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Endemism and geographic distribution of African Thismiaceae

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Background and aim – The occurrence of the enigmatic plant family Thismiaceae has never been characterized in detail, but appears to be focused in three vegetation types. This study used data from the literature, in tandem with detailed new field data from Cameroon, to document, map, and predict potential distributions of Thismiaceae species across Africa, and relate their occurrence to features of climate.
Methods – We reviewed known occurrences of Thismiaceae species across Africa; in Cameroon, Thismiaceae occurrences were studied in 22 1-ha plots (220 000 m^2), at lowland, sub-montane, and montane sites in evergreen forest, semi-deciduous forest, and woody and grassland savannah vegetation types. Assembling known occurrences from across the continent, ecological niche modeling was used to map potential geographic ranges of African Thismiaceae under present-day climate conditions across Africa.
Results and discussion – In Cameroon fieldwork, 338 individual Thismiaceae were recorded, corresponding to eleven species of *Afrothismia*. The most occupied vegetation type for Thismiaceae was sub-montane forest. Occurrence of Thismiaceae seems to depend principally on rainfall, as most specimens were recorded in areas with high rainfall, about six weeks after the first rains, toward the middle or end of the rainy season. This pattern seems to be consistent across all of the species. Soil analyses shows that *Afrothismia* was most frequent under conditions of low calcium (0.09–15.21 %) and pH of 3.58–6.16. Niche models predicted that additional Thismiaceae populations may be discovered at high-rainfall sub-montane forest sites in Democratic Republic of Congo, Rwanda, Tanzania, and Kenya. Across tropical Africa, the Thismiaceae comprise 22 species in two genera (twenty *Afrothismia* and two *Oxygyne*), recorded from seven countries. Many of these species are narrowly endemic to one or a few specific sites, so that detailed knowledge of distributional patterns is important for their conservation.

Key words – Africa, biodiversity assessment, Cameroon, endemic, lowland forest, semi-deciduous forest, sub-montane forest, Thismiaceae.

INTRODUCTION

Based on previous studies (Stone 1980, Thiele & Jordan 2002, Cheek 2003, Maas-van de Kamer 2003, Franke et al. 2004, Franke 2004, Sainge & Franke 2003, Sainge et al. 2005, Cheek & Jannerup 2005, Cheek 2006, 2009, Woodward et al. 2007, Merckx 2008, Yahara & Tsukaya 2008, Dauby et al. 2007, Sainge et al. 2013), it is clear that range restriction and endemism in the Thismiaceae are high, which is emphasized each time a new species of this family is discovered. The geographic distribution of the family extends across North and South America, Africa, Asia, Australia, and New Zealand, with species assorted among five genera. The genus *Thismia* Griff. occurs in rainforest and sub-montane forest in South America and Asia, with some species in temperate forests in Australia, New Zealand, Japan, and parts of the midwestern USA. *Haplothismia* Airy Shaw is known from the Western Ghats, India. *Afrothismia* (Engl.) Schltr. is an African genus occurring in lowland rainforest, semi-deciduous, and sub-montane forest. *Oxygyne* Schltr. is known from tropical Africa (Cameroon) and Asia (Japan), whereas *Tiputinia* Berry & Woodward is known only from Amazonian parts of Ecuador (Schlechter 1906, Jonker 1938, Maas-van de Kamer 1998, Woodward et al. 2007, Yahara & Tsukaya 2008, Merckx et al. 2006, Merckx 2008, Sainge 2012).

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Three vegetation types (lowland rain forest, sub-montane forest, and semi-deciduous forest) form the largest remaining natural landscapes in tropical Africa that remain poorly characterized in terms of biodiversity. The Thismiaceae are an excellent example, occurring at lowland rain forest, sub-montane, and semi-deciduous forest, with 63–90 species known globally (Franke 2007, Sainge 2012, Merckx et al. 2013, Sainge et al. 2013), and 22 species known from Africa; most are known from restricted areas, and often from type specimen series only, leading to their hyper-endemism at specific sites. Such narrowly endemic species are likely to be more susceptible to disturbance, population loss, and extinction (Borokini 2014), and are probably particularly vulnerable to climate change. The distribution and diversity of the family across Africa have never been summarized.

The Thismiaceae are monocotyledonous herbs; molecular studies (Merckx 2008) distinguished them as a separate clade from the Burmanniaceae. Thismiaceae, like most mycoheterotrophic plants (MHP), do not photosynthesize, but rather obtain nutrients from root fungi (Leake 1994), termed arbuscular mycorrhizal fungi (Franke 2007). The Thismiaceae, being a small group, form < 1 % of plant diversity in the forests they inhabit (Beentje 1996). Their abundance, diversity, and distribution appear to depend on seasonality of rainfall, forest type, elevation, and forest canopy structure (Sainge 2012); as such, the family has been considered as a good indicator of pristine and/or refugial forest (Cheek & Williams 1999).

African Thismiaceae (*Afrothismia* and *Oxygyne*.) are known to have populations in Cameroon (Engler 1905, Schlechter 1906, Jonker 1938, Cheek & Ndam 1996, Cheek & Williams 1999, Maas-van de Kamer 2003, Franke et al. 2004, Franke 2004, Sainge et al. 2005, Cheek 2006, Franke 2007, Merckx 2008, Sainge et al. 2010, 2013, Sainge 2012), Gabon (Dauby et al. 2007), Kenya (Cheek 2003), Malawi (Cheek 2009), Tanzania (Cheek & Jannerup 2005), Uganda (Cowley 1988), and Nigeria (Cowley 1988). However, few of these studies have been carried out across different elevations and vegetation types (Sainge 2012), which limits the degree to which their results can be interpreted as measuring species diversity.

In this study, we evaluated species composition, diversity, and endemism of the family at sites in different vegetation types across Cameroon, with comparisons across tropical Africa. We also explore which environmental variables influence Thismiaceae occurrence in tropical forests. This study reviews and updates the species list of African Thismiaceae, particularly for Cameroon. We assess species diversity and abundance at different elevations and vegetation types, and attempt to characterize ecological relationships of Thismiaceae to rainfall patterns, woody plant communities, and soil characteristics.

BACKGROUND: TAXONOMY AND NATURAL HISTORY

The geographic range and conservation status of the Thismiaceae are poorly described. This gap is likely due to their cryptic nature, which allows them to be visible only in the wet season (Jonker 1938, Franke et al. 2004, Sainge 2012), making acquisition of new data difficult. In Cameroon, this family has been studied by Sainge and collaborators since 2000 at different elevation and vegetation types (lowland, sub-montane, and montane elevations; evergreen, semi-deciduous, woody/grassland savannah, and degraded forest types; Sainge 2012). Sainge carried out a broader-scope, opportunistic, but unsuccessful survey of populations of this family in the dry seasons of 2009 and 2010 in different vegetation types across Cameroon; instead, a small population of the mycoheterotrophic Triuiridaceae (*Sciaphilia ledermannii* Engl.) was documented in Korup National Park, Cameroon. Their inconspicuous and ephemeral nature makes for the poor taxonomic documentation, described below.

The genus *Afrothismia* was established in 1906 by German botanist R. Schlechter, based on *A. winkleri* (Engl.) Schltr. This species had been collected in 1904 by the German missionary H. Winkler near the village of Muea (nicknamed 'Neu Tegel'; Engler 1905). It was described as *Thismia winkleri* Engler. In 1905, Schlechter visited Cameroon and collected *T. winkleri* Engl. and another new species from Moliwe; he moved *T. winkleri* to *Afrothismia* along with *A. pachyantha* Schltr. In 1996, S. Cable collected *A. winkleri* around the Mt Cameroon area in Southwestern Cameroon (specimen *Cable* 2830 (K); see Cable & Cheek 1998).

In 1940, W.J. Eggeling collected a variety, *A. winkleri* var. *budongensis* Cowley from Uganda (Cowley 1988). *Afrothismia zambesiaca* Cheek was described in 2009 from a dehydrated specimen collected by E. Mendonca and Wild in Malawi in 1955; *A. insignis* Cowley was collected by Polhill and Paulo in Tanzania in 1962, and Cowley cited *A. winkleri* records from Cameroon and Nigeria (Cowley 1988). The *Afrothismia winkleri* from Nigeria, turned out to be *Afrothismia hydra* (Franke 2007). In 1970, J.L. Amiet collected another new species from Mount Kala, 20 km west of Yaoundé, Centre Region, Cameroon, while studying butterflies; this specimen was preserved in alcohol and kept at the National Herbarium of Cameroon (YA) until 2006, when it was described as *A. amietii* Cheek (Cheek 2006). In 1995, A.J. de Winter collected another new species from Nyandong, in southern Cameroon, which was described as *A. gesnerioides* Maas (Maas-van de Kamer 2003). In 2002, S. Baer collected the first *Afrothismia* record for Kenya, which was described as *A. baerae* Cheek (Cheek 2003). In 2003, P. Jannerup, studying the vegetation of the Eastern Arc Mountains of Tanzania, collected a new *Afrothismia*, which was described as *A. mhoroana* (Cheek & Jannerup 2005).

Between 2000 and 2005, while studying the mycoheterotrophic plants of southwestern Cameroon as part of Franke's Ph.D. work, T. Franke and M. Sainge came across five new species of *Afrothismia*, of which four have been described fully: *A. foetheriana* Franke (Franke et al. 2004), *A. saingei* Franke (Franke 2004), *A. hydra* Sainge & Franke (Sainge & Franke 2003), and *A. korupensis* Sainge & Franke (Sainge et al. 2005). The fifth species is pending description because the alcohol-preserved material is in bad condition (*Afrothismia* sp. b). G. Dauby, a Belgian botanist, discovered another new *Afrothismia* in Gabon, described as *A. gabonensis* G.Dauby & T.Stévart (Dauby et al. 2007). Dauby et al. (2007) reported a further unidentified species of *Afrothismia*, *A. insignis* from Gabon collected by C. Wilks. In 2011, Sainge collected three new species of *Afrothismia*: *A. fungiformis* Sainge & Kenfack, *A. pusilla* Sainge & Kenfack (Sainge et al. 2013), and *Afrothismia* sp. a. Sainge later received a photograph of another *Afrothismia* that had been collected by Boupoya A. et al. (under number 674) in Gabon, and sent to Merckx for identification, which turned out to be another new species (*Afrothismia* sp. c).

The genus *Oxygyne* was also established by Schlechter after his trip to Cameroon in 1905. Besides collecting *A. winkleri* and *A. pachyantha*, Schlechter also collected specimens that he described as *O. triandra* Schltr. in 1906. Later, in 1992, while studying the vegetation of Mt Cameroon area, D. Thomas and M. Cheek collected another *Oxygyne* around Mt Etinde, not far from the type locality of *O. triandra* Schltr., but this species remains undescribed (Cheek & Willams 1999). This genus ranges broadly to Asia, with three species in Japan: *O. hyodoi* Abe & Akasawa, *O. shinzatoi* (Hatusima) Abe & Akasawa (Abe & Akasawa 1989), and *O. yamashitae* Yahara & Tsukaya (Yahara & Tsukaya 2008).

MATERIALS AND METHODS

Study sites at local scales

Our field work was concentrated in southern Cameroon, at the following sites: Korup National Park; Mt Etinde; Mt Kupe (Kupe III and Mbulle village); Mbembe Forest Reserve; Mt Oku; Transformation Reef Cameroon (TRC), Forestry Management Unit 11001, Bakogo village; Mefou National Park; PALISCO, Forestry Management Unit 10041, Mindourou; Ngovayang Massif above Mvile village; Mt Kala; and Diongo Community Forest (fig. 1, table 1; Ekwoge et al. 1999, Waterloo et al. 2000, Wanji 2001, Besong 2003, Suchel 1972, Chuyong et al. 2004, Feteke 2004, Bakoh 2008, Ndenecho 2010). In all, 22 plots of 1 ha each were established at lowland, sub-montane, and montane elevations (100–3 000 m) in evergreen, semi-deciduous, woody/grassland savannah, and degraded forests. Plots were situated at random within sites, and measured 40 m × 250 m, although opportunistic sampling outside plots yielded a few additional detections.

Since Thismiaceae, like most mycoheterotrophic plants, flower and fruit in the wet season (Jonker 1938, Franke 2004, Sainge et al. 2005), field studies were carried out in April–September 2011, with most plots visited 2–3 times: 6 weeks after the first rains, in the middle of the rainy season, and toward the end of the rains. In each plot, all woody plants ≥10 cm in diameter within each 10 m × 10 m quadrat where Thismiaceae were recorded were identified to species, and soil samples collected for nutrient analysis; such soil and woody plant sampling was fully dependent on detection of Thismiaceae. All Thismiaceae records were geo-referenced using a GPSmap 60CSx GPS unit. Numbers of individuals were recorded by species, and samples of each species collected and stored in both 70 % alcohol and silica gel; high-quality pictures of each species were taken using a Canon PowerShot SD1400 IS digital camera.

To assess influences of soil characteristics on Thismiaceae, random soil samples were collected in each of the study plots (except in Korup National Park and Mount Etinde, because samples from these sites were contaminated in the process of transportation), amounting to 20 soil samples. Since Thismiaceae grow superficially, with roots not extending below 20 cm depth, soil samples were taken at depths of 0–20 cm at each plot. Soil physical and chemical properties (pH, C, N, P, Ca, K, Mg, Fe, Al, and CEC) were characterized at the Soil Science Laboratory, IITA-IRAD Nkolbisson, Yaoundé (Sainge 2012, Sainge et al. 2013).

Herbarium specimens were studied and compared at the Missouri Botanical Garden (MO), National Herbarium of Cameroon (YA; Yaoundé), and Southern Cameroon Herbarium (SCA; Limbe). Specimens from these surveys (Sainge 2012, Sainge et al. 2013) were deposited at YA and MO. Specimens from the broader work program were deposited in B, BR, K, and WAG (herbarium acronyms follow Thiers continuously updated).

Broad-scale analyses

To provide a broader-scale perspective and understand major environmental factors affecting occurrence of African Thismiaceae, we assembled occurrence data for as many species as possible. In the end, 17 of 22 African species of Thismiaceae were included in these geographic-environmental analyses: *A. amietii*, *A. baerae*, *A. foertheriana*, *A. fungiformis*, *A. gabonensis*, *A. gesnerioides*, *A. hydra*, *A. insignis*, *A. korupensis*, *A. mhoroana*, *A. pachyantha*, *A. pusilla*, *A. saingei*, *A. winkleri*, *A. zambesiaca*, *Afrothismia* sp a. and *Oxygyne triandra.* Occurrence data were assembled from the literature and the field surveys described and cited above. Literature providing occurrence records included, for Cameroon (Engler 1905, Schlechter 1906, Jonker 1938, Cheek & Ndam 1996, Cheek & Williams 1999, Maas-van de Kamer 2003, Franke 2004, 2007, Franke et al. 2004, Sainge et al. 2005, 2010, 2013, Cheek 2006, Merckx 2008, Sainge 2012), Gabon (Dauby et al. 2007), Kenya (Cheek 2003), Malawi (Cheek 2009), Nigeria (Cowley 1988), Tanzania (Cowley 1988, Cheek & Jannerup 2005) and Uganda (Cowley 1988).

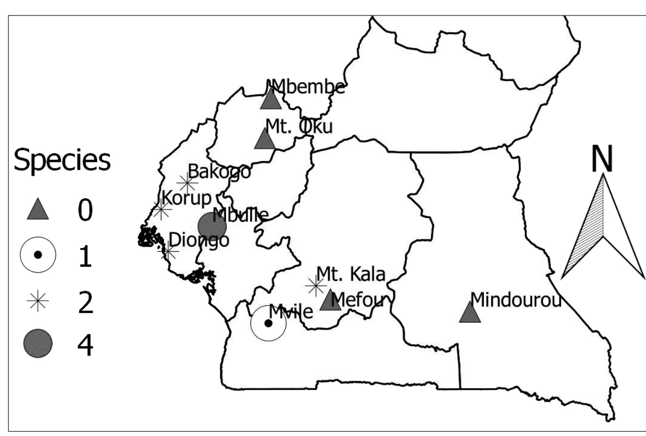

Figure 1 – Sites sampled for Thismiaceae across Cameroon, showing species richness documented at each site. Kupe III Village (Mt Kupe, close to Mbulle Village; 0 species found) is not represented on this map.

Table 1 – Summary of sampling sites, geographical coordinates, altitude, forest types and list of species in each plot where Thismiaceae were studied across Cameroon.
A. = *Afrothismia*.

Site	Plot	Geographical coordinates	Altitude (m)	Species	Forest type	Rainfall (mm)	Source for rainfall
Korup National Park	1	5.06829°N 8.85671°E	176	*A. hydra*	lowland	≥ 5 000	Chuyong et al. (2004)
	2	5.06390°N 8.85696°E	144	*A. hydra*			
	3	5.06822°N 8.85759°E	181	*A. hydra* *A. korupensis*			
Diongo Community Forest	1	4.39144°N 8.97154°E	158	*A. hydra*	lowland	≥ 4 500	Ekwoge. et al. (1999)
	2	4.39667°N 8.97115°E	236	*A. hydra* *A. foertheriana*			
	3	4.39142°N 8.97157°E	178	*A. foertheriana*			
Bakogo	1	5.49548°N 9.28052°E	258	*A. amietii* *A. korupensis*	lowland	3 500	Besong (2003)
Mt. Kupe, Kupe III Village	1	4.77563°N 9.68125°E	803	–	sub-montane	4 891	Suchel (1972)
	2	4.77596°N 9.68289°E	799	–			
Mt. Kupe, Mbulle Village	1	4.79372°N 9.67672°E	921	*A. fungiformis*	sub-montane	4 891	Suchel (1972)
	2	4.79212°N 9.67793°E	966	*A. gesnerioides* *A. saingei* *A. winkleri*			
Mount Kala	1	3.83795°N 11.34926°E	956	*A. pusilla*	sub-montane	1 500–2 000	Yerima & Van Ranst (2005)
	2	3.83518°N11.34917°E	1 093	*Afrothismia* sp. d			
Mount Mvile, Mvile Village	1	3.22585°N 10.58066°E	544	*Afrothismia* sp. a	sub-montane	2 500	Waterloo et al. (2000)
	2	3.23412°N 10.58375°E	689	*Afrothismia* sp. a			
Mefou Proposed N.P	1	3.61793°N 11.58195°E	670	–	semi-deciduous	2 000	Bakoh (2008)
	2	3.62141°N 11.57573°E	680	–			
Mbembe forest reserve Buku-up	1	6.86144°N 10.62401°E	462	–	semi-deciduous	2 000–3 000	Wanji (2001)
	2	6.88389°N 10.61010°E	351	–			
Mount Oku	1	6.22025°N 10.52755°E	2 581	–	semi-deciduous	3 050	Ndenecho (2010)
	2	6.22366°N 10.52193°E	2 350	–			
PALISCO; FMU 10041; Mindourou	1	3.42229°N 13.82726°E	729	–	semi-deciduous	1 650	Feteke (2004)
	2	3.43568°N 13.77988°E	736	–			

To provide a first exploration of the climatic niche and potential geographic distribution of African Thismiaceae, we developed simple climatic niche models in Maxent version 3.3.1 (Philips et al. 2006). Because the data were sparse, we kept our data manipulations to a minimum, and fit models on default settings, except for specifying 10 random, bootstrap replicate models. We used the median of the outputs of those models for exploration and interpretation. We used the variable jackknife procedure (Peterson & Cohoon 1999) implemented in Maxent to explore relative importance of different environmental variables.

We examined environmental variables summarizing present-day climate conditions from WorldClim "(10' or 17 km spatial resolution)" (19 bioclimatic variables from Hijmans et al. 2005, of which variables: mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter were omitted owing to known spatial artefacts). Because Thismiaceae are generally poorly known, only small numbers of occurrence records exist for individual species, so we were forced to lump species into two aggregate occurrence data sets, one for each genus; only for *Afrothismia* were data sufficient to permit calibration of rigorous models.

RESULTS

Field surveys

In all our field surveys, we recorded 338 individual stems of Thismiaceae across 22 ha of sampling, representing eleven *Afrothismia* species. Numbers of species per plot ranged 0–4, with Mbulle village being the richest, with four species (fig. 1). No Thismiaceae were recorded at Mbembe Forest

Table 2 – Summary of occurrence of Thismiaceae taxa in Africa and preliminary IUCN statuses recovered from literature (Onana 2011).
A. = *Afrothismia*. Species not included in ecological niche models for lack of occurrence data are indicated with asterisks.

Species	Countries of presence	IUCN Status	Herbarium vouchers	Reference
A. hydra Sainge & Franke	Cameroon, Nigeria	Vulnerable	*Sainge* 910 (holotype: YA; isotypes: B, K) *Franke* 02/027 (isotype: B)	Sainge & Franke (2005)
A. korupensis Sainge & Franke	Cameroon	Vulnerable	*Sainge* 991 (holotype: YA; isotype: B)	Sainge & Franke (2005)
A. amietii Cheek	Cameroon	Endangered	*Amiet* 20346/HNC (holotype: YA) *Sainge* 2021 (MO); *Sainge* 2632 (YA)	Cheek (2007)
A. saingei Franke	Cameroon	Critically Endangered	*Sainge* 1053 (holotype: YA; isotypes: B, BR) *Sainge* 2638 (YA) *Sainge* 2757 (MO)	Franke (2004)
A. foertheriana Franke, Sainge & Agarer	Cameroon	Vulnerable	*Franke & Sainge* 02/030 (holotype: YA; isotypes: B, WAG)	Franke et al. (2004)
A. gesnerioides Maas	Cameroon	Vulnerable	*de Winter* 91 (holotype: WAG) *Sainge* 1002 (isotype: B) *Sainge* 1618 & 2756 (MO)	Maas (2003)
A. pachyantha Schltr.	Cameroon	Probably extinct in the wild	*Schlechter* 15789 (holotype: B)	Schlechter (1906)
A. winkleri (Engl.) Schltr.	Cameroon	Vulnerable	*Winkler* 225 (holotype: B) *Cable* 2830 (K) *Franke* 02/034 (B) *Sainge* 1601 & 1263 (MO) *Sainge* 2637 & 2758 (YA)	Schlechter (1906)
A. fungiformis Sainge & Kenfack	Cameroon	Critically Endangered	*Sainge* 2639 (holotype: YA) *Sainge* 2760 (isotype: MO)	Sainge & Kenfack (2013)
Afrothismia sp. a	Cameroon	Not Evaluated	*Sainge* 2739 (holotype: YA)	Sainge pers. obs.
A. pusilla Sainge & Kenfack	Cameroon	Critically Endangered	*Sainge* 2827 (holotype: YA; isotype: MO)	Sainge et al. (2013)
Afrothismia sp. b*	Cameroon	Not Evaluated	*Sainge* 1003 (WAG)	Th. Franke & M. Sainge pers. obs.
Afrothismia sp. d	Cameroon	Not Evaluated	*Sainge* 2826	Sainge pers. obs.
A. baerae Cheek	Kenya	Critically Endangered	*Baer* s.n. (holotype: EA; isotype: K)	Cheek (2004)
A. gabonensis Dauby & Stévart	Gabon	Critically Endangered	*Dauby & Kaparidi* 67 (holotype: BRLU) *Dauby* 167 (isotypes: BRLU, LBV, MO, WAG)	Dauby et al. (2008)
Afrothismia sp. c	Gabon	Not Evaluated	*Boupoya, Dauby, Nzabi, Akouangoa* 674 (BRLU, LBV)	Vincent Merckx, KU Leuven, pers. com.
A. mhoroana Cheek & Jannerup	Tanzania	Critically Endangered	*Jannerup & Mhoro* 299 (holotype: K)	Cheek & Jannerup (2006)
A. insignis Cowley	Tanzania	Endangered	*Polhill & Paulo* 1811	Cowley (1988)
A. zambesiaca Cheek	Malawi	Endangered	*Mendonca &Wild* 1066 (holotype: K)	Cheek (2009)
A.winkleri var. *budongensis* Cowley*	Uganda	Endangered	*Eggeling* 4041 (holotype: K)	Cowley (1988)
Oxygyne triandra Schltr.	Cameroon	Probably extinct in the wild	*Schlechter* 15790 (holotype: B)	Schlechter (1906)
Oxygyne sp. nov.*	Cameroon	Data Deficient	K	Cheek & Williams (1999)

Reserve; Mt Oku; Kupe III village; Mefou National Park; or PALISCO, FMU 10041, Mindourou (table 1).

Endemism is high in the Thismiaceae, with almost all species being restricted entirely to one or a few known sites. In the field portion of this study, all species recorded were endemic to Cameroon except *A. hydra*, which is said to occur also in Nigeria (table 2), and all were site-specific, except for *A. korupensis*, which occurs at both Korup National Park and TRC FMU 11001 at Bakogo in South West Region, and *A. hydra* which occurs in Korup National Park and Diongo Community Forest (table 1). However, literature data complete our survey and show that two other species are not site-specific: *A. amietii*, which occurs in TRC FMU 11001 at Bakogo (table 1) and at Mt Kala in Centre Region (Cheek 2006); and *A. gesnerioides*, which occurs in three localities: at Nyandong in South Region (Maas-Van de Kamer 2003), Mt Kupe (Mbulle Village, table 1; and Kupe III Village, Franke 2007), and in Korup National Park in South West Region (table 1).

According to our field survey and to literature data, nine species of Thismiaceae are restricted to the South West Region of Cameroon (*Afrothismia korupensis*, *A. saingei*, *A. foertheriana*, *A. pachyantha*, *A. winkleri*, *A. fungiformis*, *Afrothismia* sp. b, *Oxygyne triandra* and *Oxygyne* sp. nov.). Additionally, three species are found only in the Centre region of the country at Mt Kala (*A. pusilla*, *Afrothismia* sp. d, and *A. amietii*; Cheek 2006, Sainge 2012, Sainge et al. 2013); and the South region is represented by two species of *Afrothismia* (*A. gesnerioides* and *Afrothismia* sp. a; Maas-van de Kamer 2003, Sainge 2012).

Thismiaceae populations occur in rotten leaf litter on the forest floor, with roots of some species penetrating the soil to depths of up to 20 cm. Soil characteristics were as follows: pH 3.58–6.16, Ca 0.09–15.21 %, Mg 0.10–5.13 %, K 0.07–1.04 %, Al 0.00–6.13 %, CEC 4.18–36.93 %, Fe 40.26–314.14 ug/g, Org. C 1.11–13.88 %, N 0.111–1.41 %, C/N 8.94–13.74 %, and P 0.86–38.81 %. In Cameroon, *Afrothismia* prefer ferrallitic, ferrous, ferruginous, and azonal soils (Yerima & Van Ranst 2005, Sainge 2012). Our soil analysis did not reveal any clear correlates of *Afrothismia* occurrences; however, elevated rainfall and low calcium content may favour high abundances of *Afrothismia*.

In Korup National Park, among individuals of *A. hydra*, we noted variation in numbers of tepals and stamens across three populations. In the first population, all individuals had the normal six tepals. The second population included individuals with six tepals and a single individual with ten tepals. In the third population, 90 individuals had six tepals but three individuals had seven tepals. After studying internal structure, we realized that individuals with six tepals had six stamens, those with seven tepals had seven stamens, and those with ten tepals had ten stamens, but these variations did not appear to have any taxonomic significance.

Coexisting plant species

Our investigations across all Cameroon sites where *Afrothismia* was recorded did not show any clear pattern of specific associations between *Afrothismia* and the surrounding plant community. That is, different species of green plants were associated with *Afrothismia* at different sites (electronic appendix 1). In all, 73 tree species ranging from understorey, canopy to emergent layer were recorded coexisting with ten species of Thismiaceae (*A. gesnerioides*, *A. fungiformis*, *A. saingei*, *A. winkleri*, *A. hydra*, *A. korupensis*, *A. foertheriana*, *A, amietii*, *A. pusilla*, and *A*. sp. a) at six sites (electronic appendix 1). Seven other species of mycoheterotrophic plants coexist with Thismiaceae at these sites (electronic appendix 2).

Climatic niche and potential geographic distributions

Jackknife analyses found significant contributions from several bioclimatic variables (annual mean temperature, mean diurnal range, annual precipitation, temperature seasonality, precipitation of wettest month) in delimiting the potential distribution of *Afrothismia* species. Our simple exploratory analysis showed highly suitable areas in Sierra Leone, Liberia, Ivory Coast, Nigeria, Cameroon, Equatorial Guinea, Gabon, Republic of Congo, and Democratic Republic of Congo, with much lower suitability in Guinea, Ghana, Uganda, Tanzania, and Malawi. The predictions corresponded generally to the area classified as the Guineo-Congolian region (White 2001), and isolated montane areas from Malawi to the Indian Ocean coastal belt (fig. 2).

DISCUSSION

Until recently, seventeen species of Thismiaceae were known in tropical Africa: fifteen *Afrothismia* and two *Oxygyne*. Cameroon was known to hold nine species of *Afrothismia* and two species *Oxygyne* (Sainge et al. 2010). At present, 22 species of Thismiaceae are known in Africa, with Cameroon hosting fifteen (table 2); such that Cameroon, and particularly the mountains in South West Region, appears to constitute the centre of diversity for Thismiaceae in Africa. These records may be high in Cameroon thanks to intense sampling, so true diversity patterns of Thismiaceae across Africa can be appreciated only if sampling efforts extend to appropriate montane habitats in Republic of Congo, Democratic Republic of Congo, Equatorial Guinea, Gabon, Kenya, Liberia, Malawi, Nigeria, Rwanda, Sierra Leone, Tanzania, and Uganda. Our results thus agree with Merckx et al. (2013) that some areas in Africa likely remain seriously under-collected, with considerable potential for discovery of new species with more samples.

Our modelling explorations suggest that distributions of African Thismiaceae species are influenced positively by precipitation and wet season. This result is in line with Jonker (1938) and Franke (2004), who concluded that Thismiaceae emerge chiefly in the rainy season. Our results show that submontane vegetation holds the most diverse *Afrothismia* assemblages, with four species recorded in a single locality at Mbulle (*A. winkleri*, *A. saingei*, *A. gesnerioides*, and *A. fungiformis*; fig. 1). Thismiaceae diversity and endemism thus appear to be focused in montane systems (Borokini 2014), which coincides with conclusions for other Thismiaceae in Africa and globally (Maas et al. 1986, Cheek & Jannerup 2005). The lowland forest of Korup National Park, in spite of long-term, intensive searches, holds only two species of Thismiaceae, but achieved highest abundance, with > 90 individuals of *A. hydra* recorded in a single plot. Although no Thismiaceae were collected during this study at Kupe III village, previous studies (Franke 2007, Merckx et al. 2012) have recorded a high number of Thismiaceae on this site.

Ecology and distribution

The Thismiaceae may be widespread in tropical forests, but they are poorly known because little attention is given to them and because they are cryptic. Their strictly seasonal occurrence makes for limited specimen documentation and natural history information. The greatest diversity of Thismiaceae in Africa is found in the forests of Central Africa, with Cameroon harbouring fifteen of the 22 known species in Africa. The greatest concentration of diversity of Thismiaceae worldwide is in the rainforests and sub-montane forests of South America in the Rio de Janeiro area, with seven species known to co-occur locally (Maas et al. 1986, Woodward et al. 2007, Merckx 2008).

In Cameroon, Thismiaceae occur under different ecological conditions, with greatest numbers found in closed sub-montane forest (Sainge 2012, Sainge et al. 2013) and the family is considered to be a good indicator of pristine and/or refugial ecosystems (Cheek & Williams 1999). Like most mycoheterotrophic plants, Thismiaceae are highly "sun-intolerant," growing mostly under canopy trees or heavily shaded understorey trees, such that < 1 % of sunlight reaches them (Chazdon & Fetcher 1984, Lusk et al. 2006). Rainfall patterns greatly influence occurrence of Thismiaceae, as they are collected almost invariably within six weeks after the first rains. Although our soil analysis showed that high rainfall and low calcium levels are generally important factors in the occurrence of *Afrothismia*, at the Diongo and Kupe sites, *Afrothismia* was present in spite of high calcium levels and at Mt Kala, *Afrothismia* was present in spite of low rainfall.

Threats to African Thismiaceae

Primary habitat is being degraded at alarming rates worldwide (Foster 2003), particularly in the Tropics, which prioritizes assembling detailed information on the distribution, habitat, and endemism of Thismiaceae before species are lost. The Thismiaceae face a number of threats, as they occur mostly in unclassified forests that are poorly managed. Even species occurring within protected areas are given less attention, and encroachment for agriculture, logging, and mineral exploration, and occurrence of invasive plant species can threaten their populations.

For example, the type localities of *A. winkleri*, *A. pachyantha*, and *Oxygyne triandra* have been degraded to extensive palm and banana plantations (Moliwe and Muea) in the South West Region of Cameroon. Neither of these species (*A. pachyantha* and *Oxygyne triandra*) has been recorded at those sites for over a century, so they are presumed extinct, with no detections since collection of the type specimen series. Our opportunistic sampling in disturbed habitats has yielded no records of Thismiaceae. Many Thismiaceae sites in non-protected areas, such as Bakogo and Kupe village in

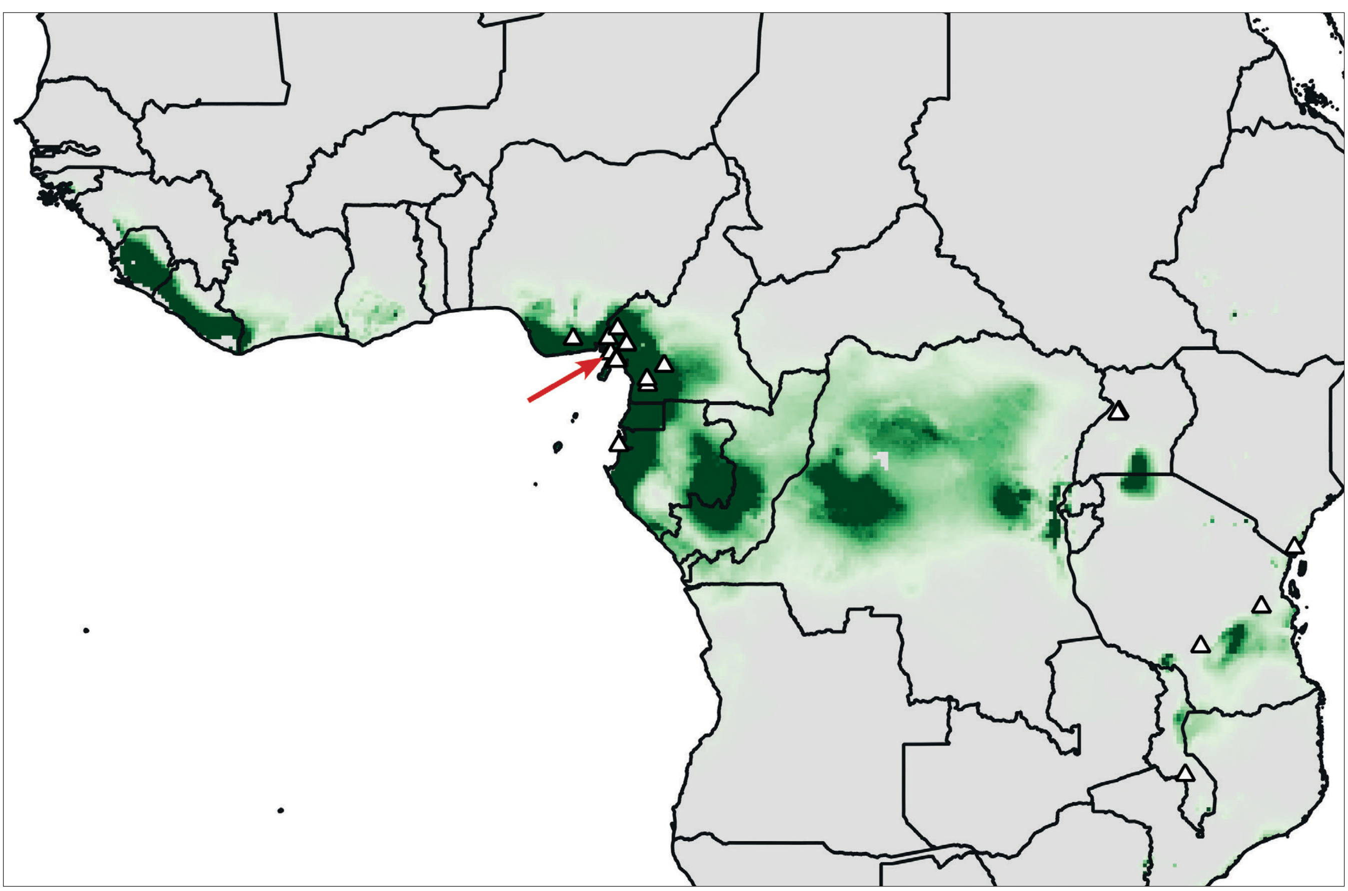

Figure 2 – Potential distribution (shading from pale to dark green) of *Afrothismia* species across Africa according to ecological niche modelling (Maxent). White triangles show the recorded species distribution of *Afrothismia*. Red arrow points to the single record of *Oxygyne*.

Cameroon, are threatened by agricultural encroachment; and the Mt Kala site is threatened by creation of a quarry nearby.

Climate change presents another suite of threats to species that are confined to isolated patches, with restricted and fine-tuned phenology, such as the Thismiaceae. Hence, even minor changes in climate could reduce potential distributional extents of Thismiaceae species dramatically, and may lead to extinctions in the long run. As a parallel example, the golden toad (*Bufo periglenes*) in Costa Rica has apparently gone extinct as a consequence of climate change caused by shifts in local distributions of moisture and cloud cover (Pounds et al. 1999, 2006).

SUPPLEMENTARY DATA

Supplementary data related to this article are available in pdf at *Plant Ecology and Evolution*, Supplementary Data site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data) and consist of the following: (1) tree species documented as coexisting with Thismiaceae at 6 sites across Cameroon; and (2) myco-heterotrophic plant species documented as coexisting with Thismiaceae across Cameroon.

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