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RESEARCH ARTICLE

Flower morphological differentiation and plant-pollinator interactions among sympatric *Aframomum* species (Zingiberaceae) with floral trumpet type in the tropical African rainforest

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Background and aims – Diversification in plant-pollinator interactions based on floral diversity is potentially a mechanism of coexistence in angiosperms. However, besides high floral diversity, some genera seemingly exhibit the same floral type in many of their species. This contradicts some expectations of competitive exclusion. We thus tested on a finer flower morphological scale whether five sympatric *Aframomum* species (61 spp., Zingiberaceae) in southeastern Gabon exhibiting the same general floral type (trumpet) were differentiated, and whether this resulted in different "pollinator niches".
Material and methods – We carried out a detailed survey measuring 18 flower morphological parameters as well as nectar volume (µl) and sugar concentration (% Brix) on five flowers per species and locality. Furthermore, we observed inflorescence phenology and pollinator activity from 8 am to 4 pm for 12 to 50 hours per species and conducted pollinator exclusion experiments.
Key results – This study proves fine-scale flower morphological and resource differentiation within the trumpet floral type. Pollination-relevant parts of the flowers, however, remain constant across species. Our pollinator observations reveal the same broad bee pollinator spectrum for all observed simultaneously flowering sympatric species.
Conclusion – As we could not detect a pollinator-based differentiation in the studied sympatric *Aframomum* species we assume that species boundaries developed randomly by genetic drift during geographic isolation in the past. The trumpet floral type and its pollinator guild, however, were maintained due to similar selection pressures in comparable habitats during isolation and are potentially an advantage for increased pollinator attraction through co-flowering.

Keywords – *Aframomum*; Africa; bee pollination; floral morphology; floral type; Gabon; pollinator sharing; tropics; Zingiberaceae.

INTRODUCTION

Floral divergence and pollinator specialization has driven angiosperm diversification and is potentially a mechanism of angiosperm coexistence (Givnish 2010). Examples of pollinator-driven divergence include *Aquilegia* L. (Ranunculaceae) (Bastida et al. 2009), *Disa* P.J.Bergius (Orchidaceae) (Johnson et al. 1998), and *Salvia* L. (Lamiaceae) (Claßen-Bockhoff et al. 2004; Wester & Claßen-Bockhoff 2007). Specialised plant-pollinator associations lead to a strict separation in pollen transfer, preventing any admixture. The association of plants with certain pollinators and the exclusion of others is reached through e.g. different spur or tube lengths, floral sizes, colours, odours, and divergences in many other floral characteristics.

We can often predict the pollinators of a flower from its floral biology (e.g. colour, scent, reward, opening time, etc.)

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(Ollerton & Watts 2000). This set of floral characteristics is called "pollination syndrome". These specialized plant-pollinator associations ensure optimization of pollen transfer based on a highly differentiated floral morphology optimizing mechanical fit between plant and pollinator (Armbruster et al. 1994; Johnson et al. 1998; Ley & Claßen-Bockhoff 2009). The plant species is either visited by one or several specific pollinators or by the same set of pollinators as its sympatric neighbours but with pollen deposited in a rather specific place on those pollinators – both guaranteeing a rather unique pollen transfer (Grant 1994). The pollinator's floral spectrum, its pollen transfer efficiency, flight radius, and pattern of floral visitation within and among plant individuals and populations shape the patterns of gene flow within and among plant species influencing their genetic differentiation and fitness, e.g. selfing versus outcrossing and/or hybridisation (Lunau 2004).

In contrast to these conspicuous floral radiations (e.g. *Disa*: Johnson et al. 1998; Marantaceae: Ley & Claßen-Bockhoff 2011; Costaceae: Ricklefs & Renner 1994, Specht et al. 2001; *Salvia*: Wester & Claßen-Bockhoff 2007) there are also plant species that exhibit morphologically very similar floral types (see selected groups of species within *Impatiens*: Grey-Wilson 1980; Marantaceae: Ley 2008; *Aframomum*: Ley & Harris 2014). These contradict our expectations of competitive exclusion (either through different pollinator species or mutual pollen incompatibility), or at least suggest a strong possibility of high rates of interspecific pollen transfer. Interspecific pollen transfer is one of the mechanisms underlying potential competition among plants for pollinators by either the interference with conspecific pollen by stigma clogging and during fertilization and/or the reduction of the amount of pollen transferred between conspecific flowers (Morales & Traveset 2008; Moreira-Hernández & Muchhala 2019). Successful interspecific pollen transfer can lead to the dilution of species boundaries, i.e. hybridisation as seen in some Marantaceae (Ley 2008).

Still, morphologically similar flowers with (near-) identical pollinator niches showing synchronized flowering can be at an advantage when the number of pollinators attracted to an area increases at an accelerating rate with an increasing number of flowers (Tachiki et al. 2010). In this case, facilitation of pollination by different species exceeds the negative influence of interspecific plant competition. In some species with morphologically very similar flowers, the flowers might differ in other than morphological traits such as the quality of their rewards (e.g. odour, nectar composition) leading at least to partially different pollinator spectra and thus further species separation (Urru et al. 2010). Due to the rather uniform appearance of these systems at first sight they remain little investigated regarding their current degree of differentiation and their ecological-evolutionary background.

Such a system of a large recent radiation of the same floral type can be found in the species-rich tropical African genus *Aframomum* (61 spp., Zingiberaceae; Dhetchuvi 1996; Harris et al. 2000; Auvray et al. 2010; Zakaria 2013; Harris & Wortley 2018). Its species are broad leaved perennial herbs from the rainforest understorey, gaps, edges, and savannas distributed from Senegal to Madagascar (Dhetchuvi 1996). They form large conspicuous flowers of five different floral types (trumpet, apron, open, short tube, collar) with one single floral type dominating (trumpet) (Ley & Harris 2014). Based solely on morphological characters and the concept of "pollination syndromes" (Ollerton & Watts 2000), first hypotheses about their pollinating species have been pronounced (Ley & Harris 2014).

The dominant floral trumpet type in about 60% of all *Aframomum* species consists of a large pink tubular flower of delicate tissue with a large landing platform and a horizontal to slightly vertical floral entrance with often conspicuous yellow nectar guides (UV patterning is not yet documented) and some variation in size between species (Ley & Harris 2014). Species of this floral type can be found throughout tropical Africa with the centre of species diversity in Cameroon and the Republic of the Congo. Here, many of these species can be found in sympatry in the same habitat (Ley & Harris 2014). This floral type was hypothesized to be pollinated by medium-sized to small bees (Ley & Harris 2014), however, direct field observations are still lacking (except Lock et al. 1977). Due to a lack of genetic studies, there is no evidence of hybridization yet. The fruits of *Aframomum* are large and conspicuously red in colour with many small black seeds and distributed by monkeys (Lekane Tsobgou 2009; Zakaria 2013).

The aim of this study was to reveal the pollination system of five *Aframomum* species with trumpet type flowers, growing in sympatry in the landscape mosaic of forest and savanna in southeastern Gabon. We perform a fine-scale morphological survey of the flowers, direct pollinator observations and pollinator exclusion experiments. For the savanna species *A. alboviolaceum* (Ridl.) K.Schum., we additionally compared floral morphology and pollinator visitation among different sites.

Specifically, we wanted to test 1) whether species exhibiting the same general floral type (trumpet) were differentiated morphologically in certain characters and/or their reward and whether this differentiation may place the species into different "pollinator niches". 2) We further wanted to detect the actual pollinator spectrum of each species through direct pollinator observations. Here, we explicitly tested for pollinator sharing (different species using the same pollinator spectrum, e.g. to increase pollinator attraction) versus pollinator exclusion (different species using a differentiated pollinator spectrum, e.g. to prevent interspecific pollen transfer). 3) Moreover, we wanted to establish the importance of pollinators for fruit set in *Aframomum*. Thus, we conducted pollinator exclusion experiments documenting fruit set in the presence and absence of pollinators.

MATERIAL AND METHODS

Study localities and material

The study was conducted in southeastern Gabon, which is characterized by a mosaic of forest and savanna (Walters 2012). The main study site was at Bakoumba (13°01′E, 1°82′S) in a secondary forest (*Musanga cecropioides* R.Br. ex Tedlie, *Aucoumea klaineana* Pierre) with open glades dominated by Marantaceae, Costaceae, and ferns. Here, four

species of the genus *Aframomum* occur in sympatry (fig. 1, supplementary file 1 table S1 for herbarium specimens). We included a fifth *Aframomum* species (*A. alboviolaceum*) that grows in the adjacent savanna. This latter species was additionally investigated at two distant sites: Franceville (13°54′E, 1°63′S) (savanna predominated by *Hyparrhenia diplandra* (Hack.) Stapf (Poaceae)) and Ossélé (13°86′E, 1°86′S) (savanna dominated by the deciduous shrub *Crossopteryx febrifuga* (Afzel. ex G.Don) Benth.).

At each locality, flowering *Aframomum* species were identified using available identification keys (Koechlin 1964; Dhetchuvi 1996) and comparing own collections with herbarium specimens of the National Herbarium of Gabon in Libreville (LBV) checked by David Harris (Royal Botanic Garden Edinburgh).

Floral phenology, morphology, and resources

Field work was conducted during the peak flowering of *Aframomum* species which is between September/October and December/January (Harris & Wortley 2018). Inflorescence phenology was monitored daily on five to 68 inflorescences of five to 48 individuals per species for 36 days at Bakoumba (15 Oct. – 19 Nov. 2015), for five days at Ossélé (10–15 Aug. 2015), and for 27 days at Franceville (25 Nov. – 20 Dec. 2015). A total of 18 morphological parameters (Ley & Harris 2014; supplementary file 1 table S2, S3) were measured on five flowers (living material) per species and locality with each flower coming from a different individual. We used a calliper with a precision of ± 0.01 cm. In addition, the amount of nectar (µl) and its sugar concentration (% Brix) were measured in the morning on newly opened bagged flowers using a capillary pipette and an Eclipse refractometer.

Pollinator observations

Pollinators were observed in one-hour intervals for 12 to 50 hours per *Aframomum* species and locality between 8 am and 4 pm. Visiting insects were termed pollinators when they entered the tubular flower and came into contact with the reproductive organs (thecae and stylar cavity). The number and respective length of visits of a pollinator to a flower was noted. At the end of each observation period at a locality, a few individuals of each pollinator species were collected for morphological measurements with Optika (size of the head, and thorax & abdomen). Bees were identified by Connal Eardley (Pretoria, South Africa). Due to a scarcity of flowering individuals no pollinators could be observed on *A. longipetiolatum* Koechlin.

Breeding system and fruit set

Natural fruiting was documented on five open and five bagged (pollinator excluded) inflorescences per species (one inflorescence per individual). Fruit set was determined after about one month by dividing the number of fruits produced per inflorescence by the number of flowers produced on each inflorescence multiplied by 100.

Statistical analysis

Morphological dissimilarity among flowers of different *Aframomum* species was studied via a principal component analysis (PCA) using 18 quantitative morphological

Figure 1 – Flowers and nectar guides on the labellum of five *Aframomum* species with trumpet type flowers from savanna (A, B) and forest (C–J) in southeastern Gabon. **A**–**B**. *Aframomum alboviolaceum*. **C**–**D**. *A. hirsutum*. **E**–**F**. *A. sericeum*. **G**–**H**. *A. subsericeum*. **I**–**J**. *A. longipetiolatum*. Scale bars = 1 cm. Photographs by Alexandra C. Ley and Elie Nzigou Doubindou.

Table 1 – Test for significant statistical differences in floral morphology between three PCA groups of five sympatric *Aframomum* species. Results of the linear mixed models and Tukey test among PCA groups: A: *Aframomum longipetiolatum*, *A. sericeum*, *A. subsericeum*, B: *A. hirsutum*, C: *A. alboviolaceum*. Levels of significance: *** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$. For an illustration of measured traits see Ley & Harris (2014).

	Morphological trait	Tukey test			linear mixed model		
		A	B	C	Transformation	χ^2	p
Overall floral size	Length of the labellum	c	b	a	exp	26.975	1.388×10^{-6} ***
	Length of the dorsal petal	b	b	a	none	22.352	1.401×10^{-5} ***
	Length of lateral petal	b	a	a	none	20.857	2.957×10^{-5} ***
	Length of calyx	b	b	a	log	10.160	0.006221 **
	Length of floral tube	b	a	a	log	23.693	7.165×10^{-6} ***
	Elongation of the floral tube	b	c	a	log	23.808	6.762×10^{-6} ***
	Length of the filament	b	b	a	log	16.626	0.0002453 ***
	Length of the style	b	a	a	none	13.544	0.001145 **
Internal organs: size and relative position	Length of style head	b	a	b	exp	12.447	0.001982 **
	Length of thecae	a	a	a	log	0.817	0.6647
	Distance below narrowing of floral tube	a	a	a	none	2.210	0.3312
	Length of opening of pollen sac	b	a	b	none	14.521	0.0007028 ***
	Width of stigmatic cavity	b	a	a	log	14.721	0.000636 ***
	Height of stigmatic cavity	b	c	b	none	13.658	0.001082 **
	Width of arch formed by lateral appendices of the anther	b	b	a	exp	12.486	0.001944 **
	Distance between thecae and labellum surface	a	b	ab	none	7.377	0.025 *
	Length of ovary	b	a	b	none	17.395	0.000167 ***
	Length of epigynale glands	b	a	b	log	12.624	0.001815 **
Resources	Nectar volume per flower (µl)	a	a	a	log	2.915	0.2328
	Nectar sugar concentration (% Brix)	b	b	a	exp	9.2207	0.009948 **

parameters and two nectar traits applying the method prcomp in R v.3.3.2 (R Core Team 2016). To show which traits are behind the group differentiation differences among PCA groups were tested for significance using linear mixed models (R package lme4; Bates et al. 2011) followed by a post-hoc Tukey test (Tukey 1957). Before analyses, traits were visually inspected for normal distribution and log or exponential transformed whenever necessary using PCA groups as fixed and the respective morphological parameter as random factor. To evaluate whether there was a correlation between nectar sugar concentration and nectar volume, a linear regression assay was performed in PAST (Hammer et al. 2001).

RESULTS

Floral morphology and resources

Based on 18 quantitative flower morphological parameters, nectar volume, and sugar concentration the five studied species with trumpet flowers were divided into three groups using principal component analysis (PCA: A, B, and C) (fig. 2) (table 1, supplementary file 1 table S2). The first two axes explained 37% and 24% of the total variance in the data, respectively (supplementary file 1 table S4). PC1 represented traits of floral size (length of calyx, labellum, petals, filament, and style) and PC2 dimensions of inner organs such as stylar head and thecae and their relative position to each other (supplementary file 1 table S5). The PCA grouping was supported by statistically significant differences in floral measurements among groups (table 1, fig. 3). Group A (*A. subsericeum* (Oliv. & D.Hanb.), *A. longipetiolatum*, *A. sericeum* Dhetchuvi & D.J.Harris) and group B (*A. hirsutum* D.J.Harris & Wortley (Pop1), *A. hirsutum* (Pop2)) contained the forest species from Bakoumba, and group C was formed by the individuals of the savanna species *A. alboviolaceum* from the three different localities (fig. 2). Within groups, it was difficult to discern individual species or populations. The three PCA groups formed a continuum along PC1, with forest group A having the largest flowers (length of labellum: ~12 cm), forest group B intermediate-sized flowers (length of labellum: ~9.4 cm), and group C from the savanna the smallest flowers (length of labellum: ~8 cm; fig. 3). Remarkably, forest group B differed markedly along PC2 from forest group A and savanna group C. Individuals of forest group B had the shortest floral tube (~2.8 cm) but

the longest extension of the floral tube (~8.2 cm) and the arc formed by the lateral extensions of the anthers was widest (1.46 ± 0.11 cm) (table 1). Furthermore, the flowers exhibited the largest distance between the thecae and the surface of the labellum (0.68 ± 0.08 cm) and the shortest ovary. The lowest nectar sugar concentration (34 ± 4.6 %) was found in individuals of savanna group C (compared to 37 to 41% in the forest species; fig. 3D, supplementary file 1 table S2).

There was considerable intraspecific variation within the savanna species *A. alboviolaceum* (supplementary file 1 fig. S1). Floral size and nectar sugar concentration varied greatly between different localities (supplementary file table S3). Flowers of *A. alboviolaceum* at Ossélé were much smaller than at Bakoumba and Franceville and had the highest nectar sugar concentration of the savanna populations (~37%; supplementary file 1 table S3).

The colour variation was independent of PCA groups ranging from white purple (*A. alboviolaceum*, *A. longipetiolatum*, *A. sericeum*) to bright purple (*A. hirsutum* (Pop1), *A. hirsutum* (Pop2)) and dark purple (*A. subsericeum*) (fig. 1, supplementary file 1 table S2). The same was true for nectar volume. It was largest in *A. longipetiolatum* (13.3 ± 2.51 µl) and smallest in *A. hirsutum* (Pop1) (4.6 ± 1.8 µl) (supplementary file 1 table S2, fig. 3C). There was a negative correlation between nectar volume and sugar concentration (linear regression test, p value = $1.16 \times 10^{-8} < 0.001$). Yellow nectar guides on the labellum at the floral entrance were present in all species (fig. 1).

Inflorescence and flower longevity

Inflorescences of the five *Aframomum* species produced one (*A. subsericeum*) to up to 20 (*A. hirsutum*) flowers (supplementary file 1 table S2). The life of an *Aframomum* flower lasted, independent of species, one day from about 8 am till the afternoon. Only in the savanna species, the rim of the floral tube wilted a bit earlier in the afternoon at around 2 pm instead of after sunset as in the forest species. One to three flowers per inflorescence opened every or every second to third day (supplementary file 1 tables S6–S8). Thus, the length of flowering of an inflorescence varied between species lasting from 1 to 3 days to 3 to 4 weeks (supplementary file 1 tables S6–S8). Through simultaneous blooming of several inflorescences per species and population there were always > 5 flowers open per species at our study localities (supplementary file 1 tables S6–S8).

Plant-pollinator interaction

The study of the pollinator community of the five *Aframomum* species revealed about 11 different pollinator species altogether. This included eight species from two hymenopteran orders (Apidae, Halictidae), a fly (Diptera), and two species of butterflies (table 2, for specimens refer

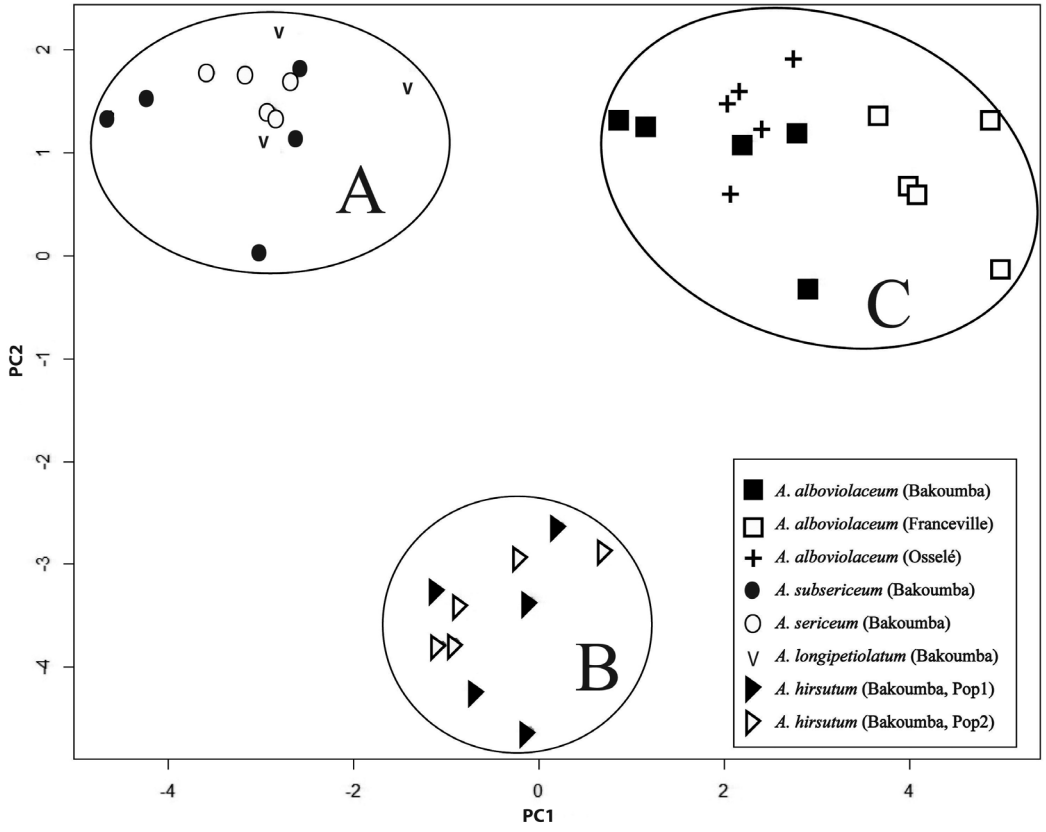

Figure 2 – PCA (principal component analysis) of 18 morphological parameters and two nectar traits in three to five individuals of five *Aframomum* species (Zingiberaceae) from southeastern Gabon.

Table 2 – List of pollinators observed on the five studied *Aframomum* species (Zingiberaceae) and average values (cm) of different measures of head, thorax and abdomen, and proboscis. Small black insects Bakoumba include: *Lipotriches* (Trinomia) sp.1, *Pseudapis* sp.1, and *Lasioglossum* sp.2; small black insects Ossélé include: *Braunsapis leptozonia* (Vachal, 1909) and *Meliponula ferruginea* (Lepeletier, 1841). Lepidoptera sp.1: Erebidae (Noctuoidea) cf.; Lepidoptera sp.2: *Leptotes* sp. (Lycaenidae) cf. L = length of head, W = width of head.

Order	Species	Number of specimens investigated	Head (cm)		Thorax and abdomen (cm)	Proboscis (cm)
			L	W		
Apidae	*Amegilla kaimosica* (Cockerell, 1947)	2	0.33 ± 0.03	0.60 ± 0.05	1.69 ± 0.12	2.43 ± 0.32
Apidae	*Apis mellifera* Linnaeus, 1758	5	0.83 ± 0.02	0.85 ± 0.04	3.13 ± 0.24	0.79 ± 0.65
Apidae	Small black insects Ossélé	6	2.15 ± 0.31	0.51 ± 0.27	0.60 ± 0.14	0.54 ± 0.16
Halictidae	*Lasioglossum* sp.1	4	0.38 ± 0.05	0.46 ± 0.02	2.08 ± 0.02	0.24 ± 0.05
Halictidae	Small black insects Bakoumba	8	0.67 ± 0.21	0.83 ± 0.15	3.04 ± 0.5	0.56 ± 0.23
Lepidoptora	Sp.1	4	2.30 ± 0.04	2.67 ± 0.03	14.10 ± 3.10	4.27 ± 0.02
Lepidoptora	Sp.2	1	1.30 ± 0.00	1.02 ± 0.00	10.21 ± 0.00	3.02 ± 0.00

to supplementary file 1 table S9). At Bakoumba, pollinator community composition was the same for the four forest and the single savanna species (table 3), consisting of two species of Halictidae and *Apis mellifera* (Apidae), the latter generally being the most frequent pollinator (except for *A. hirsutum* (Pop1)). In contrast, pollinator community composition of the savanna species *A. alboviolaceum* was completely different between the different savanna localities Bakoumba, Franceville, and Ossélé (table 3; exception: omnipresence of *Apis mellifera*). In contrast to the group of Halictidae plus *Apis mellifera* at Bakoumba, different species of Apidae prevailed at Ossélé and *Apis mellifera* was the sole pollinator at Franceville.

Most pollinator visits were observed between 9 am and 1 pm. The most frequently visited *Aframomum* individuals were those from the savanna (*A. alboviolaceum*) or more open microsites (*A. subsericeum*) (table 3). The species in more closed forests exhibited much lower visitation frequencies.

Bee pollinators would land on the upper labellum tip of the flower which is horizontally arranged and then crawl into

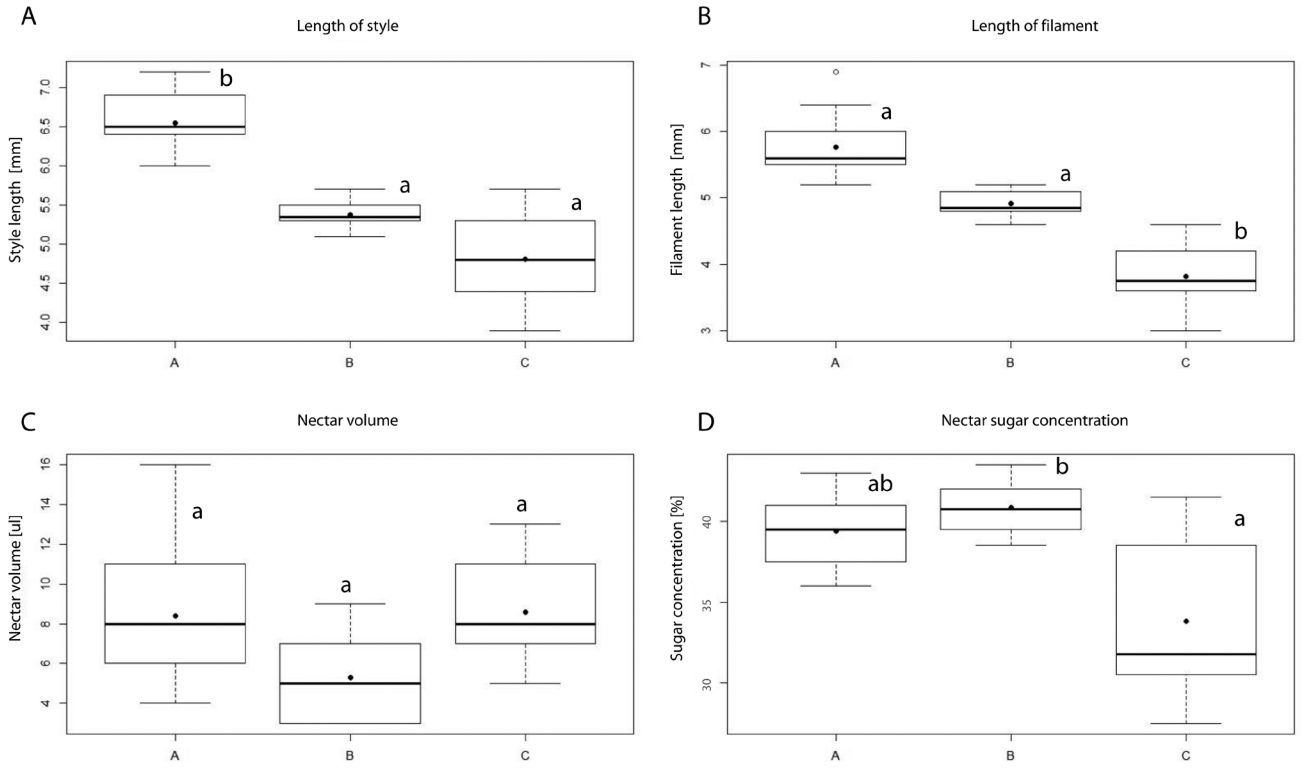

Figure 3 – Statistical comparison of the three PCA groups of *Aframomum* flowers (Zingiberaceae) (groups A, B, and C on x-axis after fig. 2). **A**. Length of style (mm). **B**. Length of filament (mm). **C**. Nectar volume. **D**. Nectar sugar concentration. Letters above boxplots indicate significant groupings based on Tukey test (see supplementary file 1 table S5).

Table 3 – Average number of visits of pollinators per flower per hour for four different species of *Aframomum* (Zingiberaceae) in two different habitats (forest/savanna) and three different savanna localities. BKB, Bakoumba; FCV, Franceville. Small black insects Bakoumba include: *Lipotriches* (Trinomia) sp.1, *Pseudapis* sp.1, and *Lasioglossum* sp.2; small black insects Ossélé include: *Braunsapis leptozonia* (Vachal, 1909) and *Meliponula ferruginea* (Lepeletier, 1841). Lepidoptera sp.1: Erebidae (Noctuoidea) cf.; Lepidoptera sp.2: *Leptotes* sp. (Lycaenidae) cf.

Family	Pollinator species	Forest BKB				Savanna BKB	Savanna FCV	Savanna Ossélé
		A. hirsutum (Pop1)	***A. hirsutum*** (Pop2)	***A. subsericeum***	***A. sericeum***	***A. alboviolaceum***	***A. alboviolaceum***	***A. alboviolaceum***
	Number of observation hours	12	12	12	12	12	50	28
Apidae	*Amegilla kaimosica* (Cockerell, 1947)	0	0	0	0	0	0	0.20 ± 0.31
Apidae	*Apis mellifera* Linnaeus, 1758	0.06 ± 0.15	0.14 ± 0.23	0.24 ± 0.42	0.07 ± 0.12	0.74 ± 0.51	0.16 ± 0.25	0.01 ± 0.02
Apidae	Small black insects Ossélé	0	0	0	0	0	0	0.14 ± 0.31
Halictidae	*Lasioglossum* sp.1	0.11 ± 0.11	0.05 ± 0.07	0.09 ± 0.17	0	0.19 ± 0.12	0	0
Halictidae	Small black insects Bakoumba	0.05 ± 0.12	0.08 ± 0.1	0.20 ± 0.26	0.03 ± 0.06	0.44 ± 0.3	0	0
Lepidoptera	sp.1 & sp.2	0	0	0	0	0	0	0.02 ± 0.09

the floral tube. Bees would stay inside the floral tube for half a minute to up to about four minutes. Also, the butterflies would crawl inside the floral tube to reach the nectar.

Fruit set in the presence and lack of pollinators

Fruits started to appear about three weeks after flowering. This initial fruit appearance was used to determine fruit set. Natural fruit set varied from 3% (*A. hirsutum* (Pop2)) to 78% (*A. alboviolaceum* at Ossélé) (table 4). It was inversely related to the number of flowers produced per inflorescence. There was no correlation between visitation rate per flower and fruit set (supplementary file 1 fig. S2). In the pollinator exclusion experiments no fruits were observed in any of the species (table 4).

DISCUSSION

Fine-scale differentiation within the uniform trumpet type flowers

The detailed morphological investigation confirmed a large size range with three specific groups within the apparent uniform trumpet type flowers from different species of *Aframomum* (this study but compare also Ley & Harris 2014 for a larger species range). The flowers of the savanna species were by far the smallest. However, in all cases the relative position of inner organs that determine pollination efficiency was rather similar (i.e. the distance between pollen sac and labellum and also the width of the arch formed by the lateral appendices of the anther), suggesting equal-sized effective pollinators for all species. The smaller corolla size in the savanna species could represent an adaptation towards elevated desiccation in the open savanna habitat just as found in leaves (Tomlinson et al. 2013). However, the overall floral type with its delicate tissue remained the same. Instead, we observed an earlier wilting in the afternoon. This, however, was at the end of the daily height of insect activity (Ley & Claßen-Bockhoff 2009). Thus, we hypothesize that the effect of strong selection forces for desiccation tolerance in the savanna on floral morphology might be dampened by the short overall flowering time of an *Aframomum* flower (max. 1 day), their phylogenetic constraints (ancestral floral type: trumpet type; Ley & Harris 2014) and the high fitness component of successful pollinator interactions achieved by the floral trumpet type (see also further on).

The detected uniform floral morphology (except for size) in the investigated trumpet type flowers leaves only floral resources as potential source of floral divergence in *Aframomum* (see e.g. Silva et al. 2020). The nectar sugar concentration influences the viscosity of nectar (Kim et al. 2011) which can limit feeding to specific pollinators. In the investigated *Aframomum* species, the nectar sugar concentration is in the range of bee pollinated species (Roubik et al. 1995; Perret et al. 2001; Ley & Claßen-Bockhoff 2009). This suggests the same specific pollinator group and not a divergence in pollinator spectrum among species. The high intraspecific variation in nectar sugar concentration found in the savanna species (30–37%) might be tied to variations in microclimate and soil (Cruden 1976; Herrera et al. 2006; Farkas et al. 2012). Still, it was rather surprising to find on average a slightly lower nectar sugar concentration under the higher temperatures of the open savanna habitat (~34%) compared to the forest species

Table 4 – Natural fruit set and fruit set under pollinator exclusion observed on five inflorescences (Inflor) (up to 10 inflorescences in *A. hirsutum*) from five different individuals per *Aframomum* species (Zingiberaceae) in southeastern Gabon. Nd, no data. Inflor, inflorescence. *, Ossélé; ⁺, Bakoumba; °, Franceville. #, in these taxa inflorescences were only observed during the first two weeks of flowering and not until the end. Thus, the number of flowers and fruits per inflorescence are only investigated and not the total numbers of flowers and fruits per inflorescence. For the latter, refer to table 1.

Species	Open flowers			Bagged flowers		
	Flowers/Inflor	Fruits/Inflor	Fruit set (%)	Flowers/Inflor	Fruits/Inflor	Fruit set (%)
*A. alboviolaceum**	3.20 ± 0.84	2.40 ± 0.55	78.00 ± 21.73	4.00 ± 1.00	0	0
A. alboviolaceum⁺	4.00 ± 0.70	2.40 ± 0.89	58.66 ± 16.69	3.40 ± 1.14	0	0
A. alboviolaceum°	nd	nd	nd	nd	nd	nd
A. hirsutum (Pop1)	5.67 ± 3.28#	0.54 ± 0.58#	8.89 ± 8.89	14.40 ± 5.32	0	0
A. hirsutum (Pop2)	6.58 ± 3.99#	0.23 ± 0.59#	3.04 ± 7.30	9.40 ± 0.71	0	0
A. subsericeum	1.00 ± 0.00	0.60 ± 0.55	60.00 ± 54.77	1.00 ± 0.00	0	0
A. longipetiolatum	nd	nd	nd	nd	nd	nd
A. sericeum	3.60 ± 0.89	2.60 ± 1.14	71.00 ± 24.36	3.80 ± 0.84	0	0

(~37%) (Zajácz et al. 2006). A further potential species differentiation might lie in the amino acid composition of the nectar (Gottsberger et al. 1989). However, this needs further investigation in *Aframomum*.

Thus, so far, based solely on the fine scale floral morphology and the nectar resource (volume and sugar concentration) of the five species with trumpet type flowers, we might expect the same pollinator spectrum for all investigated species.

Generalized bee pollinator-sharing in trumpet type flowers

In accordance with the lack of pollination-relevant differentiation in fine scale floral morphology and resources, we observed mainly the same pollinator species (mainly bees and two small butterflies) for all our studied co-flowering *Aframomum* species. However, to get to the full spectrum of bee pollinators for each *Aframomum* species, it will still be necessary to include many more sites per species as shown by the different bee pollination spectra by site in *A. alboviolaceum*.

Bee pollination in the trumpet type was already hypothesized by Ley & Harris (2014). The purple colour, tubular shape, the lengthening of the labellum as a landing platform, the yellow nectar guide, and the rather high concentration of sugar present in the flowers of *Aframomum* are ideal floral traits for bees and some small butterflies (Brisson et al. 1994; Herrera et al. 2006; Ley & Claßen-Bockhoff 2009; Ley & Harris 2014).

This strategy of different sympatric plant species attracting the same pollinators is termed "pollinator sharing" (Macior 1971). An increased local floral display is reached through the simultaneous inter- and intraspecific flowering of sparsely, thus cost-effectively, flowering individuals (see also Moeller 2004). This simultaneous flowering has proven in other plant species to attract in total a greater and more stable pollinator community to a given area through the provision of a continuously rich food resource and thereby increases the individual rate of successful pollination (Gottsberger 1989; Tachiki et al. 2010). Similar pollination patterns have been observed elsewhere in the tropics (Schemske 1981; Ley & Claßen-Bockhoff 2009; Wang et al. 2016) and might also play a role in these sparsely flowering sympatric *Aframomum* species. Additionally, adjacent habitats (here: savanna and forest) can potentially contribute to a reciprocally-enriched pollinator community (Schüepp et al. 2012; Stanley & Stout 2014).

All observed pollinating bees belong to the group of longue-tongued bees (Brisson et al. 1994; Eardley et al. 2010). The bending of the floral tube and the delicate tissue seem to exclude birds and other larger animals from visiting these flowers – at least during our observations. Other smaller insects have also been observed visiting the open accessible trumpet type flowers, however, due to their small size it is unlikely that they are relevant pollinators because on their way down into the floral tube to get to the nectar they do not come into contact with the reproductive organs. The distance between the labellum on which they walk and the thecae is simply too wide, which prevents them from coming into contact with the pollen (unless they feed on the reproductive organs and thereby come into contact with the pollen).

Using the same pollinators across trumpet type species opens the strong possibility of high rates of interspecific pollen tansfer. Still, there are constant morphological differences between species of *Aframomum* and long-accepted species concepts in the genus (Harris & Wortley 2018). We therefore assume that species are largely genetically incompatible. This incompatibility might have developed randomly by genetic drift during geographic isolation in the past (Maley 1996; Ley & Harris 2014; Couvreur et al. 2020). However, detailed experiments on cross species compatibility have still to be conducted (Wang et al. 2016). Also, the current summary of several different bee species under "small black insects Ossélé" and "small black insects Bakoumba" still hold a potential of a partial differentiation of pollinators between species.

The different composition of bee pollinator spectra by site might mirror differences in available local habitats as

breeding and feeding site for the different bee species (Viana et al. 2012). *Apis mellifera* was the only species observed at all three study localities in all habitats and on all studied species. This bee is widespread and known as a generalist pollinator (Fohouo et al. 2010; Hagen & Kraemer 2010; Giannini et al. 2015). The very high frequency of *Apis mellifera* at Bakoumba and Franceville can additionally be explained by the local presence of bee hives (Nzigou Doubindou pers. obs.). It needs to be checked whether *Apis mellifera* totally replaces a more diverse bee community at Franceville.

The visitation frequencies differed among species of pollinators and localities and thus pollinator preference and pollen transfer efficiency need further testing (Silva et al. 2020). However, both frequent and rare visitors might be effective pollinators, together contributing to the reproductive success of the species (Schemske 1981; Moeller 2004). The bee visitation frequency was highest in flowers of the savanna. This might be related to the higher solar radiation in this habitat – as bees are ectotherms (Hagen & Kraemer 2010). At localities or in years of low visitation frequency, the large number of flowers per inflorescence as found in *A. hirsutum* might be an advantage as it yields a long flowering period (an individual flower lasts a single day only) and thereby increases the probability of effective pollination.

Breeding system and fructification

All studied *Aframomum* species are xenogamous, thus they need pollinators to produce fruits as shown by our pollinator exclusion experiments. Xenogamy increases the likelihood of cross-fertilisation by which genetic diversity within a species is maintained and/or increased (Bawa 1990; Brisson et al. 1994; Ley & Claßen-Bockhoff 2009). Further tests of self and cross-species compatibility in *Aframomum* are needed to establish whether fruits can arise from selfing, probably geitonogamy, and whether pollinator sharing might facilitate hybridisation. The observed spatial isolation of style head and thecae through their respective relative position to each other in the flower rather contradicts the potential for autogamy (see Ley & Harris 2014). The potential for geitonogamy is reduced through the sparse flowering of an inflorescence (rarely more than one simultaneously open flower): geitonogamy would only be possible as a result of pollen transfer across adjacent clonal individuals.

Self-incompatibility might be one potential explanation for the detected low natural fruit set of 3–8% in the rich-flowering *A. hirsutum*, in contrast to a rather high fruit set of > 60% in all other sparsely flowering species (except *A. longipetiolatum* – no data) (compare Sutherland & Delph 1984; Ley & Claßen-Bockhoff 2013). However, the low fruit set in *A. hirsutum* could also be an effect of resource limitation. This hypothesis builds on the idea that the production of the large and thus energetically costly fruits in *Aframomum* is restricted by available resources in favour of e.g. genetically "advantageous" (i.e. outcrossed) fruits (Sutherland 1986; Horvitz & Schemske 1988). Currently, it seems as if in the studied *Aframomum* species a given inflorescence cannot bear more than one to three large fruits – but more specific data is still needed to prove or reject this idea.

SUPPLEMENTARY FILE

Supplementary file 1 – Information on the specimens of *Aframomum* collected (coll.) at the three study sites in Gabon (table S1); average morphological measurements (cm) of five sympatric *Aframomum* species (table S2); average morphological measurements (cm) of *Aframomum alboviolaceum* at three different localities (table S3); PCA statistics of morphological measurements (tables S4, S5); results of statistical differentiation between PCA groups, phenological data (tables S6, S7, S8); information on voucher specimens of pollinators and relationships of fruit set (table S9); flowers of *Aframomum alboviolaceum* from three different study sites in Gabon (fig. S1); relationship of fruit set and pollinator visitation rate per flower in five species of *Aframomum* at Bakoumba in Gabon (fig. S2).

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