

# The structure of Leguminosae-Detarioideae dominant rain forest in Korup National Park, Cameroon

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**Background and aims** – We studied a cluster of trees in the Leguminosae subfamily Detarioideae, to: (1) determine the size, structure, and tree species composition of this cluster; (2) map the size, shape, and structure of groups of individual Detarioideae tree species in the cluster.

**Location** – Lowland rain forest in southern Korup National Park, in the Southwest Region of Cameroon.

**Material and methods** – Trees in permanent plots were recorded using standard plot enumeration techniques. Outside plots, single-species tree groups were recorded by a rapid technique. From this data, detailed maps of groups of trees were prepared.

**Key results** – Detarioideae tree species occur co-dominant in a cluster of at least 32 km<sup>2</sup> with an irregular shape. The cluster contained at least 42 Detarioideae tree species; at least 29 of these occurred in groups ranging in size from 50 to 4000 m across, depending on the species. Groups usually had circular shapes, caused by ballistic seed dispersal. In a group, trees were always mixed with trees of several other Detarioideae species. Every area within the cluster contained a specific set of Detarioideae species. The percentage of Detarioideae trees  $\geq$  60 cm stem diameter on 50 ha was up to 76% in Detarioideae-rich forest, to 6% in Detarioideae-poor forest. Of all trees in the centre of the cluster, 2.8% belonged to pioneer forest species, which indicates that disturbance levels were low during the past generations of trees.

**Discussion** – The forests in the Detarioideae cluster have not been subject to substantial human and natural impacts in historic or prehistoric times. Such forests are exceptional in Africa. Detarioideae clusters may indicate glacial age forest refuges, especially clusters that contain both many different Detarioideae species and some Detarioideae species endemic to the cluster.

**Keywords** – Ballistic seed dispersal; forest refuge; glacial age; *Microberlinia*; monodominant; *Tetraberlinia*; transient dominant.

## INTRODUCTION

In tropical lowland rain forests, areas with a high richness of canopy tree species may be intermingled with areas dominated by a single canopy tree species. After major disturbance, a pioneer tree species can become established and dominate the rain forest canopy. Dominance after severe disturbances is a successional phase, which will last only

a single generation, because pioneer tree species do not regenerate in their own shade (Connell & Lowman 1989; Hart et al. 1989). Dominance also occurs in tropical regions that contain smaller numbers of species, such as forests at high altitudes, forests with low or seasonal rainfall, and mangrove forests (Connell & Lowman 1989). Persistent monodominance, a tree species persisting abundantly in the canopy of tropical rain forest on well-drained soils across

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more than one generation, appears to be favoured only by a period of low disturbance. If the dominant species comprises over 50% of the number of canopy trees (Connell & Lowman 1989) or over 80% of the basal area of canopy trees (Hart 1990), that species is considered monodominant. The dominant species successfully regenerates under its own canopy (Torti et al. 2001). The monodominant stands are surrounded by forest with a much higher diversity of canopy species (Hart et al. 1989).

Many canopy tree species in the Leguminosae subfamily Detarioideae (LPWG 2017) in African lowland rain forests form monodominant stands of a few hectares to many km<sup>2</sup> in area (Aubréville 1938, 1968; Letouzey 1968). *Gilbertiodendron dewevrei* (Detarioideae) forest is the most prominent example of monodominance, occurring in stands to many km<sup>2</sup> in area where up to 90% of canopy trees belong to this species (Gérard 1960; Hart 1990). The extent of monodominant forest has been examined using aerial photography and by recording trees along transects. An example of the use of aerial photography is the map of *Gilbertiodendron dewevrei* stands in southern Cameroon by Letouzey (1968). Gérard (1960) mapped the occurrence of *G. dewevrei* and *Julbernardia seretii* (Detarioideae) along a grid of transect lines.

The canopy of African rain forests may be dominated by several Detarioideae tree species in co-dominant stands (Aubréville 1968; Letouzey 1968; White 1983; Connell & Lowman 1989). In the tropical lowland evergreen rain forests of southern Korup National Park, in the Southwest Region in Cameroon, where the average annual rainfall is about 5100 mm, there is an example of such a Detarioideae cluster, consisting of groups of many Detarioideae species (Gartlan et al. 1986; Newbery et al. 1998, 2004, 2013). We define a Detarioideae cluster as an area of forest rich in Detarioideae trees of multiple species, surrounded by forest poor in Detarioideae trees. We define a Detarioideae group as an accumulation of trees of a single Detarioideae species, surrounded by forest where that species is absent. In such groups, the Detarioideae trees are mixed with trees of other Detarioideae species and trees of other plant families. The crown of each tree in a group would normally be adjacent to the crown of at least one other conspecific tree, or there may be a single tree of a different species in between two conspecific trees in a group. Distances between groups would generally be larger than the diameters of the groups. Such groups of conspecific trees can be documented by an observer who is familiar with the appearance of the stem and the fallen leaves of that tree species (e.g. Saint-Aubin 1961; Aubréville 1968), or they can be recorded through mapping, for example in permanent plots (e.g. Condit et al. 2000; Thomas et al. 2003).

The existence of Detarioideae clusters was known, but there were no maps, and no detailed descriptions of the structure and species composition. A comprehensive description of a Detarioideae cluster is the first step towards explanations and hypotheses on how a cluster was formed and how it is conserved. The vegetation on the African continent has been documented on vegetation maps such as White (1983) and Sayre et al. (2013) and for Cameroon, there is the detailed vegetation map of Letouzey (1968).

These vegetation maps have been prepared using aerial or satellite photography. Detarioideae clusters, however, cannot be mapped with aerial photography, because identification of tree species in species-rich tropical lowland rain forest cannot be acceptably achieved from aerial photography. A permanent plot may capture a section of a Detarioideae cluster, for example in Gabon (Engone Obiang et al. 2019), but permanent plots are usually up to only 50 ha in size, because mapping from the ground takes much time. Here we use data from a set of permanent plots of exceptionally large size, 155.75 ha, as well as a fast method to map trees of a single species without making a plot (Newbery et al. 2004, 2013) which enables us to fill the gap between small 50-ha plot maps and large vegetation maps. We prepared detailed maps of the Detarioideae cluster in southern Korup National Park, to: (1) describe the size, structure, and tree species composition of this cluster; (2) describe the size, shape, and structure of groups of individual Detarioideae tree species in the cluster. We discuss these maps and descriptions of the structure of the Detarioideae cluster and propose hypotheses on the origin and maintenance of the cluster.

## MATERIAL AND METHODS

### Tree mapping within permanent plots

Around the 5 km long “P transect” in southern Korup National Park, the 155.75 ha “P transect plots” were established (fig. 1). The methodology used in the set-up of these plots is explained in detail by Newbery et al. (2004, 2013). They consist of three plots: 1. The “P plot”, 1650 × 500 m, 82.5 ha, set up in 1990–1991, re-census in 2004–2005. 2. Six extensions to the P plot, each usually 50 m wide, 17 ha, set up in 1999–2000. 3. The “NW plot”, 750 × 750 m, 56.25 ha, set up in 2003 (fig. 1). All trees ≥ 50 cm stem diameter were registered; the diameter was recorded at 1.3 m height, or higher if the tree had buttresses. The P transect plots contained 3177 trees ≥ 50 cm stem diameter of 144 species. Trees of 10–49.9 cm stem diameter were recorded in 56 subplots of 50 × 50 m: 33 within the P plot and 23 within the NW plot, total 14 ha (fig. 1). These subplots contained 6047 trees ≥ 10 cm stem diameter of 221 species. In the P and NW plots, all trees 10–49.9 cm stem diameter were recorded, of the four most abundant Detarioideae tree species, and of selected Detarioideae tree species occurring in groups. The percentage of Detarioideae trees ≥ 60 cm stem diameter in a 50-ha sample of the NW plot was compared with that in Detarioideae-poor forest in the 50-ha KFDP plot in Korup National Park (Thomas et al. 2003, who used a 60 cm tree diameter threshold). A list of pioneer tree species in the P transect plots was prepared, using Appendix A in Hawthorne (1996), and internet databases such as African Plant Database (2021) and GBIF (2021). Pioneer species usually occur widespread; nearly all pioneer tree species listed for Ghana by Hawthorne, occur also in Cameroon.

### Tree mapping outside permanent plots

Outside the P transect plots, selected groups of trees of several Detarioideae species were mapped. A map of all *Microberlinia bisulcata* trees ≥ 50 cm stem diameter in the

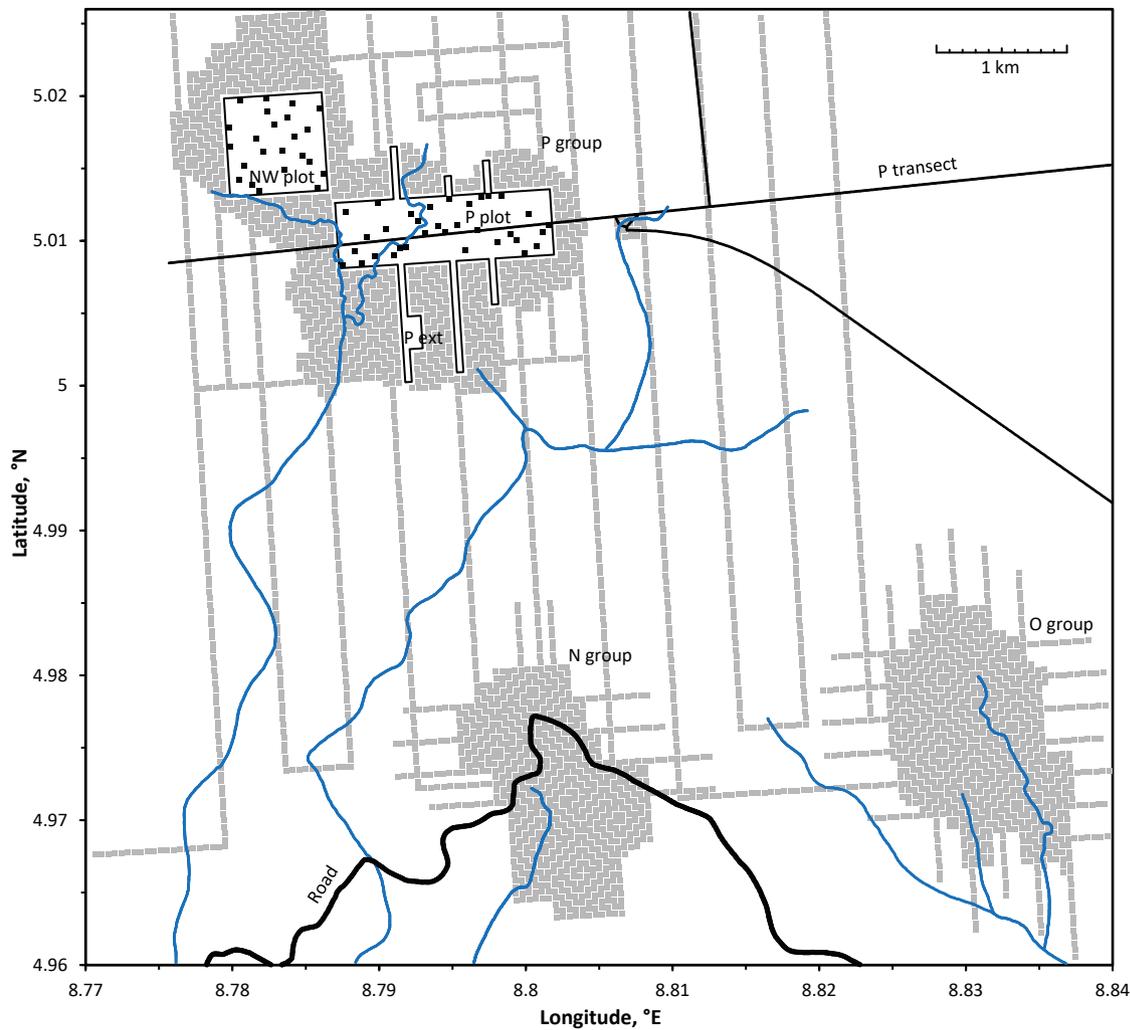
“P group”, which includes the P transect plots, was published by Newbery et al. (2004, 2013) and Burgt (2018). The stem diameters of the trees were not recorded. In 2004–2005, data for a more detailed map including smaller trees was collected, by recording coordinates and stem diameter of all *M. bisulcata* trees  $\geq 10$  cm stem diameter, at 1.3 m height; or higher if the tree had buttresses. Details of the mapping methodology are given in Newbery et al. (2004). All trees  $\geq 10$  cm stem diameter in two other *M. bisulcata* groups in the Detarioideae cluster were mapped, using the same methodology: the “N group” 4.5 km to the south and the “O group” 6 km to the southeast. The existence of part of the N group was known since 1995 (by D.M. Newbery). The northern section was mapped in 2005, the southern section in 2015 and 2016; the area further south was not mapped because the habitat was mostly periodically inundated forest, unsuitable for *M. bisulcata*. The O group was mapped in

2004–2005. The absence of *M. bisulcata* close to the three groups was recorded along 50 m wide transect lines starting at the edges, usually to 500 m long and spaced 250 m apart.

The occurrence of Detarioideae trees was recorded in an area of ca 33 km<sup>2</sup> along a series of 50-m wide transect lines, located in the cluster, and spaced 500 m apart, in 2004–2005. Occurrence was recorded for each 50 m segment. These walks were up to 9 km long; their routes were mostly rectangular in shape. The average deviation measured at the end of each walk was 3.4 m/km<sup>2</sup>; range 0.0–9.3 m/km<sup>2</sup>.

### Tree positioning

Positions were measured with 50-m tapes and thread distance meters. Line directions were taken with Suunto KB-14/360R compasses which were not adjusted for declination, pointing to the magnetic rather than the geographic north.



**Figure 1** – Map of the study area in Korup National Park, showing the NW plot, the P plot, and the six P plot extensions, where all trees over 50 cm stem diameter were recorded. Black squares within these plots are the 56 subplots of 50 × 50 m where all trees over 10 cm stem diameter were recorded. The area outside these plots was divided into 50 × 50 m squares; squares surveyed for selected Detarioideae trees are grey; white areas were not surveyed. All recorded *Microberlinia bisulcata* trees over 10 cm stem diameter were occurring in three groups: the P group, the N group, and the O group. The occurrence of Detarioideae trees was recorded along a series of 50 m wide transect lines spaced 500 m apart. The size of the map is 7.3 km north to south, by 7.9 km west to east. Blue lines are rivers.

The position of trees was recorded in metric coordinates because the P plot had been set up using that system. Metric coordinates were converted to geographical coordinates in the WGS84 format, using Garmin eTrex 30 devices. To verify the results of the conversion, the coordinates of nine trees were measured in WGS84 format, as well as calculated. The calculated coordinates were between 1 and 30 m away (average of 15 m away) from the measured coordinates. In the eastern section of the P group, the error could have been up to 50 m. For interpretation of the maps the precision was generally satisfactory because the positioning of neighbouring trees had an accuracy of 0–5 m.

## RESULTS

### The Detarioideae cluster

The Detarioideae cluster in southern Korup National Park occurred at 40 to 130 m altitude and had a size of at least 32 km<sup>2</sup> with an irregular shape. Detarioideae tree species occurred abundantly across at least 7.5 km in north-south direction and at least 4.5 km in east-west direction. These dimensions are to some extent tentative because cluster margins were indistinct as well as only partly recorded. In the Detarioideae cluster, Detarioideae trees were more abundant and attained larger stem diameters than non-Detarioideae trees, as concluded from visual interpretation of fig. 2. Dominance of Detarioideae trees increased with increasing stem diameter class and was larger when basal area was considered (fig. 3). Of the 3177 trees  $\geq 50$  cm stem diameter, 56.1% were Detarioideae and their basal area was 71.7% of total basal area. Of the 564 trees  $\geq 100$  cm stem diameter,

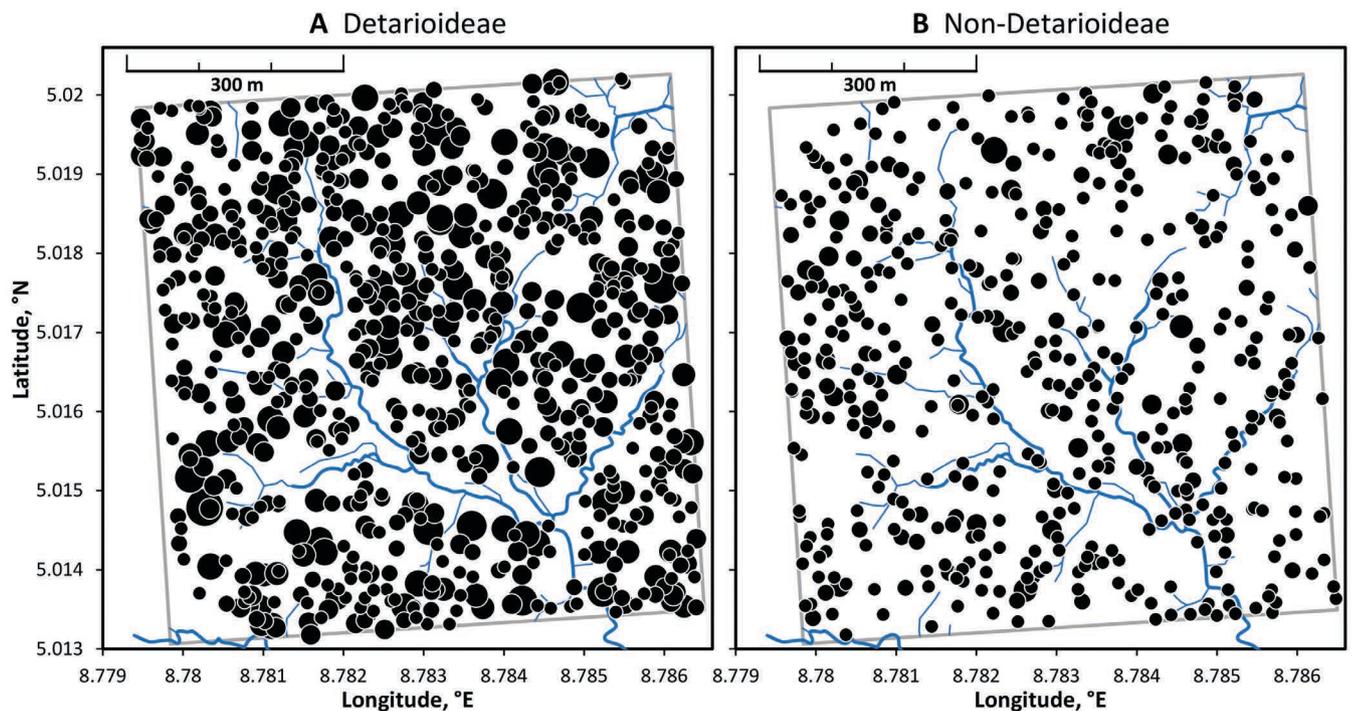
91.5% were Detarioideae, with a basal area of 92.9% of total basal area (fig. 3). The percentage of Detarioideae trees  $\geq 60$  cm stem diameter was up to 76% in Detarioideae-rich forest (in a 50-ha sample of the NW plot), to 6% in Detarioideae-poor forest in the 50-ha KFDP plot, located 9 km to the NE.

### Species composition of the cluster

The cluster contained at least 42 Detarioideae tree species (table 1). Most of these 42 species were large canopy trees, growing to stem diameters of  $\geq 100$  cm, and heights of 40–50 m. Forty Detarioideae species occurred on well-drained sandy and rocky soils. *Eurypetalum unijugum* occurred on rock outcrops, while the smallest of the 42 Detarioideae tree species, *Gilbertiodendron demonstrans*, reached about 30 cm stem diameter, and was found on periodically inundated soils. Nine of the 42 Detarioideae tree species are endemic to the Southwest Region in Cameroon (table 1). Seven of these nine species were discovered during the present study. The Detarioideae cluster contained many trees and tree species from other families (table 2). Pioneer trees were 88 in number (of 14 species), which is 2.8% of the 3177 trees (of 144 tree species)  $\geq 50$  cm stem diameter in the P transect plots (table 3).

### Structure of the cluster

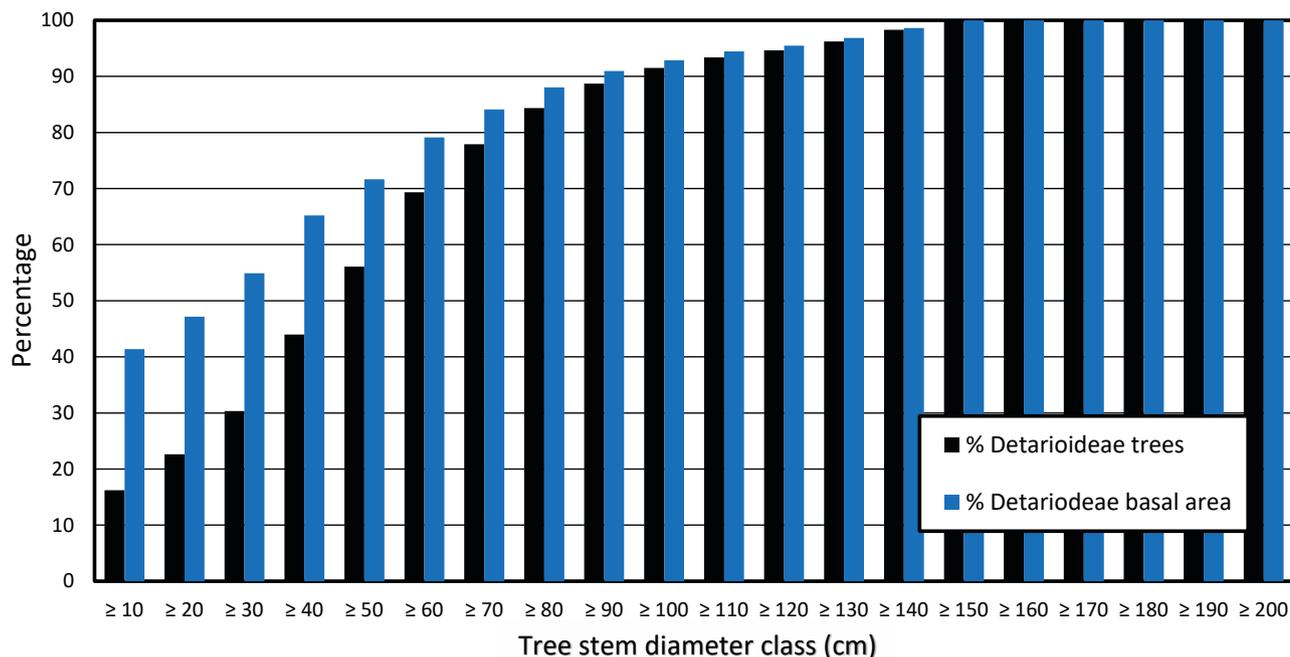
In the cluster, Detarioideae trees of at least 29 species were recorded to occur in groups (table 1). Group size depended on the species and varied between 50 and 4000 m. Maps of six Detarioideae species in the NW plot are shown in fig. 4. The NW and P plots contained 25 and 27 Detarioideae species, respectively; mostly group-forming species, with a few



**Figure 2** – Maps of all 704 Detarioideae trees (18 species) and all 490 non-Detarioideae trees (81 species)  $\geq 50$  cm stem diameter in the NW Plot. The size of a symbol is relative to the stem diameter of the tree, in 8 size classes of 20 cm: 50–69.9 cm up to 190–209.9 cm. Blue lines are streams.

**Table 1** – The 42 Detarioideae tree species recorded in the Detarioideae cluster. The 29 species marked \* were recorded to be group-forming; species not marked could still be group-forming. Main method of seed dispersal: A = animal, B = ballistic, W = wind. The nine species marked in bold are endemic to the Southwest Region of Cameroon.

A	<i>Azelia bella</i> Harms	*	B	<b><i>Englerodendron korupense</i></b> Burgt
B	<i>Annea afzelii</i> (Oliv.) Mackinder & Wieringa		B	<i>Eurypetalum unijugum</i> Harms
A	<i>Anthonotha crassifolia</i> (Baill.) J.Léonard	*	B	<i>Gilbertiodendron brachystegioides</i> (Harms) J.Léonard
A	<i>Anthonotha fragrans</i> (Baker f.) Exell & Hillcoat	*	B	<i>Gilbertiodendron demonstrans</i> (Baill.) J.Léonard
A	<i>Anthonotha lamprophylla</i> (Harms) J.Léonard	*	B	<i>Gilbertiodendron dewevrei</i> (De Wild.) J.Léonard
A	<i>Anthonotha macrophylla</i> P.Beauv.	*	B	<b><i>Gilbertiodendron newberyi</i></b> Burgt
*	B <i>Anthonotha xanderi</i> Breteler	*	B	<i>Gilbertiodendron ogoouense</i> (Pellegr.) J.Léonard
B	<i>Aphanocalyx margininervatus</i> J.Léonard	*	B	<i>Gilbertiodendron preussii</i> (Harms) J.Léonard
B	<i>Aphanocalyx microphyllus</i> (Harms) Wieringa	*	B	<i>Gilbertiodendron</i> sp. ined.
*	B <i>Baikiaea insignis</i> Benth.	*	B	<i>Hymenostegia bakeriana</i> Hutch. & Dalziel
*	B <i>Berlinia auriculata</i> Benth.	*	B	<i>Hymenostegia viridiflora</i> Mackinder & Wieringa
*	B <i>Berlinia bracteosa</i> Benth.	*	B	<i>Julbernardia seretii</i> (De Wild.) Troupin
*	B <i>Berlinia craibiana</i> Baker f.	*	B	<i>Microberlinia bisulcata</i> A.Chev.
*	B <b><i>Berlinia korupensis</i></b> MacKinder & Burgt	*	B	<i>Plagiosiphon longitubus</i> (Harms) J.Léonard
*	B <i>Bikinia letestui</i> (Pellegr.) Wieringa	W		<i>Stemonocoleus micranthus</i> Harms
A	<i>Copaifera mildbraedii</i> Harms	*	B	<b><i>Talbotiella korupensis</i></b> MacKinder & Wieringa
*	B <i>Crudia ledermannii</i> Harms	*	B	<b><i>Talbotiella velutina</i></b> Burgt & Wieringa
*	B <b><i>Cryptosepalum korupense</i></b> Burgt	*	B	<b><i>Tessmannia korupensis</i></b> Burgt
A	<i>Daniellia oblonga</i> Oliv.	A		<i>Tessmannia</i> sp. ined.
*	B <i>Didelotia africana</i> Baill.	*	B	<i>Tetraberlinia bifoliolata</i> (Harms) Hauman
*	B <b><i>Didelotia korupensis</i></b> Burgt	*	B	<b><i>Tetraberlinia korupensis</i></b> Wieringa



**Figure 3** – Percentages of Detarioideae trees in the P transect plots, compared to all trees in these plots (black bars), and percentages of Detarioideae tree basal area in the P transect plots, compared to all trees in these plots (blue bars). Percentages are given for 20 size classes, ≥ 10 cm to ≥ 200 cm stem diameter. Data for the first four size classes is from 6047 trees ≥ 10 cm recorded on 14 ha. Data for other the size classes is from 3177 trees ≥ 50 cm recorded on 155.75 ha.

**Table 2** – Numbers of trees and of tree species in the P transect plots, in the Detarioideae, in three other Leguminosae subfamilies (LPWG 2017) and in all other families combined, in four increasing size thresholds. Numbers of trees and species  $\geq 10$  cm stem diameter are from 6047 trees on 14 ha. Numbers of trees and species  $\geq 50$  cm to  $\geq 150$  cm stem diameter are from 3177 trees  $\geq 50$  cm on 155.75 ha.

(Sub-)family	Number of trees / species $\geq 10$ cm	Number of trees / species $\geq 50$ cm	Number of trees / species $\geq 100$ cm	Number of trees / species $\geq 150$ cm
Leguminosae-Caesalpinioideae	74 / 6	123 / 7	14 / 3	0 / 0
Leguminosae-Detarioideae	982 / 26	1782 / 29	516 / 10	65 / 3
Leguminosae-Dialioideae	40 / 3	16 / 3	0 / 0	0 / 0
Leguminosae-Papilionoideae	110 / 4	16 / 4	0 / 0	0 / 0
Non-Leguminosae	4841 / 181	1240 / 101	34 / 17	0 / 0
<b>Total</b>	<b>6047 / 220</b>	<b>3177 / 144</b>	<b>564 / 30</b>	<b>65 / 3</b>
% Leguminosae-Detarioideae	16.2% / 11.8%	56.1% / 20.1%	91.5% / 33.3%	100% / 100%

**Table 3** – Abundance of trees  $\geq 50$  cm stem diameter of all pioneer forest tree species in the P transect plots. Of all trees, 2.8% belonged to pioneer forest species.

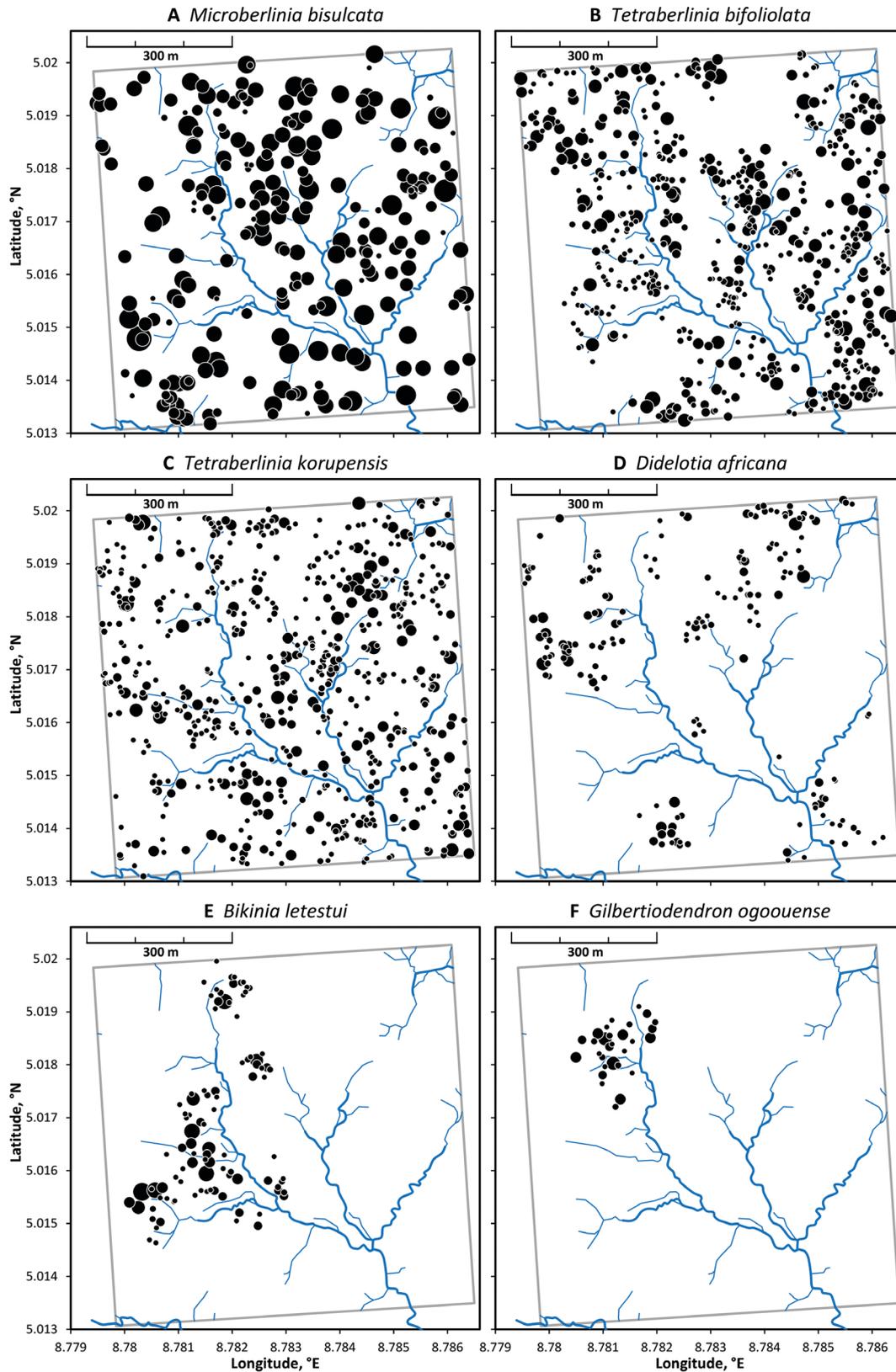
Pioneer tree species	Family	Number of trees
<i>Alstonia boonei</i> De Wild.	Apocynaceae	23
<i>Anthocleista schweinfurthii</i> Gilg	Gentianaceae	3
<i>Bridelia micrantha</i> (Hochst.) Baill.	Phyllanthaceae	1
<i>Cleistopholis staudtii</i> Engl. & Diels	Annonaceae	2
<i>Croton penduliflorus</i> Hutch.	Euphorbiaceae	6
<i>Discoglyprena caloneura</i> (Pax) Prain	Euphorbiaceae	4
<i>Lophira alata</i> Banks ex C.F.Gaertn.	Ochnaceae	4
<i>Musanga cecropioides</i> R.Br.	Urticaceae	17
<i>Nuclea diderrichii</i> (De Wild. & T.Durand) Merr.	Rubiaceae	3
<i>Psydrax subcordata</i> (DC.) Bridson	Rubiaceae	5
<i>Sapium ellipticum</i> (Hochst.) Pax	Euphorbiaceae	3
<i>Tetrapleura tetraptera</i> (Schumach. & Thonn.) Taub.	Leguminosae-Caesalpinioideae	2
<i>Zanthoxylum gillettii</i> (De Wild.) P.G.Waterman	Rutaceae	2
<i>Zanthoxylum tessmannii</i> (Engl.) J.F.Ayafor	Rutaceae	13
Number of trees of these 14 pioneer species		88
Number of trees of 130 non-pioneer species		3089
<b>Total number of trees of 144 species</b>		<b>3177</b>

non-group-forming species. In a group, trees were always mixed with trees of several other Detarioideae species. Some species occurred across large areas of the cluster, occupying over 50% of the cluster area. Some species were only found in a single group, but there may be more groups since only part of the cluster was surveyed. Distance between groups of most species was usually much more than the diameters of the groups, leaving most of the forest in the cluster unoccupied by those species. Every area within the cluster therefore contained a specific set of Detarioideae species.

*Tetramerlinia bifoliolata* and *T. korupensis* were the two most common Detarioideae tree species in the cluster. These two species occurred in oval to irregular-shaped groups of about 1.0–4.0 km in size (fig. 5). In the northern section of the cluster, *T. korupensis* occurred in an area of at least 9.3 km<sup>2</sup> and *T. bifoliolata* in 7.8 km<sup>2</sup> (fig. 5). In the central section, partly connected to the northern one, *T. korupensis*

occurred in an area of at least 7.3 km<sup>2</sup> and *T. bifoliolata* in 5.8 km<sup>2</sup>. In the southern section, the two species occurred in smaller areas. Visual interpretation of fig. 5 proves that the two *Tetramerlinia* species usually occurred together, that the shapes of the groups of these two species are partially similar, and that both species are absent in large areas. In contrast, the groups of the seven species of *Gilbertiodendron* usually occurred separate from each other.

Several other species besides *Tetramerlinia* occurred in large groups. *Anthonotha xanderi*, *Gilbertiodendron preussii*, and *Julbernardia seretii* occurred in groups of over 500 m diameter. *Microberlinia bisulcata* was recorded in three large, well-defined groups with distinct shapes and clear edges, compound circular to irregular in shape, 0.8–3 km across, and located at 2–4 km distance to each other (fig. 6). This figure proves that the trees of this species are not randomly distributed. The species is absent from most



**Figure 4** – Maps of six Detarioideae tree species in the NW plot; the four most common species and two species occurring in small groups. Maps show all trees  $\geq 10$  cm stem diameter. The size of a symbol is relative to the stem diameter of the tree, in 10 size classes of 20 cm: 10–29.9 cm up to 190–209.9 cm. Blue lines are streams. Map F adapted from Burgt et al. (2015), reprinted by permission from Springer Nature; © Springer Nature; this image 4F is not covered by the terms of the Creative Commons licence of this publication. For permission to reuse, please contact the rights holder.

of the mapped area. Detailed maps of the three groups show the distributions of trees of various size classes (figs 7, 8). No other groups were found within the area of fig. 6; however, groups of 400 m diameter or less may have been left unrecorded. The density of *M. bisulcata* trees in the three groups is compared in fig. 9. As all other Detarioideae species, *M. bisulcata* occurred in only parts of the cluster: of the at least 32 km<sup>2</sup> of the cluster, 4.4 km<sup>2</sup> was occupied by the three *M. bisulcata* groups. The species usually occurred with *Tetraberlinia bifoliolata* and *T. korupensis*, but not always: there were no *Tetraberlinia* trees in the southern part of the N group.

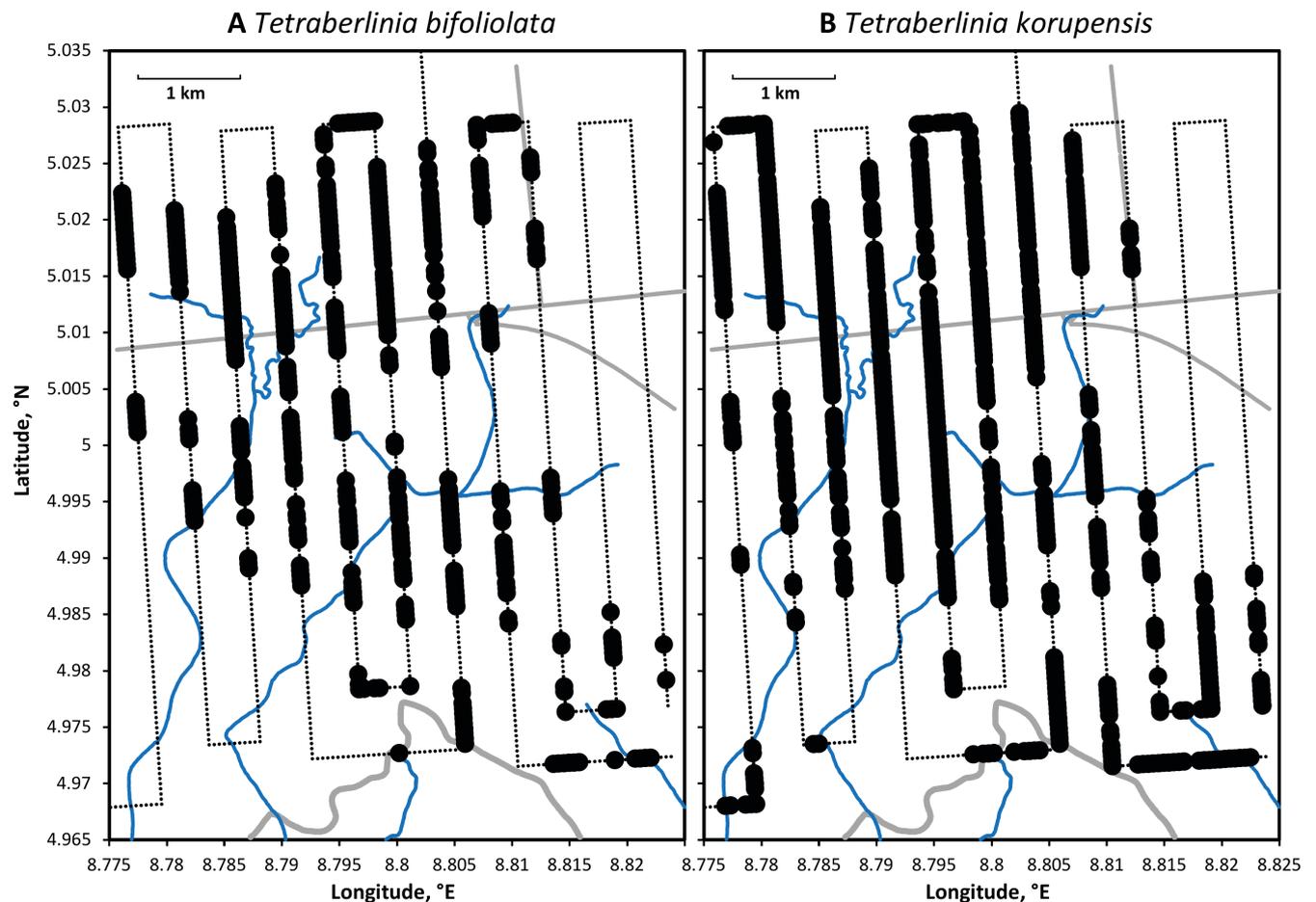
Most species occurred in groups of less than 300 m diameter. *Bikinia letestui* was recorded in about 30 groups of 50–200 m diameter, at 100–800 m distance to each other. One of the smallest groups contained 11 trees of 10–96 cm stem diameter in an area about 50 m diameter (fig. 4E). There are probably many additional, unrecorded groups of *B. letestui* in the cluster, but in some areas the species is absent. In some species group size appeared similar, for example, six groups of *Gilbertiodendron ogoouense* were all 100–200 m diameter (one of these in fig. 4F). In other species, group size was more variable, for example in *Didelotia africana* (fig. 4D). *Anthonotha fragrans* is not group-forming and occurred

commonly in both Detarioideae-rich and -poor forest; the seeds are animal-dispersed.

## DISCUSSION

### Subfamily dominance

The Detarioideae trees in the cluster in southern Korup National Park are co-dominant at the subfamily level (figs 2, 3; table 2). The three *Microberlinia bisulcata* groups (fig. 6) were in different phases of transient dominance (Newbery et al. 2013), evidenced by their clearly differing size-class frequency distributions (fig. 9). This suggests that the degree of dominance in a single group might vary from generation to generation. The O group had more trees/km<sup>2</sup> of 10–90 cm stem diameter, compared to the other two groups. The next generation in the O group may therefore show higher mature tree density, while the mature tree density in the P and N groups may be lower in the next generation. The P group had more trees/km<sup>2</sup> of 100–150 cm stem diameter. The low numbers of trees/km<sup>2</sup> around 50 cm stem diameter, in all three *M. bisulcata* groups (fig. 9), are partly caused by high growth rates and low mortality (Newbery et al. 2013). A second example of possible transient dominance was recorded for



**Figure 5** – Maps of *Tetraberlinia bifoliolata* and *T. korupensis* in the Detarioideae cluster in Korup National Park. The occurrence of both species was recorded along lines 500 m apart. Presence of the species is depicted by large dots, absence by small dots. The size of the maps is 7.74 km north to south, by 5.62 km west to east. The wide grey line is a road; narrow grey lines are footpaths. Blue lines are streams.

*Gilbertiodendron dewevrei* at around 5.001°N, 8.796°E, where 96 trees of 10–213 cm stem diameter occurred in four groups, each with different size distributions, (Map 2 in Burgt et al. 2015). Trees of this species stand relatively close to each other because of their narrow and deep crowns.

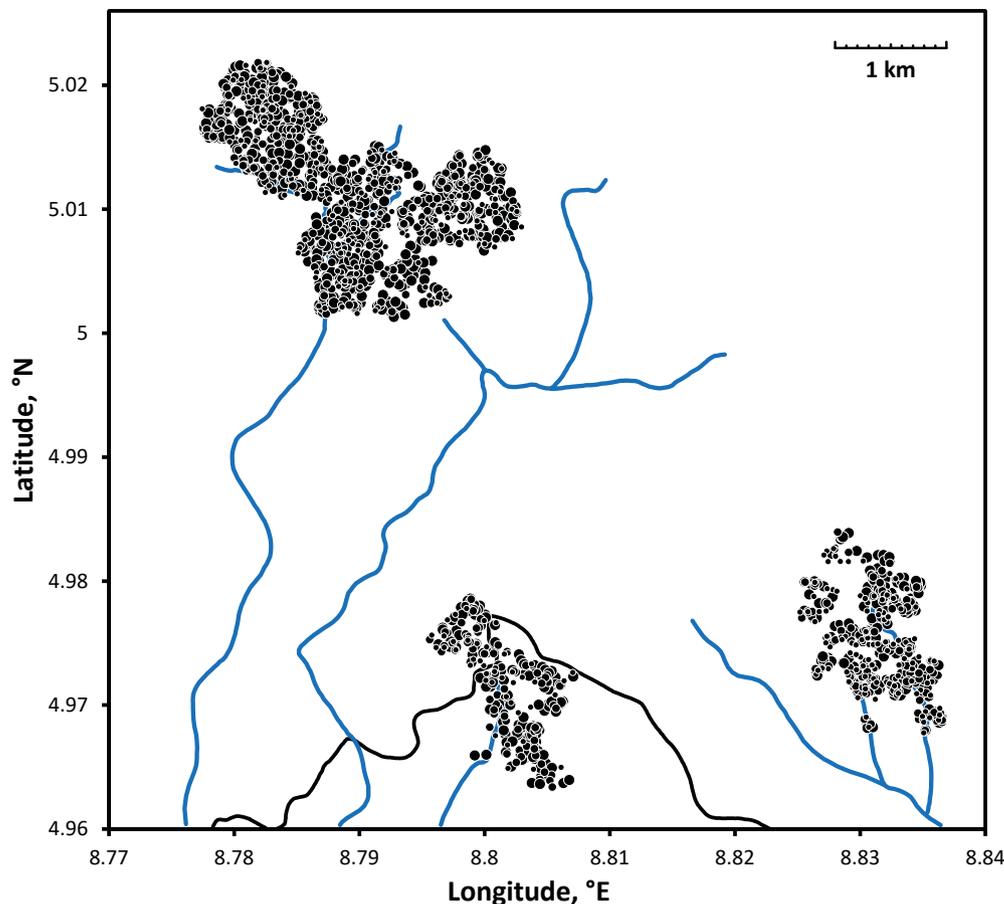
A Detarioideae cluster with a similar Detarioideae tree species composition was found by chance, around 4.925°N, 8.910°E, at 14 km southeast of the centre of the cluster in southern Korup National Park. This forest was gradually being transformed to farmland. The forest between these two clusters was partly Detarioideae-poor forest, and partly forest of unknown species composition, converted to oil palm plantations.

### Seed dispersal

Ballistic seed dispersal is the primary means of seed dispersal of the Detarioideae species in table 1 (Burgt 1997), except species in the genera *Afzelia*, *Anthonotha* (partly), *Copaifera*, *Daniellia*, and *Stemonocoleus* which have seeds dispersed by wind and/or animals (table 1). The abundant presence of Detarioideae trees within groups, the clear margins of the groups and the absence of the species in the surrounding forests (figs 4D, 4E, 7, 8) are a result of the

relatively short and strictly limited maximum ballistic seed dispersal distance and the near-absence of longer-distance seed dispersal (Hart et al. 1989; Newbery et al. 2004). Although most tropical tree species occur more grouped than a random distribution, the most distinctive groups are formed by species with ballistic seed dispersal (Condit et al. 2000; Thomas et al. 2003; Seidler & Plotkin 2006). Ten Sapotaceae tree species were recorded in the Detarioideae cluster; two of these occurred in groups and are ballistic seed dispersers: *Gluema korupensis* Burgt (Burgt & Newbery 2006) and *Lecomtedoxa klaineana* (Pierre ex Engl.) Dubard (Thomas et al. 2003). Both are canopy tree species.

The furthest of many thousands of *Microberlinia bisulcata* seedlings that were observed during the present study was 72 m, measured horizontally, from the edge of the crown of the nearest mature tree. This distance would be the longest recorded ballistic seed dispersal distance, surpassing the record of *Tetraberlinia moreliana* Aubrév. (Burgt 1997). This distance matches with 90–100 m maximum dispersal distance from the stem base of a tree, measured on two seeds in seed traps by Norghauer & Newbery (2015). *Bikinia letestui* may also disperse its seeds to relatively long distances (Burgt 1997, as *Monopetalanthus*).



**Figure 6** – Map showing the relative position of groups of *Microberlinia bisulcata* trees recorded in Korup National Park: the P group (top left; fig. 7), the N group (bottom left; fig. 8), and the O group (bottom right; fig. 8). In total, 1934 trees of 10–252 cm stem diameter were recorded. The size of the map is 7.3 km north to south, by 7.9 km west to east. The black line in the south is a road. Blue lines are rivers.

Secondary seed dispersal may further disperse a ballistic dispersed seed. Secondary dispersal by animals may occur occasionally, although seeds fully adapted for ballistic dispersal have no adaptations for animal dispersal, apart from possibly being edible. Secondary seed dispersal by water seems to have occurred: on fig. 8 (right), two small groups of *Microberlinia bisulcata* trees along two streams just south and downstream of the main group, possibly originated from seeds dispersed by water, several generations ago.

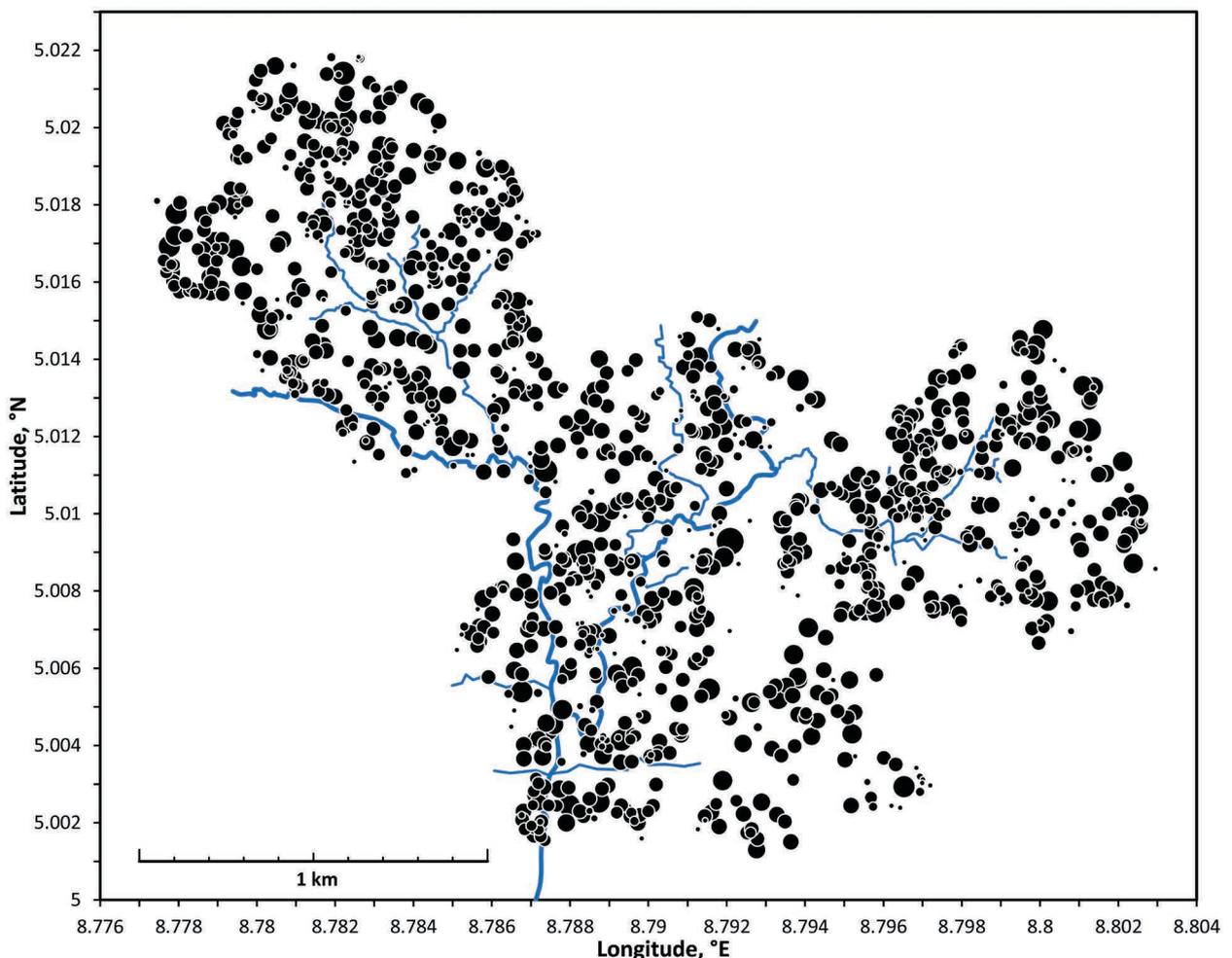
The map of the *M. bisulcata* groups (fig. 6) looks remarkably like the map of a simulation over 9500 years, by Kazmierczak et al. (2016, their fig. 5), of a 10 × 10 km forest area with a single tree species using short-distance seed dispersal and seven tree species using long-distance dispersal. This indicates that ballistic dispersal is indeed an important factor in group formation.

### Expansion of groups

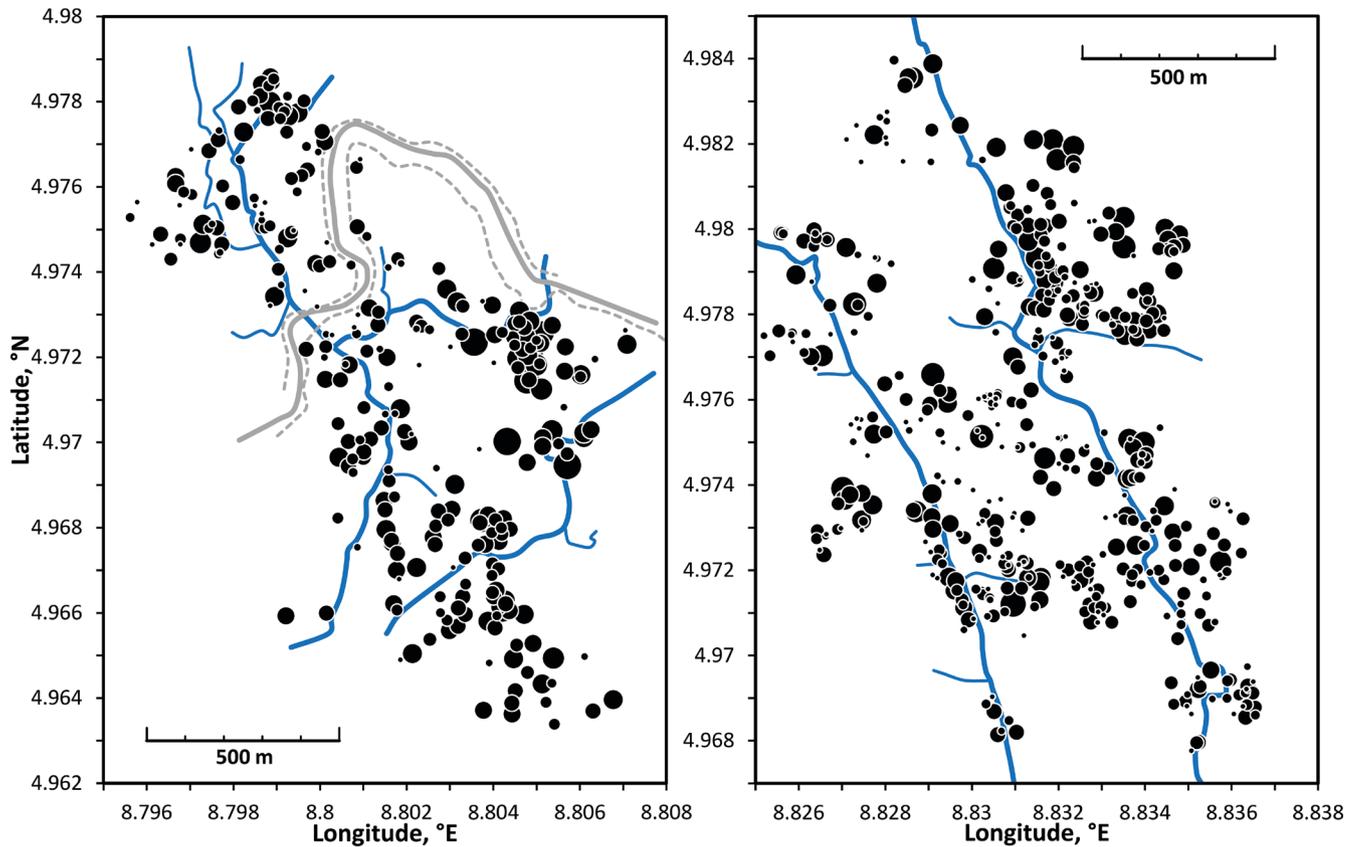
Groups of a single Detarioideae species often had a circular or oval shape; or had a composite shape but then consisted of several overlapping circular shapes (figs 4E, 7). The

circular shape of large groups was probably caused by gradual expansion in all directions. In the absence of major disturbance and strong competition, Detarioideae groups would probably gradually expand into the surrounding forest with the increase in radius per generation determined by the average ballistic seed dispersal distance of the species (Evrard 1968; Hart 1990; Newbery et al. 2004; Djuikouo et al. 2014).

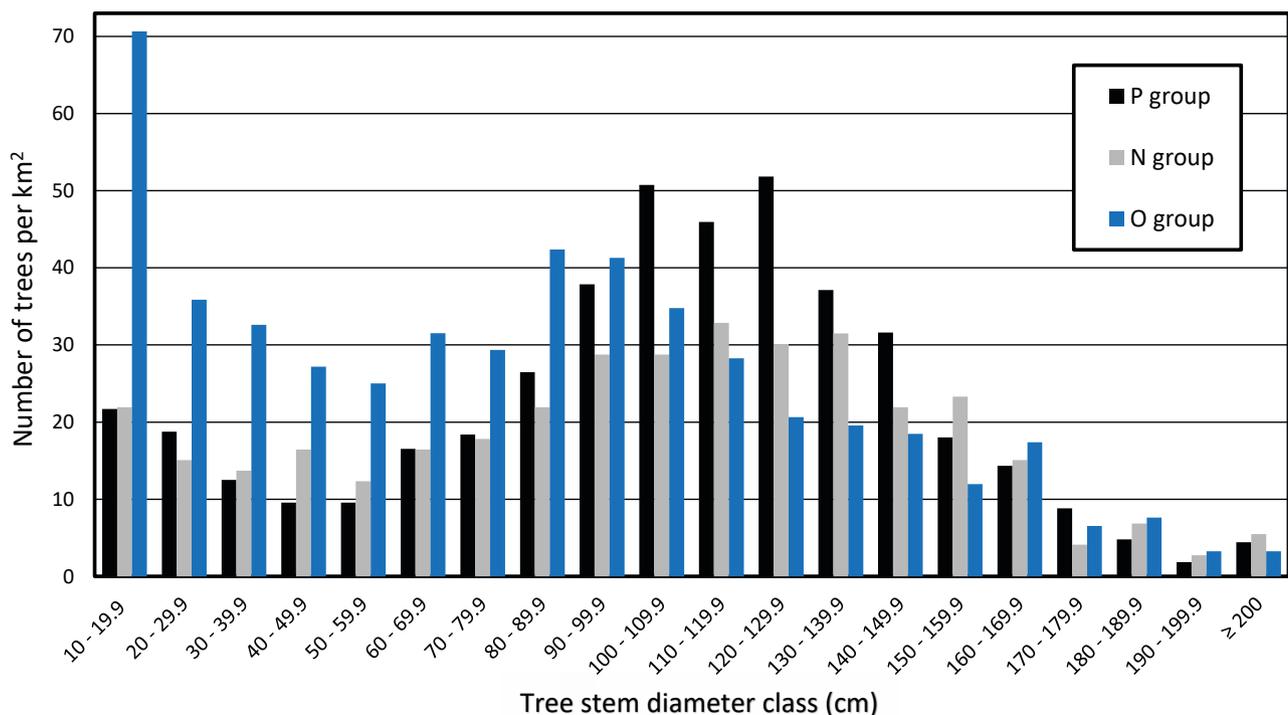
For two species, this expansion rate can be estimated. The average size at the start of maturity of *Tetraberlinia bifoliolata* is 25 cm stem diameter (Norghauer & Newbery 2015, appendix S6). In total 590 mature *T. bifoliolata* trees were recorded in the NW and P plots; the ages of these trees were estimated with Norghauer & Newbery (2015, appendix S6). The generation length, the average age of mature trees in the population, is the average age of these 590 trees: 171 years. With an estimated radial expansion rate of 50 m per generation (Newbery et al. 2004; for *Microberlinia bisulcata*, a species with similar dispersal capacity), the radial expansion rate of *T. bifoliolata* is 29 m per century, and a group of 500 m radius that has expanded with an



**Figure 7** – Map of *Microberlinia bisulcata* trees in the P group. This is the same group as Newbery et al. (2004, 2013) and Burgt (2018), now mapped in much more detail. The P group contained 1199 trees  $\geq 10$  cm stem diameter, on 2.72 km<sup>2</sup>. The size of a symbol is relative to the stem diameter of the tree, in 13 size classes of 20 cm: 10–29.9 cm up to 250–269.9 cm. Blue lines are streams. The size of the map is 2.54 km by 3.15 km.



**Figure 8** – Map of *Microberlinia bisulcata* trees in the N group (left) and the O group (right). The N group contained at least 268 trees  $\geq 10$  cm stem diameter, on 0.73 km<sup>2</sup>; the O group contained 467 trees on 0.92 km<sup>2</sup>. The size of a symbol is relative to the stem diameter of the tree, in 12 size classes of 20 cm: 10–29.9 cm up to 230–249.9 cm. Blue lines are streams, which flow approximately southwards. The grey line on the left map is a road. Thin dashed grey lines show edges of the area cleared of trees. The sizes of both maps are 1.99 km by 1.46 km.



**Figure 9** – Density of *Microberlinia bisulcata* trees in the P group, N group, and O group, in 10-cm size classes.

average rate, would be about 1700 years old. *Microberlinia bisulcata* has an average size at the start of maturity of 44 cm stem diameter (Norghauer & Newbery 2015, appendix S6). In the NW and P plots, 517 mature trees were recorded. The average age of these trees was 124 years, the generation length. The radial expansion rate of *M. bisulcata* is 40 m per century, and a group of 500 m radius would be about 1200 years old.

The *M. bisulcata* groups were apparently expanding at some of their margins during the most recent tree generation; this can be inferred from trees arranged in circles of 100–300 m diameter at the margins of the P group, especially at the northwest margin (fig. 7; Newbery et al. 2004). In the centres of these circles, there were probably one or more parent trees, allowing regeneration only beyond their canopy. Few trees of 10–50 cm stem diameter were recorded at the margins (fig. 7), which implies that the P group was expanding slower than one generation earlier, when the circles of large trees were formed. However, the mature trees at the margin might still regenerate. There were two mature *M. bisulcata* trees with abundant regeneration, both located at margins. In the P group, at 8.797°E, 5.003°N, a large tree was surrounded by eight young trees (fig. 7) and in the O group, at 8.828°E, 4.982°N, a large tree was surrounded by nine young trees (fig. 8).

Groups of some species were always small, such as those of *Bikinia letestui* and *Gilbertiodendron ogoouense* (fig. 4E, F). These small groups could be young expanding groups, or older groups that, for unknown reasons, do not expand. None of the Detarioideae tree species occurred continuously across the cluster; therefore, ecological processes, such as some form of disturbance, must have confined the trees in groups. Seed dispersal, therefore, does not fully explain the spatial distributions of the Detarioideae species.

### Formation of the cluster

The tree species composition in the cluster is comparable to that outside the cluster, except for the Detarioideae tree species that form the cluster, although the species diversity per surface area is lower in Detarioideae forest, especially for canopy tree species (Hart et al. 1989; Makana et al. 2011; Djuikouo et al. 2014; Katembo et al. 2020). Of the tree species  $\geq 10$  cm stem diameter found in the cluster, excluding Detarioideae, 82–87% occurred also in the Detarioideae-poor KFDP plot (Thomas et al. 2003; estimated because some tree species were named to genus level only). There are no significant changes in soil substrate, topography, or other environmental factors between the P group and the forest to the east and west of it that might account for the change in vegetation (Gartlan et al. 1986; Newbery et al. 1988, 1997). Soils of Detarioideae-rich forests are generally similar to those of adjacent mixed forests (Hart 1990; Katembo et al. 2020). The Detarioideae tree species occurred in a complex configuration of groups, and the groups of the various species were separated, or overlapped partially (fig. 4). This configuration of groups and their clear margins would be difficult to explain by variations in soil properties or other environmental factors.

The eight explanations for monodominance reviewed by Peh et al. (2011) may all form part of a possible explanation for Detarioideae co-dominance. Different Detarioideae tree species may become co-dominant for a different combination of reasons. Three of the eight reasons are discussed here: short-distance seed dispersal (discussed above), a low frequency of human and natural impacts over a long period of time (discussed below) and ectomycorrhizal associations. At least 21 of the 29 group-forming Detarioideae tree species in table 1 are characterised by their symbiosis with ectomycorrhizal fungi, which enhance the uptake of nutrients by tree roots. Detarioideae tree species are amongst the relatively few tree species that form ectomycorrhizal symbiosis, and this may promote dominance by these species on low-nutrient soils through a more efficient nutrient cycling (Alexander 1989; Newbery et al. 1988, 1997). Once an ectomycorrhizal tree species has become dominant, it may become easier for related species to become established, thus single-species dominance could develop towards family dominance (Connell & Lowman 1989). The selective advantages created by a Detarioideae tree species may also be advantageous for other Detarioideae tree species (Newbery et al. 1997), thus creating the cluster. A possible example is visible on the maps of the two *Tetraberlinia* species, which usually occur together (fig. 5).

A Detarioideae species may depend on some form of long-distance seed dispersal to establish new groups, for example by wind or animals. Alternatively, establishment could have been by expansion of groups through ballistic seed dispersal, over many generations, followed by fragmentation, after which few scattered trees of the group-forming species remained, from which new groups developed (Newbery et al. 1998). What the mechanism of fragmentation might have been is unknown. These two ways of group establishment do not exclude each other; both may have contributed to create a cluster of multiple Detarioideae species.

### Low disturbance levels

The current species composition of many African rain forests reflects widespread and significant past human as well as climatic impact. Many forests have been subject to historic human activities, such as clearance for small-scale cultivation. Forests that have experienced low levels of disturbance by humans and climate are exceptional in Africa (Letouzey 1960; Willis et al. 2004; Malhi et al. 2013; Biwolé et al. 2015). Any study area situated in African rain forest, within or outside a glacial age forest refugium, might have been considerably modified by human activities (White & Oates 1999). The forests around the P transect were probably never damaged by forest fires, because charcoal was found in only one of 18 pits: a distinct charcoal layer at 22 cm depth, which could have been due to a lightning strike on a single tree (Newbery et al. 1997). The forests of southern Korup National Park have never been farmed or commercially logged (Gartlan et al. 1986). Korup National Park is in an area postulated to have been a glacial-age forest refugium and has probably been under continuous forest cover during the past glacial ages when the climate was cooler and drier (Maley 1996; Maley et al. 2018).

Of all trees in the P transect plots, only 2.8% belonged to pioneer forest species (table 3). None of the 42 Detarioideae tree species from table 1 are pioneer species. This indicates that disturbance levels were low during the past generations of trees. The pioneer tree species *Lophira alata* was very rare on the P transect, indicating low levels of disturbance (Newbery & Gartlan 1996). The present study recorded only four trees of *L. alata* out of 3177 trees  $\geq 50$  cm stem diameter. Rain forests in Cameroon where this tree is common have been in cultivation in historic or prehistoric times, as demonstrated by the potsherds and charcoal frequently found in the soil (Letouzey 1960). Equally remarkable is the absence of trees of pioneer species that occur commonly elsewhere in the region, such as *Ceiba pentandra* (L.) Gaertn., *Milicia excelsa* (Welw.) C.C.Berg, and *Terminalia superba* Engl. & Diels. The relatively high occurrence of *Musanga cecropioides* (table 3) may be explained by the fact that this species is common in natural gaps in the area. The trees of *Alstonia boonei* (table 3) were all located in forest on periodically inundated soils. Gaps occur more often on such soils because the weak substrate makes them more susceptible to windfall.

The richness of Detarioideae trees and tree species in the cluster also indicates a low level of disturbance. In the African rain forests, Detarioideae trees appear to occur particularly in forests that have had no history of cultivation or clearance and have not been much affected by past climatic change. The seeds of most Detarioideae tree species are dispersed to relatively short maximum distances, which makes these species poor re-colonisers of forest after disturbance (Letouzey 1960, 1968). It is therefore probable that the Detarioideae tree species are persistently dominant and have been present in the area for many generations of trees, possibly since these species came into existence (Newbery et al. 1998). Detarioideae tree species in the *Berlinia* clade, which contains 25 of the 42 Detarioideae species listed in table 1, have lowland rain forest as their ancestral state (Estrella et al. 2020).

*Gilbertiodendron dewevrei* monodominant forests may have experienced low levels of disturbance and very little change in vegetation composition over the past 2700 years, evidenced by insignificant changes in pollen composition of forest species over that period (Tovar et al. 2019), or these forests may be a legacy of disturbance (Aubréville 1957) due to a climatic crisis 2500–2000 years cal BP (Maley et al. 2018). *Gilbertiodendron dewevrei* is present in southern Korup National Park, but not monodominant across large areas, as it does elsewhere in Central Africa. This species was found in seven groups, each consisting of 11–30 trees over 10 cm diameter. If the hypothesis of Maley et al. (2018) is correct, the presence of small groups and the absence of large groups of *G. dewevrei* in the cluster may indicate absence of disturbance.

The richness of Detarioideae trees and tree species, the scarcity of pioneer trees, and the near absence of charcoal in the soil, indicate that the forests around the P transect plots in Korup National Park probably have been subject neither to substantial human impacts nor large natural disturbances in historic or prehistoric times. Certain Detarioideae tree species have been proposed as glacial age forest refuge

indicators (Rietkerk et al. 1996; Leal 2004; Tchouto et al. 2009), as well as general species richness (e.g. Aubréville 1968), the presence of certain species of *Begonia* (Sosef 1994) and certain species of Rubiaceae (Robbrecht 1996). Detarioideae clusters may also indicate glacial age forest refuges, especially clusters that contain both many different Detarioideae species and some Detarioideae species endemic to the cluster. Because glacial age forest refuges are rich in rare plant species, Detarioideae clusters may also indicate areas important for plant conservation.

#### DATA AVAILABILITY STATEMENT

The data presented in this study are available in Dryad at:

<https://doi.org/10.5061/dryad.t85n3>

<https://doi.org/10.5061/dryad.rxwdbvr82>

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#### AUTHOR CONTRIBUTIONS

DMN designed and supervised the research in the permanent plots, and with XvdB and SN collected data in them. XvdB designed the research outside the plots, and for this XvdB and SN collected the data. SN played an essential role in the field work; he passed away on 24 February 2020. XvdB performed the present data analysis, prepared the maps, and very largely wrote the paper. DMN reviewed results, commented, and contributed to all drafts. XvdB and DMN approved the final version and take full responsibility for the paper on behalf of the deceased co-author.

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