i>Burkea africana</i>	116	0.103	0.688	0.226	0.751	0.323	0.332
<i>Baikiaea plurijuga</i>	194	0.173	0.665	0.116	0.653	0.249	0.256
<i>Combretum</i> species	214	0.191	0.657	0.148	0.697	0.484	0.479
<i>Comiphora</i> species	36	0.032	0.639	0.201	0.875	0.382	0.556
<i>Ochna pulchra</i>	26	0.023	0.635	0.087	0.962	0.567	0.673
<i>Philenoptera nelsii</i>	16	0.014	0.750	0.141	0.820	0.563	0.625
<i>Pterocarpus angolensis</i>	178	0.159	0.647	0.163	0.813	0.198	0.218
<i>Schinziophyton rautanenii</i>	75	0.067	0.653	0.137	0.875	0.243	0.300
<i>Securidaka longipedunculata</i>	2	0.002	0.625	0.125	0.962	0.375	0.625
<i>Strychnos pungens</i>	26	0.023	0.683	0.163	0.893	0.462	0.548
<i>Terminalia sericea</i>	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}	$1 - M_{\text{Sp}}$	$M = \frac{P(p)}{1 - M_{\text{Sp}}}$
<i>Baikiaea plurijuga</i>	116	0.103	0.653	0.347	0.298
<i>Burkea africana</i>	194	0.173	0.751	0.249	0.696
<i>Combretum</i> species	214	0.191	0.697	0.303	0.631
<i>Pterocarpus angolensis</i>	178	0.159	0.813	0.188	0.883
<i>Schinziophyton rautanenii</i>	75	0.067	0.875	0.125	0.627
<i>Terminalia sericea</i>	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.

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

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

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

376 The random distribution of *P. angolensis* is probably a reflection of the
377 regeneration requirements of the species. Vermeulen (1990) reports that
378 *P. angolensis* is especially sensitive to competition in the seedling and estab-
379 lishment phases. The species therefore often regenerates in areas that have been
380 cleared by human or other action. Other species would then establish them-
381 selves later.

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

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

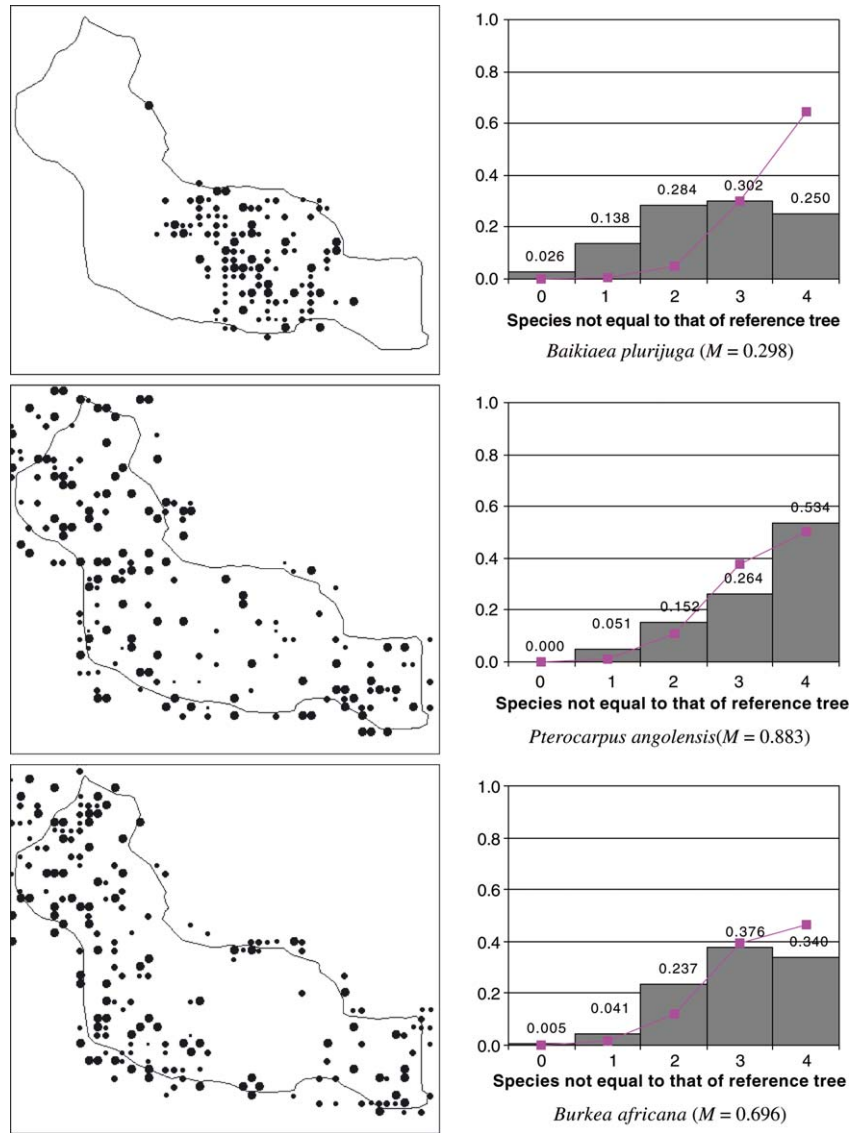


Figure 2. The dispersion of *Baikiaea plurijuga*, *Pterocarpus angolensis* and *Burkea africana*, within the study area. High values of M_i are shown in large circles and vice versa. The graphs depict the observed relative distribution of M_i values (bars), and the theoretical hypergeometric distribution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

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

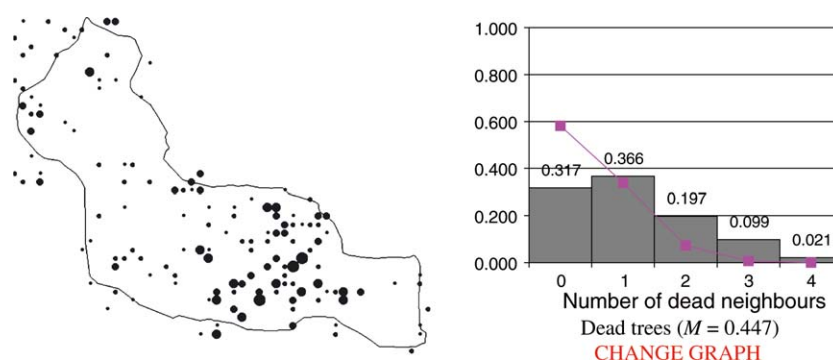


Figure 3. The aggregation of dead trees within the stand. The degree of interspersion is reflected by the size of the points, with a high degree of aggregation shown by larger points.

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

403 Conclusions

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

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

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

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431 References

- 432 Albert M. and Gadow K.v. 1998. Assessing biodiversity with new neighborhood-based parameters.
 433 In: Proceedings of the International Conference on Data Management and Modelling Using
 434 Remote Sensing and GIS for Tropical Forest Land Inventory. Jakarta, Indonesia, Oct. 26–29,
 435 1998.
- 436 Amakali M. 1992. Updated isohyetal rainfall map for Namibia. Unpublished Report. Department
 437 of Water Affairs, Namibia.
- 438 Anon 1996. Forest cover mapping, northern Namibia, phase I. Unpublished Report. Directorate of
 439 Forestry, Namibia. ■Au: Not cited in the text, please check.■
- 440 Biesele M., Bosquet J. and Stanford G. 1979. A Kalahari food staple: *Ricinodendron rautanenii*. In:
 441 Goodin J.R. and Northington D.K. (eds), Arid Land Plant Resources. International Center for
 442 Arid and Semi-Arid Land Studies, Texas Tech University, Lubbock, pp. 341–355. ■Au: Not
 443 cited in the text, please check.■
- 444 Botelle A. 1999. Estimating Manketti Nut Yields in the forest of Western Kavango, Namibia.
 445 CRIAA SA-DC, Windhoek. ■Au: Not cited in the text, please check.■
- 446 Büschel D. 1999. A study of resource utilization: a case from Namibia, Mpungu constituency,
 447 Kavango district, northern Namibia. CRIAA SA-DC Report, Windhoek, Namibia.
- 448 Chakanga M. 1995. Forest Cover Reconnaissance Mapping Project. Directorate of Forestry,
 449 Republic of Namibia, Windhoek.
- 450 Childes S.L. 1984. The population dynamics of some woody species in the Kalahari sand vegetation
 451 of the Hwange National Park. M.Sc. thesis, University of the Witwatersrand, South Africa.
- 452 Chimbelu E.G. 1983. The availability, use and Management potentials of Mungongo (*Ricinoden-*
 453 *dron rautanenii*, Schinz): A Case study of the Southern Shungu Region, Zambia. Ph.D. thesis,
 454 State University of New York, USA. ■Au: Not cited in the text, please check.■
- 455 Clark P.J. and Evans F.C. 1954. Distance to Nearest Neighbor as a Measure of Spatial Rela-
 456 tionships in Populations. *Ecology* 35(4): 445–453.
- 457 Coetzee M.E. 2001. NAMSOTER, A SOTER database for Namibia. Agroecological Zoning
 458 Programme, Ministry of Agriculture, Water and Rural Development, Namibia.
- 459 Crerar S.E. and Church J.T. 1988. Evaporation map for south West Africa/Namibia. Hydrological
 460 Report No. 11/1/8/1/H1, Department of Water Affairs, Namibia.
- 461 Dominy N.J. and Duncan B. 2001. GPS and GIS methods in an African rain forest: applications to
 462 tropical ecology and conservation. *Conserv. Ecol.* 5(2): 6. URL: [http://www.consecol.org/vol5/](http://www.consecol.org/vol5/iss2/art6)
 463 [iss2/art6](http://www.consecol.org/vol5/iss2/art6).
- 464 Department of Water Affairs. 1971. Consolidated report on reconnaissance surveys of soils of
 465 northern and central south West Africa in terms of their potential for irrigation. Report TS/30/
 466 71, Department of Water Affairs, Windhoek, Namibia.
- 467 Department of Water Affairs. 1991. Groundwater investigation in Kavango and Bushmanland,
 468 Namibia. Unpublished Report. Department of Water Affairs, Windhoek, Namibia.

- 469 De Pauw E. and Coetzee M.E. 1999. Production of an agro-ecological zones map of Namibia (first
470 approximation), Part 2: Results. *Agricola* 10: 8–68.
- 471 Du Plessis P. 2001. Strategy and action plan for promoting indigenous fruits in Namibia. Indig-
472 enous Fruit Task Team, Ministry of Agriculture, Water and Rural Development, Namibia. ■Au:
473 Not cited in the text, please check.■
- 474 Gadow K.v. 1999. Waldstruktur und Diversität. *Alg. Forst-u. J.-Ztg.* 170: 117–122.
- 475 Gadow K.v., Hui G.Y. and Albert M. 1998. Das Winkelmaß – ein Strukturparameter zur Bes-
476 chreibung der Individualverteilung in Waldbeständen. *Centralblatt das gesamte Forstwesen.*
477 115(1): 1–10.
- 478 Gadow K.v., Hui G.Y., Chen B.W. and Albert M. 2003. Beziehungen zwischen Winkelmaß und
479 Baumabständen. *Forstw. Cbl.* 122: 127–137.
- 480 Geldenhuys C.J. 1977. The effect of different regimes of annual burning on two woodland com-
481 munities in Kavango. *S. Afr. J. Forestry* 103: 32–42. ■Au: Not cited in the text, please check.■
- 482 Giess W. 1998. A preliminary vegetation map of Namibia (3rd revised edition). *Dinteria* 4: 1–112.
- 483 Goldammer J.G. 1998. Development of a national fire policy and guidelines on fire management in
484 Namibia. Namibia Finland Forestry Programme. Directorate of Forestry, Windhoek. ■Au: Not
485 cited in the text, please check.■
- 486 Graz F.P. 1996. Management of a *Pterocarpus angolensis* population under the influence of fire and
487 land use. M.Sc. thesis, University of Stellenbosch, South Africa.
- 488 Graz F.P. 1999. A preliminary terrain feature classification of the Okavango region, Namibia. *S.*
489 *Afr. J. Survey. Geo-Inf.* 1: 123–129.
- 490 Graz F.P. 2003. Fire damage to *Schinziophyton rautanenii* (Schinz) trees in North-Eastern Namibia.
491 *Dinteria* 28: 39–43.
- 492 Graz F.P. 2004. The behavior of the species mingling index M_{Sp} in relation to species dominance
493 and dispersal. *Eur. J. Forest Res.* 1: 87–92.
- 494 Graz F.P., in preparation. Description and Ecology of *Pterocarpus angolensis*. ■Au: Not cited in
495 the text, please check and also update if possible.■
- 496 Groome J.S., Lees H.M.N. and Wigg L.T. 1957. A summary of information on *Pterocarpus*
497 *angolensis*. *Forestry Abstr.* 18(2): 153–162. ■Au: Not cited in the text, please check.■
- 498 Helgren D.M. 1982. Edaphic context of the Mongongo (*Ricinodendron rautanenii*) in the North-
499 western Kalahari. *S. Afr. J. Sci.* 78: 131–132. ■Au: Not cited in the text, please check.■
- 500 Hui G.Y., Albert M. and Gadow K.v. 1998. Das *Umgebungsmaß* als Parameter zur Nachbildung
501 von Bestandesstrukturen. *Forstw. Cbl.* 117: 258–266.
- 502 Lee R.B. 1973. Mogongo: the ethnography of a major wild food resource. *Ecol. Food Nutr.* 2: 307–
503 321.
- 504 Leger S. 1997. The Hidden Gift of Nature. DED, German Development Service, Berlin, Germany.
- 505 Lewandowski A. and Pommerening A. 1997. Zur Beschreibung der Waldstruktur – Erwartete und
506 beobachtete Arten-Durchmischung. *Forstw. Cbl.* 116: 129–139.
- 507 Mitlöhner R. 1997. Pflanzeninterne Potentiale als Indikatoren für den tropischen Standort. Shaker
508 Verlag.
- 509 Newmark J. 1997. Statistics and Probability in Modern Life, 6th ed. Saunders College Publishing,
510 Fort Worth.
- 511 NFSP. 1996. Namibia Forestry Strategic Plan. Directorate of Forestry, Windhoek, Namibia.
- 512 Ollikainen T. 1992. Study on wood consumption in Namibia. Internal Report, Directorate of
513 Forestry, Windhoek.
- 514 Palmer E. and Pitman N. 1972. Trees of Southern Africa, Vol. 2. Balkema, Cape Town. ■Au: Not
515 cited in the text, please check.■
- 516 Pielou E.C. 1977. Mathematical Ecology. John Wiley & Sons, New York, 384 pp.
- 517 Rutherford M.C. 1981. Survival, regeneration and leaf biomass changes in woody plants following
518 spring burns in *Burkea africana* – *Ochna pulchra* savanna. *Bothalia* 13: 531–552.
- 519 Shackleton C.M. 2001. Managing regrowth of an indigenous savanna tree species (*Terminalia*
520 *sericea*) for fuelwood: the influence of stump dimensions and post-harvest coppice pruning.
521 *Biomass Bioenergy* 20: 261–270.

- 522 Smith T.M. and Grant K. 1986. The role of competition in a *Burkea africana* – *Terminalia sericea*
523 savanna. *Biotropica* 18: 219–223.
- 524 Staupendahl K. 2001. Das flächenbezogene Winkelmaß W_f – Ein Index zur quantitativen Bes-
525 chreibung der horizontalen Baumverteilung. In: Akca A. et al. (HRSG). Waldinventur,
526 Waldwachstum und Forstplanung – Moderne Technologien, Methoden und Verfahrensweisen.
527 Festschrift K. von Gadow. Zohab-Verlag, Göttingen. pp. 101–115.
- 528 Vermeulen W.J. 1990. A monograph on *Pterocarpus angolensis*. SARCCUS Standing Committee
529 for Forestry, Pretoria, South Africa.
- 530 Von Breitenbach F. 1968. Long-term plan of forestry development in eastern Caprivi Zipfel.
531 Unpublished Report. George, South Africa.
- 532 Wilson B.G. and Witkowski E.T.F. 2003. Seed banks bark thickness and damage in age and size
533 structure (1978–1999) of the African savanna tree *Burkea africana*. *Plant Ecol.* 167: 151–162.
- 534 Yeaton R.I. 1988. Porcupines, fires and the dynamics of the tree layer of the *Burkea africana*
535 savanna. *J. Ecol.* 76: 1017–1029.
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