Critical Appraisal

Co-dominant Detarioideae (Leguminosae) tree species in the rain forests of Korup National Park, Cameroon

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Abstract

The tropical evergreen rain forest in south Korup National Park has been little influenced by human disturbance and past climatic change. Trees of the Leguminosae subfamily Detarioideae are common. Ten new Detarioideae tree species were described in the past eleven years; most of these are (near-) endemic to Korup National Park. They had not been recorded earlier because rainforest trees are easily overlooked and difficult to collect in fertile state. A mapping method was developed to map all *Microberlinia bisulcata* trees in a large grove. This grove had a size of 272 ha and consisted of 1028 *M. bisulcata* trees > 50 cm stem diameter. *M. bisulcata* occurs co-dominant with *Tetraberlinia bifoliolata*, *T. korupensis* and at least 21 other, less abundant, grove-forming Detarioideae trees. Many other tree species from many other families are present. There are no significant changes in soil type, topography, or other environmental factors between the *M. bisulcata* grove and the forest just outside this grove. The tendency of *M. bisulcata* and other Detarioideae trees to grow in groups is related to the relatively short and strictly limited maximum distance of the ballistic seed dispersal method, characteristic of these species. Co-dominance of Detarioideae trees may also be promoted by other factors such as their ectomycorrhizal habit. Ballistic seed dispersal explains the clear edge of the grove and the complete absence of *M. bisulcata* from the surrounding forest. The semi-circles of 100 – 200 m diameter of mature *M. bisulcata* trees at the grove's edge indicate that the grove had been expanding up to the time when these trees established. The presence at the edge of only a few juveniles, indicates that the grove is not expanding much since the present *M. bisulcata* trees became adults. *M. bisulcata* has been persistently dominant in the past, but the current deficiency of regeneration indicates *M. bisulcata* may lose much of its dominance in the near future.

Preface

This is a thesis of the publications resulting from 24 years of expeditions and research (1994 to 2017) on the study of co-dominant rain forest trees from the Leguminosae subfamily Detarioideae. During those 24 years I have accomplished 47 expeditions, with a duration of two weeks to six months, to six countries in the African tropical rain forest zone: Guinea, Sierra Leone, Cameroon, Gabon, Congo-Brazzaville, and Congo-Kinshasa. These expeditions were often aimed at subjects other than the present thesis, but I have always taken the opportunity to collect observations and data on this subject. In 1994 I accomplished my first research on this subject, on the ballistic seed dispersal of the tree species *Tetraberlinia moreliana* in Gabon (Burgt 1997) as part of my MSc study of Forest Conservation at Wageningen Agricultural University in The Netherlands. From 1999 to 2000 and 2002 to 2005 I worked at the Institute of Plant Sciences at the University of Bern in Switzerland. During those years I was working in Korup National Park in Cameroon for periods of up to 6 months, researching the taxonomy, ecology, and dynamics of co-dominant Detarioideae tree species. Since 2005 I have been working at the Herbarium of the Royal Botanic Gardens, Kew; and amongst many travels to Africa I made six additional visits to Korup National Park, in part with the aim of gathering more data on this subject. Korup National Park in Cameroon is therefore the main subject of this thesis.

1. Introduction

1.1. The Leguminosae subfamily Detarioideae

The Detarioideae is a recently recognised Leguminosae subfamily. The new classification of the Leguminosae family by LPWG (2017) addresses the long-known non-monophyly of the traditionally recognised subfamily Caesalpinioideae, by recognising six robustly supported monophyletic subfamilies. Many genera previously placed in the tribe Detarieae of the subfamily Caesalpinioideae (Mackinder 2005) were transferred to the subfamily Detarioideae (LPWG 2017). The Detarioideae subfamily currently consists of 81 genera and c. 760 species (Estrella et al. 2018), occurring almost exclusively in the tropics across all continents. All tree species that are the subjects of the present thesis used to be classified in the subfamily Caesalpinioideae and are now included in the subfamily Detarioideae. Therefore, though all cited publications refer to these tree species as members of the Caesalpinioideae, the present thesis refers to them as members of the Detarioideae, even when citing from these publications.

The generic and species diversity in the Detarioideae is much higher in Africa than in America or Asia: 58% of the genera occur only in Africa, 20% in America and 12% in Asia and Australia; while 10% of the genera are present in more than one region (Estrella et al. 2017; LPWG 2017). This is even though African rain forests have a poorer flora generally than those of the American and Southeast Asian tropics (Couvreur 2015; Parmentier et al. 2007; Richards 1996: 292). Detarioideae tree species are common components of African rain forests; many are large trees (Aubréville 1970).

1.2. Dominance of tree species in African tropical rain forests

The most important single characteristic of tropical rain forests is their astonishing wealth of plant and animal species (Richards 1996: 289). Their extreme species richness has impressed scientists ever since the first explorations (Whitmore 1990: 149). Tropical lowland rain forests are ecosystems with very diverse species communities;

they contain the greatest wealth of biological and genetic diversity of any terrestrial community. In samples of one or two hectares, as well as in vast forested regions, the number of different kinds of plants is enormous: far larger than in any temperate forests (Richards 1996: 289). On the richest rain forest plots, nearly every second tree on a hectare belongs to a different species (Whitmore 1990: 29).

In some areas of tropical lowland rain forests, patches with a high richness of canopy tree species, are intermingled with patches where the canopy is dominated by a single or a few canopy tree species (Connell & Lowman 1989; Hart 1990; Richards 1996: 38). If the dominant species comprises over 50% (Connell & Lowman 1989), over 60% (Degagne et al. 2009) or over 80% (Hart et al. 1989; Hart 1990) of the number of canopy trees or basal area (or both), that species is considered monodominant.

Monodominance of tropical rain forest canopy trees is common after major disturbances, for example when most or all canopy trees in a forest patch are uprooted by strong winds. Following a major disturbance, a single pioneer tree species can become established and dominate the canopy of rain forest more than a century later. The pioneer canopy trees do not regenerate in their own shade because their seedlings and saplings are light-demanding. The invasion by a more diverse community of canopy species with shade-tolerant seedlings and saplings is apparent by their presence in the understory (Hart et al. 1989; Hart 1990). An example is the African rain forest tree *Musanga cecropioides* R.Br. ex Tedlie (Urticaceae), which may become monodominant after a large windfall, or when farmland which has been newly carved out of forest is abandoned for the first time (Jones 1955). Monodominance after severe disturbances is a successional stage, lasting only a single generation; in the absence of additional disturbances, the species composition of the forest canopy will change significantly.

Monodominance often occurs in tropical regions that have smaller species pools, such as forests at high altitudes, forests with low or very seasonal rainfall, freshwater swamp forests or mangrove forests (Connell & Lowman 1989). The existence of monodominant forests in these vegetation types is explainable by ecological theory (Peh et al. 2011b). However, a single canopy tree species may occur as dominant in tropical lowland rain forests on well-drained soils which have not recently been through some form of major disturbance. The dominant species successfully recruits and replaces itself under its own canopy. The monodominant stands are surrounded by forest with a much higher diversity of canopy species, on the same soil type (Hart et al. 1989; Torti et al. 2001). Some of these monodominant forests cover hundreds of square kilometres, while others are found locally in mixed forest as patches of only a few hectares (Richards 1996: 38). This type of monodominant forest is less easily explainable by current ecological theory (Peh et al. 2011b).

Persistent monodominance, a tree species persisting abundantly in the canopy across more than one generation, appears to be favoured only by a period of low disturbance (Hart et al. 1989; Letouzey 1960). Monodominant forests have been the subject of many studies; for an overview see Peh et al. (2011b). The *Gilbertiodendron dewevrei* (De Wild.) J.Léonard (Detarioideae) forest is the most prominent example of monodominant tropical lowland rain forest on well-drained soil in Africa. *Gilbertiodendron dewevrei* forest occurs in monodominant stands in which it comprises up to 90% of the canopy trees, in stands to hundreds of square km in size, as well as in patches of less than one hectare. All age classes are present, including many seedlings; the canopy is closed, and gaps are uncommon. The species occurs from southeast Nigeria to eastern Congo-Kinshasa (Barbier et al. 2017; Burgt et al. 2015; Gérard 1960; Hart 1990; Richards 1996; Torti & Coley 1999).

1.3. The research programme

In the rain forests of West and Central Africa, many tree species in the Leguminosae subfamily Detarioideae tend to grow in patches or clusters of a few ha to some km^2 in area (Aubréville 1968; Saint-Aubin 1961; Letouzey 1968, 1985; Richards 1996: 331; White 1983: 77). Where these patches or clusters of Detarioideae trees are well defined by one or a few related species which are structurally dominant, the trees may be said to grow in 'groves' (Newbery, Burgt & Moravie 2004). Such groves may consist of a single monodominant canopy tree species, or of several related co-dominant tree species which together dominate the rainforest canopy. In the rain forests of south Korup National Park, located in the Southwest Region in Cameroon, there is a fine example of such a Detarioideae grove which is dominated by *Microberlinia bisulcata* A.Chev. together with two more large Detarioideae tree species, *Tetraberlinia bifoliolata* (Harms) Hauman and *T. korupensis* Wieringa (Gartlan et al. 1986, Newbery & Gartlan 1996, Newbery et al. 1988, 1997, 1998, 2013). The area is under 100% forest cover with canopy trees 30 – 45 m high. Interspersed throughout the grove are other tree species, of lower abundance, in the Detarioideae and in other Leguminosae subfamilies. Tree species in many other families of plants also occur; although at lower densities than in the surrounding forest (Burgt et al. 2007, 2015).

A remarkable fact about *M. bisulcata*, is that, even though the species is dominant, its seedlings and saplings are not shade-tolerant (Newbery et al. 2013), although they are more shade tolerant than the seedlings of tree species regenerating in large gaps. Consequently, *Microberlinia bisulcata* cannot regenerate in its own shade, the way other dominant tree species can. This is discussed in chapter 5. *Microberlinia bisulcata* is one of the largest of African trees; in Korup National Park, median diameter is c. 1.1 m and maximum diameter is 2.85 m. It reaches heights of c. 45 m, crown diameters of c.70 m, and may develop large buttresses several m high and to 10 m from the stem. Maximum age was estimated at 250 years (Newbery, Burgt & Moravie 2004).

In the Detarioideae-rich forest, starting in 1990, the 155.75-ha “P transect plots” were established, Prof D.M. Newbery’s permanent plot system in Korup National Park. These plots were established for research into the ecology and dynamics of *Microberlinia bisulcata* and other Detarioideae tree species. All trees over 50 cm stem diameter in the plots were registered. Smaller trees, of 10 – 50 cm stem diameter, were recorded in 56 random located 50 m x 50 m subplots within the plots (Newbery et al. 1998, 2013). The research in the P transect plots has resulted in numerous publications on the ecology and dynamics of the Detarioideae tree population, with results on many subjects such as seedling survival, nutrient dynamics, ectomycorrhizae, mast fruiting, seed dispersal and dominance; see the literature cited in Newbery et al. (2013). As part of this research, all Detarioideae in the P transect plots were collected in flower and named, and maps of individual trees of some of the species were prepared and analysed.

The subject of the nine research papers of the present thesis (listed in chapter 6.1) is the species richness and co-dominance of tree species in the Leguminosae subfamily Detarioideae in the lowland rain forests in south Korup National Park in Cameroon. The contents of these nine papers are here discussed in relation to the general literature on the subject. These papers newly describe seven tree species from the rain forests of Korup National Park, six Detarioideae and one Sapotaceae. An additional eight new Detarioideae tree species are described from rain forests elsewhere in Central Africa.

One of the papers presents a large map of a grove of *Microberlinia bisulcata* and analyses the structure and inferred dynamics of this grove. This paper discusses how the Detarioideae co-dominant forest was established, whether the *M. bisulcata* grove is expanding and whether the species is persistently dominant. Smaller maps of several other tree species of Detarioideae, and a map of a Sapotaceae tree species, are presented in some of the nine papers.

2. Korup National Park in Cameroon

2.1. The rain forests of Korup National Park

Korup National Park in the Southwest Region in Cameroon is mostly covered in tropical evergreen rain forest; on well-drained soils generally, but patches of rain forest on periodically inundated soil commonly occur along streams (Burgt 2016). The topography in the southern part of the park, where the research for the present thesis took place, is flat to slightly sloping, with an altitude between 90 m and 130 m. The soils are mostly well-drained, infertile, and sandy to rocky, with occasional granitic rock outcrops and granitic rock boulders up to 10 m in diameter. The streams are in shallow valleys, with rapids along the rocky sections, as well as with sections where the streams are bordered by periodically inundated soils, which are nonetheless sandy and contain occasionally granitic boulders. The rainfall ranged from 4023 to 6146 mm/y and averaged 5041 mm/year (1984 – 2009) and is strongly seasonal with a single distinct dry season from December to February (Burgt et al. 2012).

The scientific exploration of the Korup National Park rain forest vegetation was for a large part organized by J.S. Gartlan, D.M. Newbery and D.W. Thomas since the 1980s (e.g. Gartlan et al. 1986; Newbery et al. 1988; Thomas et al. 2003). Their ecological research and vegetation surveys have provided considerable evidence of the plant conservation importance of Korup National Park. Their paper on the analysis of 40668 trees in 135 plots along four transects (Gartlan et al. 1986) represents a major advance in knowledge of the vegetation of Korup National Park (Burgt 2016).

2.2. Influences by past climate change and prehistoric inhabitants

Africa has had a variable climatic history, with numerous warm, wet phases interspersed with periods of cool, dry climate (Gartlan 1994; Maley 1996). During the last glacial maximum, around 18,000 years ago, the climate was cooler and drier compared to the present. These climatic conditions restricted dense equatorial forests in West and Central Africa into about eight large refuge areas and a complex mosaic of ‘microrefugia' along permanent streams, where favourable conditions persisted (Leal 2004; Maley & Brenac 1998; Sosef 1994, 1996). The Holocene marked the return to warmer and wetter conditions in West and Central Africa, and forests regained lost ground, as evidenced by increasing levels of rainforest pollen in lake sediments across the region. At present in Africa the extent of the rain forest is close to its quaternary maximum (Leal 2004; Maley 1996; Oslisly et al. 2013; Sosef 1994, 1996; Tchouto et al. 2009). Present evidence seems to indicate that the forests in Korup National Park have persisted during periods of cool, dry climate; as part of a large forest refuge (Gartlan 1986, 1994; Maley 1991).

Early researchers thought the African rain forest to be mostly primary rainforest, little influenced by past human activities, but this opinion has significantly changed (Jones 1955; Letouzey 1968: 143, 1985; Richards 1996). Prehistoric human activities were far more extensive than originally thought; the current species composition of many African rain forests may still reflect large-scale historical disturbances, such as past human activities (Biwolé et al. 2015; Brncic et al. 2007; White & Oates 1999; Willis et al. 2004; Tovar et al. 2014). Evidence of human settlements and activities such as shifting cultivation agriculture, up to 3000 years ago, was found as charcoal layers, furnaces, pottery, and banana phytoliths in forest soils beneath the present-day rainforest vegetation in Nigeria, Cameroon, Gabon, Congo-Brazzaville, and Congo-Kinshasa (Biwolé et al. 2015; Gemerden et al. 2003; Mbida et al. 2000; Richards 1963, 1973; White & Oates 1999). Pollen profiles show that humid forest trees were replaced, through increased anthropogenic burning, by light-demanding pioneer and herbaceous species, characteristic of degraded forests and savannas (Brncic et al. 2007; Oslisly et al. 2013).

The expansion of human populations into the African rainforest happened in two phases: between 2500 and 1400 years BP and between 1000 and 100 years BP; separated by a depopulation phase (Biwolé et al. 2015). Tovar et al. (2014) analysed fossil charcoal in soils of four forest types; they found amounts of charcoal starting to increase at 1100 years BP and peaking in the last 300 years BP. How much of the impact on the forest was due to human activities and how much was climate-induced disturbance is still debated, however (Biwolé et al. 2015). Hence, a picture of widespread and significant human impact on African forests is emerging wherever ecologists, archaeologists, and palynologists team up. No ecologist working in the

African rain forest should ignore the possibility that their study area, situated within or away from a glacial age forest refuge, might have been significantly modified by human activity (White & Oates 1999).

2.3. Low levels of disturbance of rain forest in Korup National Park

The rainforests in south Korup National Park were likely never damaged by forest fires, because charcoal was found in only one of 18 pits dug: a distinct charcoal layer at 22 cm deep, which could have been due to a lightning strike on a single tree (Newbery et al. 1997, 1998). In parts of the forest, logging for local use and the harvesting of natural plant products has taken place on a small scale, and hunting has reduced the populations of many animal species, but most of the forest has never been farmed or commercially logged (Chuyong et al. 2004; Gartlan 1986; Thomas 1986). No evidence of historic or prehistoric occupation has been found in south Korup National Park up to the present. The study area has no signs of severe recent or ancient human disturbance (Kenfack et al. 2014; Newbery et al. 1997, 2013).

In the African rain forests, Detarioideae trees appear to occur particularly in places that have had no history of cultivation or clearance by people and have not been much affected by past climatic change. The seeds of most Detarioideae tree species are dispersed to relatively short and strictly limited maximum distances (see chapter 4), which makes these species poor re-colonisers of forest after disturbance. When the frequency and intensity of human or natural disturbance increases, the forest will convert to a forest containing fewer Detarioideae trees and more secondary forest trees (Leal 2004; Letouzey 1957, 1960; Richards 1963; Rietkerk et al. 1996; Tchouto et al. 2009). The forests in the study area in south Korup National Park are particularly rich in Detarioideae tree species and trees (Burgt & Eyakwe 2010; Newbery et al. 2013). This suggests that there has been a relatively low intensity of human and natural disturbance in the past, compared to other rain forests in Cameroon.

Many tree species commonly encountered in secondary forests (Aubréville 1938, 1971; Gartlan 1986; Jones 1955; Letouzey 1957; Richards 1963), which occur in the Southwest Region in Cameroon according to the African Plant Database (2018), are absent or present in only low numbers in both Detarioideae-rich and Detarioideae-poor forests in the study area in Korup National Park (Newbery et al. 2013). Pioneer tree species with shade-intolerant seedlings are rare in these forests. Since these species do occur elsewhere in the Southwest Region in Cameroon, their scarcity in the study area may indicate absence of large-scale natural or human disturbance in the past, rather than unsuitable climatic or edaphic conditions. An example of such a pioneer tree species is *Lophira alata* Banks ex C.F. Gaertn., establishing itself after major disturbance. The absence of juvenile trees in mature *L. alata* forest indicates the species will disappear in the absence of future disturbances (Letouzey 1957). Forests in Cameroon where this tree is common have been in cultivation in the past, as demonstrated by the potsherds and charcoal frequently found in the soil of forest dominated by *L. alata* (Letouzey 1968: 143). The grove of *Microberlinia bisulcata* in Korup National Park is very poor in *L. alata*: in a sample of 3181 trees over 50 cm stem diameter, taken within this grove, there were only four *L. alata* trees. Letouzey (1957) recorded that about 1/3 of trees over 50 cm stem diameter were *L. alata*.

Natural disturbances currently occur at low intensity in Korup National Park. Although branchfalls and treefalls are naturally frequent, hurricanes do not occur in the area (Chuyong et al. 2004). Strong winds linked to thunderstorms may uproot all canopy trees in areas up to 1.5 ha, but this was observed only once during more than 20 years of fieldwork. In the wet season of 1999 (July–October) an area of c. 1.5 ha within the 272-ha *Microberlinia bisulcata* grove experienced a wind-throw which brought down c. 30 trees with stem diameters over 50 cm, but none were *M. bisulcata* which were left surrounding the gap. The fallen trees had a fan pattern indicating a gust coming with a thunderstorm (Newbery et al. 2010).

The result of the low impact of climatic change and the low level of human disturbance is that the forests in Korup National Park possess exceptionally high numbers of plant species in general, and endemic plant species in particular (Gartlan 1986, 1994; Thomas 1986). The park is therefore considered a site of global importance, for ecological research into the structure and processes of species-rich rain forest (Gartlan 1986, Thomas 1986). Korup National Park is a wilderness area in the sense of, for example, Watson et al. (2016), an area where natural ecological and evolutionary processes operate with minimal human disturbance.

3. The Detarioideae tree species in Korup National Park

3.1. The tree species composition of the study area

A checklist of the plant species of Korup National Park does not yet exist; the total species numbers and endemic species numbers can therefore only be roughly estimated. The Korup Forest Dynamics Plot, a 50-ha permanent plot located about 10 km NE of the study area, recorded 329,519 trees, shrubs, and saplings over 1 cm diameter at breast height, belonging to 493 tree species (Thomas et al. 2003; Kenfack et al. 2007). They estimate that the 50-ha plot includes in the order of half the tree species occurring in the park. Newbery et al. (2013) published a list of all tree species recorded in the 155.75-ha P transect plots in Korup National Park: 252 tree species over 10 cm stem diameter.

The Leguminosae family is by far the most abundant family in the tree species of the P transect plots: of the 252 tree species over 10 cm diameter, 48 are Leguminosae. The other abundant tree families are the Rubiaceae with 19 species, the Annonaceae with 12 species, the Clusiaceae with 11 species, and the Anacardiaceae, Chrysobalanaceae, Ebenaceae and Phyllanthaceae, each with 10 species (Newbery et al. 2013; families updated with African Plant Database 2018; LPWG 2017). In and around the P transect plots, Burgt & Eyakwe (2010) recorded 39 Caesalpinioideae tree species over 50 cm stem diameter, of which 35 were transferred to the Detarioideae (LPWG 2017). When comparing the number of stems, the Detarioideae are even more abundant: 56% of the trees in the P transect plots with a stem diameter of ≥ 50 cm belong to species from this subfamily.

3.2. Newly discovered tree species

There are still many new plant species being discovered in the rainforests of Africa (Burgt & Eyakwe 2010; Burgt et al. 2015; Cheek et al. 2004; Maesen & Sosef 2016; Sosef et al. 2006). The botanical exploration of tropical Africa is far from complete (Sosef et al. 2017). Knowledge of rare tropical rain forest trees remains scanty; they are hard to find and hard to identify (Kenfack et al. 2007). In Korup National Park, 14 new tree species have been discovered or co-discovered by me in the past 12 years (chapter 6.1; Burgt 2009, 2010; Ewango et al. 2016; Gautier et al. 2016; Mackinder et al. 2010). According to current knowledge, seven of these new tree species are endemic to Korup National Park or even to the P transect plots. Two new tree genera have been described from Korup National Park: *Korupodendron* (Vochysiaceae; Litt & Cheek 2002) and *Namataea* (Sapindaceae; Thomas & Harris 1999).

As a result of the collecting strategy applied in the P transect plots during the past 17 years, type collections of ten new tree species in the Detarioideae were collected by me, and subsequently described by various authors: *Anthonotha xanderi* Breteler (2010), *Berlinia korupensis* Mackinder & Burgt (2009), *Cryptosepalum korupense* Burgt (Burgt et al. 2014), *Didelotia korupensis* Burgt (2016), *Englerodendron korupense* Burgt (Burgt & Newbery 2007), *Gilbertiodendron newberyi* Burgt (Burgt et al. 2012), *Hymenostegia viridiflora* Mackinder & Wieringa (2013), *Talbotiella korupensis* Mackinder & Wieringa (Mackinder et al. 2010), *Talbotiella velutina* Burgt & Wieringa (Mackinder et al. 2010) and *Tessmannia korupensis* Burgt (2016). According to current knowledge, all species except *Anthonotha xanderi, Gilbertiodendron newberyi* and *Hymenostegia viridiflora* appear to be endemic to the Southwest Region in Cameroon or even to Korup National Park, emphasising the great importance of this park for the conservation of tree species. There are currently at least two undescribed Detarioideae tree species in Korup National Park (Burgt & Eyakwe 2010).

3.3. Rare and narrow-endemic tree species

All recently described tree species have been assessed according to the criteria of IUCN (2012). These assessments, although published, are preliminary; full assessments through the IUCN Species Information System still need to be made, after which the assessments will appear on the IUCN Red List website. Eight of the ten newly described tree species in the Detarioideae were assessed to the categories Critically Endangered (CR) or Endangered (EN). Some of these species are known from very few trees only. *Didelotia korupensis* is only known from an area of rain forest of c. 1600 m by 3000 m (c. 4 km^2), where 51 mature trees over 10 cm stem diameter have been recorded so far (Burgt 2016). In total 16 trees of *Englerodendron korupense* have been found; 12 of them were mature because old pods were found on the forest floor beneath the trees (Burgt et al. 2007).

The question may be asked why there are many rare, narrow-endemic tree species in Korup National Park. Species diversity of plants in tropical rain forest is strongly correlated with annual precipitation, and probably even more closely with non-seasonality of rainfall (Gentry 1988; Richards 1996). The species richness of Korup National Park may therefore be correlated with the high rainfall. An additional possible explanation is the relatively stable forest environment. The forests in Korup National Park have persisted during periods of cool, dry climate; as part of a large forest refuge (Gartlan 1986, 1994; Maley 1991). The refuge areas to which the African rain forests retreated during the repeated glacial periods of the Pleistocene have always been the same because the ecological and meteorological conditions have always been similar. The result of this long sequence of expansion and contraction has been that the forest refuges have become centres of diversity with high species endemism (Gartlan 1986).

The question may also be asked why these species have not been found earlier in a floristically relatively well-studied area. To have ten recently described Detarioideae tree species out of a total of 35 Detarioideae tree species over 50 cm stem diameter (Burgt & Eyakwe 2010), is unexpected, as the forests of south Korup National Park were studied during recent decades by ecologists and botanists (Gartlan et al. 1986; Newbery et al. 1998; Kenfack et al. 2007; Thomas et al. 2003). Three possible explanations as to why these ten species had been previously overlooked are discussed by Burgt & Eyakwe (2010).

Undescribed plant species will usually need to be collected fertile to be recognized and described. Tall rainforest trees are difficult to collect in fertile state; plant collecting in rainforest therefore results mostly in collections of herbs, shrubs, and small trees (Burgt & Eyakwe 2010). Tall trees in Korup National Park are generally 35 to 45 m high. The highest newly described species, *Gilbertiodendron newberyi*, can grow to 51 m high (Burgt et al. 2012). Trees of that height are difficult or even impossible to climb, even with alpine climbing techniques. Flowers are usually present only a few weeks per year and the flowering period of undescribed species is unknown. Some species, for example *Didelotia korupensis*, do not drop anything on the ground when flowering; the presence of flowers in the canopy may be difficult to notice (Burgt 2016).

Large rain forest trees are difficult to name. Large rain forest trees, especially those in plots, are frequently identified by stem and bark characteristics only, as flowers and fruits are often absent, and the leaves in the tree are too high to collect or even to be clearly seen, while the leaves on the ground are a mixture of leaves of many tree and liana species. Identification is usually aided by slashing; but slash characteristics are hardly used in botanical descriptions of trees and are therefore difficult to relate to scientific names of trees. Although slashing may have some use for known species, undescribed tree species will not be identified correctly (Burgt & Eyakwe 2010).

Botanists may easily overlook rare large forest tree species. Botanists usually walk around more or less at random looking for flowering plants. This method can work well in herbaceous vegetation: all plants can be easily observed, and many plants can be seen and compared at the same time. Botanical inventories of large and high forest trees are much more difficult. They occur in low densities, much lower than those of rare herbaceous species, simply because trees are much larger than herbs. Collecting plants by walking around at random while looking for signs of flowering or fruiting, is inadequate for finding rare large trees in a species-rich forest (Burgt & Eyakwe 2010).

4. Seed dispersal of African Detarioideae tree species

4.1. Characteristics of ballistic seed dispersal

Plant species dispersing their seeds by ballistic dispersal are represented among annuals and perennials, herbs, and trees; in open and shaded, wet and dry habitats (Stamp & Lucas 1983). In the Leguminosae, ballistic seed dispersal, also referred to as explosive seed dispersal, is found most frequently in herbs, but occurs in high forest trees, from which large seeds are thrown many metres away (Pijl 1982: 155). Detarioideae trees with explosively dehiscent pods dominate most primary and secondary dry forest and woodland types in the Zambesian Regional Centre of Endemism (Bingham 1994). Ballistic dispersal is a common feature of Detarioideae trees in the African rainforests. In Gabon, at least 73 tree species in at least 24 Detarioideae genera have explosively dehiscent pods (Burgt 1997; the number of genera was updated from African Plant Database 2018 and LPWG 2017).

The pods of those African Detarioideae rain forest tree species that exhibit the ballistic dispersal method, are usually positioned on the crown surface, beyond the outermost leaves. Depending on the species, a pod may contain 1 to 7 seeds. The seeds are discoid in shape and have a thin and smooth seed coat (Aubréville 1968; Burgt 1997). When a mature pod in the tree is exposed to sunshine or dry air, it begins to dry. Each valve consists of two woody layers with different properties. During drying, the two valves are predisposed to curl up in opposite directions, and as a result tension builds up between them. The corky connecting layer between the two valves keeps them attached and thereby flat, but as the drying continues, the tension eventually becomes too great and the pod dehisces suddenly and forcefully. Mature pods explode with a cracking noise, during periods of sunshine. The two valves twist rapidly, in opposite directions, and the seeds are ejected at speed. Many seeds drop beneath the crown of the parent tree, but some are dispersed to short distances from the edge of the crown (Burgt 1997; Burgt et al. 2015; Mackinder & Burgt 2009). The maximum ballistic dispersal distance depends on the height of the tree, the size and strength of the pod and the size and shape of the seeds. Therefore, each species has its own maximum ballistic seed dispersal distance. The maximum distance is unknown for most species, but it is probably in the range of 10 – 70 m (Burgt 1997, 2016; Mackinder & Burgt 2009; Norghauer & Newbery 2015).

Several advantages are associated with the dispersal of seeds some distance from the maternal plant (Howe & Smallwood 1982). Despite these advantages, the question is asked why many African Detarioideae tree species use a dispersal method that seems inefficient, because of a relatively short and strictly limited maximum dispersal distance, compared to many wind-, water- or animal-dispersed species. A possible answer is that, in addition to the ballistic dispersal, there may exist some type of long-distance dispersal (Burgt 1997). A second answer may be that the evolution towards reduced mobility appears to be an adaptation enabling the species to dominate stable habitats (Bingham 1994). A third possible answer is that successful dispersal may be less a function of distance than of arrival in particular kinds of sites (Willson 1993).

4.2. Ballistic seed dispersal of *Tetraberlinia moreliana* in Gabon

Observations and experiments on the ballistic dispersal of *Tetraberlinia moreliana* Aubrév. are described by Burgt (1997). *Microberlinia bisulcata* and the two *Tetraberlinia* species in Korup National Park display ballistic seed dispersal characteristics similar to those of *T. moreliana*. The crown of *T. moreliana* has the shape of a hemisphere and can attain a height of 51 m, emerging above the surrounding canopy. Pods are woody, are located on the outside of the tree crown, and have a size of 10 – 23 x 3.5 – 6.8 cm. A pod may contain 0 to 4 seeds, with an average of 2.0 seeds. The discoid seeds have a size of 19 – 30 x 19 – 26 x 5.8 – 7.7 mm and a weight of 2.4 – 3.2 g when fresh (Burgt 1997; Wieringa 1999). The seeds of *T. moreliana* are expelled from the pods with a calculated maximum initial velocity of 37.1 m s^{-1} and with an average upwards angle of 17.3° (Burgt 1997).

The dispersal distance of an explosively dispersed seed, dispersed beyond a tree's crown projection, is defined as the horizontal distance between this seed and the nearest edge of the tree's crown projection (Burgt 1997). Maximum dispersal distances of four *Tetraberlinia moreliana* trees were 60, 52, 51 and 41 m. These four trees were standing at artificial forest edges; their seeds were not deflected by leaves and branches of other trees on their descent. The nearest branches with pods were, respectively, 39, 32, 30 and

24 m above the observation areas. Maximum dispersal distance partly depends on tree height. A total of 41 seeds was found more than 50 m from one of the studied trees, over a period of 20 days. This tree produced an estimated total number of 15,000 to 20,000 seeds. Approximately 1.5-2% of these seeds were dispersed beyond 50 m from the edge of the tree crown (Burgt 1997). The farthest dispersed *T. moreliana* seed was the longest ballistic seed dispersal distance so far recorded in literature. Proof was provided that, for the farthest dispersed seed, both the starting point on the outside of the tree crown and the trajectory can be accurately calculated; while this is not possible for the many seeds found beneath or near the tree crown. The figure of the calculated trajectory of the furthest dispersed seed shows that seeds can pass over neighbouring tree tops before they enter the canopy (Burgt 1997).

4.3. Seed dispersal of Detarioideae tree species in Korup National Park

Of the 35 Detarioideae tree species over 50 cm stem diameter, found in and around the P transect plots (Burgt & Eyakwe 2010), 26 tree species use ballistic seed dispersal. Compared to *Tetraberlinia moreliana* in Gabon, there are variations amongst the dispersal capacities of these 26 species, resulting from differences in pod size, strength, and thickness, as well as in seed size. Some high tree species with strong pods located on the outside of the tree crown, for example *Bikinia letestui* (Pellegr.) Wieringa or *Gilbertiodendron newberyi*, may disperse their seeds to a somewhat longer maximum distance than *T. moreliana* (Burgt 1997; Burgt et al. 2012, 2014). Trees of *Didelotia korupensis* and *Englerodendron korupense* are lower in height, and the fruit peduncles are pendant from the branches; the distances to which their seeds disperse, will therefore be smaller (Burgt et al. 2007; Burgt 2016). Five tree species (*Anthonotha* and *Tessmannia*) use also ballistic seed dispersal, but seeds are dispersed to shorter distances than the other 26 species, because the fruits are thin and small compared to the seed size (Burgt 2016). A few other Detarioideae tree species are wind or animal dispersers (Burgt 1997). The seeds of *Afzelia bella* Harms, *Copaifera mildbraedii* Harms and *Daniellia oblonga* Oliv. (Detarioideae) are dispersed by animals and the fruits of *Stemonocoleus micranthus* Harms (Detarioideae) are dispersed by wind. These species generally do not occur gregariously.

There are many instances of secondary transport of seeds after ballistic dispersal (Pijl 1982). After ballistic dispersal, secondary dispersal can increase the dispersal distance, and can also bring seeds to a better site (Stamp & Lucas 1983). Seeds of many Detarioideae tree species are recalcitrant; they either germinate or rot within a week after dispersal. The seeds are not protected and will usually not survive handling by animals (Burgt et al. 2012; Hart et al. 1989). Also, the seeds lack arils, caruncles or any other apparent 'rewards' for animals and they are too smooth to attach to animals, thus the options for secondary dispersal, for example by animals, are limited. Plants that maximize ballistic dispersal distance cannot exhibit structural adaptations for secondary dispersal (Stamp & Lucas 1983). On the other hand, secondary dispersal of Detarioideae tree seeds will occasionally occur, for example dispersal by water currents in gullies, streams, and rivers. Seeds of various Detarioideae rain forest trees are eaten by different animal species and this may occasionally result in secondary dispersal (Burgt 1997).

It is interesting to note that primate densities were reduced in Detarioideae-rich forests (Brugière et al. 2002; Thomas 1991). The Ituri Forest of Eastern Zaire contains the richest recorded assemblage of anthropoid primates in the world (13 sympatric species). However, very few primates of any species were observed in areas of the Ituri Forest dominated by the Detarioideae tree species *Gilbertiodendron dewevrei* (Thomas 1991). Densities of three cercopithecines and one colobine monkey species were greatly reduced in Detarioideae-dominated rainforests in Gabon (Brugière et al. 2002). They suggest that several biological characteristics of Detarioideae tree species are unfavourable to monkey populations: mast fruiting which Detarioideae generally exhibit, results in periods of food scarcity, most Detarioideae produce dry fruits while fleshy fruits are preferred by monkeys and most Detarioideae produce mature leaves with low palatability. Therefore, forest habitat mosaics may support larger populations of primary consumers than homogeneous forests rich in Detarioideae (Brugière et al. 2002).

The Detarioideae tree species are not the only large tree species in Korup National Park which show ballistic seed dispersal. The Sapotaceae genera *Gluema* and *Lecomtedoxa* also use the ballistic seed dispersal method (Burgt & Newbery 2006; Burgt 2009), but the fruit morphology is very different. The fresh fruits of *Gluema korupensis* Burgt are globose or almost so, 9 – 13 cm long. When a fruit matures, tension builds up in the rubbery mesocarp, and eventually the single large seed is pressed out of the fruit at some speed. Ballistic dispersal can disperse a seed at least 18 m, measured horizontally from the edge of the crown (Burgt & Newbery 2006). The species was observed to grow in groups.

5. Co-dominance of African Detarioideae tree species

5.1. Mapping of tree species in Korup National Park

Dominance of Detarioideae tree species in the African rain forests has been recorded by many authors. Aubréville (1938, 1968) and Letouzey (1957, 1985) were amongst the first authors to describe and attempt to explain this dominance. The extent of forest dominated by *Gilbertiodendron dewevrei* in South Cameroon has been mapped from aerial photographs (Letouzey 1968: 250; Barbier et al. 2017). Gérard (1960) published a map of c. 2.5 x 3 km, showing the occurrence of *G. dewevrei* forest and *Julbernardia seretii* (De Wild.) Troupin forest along 20-m wide east-west and north-south transect lines 500 m apart. The presence or absence was recorded of trees over 50 cm girth in 20 x 100 m subplots. Their map shows that both species occur gregariously, along sections of transects of about 500 – 1000 m long. Some authors have published maps of individual trees of a single species, for example those of the 50 ha permanent plots established in tropical rain forests on all continents (Condit 1998). Although such plots are usually not located in monodominant forest, these maps still show that some tree species, both those in the Detarioideae and in other families, occur in circular groups that do not correlate with topography (Condit et al. 2000; Seidler & Plotkin 2006; Thomas et al. 2003).

Mapping methodology

A grove of *Microberlinia bisulcata* trees > 50 cm stem diameter was mapped in its entirety (Newbery, Burgt & Moravie 2004). The mapping approach used the existing P Plot (part of the P transect plots), which has a size of 1650 x 500 m (Fig. 1). From the four edges of the P Plot, a series of parallel mapping lines were walked at right angles of the plot edge using a compass. These lines were at 50 m distance to each other (the red lines in Fig. 1). The lines were not cleared of vegetation. If a *M. bisulcata* tree > 50 cm diameter was found within 30 to 40 m from both sides of the line, its position was mapped. A line ended when no more *M. bisulcata* trees were found for 150 – 200 m. Then, after walking 50 m to the left or right, a new line was followed back to the edge of the plot, 50 m away from the starting point. Many *M. bisulcata* trees were observed at least twice, the second time being when the next parallel line was walked. *M.*

bisulcata trees can be recognized easily by the pinnate leaf structure and the characteristic appearance to the bark. It is therefore unlikely that any *M. bisulcata* trees > 50 cm diameter would have been overlooked using this method (Newbery, Burgt & Moravie 2004).

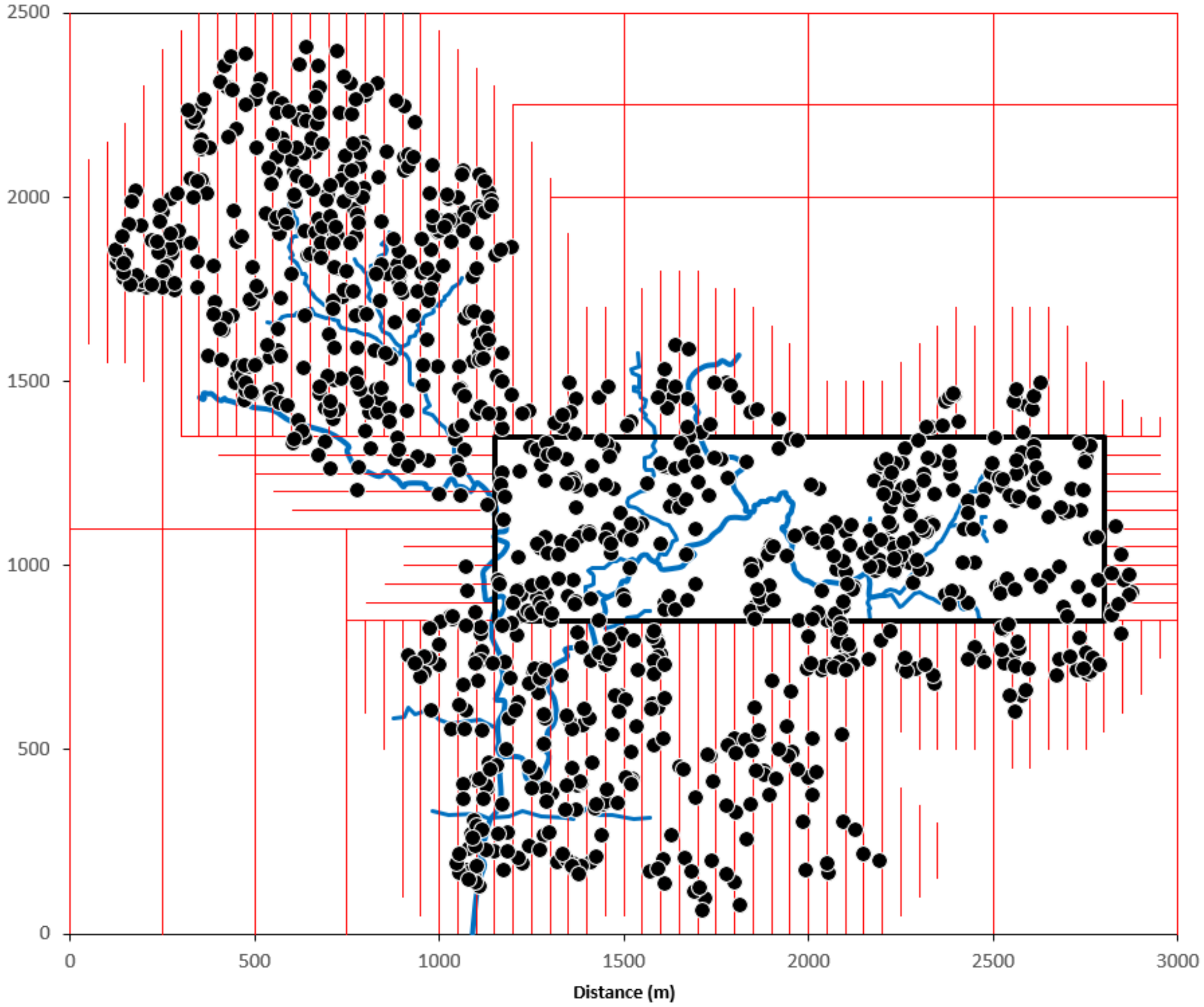

Figure 1. Map of a 272-ha grove of 1028 *Microberlinia bisulcata* trees > 50 cm stem diameter (black dots) in Korup National Park. Rivers and streams are in blue. The black rectangle is the P Plot. From: Newbery, Burgt & Moravie (2004); Newbery et al. (2013). The red lines show the mapping walks made, to map all *Microberlinia bisulcata* trees outside the P Plot.

Maps of *Microberlinia* and *Tetraberlinia* tree species

The data were used to make a map of the whole grove and to examine its structure. In the year 2000, the *Microberlinia bisulcata* grove had a size of 272 ha and consisted of

1028 trees > 50 cm diameter (Fig. 1). The largest trees were distributed across the grove, but most of them occurred at or near the edges (Newbery, Burgt & Moravie 2004; Burgt unpubl. data). Other species occurred within the grove, including the associated co-dominants *Tetraberlinia bifoliolata* and *T. korupensis*. Within the P Plot, which is completely incorporated into the 272-ha *M. bisulcata* grove, 1651 trees > 50 cm diameter were recorded; of which 294 were *M. bisulcata*, 195 *T. bifoliolata*, 279 *T. korupensis*, and 883 trees of other species. *M. bisulcata* trees are the largest in this forest: when trees over 100 cm diameter within the P Plot are considered, a total of 295 trees was recorded, of which 170 were *M. bisulcata*, 37 *T. bifoliolata*, 42 *T. korupensis* and 46 trees of other species (Newbery et al. 2013). In addition to the 272-ha grove, two other large groves of *M. bisulcata* have been mapped (one grove not entirely). These maps are not yet published. The two *Tetraberlinia* species occur in groves to 2 or 3 km diameter, much larger than the *M. bisulcata* groves (Burgt unpubl. data; Newbery et al. 2013). The edge of the *M. bisulcata* grove is therefore not an edge between forests of high and low abundance of Detarioideae trees (Newbery, Burgt & Moravie 2004).

Maps of other Detarioideae tree species

For seven other species maps have been published; these species grow in groups of 100 – 400 m diameter (Burgt et al. 2012, 2014, 2015; Burgt 2016; Mackinder & Burgt 2009; Mackinder et al. 2010). The distances between the groups is 100 – 700 m or more. The groups consist of mature trees, juvenile trees, saplings, and seedlings. It would be very unusual to find a juvenile tree, sapling, or seedling without any mature trees of the same species close by (Burgt et al. 2012). Within the area occupied by these groups, up to 30% of the trees over 50 cm stem diameter belong to a single species (Burgt et al. 2015). These seven species are not dominant, since they comprise of much less than 50% of the number of canopy trees. One of the seven species, *Berlinia korupensis,* has only been found in a single group of 14 trees on 20 ha (Mackinder & Burgt 2009). Although the *B. korupensis* trees are much more dispersed than those of the other Detarioideae tree species discussed here, they still occur clustered. The pods of *B. korupensis* are 15 – 33 cm long; much larger than those of most other Detarioideae species in Korup National Park. The seeds are also much larger and heavier and are probably dispersed to a shorter distance than the other Detarioideae species (Gérard 1960; Hart 1995). It is not known why *B. korupensis* trees occur in a more dispersed group, while having an even shorter ballistic seed dispersal distance.

The forest in the southern part of Korup National Park contains an area at least 7 × 5 km in size, rich in both individual trees and species from the Detarioideae, whereas the surrounding forest is poor in tree species from this group (Burgt et al. 2012). Of the 35 Detarioideae tree species over 50 cm stem diameter, found in this area (Burgt & Eyakwe 2010), about 24 species have been observed to occur in groups, including those of which maps were published. Together, these 24 Detarioideae tree species are co-dominant in this 7 x 5 km area. Within the P Plot (Fig. 1), where 11 of the 24 species reach stem diameters of over 50 cm, 52% of the trees over 50 cm stem diameter belong to these 11 species and their basal area is 70% of the total basal area. A few species, such as *M. bisulcata*, may be considered dominant in part of the 7 x 5 km area. However, most of the Detarioideae species cannot be considered individually dominant; their trees do occur in groups but occupy less than 50% of the number of canopy trees. Within the 7 x 5 km area of Detarioideae-rich forest, each of the 24 tree species of Detarioideae has its own characteristic distribution; some species occur throughout most of the area, some others are very rare (Burgt et al. 2012). The groups of different Detarioideae tree species often partly overlap, and smaller groups often occur completely within larger groups of other species, but their edges generally do not coincide.

In Korup National Park, *Gilbertiodendron dewevrei* also grows in small groups. A map of 96 *G. dewevrei* trees between 10 and 213 cm stem diameter was published (Map 2 in Burgt et al. 2015). The 96 trees stand in four groups, but the size of these four stands is small, each about 0.5 ha only. This is very small compared to the monodominant stands of *G. dewevrei* elsewhere in the African rain forest, which may be thousands of hectares in size (Barbier et al. 2017; Hart 1990; Letouzey 1968). Another difference is that, in Korup National Park, *G. dewevrei* forms relatively even-sized, presumably even-aged stands. The presence of many saplings and juvenile trees in two of these four stands, while the two other stands have mostly mature trees, indicates that *G. dewevrei* has a different reproduction ecology in Korup National Park compared to elsewhere in the African rain forest.

A map of a Sapotaceae tree species

The Sapotaceae provide several examples of tree species occurring in groups, most prominently in the genus *Lecomtedoxa* (Letouzey 1968: 152; 1983). The tree species in the Sapotaceae genera *Gluema* and *Lecomtedoxa* each occur in groups in the rainforest of Korup National Park (Burgt & Newbery 2006; Burgt 2009). Both species were described only recently and have not yet been investigated for ectomycorrhizal status. A map was published of 154 *Gluema korupensis* trees on c. 22 ha. The trees grow close together, in a group with a clear edge, in Detarioideae-rich forest. Solitary trees are absent, except to the northwest, along a stream. These trees may have grown from seeds dispersed by water, floating downstream from the main group of trees, and germinating on the stream bank (Burgt & Newbery 2006).

5.2. Causes of co-dominance

Gilbertiodendron dewevrei has been recorded on a wide variety of soils and the parent materials of soils underlying *G. dewevrei* forests are also diverse. The transition from *G. dewevrei*-dominated forest to mixed forest is abrupt and without associated changes in environmental characteristics. The two forest types both occur on well-drained soils with comparable soil characteristics, and the topography and climate are identical (Hart et al. 1989; Hart 1990; Makana et al. 2004; Peh et al. 2011a). Soil characteristics do not seem to cause persistent monodominance of *G. dewevrei*.

There are no significant changes in soil type or in topography between the *Microberlinia bisulcata* grove of Fig. 1 and the forest just outside this grove. In structure and physical composition, the mineral soils do not appear to differ between groves and the surrounding forest matrix (Chuyong et al. 2000; Gartlan et al. 1986; Newbery et al. 1988, 1997). The absence of *M. bisulcata* outside of the grove cannot, therefore, be readily explained by differences in known environmental factors (Newbery, Burgt & Moravie 2004).

Persistent monodominance in African lowland rain forests is not caused by prehistoric human activities. As for *Gilbertiodendron dewevrei,* potsherds and charcoal are frequent in the soil of the mixed forest in Congo-Kinshasa but are never found in the form of forest where *G. dewevrei* is strongly dominant (Léonard 1952). Hart et al. (1996) found charcoal in *G. dewevrei* forest, but it was not clear whether this originated from natural fires or human activity. As explained in chapter 2.3, the dominance of Detarioideae trees indicates the absence of large-scale natural or human disturbance in the past.

Peh et al. (2011b) evaluated eight published hypotheses on the possible causes of persistent monodominance in tropical lowland rain forests. The eight hypotheses are not mutually exclusive. Monodominance is likely to be a consequence of a combination of characteristics of the species itself and characteristics of the forest ecosystem. Every tree species may have its own set of causes to become monodominant or co-dominant. Three of the eight hypotheses are here further examined with regards to the *Microberlinia bisulcata* grove in Korup National Park. The other five hypotheses, for example the one on mast fruiting (Newbery et al. 2006b), might also be of importance.

1. Reduced rates of gap formation. A low frequency of disturbance to the forest habitat may result in a reduced rate of gap formation and a subsequent low abundance of shade-intolerant tree species, which may favour monodominant species (Connell & Lowman 1989; Hart et al. 1989; Peh et al. 2011b). It is likely that monodominant stands will expand only in regions undisturbed over long periods (Hart 1990). Gaps are uncommon in *Gilbertiodendron dewevrei* forest, and its seedlings and saplings are shade-tolerant, enabling the species to reproduce in its own shade without the need of any significant disturbance (Gérard 1960). *Microberlinia bisulcata* does not have shade-tolerant seedlings and saplings, regeneration depends therefore on some sort of disturbance (Newbery et al. 2013). Nevertheless, gaps are also uncommon in *M. bisulcata* forest (see chapter 2.3). The very large buttresses of the trees make them highly resistant to wind.

2. Ectomycorrhizal associations may promote the development of dominance, particularly where nutrients are in low or uncertain supply. Ectomycorrhizae are of selective advantage to trees on soils of low fertility. Ectomycorrhizal associations with trees can increase nutrient supplies via a more efficient exploitation of larger volumes of soils or through the direct decomposition of leaf litter (Connell & Lowman 1989). Dominance may be reinforced by the fact that only ectomycorrhizal individuals can benefit from the mycelial network (Alexander 1989). Ectomycorrhizae might also facilitate mast fruiting, which also may promote dominance (Newbery et al. 2006b). In a monodominant *Gilbertiodendron dewevrei* rain forest in southeast Cameroon, ectomycorrhizal fungi were shared between seedlings and adults; however, no evidence was obtained for nutrient transfer from trees to seedlings (Ebenye et al. 2016). In the Ituri Forest in Congo-Kinshasa, some ectomycorrhizal species, such as *Manilkara sp.*, are not dominant, and some dominant species, such as the vesicular-arbuscular mycorrhizal tree species *Cynometra alexandri* C.H. Wright, are not ectomycorrhizal (Torti et al. 2001; Alexander 1989). Ectomycorrhizal habit can therefore not be a unique explanation for monodominance but may nonetheless be an important part of a set of explanations (Torti & Coley 1999; Torti et al. 2001).

In Detarioideae-rich forest in South Cameroon, more than 150 ectomycorrhizal fungal species have been observed. Important ectomycorrhizal fungal genera are *Amanita* (Amanitaceae), *Russula* and *Lactarius* (Russulaceae) and various genera of the Cantharellaceae and Boletales (Onguene & Kuyper 2001). They observed groups of ectomycorrhizal Detarioideae trees in their study area. In Korup National Park, out of the 24 Detarioideae species which have been observed to occur in groups, 18 are ectomycorrhizal (Alexander 1989; Newbery et al. 1988; Onguene & Kuyper 2001). The remaining six species have not yet been tested; five of them were recently described as new. Those Detarioideae tree species in the study area which have not been observed to occur clustered, may or may not be ectomycorrhizal; all of them grow mixed with the ectomycorrhizal clustered Detarioideae trees.

Microberlinia bisulcata and the two *Tetraberlinia* species are ectomycorrhizal, which may promote their co-dominance. Ectomycorrhizal symbiosis might enable seedlings of *M. bisulcata* to survive several years between pulses of increased radiation (Newbery et al. 2010). However, root-sterilized *M. bisulcata* seedlings transplanted into low- and high-abundance ectomycorrhizal forest plots became well inoculated with ectomycorrhizae (Newbery et al. 2000), thus demonstrating no limitation of inoculum for *M. bisulcata* to establish well away from existing adults. Ectomycorrhizal spores are windborne and therefore probably not a limited resource in both Detarioideae-rich and Detarioideae-poor forest (Torti et al. 1999). The shape of the *M. bisulcata* grove appears not to be determined by the occurrence of ectomycorrhizae specific to this tree species (Newbery, Burgt & Moravie 2004).

3. Limited seed dispersal distance. Trees of a species with limited seed dispersal occur in clusters, whereas a species with long-distance seed dispersal will exhibit less clustering or even spatial randomness. Ballistic dispersal, compared with other dispersal methods, generally leads to the most aggregated clustering of trees (Seidler and Plotkin 2006). The gregarious habit of seedlings beneath and near parent trees due to limited seed dispersal, observed in many monodominant species, may explain the existence of dominant stands (Connell & Lowman 1989; Hart 1990; Newbery, Burgt & Moravie 2004). The tendency of *Microberlinia bisulcata* and other Detarioideae trees to grow in groups is related to the relatively short and strictly limited maximum dispersal distance of the ballistic seed dispersal method (Burgt et al. 2007, 2012, 2015; Stamp & Lucas 1983; Wieringa 1999). It is interesting to note that the tree species *Gluema korupensis* and *Lecomtedoxa plumosa* Burgt (Sapotaceae) in Korup National Park also display ballistic dispersal and clustered stands, although these species have a different fruit morphology and expulsion mechanism (Burgt & Newbery 2006; Burgt 2009).

5.3. Establishment and expansion of Detarioideae tree groves

Establishment and sizes of groves

A single accidental secondary dispersal event could send a seed much further than the maximum ballistic dispersal distance and might establish the species at new locations (Newbery et al. 2013). Secondary dispersal of seeds of *Microberlinia bisulcata* and the two *Tetraberlinia* species has not been observed (Newbery, Burgt & Moravie 2004) and is certainly rare, but will occur now and then. One of the other two *Microberlinia bisulcata* groves which have been mapped in Korup National Park since 2004 (Burgt unpubl. data), shows the possibility of water dispersal: along the two streams flowing through this grove, two groups were found, of 6 and 31 trees, 100 to 200 m downstream from the edge of the grove. Another way separate groves may form is by expansion of a grove, followed by fragmentation and near-extinction, resulting in only a few scattered trees remaining, from which several groves would then start to form by renewed expansion.

It is interesting to compare *M. bisulcata* with *Bikinia letestui*. These species are similar to each other in tree size and crown architecture, as well as in leaf, pod, and seed sizes, but may easily be separated by their flowers, leaflet shape and bark. Nevertheless, *Bikinia letestui* occurs in groves of usually less than 10 mature trees, on areas of 0.25 ha to 5 ha in size, where saplings and juvenile trees occur mixed with mature trees of all sizes (Burgt unpubl. data; Saint Aubin 1963: 53; Wieringa 1999). These groves are therefore very different in size and structure from those of *M. bisulcata*. The seedlings of *Bikinia letestui* are likely shade-tolerant, enabling the species to regenerate in its own shade. Nevertheless, seedlings of the two *Tetraberlinia* species are also shade-tolerant;

they survived much better (21% after 7 years) than those of *M. bisulcata* (4% after 7 years) (Newbery et al. 2006), while the grove size of the *Tetraberlinia* species is larger than those of *M. bisulcata*. The fact that these similar tree species occur with pronounced differences in grove structure and sizes, highlights that the ecological characteristics which determine the size of groves of various species are not fully understood.

The 24 grove-forming Detarioideae tree species are growing together in a 7 x 5 km area of Detarioideae co-dominant forest. The 24 species show a large inter-specific variability in grove size, while the sizes of groves of a single species seem similar. The light-demanding requirements of most of the 24 grove-forming Detarioideae tree species have not been precisely determined, but the impression is that most of them are shade-tolerant. The abundance of saplings and juvenile trees of these species (except *Microberlinia bisulcata*; see below) indicate these species successfully recruit and replace themselves under their own canopy, thus maintaining their local abundance. A single species never reaches monodominance across areas larger than a hectare. None of the 24 species has unique ecological characteristics enabling it to outcompete the other species; even *Microberlinia bisulcata* has not been able to outcompete any of the other 23 species. Areas of up to 250 m x 250 m without *M. bisulcata* but rich in other Detarioideae trees, occur within all three mapped groves (Burgt unpubl. data). Which species replaces a large tree after it perishes may be determined for a large part by chance, rather than by the ecological characteristics of the replacing species.

Directly to the east of the 7 x 5 km area of Detarioideae-rich forest, also within Korup National Park, there is an area of Detarioideae-poor forest of about the same size, which, judged by the species composition, is also little influenced by past human activities and past climatic change. Perhaps this area of Detarioideae-poor forest, notwithstanding its species composition, was not under forest cover during recent ice ages, and the Detarioideae tree species have not yet been able to reach that forest due to their limited seed dispersal.

Expansion of the *Microberlinia bisulcata* grove

Microberlinia bisulcata occurs in Korup National Park in dense stands, surrounded by rain forest where trees of this species are completely absent. The 272-ha grove which was mapped in its entirety has a well-defined edge. Ballistic seed dispersal, combined with the apparent infrequency of any form of longer-distance seed dispersal, explains the clear edge of the *M. bisulcata* grove and the complete absence of *M. bisulcata* from the forest that surround the grove (Newbery, Burgt & Moravie 2004). Ballistically dispersed species can achieve a regular and radial expansion of juvenile trees around adults: the edge of a monodominant forest patch expanding and invading the surrounding mixed forest (Connell & Lowman 1989; Hart 1990; Newbery, Burgt & Moravie 2004).

From its pod and seed size, *M. bisulcata* would be expected to display a comparable maximum dispersal distance as *Tetraberlinia moreliana*, 60 m from the edge of the crown (Burgt 1997), and this is confirmed by the fact that its seedlings at the edge of the grove occur only up to 40 – 50 m from the crowns of the adult trees. The restricted dispersal of *M. bisulcata* means that the next generation establishes either inside the grove or within 40 – 50 m of the edge of the outmost tree crowns (Newbery, Burgt & Moravie 2004). Ballistic seed dispersal was evident from the *Microberlinia bisulcata* trees > 50 cm diameter standing in semi-circles of 100 – 200 m diameter at the grove's edge and from the internal circles of *M. bisulcata* trees of the same diameter. Within these circles, round or oval areas without *M. bisulcata* trees indicated where parent trees had most likely died and were then replaced by trees of other species. Some circles were much larger and these probably originated from either more than one parent tree or after two generations. These semi-circles of trees on the edge of the grove show that the grove had been expanding up to the time when the present adult trees established (Newbery, Burgt & Moravie 2004).

Although the grove has been observed for only c. 20 years, while its trees live to typically 200 – 250 years (Newbery et al. 2013), an estimate may be made of its expansion rate. The circles of *Microberlinia bisulcata* trees of 100 – 200 m diameter at the grove's edge, and the maximum ballistic seed dispersal distance, suggest a radial expansion rate of c. 50 m per generation (Newbery, Burgt & Moravie 2004). The *M. bisulcata* trees could begin seeding at 42 – 44 cm diameter. The average age when *M. bisulcata* matures was estimated from stem growth rates at c. 65 years, or c. 51 years when using dendrochronology (Norghauer & Newbery 2015; Newbery et al. 2013). The grove could expand, therefore, at a maximum rate of about 100 m per century (Newbery, Burgt & Moravie 2004).

The expansion rate of *Gilbertiodendron bambolense* Burgt in Congo-Kinshasa was estimated at 100 m per two or three centuries (Evrard 1968: 102; cited as *G. ogoouense* (Pellegr.) J.Léonard). The relatively large and heavy seeds of *G. dewevrei* disperse to a maximum ballistic seed dispersal distance of between 5 m and 10 m from the crown edge (Hart et al. 1989; Hart 1995). Seedlings are never found further than 20 m from the edge of the tree crown (Gérard 1960: 125). The comparatively short maximum ballistic seed dispersal distance explains the sharp boundary between monodominant *G. dewevrei* forest and mixed forest. Because of the limited means of dispersal, patches of *G. dewevrei* would likely expand into adjacent mixed forest (Hart et al. 1989; Hart 1995; Djuikouo et al. 2014).

5.4. Ecology and dynamics of co-dominance in Korup National Park

The current state of the *Microberlinia bisulcata* grove

Seedlings, saplings, and juvenile trees of the two *Tetraberlinia* species occur abundantly in Korup National Park; the diameter frequency distributions show the number of trees decreasing with an increase in stem diameter. However, the diameter frequency distribution of *Microberlinia bisulcata* is typically bell-shaped, with the maximum number of trees occurring at 90 – 120 cm stem diameter (Newbery et al. 1998). Although *M. bisulcata* produces large seedling banks through a 2 or 3-year mast fruiting cycle (Newbery et al. 2006b), saplings and juvenile trees are rare in comparison to the numbers of mature trees (Newbery et al. 1998, 2013). The poor recruitment of *M. bisulcata* is the result of its very low seedling survival (Newbery et al. 2006a). The seedlings and saplings are shade-intolerant, while the 272-ha grove has a continuous canopy with few gaps. As a result, there are few saplings and juvenile trees within this *M. bisulcata* grove. In the recent past few trees have reached maturity, and in the coming decades few trees will reach maturity. The presence, at the edge of the grove, of only one semi-circle of juvenile trees, and just a few solitary juveniles, indicates that the grove is not expanding much since the present *M. bisulcata* trees became adults (Newbery, Burgt & Moravie 2004). Unless many more saplings and juvenile trees will be able to establish before the current mature trees die, *M. bisulcata* will be much less dominant in the next generation (Newbery et al. 2004).

A possible hypothesis is that periods of multiple extreme events, not single separated ones, have the most important effects on forest composition, patterns, and dynamics (Newbery & Gartlan 1996; Newbery et al. 1998). Waves of recruitment would result from periods of multiple extreme events, in the form of repeated climatic disturbances. *M. bisulcata* may need increased light over several periods to recruit successfully (Newbery et al. 2010). Waves of enhanced recruitment may have happened in past centuries, but their signature was subsequently blurred by variance in growth rates. Nevertheless, one distinctive mode in *M. bisulcata* tree size at 90 – 120 cm stem diameter, and a corresponding average age of c. 200 years, is evident (Newbery et al. 2013). The dominance of *M. bisulcata* is most likely due to an epoch of unusually dry years, which allowed its shade-intolerant seedlings and saplings to outcompete other species (Newbery et al. 1998). Each period of events led to a wave of release and recruitment of *M. bisulcata*. Canopy openings allow the light-demanding and fast-growing ectomycorrhizal *M. bisulcata* to establish. At each step the saplings would make increments in height and stem growth towards the canopy. With only single events, or events too far apart, saplings would stagnate and die in the shade (Newbery, Burgt & Moravie 2004). Recruitment appears to have been much poorer in the last 50 years than before, and this implies that large disturbance events were absent (Newbery, Burgt & Moravie 2004).

The future of the *Microberlinia bisulcata* grove

The crucial issue is why *Microberlinia bisulcata* is presently not replacing itself and why there is an unusual peak in the frequencies of its largest trees today. The *M. bisulcata* trees could begin seeding at 42–44 cm diameter (Norghauer & Newbery 2015). If the average stem diameter at maturity is taken as 43 cm, then the grove consisted of 1052 mature trees and 146 juvenile trees (12%) over 10 cm diameter. The density of juvenile *M. bisulcata* trees, both inside and at the edge of the grove, is not enough for complete replacement of the current set of mature trees. Even 100% survivorship of its juveniles would be insufficient to retain its dominance (Newbery et al. 1998). Juvenile trees of *M. bisulcata* have high growth rates and high survival: annualized mortality rate 1991–2005 was 0.13 x that of the other tree species (Newbery et al. 2010); but even that would not be enough to fully compensate for their low densities.

The scarcity of saplings and juvenile trees indicates that the *Microberlinia bisulcata* groves have a reproduction ecology that is different from the *Tetraberlinia* groves and the *Gilbertiodendron dewevrei* groves. At present, the trees in the *M. bisulcata* grove are very dominant, regarding numbers of canopy trees, biomass, basal area, and crown projection area. Dominance by *M. bisulcata* need not necessarily be a persistent feature, however. It could also be transient, in the sense that high abundance fluctuates over time. Transient dominance means that trees alter the habitat in ways that are increasingly to the species' own advantage, but later those enforced conditions become selective against its continuation. Transient dominance implies that recruitment does not occur continuously, but in waves (Newbery et al. 2013).
Such transient dominance may explain why *M. bisulcata* does not occur all over the forest. At the rate of expansion of about 100 m per century of *Microberlinia bisulcata*, the edges of the three known groves would meet in about two millennia, since these groves are situated at about 2 to 4 km from each other. Perhaps periods with an absence of disturbance, which would be favoured by other persistent dominant species, resulted in slower expansion or even contraction of the *M. bisulcata* groves.

The structure of one of the other two *Microberlinia bisulcata* groves in Korup National Park, which has now been completely mapped (Burgt unpubl. data), is somewhat different from that of the grove of Fig. 1. The shape is less regular and there are many more juvenile trees present: there were 349 mature trees in this grove, and 136 juvenile trees (28%) over 10 cm diameter. Their number is still less than the number of mature trees and therefore the regeneration in this grove as well seems insufficient to maintain the dominance of the species. The differences in numbers of juvenile trees in the two groves indicate that there must have been differences in their past reproduction ecology. Rainfall in the dry season is by thunderstorms, which could pass over only one of the two groves; consequently, droughts may have affected one grove more than the other grove.

Microberlinia bisulcata has been persistently dominant in the past, because the slow expansion rate of the grove, at a maximum rate of about 100 m per century (Newbery, Burgt & Moravie 2004), shows that the grove has been there for many generations of trees. The current deficiency of regeneration indicates *M. bisulcata* may lose much of its dominance. The trees in the *M. bisulcata* grove currently occur in dense stands, and individual *M. bisulcata* trees may not be replaced by a *M. bisulcata* tree of the next generation, since *M. bisulcata* only regenerates beyond the crown projection of mature trees. Saplings were found to be located at an average distance of 43 m from adults (Newbery et al. 2010), while crown radius of mature trees is 10 – 30 (– 41) m. As a result, the next generation grove might contain much less *M. bisulcata* trees. However, the remaining trees would occur much less dense and would therefore have much better opportunities for reproduction. Within a few generations, the *M. bisulcata* grove could become dense again. The result of such intermittent recruitment would be that the *M. bisulcata* grove is transiently dominant instead of persistently dominant. (Newbery et al. 2013).

In *Gilbertiodendron dewevrei* forest in Congo-Kinshasa, all age classes are present. The shade-tolerant saplings and juvenile trees occur abundantly, indicating the species successfully recruits and replaces itself under its own canopy. *G. dewevrei* therefore may be considered persistently monodominant and the forest is considered relative stable; the composition and structure of the forest is not expected to change much over long periods of time (Gérard 1960; Hart 1990). This is also true for the adjacent mixed forest; both the monodominant and mixed forests are likely to maintain their major canopy dominants during subsequent generations (Makana & Hart 1998); except at the edge between the two forest types, where a slow expansion of *G. dewevrei* forest may take place.

5.5. The species richness of the Detarioideae forest

Two recent studies have made plots in monodominant *Gilbertiodendron dewevrei* forest, and adjacent mixed forest to study the stand structure and species diversity (Djuikouo et al. 2014; Makana et al. 2004, 2011). The results of both studies are contradictory. Djuikouo et al. (2014) concluded that 9 plots of 1 ha each in mixed forest in the Dja Reserve in Cameroon, were significantly more diverse in numbers of species (average 109 species over 10 cm stem diameter per ha) compared to 9 plots of 1 ha in *G. dewevrei* forest (47 species). In contradiction with this, Makana et al. (2004) concluded that the monodominant forest of the Ituri region in Congo-Kinshasa is just as species rich as the nearby mixed forest: mixed forest had 410 species over 1 cm stem diameter on 10 ha, and monodominant forest 403 species. Djuikouo et al. (2014)

suggest that the discrepancy between these results is probably because their plots were selected in such a way that the entire 1 ha plot was within a homogeneous area forest.

The strong dominance of *Gilbertiodendron dewevrei* in monodominant forest is associated with a reduction in the abundance of other canopy tree species. In monodominant forest, most other large tree species are rare due to the abundance of *G. dewevrei*. Forests in Ituri appear species poor at smaller scales and in the larger size classes, but quite diverse at larger scales and when all trees over 1 cm stem diameter are considered (Makana et al. 2004, 2011). *Gilbertiodendron dewevrei* only reduces rather than eliminates the presence of mixed-forest species (Djuikouo et al. 2014; Makana et al. 2011). Except for the absence of *G. dewevrei* from mixed forest, the same tree species occur in both mixed and monodominant forest, although at different densities (Hart et al. 1989; Hart 1990).

Apart from *Microberlinia bisulcata*, there are no other important differences in tree species composition between the inside and outside of the grove (Gartlan et al. 1986; Newbery & Gartlan 1996; Newbery et al. 1997). A credible hypothesis is therefore that all plant species occurring in the Detarioideae-poor forest in Korup National Park, also occur in the Detarioideae-rich forest, although often at a much lower frequency. According to this hypothesis, the Detarioideae-rich forest would be richer in species compared to the Detarioideae-poor forest, because most of the 32 Detarioideae tree species so far found in the Detarioideae-rich forest do not occur in the Detarioideae-poor forest.

6. The original contribution to knowledge represented by the published work

6.1. The papers used in this thesis

Nine publications were selected for the present thesis: one single-authored paper, six first-authored papers and two co-authored papers. Seven papers describe in total 15 new Detarioideae tree species from Korup National Park in Cameroon and elsewhere in the Central African rain forests. These papers contain sections on the ecology and grove-formation of the newly described species. The paper Newbery, Burgt & Moravie (2004) is included because this paper explains a large amount of my personal observations and thoughts. A paper newly describing a co-dominant Sapotaceae tree species in Korup National Park is included, because it provides an interesting comparison with the co-dominant Detarioideae tree species. Several additional first-authored and co-authored publications are cited.

Newbery, D.M.; Burgt, X.M. van der; Moravie, M.-A. 2004. Structure and inferred dynamics of a large grove of *Microberlinia bisulcata* trees in Korup National Park, Cameroon. *Journal of Tropical Ecology* 20: 131 – 143. https://doi.org/10.1017/S0266467403001111

Burgt, X.M. van der; Newbery, D.M. 2006. *Gluema korupensis* (Sapotaceae), a new tree species from Korup National Park, Cameroon. Kew Bulletin 61 (1): 79 – 84. http://www.jstor.org/stable/20443247

Burgt, X.M. van der; Newbery, D.M. 2007. *Englerodendron korupense* (Leguminosae-Caesalpinioideae), a new tree species from Korup National Park, Cameroon. *Adansonia* 29 (1): 59 – 65. http://sciencepress.mnhn.fr/en/periodiques/adansonia/29/1/englerodendron-korupense-fabaceae-caesalpinioideae-une-nouvelle-espece-d-arbre-du-parc-national-de-korup-au-cameroun

Mackinder, B.A.; Burgt, X.M. van der 2009. *Berlinia korupensis* (Leguminosae - Caesalpinioideae), a new tree species from Cameroon. *Kew Bulletin* 64: 129 – 134. https://doi.org/10.1007/s12225-009-9100-z

Burgt, X.M. van der; Eyakwe, M. 2010. Searching for undescribed large tree species in the rainforests of Korup National Park, Cameroon. In: Burgt, X.M. van der; Maesen, J. van der; Onana, J.-M. (eds.) 2010. *Proceedings of the 18th AETFAT Congress, Yaoundé, Cameroon.* Pp. 741 – 747. http://shop.kew.org/systematics-and-conservation-of-african-plants-proceedings-of-the-18th-aetfat-congress-12455

Burgt, X.M. van der; Eyakwe, M.; Motoh, J. 2012. *Gilbertiodendron newberyi* (Leguminosae: Caesalpinioideae), a new tree species from Korup National Park, Cameroon. *Kew Bulletin* 67 (1): 51 – 57. https://doi.org/10.1007/s12225-012-9345-9

Burgt, X.M. van der; Poundje, M.; Sene, O. 2014. *Cryptosepalum korupense* sp. nov. (Leguminosae – Caesalpinioideae), a tree species from the Southwest Region in Cameroon. *Adansonia* sér. 3, 36 (1): 73 – 81. https://doi.org/10.5252/a2014n1a7

Burgt, X.M van der; Mackinder, B.A.; Wieringa, J.J.; Estrella, M. de la 2015. The *Gilbertiodendron ogoouense* species complex (Leg. – Caesalpinioideae), Central Africa. *Kew Bulletin* 70: 29; 42 pp. https://doi.org/10.1007/s12225-015-9579-4

Burgt, X.M van der 2016. *Didelotia korupensis* and *Tessmannia korupensis* (Fabaceae – Caesalpinioideae), two new tree species from Korup National Park in Cameroon. *Blumea* 61: 51 – 58. https://doi.org/10.3767/000651916X691402

6.2. Original methodology and discoveries presented in these papers

The mapping methodology developed for recording large tree species in tropical rain forest enables mapping of areas much larger than 50 ha; the size of many permanent plots in tropical rain forest. The map prepared by Newbery, Burgt & Moravie (2004), of a 272-ha grove of dominant *Microberlinia bisulcata*, is by far the largest map ever published of individual trees of a single species in tropical rain forest. A rapid mapping method was developed (see chapter 5). Precise mapping of individual trees can usually only be done from the ground. Mapping by satellite has many possibilities, but individual trees in tropical rain forest may not be identified and recorded accurately.

Analysis of this map resulted in several new conclusions. The *M. bisulcata* grove has a well-defined edge. Ballistic seed dispersal explains the clear edge and the complete absence of *M. bisulcata* from the surrounding forest. Ballistic seed dispersal was evident from the *M. bisulcata* trees > 50 cm diameter standing in semi-circles of 100 – 200 m diameter at the grove's edge. They indicate that the grove had been expanding up to the time when the present adult trees established. The presence, at the edge of the grove, of only one semi-circle of juvenile trees, and just a few solitary juveniles, indicates that the grove is not expanding much since the present *M. bisulcata* trees became adults. *M. bisulcata* has been persistently dominant in the past, but the current deficiency of regeneration indicates *M. bisulcata* may lose much of its dominance in the future (Newbery, Burgt & Moravie 2004).

During the present research, I newly described 15 Detarioideae tree species. Seven of these occur in Korup National Park (and are also listed in chapter 3.2), the others occur elsewhere in West and Central Africa: *Berlinia korupensis* Mackinder & Burgt, *Cryptosepalum korupense* Burgt, *Didelotia korupensis* Burgt, *Englerodendron korupense* Burgt, *Gilbertiodendron bambolense* Burgt, *Gilbertiodendron breteleri* Burgt, *Gilbertiodendron ebo* Burgt & Mackinder, *Gilbertiodendron maximum* Burgt & Wieringa, *Gilbertiodendron minkebense* Burgt & Estrella, *Gilbertiodendron newberyi* Burgt, *Gilbertiodendron quinquejugum* Burgt, *Gilbertiodendron sulfureum* Burgt, *Gilbertiodendron tonkolili* Burgt & Estrella, *Talbotiella velutina* Burgt & Wieringa, *Tessmannia korupensis* Burgt (for references see chapter 3.2; Burgt et al. 2015; Estrella et al. 2012). Maps of groups of trees were published of five of these 16 new species; seven more tree species were observed in the forest to grow in groups.

Two Sapotaceae tree species, *Gluema korupensis* and *Lecomtedoxa plumosa*, were newly described during the present research. Both species, and indeed both genera, were first described to use ballistic seed dispersal by Burgt & Newbery (2006) and Burgt (2009). Both newly described species were shown to grow in groves. A map was published of a 20-ha grove of 154 *Gluema korupensis* trees.

Before the publication of Burgt et al. (2015), the herbarium specimens of the central African tree species *Gilbertiodendron ogoouense* showed a large variability. For example, in the Flore du Gabon and the Flore du Cameroun (Aubréville 1968, 1970), *G. ogoouense* keys out having 2 – 8 pairs of leaflets; while the herbarium specimens had 2 – 11 pairs of leaflets. Burgt et al. (2012, 2015) have split *G. ogoouense* into eleven species: *G. ogoouense* itself, nine newly described species and one reinstated species and present a key to name fertile and sterile material collected from the canopy of mature trees. All newly described species are likely grove-forming; several were indeed observed to be grove-forming by me.

6.3. Future research on co-dominant Detarioideae tree species

After publishing the map and analysis of the 272-ha *Microberlinia bisulcata* grove (Newbery, Burgt & Moravie 2004), tree diameters were measured of all 1028 trees in this grove. Two nearby groves, each at 2.5 and 4 km distance to the first grove, were also mapped (one grove only partly). The surrounding forest was surveyed along transect lines 500 m apart, with a length of about 70 km (Burgt, unpublished data). This dataset will be analysed and published in a future paper.

Gilbertiodendron dewevrei is one of the most-studied monodominant Detarioideae tree species, but large maps depicting individual trees do not yet exist. The mapping methodology developed by Newbery, Burgt & Moravie (2004) for mapping large tree species in tropical rain forest could be used to map an area of monodominant *Gilbertiodendron dewevrei* forest, including a section of a grove's edge. Such a map might increase understanding of the ecology and dynamics of the species.

Detarioideae rain forest tree species occur in dense groves, while the forest in between these groves is completely empty of that species. It is not clear how the ecology and dynamics of Detarioideae rain forest tree species leads to this distribution of trees. Long-distance seed dispersal might be an option, although this was never observed and will happen at best only occasionally. Another option is a long period of slow expansion, followed by a near-extinction event, leading to only a few scattered trees of a Detarioideae rain forest tree surviving in the forest, after which a second period of slow expansion would occur. Further field research, possibly including molecular techniques, might provide better understanding into the dynamics of grove formation. Molecular techniques have recently been used to date the occurrence of long-distance dispersal events and may be used to determine when a grove was established through long-distance dispersal, as well as determine the parent grove.

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Appendix 1. Statements of contribution of the papers used in this thesis

Paper 1. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Newbery, D.M.; Burgt, X.M. van der; Moravie, M.-A.; 2004. Structure and inferred dynamics of a large grove of *Microberlinia bisulcata* A.Chev. trees in Korup National Park, Cameroon. Journal of Tropical Ecology 20: 131 – 143. https://doi.org/10.1017/S0266467403001111

Background: A 272-ha grove of 1028 dominant *Microberlinia bisulcata* (Detarioideae) adult trees > 50 cm stem diameter was mapped in its entirety in the southern part of Korup National Park, Cameroon. The distribution of trees within this grove was analysed. Past events possibly contributing to the current structure are discussed.

Contribution of the candidate: I, Xander van der Burgt, made the following contributions:

- I mapped, or verified the positions, of all *Microberlinia* trees > 10 cm stem diameter.
- I wrote parts of the methods section.
- My thoughts on the structure and inferred dynamics contributed to the discussion.

Statement of contribution: As first author of this paper, I, David M. Newbery, hereby endorse this statement of contribution by Xander van der Burgt.

Name, institute, email address	**Signature**	**Date**
Prof.em. Dr. David M. Newbery Institute of Plant Sciences University of Bern, Switzerland David.newbery@ips.unibe.ch	D. McC. Newbery	11. Sept., 2017

M.-A. Moravie, one of the co-authors, has deceased.

Paper 2. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Burgt, X.M. van der; Newbery, D.M.; 2006. *Gluema korupensis* (Sapotaceae), a new tree species from Korup National Park, Cameroon. Kew Bulletin 61 (1): 79 – 84. http://www.jstor.org/stable/20443247

Background: The paper describes a new species in the genus *Gluema,* from Korup National Park.

Contribution of the candidate: I, Xander van der Burgt, took the leading role in this study and in the preparation of the manuscript. I made the following contributions:

- I determined the species to be new to science.
- I wrote the paper, including the description of the new species.
- I studied all cited herbarium specimens and prepared the distribution map.
- I generated the conservation assessment for the species.
- I prepared the line drawing.
- I collected flowering and fruiting type specimens of the new species.
- I recorded a group of 154 *Gluema korupensis* trees, and prepared a map of this group.
- I communicated with the journal and addressed the comments of the reviewers.

Statement of contribution: As co-author of the listed paper, I, David M. Newbery, hereby endorse this statement of contribution by Xander van der Burgt.

Name, email address	**Signature**	**Date**
Prof.em. Dr. David M. Newbery Institute of Plant Sciences University of Bern, Switzerland david.newbery@ips.unibe.ch	D.McC.Newbery	11 Sept, 2017

Paper 3. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Burgt, X.M. van der; Eyakwe, M.B.; Newbery, D.M.; 2007. *Englerodendron korupense* (Leguminosae-Caesalpinioideae), a new tree species from Korup National Park, Cameroon. Adansonia 29 (1): 59 – 65. http://sciencepress.mnhn.fr/en/periodiques/adansonia/29/1/englerodendron-korupense-fabaceae-caesalpinioideae-une-nouvelle-espece-d-arbre-du-parc-national-de-korup-au-cameroun

Background: The paper describes a new species in the genus *Englerodendron,* from Korup National Park.

Contribution of the candidate: I, Xander van der Burgt, took the leading role in this study and in the preparation of the manuscript. I made the following contributions:

- I determined the species to be new to science.
- I wrote the paper and the description of the new species.
- I studied all cited herbarium specimens and prepared the distribution map.
- I generated the conservation assessment for the species.
- I collected flowering and fruiting type specimens of the new species.
- I communicated with the journal and addressed the comments of the reviewers.

Statement of contribution: As co-authors of the listed paper, we hereby endorse this statement of contribution by Xander van der Burgt.

Name, email address	**Signature**	**Date**
Moses Eyakwe moseseyakwe@yahoo.com		01/09/2017
Prof.em. Dr. David M. Newbery Institute of Plant Sciences University of Bern, Switzerland david.newbery@ips.unibe.ch	D. McC. Newbery	11 Sept, 2017

Paper 4. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Mackinder, B.A.; Burgt, X.M. van der; 2009. *Berlinia korupensis* (Leguminosae - Caesalpinioideae), a new tree species from Cameroon. *Kew Bulletin* 64: 129 – 134. https://doi.org/10.1007/s12225-009-9100-z

Background: The paper describes a new tree species of *Berlinia* from Korup National Park in Cameroon.

Contribution of the candidate: I, Xander van der Burgt made the following contributions:

- I collected all herbarium specimens and ecological data for the new species.
- I wrote the section on the habitat and ecology of the new species.
- I prepared a map showing a group of *Berlinia korupensis* trees.

Statement of contribution: As first author of this paper, I, Barbara Mackinder, hereby endorse this statement of contribution to the paper by Xander van der Burgt.

Name, institute, email address	**Signature**	**Date**
Dr. Barbara Mackinder Royal Botanic Garden Edinburgh B.Mackinder@rbge.ac.uk	B. Mackinder	30 July 2017

Paper 5. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Burgt, X.M. van der; Eyakwe, M.; 2010. Searching for undescribed large tree species in the rainforests of Korup National Park, Cameroon. In: Burgt, X.M. van der; Maesen, J. van der; Onana, J.-M. (eds.) 2010. Proceedings of the 18th AETFAT Congress, Yaoundé, Cameroon. Pp. 741 – 747. http://shop.kew.org/systematics-and-conservation-of-african-plants-proceedings-of-the-18th-aetfat-congress-12455

Background: The paper refers to the discovery of 11 undescribed Detarioideae tree species in the study area in Korup National Park in recent years, by Xander van der Burgt and various other researchers. Reasons are discussed why these tree species were not discovered earlier.

Contribution of the candidate: I, Xander van der Burgt, took the leading role in this study and in the preparation of the manuscript. I made the following contributions:

- I wrote the paper.
- I determined the reasons why these tree species were not discovered earlier.
- I prepared the map illustrating the rarity of two of these new species.
- I communicated with the publisher and addressed the comments of the reviewers.

Statement of contribution: As co-author of the listed paper, I hereby endorse this statement of contribution by Xander van der Burgt.

Name, email address	**Signature**	**Date**
Moses Eyakwe moseseyakwe@yahoo.com		01|09|2017

Paper 6. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Burgt, X.M. van der; Eyakwe, M.; Motoh, J.; 2012. *Gilbertiodendron newberyi* (Leguminosae: Caesalpinioideae), a new tree species from Korup National Park, Cameroon. *Kew Bulletin* 67 (1): 51 – 57. https://doi.org/10.1007/s12225-012-9345-9

Background: The paper describes a new species in the genus *Gilbertiodendron,* from Korup National Park.

Contribution of the candidate: I, Xander van der Burgt, took the leading role in this study and in the preparation of the manuscript. I made the following contributions:

- I determined the species to be new to science.
- I wrote the paper and the description of the new species.
- I studied all cited herbarium specimens and prepared the distribution map.
- I generated the conservation assessment for the species.
- I prepared the line drawing.
- I collected flowering and fruiting type specimens of the new species.
- I recorded some groups of trees, of two *Gilbertiodendron* species, and prepared maps.
- I communicated with the journal and addressed the comments of the reviewers.

Statement of contribution: As co-author of the listed paper, I, Moses Eyakwe, hereby endorse this statement of contribution by Xander van der Burgt.

Name, institute, email address	**Signature**	**Date**
Moses Eyakwe moseseyakwe@yahoo.com		01/09/2017

Jackson Motoh, one of the co-authors, has deceased.

Paper 7. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Burgt, X.M. van der; Poundje, M.; Sene, O.; 2014. *Cryptosepalum korupense* sp. nov. (Leguminosae – Caesalpinioideae), a tree species from the Southwest Region in Cameroon. Adansonia sér. 3, 36 (1): 73 – 81. https://doi.org/10.5252/a2014n1a7

Background: The paper describes a new species in the genus *Cryptosepalum,* from Korup National Park.

Contribution of the candidate: I, Xander van der Burgt, took the leading role in this study and in the preparation of the manuscript. I made the following contributions:

- I determined the species to be new to science.
- I wrote the paper and the description of the new species.
- I studied all cited herbarium specimens and prepared the distribution map.
- I generated the species conservation assessment.
- I prepared the line drawing.
- I collected flowering and fruiting type specimens of the new species.
- I prepared a map showing a group of individual trees.
- I communicated with the journal and addressed the comments of the reviewers.

Statement of contribution: As co-authors of the listed paper, we hereby endorse this statement of contribution by Xander van der Burgt.

Name, email address	**Signature**	**Date**
Maguy Poundje IRAD - National Herbarium of Cameroon Yaoundé, Cameroon poundjemaguy@yahoo.fr		10 Sept 2017
Olivier Sene IRAD - National Herbarium of Cameroon Yaoundé, Cameroon olivier_sene@yahoo.		29 Aug 2017

Paper 8. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Burgt, X.M van der; Mackinder, B.A.; Wieringa, J.J.; Estrella, M. de la; 2015. The *Gilbertiodendron ogoouense* species complex (Leguminosae – Caesalpinioideae), Central Africa. *Kew Bulletin* 70: 29; 42 pp. https://doi.org/10.1007/s12225-015-9579-4

Background: The paper describes a complex of 14 related tree species in the genus *Gilbertiodendron,* occurring in Africa from Cameroon to Angola (Cabinda). Eight species are newly described in the paper, and one species is reinstated.

Contribution of the candidate: I, Xander van der Burgt, took the leading role in this study and in the preparation of the manuscript. I made the following contributions:

- I determined 7 species to be new to science and one species to be reinstated.
- I wrote the introduction and the key to the 14 species.
- I produced the comparative table of morphological characters.
- I wrote all 14 species descriptions.
- I studied all cited herbarium specimens and prepared all 14 distribution maps.
- I generated all 14 species conservation assessments.
- I worked with the botanical artist, who prepared 12 line drawings.
- I prepared 2 line drawings.
- I collected flowering and fruiting type specimens of one of the new species.
- I mapped two groups of *Gilbertiodendron* trees and prepared maps for the manuscript.
- I communicated with the journal and addressed the comments of the reviewers.

Statement of contribution: As co-authors of the listed paper, we hereby endorse this statement of contribution by Xander van der Burgt.

Name, institute, email address	**Signature**	**Date**
Dr. Barbara Mackinder Royal Botanic Garden Edinburgh b.mackinder@rbge.ac.uk	B. Mackinder	30 July 2017
Dr. Jan Wieringa Nationaal Herbarium Nederland jan.wieringa@naturalis.nl		28 July 2017
Dr. Manuel de la Estrella Royal Botanic Gardens, Kew mdelaestrella@gmail.com		29 July 2017

Paper 9. Statement of contribution

Paper to be considered as part of the PhD by Published Work:
Burgt, X.M van der; 2016. Didelotia korupensis and *Tessmannia korupensis* (Fabaceae – Caesalpinioideae), two new tree species from Korup National Park in Cameroon. Blumea 61: 51 – 58. https://doi.org/10.3767/000651916X691402

Background: The paper describes two new Detarioideae tree species from Korup National Park in Cameroon.

Contribution of the candidate: I, Xander van der Burgt, am the single author of this paper:

- I determined the two species to be new to science.
- I compared the morphological characters of both species with their morphologically nearest relative.
- I wrote the paper, including the two species descriptions.
- I studied all cited herbarium specimens and prepared the two distribution maps.
- I generated the two species conservation assessments.
- I prepared the two line drawings.
- I took all photos of the two new species.
- I collected all flowering and fruiting specimens of both new species.
- I mapped a group of 43 *Tessmannia korupensis* trees and prepared a map for the manuscript.
- I communicated with the journal and addressed the comments of the reviewers.