Spatio-temporal Pattern of Specialization of Sunbird-flower Networks on Mt. Cameroon

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Abstract

Differences in bird-flower interaction specialization across continents serve as a common example of evolutionary trajectory specificity. While New World hummingbird-flower networks have been subject to numerous studies and are considered highly specialized, our knowledge of network specialization for their Old World counterparts, sunbirds (Nectariniidae), is completely insufficient. A few studies from tropical Africa indicate that sunbird-flower networks are rather generalized. Unfortunately, these studies are limited to dry seasons and high elevations around the tree-line, the environments where also niche-based hypotheses often predict lower resource partitioning. In our study, we explore the specialization of sunbird-flower networks and their spatio-temporal variability on Mt. Cameroon (Cameroon). Using a combination of automatic video recording and personal observations, we constructed eight comprehensive sunbird-flower networks in four forest types occurring in different elevations and in both the dry and wet season. As reported by previous studies the montane forest plants, birds and whole networks were highly generalized. Nevertheless, we observed much higher specialization in forests in lower elevations. The wet season was also characterised by higher, but not significant, specialization. While less specialized flowering trees dominated in dry season networks, more specialized herbs and shrubs were visited during the wet season. Whereas our findings do not support the generally accepted assumption that Old World bird-flower networks are rather generalized, we need further studies to understand the differences in bird-flower specialization on individual continents.

Introduction

Studies on global patterns of plant-pollinator network specialization help us to understand spatial differences resulting from specific environmental conditions and/or evolutionary history. Nevertheless, global syntheses are suffering from the absence of datasets from large areas, making the picture incomplete (Vizentin-Bugoni et al. 2018). For example, as highlighted by Ollerton (2012), one of the most complex global studies on specialization in plant-pollinator networks along latitudinal gradients (Schleuning et al. 2012) suffers from large data deficits from tropical Africa and Asia. Continental tropical Africa and tropical Asia are represented by only one and two plant-pollinator networks, respectively. Similar data deficit can be found in the synthesis of bird-flower specialization, which compares hummingbird, sunbird, and honeyeater networks around the world (Zanata et al. 2017). In Africa, there were just three quantitative pollination networks from specific South African biomes, and just two for sunbirds from tropical Africa, where, paradoxically, we find the highest sunbird diversity (Cheke et al. 2001).

Specialization in plant-pollinator networks reflects resource (niche) partitioning among species, which can be driven by the tendency of plants and pollinators to use only a subset of potential resources, and by inter-plant or inter-bird interactions, such as competition (Blüthgen et al. 2006). A few studies on African sunbird-flower networks indicate that they are less specialized than hummingbird-flower networks (Zanata et al. 2017; Nsor et al. 2019). Nevertheless, other studies, which did not use the network analytical framework, revealed many similarities that should result in similar network specialization. It is generally accepted that both hummingbirds and sunbirds are similarly specialised for nectarivory in many traits such as bill length, tongue structure, digestive tract functioning, etc. (Stiles 1981). Even the ability to hover, which was for a long time considered as a hummingbird privilege (Stiles 1981; Fleming and Muchhala 2008), was documented in sunbirds (Geerts and Pauw 2009a; Wester 2014). Moreover, it has been shown that plants adapted to hovering sunbirds occur also in African tropics (Janeček et al. 2011; Bartoš and Janeček 2014; Seifová et al. 2021) and that sunbirds are also driving away insects from the food plants in their territories (Ollerton and Nuttman 2013; Tropek et al., 2013) as hummingbirds

do (Jacobi and Antonini 2008). In both bird groups, we can find high variability in morphological and behavioral nectarivory related traits such as in bill length, bill curvature or ability to hover, which enable resource partitioning (Paton and Collins 1989; Janečková et al. 2021; see also Adler et al. 2013). Resource partitioning itself was also documented in both hummingbird and sunbird assemblages composed of species with different functional traits (Feinsinger et al. 1985; Geerts and Pauw 2009b; Janeček et al. 2012). Considering plants, a wide spectrum of growing forms and degree of specialization (Fleming and Muchhala 2008) was recorded in both American and African flora. Hummingbirds and sunbirds interact with non-specialized plant species, often canopy trees (Maruyama et al. 2014; Nsor et al. 2019; Chmel et al. 2021) but also with highly specialized ornithophilous plants, often herbs, shrubs, and epiphytes (Cronk and Ojeda 2008; Janeček et al. 2015; Chmel et al. 2021). Resource (i.e. bird) partitioning among plant species was documented in both systems (Stiles 1981)

Our present ideas on sunbird-flower network specialization look even more anecdotal if we take into account the growing evidence of high spatiotemporal variability in plant-pollinator networks (Burkle and Alarcón 2011; CaraDonna et al. 2017). It was shown that specialization in pollination networks can change with climate along a relatively narrow latitudinal gradient within the Aegean Sea region (Petanidou et al. 2018). There was observed an increased proportion of specialized plants and flower visitors along the elevational gradient in the Andes (Colombia; Cuartas-Hernández and Medel 2015). On the contrary, in the Alps (Germany; Hoiss et al. 2015), on El Teide (Canary Islands; Lara-Romero et al. 2019) and on Mt. Kilimanjaro (Tanzania; Classen et al. 2020) was reported decreasing specialization in plant-pollinator networks with increasing elevation. Additionally, Popic (2013) showed that rainy periods increase the specialization of flower-visitor networks.

There are several studies on the factors affecting the specialization of bird-flower interaction networks, however, almost all of them are on hummingbird-plant networks (e.g., Maglianesi et al. 2014; Cuartas-Hernández and Medel 2015; Maruyama et al. 2018). The observed pattern along elevational gradients, serving as an exceptional field laboratory characterized by rapid environmental changes, differs depending on the metrics used and the location under study. Using the species level specialization index (d'), Maglianesi et al. (2015) showed greater specialization of hummingbirds at low (0 m a.s.l.) and middle (1000 m a.s.l.) elevations, compared to high elevations (2000 m a.s.l.). In the same study area, the complementarity specialization index (H'_2), which considers both plant and visitor specialization, was the highest at middle elevations (Maglianesi et al. 2014). In contrast, Partida-Lara et al. (2018) demonstrated, on a similarly long elevational gradient, that the highest complementary specialization is found at high elevations. Sonne et al. (2019) showed a more complex pattern along a more expansive elevational gradient (0-4000 m.a.s.l.), where there was a dominance of curved-bill specialists in lowlands, long-straight bill specialists at high elevations and relatively low hummingbird species level specialization at middle elevations. In contrast, Pellissier et al. (2017) demonstrated a decrease in hummingbird-flower network connectance (i.e., increase of specialization) at high elevations.

Studies on the temporal variability of bird-flower network specialization are rather rare. Partida-Lara et al. (2018) found similar complementarity specialization in hummingbird networks across a one-year period. Maruyama et al. (2014) found plant and hummingbird phenological overlap is important for network modularity. Nevertheless, many studies not directly targeting plant-bird networks presented various phenological patterns, which should be reflected in temporal changes in network specialization. Independent studies demonstrated that flowering intensity and nectar availability for birds can vary considerably from season to season, not only for hummingbirds (Wolf 1970; Araujo and Sazima 2003; Abrahamczyk and Kessler 2010) but also for sunbirds (Collins and Rebelo 1987) and honeyeaters (Collins and Briffa 1982; Collins 1985; Comer and Wooller 2002). Specific flowering

patterns of individual plant groups can also contribute to these patterns. For example, tropical trees (Janzen 1967; Bentes et al. 2008) and specialized ornithophilous herbs can predominantly bloom in certain seasons of the year (Janeček et al. 2015). Unfortunately, all published sunbird-flower networks from tropical Africa were studied in the dry season (Zanata et al. 2017; Janeček et al. 2012; Nsor et al. 2019). We assume that this can largely bias our general conclusions on sunbird-flower interactions.

Here we aim to explore the specialization of sunbird-flower interactions on Mt. Cameroon, the highest peak of West Africa. We specifically explore the sunbird-flower networks in different forest types occurring in different elevations and in two contrasting seasons (wet and dry). Our goal was to focus on two main questions. 1/ Are birds, plants and the whole networks at higher elevations more or less specialized? Lower specialization can arise from broader niches and lower resource partitioning in the harsher, less predictable environments of higher elevations (Rasmann et al. 2014). In contrast, birds are relatively reliable pollinators in cold weather, and consequently there can be more specialized bird-pollinated plants, which on the contrary, enable better niche separation at higher elevations (Cruden 1972; Huang et al. 2017). 2/ Are the birds, plants and the whole networks more specialized in the wet season? Higher specialization can be expected as many specialized ornithophilous plants only bloom in the wet season (Cruden 1972; Janeček et al. 2015) and can enable more precise niche segregation (Abrahamczyk and Kessler 2010).

Materials And Methods

Study site

Our study was performed on the south-western slope of Mt. Cameroon (Cameroon, Fig. 1), which is the highest mountain of West-Central Africa (4040 m a.s.l.) and an important biodiversity hotspot (Küper et al. 2004). The lowest elevations of the south-western slope are used for plantations, but from approximately 400 m a.s.l. to the treeline (2200 m a.s.l.) we can find the primary tropical forest (Cable and Cheek 1998). The study was performed in four forest types: 1/ Lowland forest (LF) in the locality Drink Gari (650 m a.s.l.) where members of the plant subfamily Caesalpiniaceae (family Fabaceae) are common, 2/ Mid-elevation forest in the locality PlanteCam camp (1100 m a.s.l.) partly disturbed by elephants with common occurrence of *Kigelia africana*, *Macaranga occidentalis* and *Voacanga africana*, 3/ Submontane forest in the locality Crater Lake (1500 m a.s.l.) which is strongly disturbed by elephants and in consequence is mixed with large elephant pastures with common occurrence of *Aframomum* spp., 4/ Montane forest around the Mann's Spring (2200 m a.s.l.) close to the treeline with occurrence of montane species as *Syzygium staudtii*, *Nuxia congesta* or *Schefflera* spp. (Fig. 1). Data were collected during four expeditions across three years. One was organized in 2018 and 2020 and two in 2019. During each expedition, we collected data from two sites. As a consequence, the data were collected during two expeditions to each site, one in the dry season (end of January – mid- March) and one in the wet season (end of July - mid-September). Six transects (200 x 10 m) were established at each site, and the abundance of plants in flower within each transect was estimated.

Observation of sunbird-plant interactions

We considered each plant individual as one observation unit. For lianas, where determining an individual in the field was impossible, we defined individuals as those which had flowering parts not obviously connected to another such part. We considered individual plant species to be potentially bird-visited if the nectar amount in a

covered flower after 24 hrs was higher than 0.3 μl /per flower (unpublished data, see also Janeček et al. 2021) and if it flowered in at least 3 replications on the six transects, or if it occurred less frequently but was commonly flowering outside of the transects. Sunbird-plant interactions were observed using two complementary methods. The first method utilised security cameras (Vivotek IB8367RT) to observe herbs and small shrubs. We aimed to record 10 individuals of each plant species and each individual for two days (from 6:00 till 18:00). The rarity of some species, together with logistical and/or technical problems related to the harsh weather of Mt. Cameroon, resulted in different total recording times for individual plants (Online Resource 1). Finally, the mean video observation period was 152 hrs. per plant species. Floral visitors were identified in the video material either manually or using the automatic movement detecting software MotionMeerkat (Weinstein 2015). The second method was direct observation of trees and tall shrubs (i.e., those that were not suitable for the camera's field of view). We aimed to observe eight individuals per plant species, each of them for eight hours distributed equally throughout the day. As we could not always find a sufficient number of individuals, the mean observation time per species was 68 hrs (Online Resource 1). Tall trees were usually observed from a neighboring tree, on which the observer climbed using single-rope climbing technique.

Assessment of interaction abundances

We quantified plant abundance to estimate the total number of interactions in the studied area. To do this, we counted all flowering individuals inside six 200 x 10 m transects on each site during each expedition, giving us data on flowering plant abundance from 1.2 hectares. The values in individual cells of bird-plant interaction matrices were then calculated as visitation frequency per plant per hour multiplied by plant abundance per hectare. To achieve the integer values needed for calculations of some specialization indices, often very low frequencies per hour and hectare were arbitrarily multiplied by 10000 and rounded up. For plants which were relatively common, but did not appear on transects, we arbitrarily set their abundance as 1 individual per 2 hectares.

Specialization matrix

To describe the specialization of sunbird flower networks, we used indices currently in standard use, most of them were also used in the most complex worldwide study on specialization in bird-flower networks (Zanata et al. 2017). On the species level, we calculated the Blüthgen's standardized species specialization d' (Blüthgen et al. 2006) and normalized degree **ND** (Freeman 1979) for sunbirds and plants. The index d' is related to Shannon diversity, but compares the distribution of the interactions with each partner to the overall partner availability d' ranges from 0 (max. generalization) to 1 (max. specialization). Normalized degree ND is simply the proportion of species it interacts with out of the total possible in the network (Freeman 1979; González et al. 2010). On the network level, we used connectance (**C**), which is the proportion of realized to all possible interactions in the network, complementary specialization (H_2'), which is a generalization of d' for the whole network and similarly as d' ranges from 0 for fully generalized to 1 (max. specialized) networks (Blüthgen et al. 2006; González et al. 2015), and Newman's weighted modularity measure comparing the density of connections inside and between modules (**Q**). Q ranges from 0 for randomly arranged networks to 1 for networks with perfectly defined modules (Newman 2004, 2006; Dorman and Strauss 2014). The modules were detected using Beckett's algorithm (Beckett 2016).

Statistical analyses

Specialization indexes were calculated using the package bipartite 2.15 (Dorman et al. 2008) in R 4.0.0 (R Core Team 2020). Observed values of network-level matrices H_2' and Q were tested by comparison with null models. Values for null models were computed from 1000 networks generated by the Vaznull algorithm (Vázquez et al. 2007). The Vaznull algorithm is relatively conservative and preserves connectance and marginal totals of the observed network.

Because the values of some species level indices were not normally distributed we used for statistical analyses of plant and sunbird specializations in individual forest types and seasons a nonparametric permutation ANOVA. Elevation and season were treated as fixed factors. Permutation tests were performed using the PERMANOVA + program for PRIMER (Anderson et al. 2008). These analyses are almost the same as the traditional ANOVA. The small difference is that the F ratio in permutation ANOVA does not have the known distribution under the true null hypothesis and consequently it is denoted as pseudo F ($F_{ps.}$). Permutation P value ($p_{perm.}$) is calculated as the proportion of $F_{ps.}$ values achieved by permutations which are greater or equal to the observed $F_{ps.}$

Results

In total, the plants were observed for 15767 hours with 8205 sunbird-plant interactions recorded. We observed 12 sunbird species interacting with 49 plant species. The number of interacting sunbirds differs at individual elevations (Fig. 2). The highest number of sunbirds (9 species) was observed in lowland forest in the dry season. In contrast, only two sunbird species were visiting plants in submontane and montane forest. The numbers of visited plants were higher in the mid-elevation and submontane forests and in the dry season (Fig. 2). Trees were the most visited growth form in the dry season, whereas no tree was part of sunbird-flower networks in the wet season (Fig. 2). The species level sunbird specialization (d') significantly differed among elevations (Table 1). We detected the lowest sunbird d' specialization in the mountain forest, whereas the specialization was higher and similar in forests growing in lower elevations (Fig. 3a). Normalised degree differed among forest types with the highest values in montane and submontane forests (Table 1, Fig. 3b). The species level plant specialization (d') significantly differed among individual forest types (Table 1). Plant specialization was highest in the lowland forest network and decreased towards higher altitudes (Fig. 3c). The opposite pattern was found for plant normalized degree, which was lowest and highest in low and high elevations respectively (Table 1, Fig. 3c).

Table 1

Effect of season and forest type on bird and plant specialization expressed as Blüthgen's specialization index (d') and normalized degree (ND). Permutation Anova. * $0.01 < p < 0.05$; ** $p < 0.01$

	Bird d'		Bird ND		Plant d'		Plant ND	
	$F_{ps.}$	$p_{perm.}$	$F_{ps.}$	$p_{perm.}$	$F_{ps.}$	$p_{perm.}$	$F_{ps.}$	$p_{perm.}$
Season	2.34	0.145	0.19	0.667	0.01	0.916	0.50	0.487
Forest	4.18	0.012*	5.27	0.004**	4.85	0.004**	12.72	0.001**
Forest*season	0.50	0.689	0.14	0.926	1.55	0.224	0.32	0.790

The lower specialization in high elevations was also obvious considering the network-level indices. Connectance (C) was higher in the two upper forest types (Table 2). Both observed complementary specialization (H_2') and modularity (Q) were much lower in mountain forest. H_2' and Q significantly differed from values predicted by null

models in all but one network, indicating that networks were specialized and modular (Table 2). The only exception was the wet season network in lowland forest, where the difference between the observed and null model predicted complementary specialization was not significant. H_2' was higher values of all elevations in the wet season (Table 2).

Table 2

Network level specialization indices and they differences from the null models (Δ values) for networks in individual forest types and seasons. H_2' - network specialization index; Q – modularity; C – connectance. Observed values marked by asterisk differ from the null model prediction * $0.01 < p < 0.05$; ** $p < 0.01$.

	Lowland forest		Mid-elevation forest		Submontane forest		Mountain forest	
	dry	wet	dry	wet	dry	wet	dry	wet
$H_2'_{OBS}$	0.40**	0.43	0.17**	0.48**	0.37**	0.66**	0.08**	0.10**
$\Delta H_2'$	0.28	0.13	0.16	0.40	0.37	0.64	0.08	0.10
Q_{OBS}	0.30**	0.26*	0.10**	0.30**	0.11**	0.15**	0.02**	0.01**
ΔQ	0.23	0.15	0.09	0.25	0.11	0.14	0.02	0.01
C	0.33	0.37	0.45	0.44	0.78	0.71	0.89	0.75

Discussion

This study represents the largest collection of comprehensive sunbird-flower networks in tropical Africa to date. Rather than arriving at a clear general conclusion regarding their specialization, we have revealed high spatiotemporal variability. Most of these networks were much more specialized, irrespective of the index used, than those of the two other published studies on quantitative networks in tropical Africa (Zanata et al. 2017; Nsor et al. 2019). Nevertheless, these studies are fully consistent with our results if we consider when and where they were performed. The first one was carried out in Bamenda highlands (Cameroon) in shrubby vegetation along a small stream at an elevation around 2200 m a.s.l. (Janeček et al. 2012; Zanata et al. 2017) and the second in the montane forest on the Mambilla Plateau (Nigeria), around 1650 m a.s.l. (Nsor et al. 2019). Moreover, both studies were performed in the dry season. Our montane dry season network was also characterised by substantially lower specialisation than other networks. The differences between our high network-level specialization and the lower specialization of networks in South Africa, measured as H_2' , Q or C (Zanata et al. 2017) can be explained by three hypotheses, all of which warrant testing in the future. This low specialization can result from 1/ the latitudinal pattern and specialization decreasing towards higher latitudes, but this hypothesis is still contentious (e.g., Ollerton and Cranmer 2002), 2/ the specific properties of Austro-temperate flora in South Africa, which is closely related to the flora of Australia (Linder 2014), 3/ sampling, as all studies used in Zanata et al. (2017) from south Africa were constrained by sampling a targeted subset of plants in the community, e.g., *Salvia* and *Lycium* (Wester 2013), *Protea* (Schmid et al. 2016) or *Aloe* (Botes et al. 2008).

Our findings from the montane forest are in agreeance with other pollination-network studies showing the lowest number of potential visitors (Ramos-Jiliberto et al. 2010), and both lower group- (Miller-Struttmann and Galen 2014) and network levels (Hoiss et al. 2015) specialization at high elevations. The same pattern has also been demonstrated in hummingbird-flower networks (Maglianesi et al. 2015). However, this distribution of specialization is not consistently observed in hummingbird networks. For example, Partida-Lara et al. (2018)

revealed the opposite pattern (i.e. the lowest specialization in low elevations), suggesting that local conditions are important. Their study was performed on a gradient with different vegetation types at individual sampling elevations, with the lowest number of interacting species in lowland deciduous seasonal forest. We assume that the differences in elevational patterns between sunbird – and hummingbird networks can arise from the diversification of two, in many aspects distinct, phylogenetic lineages. Curve-billed hummingbirds (prevailing in the Phaethornithinae) and long-straight hummingbirds (prevailing in the Trochilinae) differ in elevational distribution and specialization, which in turn could generate low specialisation at mid elevations (Sonne et al. 2019). In contrast, although the phylogeny of sunbirds is yet to be properly resolved, groups of sunbird species do not display any obvious patterns of specialization and elevational distribution (Cheke et al. 2001). From a niche theory perspective, our data are consistent with the altitudinal niche-breadth hypothesis in plant-pollinator interactions (Rasman et al. 2014), which states that niches are broader in harsher montane environments. The mechanism behind this pattern is not necessarily simply the harsh environments and the associated effort to use resources per se. Additionally, the increasing abundance of birds with elevation can also play a role, as was demonstrated on Mt Cameroon (Ferenc et al. 2016). Further evidence showing that bird pollinators are generalized when abundant was also found by Simmons et al. (2019). Nevertheless, our data does not support the idea of a simple linear pattern along the whole gradient. The highest specialization was found in wet season network in submontane forest, 1500 m a.s.l. This may result from the occurrence of an extremely specialized plant species *Thonningia sanguinea*, which is almost exclusively visited by *Cyanomitra oritis* (among bird visitors) and at the same time, is the most frequently visited nectar source of this sunbird. These findings support the idea that sunbirds can be effective pollinators of this species (Quintero et al. 2017). Another potentially important factor is forest disturbance. The submontane forests in these elevations are largely disturbed by elephants and forest patches are mixed with large areas of elephant-induced clearings. This habitat heterogeneity and the floral richness which comes with it (this elevation has the highest number of visited plants and number of visited plants per one sunbird species), in turn facilitates greater niche differentiation.

The seasonal comparison shows that the existing ideas on sunbird-flower network specialization in tropical Africa are likely biased, as other studies to date were performed exclusively in the dry season (Janeček et al. 2012; Nsor et al. 2019). Our study from Mt. Cameroon shows that the wet season differs from the dry season in several important aspects which potentially drive higher wet season specialization. The wet season often has more flowering ornithophilous herbs, for example, *Impatiens* spp. (see also Janeček et al. 2015), whereas massive flowering trees act as significant nectar sources in the dry season (Fig. 2). There are also a smaller number of flowering plant individuals in the wet season, where nectar production per hectare is several times lower (unpublished data). It would appear that the wet season is not only a much less comfortable environment for field work, but also for sunbirds. Similarly, hummingbird networks showed higher specialization under resource shortage (Tinoco et al. 2017), as has also been shown for whole plant-pollinator networks (Souza et al. 2018). Peaks in the number of hummingbird-visited plants were recorded both in wet (Araujo and Sazima 2003) and dry (Partida-Lara et al. 2018) seasons. As such, we need more data to determine whether this pattern is also site-specific for sunbirds. However, it is common for trees to flower in the dry season in tropical forests in various geographic areas (Janzen 1967; Nsor et al. 2019). In terms of bird-plant coevolution, we can expect that the wet season will impart much stronger selection pressures on plant and bird traits related to ornithophily or nectarivory, respectively, as there is a higher abundance of ornithophilous plants and a general lack of resources compared to the dry season. We believe additional studies in the wet season are crucial for understanding the ecology and evolution of sunbird-plant interactions. We agree with the opinion of other authors (e.g., Ollerton 2012) that

conclusions about global patterns of specialization should be made with caution, particularly when datasets do not account for spatiotemporal variability.

Despite presenting more sunbird-flower networks than all previously published studies from tropical Africa, our knowledge of sunbird-flower network specialization is still in its infancy. Furthermore, there is a significant knowledge gap surrounding sunbird food plants. This is illustrated by the fact that the most comprehensive information on food plants in the sunbird monograph by Cheke et al. (2001), also used by Fleming and Muchhala (2008) for an evaluation of sunbird specialization, reports only 2 of the 49 food plant species that were visited by sunbirds during our observations on Mt. Cameroon. Moreover, the idea that forest-dwelling sunbirds, in contrast to hummingbirds, feed more often on canopy and subcanopy trees (Fleming and Muchhala 2008) appears valid only when applied to the dry season. Moreover, it seems that similarly to hummingbirds (Feinsinger 1976) also sunbird communities are composed of more assemblages with some species (such as Cameroon sunbird) exploring more specialized flowers in the forest interior whereas others feed on more generalized canopy trees. Another unexploited, but important aspect of sunbird ecology on Mt. Cameroon is the local migrations. It seems that in the dry season at least some individuals of Cameroon sunbird migrate to lower elevations. Ursula's sunbird disappeared from the mid altitudinal forest in the wet season but we did not find it at any other elevation. Thus, because it is an endemic species occurring only in Cameroonian Highlands and Bioko, we can speculate that it migrates to some less rainy Mt. Cameroon slopes. Nevertheless, both organisation of sunbird assemblages and local migration can be solved only by additional studies. This knowledge will be crucial for the effective conservation of Mt. Cameroon sunbird and plant assemblages.

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Figures

Figure 1

Study sites on Mt. Cameroon. (a) Mt. Cameroon. DG - Drink Gari, PC - PlanteCam Camp; CL - Crater Lake; MS - Mann's Spring. (b) Lowland forest around DG in dry season. Whitish trees are *Berlinia bracteosa* in flower. (c) Mid-elevation forest around PC, *Impatiens frithii* seen in frame, a flowering epiphytic ornithophilous species. (d) Submontane forest around CL with large patches of herbaceous vegetation maintained by forest elephants. (e) Montane forest in the dry season near MS. The tree on the left-hand side is a flowering *Schefflera abyssinica*.

Figure 2

Sunbird-flower networks on Mt. Cameroon at four elevations in dry and wet seasons. PLANTS: Aca dec - Acanthopale decempedalis; Afr sp. - Aframomum sp; Ant sca - Anthocleista scandens; Ant fra - Anthonotha fragrans; Ber bra - Berlinia bracteosa; Ber rac - Bertiera racemosa; Bri owa - Brillantaisia owariensis; Che lai - Chesallia laikomensis; Cla ani - Clausena anisata; Cle syl - Clerodendrum sylvanum; Cos dub - Costus dubius; Cor aur - Cordia aurantiaca; Dic ves - Dicranolepis vestita; Dis gra - Dischistocalyx grandiflora; Eng gab - Englerina gabonensis; Hei cri - Heinsia crinita; Hug mic - Hugonia micans; Hyp tri - Hypoestes triflora; Imp bur - Impatiens burtonii; Imp hia - Impatiens hians var. hians; Imp eti - Impatiens etindensis; Imp fri - Impatiens frithii; Imp nia - Impatiens niamniamensis; Imp sak - Impatiens sakeriana; Ixo fol - Ixora foliosa; Ixo gui - Ixora guineensis; Jas pre - Jasminum preussii; Kig afr - Kigelia africana; Lee gui - Leea guineensis; Mim sol - Mimulopsis solmsii; Mus ten -

Mussaenda tenuiflora; Nux con - Nuxia congesta; Pav rig - Pavetta rigida; Phr kam - Phragmanthera kamerunensis; Ple dec - Plectranthus decurrens; Ple kam - Plectranthus kamerunensis; Psy hyp - Psychotria hypsophila; Psy dun - Psydrax dunlapii; Rhi sp. - Rhipidoglossum sp.; Sab pil - Sabicea pilosa; Sch mag - Schumanniphyton magnificum; Sch aby - Schefflera abyssinica; Syz sta - Syzygium staudtii; Syz sp. - Syzygium sp.; Tab bra - Tabernaemontana brachyantha; Tab ven - Tabernemontana ventricosa; Tho san - Thonningia sanguinea; Thu fas - Thunbergia fasciculata; Voa afr - Voacanga africana; SUNBIRDS: Ant col - Anthodiaeta collaris; Ant rec – Anthreptes rectirostris; Ant sei - Anthreptes seimundi; Cha rub - Chalcomitra rubescens; Cin bat - Cinnyris batesi; Cin joh - Cinnyris johannae; Cin min - Cinnyris minullus; Cin urs - Cinnyris ursulae; Cin rei - Cinnyris reichenowi; Cya cya - Cyanomitra cyanolaema; Cya oli - Cyanomitra olivacea; Cya ori - Cyanomitra oritis

Figure 3

Specialization of birds (a,b) and plants (c,d) in the individual forest types on Mt. Cameroon. d' – Blüthgen´s specialization index; ND – normalized degree. The significant pair-wise differences between individual forest types are reported. LF – lowland forest; MEF – mid-elevation forest; SF-submontane forest; MF-montane forest.

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