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Biodiversity patterns of butterflies and moths on Mount Cameroon

Ph.D. Thesis

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ANNOTATION

Biodiversity patterns of butterflies and moths are investigated on the southwestern slope of Mount Cameroon, the only continuous elevational gradient of near-pristine forests in the Afrotropics. Three distinct seasons between 2014 and 2017 are sampled by two standardised methodologies (i.e., bait-trapping and manual catching of selected groups of moths at light). First, the effects of seasonality and forest habitat associations on butterflies and moths are investigated in the lowland rainforest. Then, the impacts of elephant-made natural disturbances on tree, butterfly, and moth diversities at mid-elevations is evaluated. The thesis also includes faunistic records of species never reported from the area, combining them with life history notes on selected taxa and species description of nine new species of *Alucita*. Finally, the last chapter focuses on the biodiversity of birds, trees, and butterflies in the last large patch of coastal forest of the studied area, and discusses its current conservation status.

DECLARATION [IN CZECH]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 11/03/2019 …………………………….

Vincent Maicher

This thesis originated from a partnership of the Faculty of Science, University of South Bohemia and the Institute of Entomology, Biology Centre CAS, as part of doctoral studies in the Entomology study program.

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This thesis is dedicated to the memory of Philippe and Louise Maicher.

"Je m'habille de nos rêves
Orphelin jusqu'aux lèvres"
Jojo, 1977

LIST OF PAPERS AND AUTHORS' CONTRIBUTION

The thesis is based on the following publications/manuscripts:

I. Maicher, V., Sáfián, Sz., Murkwe, M., Przybyłowicz, Ł., Janeček, Š., Fokam, E.B., Pyrcz, T., & Tropek, R. (2018) Flying between raindrops: Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon. *Ecology and Evolution*, **8,** 12761-12772 **(IF=2.537)**
VM participated in the sampling planning and data collection (attended all sampling expeditions), identified most fruit-feeding moths and most groups of moths caught at the light (all but Arctiinae), analyzed data and crucially participated in results interpretation, and led the writing of the manuscript.

II. Delabye, S., **Maicher, V.**, Sáfián, Sz., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Murkwe, M., Šebek, P., & Tropek, R. Response of butterfly and moth communities to habitat structure in lowland rainforests of Mount Cameroon. *Manuscript.*
VM participated in sampling, identification of most fruit-feeding moths, and manuscript preparation.

III. Maicher, V., Delabye, S., Murkwe, M., Kobe, I.N., Doležal, J., Altman, J., Desmist, J., Fokam, E.B., Pyrcz, T., & Tropek, R. Does rainforest biodiversity stand on the shoulders of giants? Effect of disturbances by forest elephants on trees and insects on Mount Cameroon. *Manuscript.*
VM participated in the sampling planning, collected a large part of the data (directly led two sampling expeditions), identified a large part of the

fruit-feeding moths and most groups of moths caught at the light (all but Lymantriinae), analyzed data, interpreted results, and led the writing of the manuscript.

IV. Maicher, V., Sáfián, Sz., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., Kobe, I.N., Janeček, Š., Mertens, J.E.J., Fokam, E.B., Pyrcz, T., Doležal, J., Altman, J., Hořák, D., Fiedler, K., & Tropek, R. Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *Submitted manuscript*.
VM participated in the sampling planning and data collection (attended five of the six expeditions), identified most fruit-feeding moths, as well as moths caught at the light (all but Arctiinae and Lymantriinae), analyzed data, participated in results interpretation, and led the writing of the manuscript.

V. Ustjuzhanin, P., Kovtunovich, V., Sáfián, Sz., **Maicher, V.**, & Tropek, R. (2018) A newly discovered biodiversity hotspot of many-plumed moths (Lepidoptera, Alucitidae) in the Mount Cameroon area: first report on species diversity, with description of nine new species. *Zookeys*, **777**, 119-139. **(IF=0.938)**
VM collected most of the presented specimens and participated in the manuscript preparation.

VI. **Maicher, V.**, Sáfián, Sz., Ishmeal, K.N., Murkwe, M., Kimbeng, T.J., Janeček, Š., & Tropek, R. (2016) Two genera and nineteen species of fruit-feeding erebid moths (Lepidoptera: Erebidae) recorded in Cameroon for the first time. *Entomological News*, **126,** 64-70. **(IF=0.456)**
VM crucially participated in collection and identification of the presented material and led the writing of the manuscript.

VII. Przybyłowicz, Ł., **Maicher, V.**, Laszlo, G., Sáfián, Sz., & Tropek, R. Amerila (Lepidoptera: Erebidae: Arctiinae) of Cameroon: faunistic and taxonomic summary, and first illustration of female genitalia. *Submitted manuscript.*
VM crucially participated in collection of the presented specimens, as well as in the manuscript preparation.

VIII. Ferenc, M., Sedláček, O., Tropek, R., Albrecht, T., Altman, J., Doležal, J., Janeček, Š., **Maicher, V.**, Motombi, F.N., Murkwe, M., Sáfián, Sz., & Hořák, D. (2018) Something is missing at the bottom: Importance of coastal rainforests for conservation of trees, birds and butterflies in the Mount Cameroon area. *African Journal of Ecology*, **56**(3), 679-683. **(IF=0.875)**
VM participated in collection of butterflies, in results interpretation, and the manuscript preparation.

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Our light set-up at the PlantiCam camp (ca., 650 m asl.). It attracted moths from dusk till dawn, while a lepidopterist systematically collected the pre-selected groups © V. Maicher

CHAPTER I

General introduction

Biodiversity is not evenly distributed in the world (von Humboldt, 1849). From arid deserts and luxuriant tropical rainforests, to lowland forests and alpine grasslands, sharp environmental changes are easily noticeable. For more than two centuries, the early foundations of biogeography have been assembled by generations of explorers and naturalists such as Willdenow, von Humboldt, Wallace, and Darwin, detailing multiple examples of environmental variations along latitude and elevation (see Lomolino, 2001 for an historical perspective). The negative correlations of species richness with decreasing latitude and increasing elevation are among the most universal ecological relationships known. They were first interpreted to be driven by a decrease in favourable climatic conditions with decreasing latitude and increasing elevation (Wildenow, 1805).

Understanding the patterns and causes of the global distribution of biodiversity is a central aspect of ecological research (Rosenzweig, 1995; Gaston, 2000; Hillebrand, 2004). However, studies of biodiversity along latitude are among the most challenging and costly ecological approaches. Contrastingly, elevational gradients aggregate steep changes in climatic conditions over a short spatial scale (see Körner, 2007 for a review of these effects) and are logistically easier to sample. Since elevational gradients are relatively widespread over the globe, they quickly impose themselves as an ideal alternative for biogeographical studies (Rahbek, 1995, 2005), offering the possibility to readily investigate the causes of spatial variation in species diversity.

The effects of increasing elevation on insects has been comprehensively documented. It affects their morphology, ecophysiology, activity, reproduction, spatial distribution, diversity, and abundance (see Hodkinson, 2005 for review of these effects). In this context, the study of biodiversity changes along elevational gradients has offered many opportunities to understand efficiently the processes involved over small spatial scales, while preventing confusion between historical and biogeographical effects between localities (Hodkinson, 2005; Rasmann *et al.*, 2014).

~ . LEPIDOPTERA AS A BIOLOGICAL MODEL FOR BIODIVERSITY STUDIES . ~

With almost 160,000 species described, Lepidoptera is currently the fourth most diverse order of insects (Kristensen *et al.*, 2007; van Nieukerken *et al.*, 2011). From this richness, more than 95% are moths with their adults active mostly at night. For centuries, they have attracted increasing interest from researchers due to their ease of sampling, abundance, diversity of life histories, as well as their worldwide distribution and species richness, offering opportunities for large-scale meta-analyses (Kristensen *et al.*, 2007). Together with their wide spread popularity among collectors and naturalists, both butterflies and moths are particularly suitable biological models to study various aspects of insect diversity.

Furthermore, Lepidoptera are involved in a broad range of ecological interactions, highlighting them as keystones of many ecosystems. Both caterpillars and adults are primary consumers. Concerning caterpillars, only a marginal proportion consume food sources other than living plant tissues (e.g., other invertebrates, animal and plant detritus; Powell *et al.*, 1999), while adults often depend on specific resources (e.g., nectar, overripe fruits, and sweet saps; Powell *et al.*, 1999; Krenn, 2010). Lepidoptera are also important prey for many groups of predators (Kalka *et al.*, 2008; Karhu and Neuvonen, 1998; Sam *et al.*, 2017), parasitoids (Klemola *et al.*, 2010), and pathogens (Hawkins *et al.*, 1997). To overcome these pressures, Lepidoptera evolved a whole series of adaptive defensive traits in both larval and adult stages. Caterpillars evolved a suite of chemical, physiological, morphological, and behavioural traits allowing them to escape or repel natural enemies (Greeney *et al.*, 2012), while adults often bear adaptive auditory organs and deflective or intimidating features to escape predation (Stevens, 2005; ter Hofstede and Ratcliffe, 2016). Additionally, Lepidoptera are involved in tight evolutionary interactions both as plant-herbivores (Agrawal, 2007) and plant-pollinators (Bawa, 1990), sometimes resulting in co-speciation dynamics. From this remarkable ubiquity at all ecological levels, Lepidoptera have long been recognized as a key group to study general biodiversity patterns and the ecological processes shaping them.

Methodologies to sample Lepidoptera are well-developed. Various methods allow the sampling of all Lepidoptera life stages, in both understorey and canopy (e.g., Blanton, 1990; Raimondo *et al.*, 2009; Zandt, 1994). However, for the sake of simplicity, we will focus on the two methods applied during these studies. Both bait trapping and light trapping (including both automatic light trapping and manual catching at a light source) are among the most widely used tools for sampling adult Lepidoptera: the former takes advantage of the attraction of butterflies and moths to various food baits (Freitas *et al.*, 2014), while the latter takes advantage of the attraction of most moths to light sources (Baker and Sadovy, 1978). The efficiency of these methods remains unmatched, offering an opportunity to record a large number of individuals in a very short time, and with relatively small sampling effort (Beck and Linsenmair, 2006; Freitas *et al.*, 2014). Nonetheless, these methods have various limitations. Firstly, it is known that both bait and light trapping selectively sample Lepidoptera communities. Bait trapping only attracts feeding adults, while different baits will attract different species and become degraded in the field in a relatively short time (Freitas *et al.*, 2014). Comparatively, light trapping attracts flying adult moths, but its efficiency is greatly impacted by the light source used for attraction. Generally, light with smaller wavelengths will attract larger moths on average (van Langevelde *et al.*, 2011). Both methods are also highly sensitive to environmental variables such as temperature, precipitation, vegetation density, moon phases, and cloud cover (Yela and Holyoak, 1997). Despite these limitations, these methods remain two important tools offering readily interpretable datasets for the study of Lepidoptera biodiversity and ecology (Yela & Holyoak, 1997; Beck & Linsenmair, 2006).

~ · THE MOUNT CAMEROON ALTITUDINAL GRADIENT · ~

Culminating at 4,095 m asl., Mount Cameroon is the highest mountain in West Africa. Its southwestern slope is also the only continuous forested elevational gradient on the continent ranging directly from the lowland (ca. 300 m asl.) to the tree line at 2,200 m asl., with minimal human impact along the full forested elevational range (Fig. 1). Mount Cameroon is an active volcano of Hawaiian type, with frequent eruption every ten to thirty years (Proctor *et al.*, 2007). During eruptions, thick lava slowly flows down through the forest from multiple fissure segments on the mountain flanks, sometime reaching the seashore as happened in 1999 (Fig. 1). These repeated eruptions and the associated fires and ashfalls at high elevation are most likely responsible for compressing the forest line below its climatic limit in comparison with other similar altitudinal gradients in the tropics (Jacob *et al.*, 2015; Proctor *et al.*, 2007).

The climate on the southwestern slope of Mt. Cameroon is categorized as perhumid (Martin, 1991). While it is not rare for more than ten meters of rain to fall within a year, the southwestern slope is among one of the rainiest places worldwide (Fig. 2). Seasonality is characterised by one dry and one wet season per year, mainly caused by the alternation of a southward continental dry wind during the dry season (*Harmattan*) and a northward maritime wet wind during the wet season (*monsoon*). Contrastingly, the northern slope is significantly drier due to the interference of the bulk of the mountain with the maritime clouds (Fraser *et al.*, 1998). Temperature remains rather constant throughout the year and linearly declines with elevation by 0.4°C every 100 m (Fig. 2). The mean relative humidity is high on the southwestern slope, and ranges between 75 % and 80 % yearly (Proctor *et al.*, 2007).

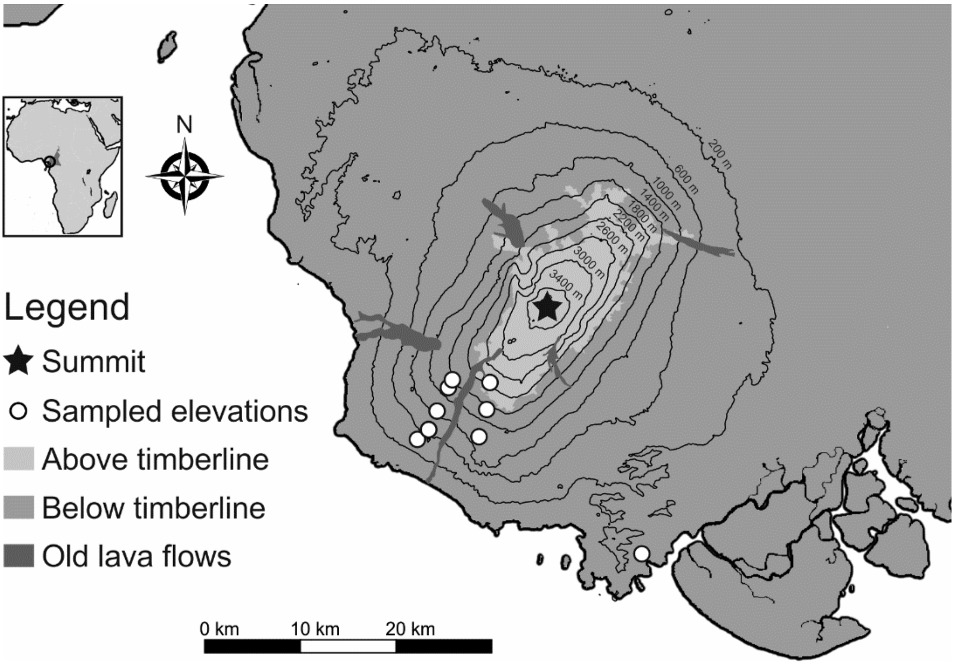

Fig. 1. Map of Mount Cameroon including the sampled elevations for this thesis (figure from Chapter V, modified).

Since 2009, most of the forests on the southwestern slope of Mount Cameroon are included within the limits of the Mount Cameroon National Park (MCNP), with the exception of the coastal forests. In fact, the last large patch of coastal forest is located 20 km South-East. The Bimbia-Bonadikombo community forest is an area under community forest status of exceptional habitat heterogeneity. Within a few kilometers, it encompasses coastal forest and freshwater swamp forest as well as patches of mangroves along the seashore. However, despite its community forest status, human pressure on the forest is high, and land-use change for agriculture, as well logging and poaching is currently ongoing (**Chapter IX**).

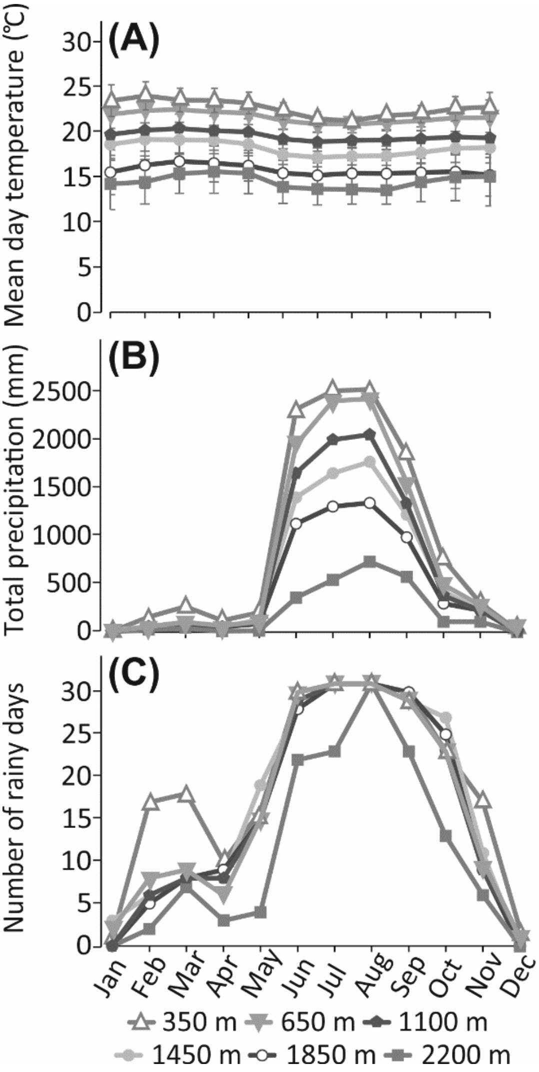

Fig. 2. Weather on Mount Cameroon. (A) Mean daily temperature; (B) monthly precipitation in 2015; and (C) number of rainy days (>2 mm of rainfall) measured by dataloggers in 2015 (from Chapter V).

In contrast, human impact within the current limits of the MCNP is low. The vegetation of Mount Cameroon has been described in detail by Cable and Cheek (1998) and completed on the southwestern slope by Proctor *et al.* (2007) with characterisation of the different soil profiles along the elevational gradient. On the studied slope, tropical lowland evergreen forest extends up to 800 m asl. characterised by a tall canopy and a scarce understorey with local emergence of very large trees. From 800 to 1,700 m asl., low density upland and submontane forest are punctuated by extensive areas dominated by ferns and elephant grass, while montane forests with trees of large stature dominate above 1,700 to the tree line at 2,200 m asl. (Cable and Cheek, 1998; Proctor *et al.*, 2007). Interestingly, the observed forest gaps at mid-elevation are partly caused by volcanism and burial of the forest by ashes (Proctor *et al.*, 2007), but also by the presence of a small population of forest elephants (*Loxodonta cyclotis*) disturbing the vegetation at mid-elevation (**Chapter IV**).

LEPIDOPTERA, TROPICAL RAINFORESTS, AND SEASONALITY

Temporal aspects of insect life history strategies are an important feature (Kishimoto-Yamada and Itioka, 2015; Wolda, 1988). While insects show strong phenological synchrony with the most favourable seasons in temperate regions (i.e., in their emergence, growth, dispersion, and reproduction), seasonality in insect life-cycles is also a common feature of many species in the tropics (Wolda and Fisk, 1981; Wolda, 1988, 1980, 1978). Tropical areas are typically subject to alternation of one or two dry and wet season(s) every year. Long-term field surveys (>10 years) have shown that adult butterfly communities are subject to annual or biannual peaks of species richness and cycles in community similarity, mostly driven by host-plant availability as well as temperature and rainfall (e.g., DeVries *et al.*, 2012; Grøtan *et al.*, 2014, 2012; Intachat *et al.*, 2001; Valtonen *et al.*, 2013). Precisely, the recorded peak of species richness was repeatedly recorded with a time lag of two to three months after the onset of the rainy season(s) (Grøtan *et al.*, 2014, 2012; Intachat *et al.*, 2001; Valtonen *et al.*, 2013). Valtonen *et al.* (2013) reported that this delay was correlated with a peak in vegetation greenness. While the first rains are often associated with leaf flushing in the tropics (Hill *et al.*, 2003; Valtonen *et al.*, 2013), and many caterpillars preferentially feed on young leaves, the observed time lag was proposed to be driven by the lower mortality rate of caterpillars (Valtonen *et al.*, 2013). Regardless, changes in the weather conditions can also negatively and positively influence both caterpillar and adult Lepidoptera species richness and abundance by influencing caterpillar mortality and survival (**Chapter II**).

While temporality is a crucial dimension structuring local communities, small-scale spatial mechanisms are also important (Cottenie, 2005). Lepidoptera communities, for instance, are tightly connected to the local species richness and community composition of plants (Novotny *et al.*, 2002; Valtonen *et al.*, 2017). On the other hand, vegetation structure influences micro-climatic conditions (such as light availability, temperature, and humidity) and micro-habitat heterogeneity as well as the abundance of individual Lepidoptera species and community assemblages (Braga and Diniz, 2015; Checa *et al.*, 2014). In the context of rainforests, the canopy provides Lepidoptera a large array of resources and microhabitats for both adults and caterpillars (Novotný *et al.*, 2003). While there is a plethora of evidence of vertical stratification of Lepidoptera communities (e.g., Ashton *et al.*, 2016a; Basset *et al.*, 2003), the vertical differentiation of a population between both strata can be to such an extent that two subpopulations are in fact totally isolated from each other (Nice *et al.*, 2019). However, knowledge on the relative contribution of all these mechanisms is still lacking. As an illustration, while the fruit-feeding butterfly guilds have been widely used to characterize butterfly habitat association, no comparative study has yet been done on fruit-feeding moths. Since these two groups differ strikingly in their ecology, one might expect different responses to habitat characteristics (**Chapter III**), as well as different responses to disturbances (**Chapter IV**).

~ . DIVERSITY PATTERNS OF TROPICAL LEPIDOPTERA ALONG ELEVATION . ~

Historically, a linear decline of species richness with elevation was for nearly a century the accepted pattern. However, reviews from Rahbek (2005, 1995) challenged this traditional view, emphasizing that a mid-elevational peak of species richness was in fact far more common than previously thought. In this context, Lepidoptera have greatly contributed to building our understanding of the spatial distribution of species along elevational gradients. As one of the hot-topics of the last decades, several dozens of studies have been conducted along elevational gradients in all tropical biomes (e.g., Ashton *et al.*, 2011a; Ashton *et al.*, 2016b; Beck and Chey, 2008; Beck and Kitching, 2009; Brehm, 2002; Brehm & Fiedler, 2003, 2005, Brehm *et al.*, 2003, 2005, 2007, 2013; Hilt & Fiedler, 2005; Hilt, 2005; Hilt *et al.*, 2007; Fiedler *et al.*, 2008; Beck *et al.*, 2011; Ignatov *et al.*, 2011 Odell, *et al.*, 2016). In the Afrotropics however, only a small set of studies have been conducted on the Lepidoptera of Mount Kilimanjaro, Tanzania (e.g., Axmacher *et al.*, 2009, 2004; Axmacher and Fiedler, 2009; Peters *et al.*, 2016).

The majority of elevational patterns of Lepidoptera diversity fall into the four categories defined by McCain and Grytnes (2010). A recent meta-analysis of the elevational patterns of Geometridae along 26 elevational gradients aimed to document the patterns of species richness encountered worldwide (Beck *et al.*, 2017). Among the 19 most complete elevational gradients, 16 showed a peak of species richness at mid-elevations, one a low-plateau, one a low plateau with a mid-peak, and one showed an increasing pattern with elevation (*sensu* McCain and Grytnes, 2010). The main causes explaining species richness patterns along elevational gradients were categorized within four groups by Grytnes and McCain (2007): climatic, historical, biotic, and spatial hypotheses. The meta-analysis performed by Beck *et al.* (2017) found very low support for the overall patterns to be explained by any single driver. However, the species-area relationship (i.e., larger areas contain more species), associated with a general decrease of productivity, was well-supported for explaining elevational patterns but remains to be tested on other groups of Lepidoptera.

Mechanistic approaches were often used to explain the peak of species richness at mid-elevation. The increasing overlap of species ranges at mid-elevation along an altitudinal gradient can produce a mid-elevation peak of species richness without interference of any biotic or abiotic factors (Colwell *et al.*, 2016, 2005, 2004; Colwell and Hurtt, 1994; Colwell and Lees, 2000). This geometric approach, called the *mid-domain effect*, was tested by Brehm *et al.* (2007) and Beck *et al.* (2017) on Geometridae. Generally, the geometric models alone failed to explain the whole pattern. The authors concluded that the mid-domain effect was most likely a modulating parameter of other environmental factors. In this context, Colwell *et al.* (2016) unify the concept of '*environmental favourability*' (i.e., a unimodal gradient of favourability for a given taxon) and the mid-domain effect within the so-called *mid-point attractor*. According to this model, taxa are "attracted" toward a mid-point attractor along the elevation, concentrating and overlapping elevational ranges around this point. For both butterflies and moths, the mid-point attractor accurately reproduces the low- or mid-elevational peak of species richness, allowing us to understand how geometric constraints can parsimoniously contribute to shape the often-found peak of species richness at low elevation (Colwell *et al.*, 2016).

Understanding the mechanisms shaping altitudinal patterns of diversity have several important applications. During the last decade, authors often used elevational gradients to detect the impacts of climate change on species elevational ranges in order to predict extinction risks (Colwell *et al.*, 2008). An important number of these studies have been done using Lepidoptera as a biological model to explore these impacts on species elevational distribution in the tropics (e.g., Chen *et al.*, 2009; Chen *et al.*, 2011a; Chen *et al.*, 2011b; Colwell *et al.*, 2008). Nevertheless, very little is known to which extent the overall patterns of diversity and species elevational range vary seasonally. Since it is acknowledged that the weather conditions influence Lepidoptera phenology, one might expect the overall patterns of species distribution to seasonally change as well. In this context, studies exploring seasonal patterns of diversity along the full elevational range are still critically lacking (**Chapter V**).

~ · A HYPER-DIVERSE, BUT UNKNOWN AND THREATENED ECOSYSTEM · ~

Mount Cameroon belongs to the eastern part of the Guinean Forests of West Africa, a hotspot of biodiversity (Mittermeier *et al.*, 2004). It is an important centre of endemicity for a wide range of taxa (Mittermeier *et al.*, 2011; Myers *et al.*, 2000). However, despite its remarkable importance at the global scale, West African forests are disappearing at an alarming rate. Currently, only 10-15% of the initial primary forest is estimated to remain in West Africa (Myers *et al.*, 2000; Oates *et al.*, 2004; Sloan *et al.*, 2014). The forests of the mainland of the Gulf of Guinea especially, supporting one of the highest human population densities in tropical Africa (ca. 100 inhabitants km^{-2}), are under increasing human pressure. Deforestation for commercial logging or agriculture are the main causes of forest disappearance and fragmentation (Cronin *et al.*, 2014; Oates *et al.*, 2004). While the Biafran forests and highlands currently encompass 18 protected areas, with a surface area of 17,500 km^2, habitat loss at their fringe, illegal logging, and poaching are still common and continue to put these ecosystems under high human pressure (Cronin *et al.*, 2014).

On the other hand, our knowledge of these ecosystems is still very poor. In an extensive field survey at several elevations, Cable & Cheek (1998) recorded 2,435 species of plants solely in the Mount Cameroon area limited to the Southern half of the mountain, as well as patches of coastal forests on the South-East and patches of lowland forests on the North and North-West foothills; ca. 2,700 km^2. This number approximates the total number of plant species known from the British Isles (over 3,000 species; Preston *et al.*, 2002). Their extensive survey and data compilation didn't include the Northern slope of the mountain, suggesting that the current total number of plant species from the Mount Cameroon area is still most likely underestimated (Cable & Cheek, 1998). Concerning Lepidoptera, whilst the diversity of butterflies from Cameroon is relatively well-known (Larsen, 2005; Williams, 2018), with several endemics known from Mount Cameroon (e.g., *Charaxes musakensis*, *Lepidochrysops liberti*, *Ceratrichia fako*), our knowledge of the diversity of moths is comparatively low and mostly based on scarce publications of species descriptions and faunistic records. De Vries & De Vries (2018), from a vast compilation of available literature, report more than 2,500 species of moths from the whole Cameroonian region, again roughly corresponding to the total number of moth species recorded nowadays on the British Isles (Manley, 2015). Although it is intuitively clear that a sampling bias may explain this pattern, the recent descriptions from Mount Cameroon of new species of butterflies, and even new genera of a supposedly well-known moth family (Sáfián and Tropek, 2016; Yakovlev and Sáfián, 2016), support the idea that moths from the Cameroonian region are still poorly known.

Further evidence of this lack of knowledge is illustrated by the fact that no invertebrate species is known to be extinct from the entire West Africans forests (Larsen, 2008; Miller and Rogo, 2001), despite the obvious decline of various natural habitats. Crucially, we could be facing an irreversible loss of species diversity, as well as an unquantifiable loss of knowledge regarding the ecology and spatial distribution of unknown species. In this context, a systematic survey of the Lepidoptera fauna from the Mount Cameroon region would provide a strong baseline to assess the diversity of a hyper-diverse group of insects of major ecological importance (**Chapter VI, VII, & VIII**).

~ · AIMS OF THE THESIS · ~

Mount Cameroon is the only elevational gradient in the whole Afrotropics where butterflies and moths have been standardly sampled simultaneously along a full elevational range starting from sea level to the tree line (ca. 2,200 m asl.). The combination of extreme seasonality on its southwestern slope, together with the presence of the only continuous elevational gradient of nearly pristine forests on the whole continent, provides a unique opportunity to investigate Lepidoptera biodiversity changes at both spatial and temporal scales. Using a multi-taxa approach and two standardized sampling methods, replicated along the full forested elevational range and during three distinct seasons, we applied a sampling effort of Lepidoptera, unmatched on the whole continent, to answer distinct ecological questions:

1/ While the effects of seasonality on Lepidoptera phenology has been well-studied in lowland rainforests across the globe, none of these studies come from an area with such high rainfall concentrated in a few months (>7,000 mm from June to August in 2015; Fig. 2). Since annual cycles of species richness and community similarity have been shown to be influenced by weather conditions and host-plant availability, we question how adult Lepidoptera phenology can be influenced by an extremely wet tropical climate such as the one observed in the lowland forest of Mount Cameroon (**Chapter II**).

2/ Furthermore, although elevational gradient patterns of diversity have been well-studied during the past decades, the effects of seasonality on biodiversity patterns along the full elevational range remain unclear. While seasonality is sometimes simply ignored, authors rather cope with it by routinely pooling their samples. Since investigating the effects of climate change on species distribution in tropical mountains is increasingly important, improving our understanding of short-term temporal dynamics linked to seasonal cycles is needed. We therefore assess how the spatial distribution of Lepidoptera species diversity along the full forested elevational gradient is influenced by seasonal dynamics (**Chapter V**).

3/ Understanding how small-scale ecological mechanisms shape biodiversity is crucial for establishing efficient local biodiversity conservation strategies. The forest habitat association of Lepidoptera has been comprehensively documented using the fruit-feeding butterfly guild as a biological model. Nevertheless, the habitat association of fruit-feeding moths has so far been ignored, despite these representing the vast majority of Lepidoptera diversity. Focusing on both understorey and canopy strata, we investigate how forest openness, structure, and diversity influence local communities of fruit-feeding butterflies and moths (**Chapter III**). By extension, the existence of a small population of forest elephants on the southwestern slope raises the question of how natural disturbances caused by this endangered megaherbivore influence forest structure, and to which extent it influences tree and Lepidoptera diversity as well. Taking advantage of the exclusion of the elephant population from an entire forested area, we examine how they may influence rainforest structure, and to which extent it impacts tree and Lepidoptera diversity (**Chapter IV**).

4/ Large inventories of Lepidoptera in Afrotropical rainforests often contain a large number of unknown species as well as new data on individual species' geographical distribution. Taking advantage of our large Lepidoptera samples from an under sampled area, we scrutinize the diversity of selected moth groups (**Chapter VI, VII, & VIII**).

5/ The extent of the Mount Cameroon National Park stops at the lowland forest on its southwestern slope (ca. 300 m asl.). Most of the coastal forests of the region today are highly disturbed or simply deforested. Overall, only a last large patch of coastal forest, of exceptional heterogeneity ca. 20 km South-East, is nowadays protected under community forest status. Despite this, intensive logging and poaching are still ongoing. We therefore assess the local diversity of trees, birds, and butterflies, and compare it with the diversity of these groups in the Mount Cameroon lowland forests, questioning the relevance of excluding this area from full protected status (**Chapter IX**).

To answer these aims, the thesis is organised as follow:

- Firstly, the thesis focuses on lepidopteran biodiversity in lowland and upland forests, as the most species rich habitats of the mountain. **Chapter II** reveals the strong seasonality of the local lepidopteran communities. **Chapter III** describes in detail the habitat associations of fruit-feeding butterflies and moths, showing relatively similar relationships of both groups to their habitats. **Chapter IV** explores the impacts of elephant-made natural disturbances on forest habitats at mid-elevation, detailing their strong effects on forest structure and diversity of tree, butterfly, and moth communities.
- **Chapter V** extends our analyses into higher elevations, describing the elevational biodiversity patterns along the complete forested elevational gradient of several Lepidoptera taxa in three different seasons, and describe how these diversity patterns, as well as the elevational ranges of individual species change seasonally.
- **Chapters VI, VII, and VIII** include faunistic records of species never reported from the area and combine them with taxonomy and life history notes on selected taxa. Finally, a new hotspot of many-plumed moths is described and is supplemented by descriptions of nine new species in the genus *Alucita*.
- **Chapter IX** focuses on the biodiversity of the coastal forests in the studied area for birds, trees, and butterflies. It discusses its current conservation status and provides clues for a possible future conservation strategy improvement.

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Male Epiphora feae Aurivillius, 1910 *caught during the transition from dry to wet season around the PlanteCam camp (ca., 1,100 m asl.) © V. Maicher*

CHAPTER II

Flying between raindrops: Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon

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ORIGINAL RESEARCH

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Flying between raindrops: Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon

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Abstract

Although seasonality in the tropics is often less pronounced than in temperate areas, tropical ecosystems show seasonal dynamics as well. Nevertheless, individual tropical insects' phenological patterns are still poorly understood, especially in the Afrotropics. To fill this gap, we investigated biodiversity patterns of Lepidoptera communities at three rainforest localities in the foothills of Mount Cameroon, West Africa, one of the wettest places in the world. Our multitaxa approach covered six lepidopteran groups (fruit-feeding butterflies and moths, the families Sphingidae, Saturniidae, and Eupterotidae, and the subfamily Arctiinae of Erebidae) with diverse life strategies. We sampled adults of the focal groups in three distinct seasons. Our sampling included standardized bait trapping (80 traps exposed for 10 days per locality and season) and attraction by light (six full nights per locality and season). Altogether, our dataset comprised 20,576 specimens belonging to 559 (morpho)species of the focal groups. The biodiversity of Lepidoptera generally increased in the high-dry season, and either increased (fruit-feeding moths, Arctiinae, Saturniidae) or decreased (butterflies, Sphingidae) in the transition to the wet season in particular groups. Simultaneously, we revealed a strong species turnover of fruit-feeding Lepidoptera and Arctiinae among the seasons, indicating relatively high specialization of these communities for particular seasons. Such temporal specialization can make the local communities of butterflies and moths especially sensitive to the expected seasonal perturbations caused by the global change. Because of the key role of Lepidoptera across trophic levels, such changes in their communities could strengthen this impact on entire tropical ecosystems.

KEYWORDS
Afrotropics, biodiversity patterns, Lepidoptera, multitaxa approach, phenology, seasonality

1 | INTRODUCTION

Understanding the spatial and temporal dynamics of biodiversity is one of the main goals of current ecology (Magurran, 2007; Rosenzweig, 1995). Although spatial patterns of biodiversity have been widely studied, research on its temporal dynamics in natural conditions remains strongly challenging and thus much less common. This is especially valid for the tropics, where the seasonal biodiversity patterns still remain poorly understood (Kishimoto-Yamada & Itioka, 2015).

In tropical rainforests, phenology of individual insect species, as well as of whole ecosystems, follows the regional seasonality typically represented by swapping of the wet and dry seasons (Kishimoto-Yamada & Itioka, 2015; Wolda, 1988). Various tropical areas, usually with one or two annual rainy seasons, exhibit annual or biannual peaks of adult Lepidoptera species richness, as well as phenological patterns in their communities' composition (Cruz-Neto, Machado, Duarte, & Lopes, 2011; DeVries, Murray, & Lande, 1997; DeVries, Alexander, Chacon, & Fordyce, 2012; Devries & Walla, 2001; Grøtan, Lande, Engen, Sæther, & DeVries, 2012; Grøtan, Lande, Chacon, & Devries, 2014; Hilt, Brehm, & Fiedler, 2007; Intachat, Holloway, & Staines, 2001; Valtonen et al., 2013). However, until lately, our knowledge on the phenology of tropical rainforests insects, including Lepidoptera (i.e., butterflies and moths), suffered from a lack of comprehensive studies. Available detailed studies described seasonal changes of some selected lepidopteran groups and proposed mainly weather conditions and host–plant availability as the main drivers of Lepidoptera phenology in tropical rainforests (e.g., Intachat et al., 2001; DeVries et al., 2012; Grøtan et al., 2012; Grøtan et al., 2014; Valtonen et al., 2013). Several of them detected the main peak of adult Lepidoptera abundances (Intachat et al., 2001) and species richness (Grøtan et al., 2014, 2012 ; Valtonen et al., 2013) with a time lag of two or three months after the beginning of the wet season. Regardless, both temperature and rainfall fluctuations were revealed to influence lepidopterans' abundances and species richness in both directions (Grøtan et al., 2014, 2012 ; Kishimoto-Yamada & Itioka, 2015; Wolda, 1988). A decreasing day temperature and increasing precipitation in the early rainy season negatively affect adults' activity (Holyoak, Jarosik, & Novák, 1997; Ribeiro & Freitas, 2010), while strong rainfalls and high humidity increase the mortality of early life stages by increasing the activity of pathogens, or by direct disturbance of caterpillars in their host plants (Hill, Hamer, Dawood, Tangah, & Chey, 2003; Intachat et al., 2001). On the other hand, rainfalls often trigger sprouting of young leaves important for caterpillars, especially in their earliest developmental stages (Hill et al., 2003; Valtonen et al., 2013), whereas the wettest part of the year also coincides with a higher predation rate on caterpillars (Molleman, Remmel, & Sam, 2016). Similarly, mass flowering in the late rainy and high-dry seasons was described to support the biodiversity of adult geometroid moths (Intachat et al., 2001) and Sphingidae (Cruz-Neto et al., 2011).

Individual groups of tropical Lepidoptera can differ in their phenological patterns (Ribeiro, Prado, Brown, & Freitas, 2010). The highest species richness of particular tropical lepidopteran groups was detected in different seasons: high-dry season for Sphingidae (Cruz-Neto et al., 2011; Owen, 1969), geometrids (Hilt et al., 2007) and butterflies (Aduse-Poku et al., 2012; DeVries et al., 2012; Grøtan et al., 2014, 2012 ; Ribeiro et al., 2010), transition from wet to dry seasons for butterflies (Valtonen et al., 2013), and wet season for butterflies (Checa, Rodriguez, Willmott, & Liger, 2014; DeVries et al., 1997; Devries & Walla, 2001). No specific seasonal patterns of species richness were revealed for Sphingidae (Beck & Linsenmair, 2006), Arctiinae (Hilt et al., 2007), butterflies (Larsen, Riley, & Cornes, 1979; Molleman, Kop, Brakefield, Vries, & Zwaan, 2006; Owen & Chanter, 1972), pyraloids (Fiedler & Schulze, 2004; Schulze & Fiedler, 2003), and macro-heterocerans (Tikoca et al., 2016). An overwhelming majority of these group-specific patterns came from single-taxon studies carried out in different tropical localities or even areas, often with different seasonality. It is thus very difficult to separate the effects of biogeography and individual lepidopteran groups' phenology with the current knowledge.

Moreover, most of the tropical Lepidoptera seasonality studies originated from South and Central America and Southeast Asia. Publications on the temporal dynamics of Afrotropical Lepidoptera are still relatively scarce and mostly focused on butterflies only (e.g., Owen & Chanter, 1972; Larsen et al., 1979; Molleman et al., 2006; Namu, Githaiga, Kioko, Ndegwa, & Hauser, 2008; Aduse-Poku et al., 2012; Valtonen et al., 2013; but see Owen, 1969; Axmacher, Kühne, & Vohland, 2008). Recently, it was predicted that the global change will strongly affect the seasonality of rainfall in the tropics during the next century, with expected strong changes in the amount of precipitation in equatorial Africa (Feng, Porporato, & Rodriguez-Iturbe, 2013). Together with the expected shifts in the seasonality timing (Feng et al., 2013), the Afrotropical Lepidoptera communities' phenology ought to shift or completely change, with unpredictable consequent effects on the related trophic levels. To predict such changes, it is firstly necessary to identify the current seasonal patterns of communities.

Here, we bring a detailed study of several taxonomical groups of adult lepidopterans from three different seasons in the lower altitudes of Mount Cameroon, West Africa. We address the following questions: (a) How does the extreme seasonality affect species richness, abundance, and diversity of local lepidopteran communities? (b) Are there any phenological patterns in community compositions of individual lepidopteran groups? (c) Are the phenological patterns caused by interseasonal species turnover or community nestedness? (d) Are these phenological patterns consistent across a few unrelated lepidopteran groups?

To answer these questions, we combined an extensive standardized sampling by fruit-baited traps with attraction by light. Considering the extreme seasonality within the study area, we expected continuously increasing biodiversity of individual focal groups after the extreme wet season, with the peak in the dry season for butterflies, and in the beginning of the wet season for moths. Simultaneously, we also expected relatively high interseasonal specialization of communities. Our study represents the first multitaxa survey of butterflies (Figure 1) and several moth groups using standardized sampling at light and by bait traps in the Afrotropical region. Simultaneously, our bait trapping is among the most intensive worldwide. Because Mount Cameroon is one of the rainiest regions in the world, with a strong discrepancy between high-dry and high-wet seasons (Proctor, Edwards, Payton, & Nagy, 2007), we expected distinct seasonal patterns of both species richness and community composition.

2 | MATERIALS AND METHODS

2.1 | Study area and sites

Mount Cameroon is the highest mountain in West and Central Africa, rising directly from the seashore to its peak at 4,095 m a.s.l. It is located in the southwestern part of the Cameroon Volcanic Line (also known as Gulf of Guinea Highland), being the only active volcano in the region. Its slopes, excluding the eastern one adjoining the town of Buea, are covered by continuous tropical rainforests from lowland (often ~300 m a.s.l., although in some areas disturbed up to 700 m a.s.l.) to the timberline (~2,100–2,400 m a.s.l.), where the rainforest is replaced by montane and subalpine grasslands. Mount Cameroon is recognized as a hotspot of biodiversity and endemism for a wide range of taxa (Cronin, Libalah, Bergl, & Hearn, 2014), including Lepidoptera (Heppner, 1991; Maicher et al., 2016; Ustjuzhanin, Kovtunovich, Sáfián, Maicher, & Tropek, 2018; Yakovlev & Sáfián, 2016). The region is characterized by strong seasonality, mostly driven by the northward wet air movement during summer (monsoon), and the southward dry air movement from the Sahel during winter (harmattan) (Lefèvre, 1967). Annual precipitation usually exceeds 10,000 mm at the lower elevations of the southwestern slopes (making it one of the rainiest places in the world), with most of the rainfall concentrated between June and September, when monthly precipitation usually exceeds 1,500 mm (Lefèvre, 1967). Conversely, any rains between mid-November and February are rare, especially at higher elevations. Two short transition seasons occur in March/May and October/November with a gradual increase and decrease of rainfall, respectively (Molua & Lambi, 2006).

FIGURE 1 *Euphaedra permixtum* (Butler, 1873) is a fruit-feeding butterfly typical for many tropical forests of West and Central Africa. Photo by Jan Mertens

All our material was sampled inside the Mount Cameroon National Park, at three sampling sites in the southwestern foothills of Mount Cameroon: around the Bamboo Camp (N 04.08990°, E 09.05174°; 350 m a.s.l.), the Drink Gari Camp (N 04.10221°, E 09.06304°; 650 m a.s.l.), and the PlanteCam Camp (N 04.11750°, E 09.07094°; 1,100 m a.s.l.). The first two sites are covered by a lowland rainforest with closed high canopy and relatively scarce understorey layers, while the forest around the PlanteCam Camp is already of an upland character, including a mixture of both lower and higher elevation forest elements. The latter locality is also relatively strongly affected by natural disturbances by forest elephants (*Loxodonta cyclotis*), reducing tree densities and creating forest openings dominated by various grasses, herbs, and ferns (Proctor et al., 2007). Such open areas were, however, avoided as much as possible during our sampling.

2.2 | Lepidoptera sampling

All lepidopterans were sampled from 2014 to 2016, combining bait trapping and manual catching of specimens attracted by light. To cover most of the main seasonality aspects, lepidopterans were sampled in three different seasons: a transition from wet to dry seasons (November/December 2014), a high-dry season (January/February 2016), and a transition from dry to wet seasons (April 2015). We did not sample during the high-wet season as it would be impossible to keep the traps baited and the lights working during the heavy rains.

Within each of the three sites, fruit-feeding lepidopterans were sampled in 16 circular plots placed in continuous forest or larger forest patches with a minimum distance of 150 m between each other (the same plots as in Ferenc et al., 2016). Within each plot (20 m radius), five Van Someren–Rydon type traps were exposed (modified IKEA PS Fångst hanging storage devices: height 75 cm, diameter 23 cm; first used by Sáfián, Csontos, & Winkler, 2011). Of these, four understory traps were installed as close to the ground as possible, and one canopy trap was set at a 20(±5) m height. Altogether, 80 traps were thus exposed at each site in each season. Each trap was baited by ca 0.3 L of fermented mashed bananas, refreshed daily, and completely replaced every three to five days according to bait condition. All the traps were exposed for 10 consecutive days within each sampling season. Every day, all captured butterfly and moth specimens were removed, killed, identified, and counted. Altogether, this study includes material collected by 240 traps, each exposed for 30 days (i.e., 7,200 "trap-days" in total).

Within each of the three sites, moths were attracted by light in three plots selected to cover the main available forest habitats. These plots were placed at least a few 100 m distant from each other. In each of the three plots, the sampling was performed for two entire nights from dusk till dawn (6–7 p.m./a.m. depending on the season) per site and season, making 54 complete nights of light catching in total. Five nights before and after a full moon were avoided. Moths were attracted by an energy-saving bulb (M036 produced by Hadex, Czechia: 4100 K, 5300 lm, 105 W, 230 V, 5U) placed in the center of two perpendicularly placed white sheets (1.5 × 1.5 × 1.8 m, the cloth type B produced by Entosphinx, Czechia). Each night, all individuals of the four focal moth groups (Arctiinae, Eupterotidae, Saturniidae, and Sphingidae) were caught by a jar saturated by vapors from an ammonia solution and stored for later identification.

For all analyses, we treated the six focal lepidopteran groups separately: bait-trapped butterflies (mostly Satyrinae and Limenitidinae subfamilies of Nymphalidae, hereafter referred to as *butterflies*), bait-trapped moths (mostly Erebidae, hereafter referred to as *fruit-feeding moths*), and light-attracted families Sphingidae, Saturniidae, and Eupterotidae, and the subfamily Arctiinae of Erebidae. Part of the material (most butterflies and some bait-trapped moths, i.e., common Erebinae and Calpinae) was identified directly in the field; the rest was later mounted and identified into (morpho)species in a laboratory combining morphological features and genitalia dissections. Voucher specimens are stored in the Institute of Entomology, Biology Centre, Czech Academy of Sciences, České Budějovice, Czechia (bait-trapped butterflies and moths), and the Nature Education Centre, Jagiellonian University, Kraków, Poland (all other focal groups, as well as a portion of the bait-trapped species).

2.3 | Species richness and diversity

All the following analyses were performed using the software R v. 3.4.3 (R core Team, 2017).

To estimate the completeness of the samples, individual-based rarefaction curves of the species richness and sample coverage (i.e., the probability that a newly sampled individual would belong to the previously sampled species; Chao & Jost, 2012) curves were computed for each group in each season with the *iNEXT* package using 50 randomizations (Chao et al., 2014; Hsieh, Ma, & Chao, 2016). For an estimation of the total species richness of each focal group in each season, the bias-corrected Chao1 species richness estimator was computed with the *SpadeR* package (Chao, Ma, Hsieh, & Chiu, 2016).

To avoid the known problems with incomplete inventories and to allow better comparability with other studies, our interseasonal biodiversity comparisons were based on four different metrics, all based on the critical review by Beck and Schwanghart (2010). To compare communities, we used the following indices: (a) *abundance*, that is, the number of sampled individuals; (b) *species richness*, that is, the number of recorded species; (c) the *bias-controlled effective number of species* (eHbc) based on bias-corrected Shannon's entropy, currently considered as one of the most suitable measures of biodiversity in potentially undersampled communities (Beck & Schwanghart, 2010), and (d) *Fisher's* α, the diversity index often used in entomological studies of biodiversity for its relative independence on sample size and robustness for comparisons of incomplete inventories. The latter two indices were computed using the *entropart* (Marcon & Hérault, 2015) and *vegan* (Oksanen et al., 2017) packages, respectively.

To test the interseasonal differences in all four measures, the generalized linear mixed-effect models (GLMM) were applied, with *season* as a fixed factor, and *sites* and *plots* (nested in *sites*) as random-effect variables. Each sample was comprised of all specimens collected within each plot in the 10 sampling days for the bait-trapped material (i.e., all five traps and 10 days of bait trapping per plot were pooled to form a sample), and within each plot in two sampling nights for the light-attracted material (i.e., the two sampling nights per plot were pooled to form a sample). Species richness and abundance were fit into the models with negative binomial distribution (O'Hara & Kotze, 2010), and eHbc and Fisher's α were log-transformed in order to improve the parametric test assumptions, based on the models' residuals. The pairwise post hoc comparisons of the least square means with Tukey adjustment were then applied among the particular sampled seasons. All models were computed using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). To quantify the proportion of variance explained by seasonality after excluding the effects of the random factors, we have also computed its marginal R^2 from all significant models using the *piecewiseSEM* package (Lefcheck, 2016).

2.4 | Species turnover

To quantify the interseasonal changes in species composition, we used measures of beta-diversity. Beta-diversity was partitioned into two additive components: (a) interseasonal *species turnover* and (b) *nestedness* of communities occurring in individual seasons (Baselga, 2010, 2012). The first represents the part of the total dissimilarity caused by species turnover among individual seasons. The latter represents the part of the total dissimilarity caused by the fact that the species-poorer community is a subset of the richer one. For each group, the incidence-based Sørensen dissimilarity index ($\beta_{\text{sør}}$; Baselga, 2010) was used as an estimation of the total dissimilarity between all pairwise combinations of the seasons. $\beta_{\text{sør}}$ was then partitioned into the Simpson dissimilarity index (β_{sim}), reflecting the dissimilarity caused by the species turnover, and into the nestedness (β_{nes}), reflecting the dissimilarity caused by the communities' nestedness. All the indices were computed with the *betapart* package (Baselga & Orme, 2012).

2.5 | Community composition

Interseasonal changes in species composition of the sampled communities were analyzed by multivariate ordination methods (Šmilauer & Lepš, 2014). For all analyses, material from all five traps per plot and 10 sampling days per season was pooled. To reveal if individual samples (plots) cluster mainly according to the sampling season, Nonmetric Multidimensional Scaling analyses (NMDS) with Bray–Curtis dissimilarity matrices were run for each focal group separately. Because NMDSs revealed a strong influence of the sampling sites on the communities' composition of all focal groups, the influence of season was tested by partial canonical correspondence analyses (CCA) with *season* as the explanatory variable and *site* as the covariate. The log-transformed ($n + 1$) abundances of individual Lepidoptera species were used as the response variables (Šmilauer & Lepš, 2014). All ordination analyses were tested by Monte Carlo permutation tests with 999 permutations. All ordination analyses were performed in Canoco 5 (ter Braak & Šmilauer, 2012).

3 | RESULTS

3.1 | Total species richness and abundance

In total, 20,576 individuals of all focal groups were collected. From these numbers, 16,062 individuals (10,425 butterflies, 5,637 fruit-feeding moths) belonging to 403 (morpho)species (117 butterflies, 286 fruit-feeding moths) were bait-trapped, and 4,514 individuals (3,645 Arctiinae, 517 Sphingidae, 252 Saturniidae, and 100 Eupterotidae) of 156 (morpho)species (86 Arctiinae, 38 Sphingidae, 15 Saturniidae, and 17 Eupterotidae) of the focal moth groups were attracted by light (Table 1).

For both bait-trapped taxa, the individual-based rarefaction curves closely approach the asymptote, indicating relatively well-sampled communities, especially concerning butterflies (Supporting Information Figure S1–S3). Concerning the light-attracted moth groups, the individual-based rarefaction curves and Chao1 estimators suggested relatively lower sampling coverage (Supporting Information Figure S1–S3, Table 1). However, the sample coverages of all individual groups in each season are generally well over 90%, indicating well-sampled communities (Supporting Information Figure S1–S3, Table 1), except for Eupterotidae with relatively undersampled communities during the high-dry season and the transition from dry to wet seasons.

Both total abundance and species richness per site were lowest during the transition from wet to dry seasons for all focal groups, except Eupterotidae for whom total abundance was lower during the high-dry season (Table 1, Figure 2). Total abundance was highest in the high-dry season for butterflies, Sphingidae and Saturniidae, and in the transition from dry to wet seasons for fruit-feeding moths and Arctiinae. Eupterotidae were most abundant during the transition from wet to dry seasons (Table 1, Figure 2). The Chao1 followed the same patterns as total species richness for all groups, except Saturniidae with the highest Chao1 in the transition from wet to dry seasons (Table 1). The

TABLE 1 Summary of abundance and diversity of individual focal groups of Lepidoptera in different seasons on Mount Cameroon

Focal group	Season	Total abundance	Total number of species	eHbc[a]	Fisher's α	Chao1 (±SE[b])	SC[c]
Butterflies	Wet to dry	1,701	88	**37.57**	**19.68**	99.7 (±7.9)	**0.99**
	Dry	**6,789**	**101**	36.33	16.83	**106.6 (±5.3)**	**0.99**
	Dry to wet	1,935	88	33.94	18.99	102.2 (±8.6)	**0.99**
	Total	10,425	117	44.1	18.46	130.0 (±9.3)	0.99
Fruit-feeding moths	Wet to dry	1,238	146	42.54	43.02	239.1 (±33.3)	0.95
	Dry	1,841	152	**44.74**	39.29	203.3 (±18.1)	**0.97**
	Dry to wet	**2,558**	**186**	43.89	**46.11**	**267.3 (±26.5)**	**0.97**
	Total	5,637	286	57.9	63.62	443.5 (±42.8)	0.98
Arctiinae	Wet to dry	845	60	27.35	14.76	63.0 (±2.9)	**0.99**
	Dry	1,248	62	20.62	13.71	75.1 (±9.0)	**0.99**
	Dry to wet	**1,552**	**79**	**31.92**	**17.59**	**91.0 (±7.9)**	**0.99**
	Total	3,645	86	32.8	15.79	102.5 (±12.9)	0.99
Sphingidae	Wet to dry	111	16	6.2	5.13	25.0 (±8.0)	0.92
	Dry	**262**	**24**	**7.12**	**6.43**	**36.0 (±10.7)**	**0.96**
	Dry to wet	144	20	5.26	6.31	33.6 (±11.1)	0.92
	Total	517	38	7.09	9.45	60.62 (±14.9)	0.97
Saturniidae	Wet to dry	40	7	5.09	2.46	8.0 (±2.2)	0.95
	Dry	**132**	**11**	2.95	2.85	14.0 (±4.1)	**0.97**
	Dry to wet	80	**11**	**7.29**	**3.45**	**20.9 (±10.1)**	0.94
	Total	252	15	7.14	3.49	20.0 (±6.0)	0.98
Eupterotidae	Wet to dry	**54**	**14**	11.87	6.13	**15.5 (±2.2)**	**0.93**
	Dry	15	9	**13.35**	**9.5**	13.7 (±5.2)	0.62
	Dry to wet	31	10	9.7	5.12	12.9 (±4.1)	0.87
	Total	100	17	12.5	5.88	20.0 (±4.1)	0.96

Note. The highest values of each diversity measure for each focal group are indicated in bold.

[a] The bias-controlled effective number of species based on bias-corrected Shannon's entropy. [b] Standard error. [c] Sampling coverage.

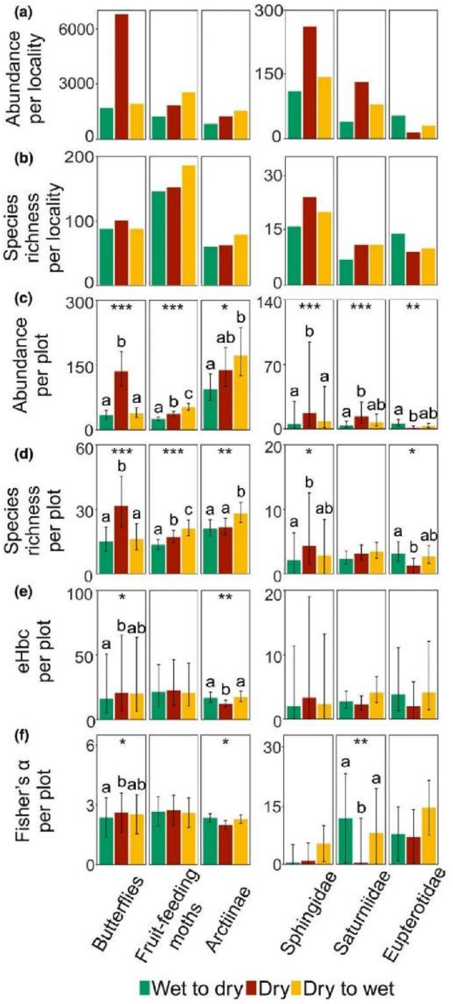

FIGURE 2 Mean (a) abundance and (b) species richness per locality during distinct sampling seasons. Results of GLMMs of (c) abundance, (d) species richness, (e) bias-controlled effective number of species, and (f) Fisher's α per sampling plot, sampled by standardized bait trapping (butterflies and fruit-feeding moths) and light attraction (Arctiinae, Eupterotidae, Sphingidae, and Saturniidae). Means per plot with 95% unconditional confidence intervals are visualized. The GLMM results of individual models are included (the type II Wald χ^2 tests: $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$); see Table 2 for more detailed results

total eHbc showed different patterns (Table 1). It was highest either in the high-dry season (for fruit-feeding moths, Sphingidae and Eupterotidae), in the transition from wet to dry seasons (for butterflies), and in the transition from dry to wet seasons (for Arctiinae and Saturniidae). Fisher's α followed a similar pattern, except for fruit-feeding moths with the highest value in the transition from dry to wet seasons.

3.2 | Local species richness and diversity

The GLMMs of abundance and species richness per sampling plot (Figure 2, Table 2) revealed the high-dry season communities significantly most abundant and richest for butterflies and Sphingidae, and poorest for Eupterotidae. Fruit-feeding moths and Arctiinae were shown to be significantly richest in individual plots in the transition from dry to wet seasons. Saturniidae did not reveal any significant interseasonal pattern in species richness per plot but were most abundant in the high-dry season. Similarly, the high-dry season eHbc per plot (Figure 2) was significantly highest for butterflies and significantly lowest for Arctiinae. The other biodiversity models did not show any significant effects of seasonality on the diversity of the individual focal groups. Seasonality was revealed also as the crucial factor influencing abundance of the studied groups, as the proportion of its explained conditional variability exceeded 39% for all of them, except Sphingidae for whom it explained 10% of the variability. The proportion of variability in species richness explained by seasonality was lower, but still exceeded 26% for all the significant models, except for Sphingidae again with 8% of the explained variability (Table 2).

3.3 | Beta diversity

The pairwise Sørensen total dissimilarities varied greatly among taxa (Table 3). The communities of fruit-feeding moths, Sphingidae, Saturniidae, and Eupterotidae, were shown as the most dissimilar among the seasons ($\beta_{sør}$ ranging from 0.25 and 0.61). The beta-partitioning of the total dissimilarity revealed that the majority of the total dissimilarity among the sampled seasons can be explained by species turnover (more than 80% of $\beta_{sør}$ for all season combinations) for fruit-feeding moths and Sphingidae. For Saturniidae and Eupterotidae, the total dissimilarity between the two transition seasons was mostly explained by the nestedness in the transition from dry to wet seasons for Saturniidae (57% of $\beta_{sør}$), while Eupterotidae revealed the opposite pattern (60% of $\beta_{sør}$).

The communities of butterflies and Arctiinae were relatively more similar among the sampled seasons ($\beta_{sør}$ ranging from 0.15 and 0.19). This dissimilarity was mainly explained by the species turnover, especially between the transition from wet to dry seasons and the high-dry season for Arctiinae (94%), and between the two transition seasons for butterflies (100%).

TABLE 2 Summaries of the GLMMs results for individual models

Focal group	Response variable	χ^2	*df*	*p*-Value	Marginal R^2
Butterflies	Abundance	364.1	2	<0.01	0.79
	Species richness	289.59	2	<0.01	0.43
	eHbc	8.42	2	0.01	0.02
	Fisher's α	6.99	2	0.03	0.02
Fruit-feeding moths	Abundance	61.33	2	<0.01	0.59
	Species richness	40.07	2	<0.01	0.29
	eHbc	0.72	2	0.70	–
	Fisher's α	1.12	2	0.57	–
Arctiinae	Abundance	7.11	2	0.03	0.90
	Species richness	11.63	2	<0.01	0.26
	eHbc	9.71	2	<0.01	0.26
	Fisher's α	6.71	2	0.03	0.20
Sphingidae	Abundance	13.9	2	<0.01	0.10
	Species richness	8.74	2	0.01	0.08
	eHbc	4.81	2	0.09	–
	Fisher's α	5.20	2	0.07	–
Saturniidae	Abundance	14.43	2	<0.01	0.39
	Species richness	2.04	2	0.36	–
	eHbc	4.23	2	0.12	–
	Fisher's α	11.38	2	<0.01	0.22
Eupterotidae	Abundance	12.45	2	<0.01	0.47
	Species richness	6.99	2	0.03	0.27
	eHbc	4.58	2	0.10	–
	Fisher's α	3.04	2	0.22	–

3.4 | Species composition

The partial CCAs (Figure 3, Table 4) revealed significant interseasonal differences in the community composition for butterflies, fruit-feeding moths, and Arctiinae, with relatively well-separated communities of all three sampled seasons (although a small overlap between both transitions was detected for butterflies). No significant interseasonal differences in the community composition were revealed for Sphingidae, Saturniidae, and Eupterotidae.

4 | DISCUSSION

We identified seasonality as a crucial factor for forming adult communities of Lepidoptera in the studied West African tropical rainforest, although the phenological patterns slightly differed among the particular groups studied. Both species richness and abundance were generally lower at the end of the wet season and increased toward the high-dry season. Whereas we do not have any data from the high-wet season itself, the low abundance and diversity of adult Lepidoptera can be related to the climatic harshness of the high-wet season on Mount Cameroon (one of the wettest places in the world, see above). These patterns corroborate with several studies of sphingids (Cruz-Neto et al., 2011; Owen, 1969) and butterflies (Aduse-Poku et al., 2012; DeVries et al., 2012; Grøtan et al., 2014, 2012 ; Ribeiro et al., 2010) from other tropical areas. Richer and more abundant communities during wet seasons are known for Neotropical fruit-feeding butterflies (Checa et al., 2014; DeVries & Walla, 2001; DeVries et al., 1997). These studies, however, did not originate from areas with such strong seasonality and extreme wet season.

The high abundance and diversity of adult tropical lepidopterans in the dry season are often interpreted by requirements of their adult and larval stages. During the wet season, adults have less time for various activities including feeding, mating, and dispersal behavior, particularly in sun-dependent butterflies. Although there are no studies of vegetation phenology on Mount Cameroon, the flowering peak of many abundant trees, representing the main source of nectar in the local communities, seems to be during the high-dry season according to our experience. But the high humidity and strong precipitation can also affect caterpillars both negatively (such as higher activity of pathogens, higher predation rate, or mechanical disturbance by strong rains; Janzen, 1993; Intachat et al., 2001; Hill et al., 2003; Molleman et al., 2016) and positively (by common mass sprouting of young leaves of various host plants). In the extreme wet season on Mount Cameroon, we hypothesize that negative effects

TABLE 3 Partitioning of beta-diversity among the sampled seasons and for individual focal groups of Lepidoptera into nestedness and species turnover

Total dissimilarity and nestedness		
Butterflies		
Dry to wet (88)	0.18 (32%)	
Wet to dry (88)	0.16 (37%)	0.15 (0%)
	Dry (101)	Dry to wet (88)
Fruit-feeding moths		
Dry to wet (186)	0.46 (13%)	
Wet to dry (146)	0.44 (2%)	0.44 (17%)
	Dry (152)	Dry to wet (58)
Arctiinae		
Dry to wet (79)	0.19 (**58%**)	
Wet to dry (60)	0.16 (6%)	0.19 (**66%**)
	Dry (62)	Dry to wet (79)
Sphingidae		
Dry to wet (20)	**0.50** (10%)	
Wet to dry (16)	**0.55** (20%)	**0.61** (8%)
	Dry (24)	Dry to wet (20)
Saturniidae		
Dry to wet (11)	0.36 (0%)	
Wet to dry (7)	0.44 (36%)	0.33 (**57%**)
	Dry (11)	Dry to wet (11)
Eupterotidae		
Dry to wet (10)	0.47 (6%)	
Wet to dry (14)	0.39 (43%)	0.25 (**60%**)
	Dry (9)	Dry to wet (10)

Note. The values represent the pairwise Sørensen dissimilarity indices (in bold if >0.50). The proportions in parentheses represent the part of total dissimilarity caused by the nestedness (in bold if >50%), while the remaining part represents the species turnover. The numbers in parentheses behind the seasons stand for the number of collected species.

dominate, as the extremely low solar radiation negatively influences foodplants' photosynthesis and high water stress decreases production of new plant tissues (van Schaik, Terborgh, & Wright, 1993; Wright, 1996). Although no exact data exists, we experienced the main vegetation sprouting in the transition from dry to wet season, while in the beginning of the dry season many herbs are also growing and flowering. Considering the dramatic rainfall discrepancy between the high-dry and high-wet seasons on Mount Cameroon, we hypothesize that the highest abundance and diversity of most studied lepidopteran groups during the transition from dry to wet

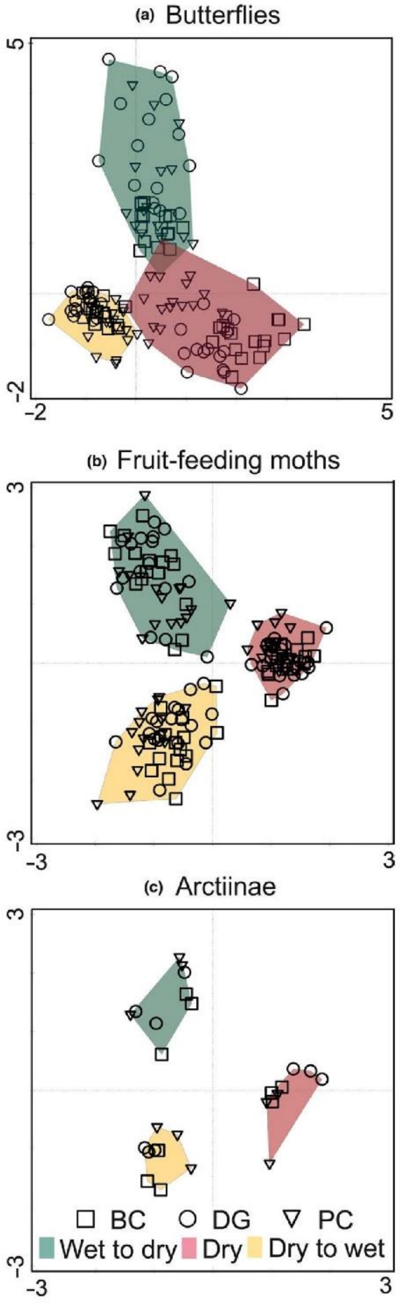

FIGURE 3 Ordination diagrams of the partial CCA with *season* as the explanatory variable, and *site* as the covariate. Individual samples from different seasons (distinguished by polygons of different colors) and localities (distinguished by different symbols) are visualized. Only the three focal groups with the significant influence of season are shown: (a) butterflies, (b) fruit-feeding moths, and (c) Arctiinae. See Table 4 for all analyses results

TABLE 4 Summary of the partial CCAs exploring the effect of seasons on community composition for individual Lepidoptera groups

	All axes eigenvalues	Explained variation (%)	Pseudo-*F*	*p*-Value
Butterflies	1.73	12.1	10.7	0.005
Fruit-feeding moths	3.79	8.5	7.6	0.005
Arctiinae	1.18	15.5	3.2	0.001
Sphingidae	2.03	4.9	1.5	1
Saturniidae	2.21	14.3	3.0	0.5
Eupterotidae	3.47	0.7	1.1	1

Note. The numbers show the eigenvalues accounted for all axes, as well as the adjusted variation explained by the effect of seasonality. The pseudo-*F* statistics and *p*-values were obtained by Monte Carlo tests with 999 permutations.

seasons reflect a suitable compromise for adults and resprouting of vegetation before the heavy rains. Altogether, the adults' activity seems to be favorable during the high or late dry season, allowing concentration of the main abundance of caterpillars into the beginning of the wet season in the studied area. On the other hand, we do not have any data on caterpillar activity or abundance to support this hypothesis. Simultaneously, we cannot dismiss the biannual adult lepidopterans pattern with its second peak in the high-wet season known from some other studies (Checa et al., 2014; DeVries et al., 1997; Devries & Walla, 2001) as we do not have any data from this period. However, considering the extreme local rainfalls during the high-wet season, such a pattern is not very probable.

Our interpretation of the seasonal patterns of abundance and species richness of adult Lepidoptera can be also seen through particular differences among the groups: both measures increased for fruit-feeding moths and Arctiinae, and decreased for all other groups but Eupterotidae during the transition from dry to wet seasons. A simple explanation can be proposed for fruit-feeding butterflies, the only focal group with day-time activity. Their adults strongly depend on sunshine, decreasing toward the high-wet season. The potential artifact of thirsty adult butterflies entering the baited traps in search for water during the high-dry season (Freitas et al., 2014) can be doubted by the different pattern observed for fruit-feeding moths. Nevertheless, such different biodiversity patterns of fruit-feeding butterflies and moths, belonging to the same trophic guild, were unexpected. Although the peak of fruit-feeding butterflies' biodiversity during the dry season has already been repeatedly documented (Aduse-Poku et al., 2012; DeVries et al., 2012; Grøtan et al., 2014, 2012 ; Ribeiro et al., 2010), no comparable study on fruit-feeding moths exists to our knowledge. As we know from our observations, many fruit-feeding moth taxa (e.g., *Deinypena*, *Hesperochroa*, *Pseudoarcte*) are only moderately attracted to artificial light; it is thus impossible to speculate on these patterns by comparing them with light-attracted moths. Yet, it can be hypothesized that the differences are driven by the different use of resources by the two groups. A substantial part of the recorded butterflies was composed of relatively large and mobile species (e.g., *Charaxes*, *Euphaedra*, *Cymothoe*) with potentially high demands for energy, while the recorded communities of fruit-feeding moths were mostly composed of smaller species with lower energetic demands on average (Niven & Scharlemann, 2005). However, during the wet season, including its beginning, there are abundant fleshy fruits on the ground (pers. observ.), resembling studies from Ghana (Lieberman, 1982) and Rwanda (Sun et al., 1996). Nevertheless, Adamescu et al. (2018) demonstrated both the same and different patterns in different Afrotropical forest communities, and without any local quantitative data, we rather avoid any generalizations. Nevertheless, we hypothesize that the differing biodiversity patterns reflect differences in dependency on direct sunshine among the two fruit-feeding groups. It can be also hypothesized that these different biodiversity peaks could be caused by seasonal food niche partitioning, but no studies on tropical Lepidoptera are yet related to this topic.

The other two focal taxa with feeding adults also differed in their biodiversity patterns during the transition from dry to wet seasons: abundance and species richness increased for Arctiinae, while decreased for Sphingidae. Because most Arctiinae in our material were lichen moths (Lithosiini) with well-developed proboscides and probably feeding on various sugar resources similarly to the fruit-feeding moths (although some minor arctiin groups include nonfeeding adults, Schulze, Linsenmair, & Fiedler, 2001), we offer similar explanations as discussed above. The only quantitative study on this group in the tropics revealed no specific biodiversity pattern related to seasonality in southern Ecuador (Hilt et al., 2007). In contrast, the dry season biodiversity and abundance peaks of Sphingidae were well documented in different tropical areas, usually interpreted in relation to a synchronicity with flowering of plants with specialized flowers and consequent saturation of local communities by dry season vagrants (e.g., Owen, 1969; Cruz-Neto et al., 2011). On Mount Cameroon, no proper dataset on the flowering phenology exists. However, we observed flowering peaks of individual sphingophilous plants (e.g., *Ixora*, *Schumanophyton*, *Tabernaemontana*) during the dry season. Simultaneously, several vagrant hawkmoths (e.g., *Nephele aequivalens* (Walker, 1856), *Phylloxiphia bicolor* (Rothschild, 1894), *Pierreclanis admatha* (Pierre, 1985) were detected during the high-dry season only. We thus hypothesize that flowering of these specialized plants might, at least partially, explain the observed patterns.

The two focal taxa with nonfeeding adults, Saturniidae and Eupterotidae, did not show any consistent seasonal patterns of biodiversity nor abundance. Despite the lack of comparative studies, this could be related to their short-living adults and the related strong temporal species turnover, as shown in our study as well. Simultaneously, a lower seasonal stress can be expected for the short-living adults; their phenology can thus be driven by different mechanisms than for the other Lepidoptera groups.

For all taxa, we also revealed a strong effect of seasonality on their community compositions, caused mainly by the strong interseasonal species turnover. The fruit-feeding Lepidoptera and Arctiinae showed distinct phenological guilds in all three sampled seasons, indicating a strong seasonal specialization of communities. For fruit-feeding butterflies, this is consistent with long-term studies conducted in other tropical regions (Grøtan et al., 2014, 2012 ; Valtonen et al., 2013), while no similar studies exist for fruit-feeding moths. The distinct seasonality of Arctiinae contradicts with Hilt et al. (2007), who reported many tropical Arctiinae occurring all year-long. The communities of Sphingidae, Saturniidae, and Eupterotidae showed relatively high interseasonal dissimilarities, but no significant differences in community composition patterns. We consider this as an artifact of the relatively low species richness together with the presence of several abundant phenological generalists in all these groups (e.g., Sphingidae: *Polyptychus nigriplaga* Rothschild & Jordan, 1903; Saturniidae: *Imbrasia epimethea* (Drury, 1773); Eupterotidae: *Stenoglene* sp.). Concerning Sphingidae, previous studies revealed no distinct seasonality of their communities as well (Beck & Linsenmair, 2006; Owen, 1969). We do not know any similar study for the other two groups. Contrastingly, we found a relatively large proportion of Sphingidae and Saturniidae to be specialized for the high-dry and transition from dry to wet seasons on Mount Cameroon.

The strong interseasonal patterns found by our study can indicate a high sensitivity of the local communities to the expected consequences of the global change. The annual variability of the precipitation timing, length, and magnitude has been increasing in the tropics over the past decades (Feng et al., 2013). The combination of the changing climatic conditions and consequent shifts in host plants' phenology (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007) could cause serious, but hardly predictable, changes on seasonally specialized Lepidoptera communities in the Mount Cameroon area. Considering that Lepidoptera play key roles in all their developmental stages as primary consumers, pollinators and prey, such expected changes of their seasonal patterns might affect entire ecosystems through both top-down and bottom-up effects.

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CONFLICT OF INTEREST

None declared.

AUTHORS CONTRIBUTION

R.T., Sz.S., and V.M. conceived and designed the study; V.M., Sz.S., M.M., E.B.F., S.J., and R.T. collected the material; V.M., Sz.S., M.M., L.P., T.P., and R.T. processed and identified the material; V.M. and R.T. analyzed the data, interpreted the results, and wrote the first manuscript draft; and all authors provided critical feedback and helped shape the final manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sc1dr77.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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One of our eighty bait-traps set in the understorey. It was exposed and emptied from trapped butterflies and moths everyday for ten days © V. Maicher

CHAPTER III

Response of butterfly and moth communities to habitat structure in lowland rainforests of Mount Cameroon

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ABSTRACT

Revealing factors responsible for structuring communities is one of the main aims of community ecology. However, while the impact of different rainforest habitat characteristics on structuring tropical rainforest fruit-feeding butterfly communities have been well-documented, no previous assessment of the impacts of environmental factors on fruit-feeding moth communities have been performed yet. To describe habitat association, we measured 37 habitat descriptors, falling into three categories: *forest openness*, *forest structure*, and *plant diversity*. We then investigated how these habitat descriptors shape both fruit-feeding butterfly and moth species richness and composition in three lowland rainforest localities of Mount Cameroon, West Africa. We sampled both groups in the understorey and the canopy by standardized bait trapping in three seasons (80 traps set for 10 days per season and locality). In total, 16,062 specimens belonging to 403 (morpho)species were trapped. Both butterfly and moth community compositions appeared to be mainly structured by forest openness characteristics and to a lower extent by plant diversity. Both of these descriptors predicted well moth species richness, whereas forest structure was rather found to influence the canopy butterfly and moth species richness. Understorey and canopy communities were also distincts, indicating a vertical stratification of both Lepidoptera groups. Interestingly, whilst the ecology of these two groups differs, larval host-plant specificity, sensitivity to microclimatic conditions, and habitat heterogeneity are proposed to be the main factors affecting their spatial distribution in tropical rainforest.

INTRODUCTION

Revealing factors responsible for structuring communities belongs among the essential aims of community ecology (Agrawal *et al.*, 2007). They differ among scales: climate or environmental productivity are crucial on larger scales, whilst biotic interactions and microhabitat characteristics prevail on smaller scales (Benton 2009). Recently, considerable attention has been paid to the large-scale patterns of biodiversity, resulting in some general relationships consistent among different taxa (Gaston 2000, Hillebrand & Thomas 2004, Tittensor *et al.*, 2010). Nevertheless, knowledge of small-scale mechanisms is also important for our understanding of the dynamics and structure of local communities (Cottenie 2005). This is particularly true for developing local biodiversity conservation strategies. Since local mechanisms vary among studied taxa and areas (Webb & Peart 1999, Tews *et al.*, 2004, Siefert *et al.*, 2012, Stein *et al.*, 2014), more data are needed, especially from understudied regions, such as the Afrotropics.

Insect herbivores are one of the most species-rich and abundant ecological guilds in tropical rainforests, with both top-down and bottom-up effects on the entire ecosystem (Dyer & Letourneau 1999, Novotny *et al.*, 2010). Their diversity strongly correlates with plant diversity (Novotny, Basset, *et al.*, 2002a, Novotny & Basset 2005, Basset *et al.*, 2012), nevertheless the species composition of herbivorous insect communities can be both directly and indirectly influenced by various other factors, often related to vegetation. A more diverse plant community surely offers host plants to a broader spectrum of herbivorous insects (Novotný *et al.*, 2006). Simultaneously, a diverse plant community will also offer more heterogeneous microhabitat conditions through its structural complexity (such as host plants' architecture), and thus more complex fundamental niches (Lawton 1983, Tews *et al.*, 2004). However, the particular role of individual components of vegetation structure in shaping communities of tropical herbivorous insects are scarcely studied. In tropical rainforests, Lepidoptera communities are highly influenced by the species richness and composition of the local plant communities (e.g., Novotny *et al.*, 2002b). The positive correlation between plant and Lepidoptera species richness is commonly described (Brehm *et al.*, 2007, Nyafwono *et al.*, 2014a, 2015; but see Axmacher *et al.*, 2004), while vegetation structure has also been linked to the structure of Lepidoptera communities. For instance, the stratification of vegetation directly causes discrete vertical stratification of Lepidoptera communities (Devries & Walla 2001, Fermon *et al.*, 2005, Aduse-Poku *et al.*, 2012). Simultaneously, canopy openness, especially the extent of canopy gaps, is another environmental factor increasing Lepidoptera diversity as a consequence of higher habitat heterogeneity (Spitzer *et al.*, 1997, Hill *et al.*, 2001, Hilt & Fiedler 2005, Nyafwono *et al.*, 2015). These vegetation-related characteristics together are responsible for the microclimatic conditions of habitats, especially light availability, temperature, and humidity, all crucial factors structuring tropical Lepidoptera assemblages (Koh & Sodhi 2004, Beck & Chey 2008).

However, the relative importance of these habitat characteristics in structuring butterfly and moth community is not fully understood in most tropical rainforests. Despite the dependence of herbivorous communities on vegetation diversity, microclimatic conditions linked to forest openness can also be important predictors of community composition and species richness, both for tropical butterflies (Spitzer *et al.*, 1997, Tropek & Konvicka 2010, Vlasanek *et al.*, 2013, Koh & Sodh, 2004, Houlihan *et al.*, 2013) and moths (Hilt and Fiedler 2005, Fermon *et al.*, 2005, Brehm *et al.*, 2003, 2007, Beck & Chey, 2008). On the contrary, plant community composition was a significantly better predictor for butterfly community composition than vegetation structure and forest openness, with however no correlation between species richness of trees and butterflies (Valtonen *et al.*, 2017). Similarly, tree diversity is known to be the most important factor predicting moth community diversity, with a positive correlation with moth species richness (e.g., Beck *et al.*, 2002, Brehm *et al.*, 2003; although a negative correlation was found by Axmacher *et al.*, 2004). Whilst vegetation structure was not found to impact tropical moth community composition (Brehm *et al.*, 2003), it was, together with forest openness shown to predict community composition of tropical butterflies (Nyafwono *et al.*, 2014b, 2015, Spitzer *et al.*, 1993).

We studied habitat associations of fruit-feeding butterfly and moth communities, a species-rich guild of tropical insects, in lowland rainforests of the comparatively understudied Afrotropics. Owing to straightforward and well-standardized sampling methods, these two groups are frequently used as bioindicators in numerous ecological studies (Bonebrake *et al.*, 2010, Lucci Freitas *et al.*, 2014). Our intensive sampling in three forest localities in the foothills of Mount Cameroon, together with detailed data on forest composition and structure, allows for a robust analyses of habitat determinants of species richness and community composition of butterflies and moths. To the best of our knowledge, we present the first comprehensive study of habitat associations of fruit-feeding moths in tropical rainforests. Because Lepidoptera communities are known to be vertically stratified, we also focus on differences in habitat associations between canopy and understorey communities; as well as capturing seasonal effects. Generally, we focus on the relative importance of three main habitat components (plant diversity, forest structure, and forest openness) for both lepidopteran groups. We hypothesize that according to their differential use of habitat, butterfly communities will be more influenced by forest openness, whereas moth communities will be better predicted by plant diversity.

Table 1. Measured habitat descriptors. * indicate variables selected via Pearson’s correlation and used for the GLMM analyses.

Variable	Code	Definition/way of evaluation	Range	Average	SD
Forest structure					
Tree number	Tnb	Number of all trees >10 cm DBH (individuals/plot)	33–112	64.54	16.11
*Live tree number	LTnb	Number of live trees >10 cm DBH (individuals/plot)	33–110	62.56	15.43
Dead tree number	DTnb	Number of dead trees >10 cm DBH (individuals/plot)	0–11	1.98	2.79
Tree basal area	TBA	Cumulative area of all tree trunks and stems >10 cm DBH; calculated from measured DBH (m^2)	2.73–9.34	5.36	1.46
Dead tree basal area	DTBA	Cumulative area of all live tree trunks and stems >10 cm DBH; calculated from measured DBH (m^2)	0–0.93	0.14	0.24
Live tree basal area	LTBA	Cumulative area of all dead tree trunks and stems >10 cm DBH; calculated from measured DBH	2.72–9.34	5.19	1.49
Stand wood volume	SWV	Product of tree height and basal area (m^3)	33.12–	118.90	52.40
*Dead tree wood volume	DTWV	Product of tree height and basal area (m^3)	0–7.14	0.94	1.77
*Live tree wood volume	LTWV	Product of tree height and basal area (m^3)	32.54–	118.17	52.11
Maximum Diameter at Breast	MxDBH	Measured (cm)	58.7–200	106.26	34.01
*Mean Diameter at Breast Height	MnDBH	Calculated from measured DBH (cm)	19.99–34.41	25.95	3.31
Maximum tree height	MxTH	Estimated height of the highest tree (m)	17–48	33.08	6.21
*Mean tree height	MnTH	Calculated from estimated heights of individual trees (m)	8.61–18.89	13.92	2.48
Stem Slenderness Index	SSI	Averaged per plot of the ratio of estimated tree height to measured DBH for each tree	0.43–0.90	0.64	0.11
Forest openness					
Maximum canopy openness	MxCO	Maximum percentage of open sky from beneath a forest canopy (%)	2.24–12.88	4.87	2.53
Mean canopy openness	MnCO	Mean percentage of open sky from beneath a forest canopy (%)	2.46–20.31	6.86	4.43
*Herb layer cover	E1	Herbs defined as all non-woody plants rooted in the soil; visually estimated over the entire plot area	20–90	48.65	16.07
*Shrub layer cover	E2	Shrubs defined as all woody plants not exceeding the height of 4 m and with DBH < 10 cm rooted	10–60	40.31	14.71
Herb and shrub layer cover	E1+E2	Visually estimated by the same observer (%)	50–90	69.06	11.74
Maximum Leaf Area Index	MxLAI	Maximum effective leaf area index integrated over the zenith angles 0 to 75°	1.99–4.74	3.73	0.72
Mean Leaf Area Index	MnLAI	Mean effective leaf area index integrated over the zenith angles 0 to 75°	2.67–5.31	4.28	0.63
Maximum amount of transmitted	MxTDR	Maximum amount of direct solar radiation transmitted by the canopy (%)	3.70–21.43	9.16	4.46
Mean transmitted direct solar	MnTDr	Mean amount of direct solar radiation transmitted by the canopy (%)	4.46–41.49	14.55	8.37
Maximum amount of transmitted	MxTDf	Maximum amount of diffuse solar radiation transmitted by the canopy (%)	3.57–17.70	7.74	3.64
Mean transmitted diffuse solar	MnTDf	Mean amount of diffuse solar radiation transmitted by the canopy (%)	3.75–31.04	11.51	7.02
Maximum of total solar radiation	MxTT	Maximum sum of direct and diffuse solar radiation transmitted by the canopy (%)	3.64–22.47	8.67	4.47
*Mean total solar radiation	MnTT	Mean sum of direct and diffuse solar radiation transmitted by the canopy (%)	4.1–39.94	13.29	8.07
Plant diversity					
*Tree species richness	TSR	Number of tree species	13–35	20.21	4.40
*Herb species richness	HSR	Number of herb species	25–101	66.25	19.00
Tree DCA CaseR1	TDCAR1	Case scores derived from the tree count produced by a detrended correspondence analysis–Axis 1	0.09–1.99	1.02	0.50
Tree DCA CaseR2	TDCAR2	ditto–Axis 2	0–2.47	0.84	0.53
Tree DCA CaseR3	TDCAR3	ditto–Axis 3	0–2.49	1.66	0.38
Tree DCA CaseR4	TDCAR4	ditto–Axis 4	0.83–1.32	1.12	0.11
Herb DCA CaseR1	HDCAR1	ditto–Axis 1	0.01–1.94	0.69	0.39
Herb DCA CaseR2	HDCAR2	ditto–Axis 2	0–3.97	1.47	1.38
Herb DCA CaseR3	HDCAR3	ditto–Axis 3	0.68–2.75	1.45	0.47
Herb DCA CaseR4	HDCAR4	ditto–Axis 4	0.61–2.34	1.40	0.28

Study area

Our study was conducted on the southwestern slope of Mount Cameroon (N 04.21519°, E 09.17340°), Southwest Region, Cameroon. It is the highest mountain of West/Central Africa (4,095 m asl) and the only recently active volcano within the Cameroon Volcanic Line. It offers a continuous altitudinal gradient of natural tropical forests from lowlands (~300–400 m asl on the southwestern slopes) up to a natural timberline (~2,100–2,300 m asl on the same slope). The region has a humid tropical climate with a one dry (late December–February) and one wet (June–September) seasons separated by two transition seasons in March–May and October–November, with a progressive rainfall increasing and decreasing, respectively. The mean annual temperature is 23.3 ± 0.7°C at 300 m asl (decreasing by ca 0.5°C per 100 altitudinal meters; Chapter V) and the mean annual rainfall often surpasses 10,000 mm in the foothills (Maicher *et al.*, Chapter V), making the southwestern slope of Mount Cameroon one of the rainiest places on Earth. Its climate, relative isolation, and heterogeneity of environments along its altitudinal gradient make it a biodiversity hotspot for many organisms, including Lepidoptera (Larsen 2005, Maicher *et al.*, 2016, Sáfián & Tropek 2016, Ustjuzhanin *et al.*, 2018).

Our study was carried out at three sampling localities at lower elevations of the mountain, all inside the Mount Cameroon National Park. These study sites are the same as those examined in Maicher *et al.*, (2018): the Bamboo Camp (N 04.08990°, E 09.05174°; 350 m asl), the Drink Gari Camp (N 04.10221°, E 09.06304°; 650 m asl), and the PlanteCam Camp (N 04.11750°, E 09.07094°; 1100 m asl). The latter locality is naturally disturbed by forest elephants (Loxodonta cyclotis), which reduces the density of trees and forms clearings occupied by various herbs, grasses and ferns (Proctor, 2007). The non-forest habitats were avoided during our sampling as we targeted forest Lepidoptera only. Whereas the forest has a typical upland composition due to the presence of both lower and higher elevations plant species, the two lower localities are covered by forest with relatively scarce understorey and closed high canopy layers, typical of lowland rainforests.

METHODS

Lepidoptera sampling

The sampling of fruit-feeding butterflies and moths is described in Maicher *et al.*, (2018). Both groups were collected using Van Someren-Rydon type traps (modified IKEA PS Fångst hanging storage devices: height 75 cm, diameter 23 cm; first used by Sáfián *et al.*, 2011) baited with ca 0.3 l of fermented mashed bananas. Within each sampling locality, 16 plots (radius of 20 m; i.e., 9.68 ha covered by all 48 plots) were established in forest habitats, with a minimal distance of 150 m between them. Within each plot, five traps were installed: four were exposed in the understorey as close to the ground as possible, and one was set in the canopy at 20 (±5) m height.

Our sampling was repeated in three different seasons: a transition from wet to dry seasons (November/December 2014), a high-dry season (January/February 2016), and a transition from dry to wet seasons (April 2015). During each season, the traps were exposed for ten consecutive days; every day all traps were checked, and all captured butterflies and moths were removed, killed, and either identified in the field, or dried and identified later in the lab using morphological features. All traps were rebaited every third or fourth day according to weather conditions, the bait was also checked daily and refilled if necessary. Voucher specimens are deposited in the Nature Education Centre of the Jagiellonian University, Kraków, Poland.

Habitat characteristics

The sampled plots were characterized by 37 habitat descriptors separated into three categories: 1/ forest structure, 2/ forest openness, and 3/ plant diversity; all particular habitat descriptors are described in Table 1.

In each plot, for both dead and live trees >10 cm DBH, height was estimated and DBH was measured, these values were used for the quantification of 14 characteristics of forest structure (Table 1). Consequently, to quantify light transmitted through the canopy - five hemispherical photographs per plot (i.e., 240 photographs together) were taken by Nikon F9 digital camera with Nikkor fisheye lens. Each photography point was fixed at 1.8 m above ground, one in the plot center and four in its cardinal direction points 10 m from the center. All photographs were converted to black and white bitmaps using automatic thresholding implemented in SideLook 1.1 (Nobis & Hunziker 2005). Transmitted direct, diffuse, total solar radiation, and canopy openness were calculated with Gap Light Analyzer software (Frazer *et al.*, 1999). Together with herb and shrub layer coverage estimates, as well as the total coverage of these two layers, 13 characteristics of forest openness were quantified (Table 1). Finally, all trees and herbs were identified to species, and their species richness, together with ordination scores of tree and herb communities derived from detrended correspondence analyses (DCA), composed 10 characteristics of plant diversity (Table 1).

Data analyses

In all analyses, butterfly and moth communities were analyzed separately. All analyses were firstly run for the pooled dataset, followed by an analysis of each strata separately (canopy and understorey communities).

The influence of individual habitat characteristics on the species richness of both communities were tested in the lme4 package (Bates *et al.*, 2015) in R 3.5.2 (R Core Team, 2018) by Generalized Linear Mixed Models (GLMM) with log link function and Poisson error distribution of the dependent variable (species richness in individual plots per ten consecutive sampling days). Firstly, we tested collinearity among the explanatory variables within the three groups of habitat characteristics. Altogether, ten habitat characteristics which did not correlate with one another (Pearson $\rho \leq |0.7|$; Table 1) were included into the models. The sampling localities were treated as a random effect factor, whilst all the tested habitat characteristics were treated as fixed effects. All possible combinations of the preselected habitat characteristics within these three sets were fitted into GLMM models, and compared with each other, as well as with a null model (i.e., locality with fixed factor as the only explanatory variable). The model comparisons were based on the corrected second-order Akaike's information criterion (AICc; Sugiura 1978, Anderson & Burnham 2002). The most plausible models (ΔAICc < 2) were considered as significant and are listed in Table 2. Simultaneously, the Akaike's information criteria weight (wi) was used to express the conditional probabilities of individual model (i) to be the most plausible for explaining the analyzed relationships (Wagenmakers & Farrell 2004).

The relative importance (i.e., both marginal and conditional effects) of the three groups of habitat characteristics on lepidopteran community composition was analyzed by variance partitioning in partial Canonical Correspondence Analyses (CCA) in CANOCO 5.0 (Braak & Smilauer 2012, Šmilauer & Lepš 2014). Prior to the analyses, the response variables (i.e., lepidopteran species abundances in individual plots after ten days of trapping in each sampled season) were log-transformed and rare species were downweighted with sampling localities as a covariate in order to filter out non-focal variability. Within each group of habitat characteristics, the significant variables were selected by a step-by-step forward selection procedure, based on Monte-Carlo permutation tests (999 permutations; $p<0.05$). The proportion of variation in communities explained by each group of habitat characteristics, the variation shared between one or several sets, and the unexplained variation were calculated by variation partitioning (Borcard *et al.*, 1992), with the adjusted Ra2 as the measure of variability explained by the particular group of characteristics (conditional effect) or their combinations (marginal effect; Peres-Neto *et al.*, 2006).

RESULTS

Altogether, 3,098 standing trees >10 cm DBH of 136 tree species were measured within the 48 plots (Table 1).

Concerning Lepidoptera, we recorded 10,425 and 5,637 specimens belonging to 117 and 286 (morpho)species of butterflies and moths, respectively. From these 7,889 and 4,617 specimens of 103 and 227 (morpho)species of butterflies and moths, respectively, were caught in understorey; whilst 2,534 and 1,022 specimens of 67 and 151 (morpho)species of butterflies and moths, respectively, were caught in canopy.

Table 2. Best plausible models explaining species richness of individual groups of fruit-feeding Lepidoptera. Models are ranked according to their second-order Akaike's information criteria (ΔAICc <2). Parameter estimates and model weight (wi) are reported, together with positive (+) or negative (-) effects of each significant habitat characteristics (see Table 1 for their full names and definitions). The different models of the characteristic groups where the null models were included among the best ones are left blank (see Table S2-S3 for details of the models).

	Forest structure	Effect	ΔAICc	*wi*	Forest openness	Effect	ΔAICc	*wi*	Plant diversity	Effect	ΔAICc	*wi*
All butterflies												
Understory butterflies												
Canopy butterflies	~ MnTH	MnTH +	0	0.3								
	~ DTWV + MnTH	DTWV - ; MnTH +	0.58	0.2								
	~ LTnb + MnTH	LTnb + ; MnTH +	0.81	0.2								
	~ LTnb + DTWV + MnTH	LTnb + ; DTWV - ; MnTH +	1.58	0.1								
	~ LTnb + MnDBH + MnTH	LTnb + ; MnDBH + ; MnTH +	1.61	0.1								
	~ LTWV + MnTH	LTWV + ; MnTH +	1.93	0.1								
	~ MnDBH + MnTH	MnDBH + ; MnTH +	1.96	0.1								
All moths	~ LTnb + LTWV + MnDBH	LTnb - ; LTWV + ; MnDBH -	0	0.6	~ E1	E1 +	0	1	~ TSR	TSR -	0	0.6
	~ LTnb + LTWV + MnDBH + MnTH	LTnb - ; LTWV + ; MnDBH - ; MnTH +	1.85	0.2					~ TSR + HSR	TSR - ; HSR +	0.98	0.4
	Null model		1.93	0.2								
Understory moths												
Canopy moths	~ LTnb + DTWV + LTWV + MnDBH	LTnb - ; DTWV - ; LTWV + ; MnDBH -	0	0.2	~ MnTT	MnTT +	0	0.4	~ TSR + HSR	TSR - ; HSR +	0	0.7
	~ LTnb + DTWV + LTWV + MnDBH + MnTH	LTnb - ; DTWV - ; LTWV + ; MnDBH - ; MnTH +	0.46	0.2	~ E2 + MnTT	E2 + ; MnTT +	1.41	0.2	~ TSR	TSR -	1.56	0.3
	~ DTWV	DTWV -	0.83	0.1	~ E1 + MnTT	E1 + ; MnTT +	1.43	0.2				
	~ LTnb + DTWV	LTnb - ; DTWV -	0.88	0.1	~ E1 + E2 + MnTT	E1 + ; E2 + ; MnTT +	1.98	0.2				
	~ DTWV + MnTH	DTWV - ; MnTH +	1.19	0.1								
	~ LTnb + DTWV + MnTH	LTnb - ; DTWV - ; MnTH +	1.39	0.1								
	~ LTnb + DTWV + LTWV	LTnb - ; DTWV - ; LTWV +	1.68	0.1								

Determinants of species richness

In most of our species richness model comparisons, the null models were included among the most plausible models according to AIC (Table 2). Simultaneously, the null models were almost always (except the species richness of the pooled and the canopy moths, see below) the most plausible ones, or had comparable AIC weights to the models with higher AIC (i.e., had always higher or comparable conditional probability to be the most plausible model; Wagenmakers & Farrell, 2004). In such cases, we avoided interpretation of the particular relationships of species richness to individual habitat characteristics.

The effect of habitat characteristics on the species richness of pooled fruit-feeding butterflies was thus rather marginal and probably related to other factors. One exception was the relationship of canopy butterfly species richness to forest structure variables where seven plausible models were selected without the null model (Table 2). The positive effect of mean tree height (MnTH) to species richness was included in all of them. According to individual plausible models, species richness of canopy butterflies was positively related to the number of living trees (LTnb), wood volume (LTWV), and mean DBH (MnDBH), and negatively to dead trees wood volume (DTWV).

Pooled fruit-feeding moth species richness was significantly related to forest openness and plant diversity habitat characteristics (Table 2). The forest openness models showed a positive relationship to herb layer cover (E1). The plant diversity models showed a negative relationship of total moth species richness to tree species richness (TSR), and a positive relationship to herb species richness (HSR). The null model was selected among the most plausible forest structure models, but both its AIC and AIC weight were substantially lower than of the best model; we thus considered the positive relationship of all moth species richness to live tree wood volume (LTWV), and negative relationship to number of living trees (LTnb) and mean DBH (MnDBH) as substantial.

None of the habitat characteristics groups had a significant influence on the species richness of understorey moths, however, all habitat characteristic groups showed a significant relationship to species richness of canopy moths. For forest structure, seven most plausible models were selected, where canopy moth species richness was negatively related to dead tree wood volume (DTWV), whilst particular models also included a positive relationship to live tree wood volume (LTWV) and mean tree height (MnTH), and a negative relationship to live tree number (LTnb), and mean DBH (MnBDH). Forest openness analyses showed a positive relationship of canopy moth species richness to mean total solar radiation (MnTT) included in all four plausible models (Table 2), as well as to both herb cover (E1) and shrub cover (E2) layers included in particular models. Lastly, canopy moth species richness was related positively to herb species richness (HSR), whereas negatively to tree species richness (TSR).

Determinants of community composition

For the pooled butterflies and the pooled moths, the forest openness descriptors showed significant conditional effects on community composition and explained the highest proportions of variability (Fig 1A, C). Its marginal effects were prevailingly shared with the plant diversity variables in both cases, while conditional effects of plant diversity were just marginally significant, or not significant at all. The shared explained variation among the forest openness and forest structure variables was important for the pooled butterfly communities only, whereas the conditional effects of the forest structure variables were marginally significant or non-significant for both lepidopteran groups.

In contrast, for the composition of understorey communities of both butterflies and moths, both plant diversity and forest openness descriptors significantly explained most of the variation, mainly through shared variation. However, the independent variation explained by plant diversity was higher than the independent variation explained by forest openness for both understorey communities (Fig 1B, D).

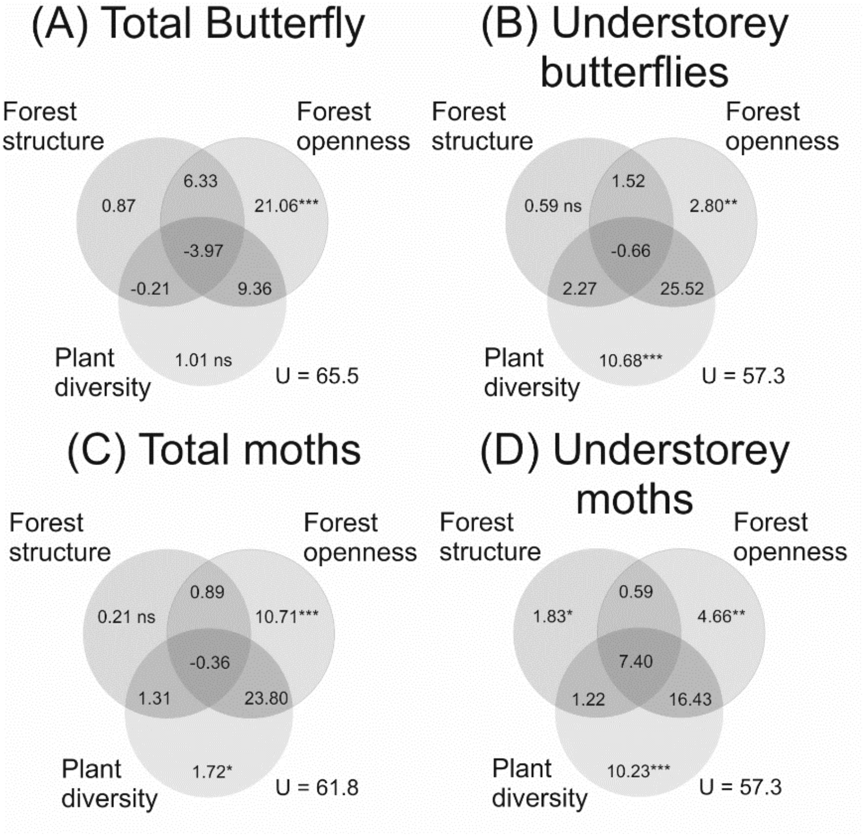

Fig. 1. Venn diagrams showing the partition of the variation (Ra2 in %) in (A) total butterfly community composition, (B) understorey butterfly community composition, (C) total moth community composition, and (D) understoy moth community composition. U is the residual variation. The joint fraction and residuals could not be tested for significance because these were obtaitned by subtraction. Negative values are interpreted as zeros (Šmilauer & Lepš, 2014). The significance values are represented as ***P < 0.001, **P < 0.01, *P < 0.05, ns P > 0.05.

Table 3. Results of partial CCAs showing the influence of the habitat characteristics on the community composition of individual groups of fruit-feeding Lepidoptera. Final models were selected by step-by-step forward selection procedure and used for later variation partitioning. Pseudo-F, p value and adjusted explained variation (Ra2 in %) are reported for individual models. See Table 1 for the habitat characteristics full names and definitions.

Community	**Final model**	**pseudo-F**	**p**	**Ra^2**
All butterflies	~ DTnb + MxTDf + MnLAI + TSR + HSR	4.6	0	31.7
Canopy	~ SSI	3.7	0	10.5
Understory	~ DTnb + MnCO + HSR + TDCAR3 + TDCAR2 +	5.1	0	34.2
All moths	~ DTBA + MxTDf + MnLAI + E1 + MxCO + HDCAR2	2.5	0	30
Canopy moths	No forward-selected variables	-	-	-
Understory	~ Tnb + MnDBH + SSI + MxTDF + MxLAI + MxTDr +	2.4	0	21

Finally, whilst none of the habitat descriptors were important for the composition of canopy moth communities, the forest structure variables significantly affected community composition of butterflies in the canopy (Table 3).

DISCUSSION

The communities of both fruit-feeding butterflies and moths displayed similar associations to their habitats on Mount Cameroon. Community composition of both groups, as well as species richness of the pooled moths, were driven mainly by the openness of the forest and by plant diversity. In contrast, canopy butterfly species richness was significantly related with forest structure only, while the canopy moths depended on forest structure, canopy openness, and plant diversity. Based on previous studies, we did not expect this similarity between these two groups of Lepidoptera. Whilst we hypothesized that butterfly communities will be mostly influenced by canopy openness and moths by plant diversity, it appears that the three habitat descriptors play an important role in shaping communities of both fruit-feeding butterflies and moths, and that these effects are vertically stratified.

Habitat characteristics influencing fruit-feeding butterfly species richness and composition differed between the understorey and canopy. Similar effects of canopy openness and plant diversity in shaping butterfly community composition have been reported from the understorey in Afrotropical rainforests (Nyafwono *et al.*, 2014b, 2015). One possible explanation of the importance of canopy openness in the understorey strata is that adult butterflies rely on solar radiation for their thermoregulation and flying activities (Clench, 1966). Many butterfly species use sunny parts (i.e., forest gaps, canopy openings, or small light spots under sparse canopy) of their habitats for basking, nectaring, mating, and ovipositing (Uehara-Prado *et al.*, 2007; Spitzer *et al.*, 1997; Tropek & Konvicka, 2010, Vlašanek, *et al.*, 2013). Similarly, many of their larval food plants grow in sunny microhabitats as well (Hill *et al.*, 2001). Interestingly, the importance of plant diversity was relatively low for fruit-feeding butterflies, influencing species composition only. This finding is in conflict with several other studies showing plant community richness is the main driver of butterfly community richness and composition (e.g., Valtonen *et al.*, 2017, Nyafwono *et al.*, 2014b). The direct dependence of butterfly communities on the local plant communities is indisputable, as caterpillars depend on their foodplants and are relatively host-specialized (Novotny *et al.*, 2002a). However, low host specificity resulting from the prevalence of closely-related plant species could explain this pattern, as Lepidoptera are more likely to share hosts under these conditions (Novotný *et al.*, 2002a). On the other hand, variables linked to forest structure such as forest height, density, and size of living trees became the most important factors influencing canopy butterfly species richness and composition. Vertical stratification of butterfly communities has already been repeatedly observed (e.g., DeVries *et al.*, 2001, 2012; Molleman *et al.*, 2006; Nice *et al.*, 2019), whilst forest structure has also been shown to influence fruit-feeding butterfly activity in West Africa (Fermon *et al.*, 2003). Indeed, the combined presence of a high number of young leaves, sap fluids, nectar and fruits, as well as the high occurrence of epiphytes and lianas in the rainforest canopy is likely to attract many butterfly species (Novotný *et al.*, 2003). Therefore the increases in butterfly species richness related to taller, more abundant and larger living trees likely reflects an increase in available microhabitats and resources.

Similar to fruit-feeding butterflies, the habitat associations of fruit-feeding moth communities were again mostly explained by forest structure and plant diversity. While the habitat association of fruit-feeding moths has to date never been reported, comparisons of our results with studies on light-attracted moths of all adult-feeding guilds can still be made. In contrast to butterflies, moths are generally not dependent on solar radiation as most of their adults are not active during daytime (Ribeiro and Freitas, 2010). However, temperature shapes moth communities, and has even been shown to be a better predictor than tree diversity or forest structure along an altitudinal gradient in Borneo (Beck and Chey, 2008) and in South and Central America (Brehm *et al.*, 2003, 2007). Moreover, microclimatic conditions are also crucial for the development of larval moths. For instance, high rainfall and humidity can increase caterpillars' mortality by mechanical disturbance from their host-plant or by increasing pathogen activity (Hill *et al.*, 2003). However, many of the fruit-feeding moths we sampled from the canopy were relatively large in size (e.g., Ogovia tavetensis, Sphingomorpha chlorea), particularly mobile and well-adapted to canopy foraging. The increases in species richness with living tree wood volume could as be attributable to an increase in available niches. Moreover, since a majority of moth species feed on tree (or vascular plant) species, a greater diversity of tree species should support more moth species (e.g., Beck *et al.*, 2002; Brehm *et al.*, 2007). While Peters *et al.* (2016) found a positive relationship between moth and plant species richness in Africa, Axmacher *et al.* (2004) found a negative association between the diversity of Geometridae and the number of dicotyledons in Mount Kilimanjaro, although this was the only reported negative relationship. The authors suggested that this correlation could be explained by the young age and the geographical isolation of Mt Kilimanjaro's montane forests. This hypothesis could however hardly explain the similar relationship found in the lowland forests of Mount Cameroun.

Communities of both butterflies and moths sampled in the understorey and canopy differed in their relationship to habitat characteristics. Whilst species richness of both butterflies and moths in understorey showed no relationship to habitat descriptors, canopy communities of both groups were influenced by forest structure and canopy fruit-feeding moths by forest openness and plant diversity as well. The individual traits of forest structure which act to influene the species richness of both groups also differ. Fruit-feeding butterfly species richness was positively influenced by an increasing density of large trees, while fruit-feeding moths species richness generally responded negatively to tree density. Many fruit-feeding butterfly species are highly specialized canopy foragers, thus rarely frequenting the understorey (Nice *et al.*, 2019). However, herb layer coverage was the only forest openness predictor which was positively correlated with moth species richness. Thereby, it is possible to hypothesize that many fruit-feeding moths species prefer more open forest habitats and are likely to forage close to the ground (Willott *et al.*, 1999).

The commonly observed vertical stratification of fruit-feeding butterflies in tropical rainforests can be as well generalized to fruit-feeding moths. This stratification is mostly driven by a strong habitat association for both groups. Although both fruit-feeding butterflies and moths have slightly different responses to habitat structure, their general sensitivity to forest structure and plant diversity is surprisingly similar. Whilst the ecology of butterflies and moths differ in many ways, a combination of larval host-plant specificity, sensitivity to microclimatic conditions, and habitat heterogeneity is likely to explain the observed patterns for both groups. Moreover, the relative importance of these effects seemed to be even more amplified in the canopy strata. The high habitat association detected for both fruit-feeding butterflies and moths highlight the need to sample both understorey and canopy strata in order to cover the full diversity of both groups.

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SUPPLEMENTARY MATERIAL

Table S1. Pearson correlation coefficients of measured characteristics for (a) forest structure, (b) forest openness, and (c) plant diversity. coefficients exceeding 0.7 and selected variables are highlighted. Variable names are presented in Table 1.

(A) Forest structure

Forest structure	Tnb	LTnb	DTnb	TBA	**DTWV**	**LTWV**	MxDBH	**MnDBH**
LTnb	**0.99**							
DTnb	0.32	0.16						
TBA	0.28	0.33	-0.23					
DTWV	0.06	-0.07	**0.72**	-0.21				
LTWV	-0.04	0.02	-0.35	**0.88**	-0.20			
MxDBH	-0.23	-0.18	-0.38	0.69	-0.25	**0.83**		
MnDBH	-0.55	-0.50	-0.43	0.56	-0.21	0.63	0.55	
MnTH	-0.35	-0.31	-0.33	0.32	0.13	0.59	0.41	0.53

(B) Forest openness

Forest openness	MnCO	MxCO	**E1**	**E2**	E1E2	MnLAI	MxLAI	MnTDr	MxTDr	MnTDf	MxTDf	**MnTT**
MxCO	**0.94**											
E1	0.56	0.54										
E2	-0.56	-0.55	-0.38									
E1E2	0.28	0.26	**0.74**	0.25								
MnLAI	**-0.88**	**-0.82**	-0.58	0.55	-0.34							
MxLAI	-0.67	-0.57	-0.59	0.45	-0.37	**0.86**						
MnTDr	**0.93**	**0.84**	0.58	-0.42	0.39	**-0.77**	-0.60					
MxTDr	**0.90**	**0.84**	0.56	-0.43	0.33	**-0.76**	-0.61	**0.94**				
MnTDf	**0.97**	**0.93**	0.63	-0.50	0.39	**-0.84**	-0.64	**0.96**	**0.91**			
MxTDf	**0.92**	**0.97**	0.59	-0.51	0.34	**-0.79**	-0.57	**0.89**	**0.87**	**0.95**		
MnTT	**0.95**	**0.87**	0.57	-0.47	0.35	**-0.80**	-0.62	**0.99**	**0.93**	**0.97**	**0.90**	
MxTT	**0.93**	**0.89**	0.56	-0.48	0.30	**-0.80**	-0.63	**0.94**	**0.99**	**0.93**	**0.91**	**0.94**

(C) Plant diversity

Plant diversity	**TSR**
HSR	-0.30

Table S2. Plausible candidate models (ΔAIC < 2) explaining the butterfly species richness, separately for both understory and canopy communities. Models are ranked according to their 2nd-order Akaike's information criterion (AICc). Parameter estimates (coefficients), number of parameters (k), and model weight (wi) are reported. GLMMs were fit with localities as random factor. Variable names are presented in Table 1.

	Intercept	**Parameter estimates**										***K***	**logLik**	**AICc**	**ΔAICc**	***wi***
		LTnb	**DTWV**	**LTWV**	**MnDBH**	**MnTH**	**E1**	**E2**	**MnTT**	**TSR**	**HSR**					
	All butterfly community															
Forest structure	3.698											2	-158.45	321.17	0	0.36
	3.606	0.002										3	-158.04	322.63	1.46	0.17
	3.687		0.012									3	-158.07	322.69	1.52	0.17
	3.655			<0.001								3	-158.17	322.89	1.72	0.15
	3.511					0.014						3	-158.23	323	1.83	0.15
Forest openness	3.608						0.004		-0.013			4	-155.86	320.65	0	0.26
	3.561						0.003					3	-157.07	320.68	0.03	0.25
	3.698											2	-158.45	321.17	0.52	0.2
	3.42						0.004	0.003				4	-156.37	321.66	1.02	0.16
	3.477						0.005	0.002	-0.013			5	-155.26	321.96	1.31	0.13
Plant diversity	3.698											2	-158.45	321.17	0	0.44
	3.555										0.002	3	-157.43	321.41	0.25	0.39
	3.625									0.004		3	-158.27	323.08	1.92	0.17
	Understory butterfly community															
Forest structure	3.433		0.023									3	-154.4	315.34	0	0.36
	3.456											2	-155.57	315.41	0.07	0.35
	3.378		0.027	<0.001								4	-154.13	317.2	1.85	0.14
	3.646		0.024			-0.015						4	-154.17	317.27	1.92	0.14
Forest openness	3.456											2	-155.57	315.41	0	0.45
	3.328						0.003					3	-154.64	315.82	0.41	0.37
	3.363						0.004		-0.01			4	-154.14	317.21	1.8	0.18
Plant diversity	3.456											2	-155.57	315.41	0	0.458
	3.295									0.008		3	-154.9	316.34	0.93	0.288
	3.337										0.002	3	-155.02	316.59	1.18	0.254
	Canopy butterfly community															
Forest structure	1.586					0.077						3	-128.52	263.59	0	0.25
	1.561		-0.029			0.081						4	-127.62	264.17	0.58	0.18
	1.284	0.003				0.084						4	-127.74	264.41	0.81	0.16
	1.266	0.003	-0.029			0.087						5	-126.87	265.17	1.58	0.11
	0.827	0.005			0.019	0.074						5	-126.89	265.21	1.61	0.11
	1.615			0.001		0.07						4	-128.3	265.52	1.93	0.09
	1.447				0.008	0.071						4	-128.31	265.55	1.96	0.09
Canopy openness	2.662											2	-133.89	272.05	0	0.36
	2.521						0.003					3	-133.36	273.27	1.22	0.2
	2.741								-0.009			3	-133.64	273.82	1.77	0.15
	2.56							0.003				3	-133.65	273.85	1.8	0.15
	2.591						0.005		-0.018			4	-132.51	273.94	1.89	0.14
Plant diversity	2.662											2	-133.89	272.05	0	0.53
	2.502										0.002	3	-133.45	273.44	1.39	0.26
	2.806									-0.007		3	-133.66	273.86	1.81	0.21

Table S3. Plausible candidate models (ΔAIC < 2) explaining the moth species richness, separately for both understory and canopy communities. Models are ranked according to their 2nd-order Akaike's information criterion (AICc). Parameter estimates (coefficients), number of parameters (k), and model weight (wi) are reported. GLMMs were fit with localities as random factor. Variable names are presented in Table 1.

	Intercept	Parameter estimates										*K*	logLik	AICc	ΔAICc	*wi*
		LTnb	DTWV	LTWV	MnDBH	MnTH	E1	E2	MnTT	TSR	HSR					
	All moth community															
Forest structure	4.696	-0.01		0.002	-0.034							5	-164.81	341.05	0	0.56
	4.491	-0.01		0.002	-0.036	0.019						6	-164.43	342.9	1.85	0.22
	3.692											2	-169.36	342.98	1.93	0.21
Canopy openness	3.501						0.004					3	-166.39	339.32	0	1
Plant diversity	4.024									-0.017		3	-166.27	339.08	0	0.62
	3.925									-0.018	0.002	4	-165.57	340.06	0.98	0.38
	Understory moth community															
Forest structure	3.331											2	-164.23	332.72	0	0.37
	3.701				-0.014							3	-163.19	332.92	0.2	0.34
	3.582					-0.018						3	-164.02	334.58	1.86	0.15
	3.744			0.001	-0.019							4	-162.87	334.66	1.94	0.14
Canopy openness	3.16						0.004					3	-162.65	331.84	0	0.38
	3.331											2	-164.23	332.72	0.88	0.25
	3.466							-0				3	-163.23	333	1.16	0.21
	3.267						0.003	-0				4	-162.38	333.69	1.85	0.15
Plant diversity	3.331											2	-164.23	332.72	0	0.36
	3.537									-0.01		3	-163.41	333.37	0.65	0.26
	3.197										0.002	3	-163.71	333.96	1.24	0.19
	3.406									-0.012	0.003	4	-162.54	334.01	1.29	0.19
	Canopy moth community															
Forest structure	4.044	-0.01	-0.068	0.003	-0.046							6	-153.26	320.57	0	0.22
	3.408	-0.01	-0.07	0.003	-0.053	0.06						7	-152.12	321.03	0.46	0.17
	2.608		-0.074									3	-157.43	321.4	0.83	0.14
	2.861	-0	-0.073									4	-156.26	321.45	0.88	0.14
	1.814		-0.072			0.057						4	-156.41	321.76	1.19	0.12
	2.085	-0	-0.071			0.055						5	-155.26	321.96	1.39	0.11
	2.751	-0.01	-0.062	0.001								5	-155.41	322.25	1.68	0.09
Canopy openness	2.218								0.037			3	-154.53	315.61	0	0.42
	2.024							0.004	0.042			4	-154.04	317.02	1.41	0.21
	2.107						0.003		0.032			4	-154.05	317.04	1.43	0.21
	1.769						0.005	0.005	0.038			5	-153.08	317.59	1.98	0.16
Plant diversity	3.35									-0.058	0.005	4	-148.57	306.08	0	0.69
	3.657									-0.056		3	-150.55	307.64	1.56	0.31

The montane forest around the Elephant camp (ca., 1.850 m asl.) is naturally disturbed by elephants © Š. Janeček

CHAPTER IV

Does rainforest biodiversity stand on the shoulders of giants? Effect of disturbances by forest elephants on trees and insects on Mount Cameroon

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ABSTRACT

Disturbances are a major component in tropical forests. Among the natural disturbances occurring in tropical rainforests, the ones induced by Megaherbivores can be staggering. While most of the studies have focused on the impact of forest elephants in savannahs, very few studies explored the impacts of forest elephants on their ecosystems. Moreover, their potential impacts on insect diversity is poorly understood. By comparison of already collected datasets in the disturbed forests and replications in the undisturbed forests, we assessed the effects of forest elephant disturbances on both tree and Lepidoptera communities. Forest elephant disturbances induce strong forest structural shift by reducing the tree density, size, and canopy cover of tallest trees. They also decrease tree species richness and alter the tree species composition, possibly by top-down control on tree recruitment. Overall, these changes also impact Lepidoptera communities, They increases the species richness of several groups as well as induces strong changes in community composition of all of them. Analyses of species ranges also shown that disturbed forests gather more range restricted species. While the populations of forest elephants are nowadays highly threatened, their future extinction from protected areas could have unexpected consequences at several ecological levels.

INTRODUCTION

Disturbances are major driving forces of diversity and dynamics of forest ecosystems (Burslem and Whitmore, 2006). The traditional view considering tropical rainforests as relatively stable ecosystems has been gradually replaced by a dynamic representation of tropical rainforests, alternating between disturbances and recovery phases (Chazdon, 2003). Natural disturbances can affect forest structure and tree assemblages through several pathways. For instance, a canopy opening resulting from a tree fall can temporarily modify resource availability (light, water, and soil nutrients) to the benefit of understorey plants (Schnitzer *et al.*, 1991). Usually, it leads to an increase in plant recruitment and growth during the first years until understorey saturation. This recovery phase will be maintained until a few individuals grow enough to close the canopy gap and reduce light availability to the lower strata (Schnitzer *et al.*, 2008). In this context, repeated disturbances are often seen as an important process for maintaining the diversity of pioneer plant species in tropical rainforests.

Tree community composition and forest structure is one of the main factor shaping insects communities (Nyafwono *et al.*, 2015; Valtonen *et al.*, 2017). By changing the biotic and abiotic conditions of the forest, natural disturbances have both direct and indirect effects on insect communities. Generally, they affect the density of individual species with both positive and negative responses to particular disturbances (Schowalter, 2011). Extreme disturbance events such as forest fires and floods will have intense direct effects being able to wipe out terrestrial insects from a locality (Paquin and Coderre, 1997). On the other hand, changes in horizontal and vertical microclimatic conditions following canopy openings can also impact insects locally. Increasing light penetration to the ground, for instance, significantly decreases humidity, driving insect community shift in favour of xerophilic species (Grimbacher and Stork, 2009). While these direct effects are relatively well-documented, indirect impacts of natural disturbances are harder to assess. They alter both resource availability and quality, as well as exposure to predators and parasites (see Schowalter, 1985 for a review of these effects). Simultaneously, an increase in forest heterogeneity may affect diversity positively by increasing the number of available niches within a locality (e.g., Hamer *et al.*, 1997; Hamer and Hill, 2000). But in contrast to the well-documented effects of natural disturbances on tree diversity (Schnitzer *et al.*, 2008), data on the expected cascade effects on insect diversity are still lacking in species-rich ecosystems such as tropical rainforests.

Megaherbivores, i.e., animal with body mass ≥ 1,000 kg, substantially alter various tropical ecosystems (Terborgh *et al.*, 2016). As large biomass consumers, they impact habitat structures and composition by top-down control on tree recruitment (Sankaran *et al.*, 2013). Amongst all megaherbivores, the effects of savannah elephants on their habitats are maybe the most studied. They alter their habitats mainly through two levels. First, as fruit-consumers, savannah elephants are important seed-dispersers able to spread seeds several kilometres away from the parent tree (e.g., Campos-Arceiz & Blake, 2011). Savannah elephants also increase tree mortality through grazing and repeated damage such as trampling and debarking (Rutina and Moe, 2014). On the other hand, meta-analysis of elephant-made disturbances on woody vegetation in savannah landscapes has shown that their impacts are regulated by climatic conditions, where woody vegetation is more negatively impacted in arid savannahs (Guldemond and Van Aarde, 2008). All these habitat modifications also implement changes in insect communities. Directly, trampling can affect insect communities by increasing the abundance of individuals with a high-level threshold to disturbance (Samways and Grant, 2008; Samways and Kreuzinger, 2001), while elephant dung piles support diversity of many insects (Botes *et al.*, 2006). Through their ability to radically transform their habitats at several ecological levels, savannah elephants play a key role in maintaining ecological processes (Kerley and Landman, 2006).

Comparatively, the effects of forest elephants on both tree and insect communities have received much less attention although their populations are decreasing at an alarming rate. In Central Africa, including Cameroon, the forest elephant population is essentially scattered into fragmented populations. The total number of individuals is estimated to have decreased by more than 62% between 2002 and 2012, occupying only 25% of its potential area (Maisels *et al.*, 2013). Poaching for ivory as well as deforestation and habitat fragmentation are the main threats leading to this concerning drop in the number of individuals. Even the largest metapopulation from Gabon, has dramatically reduced since 2004 by more than 80% of its individuals (Poulsen *et al.*, 2017). This decline in forest elephant population has already left extensive areas, included protected ones, empty of forest elephants. However, our knowledge on how rainforest ecosystems are responding to elephant disappearance is still very limited (Poulsen *et al.*, 2018)

Similarly to savannah elephants, forest elephants also transform their habitats (Poulsen *et al.*, 2018). However, their impact on woody plant species is ubiquitous, with both negative and positive impacts on tree density and diversity (Campos-Arceiz and Blake, 2011; Hawthorne and Parren, 2000; Poulsen *et al.*, 2018). Generally, forest elephants inhibit the growth of young saplings and reduce the diversity of large ones (Terborgh *et al.*, 2016), whilst being more efficient seed dispersers than their savannah counterparts (Campos-Arceiz and Blake, 2011; Yumoto *et al.*, 1995). In terms of forest succession, their presence can inhibit forest regeneration and maintain forest gaps (Omeja *et al.*, 2014). Preferential browsing of forest elephants also repetitively maintains bare ground and their trampling repeatedly destroys seeds and small saplings (Terborgh *et al.*, 2016). However, as far as we know, no studies have been done exploring the impacts of disturbances by elephants on rainforest insect communities.

Mount Cameroon provides a unique opportunity for studying the impacts of forest elephants on rainforest biodiversity. Despite their large size, forest elephants are especially difficult to monitor in tropical rainforests and are often tracked down by indirect evidences (e.g., dungs, elephant trails). However, on the southwestern slope of Mount Cameroon, a small population of forest elephants restrict their movement around two crater lakes. Additionally, the combined effects of water scarcity and the presence of a wide corridor of bare lava rocks not crossed by elephants split the forest into two blocks, with disturbed and undisturbed forests within a minimum distance. These unusual conditions present an opportunity for a design resembling a long-term exclosure experiment in natural conditions performed on a much larger-scale than any artificial exclosure study so far.

We hypothesize that forest elephants are keystone engineers in forming and maintaining diversity of tree and insect communities in tropical rainforests. We firstly hypothesize that both disturbed and undisturbed forests have different forest structures, with the disturbed forest being characterised by the presence of larger trees escaping elephant damage and either a sparse or dense understorey depending on the recent elephant activities. We also expect that forest elephants filter tree recruitment and decrease local tree species richness and alter tree community composition. Consequently, we suppose that these habitat changes impact insect biodiversity. Because of the combined effects of an increase in micro-habitats heterogeneity and changes in microclimatic conditions, as well as the cohabitation of large trees and pioneer plants, we expect the disturbed forest to be species-richer and composed of distinct insect assemblages.

MATERIAL AND METHODS

Study sites

Mount Cameroon (Southwestern Province, Cameroon) is the highest mountain in West and Central Africa. It is an active volcano rising from sea level at the Gulf of Guinea seashore up to 4,095 m asl. The Southwestern slope includes one of the only complete forested altitudinal gradients in the whole Afrotropics (extending from ca. 300 m asl. up to the tree line at 2,200 m asl.). Mount Cameroon is also part of the Guinean Forests of West Africa hotspot of diversity (Mittermeier *et al.*, 2011), including numerous endemic tree and insect species (e.g., Cable & Cheek, 1998; Sáfián and Tropek, 2016; Yakovlev and Sáfián, 2016; Ustjuzhanin *et al.*, 2018). Since 2009, most of the Mount Cameroon rainforests are now protected within the Mount Cameroon National Park (MCNP) including a large patch of lowland rainforest on the Southwestern slope.

Due to its coastal location on the Atlantic front, the southwestern slope of Mount Cameroon belongs to one of the rainiest places on Earth, with annual rainfall often exceeding 10,000 mm (Fraser *et al.*, 1998; Maicher *et al.*, 2019). The seasonality is characterized by the alternation of a single dry (late December to February), and a single wet season concentrating most of the annual rainfall (June to September). Contrastingly, the opposite North-Eastern slope is drier since the north-east maritime winds are partially blocked by the mountain (Fraser *et al.*, 1998). Despite the heavy precipitation during the wettest parts of the year, the river network is rather low on the Southwestern slope. Because of the ground porosity, most of the rain water percolates and is retained within large underground reservoirs rushing downslope into large springs during the wet season (Ako *et al.*, 2012). However, most of the dry up during the high-dry season on the Southwestern slope and the water remains contained underground emerging only at lower elevations. During this season, only two large crater lakes at mid-elevation remain filled with water.

Natural disturbances

Volcanism is a major factor of natural disturbance in the rainforests of Mount Cameroon. Frequent eruptions occur every ten to thirty years on the mountain flanks, where lava slowly flows down from multiple fissured segments. The increasing number of isolated trees and dead trees close to the tree line suggest that volcanism and repeated burning are responsible for compressing the tree line downward, below its climatic limit (Jacob *et al.*, 2015). Besides compressing the tree line downward, repeated volcanic events and lava flows also impact the forest at lower elevations through periodic forest fires and ash-falls (Proctor *et al.*, 2007). Remarkably, on the studied Southwestern slope, two eruptions in 1982 and 1999 created a wide corridor of bare lava rocks crossing the rainforest down to the sea coast (Fig. 1).

In addition to volcanic activity, a small population of forest elephants (*Loxodonta cyclotis*) also has a strong impact on vegetation above ca. 800 m asl. on the Southwestern slope (Cable & Cheek, 1998; Proctor *et al.*, 2007). This population is completely isolated from the nearest populations of the Korup National Park and the Banyang-Mbo Wildlife Sanctuary, as well as from the much larger metapopulations in the Congo Basin (Blanc, 2008). The number of individuals is estimated to be around 130 individuals by the Cameroonian Ministry of Forestry and Wildlife (2014). By the combined effects of the patchy availability of water reservoirs and the presence of the recent lava flows as natural obstacles, the Mount Cameroon forest elephant population is concentrated in a few areas with a local density high enough to have a strong impact on vegetation (Fig. 1). As a result, from either side of the main lava flows, extensive clearings and disturbed sparse forests supplement the typical closed-canopy on the west, while the forests ca. 5 km on the east remain free from their presence. Hence the forests are divided into two areas, with affected and non-affected forests (hereafter referred as ‘disturbed’ and ‘undisturbed forests’ respectively) within relatively short distances (Fig. 1).

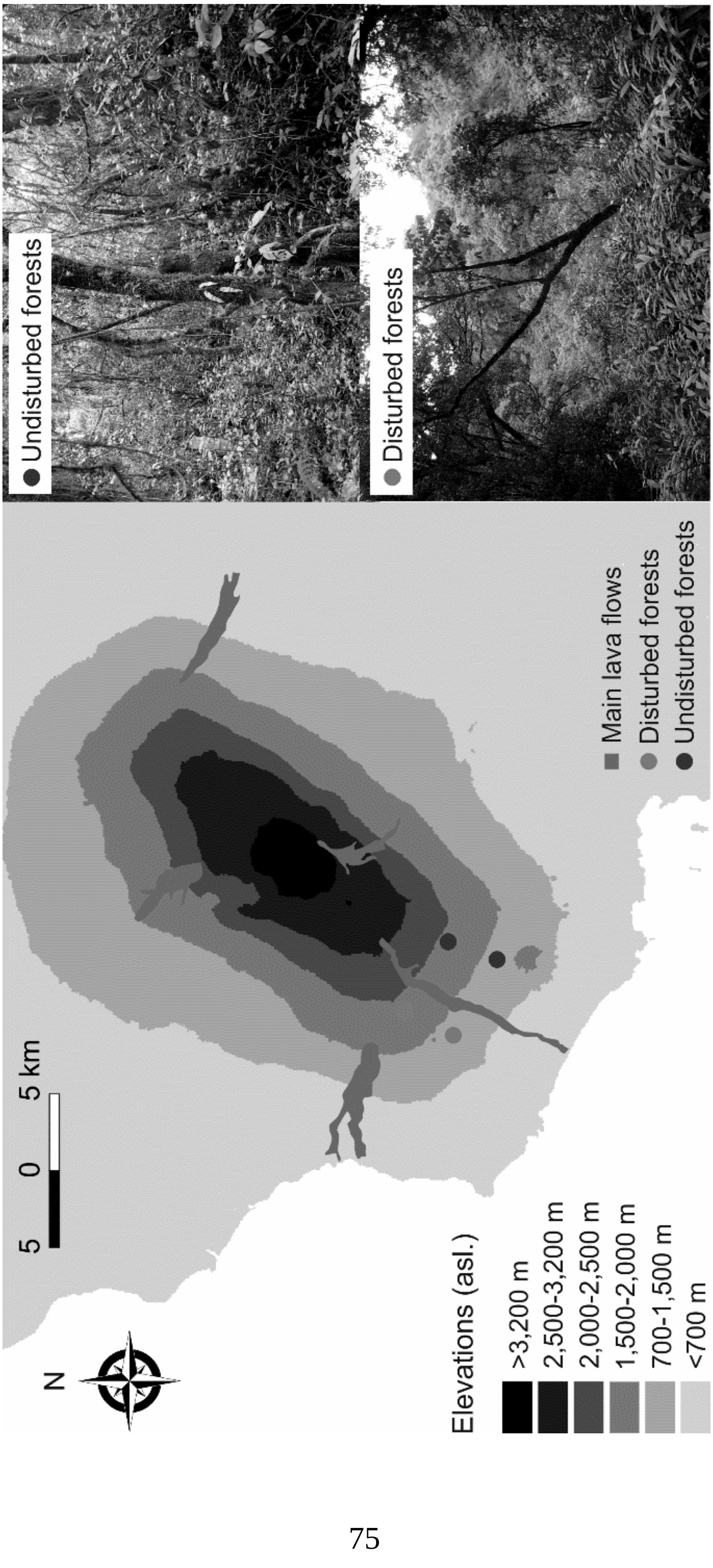
N
5
0
5 km
Elevations (asl.)
>3,200 m
2,500-3,200 m
2,000-2,500 m
1,500-2,000 m
700-1,500 m
<700 m
■ Main lava flows
● Disturbed forests
● Undisturbed forests
● Undisturbed forests
● Disturbed forests

Fig. 1. Map of Mount Cameroon with location of the main old lava flows, as well as sampled forests both disturbed and undisturbed by elephants. Both pictures were taken at 1,850 m asl.

To investigate the effects of forest elephant disturbances, two elevations were sampled, corresponding to upland forest (1,100 m asl.) and montane forest (1,850 m asl.). In the undisturbed forests, sixteen circular plots were already established (20 m radius, 150 m from each other; the same as in Djomo Nana *et al.*, 2015). Among them, eight adjacent plots were randomly selected. To then compare both disturbed and undisturbed forests, eight plots per elevation were established in the undisturbed forest following the same protocol as in the disturbed forests. Altogether, the 32 sampled plots cover a surface area of 4.02 ha.

Similarly, three additional distinct plots separated by a few meters from each other were also already established in both disturbed forests (Maicher *et al.*, in review). Following the same protocol, three additional plots per elevation were installed in the undisturbed forests.

Tree diversity and forest structure

To assess the tree diversity in both disturbed and undisturbed forests, all living and dead trees with diameter at breast height (DBH, at 1.3 m) ≥10 cm were labelled with numbered aluminium tags and identified to (morpho)species level in each of the eight circular plots. The tree diversity dataset in the disturbed forests was excerpted from Djomo Nana *et al.* (2015), whilst trees in the undisturbed forests were tagged and identified in 2017.

To study the impacts of elephant disturbances on the forest structure, each of these plots were characterised by twelve forest structure descriptors. Within each plot, all species were recorded and all living and dead trees with DBH ≥10 cm counted. Consequently, DBH and basal area of each of these trees was measured and averaged per plot (mean DBH and mean basal area), while height of the tree was estimated from the ground and averaged per plot (mean height) and the maximal tree height per plot recorded. From these measurements, two additional indices were computed for each tree: Stem Slenderness Index (SSI) was calculated as the ratio between tree height and DBH, and tree volume as the product of tree height and basal area. Both measurements were then averaged per plot (mean SSI and mean tree volume). Finally, following Grote (2003), a proxy of shrub, lower canopy, and upper canopy strata coverages was estimated per plot by summing the DBH of three tree height categories: 0-8 m; 8-16 m; >16 m.

Insect sampling

Lepidoptera (butterflies and moths) were selected as the target insect group because they are species-rich, with relatively well-known ecology and resolved taxonomy, and are easily attractable by standardised methods. The Lepidopteran dataset in the disturbed forests was directly extracted from Maicher *et al.* (2019), while the same sampling protocols were repeated in the undisturbed forests.

Lepidopterans were collected by two methods. Fruit-feeding Lepidopterans were sampled by five bait-traps (four in the understory, one in the canopy, baited by fermented bananas; see Maicher *et al.*, 2019 for details) in each of the eight circular plots. All butterflies and moths (hereafter referred to as butterflies and fruit-feeding moths) were removed daily from the traps for ten consecutive days and identified to (morpho)species.

Simultaneously, moths were attracted by a light (see Maicher *et al.*, 2019 for details) in each of the three plots during six complete nights per elevation (i.e., two night per plots). Six target moth groups (Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae, and Eupterotidae; hereafter referred as light-attracted moths) were collected manually and identified into (morpho)species. All voucher specimens will be deposited in the Nature Education Centre, Kraków, Poland.

To partially cover the seasonality, the entire sampling design was repeated during two transition seasons in both disturbed and undisturbed forest blocks (i.e., transition from wet to dry season: November/December 2014 and 2017 for the disturbed and undisturbed forests, respectively; and transition from dry to wet season: April/May 2015 and 2017 for the disturbed and undisturbed forests, respectively).

Diversity analyses

First, to account for sampling completeness of all focal groups (i.e., trees, butterflies, fruit-feeding moths, and light-attracted moths), the bias-corrected Chao1 species richness estimator as well as the sampling coverage were calculated to evaluate our data quality. Chao1 was computed using the package SpadeR (Chao *et al.*, 2016), and sampling coverage using the package iNEXT (Hsieh *et al.*, 2019), both in R 3.5.1 (R Core Team, 2018). For all focal groups in all seasons and at all elevations, the sampling coverage was always ≥0.84, indicating a good coverage of the sampled communities (Table S1). Subsequently, recorded species richness was used for analyses.

To analyse the effects of disturbances on the tree species richness recorded per plot and the Lepidoptera species richness after one day or night sampling at each plot, Generalized Estimated Equations (GEE) were computed using the geeglm function in the geepack package (Højsgaard *et al.*, 2006). For trees, plots were used as the sample using an independent covariance structure, with the factors disturbance, elevation, and their interaction included as explanatory variables. For lepidopterans, because of the temporal pseudo-replicative sampling design, one sampling day (butterflies and fruit-feeding moths) or night (light-attracted moths) per plot were used as a sample under a first-order autoregressive relationship “AR(1)” covariance structure. The factors disturbance, season, and elevation, as well as the interactions disturbance*season and disturbance*elevation were included as explanatory variables. All models were conducted with a Poisson distribution and log-link function. Pairwise post-hoc comparisons of the estimated marginal means were compared by Wald χ^2 tests. Estimated marginal means and 95% confidence intervals were used for plotting.

Differences in composition of communities between the disturbed and undisturbed forests were analysed by multivariate ordination methods, separately for all four focal groups. Firstly, the main patterns in species composition of individual plots were visualized by Non-Metric Multidimensional Scaling (NMDS) in Primer-E v6 (Clarke & Gorley, 2006). NMDS were generated using the Bray-Curtis similarity index, computed from the square-root transformed abundance recorded per plot. Then, the influence of disturbances was tested by constrained partial Canonical Correspondence Analyses (CCA) with elevation as covariate (Šmilauer & Lepš, 2014). The log-transformed abundances of individual species were used as the response variables. Significance of all partial CCAs were tested by Monte Carlo permutation tests with 9,999 permutations.

Finally, the impacts of disturbance on forest structure descriptors were analysed by partial Redundancy Analyses (RDA). Prior to the analyses, preliminary checking of the pairwise multicollinearity table between structure descriptors was investigated. Only forest structure descriptors with pairwise collinearity <0.80 were included in these analyses (i.e., tree species richness per plot, number of dead trees, mean DBH, mean height, maximum height, mean SSI, and the summed DBH of the trees >16 m). The log-transformation of these habitat descriptors were used as the response variables (Šmilauer & Lepš, 2014). RDA was then run with disturbance as an explanatory variable and elevation as covariate. Significance of the partial RDA was tested by Monte Carlo permutation tests with 9,999 permutations. CCAs, variation partitioning, and RDA were performed with the software Canoco 5 (ter Braak & Šmilauer, 2012).

Species distribution range

To analyse if the elephant disturbance supports rather species with restricted range or widely distributed generalists, we used the number of Afrotropical countries with known record of each tree and Lepidoptera species as a proxy for their distribution range; we are not aware of any more precise existing dataset covering all studied groups for the Afrotropics. Because of the considerably limited knowledge on many groups of Afrotropical Lepidoptera, we considered only butterflies, Sphingidae and Saturniidae moths (the latter two pooled together and referred to as moths in this analysis). This ranking was excerpted from the RAINBIO database for trees (Dauby *et al.*, 2016), Williams (2018) for butterflies, and Afromoths.net for moths (De Prins & De Prins, 2018); all considered as comprehensive databases for these focal groups. Non-native tree species were not considered for these analyses. In total, 73 species of trees were included in the distribution range analyses.

To consider also the relative abundances of individual species in the communities, the distribution range of each species was multiplied by the number of collected individuals per sample (i.e., plot for trees and butterflies; sampling night for moths), and subsequently divided by the total number of individuals recorded at each sample. The “mean distribution ranges” per sample were then compared between disturbed and undisturbed forests by GEE analyses (with normal distribution; independent covariance structure) following the same model design as for comparisons of species richness of trees and individual lepidopteran groups.

RESULTS

In total, 2,025 trees were identified to 97 species in all sampled plots (Table S1). For target insect groups, 7,853 individuals belonging to 437 species were identified (Table S1).

Effects of elephant disturbances on structure of rainforests

The partial RDA ordination analysis showed that both disturbed and undisturbed forests differed in the forest structure descriptors (Fig. 2). In total, the first two canonical axes explained 18.5% of adjusted variation (all axes eigenvalues: 0.83; Pseudo-F = 7.8; p = 0.002). The plots disturbed by elephants were negatively correlated with tree species richness, mean SSI, tree maximum and mean height, and sum of DBH of trees >16 m. In contrast, the elephant disturbed forests were characterised by higher mean DBH (Fig. 2). Number of dead trees seemed to have no relationship to the elephant disturbances.

Effect of elephant disturbances on tree diversity

Elephant disturbances affected species richness of trees recorded both per sampled elevation and plot. In both upland and montane forests, elephant disturbances decreased total recorded tree species richness, as well as Chao1, nearly to half the values in the undisturbed forests (Table S1). Additionally, elephant disturbances significantly decreased tree species richness per plot at both elevations (Tables 1 and S1; Fig. 3b). Whilst both elevation and disturbances were significantly associated with a decrease in species richness, the interaction disturbance*elevation was not significant, indicating a similar decrease in of species richness at both elevations (Table 1).

Tree species composition also differed between forests disturbed and undisturbed by elephants. Although the first NMDS axis can be related to elevation, the tree communities of the disturbed and undisturbed forests are relatively well-separated (Fig. 4a). It also showed that upland forest tree assemblages were the most dissimilar (Fig. 4a). The significance of elephant disturbance was confirmed by the partial-CCA (Table 2).

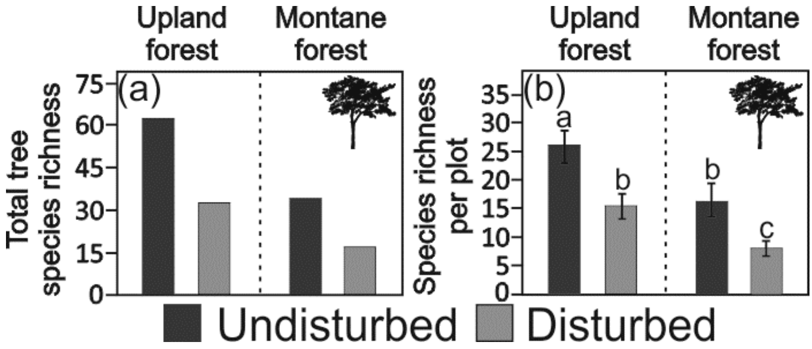

Fig. 3. Recorded species richness of trees (a) in the sampling site (raw values) and (b) per plot estimated by GEE (estimated means with 95% unconditional confidence intervals). The GEE results are summarized in Table 2. The letters visualize results of the post-hoc pairwise comparisons for the effect of disturbances.

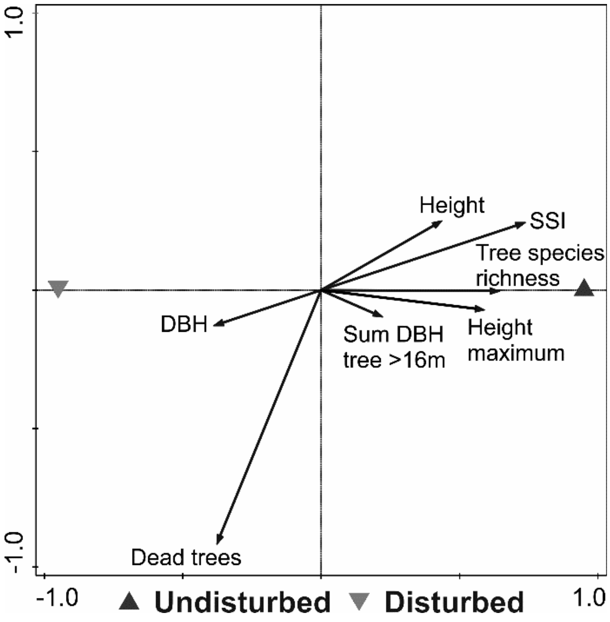

Fig. 2. Ordination diagram of the two first partial-RDA axes summarizing the effects of habitats descriptors on forest structure after removing the effects of elevation.

Table 1. Results of GEEs of tree and insect species richness per sample between forest disturbed and undisturbed by elephants, with included effects of elevation, season, and their interactions into the models (*p <0.05; **p <0.01; ***p <0.001). See methods for the details of the models.

Focal group	Source	df	Wald χ2	p-value	
Trees	Disturbance	1	21.9	<0.001	***
	Elevation	1	51.9	<0.001	***
	Disturbance*Elevation	1	1.3	0.25	
Butterflies	Disturbance	1	4.7	0.031	*
	Season	1	0	0.964	
	Elevation	1	10.2	0.001	**
	Disturbance*Season	1	7.4	0.007	**
	Disturbance*Elevation	1	45.1	<0.001	***
Fruit-feeding moths	Disturbance	1	3.3	0.069	
	Season	1	3.2	0.072	
	Elevation	1	27.3	<0.001	***
	Disturbance*Season	1	149.7	<0.001	***
	Disturbance*Elevation	1	7.2	0.007	**
Light-attracted moths	Disturbance	1	6.2	0.012	*
	Season	1	2.5	0.112	
	Elevation	1	2.4	0.123	
	Disturbance*Season	1	8.9	0.003	**
	Disturbance*Elevation	1	67.0	<0.001	***

Table 2. Results of partial CCAs testing the effect of forest elephant disturbances on composition of the focal groups communities.

	All axes eigenvalues	Adjusted explained variation (%)	Pseudo-F	p-value
Trees	4.55	8.59	3.8	<0.001
Butterflies	2.75	5.51	4.6	<0.001
Fruit-feeding moths	5.27	3.54	3.2	<0.001
Light-attracted moths	2.96	7.30	4.5	<0.001

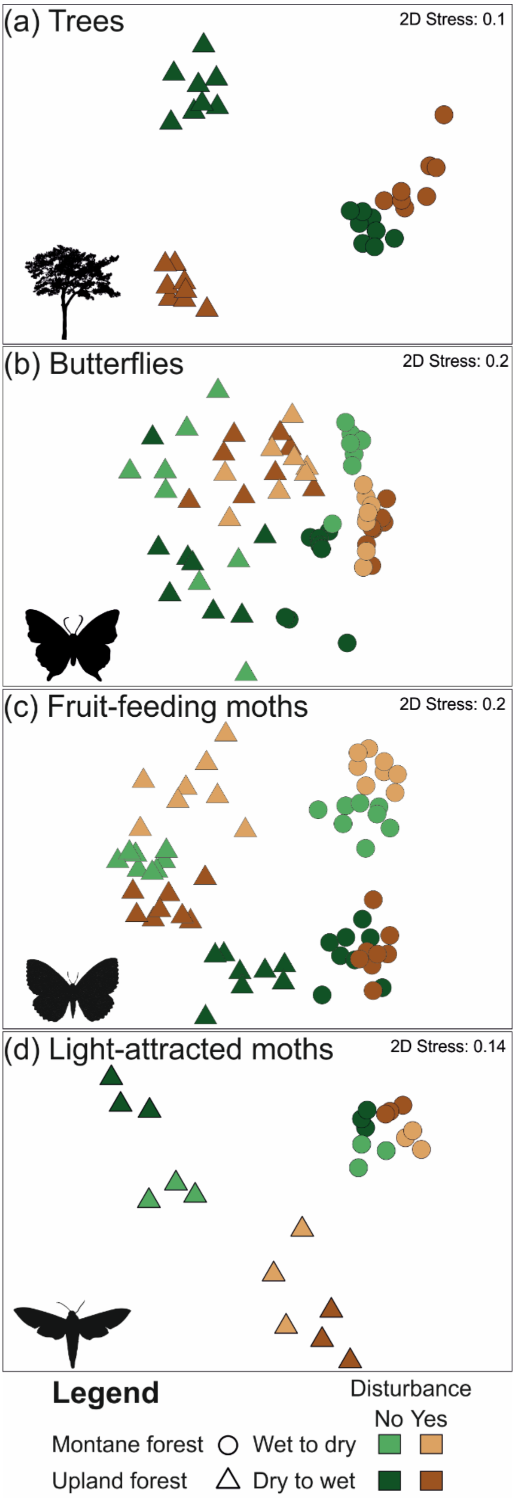

Fig. 4. Unconstrained ordination diagrams from non-metric multidimensional scaling (NMDS, based on the Bray-Curtis similarity index) of the individual focal group community compositions at the sampled plots.

Effect of elephant disturbances on insect diversity

The responses of individual insect groups species richness recorded per sampled elevation (gamma diversity) to elephant disturbances were rather inconsistent. Butterflies and fruit-feeding moths showed lower total species richness in the disturbed forests of both elevations during the transition from wet to dry season, which changed to become higher or comparable to the undisturbed forests during the transition from dry to wet season (Table S1; Fig. 1). Light-attracted moths were species-richer in the disturbed upland forest than in the undisturbed upland forest during both sampled seasons but species poorer in the montane forest during both sampled seasons (Table S1).

The effects of elephant disturbances on the species richness per plot (alpha diversity) differed among the studied insect groups. GEEs showed a significant positive effect of elephant disturbances on species richness per plot and night for butterflies and light-attracted moths (Table 1; Fig. 5). No significant effect of disturbance was detected for the fruit-feeding moths (Table 1). In addition, the effect of elevation was significant for both butterflies and fruit-feeding moths (Table 1). Despite the insignificant effect of disturbance on species richness of fruit-feeding moths, the interactions disturbance*season and disturbance*elevation were significant for all insect groups (Table 1). For butterflies and light-attracted moths, pairwise post-hoc comparisons of disturbed and undisturbed forests showed that the species richness per sample was significantly higher in the disturbed upland forest, and significantly lower or non-significantly different in the montane forest (Fig. 1). In contrast, fruit-feeding moth samples from the disturbed forests were significantly species-poorer in the transition from wet to dry season at both elevations, but significantly richer during the transition from dry to wet season (Fig. 1).

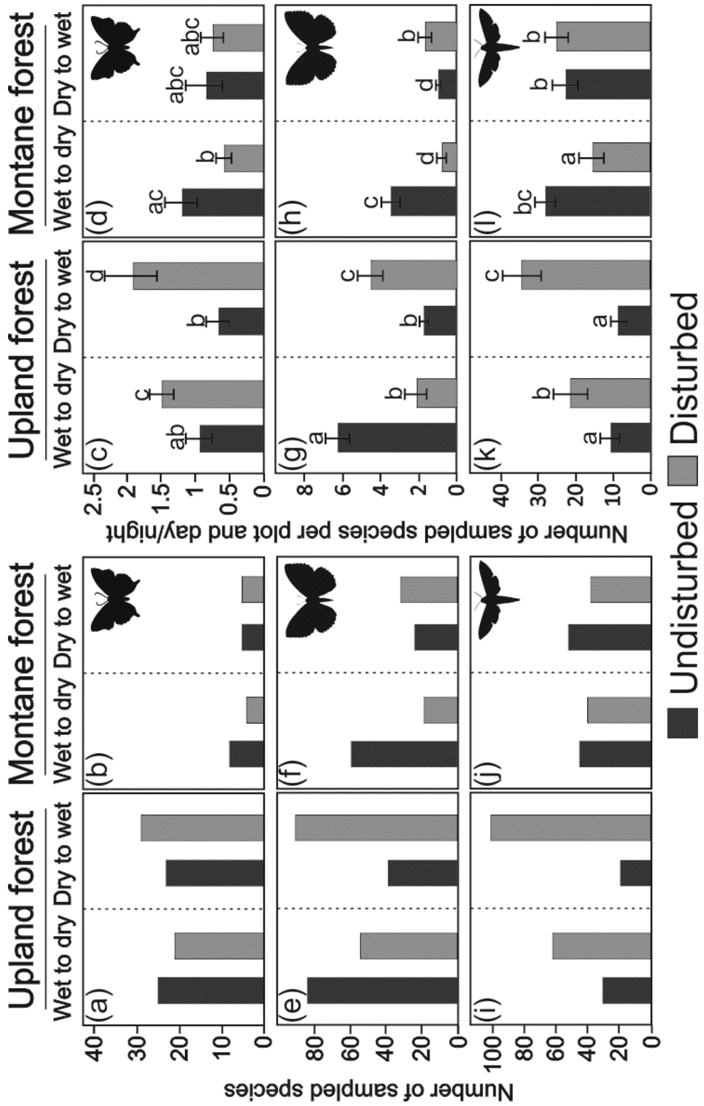

Fig. 5. Recorded species richness per sampled site and season (left panels) and per a sampling day or night at individual plots estimated by GEEs (right panels; estimated means with 95% unconditional confidence intervals are visualized) for butterflies (a-d), fruit-feeding moths (e-h), and light-attracted moths (i-l). Results of GEEs are summarized in Table 1. The letters visualize results of the post-hoc pairwise comparisons for the effect of disturbances.

Elephant disturbances affected species composition of all focal insect groups. The partial CCAs showed a significant effect of elephant disturbances on the species composition of all insect groups (Table 2). For both butterflies and fruit-feeding moths, elevation can be related to the first NMDS axis, as the samples are split between upland and montane forests along the first ordination axis (Fig. 4b-c). Contrastingly, the first NMDS is only weakly related to elevation for the light-attracted moths (Fig. 4d). Butterfly samples from disturbed and undisturbed upland forests were not clearly separated, while samples from both montane forests were well-split (Fig. 4a). In addition, the disturbed upland and montane forest plots were less heterogenous than in both undisturbed forest types. For the fruit-feeding and light-attracted moth samples, plots disturbed by elephants were well-separated from the undisturbed ones in both forest types, while the plots dispersion was comparable between disturbed and undisturbed forests (Fig. 4c-d). Among all insect groups, light-attracted moths species composition responded the most similarly to trees to elephant disturbances, with well-separated upland disturbed and undisturbed forest types and comparatively less heterogenous montane forest samples (Fig. 4a,d).

Effect of elephant disturbances on distribution range

Elephant disturbances, as well as elevation, did not show any significant effect on tree distribution range, (Table 3), but their interaction showed a marginally significant effect. In the undisturbed forests, the mean tree distribution range is positively associated with increasing elevation, while being negatively associated with increasing elevation in the undisturbed forests. However, none of the pairwise post-hoc comparisons were detected to besignificant (Fig. 6a).

Patterns of mean distribution range differ between both insect groups. For butterflies, both elephant disturbances and elevation significantly decreased the mean distribution range (Fig. 6b). The interaction disturbance*elevation was also significant in the GEE model (Table 3).

Pairwise post-hoc comparisons showed a strong decrease in mean butterfly distribution ranges in both forests disturbed by elephants, with a steeper decrease in the forests undisturbed by elephants (Fig. 6b). Contrastingly, the moths mean distribution range was significantly altered by elephant disturbances and seasonal factors, while the interaction disturbance*elevation was also significant (Table 3). Pairwise post-hoc comparisons showed that light-attracted moths in the undisturbed upland forest had a significantly lower distribution range than in the disturbed upland forest and in both disturbed and undisturbed montane forests (Fig. 6c).

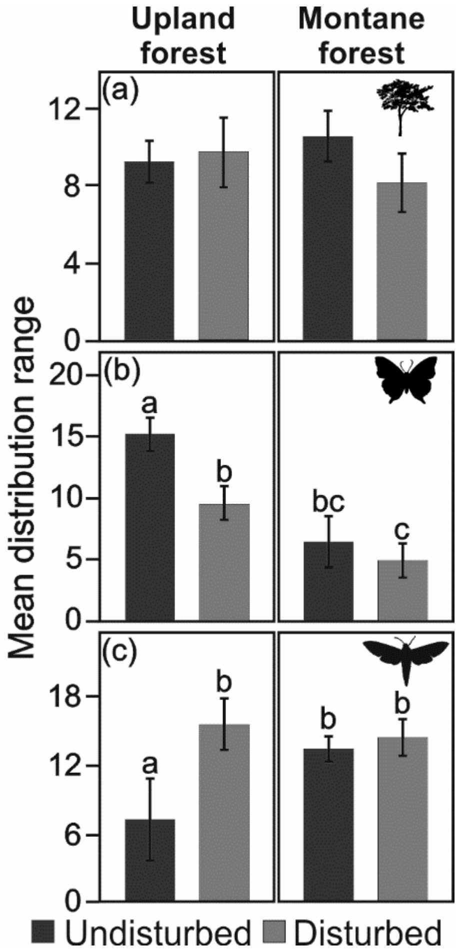

Figure 6. Mean distribution range per plot for trees (a), per plot for butterflies (b), and per night for moths (c) estimated by GEEs. The barplots visualize the estimated means per plot with 95% unconditional confidence intervals. Results of GEEs are summarized in Table 3. The letters visualize the results of the post-hoc pairwise comparisons for the effect of disturbances.

Table 3. Results of GEEs comparing average distribution range of trees and insects per sample (*p <0.05; **p <0.01; ***p <0.001). See Methods for the GEEs details.

Focal group	Source	df	Wald χ2	p-value	
Trees	Disturbance	1	1.4	0.230	
	Elevation	1	0.0	0.860	
	Disturbance*Elevation	1	3.9	0.050	*
Butterflies	Disturbance	1	9.5	0.002	**
	Elevation	1	67.6	<0.001	***
	Season	1	2.5	0.115	
	Disturbance*Elevation	1	7.3	0.007	**
	Disturbance*Season	1	0.2	0.654	
Moths	Disturbance	1	5.1	0.024	*
	Elevation	1	0.8	0.372	
	Season	1	6.9	0.009	**
	Disturbance*Elevation	1	12.4	<0.001	**
	Disturbance*Season	-	0.5	0.462	

Discussion

Forest elephants are deeply altering rainforest biodiversity. The forest elephant presence modifies the forest structure, reducing the mean tree height as well as the canopy cover of tall trees in favour of an increase in average of small trees of large stature. Confirming our first hypothesis, the observed shift in forest structure can be interpreted by a combination of direct and indirect effects driven by forest elephants. Because of their large body sizes and herd movement, most of the trees within their area are being damaged (Terborgh *et al.*, 2016). Elephants break stems and sometime uproot trees on their way, while repeated trampling denude the ground and degrade the seed bank (Terborgh *et al.*, 2016). All these direct damages are likely to indirectly increase tree susceptibility to pathogens and ultimately tree mortality. Although the number of dead trees seemed to poorly characterise the disturbed forests, the strong reduction in tree density observed within the disturbed plots support this hypothesis. Thereby, the presence of a few large trees can be explained by the fact that only a small portions of trees escape foraging breakage compared to young saplings (Terborgh *et al.,* 2016).

In addition to alter the forest structure, the presence of elephants decreases the tree species richness and induces a shift in tree community composition, confirming our second hypothesis. Forest elephants are generalist herbivores, consuming a wide range of plant species and tissues (Blake, 2002). Nevertheless, there is strong evidences of preferential browsing by forest elephants for selected species of trees and lianas (Blake, 2002). Thereby, the selective browsing of palatable species can affect tree recruitment and impact community-level assemblages, explaining the observed tree compositional change in the disturbed forests. While repeated grazing has durable effects on tree assemblages, it is likely that the impact of forest elephant on rainforest structure and tree assemblages is likely to be long-lasting (Chazdon, 2003).

The effects of elephant disturbances on insect species richness differ among groups, but significantly changes the species composition of all of them. While disturbed forests gather more species of butterflies and light-attracted moths, the effects of disturbances also differ between elevation and sampled seasons for all groups. Butterflies rely on forests gaps and openings for their thermoregulation (Clench, 1966), the decrease of canopy cover of tall trees in the disturbed forest is therefore likely to be beneficial to several butterflies species. While this hypothesis can hardly explain the increase in species richness of light-attracted moths, the increase in both fruit-feeding butterflies and light-attracted moths is proposed to be driven by the increase in forest heterogeneity, likely to support greater number of species (Braga and Diniz, 2015; Tews *et al.*, 2004). While herbivorous insects, and especially Lepidoptera, are tightly connected to their host-plants (Novotný *et al.*, 2006), the observed shift in tree community composition is probably the main driver of the changes in Lepidoptera assemblages.

Lepidoptera communities are highly seasonal on Mount Cameroon (Maicher *et al.*, 2018). While forests at different stages of recovery also shown different fruit-feeding butterflies seasonality (Nyafwono *et al.*, 2014), it appears that forest elephant disturbances could as well impact Lepidoptera phenology. Since Lepidoptera phenology is regulated by the alternation of wet and dry seasons, and especially rainfall (Grøtan *et al.*, 2014; Valtonen *et al.*, 2013), it can be proposed that changes in forest structure directly influence Lepidoptera life-cycles, or that the changes in species communities implement species with different seasonal timing of adult emergence in the disturbed forests.

Since natural disturbances are an intrinsic part of forest dynamics, management of protected areas must be based on our understanding of the natural processes involved within. Recently, Poulsen *et al.* (2018) discussed the fate of Afrotropical rainforests in a world without forest elephants. The authors hypothesized that their loss would increase stem density, reshape tree species composition, and decrease the abundance of large trees. At the light of our results, we concur with the authors hypotheses. Although more comparative studies are required, forest elephant disappearance is likely to induce a start of recovery succession, enclosing the forest gaps by increasing tree densities and tree heights, and increases habitats homogeneity at the landscape level. However, forest regeneration will also have unexpected consequences on herbivorous insect species depending on disturbed forest habitats. On this particular aspect, the potential disappearance of several range restricted insect species is concerning.

In this context, forest elephant population contributes to maintain rainforest heterogeneity and tree diversity. Thereby, the maintenance of forest elephant populations in Central African tropical rainforests could help to prevent species extinction at the landscape level (Braga and Diniz, 2015). While habitat heterogeneity increases the number of resources and available niches, and ultimately sustain a greater number of insect species, their alarming disappearance in Central Africa is of upmost concern. In this regard, forest elephants can be qualified as keystone-species *sensu* Mills *et al.* (1993). Hawthorne and Parren (2000) demonstrated that the disappearance of forest elephants from several Ghanaian forests did not have any remarkable on plant populations at the country level. From this finding, the authors challenged the traditional view of general collapse of rainforests without forest elephants. Regardless of the fact that the forest elephant population of Ghana has critically decline since then, we add that the disappearance of forest elephants from extensive areas might already have unwanted impacts on insect populations. Although highly speculative, the alteration of herbivorous insect communities associated to forest elephant populations might escalate to other trophic levels and ultimately to forest ecosystems functioning.

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SUPPLEMENTARY MATERIAL

Table S1. Summary of abundance and diversity of trees and insects in different seasons on disturbed and undisturbed forests by elephants on Mount Cameroon.

		Undisturbed				Disturbed			
		Upland forest		Montane forest		Upland forest		Montane forest	
		Wet to dry	**Dry to wet**	**Wet to dry**	**Dry to wet**	**Wet to dry**	**Dry to wet**	**Wet to dry**	**Dry to wet**
Trees	**No. individuals**	802		438		511		274	
	No. species	62		32		32		16	
	Chao 1 (±SE)	70(±6)		34(±3)		33(±1)		19(±5)	
	Sampling coverage	0.98		0.99		0.99		0.99	
Butterflies	**No. individuals**	74	67	355	95	255	193	68	119
	No. species	25	23	8	5	21	29	4	5
	Chao 1 (±SE)	32(±6)	30(±6)	10(±4)	6(±1)	33(±13)	35(±5)	4(±1)	5(±1)
	Sampling coverage	0.88	0.85	0.99	0.99	0.97	0.95	1.00	0.99
Fruit-feeding moths	**No. individuals**	1,806	184	458	93	192	499	101	144
	No. species	85	39	60	24	55	92	19	32
	Chao 1 (±SE)	182(±43)	60(±14)	102(±21)	56(±26)	86(±16)	153(±27)	25(±6)	112(±58)
	Sampling coverage	0.98	0.91	0.94	0.85	0.86	0.92	0.94	0.85
Light-attracted moths	**No. individuals**	326	61	633	473	208	469	383	597
	No. species	30	19	45	52	62	101	40	38
	Chao 1 (±SE)	38(±7)	44(±24)	66(±16)	84(±22)	96(±17)	168(±28)	54(±10)	44(±6)
	Sampling coverage	0.97	0.84	0.98	0.96	0.86	0.90	0.96	0.99

The grassland at 3,000 m asl. above the tree line *on the Eastern slope © V. Maicher*

CHAPTER V

Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon

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ABSTRACT

Aim Temporal dynamics of biodiversity along tropical elevational gradients are unknown. We studied seasonal changes of Lepidoptera biodiversity along the only complete forest elevational gradient in the Afrotropics. We focused on shifts of species richness patterns, seasonal turnover of communities, and seasonal shifts of species' elevational ranges, the latter often serving as indicator of the global change effects on mountain ecosystems.

Location Mount Cameroon, Cameroon.

Taxon Butterflies and moths (Lepidoptera)

Methods We quantitatively sampled nine groups of Lepidoptera by bait-trapping (16,800 trap-days) and light attraction (126 complete nights) at seven elevations evenly distributed along the elevational gradient from sea level to timberline. Sampling was repeated in three seasons.

Result Altogether, 42,936 specimens of 1,099 species were recorded. A mid-elevation peak of species richness was detected for all groups, but Eupterotidae. This peak shifted seasonally for six of them, mostly ascending after the beginning of the dry season. Seasonal shifts of species' elevational ranges were mostly responsible for these diversity patterns shifts along elevation: we found general upward shifts in butterflies, fruit-feeding moths and Lymantriinae from beginning to end of the dry season. Oppositely, Arctiinae shifted upwards during the wet season. The average seasonal shifts of elevational ranges often exceeded 100 meters and were even several times higher for numerous species.

Main conclusion We report seasonal uphill and downhill shifts of several groups of Lepidoptera. The reported shifts can be driven by both delay in weather seasonality and shifts in resources availability, causing delay of adult hatching and/or adult migrations. These community shifts may lead to misinterpretations of tropical insects' diversity patterns along altitude if seasonality is ignored. More importantly, considering the surprising extent

of intra-annual elevational shifts of species, we encourage authors to take account of natural dynamic as well while investigating global change impact on communities of Lepidoptera in tropical mountains.

INTRODUCTION

Research on biodiversity patterns along elevational gradients, especially in the species-rich tropics, has crucially contributed to our understanding of ecological mechanisms influencing species distribution and co-existence (McCain & Grytnes, 2010). Generally, increasingly unfavourable climatic conditions, reduction of habitat area, and constraints in resource diversity and amount have repeatedly been linked with the diversity decrease of many taxa towards the highest elevations (McCain & Grytnes, 2010). Simultaneously, it has become evident that species richness of many groups, including Lepidoptera (Pyrcz & Wojtusiak, 2002; Pyrcz *et al.*, 2009; Beck *et al.*, 2017), peaks at mid-elevations (McCain & Grytnes, 2010; Colwell *et al.*, 2016). Colwell *et al.* (2016) explained this phenomenon by combined effects of geometric constraints and a unimodal gradient of environmental favourability. So far, the majority of datasets on tropical Lepidoptera originated from the Neotropics, South-East Asia, and North Australia (e.g., Beck *et al.*, 2017). Consequently, a large knowledge gap remains in the generally understudied Afrotropics (Beck *et al.*, 2017), with the only exception of data from Mount Kilimanjaro (Axmacher *et al.*, 2004, 2009; Peters *et al.*, 2016), hindering our general understanding of lepidopteran biodiversity organisation along elevation.

Despite the historical concept of ‘aseasonal’ tropics, tropical insect biodiversity is known to be strongly seasonal (Wolda, 1988). Several studies have shown temporal changes in the demography of individual species that contribute to a phenological turnover at the community level (Grøtan *et al.*, 2012, 2014; Valtonen *et al.*, 2013; Maicher *et al.*, 2018). These phenological changes of tropical Lepidopteran communities are often driven by wet and dry season cycles influencing availability of resources for both caterpillars and adult butterflies and moths (Grøtan *et al.*, 2012, 2014; Valtonen *et al.*, 2013; Maicher *et al.*, 2018). On the other hand, at higher elevations, Lepidopteran phenology may be more strongly driven by seasonal changes of temperature as one of the main constraints for mountain insects (i.e., Boulter *et al.*, 2011; Bishop *et al.*, 2014; Wardhaugh *et al.*, 2018). Such different pressures on communities at various elevations might substantially influence the spatial distribution of species diversity along elevation, as well as its temporal dynamics. However, because of the apparent logistic problems with sampling on most tropical mountains, these phenological aspects have been ignored in most studies of tropical elevational biodiversity patterns. Most studies have focused on patterns of biodiversity along tropical elevational gradient within a single season, or even neglected local seasonality at all. In our opinion, to fully understand organisation of tropical biodiversity, we need to include its temporal aspects.

Biodiversity of tropical mountains has also recently been discussed in terms of global change, predicting to strongly impact their environments and communities (Colwell *et al.*, 2008; Laurance *et al.*, 2011). Predicted local increases in temperature should shift the climatic niches of many species uphill followed by multiple cascade effects leading to local or even global extinctions, especially of summit species (Sheldon *et al.*, 2011; Colwell *et al.*, 2008). Recently, such upward shifts of Lepidopteran elevational ranges related to the global climate change have been repeatedly reported from tropical mountains (Wilson *et al.*, 2005; Chen *et al.*, 2009, Chen, Hill, Ohlemüller, *et al.*, 2011; Chen, Hill, Shiu, *et al.*, 2011; Laurance *et al.*, 2011). However, these studies have consistently neglected the seasonal dynamics of species' ranges since data were either collected during a single season only or were lumped across seasons. Nevertheless, seasonality is known to strongly affect distribution, abundance, and diversity of Lepidopteran communities in tropical ecosystems (Grøtan *et al.*, 2012, 2014; Valtonen *et al.*, 2013, Maicher *et al.*, 2018). Therefore, it remains questionable how the described elevational range shifts might be related to natural seasonal dynamics together with potential sampling biases arising from the lack of temporal replicates. Unfortunately, knowledge of natural intra-annual shifts of elevational ranges is very poor, although crucial for the evaluation of global change impacts.

Here, we report the first extensive and standardized study of temporal biodiversity patterns of nine lepidopteran groups along an elevational gradient of Mount Cameroon, i.e., the only continuous forested gradient from lowland to timberline in the entire Afrotropics. To our knowledge, it is the second comprehensive dataset on terrestrial insects along altitude in West/Central Africa (Mongyeh *et al.*, 2018). The combination of local extremely seasonal climate and rich biodiversity (Ferenc *et al.*, 2018; Ustjuzhanin *et al.*, 2018) offers the unique opportunity to study spatial and temporal biodiversity patterns. We predicted inter-seasonally different biodiversity patterns caused by the extreme local seasonality. We also quantified shifts of individual species' ranges, which we expected to represent an important part of the inter-seasonal community differences. In addition to understanding the local biodiversity dynamics, it should allow us to better evaluate and understand potential shifts related to global climate change.

MATERIALS AND METHODS

Study sites

All material was collected at seven different elevations (Table 1; Fig. S1 in Appendix S1; Ferenc *et al.*, 2016) on the southwestern slopes of Mount Cameroon, Southwestern Province, Cameroon, the highest mountain of West/Central Africa (4,095 m asl) and an important hotspot of biodiversity and endemism for many taxa including Lepidoptera (Maicher *et al.*, 2016; Ustjuzhanin *et al.*, 2018). Mostly included inside Mount Cameroon National Park, its southwestern slope is the only continuous elevational gradient of near-pristine tropical rainforests from lowland (ca 350 m asl) to the timberline (ca 2,100–2,300 m asl) on the entire continent.

Table 1. Summary of the sampled localities on Mount Cameroon (BBCF: Bimbia-Bonadikombo community forest; MCNP: Mount Cameroon National Park). The coordinates are in WGS84.

	Elevation (m asl)	Latitude	Longitude	Vegetation type	Locality
Mexico Camp	30 m	N 03.9818°	E 09.2625°	Coastal forest	BBCF
Bamboo Camp	350 m	N 04.0899°	E 09.0517°	Mosaic of primary and secondary lowland forest	MCNP
Drink Gari	650 m	N 04.1022°	E 09.0630°	Primary lowland forest	MCNP
PlanteCam Camp	1,100 m	N 04.1175°	E 09.0709°	Upland forest locally disturbed by elephants	MCNP
Crater Lake	1,450 m	N 04.1443°	E 09.0717°	Submontane forest locally disturbed by elephants	MCNP
Elephant Camp	1,850 m	N 04.1453°	E 09.0870°	Montane forest locally disturbed by elephants	MCNP
Mann's Spring	2,200 m	N 04.1428°	E 09.1225°	Montane forest close to the timberline	MCNP

The study area lies in a perhumid tropical climate essentially influenced by alternation of south-west maritime winds (monsoon) and north-east continental dry winds (harmattan), with well-pronounced seasonality consisting of one wet (June–September) and one dry season (late December–February), separated by relatively short transition seasons (Fraser *et al.*, 1998; Fig. 1, Table S1 in Appendix S2). The southwestern slope foothills are one of the rainiest places in the world, with annual precipitation often exceeding 10,000 mm (Fraser *et al.*, 1998). Most rainfall occurs between June and September, with monthly precipitation over 1,500 mm. Rainfall is rare from November to February, especially at higher elevations (Fraser *et al.*, 1998; Fig. 1, Table S1 in Appendix S2).

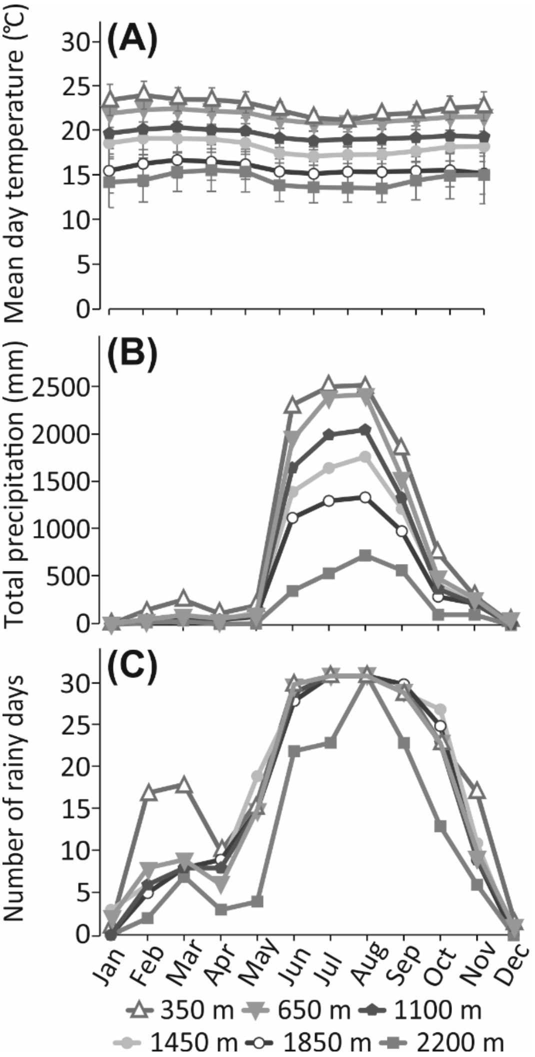


Fig. 1. Weather on Mount Cameroon. (A) Mean daily temperature; (B) monthly precipitation in 2015; and (C) number of rainy days (>2 mm of rainfall) in 2015.

Six sampling elevations (350 m, 650 m, 1,100 m, 1,450 m, 1,850 m, and 2,200 m asl) constituted the main transect along a line ranging from the lowland forest up to the natural timberline on the southwestern slope (Table 1). The lowest sampling elevation (30 m asl) was set in the Bimbia-Bonadikombo Community Forest (Table 1; Ferenc *et al.*, 2018), separated from the main transect line by ca 25 km of farmlands, extensive agroforests, inhabited areas, and degraded secondary growth (Fig. S1 in Appendix S1).

Lepidoptera sampling

At each sampling elevation, lepidopterans were collected following two sampling protocols. Fruit-feeding Lepidoptera (hereafter *butterflies* and *fruit-feeding moths*) were sampled using bait-traps, while selected groups of Lepidoptera (Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae, and Eupterotidae) were attracted by light and manually collected. Between 2014 and 2017, each elevation was sampled at three distinct seasons: transition from wet to dry season (late October/early December), high dry season (January/February), and transition from dry to wet season (April/May). Unfortunately, no sampling of Lepidoptera was logistically feasible during the high wet season because of Mount Cameroon's extreme weather conditions (Fig. 1).

For our sampling, we used the plots already described in Ferenc *et al.* (2016, 2018). Within each of the seven elevations, 16 forest plots were established, minimally 150 m apart from each other. At each plot, five bait traps were installed (modified IKEA PS Fångst: height 75 cm, diameter 23 cm; first used by Sáfián *et al.*, 2011), and baited with fermented mashed bananas. Four traps were installed in the understorey layer, as close to the ground as possible, and one trap was hung up into the canopy at 20(±5) m height. The banana bait (ca 0.3 l) was refreshed every day and renewed every three to five days, depending on its quality. All traps were exposed for ten consecutive sampling days within each season, during which all trapped butterflies and moths were removed and counted daily. This resulted in 16,800 trapping days.

Moths were also attracted by an energy-saving bulb (type M036, produced by Hadex, Czechia: 4100 K, 5300 lm, 105 W, 230 V, 5U) hung at the junction of two perpendicularly placed white sheets (1.5 x 1.5 x 1.8 m, the cloth type B, produced by Entosphinx, Czechia) powered by a portable generator. At each elevation, three distinct plots were selected at a distance of a few hundred metres from each other, to partially cover the local forest heterogeneity. The focal moth groups were sampled from dusk till dawn in two nights per plot, i.e., 126 complete nights altogether. The five nights before and after the full moon were avoided.

Most butterflies and some common bait-trapped moths (especially Calpinae and Erebinae) were identified in the field. All other specimens were dried by silica gel, stored in glassine envelopes, and later identified to (morpho)species level, using both external morphology and genitalia features. Voucher specimens are stored in the Nature Education Centre, Jagiellonian University, Krakow, Poland.

Weather data

We recorded mean daily temperature, total monthly precipitation, and the number of rainy days (defined as >2 mm rainfall per 24 hours) at all elevations but the lowest. Temperature was recorded by three DRL26 automatic dendrometers (EMS, Brno, Czechia) per elevation, with built-in growth and temperature dataloggers, placed on trunks (ca 40 cm DBH, min. 150 m from each other) at 1 m above ground under closed forest canopy. Temperature was recorded every hour from January 2015 to December 2016. Precipitation was recorded using Minikin ERi with Pronamic Pro Rain Gauge (EMS, Brno, Czechia; it registers actual time of tipping, not number of pulses within a time interval) during 2015. One rain gauge per elevation was installed in a larger canopy gap with regularly cleared understorey vegetation.

Elevational patterns of species diversity

The nine focal groups were treated separately in all analyses: bait-trapped butterflies and fruit-feeding moths, and light-attracted Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae, and Eupterotidae. Except where mentioned otherwise, all statistical analyses were performed in R v. 3.4.4 (R Core Team, 2018).

Diversities of the focal groups at each elevation and season were characterized by two measures: 1/ observed *species richness*; and 2/ bias-corrected *Chao1* species richness estimator. Sampling completeness was estimated from the sampling coverage (*iNEXT* package, Hsieh *et al.*, 2016). Generalized linear mixed-models (GLMMs, tested using type II Wald $\chi2$ tests, negative binomial distribution; *lme4* package, Bates *et al.*, 2015) were applied to test changes of *species richness* with elevation; *elevation* was applied as fixed factor, and *season* and *plot* (nested in elevation) as random factors. For both bait-trapped groups, a sample corresponded to the pooled five traps and ten trapping days at each plot per season; whereas for the light-trapped groups, a sample corresponded to the pooled two sampling nights at each plot per season. Differences among individual elevations were tested by post-hoc pairwise comparisons of the least square means with Tukey adjustments.

Seasonal patterns and seasonal shifts

Seasonal changes of *species richness* elevational patterns were tested by GLMMs with *elevation*, *season* and their interaction as fixed factors, and plot (nested in elevation) as a random factor. *Species richness* per plot in ten sampling days or two sampling nights was fit into negative binomial models. Simultaneously, main gradients in community composition at each elevation and season were analysed by Nonmetric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarity matrices after square-root transformations of individual species abundances per plot and season. Differences in species composition among elevations and seasons were tested by sequential permutational analyses of variance (PERMANOVA) using 9,999 permutations. Both NMDS and PERMANOVAs were performed in Primer-E v6 with PERMANOVA+ (Clarke & Gorley, 2006). In the six groups with significant effects of season and elevation interaction on species richness (both fruit-feeding groups, Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae), we further focused on the details of their inter-seasonal changes.

To determine if the changes are caused rather by species turnover or shifts of species' elevational ranges, we firstly quantified proportions of three species categories at each particular elevation and season: (1) *settled species*: those recorded at the same elevation in the previous season as well; (2) *shifted species*: those recorded only at any different elevation(s) in the previous season; and (3) *newly emerged species*: those not recorded in the previous season at all. Finally, we analysed inter-seasonal shifts of species' elevational ranges. We used three measures of elevational range calculated for each season separately: the species' (1) *highest elevation* (i.e., the uppermost record), (2) *lowest elevation* (i.e., the lowest record), and (3) *weighted mean elevation* (i.e., the average of elevations for all individuals of a given species, Menéndez *et al.*, 2014). Changes of these elevational measures among every two seasons were tested for species recorded in >1 season using non-parametric Wilcoxon signed-rank tests. The lowest sampling locality was excluded from both previous analyses because it is relatively isolated from the main transect and any inter-seasonal migration of specimens is thus much less probable.

RESULTS

Lepidoptera biodiversity and its elevational patterns

In total, 42,936 specimens identified to 1,099 morphospecies were collected (Table S1 in Appendix S3). Bait-trapping brought 25,338 individuals (17,322 fruit-feeding butterflies, and 8,016 fruit-feeding moths) of 541 morphospecies (138 fruit-feeding butterflies, and 403 fruit-feeding moths). Light-sampling gathered 17,598 individuals (9,203 Arctiinae; 4,451 Lymantriinae; 1,632 Notodontidae; 1,111 Lasiocampidae; 611 Sphingidae; 385 Saturniidae; 205 Eupterotidae) of 561 morphospecies (121 Arctiinae; 207 Lymantriinae; 97 Notodontidae; 56 Lasiocampidae; 40 Sphingidae; 20 Saturniidae; 20 Eupterotidae). Because of the relatively high sampling coverages of all groups but

Eupterotidae at most elevations and seasons (Table S1 in Appendix S3), and since their observed *species richness* is mostly included within the *Chao1* 95% confidence intervals (including those few with sampling coverages <0.7), only the observed *species richness* was subsequently used for the analyses and interpretations of diversity patterns.

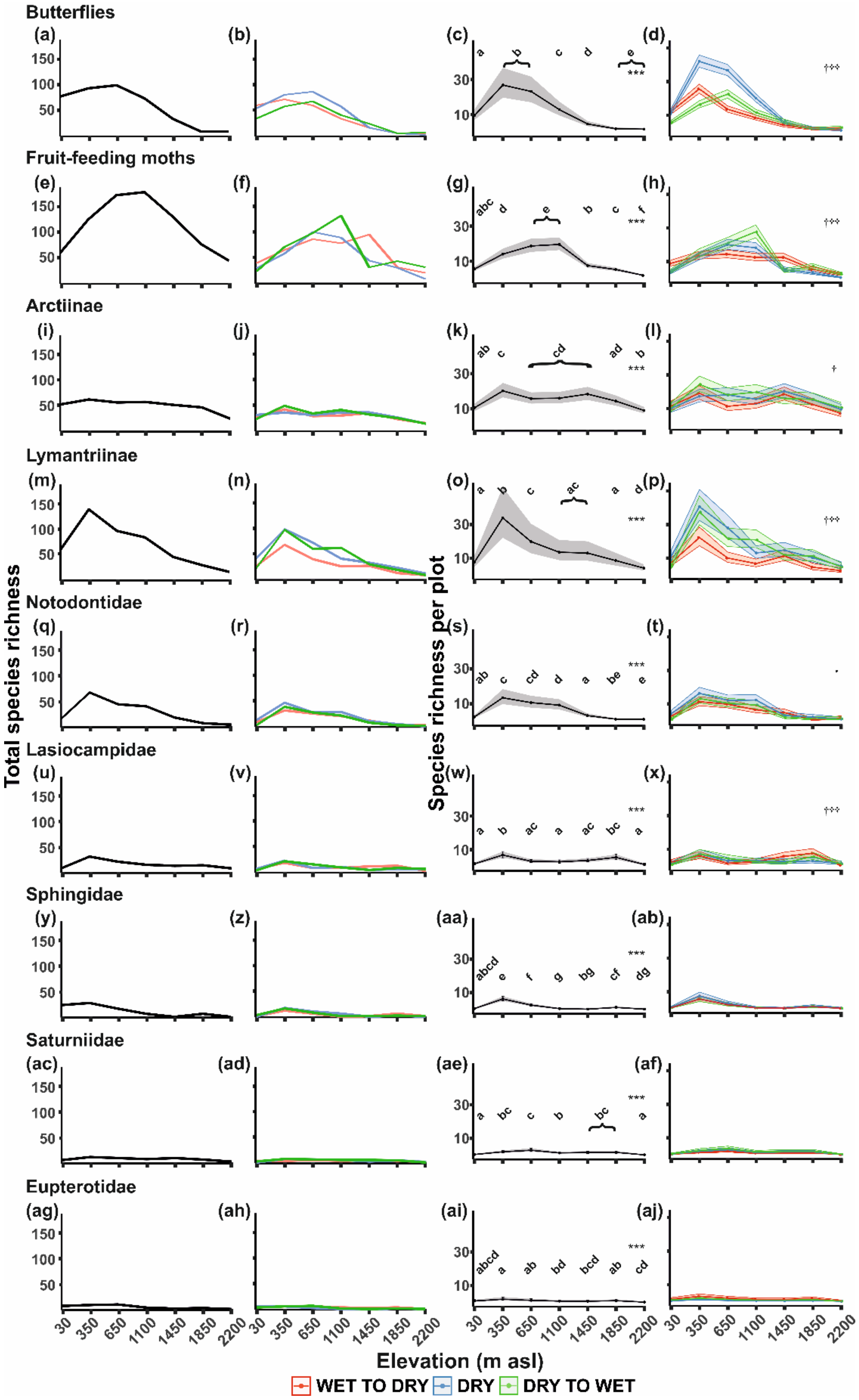
Species richness per elevation peaked between 350 and 1,100 m asl for all groups (350 m asl: Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae; 650 m asl: butterflies, Eupterotidae; 1,100 m asl: fruit-feeding moths), and then linearly towards the higher elevations (Fig. 2). *Elevation* also significantly affected *species richness* per plot of all focal groups (Fig. 2; Table S1 in Appendix S4), with its peaks at the mid-lower (butterflies, Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae; the low-plateau mid-elevation peak *sensu* McCain & Grytnes, 2010) or medium elevations (fruit-feeding moths) or showing a low elevation plateau (Eupterotidae). Over the mid-elevations, *species richness* monotonously decreased towards the higher elevations for all groups but Eupterotidae. The lowest elevation was always, except for Eupterotidae, significantly species-poorer than 350 m, often comparably poor as the highest elevations (Fig. 2).

Seasonal changes of weather

Monthly changes of both temperature and precipitation are visualised in Fig. 1 and listed in Table S1 in Appendix S2. Both weather measures expectedly decreased with elevation and changed with season. While mean daily temperatures did not fluctuate strongly (few degrees’ differences between wet and dry seasons), precipitation and the number of rainy days dramatically varied with season. Especially in the lowlands, rain fell virtually daily between June and September, exceeding 2,300 mm at 350 m asl from June till August. Precipitation decreased monotonously with elevation, the lowest measured elevation was five times rainier than the timberline. At the timberline, monthly precipitation still exceeded 500 mm during the wet season (Fig. 1, Table S1 in Appendix S2).

Seasonal changes of elevational diversity patterns

Seasonal shifts in species richness peaks were consistent for both species richness per elevation and per plot for all focal groups. The effect of interactions between elevation and season on species richness per plot was significant for butterflies, fruit-feeding moths, Arctiinae, Lymantriinae, and Lasiocampidae, and marginally significant for Notodontidae (Fig. 2, Table S2 in Appendix S4); only these groups were analysed further. Species richness peaks of butterflies, fruit-feeding moths, and Notodontidae ascended along elevation from the transition from wet to dry to the transition from dry to wet seasons; Lymantriinae showed a similar biodiversity peak ascent, yet only after the full-dry season. Oppositely, Lasiocampidae showed a high-elevation peak at the transition from wet to dry and the mid-lower elevation peak in the other sampled seasons, whilst species richness of Arctiinae changed locally without any easily interpretable temporal pattern.


Butterflies
(a)
(b)
(c)
a
b
c
d
e
***
(d)
†**
Fruit-feeding moths
(e)
(f)
(g)
abc
d
e
b
c
f
***
(h)
†**
Arctiinae
(i)
(j)
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ab
c
cd
ad
b
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(l)
†
Lymantriinae
(m)
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Notodontidae
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(s)
ab
c
cd
d
a
be
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(t)
Lasiocampidae
(u)
(v)
(w)
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bc
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(x)
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Sphingidae
(y)
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Saturniidae
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Eupterotidae
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(ah)
(ai)
abcd
a
ab
bd
bcd
ab
cd
***
(aj)
150
100
50
30
10
Total species richness
Species richness per plot
30
350
650
1100
1450
1850
2200
Elevation (m asl)
WET TO DRY
DRY
DRY TO WET

Fig 2. Changes of Lepidoptera species richness with elevation and season for individual focal groups in Mount Cameroon. The four columns represent total species richness per elevation, total species richness per elevation and season, GLMM results for species richness per plot and elevation (Table S1 in Appendix S4), and GLMM results per plot, elevation and season (Table S2 in Appendix S4). The latter two columns show means per plot with 95% unconditional confidence intervals; asterisks visualise results of individual tests (effects of altitude in the third column: * p<0.05; ** p<0.01; *** p<0.001; and of interaction between altitude and season in the fourth column: . p<0.01; † p<0.05; †† p<0.01; ††† p<0.001). Letters visualise results of the post-hoc pairwise comparisons.

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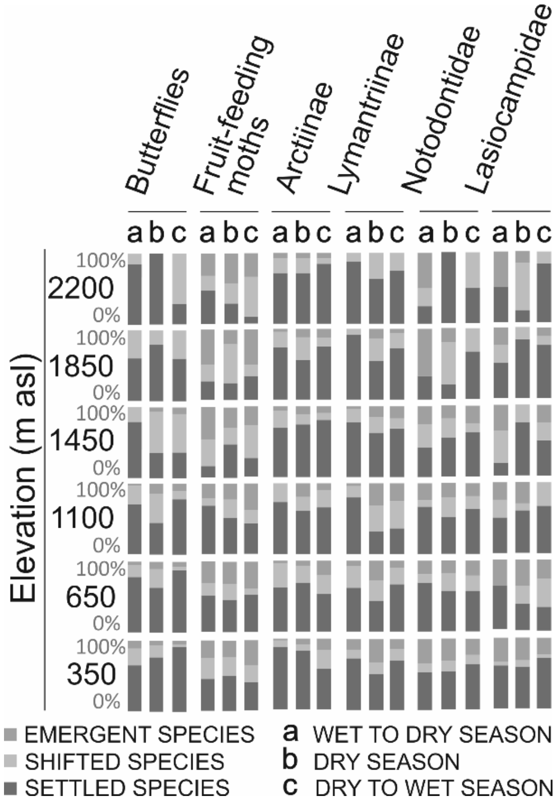


Fig 3. Proportion of Lepidoptera species at each elevation of Mount Cameroon which already occurred at the same elevation in the previous season (settled species, red), occurred only at some different elevation in the previous season (shifted species, yellow), and did not occur anywhere in the previous season (emerged species, green). Only the focal groups with a significant effect of elevation-season interaction on species richness are shown.

The inter-seasonal shifts of butterfly biodiversity peak are clearly composed by the shifts of species' distribution along elevation (Fig. 3). The proportion of newly emerging and shifted species of other groups varies among elevations and seasons, although especially in fruit-feeding moths the inter-seasonal community turnover is substantially related to the emergence of new species' adults (Fig. 3).

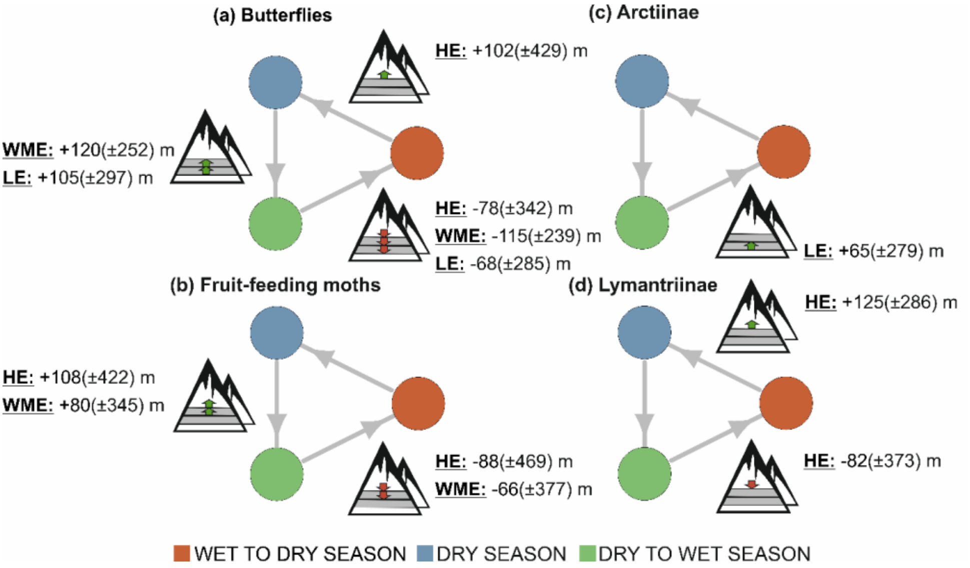


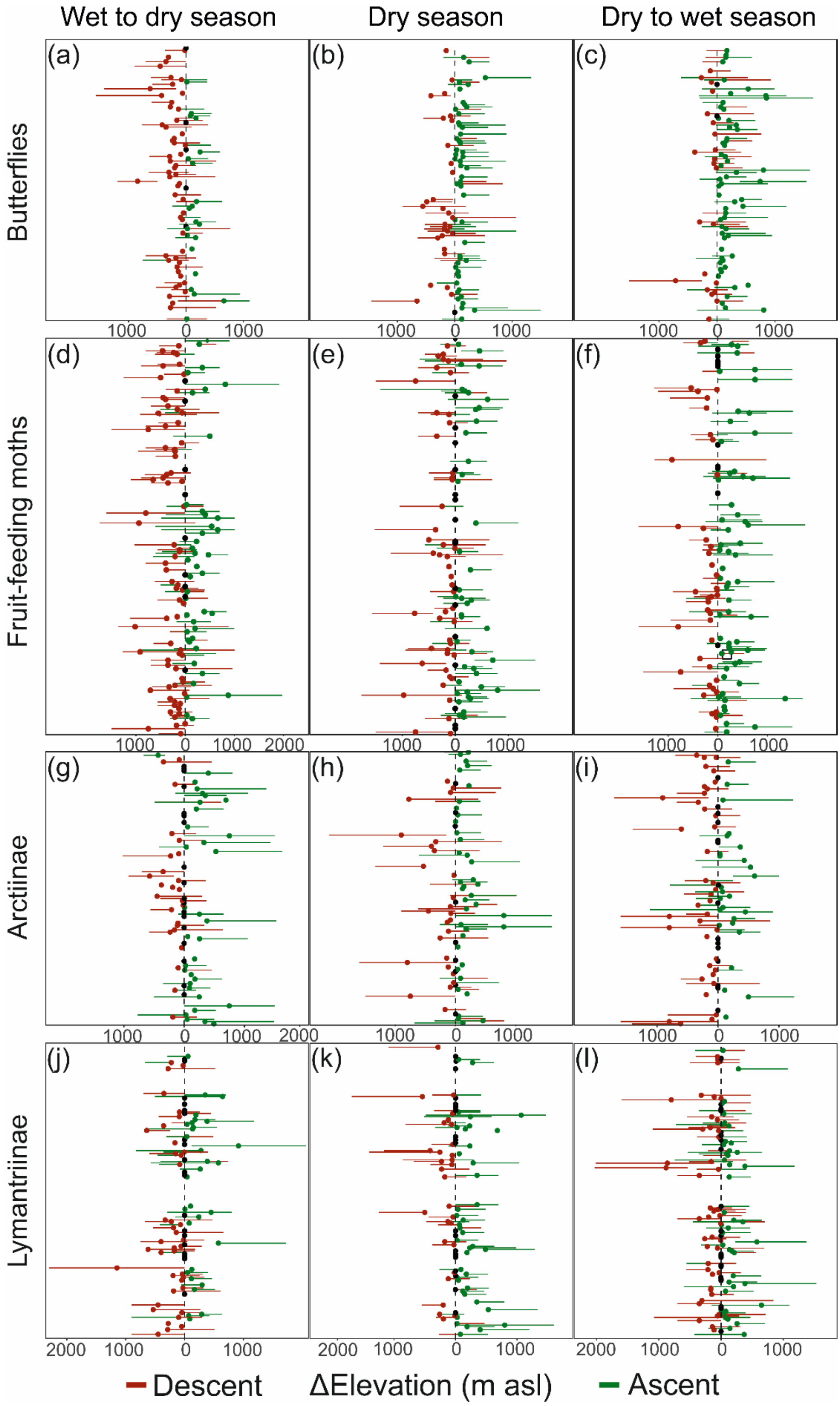
Fig 4. Significant inter-seasonal shifts of mean *highest elevation* (HE), *weighted mean elevation* (WME), and *lowest elevation* (LE) of species' ranges for (a) butterflies, (b) fruit-feeding moths, (c) Arctiinae, and (d) Lymantriinae on Mount Cameroon. The arrows and values (mean with SD) visualise significant shifts (Wilcoxon signed-rank test, Table S1 in Appendix S6) of the individual range measures' shifts.

The strong relationship of community composition to season was also confirmed by NMDS and PERMANOVA. The NMDS ordinations arranged the communities along elevation for all groups, although their "elevational organisation" along the first axes was in some cases disrupted by the lowest (mainly Notodontidae, Sphingidae and Saturniidae) and/or highest (mainly butterflies, Lasiocampidae, Sphingidae and Eupterotidae) elevation communities (Fig. S1 in Appendix S5). These two elevations also differed from the rest of the gradient on the second ordination axes for some groups (Fig. S1 in Appendix S5). The PERMANOVAs detected significant, although rather weak, effect of seasonality on the community composition of all focal groups (Table S1 in Appendix S5). The elevation and season interactions were significant for all groups as well, indicating seasonally different community turnover along elevation (Table S1 in Appendix S5).

Seasonal changes of elevational ranges

Significant seasonal shifts of the used metrices of species' elevational ranges were detected only in communities of butterflies, fruit-feeding moths, Arctiinae, and Lymantriinae (Fig. 4, Table S1 in Appendix S6). During the non-sampled wet season (i.e., between the sampled transition seasons), *highest elevation* of all named groups but Arctiinae significantly decreased, together with mean elevation of butterflies and fruit-feeding moths. Contrastingly, *lowest elevation* of Arctiinae significantly increased during the same period, whilst all three metrices did not significantly differ among the other seasons.

Fig 5. Seasonal shifts of species' elevational ranges on Mount Cameroon for individual focal groups of Lepidoptera where at least one significant inter-seasonal shift of the elevational range was detected. Dots represent the weighted mean elevations, while the whiskers represent absolute values of shift of the lowest (left whisker) or highest (right whisker) elevations. Green colour indicates an ascent, and red colour a descent, of elevational range measures. The changes are always related to the previous sampled season.



Wet to dry season
Dry season
Dry to wet season
Butterflies
Fruit-feeding moths
Arctiinae
Lymantriinae
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
1000
0
1000
2000
Descent
ΔElevation (m asl)
Ascent

After the wet season, all elevational range measures continuously shifted upwards for all other groups. These ascents started with the significant increase of *highest elevation* of butterflies and Lymantriinae at the dry season beginning, followed by the significant increase of *mean elevation* and *lowest elevation* of butterflies and *mean elevation* and *highest elevation* of fruit-feeding moths towards the wet season beginning. These general shifts are clearly visible for individual species' ranges as well (Fig. 5). The average values of inter-seasonal shifts of elevational ranges were mostly >100 m asl for all significant comparisons (Fig. 4), and often much higher for individual species' ranges (Fig. 5).

DISCUSSION

Biodiversity patterns along elevation

Unsurprisingly, the biodiversity of all sampled groups of butterflies and moths changed along elevation on Mount Cameroon. In concordance with numerous studies on Lepidoptera and other organisms (e.g., Colwell *et al.*, 2016; Beck *et al.*, 2017), the highest species richness of most studied lepidopteran groups was detected in lowlands (butterflies, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae) or mid-elevations (fruit-feeding moths, Arctiinae, Saturniidae, Eupterotidae). Such patterns are consistent with diversity patterns of dung beetles (mid-elevation peak at 1,100 m asl; Mongyeh *et al.*, 2018) and birds (monotonous decline above 350 m asl; Ferenc *et al.*, 2016) on Mount Cameroon. The observed patterns are also concordant with the lepidopteran studies on Mount Kilimanjaro, the only other sampled elevational gradient for moths in the Afrotropics, where a monotonous decline of moth diversity above 1,000 m asl was described (Axmacher *et al.*, 2004; Peters *et al.*, 2016). Unfortunately, as there are no natural forest habitats below these elevations on Mount Kilimanjaro, we cannot state if the described patterns are part of the linear diversity decrease along elevation, or rather fits to the mid-elevation peak (cf. McCain & Grytnes, 2010). All our focal groups also showed a linear decrease above 1,000 m asl, regardless of whether their species richness peaks occurred in the lowlands or at mid-elevations.

The observed low diversity of all studied groups in the lowest elevation matches with what has often been observed in various tropical areas (Colwell *et al.*, 2016). Nevertheless, the studied coastal forest has been shrinking due to recent logging (Ferenc *et al.*, 2018) which might have already decreased its biodiversity. On the other hand, its species richness of birds is fully comparable with the lowland forests inside the Mount Cameroon National Park, whilst its tree species richness is even higher (Ferenc *et al.*, 2018). Simultaneously, the sampled plots were located in primary coastal forest with minimal human influence during the sampling time.

Seasonal diversity shifts along elevation

The diversity patterns of most focal groups differed among the sampled seasons. Generally, species richness of some groups increased towards dry and/or transition from dry to wet season in lowlands and mid-elevations, as already described in Maicher *et al.* (2018). These authors mostly explained it by the locally extreme precipitation during the wet season constraining all larval, pupal and adult stages, thus causing emergence of most adults during the dry season (Maicher *et al.*, 2018). By extending the sampling to the complete rainforest elevational gradient, we have now shown that these increases of species richness differ seasonally among elevations, altogether causing the seasonal shifts of diversity peaks. A few groups displayed a seasonal switch between the “low-elevation plateau with a mid-peak” (sensu McCain & Grytnes, 2010) and the mid-elevation peak among the sampled seasons. This highlights the necessity of considering seasonal dynamics in interpretations of the elevational patterns of tropical diversity.

Detailed studies of temporal changes of diversity along tropical elevational gradients are scarce, mainly because of the logistical difficulties of sufficient sampling of each elevation, even once. Janzen (1973) was the first to explore changes of tropical arthropod diversity in different elevations and seasons. Although his localities' selection and sampling effort standardisation were not optimal to test the seasonal diversity shifts along elevation, his results showed a decrease of beetle diversity in mid-elevations during the wet season, and no seasonal shift of heteropteran diversity in Costa Rica. To our knowledge, the only recent study of seasonal shifts of tropical insect diversity along elevation was performed in the wet tropics of Australia (Wardhaugh *et al.*, 2018). Despite the strong effect of seasonality on species richness and abundance of beetles, both peaking during the high-wet season, no consistent seasonal shift of beetles' abundance or species richness along elevation was observed. This lack of seasonal shifts was explained by the potentially insufficient length of the studied elevational gradients (<1,000 m asl). Nevertheless, our results demonstrated seasonal shifts of diversity even below 1,000 m asl. Because we are not aware of other comprehensive datasets from the tropics, it is impossible to make any generalising conclusions. However, two studies of seasonal shifts of arthropod diversity in subtropical mountains in southern Africa are consistent with our results; an upward shifts of diversity peaks were unveiled in a multiple-year study of ants (Bishop *et al.*, 2014), as well as in a study of spiders along the wetter of two studied slopes (Foord & Dippenaar-Schoeman, 2016), both in south African mountains. In the latest, a different pattern of spider diversity shift was detected on the slope with drier climate and a less pronounced seasonality (Foord & Dippenaar-Schoeman, 2016). Additionally, Meyer *et al.* (2015) revealed seasonal differences in ground-dwelling arthropod communities along an elevation gradient in subtropical Southwestern US but did not scrutinise their patterns or drivers. These studied areas are also characterised by intra-annual cycles of dry and wet seasons similar to our perhumid tropical locality; we can thus speculate that precipitation changes play a key role in driving the seasonal shifts of Lepidopteran communities.

To our knowledge, the only study on seasonal shifts of individual lepidopteran species along elevation was performed by Janzen (1987) in Costa Rica. The author reported migrations of sphingids to higher elevations (“elevations hundreds to thousands of metres higher than where the larval host plants of these species occur”) during the high dry season. Janzen (1987) hypothesised that sphingids fly through mountain passes to moist refugia, but simultaneously admitted having no direct evidence on either such migration itself nor its drivers. The few other reports on tropical lepidopteran species’ shifts reviewed by Hsiung *et al.* (2018) are also not supported by any detailed data or evidence, similarly to a report on altitudinal migration of a tropical wasp Polistes instabilis in Costa Rica (Hunt *et al.*, 1999). On the other hand, similar seasonal species’ range shifts are known for many species of tropical birds and bats (Hsiung *et al.*, 2018), mostly explained by migrations.

Drivers of the elevational shifts

We found that the phenological patterns of diversity, previously described for six lepidopteran groups in the lowland rainforests of Mount Cameroon (Maicher *et al.*, 2018), change along elevations: the species richest communities are phenologically delayed at higher elevations when compared to the lower sites for several groups. We thus expect that interpretation of the seasonal shifts of both species richness and species’ elevational ranges should be related to a seasonal delay of some crucial conditions between the beginning and end of the dry season. Unfortunately, we do not have detailed phenological data from the wet season allowing us to explain the recorded general descent of biodiversity peaks and species’ elevational ranges of most focal groups.

The phenological delay at higher elevations can depend on two main factors affecting the fundamental niches of particular species: relative delays in weather seasonality and shifts in resources availability. Among the measured weather variables, precipitation is often the strongest parameter affecting phenology of Lepidoptera (as well as some other insects), as shown in numerous long-term studies from tropical rainforests (e.g., Grøtan *et al.*, 2012, 2014; Valtonen *et al.*, 2013). Although temperature can also influence Lepidoptera phenology in lowland tropical rainforests (Grøtan *et al.*, 2014), this parameter does not seasonally vary so strongly among elevations on Mount Cameroon (Fig. 1; this is known from other tropical mountains as well, Sheldon *et al.*, 2018). However, on Mount Cameroon, the wet season precipitation is of such intensity along the whole gradient that it hardly allows activity of lepidopteran species' adults, except for some wet-season specialists (Maicher *et al.*, 2018). Precipitation rather than temperature explained phenological shifts of beetles' abundance and species richness along altitude in tropical Australia (Wardhaugh *et al.*, 2018). Similarly, we expect elevational rather than seasonal changes of temperature to drive changes of the observed lepidopteran communities. Generally, insect species' life-histories differ among elevations (Hodkinson, 2005). Warmer temperatures of lower elevations hasten larval development (Gilbert & Raworth, 1996) and can thus cause phenologically hastened emergence of adults.

On the other hand, temporal changes in weather conditions and availability of resources for both adults and caterpillars might initiate seasonal adult migration (Janzen, 1987; Hsiung *et al.*, 2018). Janzen (1987) guessed a lack of food resources (both nectar flowers for adults and food plant foliage for larvae) during the dry season and the temperature drop in the wet season as the main drivers of the seasonal two-way migration. Although our data sampling is not suitable to distinguish if any of the described shifts of species' elevational range has been caused by a phenologically delayed emergence of adults in the higher elevations, or by a seasonal up- or down-slope migration of individuals, we expect a combination of both drivers behind the described patterns. While we cannot prove the migration of sphingid species towards higher elevations, we observed the presence of older butterfly specimens (i.e., most probably migration rather than emergence) at higher elevations of Mount Cameroon for some species of skippers (e.g., Coeliades libeon) and papilionids (e.g., Papilio zoroastres), not covered by our sampling protocol.

Implications for global change impact studies

Temporal changes of diversity along tropical elevational gradients have become a widely used tool for studying the global change impacts, despite the above-mentioned insufficient knowledge of their seasonal dynamics. Current consensus predicts that global change will cause uphill shifts of tropical montane species, due to their relatively narrow thermal tolerance (Forero-Medina *et al.*, 2011; Laurance *et al.*, 2011). Shifts of microclimatic conditions can result in subsequent extinctions of mountaintop species (Colwell *et al.*, 2008). Such predictions have recently been confirmed by observed upward shifts of ranges of tropical frogs (Pounds *et al.*, 1999), birds (Freeman & Class Freeman, 2014), and moths (Chen *et al.*, 2009; Chen, Hill, Shiu, *et al.*, 2011). A recent multi-taxonomical meta-analysis estimated the median rate of uphill shift to be 11 metres per decade (Chen, Hill, Ohlemüller, *et al.*, 2011).

Even though insects are a hyper-diverse group of bioindicators, there are only two on elevational shifts based on one single dataset from the humid tropics (Chen *et al.*, 2009; Chen, Hill, Shiu, *et al.*, 2011). Their authors resampled communities of geometrid moths along the elevational gradient of Mount Kinabalu, Borneo, Malaysia, 42 years after the first data collection. They detected an average upward shift of species' mean elevational ranges by 67 m (Chen *et al.*, 2009). However, results varied according to the elevational specialisation of lepidopteran species. The upper elevation species' highest elevational range decreased by 179 m, whilst their lowest elevational range increased by 121 m (Chen, Hill, Shiu, *et al.*, 2011). Both highest and lowest elevational ranges of all other geometrid species increased by 152 m and 77 m, respectively (Chen, Hill, Shiu, *et al.*, 2011).

However, our study shows that such shifts of species' elevational ranges can be part of the lepidopteran communities' seasonal dynamics. We detected range shifts of often >100 m asl (and even several times higher for particular species) within natural seasonal changes. Although we fully understand that any study of long-term changes may have many constraints, especially if they include comparisons with historical data, we consider a sufficient knowledge of the natural dynamics as an essential requirement. Far from doubting the global change effects on biodiversity, we question the available evidence for the long-term range shifts of tropical moths, considering the unexpectedly high natural dynamics of both diversity and species' elevational distribution on the tropical mountain in our study. Any sampling shortcut that ignores the main seasonal dynamics can bias our understanding of the global change effects on tropical insect communities. Consequently, misconceptions might even negatively affect any potential preventive actions. Since the global change has already altered the seasonal precipitation regimes in many tropical areas (Feng *et al.*, 2013), we call for an urgent attention to the natural seasonal dynamics of tropical diversity along elevational gradients. Only such background data would enable us to fully understand the ongoing and predicted effects of the global change also on tropical montane biodiversity.

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SUPPLEMENTARY MATERIAL

Appendix S1. Map of Mount Cameroon with the seven sampled elevations.

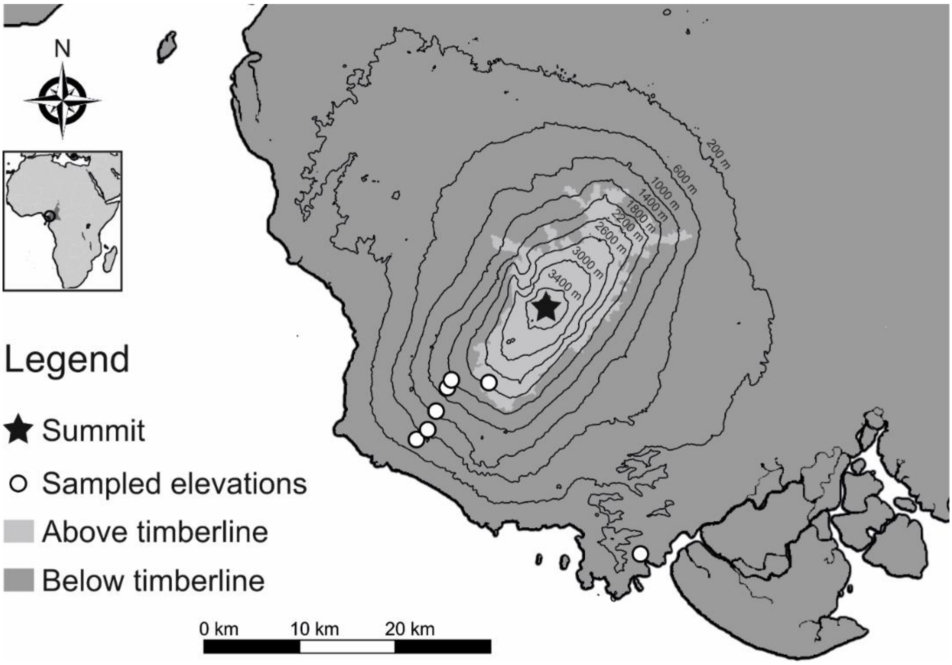


Fig. S1. Map of Mount Cameroon with the seven sampled elevations.

Appendix S2. Details of the collected weather data.

Table S1. The measured monthly values for mean day temperature (±SD), monthly precipitation, and number of rainy days (>2 mm) measured by dataloggers at individual sampled elevations but the lowest (i.e., 30 m asl) on Mount Cameroon.

Elevation (asl)	Weather measures	Months											
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
350 m	Mean day temperature (°C) 2015-2016	24.1 (±1.8)	24.4 (±1.6)	24.2 (±1.3)	23.9 (±1.3)	23.7 (±1.2)	22.6 (±0.9)	22.2 (±0.8)	22.2 (±0.5)	22.3 (±0.6)	22.8 (±1.0)	23.2 (±1.3)	23.5 (±1.6)
	Total precipitation (mm) in 2015	7.0	158.0	267.0	120.5	205.0	2327.0	2516.0	2535.0	1852.5	759.5	305.0	18.0
	Number of rainy days in 2015	1	17	18	10	16	30	31	31	30	23	17	2
650 m	Mean day temperature (°C) 2015-2016	21.9 (±2.0)	22.3 (±1.9)	22.5 (±1.4)	22.2 (±1.4)	22.1 (±1.2)	21.2 (±0.9)	20.8 (±0.8)	20.9 (±0.6)	21.0 (±0.7)	21.2 (±1.1)	21.5 (±1.4)	21.6 (±1.9)
	Total precipitation (mm) in 2015	9.5	61.0	104.0	68.5	110.0	1958.5	2412.5	2433.5	1562.0	496.0	281.5	5.0
	Number of rainy days in 2015	2	8	9	6	15	30	31	31	29	23	10	1
1100 m	Mean day temperature (°C) 2015-2016	19.7 (±2.3)	20.2 (±2.3)	20.3 (±1.5)	20.1 (±1.6)	20.0 (±1.4)	19.2 (±1.0)	18.9 (±1.0)	19.0 (±0.8)	19.1 (±1.0)	19.2 (±1.3)	19.4 (±1.7)	19.3 (±2.1)
	Total precipitation (mm) in 2015	1.5	56.5	103.0	60.5	105.0	1660.0	2007.0	2061.5	1342.0	381.5	224.0	7.5
	Number of rainy days in 2015	0	6	8	8	15	29	31	31	29	23	9	1
1450 m	Mean day temperature (°C) 2015-2016	18.6 (±1.7)	19.1 (±1.8)	19.1 (±1.4)	19.0 (±1.4)	18.6 (±1.2)	17.5 (±1.1)	17.1 (±1.0)	17.3 (±0.9)	17.3 (±1.0)	17.7 (±1.2)	18.2 (±1.5)	18.2 (±1.7)
	Total precipitation (mm) in 2015	15.5	60.5	101.5	56.5	130.5	1407.5	1659.5	1777.5	1226.5	425.5	233.5	1.5
	Number of rainy days in 2015	3	6	8	8	19	28	31	31	29	27	11	0
1850 m	Mean day temperature (°C) 2015-2016	15.5 (±2.4)	16.3 (±2.5)	16.7 (±2.0)	16.5 (±2.1)	16.2 (±1.7)	15.4 (±1.4)	15.2 (±1.3)	15.4 (±1.3)	15.4 (±1.4)	15.5 (±1.6)	15.6 (±1.8)	15.2 (±2.3)
	Total precipitation (mm) in 2015	0.5	45.5	75.0	56.0	85.5	1130.5	1312.0	1349.0	991.5	298.5	226.0	5.5
	Number of rainy days in 2015	0	5	8	9	15	28	31	31	30	25	9	0
2200 m	Mean day temperature (°C) 2015-2016	14.2 (±2.8)	14.4 (±2.4)	15.3 (±2.1)	15.6 (±2.3)	15.4 (±2.2)	13.9 (±1.8)	13.6 (±1.7)	13.6 (±1.6)	13.5 (±1.5)	14.4 (±2.1)	15.0 (±2.6)	15.0 (±3.2)
	Total precipitation (mm) in 2015	1.5	25.0	38.5	10.5	16.0	359.0	544.0	735.5	577.0	107.5	107.0	0.0
	Number of rainy days in 2015	0	2	7	3	4	22	23	31	23	13	6	0

Appendix S3. Summary table of the results per elevations, season, and focal groups.

Table S1. Summary of the results per elevations, season, and focal groups.

Focal group	Elevation (asl)	Season	Abundance	Species richness	Chao1 (±SE)	SC
Fruit-feeding butterflies	30 m	Wet to dry	402	60	66.18 (±4.38)	0.96
	350 m		792	**72**	85.60 (±8.74)	0.98
	650 m		499	60	**81.00 (±12.20)**	0.96
	1,100 m		410	34	43.43 (±7.25)	0.97
	1,450 m		738	5	5.00 (±0.45)	1,0
	1,850 m		209	5	5.00 (±0.00)	1,0
	2,200 m		**957**	3	3.00 (±0.41)	1,0
	30 m	Dry	292	54	69.3 (±9.56)	0.94
	350 m		**3026**	81	87.87 (±5.56)	1,0
	650 m		1932	**87**	**96.43 (±7.26)**	0.99
	1,100 m		1831	58	65.33 (±5.67)	0.99
	1,450 m		1520	16	18.50 (±3.15)	1,0
	1,850 m		505	5	5.00 (±0.22)	1,0
	2,200 m		32	2	2.00 (±0.00)	1,0
	30 m	Dry to wet	120	34	52.2 (±13.14)	0.88
	350 m		538	58	63.05 (±3.78)	0.97
	650 m		1021	**68**	**81.91 (±8.68)**	0.98
	1,100 m		376	41	76.00 (±25.59)	0.96
	1,450 m		706	24	29.00 (±6.63)	0.99
	1,850 m		255	5	8.00 (±4.38)	0.99
	2,200 m		**1123**	7	13.00 (±7.07)	1,0
Fruit-feeding moths	30 m		**899**	39	115.0 (±50.2)	0.98

	350 m	Wet to dry	406	65	93.1 (±14.6)	0.93
	650 m		443	86	**145.0 (±26.2)**	0.91
	1,100 m		390	78	131.1 (±25.3)	0.91
	1,450 m		248	**95**	131.6(±15.1)	0.83
	1,850 m		156	31	54.0 (±16.4)	0.9
	2,200 m		68	20	28.0 (±7.6)	0.85
	30 m	Dry	79	29	41.0 (±9.2)	0.82
	350 m		484	57	96.6 (±22.0)	0.95
	650 m		618	**100**	**174.2 (±30.1)**	0.92
	1,100 m		**739**	89	135.6 (±21.2)	0.95
	1,450 m		139	43	97.2 (±32.7)	0.83
	1,850 m		69	30	46.0 (±11.0)	0.76
	2,200 m		8	8	14.5 (±8.1)	0.28
	30 m	Dry to wet	152	23	40.3 (±15.0)	0.93
	350 m		887	71	160.0 (±44.8)	0.96
	650 m		636	98	144.9 (±20.5)	0.94
	1,100 m		**1036**	**132**	**200.1 (±25.1)**	0.95
	1,450 m		229	31	57.2 (±18.2)	0.93
	1,850 m		270	43	68.2 (±15.5)	0.92
	2,200 m		60	31	135.0 (±71.0)	0.65
Arctiinae	30 m	Wet to dry	147	26	33.9 (±7.4)	0.95
	350 m		423	**42**	45.9 (±3.7)	0.98
	650 m		158	29	**52.8 (±20)**	0.92
	1,100 m		264	30	33.0 (±3.0)	0.97
	1,450 m		**785**	33	43.6 (±10.2)	0.99
	1,850 m		375	23	28.9 (±6.4)	0.98
	2,200 m		360	14	28.9 (±13.5)	0.98
	30 m		93	31	63.3 (±26)	0.85
	350 m		333	35	44.9 (±8.3)	0.97

	650 m	Dry	566	29	33.1 (±4.8)	0.99
	1,100 m		384	**36**	**47.9 (±9.1)**	0.97
	1,450 m		489	35	47.4 (±10.6)	0.98
	1,850 m		586	25	42.9 (±23.5)	0.99
	2,200 m		**671**	14	14.4 (±1.3)	1.00
	30 m	Dry to wet	145	23	25.5 (±2.7)	0.96
	350 m		697	**49**	54.0 (±4.4)	0.99
	650 m		429	34	**94.3 (±70.9)**	0.97
	1,100 m		425	41	69.1 (±23.1)	0.97
	1,450 m		308	31	47.6 (±14.7)	0.97
	1,850 m		687	24	36.4 (±17.1)	0.99
	2,200 m		**878**	13	13.0 (±0.5)	1.00
Lymantriinae	30 m	Wet to dry	87	26	40.9 (±12.3)	0.87
	350 m		238	**67**	**123.6 (±28.5)**	0.87
	650 m		92	39	79.6 (±23.5)	0.74
	1,100 m		64	25	36.8 (±9)	0.82
	1,450 m		**265**	27	81.7 (±34.8)	0.96
	1,850 m		116	12	13.9 (±2.6)	0.97
	2,200 m		36	8	17.7 (±9.8)	0.86
	30 m	Dry	122	41	60.8 (±12.1)	0.85
	350 m		**509**	**98**	131.9 (±15.3)	0.93
	650 m		333	72	**150.1 (±46.6)**	0.92
	1,100 m		139	41	61.1 (±12.6)	0.87
	1,450 m		195	32	41.9 (±8.3)	0.95
	1,850 m		251	22	62.3 (±48.8)	0.96
	2,200 m		202	11	23.4 (±17)	0.98
	30 m		53	22	49.6 (±22.7)	0.76
	350 m		**490**	**96**	**158.1 (±28.8)**	0.92
	650 m		252	60	84.1 (±13.7)	0.91

	1,100 m	Dry to wet	307	63	94.1 (±16.8)	0.92
	1,450 m		255	29	38.9 (±8.3)	0.96
	1,850 m		318	18	22.4 (±7.1)	0.99
	2,200 m		127	8	8.4 (±1.3)	0.99
Notodontidae	30 m	Wet to dry	25	9	11.1 (±3.2)	0.89
	350 m		103	**31**	**50.4 (±14.2)**	0.87
	650 m		**106**	26	36 (±8.9)	0.92
	1,100 m		70	21	33.3 (±10.5)	0.86
	1,450 m		50	13	17.0 (±4.7)	0.90
	1,850 m		15	3	3.9 (±1.9)	0.88
	2,200 m		63	4	6.9 (±4.2)	0.95
	30 m	Dry	49	13	44.3 (±38.7)	0.84
	350 m		147	**48**	60.8 (±7.6)	0.87
	650 m		**158**	29	52.8 (±20)	0.92
	1,100 m		157	30	**85.8 (±49.5)**	0.90
	1,450 m		39	11	23.1 (±16.7)	0.87
	1,850 m		42	7	12.8 (±6.9)	0.91
	2,200 m		129	1	1.0 (±0.0)	1.00
	30 m	Dry to wet	5	3	3.2 (±0.6)	0.90
	350 m		119	**40**	**73 (±20.8)**	0.83
	650 m		96	28	45.8 (±14.2)	0.88
	1,100 m		**142**	22	46.8 (±24)	0.93
	1,450 m		17	8	9.0 (±1.6)	0.85
	1,850 m		13	4	4.4 (±1.2)	0.93
	2,200 m		87	2	2.0 (±0.4)	1.00
Lasiocampidae	30 m	Wet to dry	34	6	6.9 (±2.1)	0.94
	350 m		49	**18**	25.9 (±6.9)	0.82
	650 m		13	8	**27.3 (±15.8)**	0.48
	1,100 m		39	8	25.5 (±23.0)	0.85
	1,450 m		154	11	18.9 (±11.5)	0.97
	1,850 m		**206**	12	12.9 (±1.8)	0.99
	2,200 m		9	2	2.0 (±0.4)	1.00

	30 m	Dry	9	6	13.1 (±10.4)	0.58
	350 m		**60**	**22**	**38.3 (±14.6)**	0.84
	650 m		30	8	8.1 (±0.5)	0.97
	1,100 m		22	10	13.9 (±4.6)	0.79
	1,450 m		25	4	4.0 (±0.4)	1.00
	1,850 m		53	6	6.9 (±2.1)	0.96
	2,200 m		18	6	10.2 (±6.8)	0.84
	30 m	Dry to wet	11	3	3.0 (±0.5)	1.00
	350 m		68	**21**	25.8 (±4.7)	0.90
	650 m		32	15	**39.2 (±23.4)**	0.69
	1,100 m		20	9	20.8 (±16.3)	0.76
	1,450 m		19	4	4.4 (±1.2.0)	0.95
	1,850 m		**224**	8	9.9 (±3.7)	0.99
	2,200 m		16	6	10.2 (±6.7)	0.82
Sphingidae	30 m	Wet to dry	20	1	1.0 (±0.0)	1,0
	350 m		**93**	**12**	13.2 (±1.8)	0.96
	650 m		21	6	**16.0 (±10.1)**	0.77
	1,100 m		0	0	-	-
	1,450 m		3	1	1.0 (±0.0)	1,0
	1,850 m		21	6	12.0 (±7.0)	0.82
	2,200 m		2	1	1.0 (±0.0)	1,0
	30 m	Dry	0	0	-	-
	350 m		**137**	**17**	19.5 (±3.1)	0.96
	650 m		114	10	**25.0 (±13.5)**	0.95
	1,100 m		11	6	9.0 (±4.1)	0.65
	1,450 m		0	0	-	-
	1,850 m		19	2	2.0 (±0.0)	1,0
	2,200 m		0	0	-	-
	30 m	Dry to wet	4	3	3.5 (±1.2)	0.63
	350 m		74	**16**	**19.0 (±3.4)**	0.92
	650 m		**75**	8	15.5 (±8.1)	0.92
	1,100 m		1	1	1.0 (±0.0)	1,0

	1,450 m		1	1	1.0 (±0.0)	1,0
	1,850 m		10	2	2.0 (±0.3)	1,0
	2,200 m		5	1	1.0 (±0.0)	1,0
Saturniidae	30 m	Wet to dry	4	3	3.5 (±1.2)	0.63
	350 m		8	3	3.0 (±0.4)	1,0
	650 m		**27**	**5**	6.0 (±2.2)	0.93
	1,100 m		5	3	3.0 (±0.1)	0.9
	1,450 m		5	**5**	**15.0 (±10.0)**	0.11
	1,850 m		7	3	3.0 (±0.2)	0.89
	2,200 m		1	1	1.0 (±0.0)	1,0
	30 m	Dry	0	0	-	-
	350 m		**84**	**7**	**9.0 (±2.8)**	0.95
	650 m		41	6	7.5 (±2.5)	0.93
	1,100 m		16	5	8.0 (±4.4)	0.82
	1,450 m		14	2	2.0 (±0.0)	1,0
	1,850 m		22	4	5.0 (±2.2)	0.92
	2,200 m		1	1	1.0 (±0.0)	1,0
	30 m	Dry to wet	4	2	2.0 (±0.3)	1,0
	350 m		16	**7**	**7.3 (±0.9)**	0.89
	650 m		**55**	6	7.0 (±2.2)	0.96
	1,100 m		9	5	5.3 (±0.9)	0.82
	1,450 m		38	5	5.0 (±0.2)	0.98
	1,850 m		28	4	4.0 (±0.4)	1,0
	2,200 m		0	0	-	-
Eupterotidae	30 m	Wet to dry	6	4	4.8 (±1.6)	0.76
	350 m		23	**6**	6.2 (±0.7)	0.96
	650 m		14	**6**	**13.4 (±10.8)**	0.72
	1,100 m		18	4	4.0 (±0.5)	1.00
	1,450 m		**52**	3	3.4 (±1.3.0)	0.98
	1,850 m		18	4	4.0 (±0.5)	1.00
	2,200 m		1	1	1.0 (±0.3)	1.00
	30 m		6	**6**	**18.5 (±11.2)**	0.07
	350 m		**11**	**6**	13.3 (±10.6)	0.65

	650 m		3	3	5.0 (±2.9)	0.33
	1,100 m	Dry	1	1	1.0 (±0.3)	1.00
	1,450 m		0	0	-	-
	1,850 m		3	2	2.3 (±0.9)	0.83
	2,200 m		1	1	1.0 (±0.3)	1.00
	30 m		7	4	5.7 (±3.2)	0.76
	350 m		14	6	7.9 (±3.5)	0.87
	650 m		**15**	**7**	**14.5 (±10.9)**	0.74
	1,100 m	Dry to wet	2	2	2.5 (±1.1)	0.67
	1,450 m		5	1	1.0 (±0.1)	1.00
	1,850 m		4	2	2.0 (±0.4)	1.00
	2,200 m		1	1	1.0 (±0.3)	1.00

Appendix S4. Detailed results of the GLMMs models.

Table S1. Results of the general mixed-effect models (GLMM) with elevation as fixed effect, and season and plots nested in elevations as random effect. The type II Wald χ2 tests were applied for the models testing, while the "delta" method (Barton, 2018) was applied for the marginal R^2 calculations.

Focal group	χ2	df	p-value	Marginal R^2
Butterflies	1418.5	6	<0.01	0.82
Fruit-feeding moths	586.9	6	<0.01	0.70
Arctiinae	66.6	6	<0.01	0.46
Lymantriinae	176.3	6	<0.01	0.65
Notodontidae	311.8	6	<0.01	0.77
Lasiocampidae	77.2	6	<0.01	0.39
Sphingidae	168.4	6	<0.01	0.52
Saturniidae	53.8	6	<0.01	0.53
Eupterotidae	28.9	6	<0.01	0.28

Table S2. Results of the general mixed-effect models (GLMM) with elevation, season, and their interaction as fixed effects, and plots nested in elevations as random effect. The type II Wald χ2 tests were applied for the models testing, while the "delta" method (Barton, 2018) was applied for the marginal R^2 calculations (n.s.: not significant).

Focal group	Fixed effects	χ2	df	p-value	Marginal R²
Fruit-feeding butterflies	Elevation	1458.8	6	<0.01	0.89
	Season	315.1	2	<0.01	
	Elevation * Season	195.7	12	<0.01	
Fruit-feeding moths	Elevation	617.2	6	<0.01	0.84
	Season	28.6	2	<0.01	
	Elevation * Season	199.3	12	<0.01	
Arctiinae	Elevation	75.9	6	<0.01	0.55
	Season	12.5	2	<0.01	
	Elevation * Season	24.3	12	0.02	
Lymantriinae	Elevation	209.6	6	<0.01	0.83
	Season	117.6	2	<0.01	
	Elevation * Season	51.9	12	<0.01	
Notodontidae	Elevation	307.0	6	<0.01	0.81
	Season	15.6	2	<0.01	
	Elevation * Season	19.1	12	0.08	
Lasiocampidae	Elevation	76.2	6	<0.01	0.49
	Season	3.5	2	0.17	
	Elevation * Season	30.3	12	<0.01	
Sphingidae	Elevation	175.1	6	<0.01	0.53
	Season	3.0	2	0.22	
	Elevation * Season			n.s.	
Saturniidae	Elevation	49.6	6	<0.01	0.55
	Season	8.1	2	0.02	
	Elevation * Season			n.s.	
Eupterotidae	Elevation	28.7	6	<0.01	0.37
	Season	18.6	2	<0.01	
	Elevation * Season			n.s.	

Appendix S5. Results of PERMANOVAs and nonmetric multidimensional scaling (NMDS) two-dimensional plots of each focal group.

Fig S1. Nonmetric multidimensional scaling (NMDS) two-dimensional plots of bait-trapped (a) butterflies and (b) fruit-feeding moths; and light attracted (c) Arctiinae, (d) Lymantriinae, (e) Notodontidae, (f) Lasiocampidae, (g) Sphingidae, (h) Saturniidae, and (i) Eupterotidae collected in Mount Cameroon. Ordinations are based on matrices calculated with the Bray-Curtis similarity index of square root transformed data. A low stress values indicate a high goodness-of-fit of the ordinations.

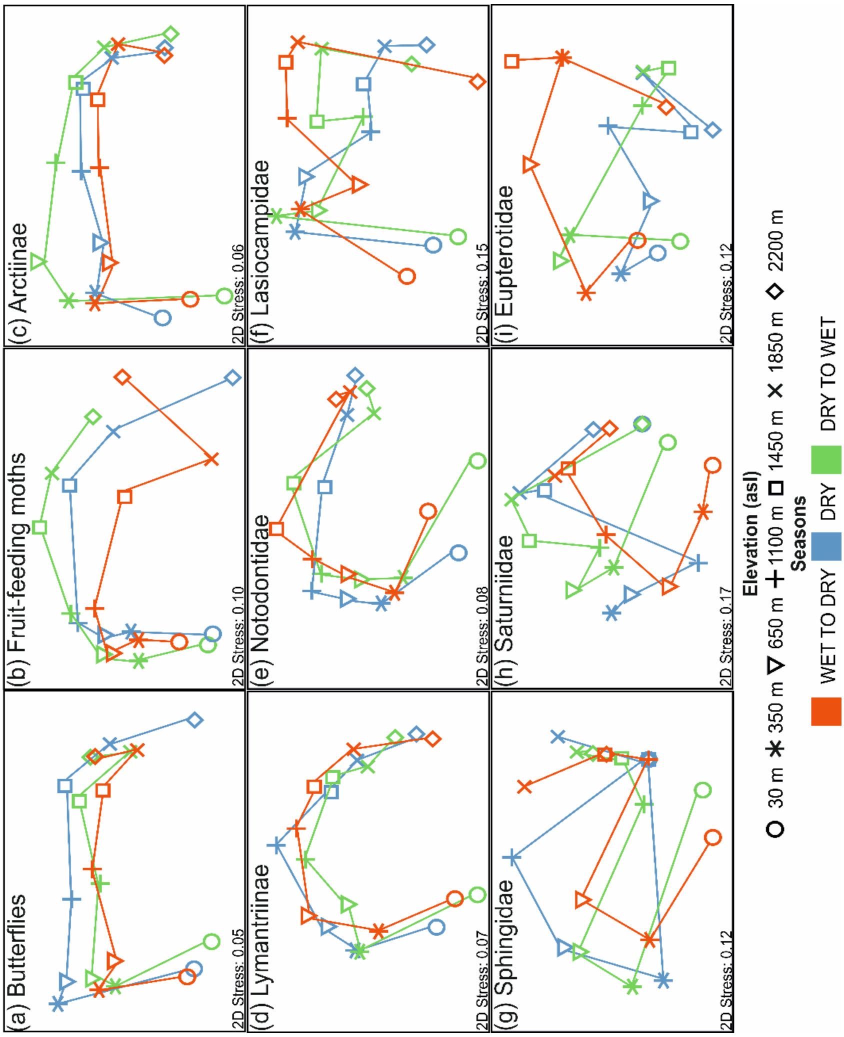


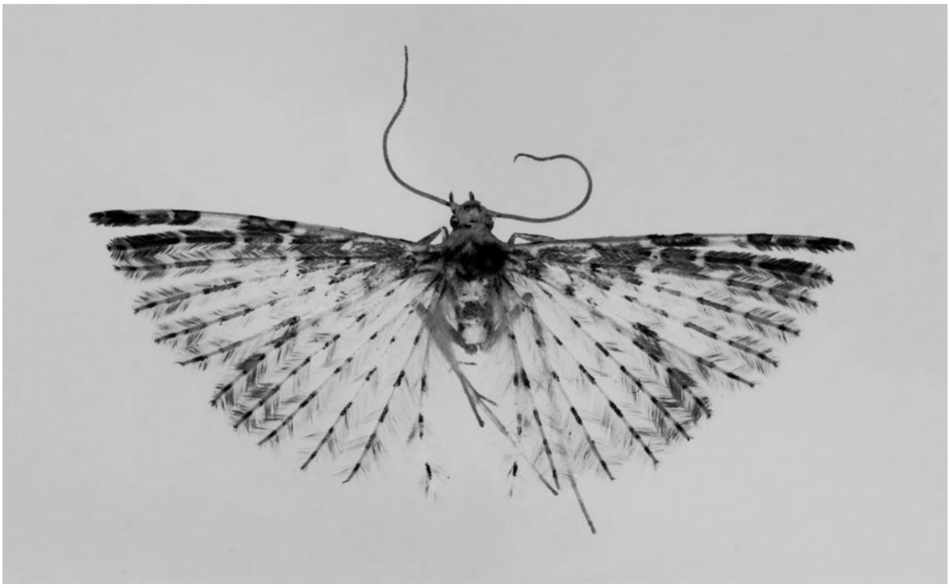
Table S1. Results of sequential PERMANOVAs carried out on all the focal groups.

Taxon	Source	df	Sums of square	Pseudo-F	p
Butterflies	Elevation	6	544,290	92.40	<0.01
	Season	2	37,716	19.21	<0.01
	Elevation x Season	12	136,040	11.55	<0.01
	Residuals	315	309,260		
Fruit-feeding moths	Elevation	6	352,950	33.11	<0.01
	Season	2	63,868	17.98	<0.01
	Elevation x Season	12	170,090	7.98	<0.01
	Residuals	315	559,590		
Arctiinae	Elevation	6	126,520	31.66	<0.01
	Season	2	9,106	6.84	<0.01
	Elevation x Season	12	25,064	3.14	<0.01
	Residuals	42	27,971		
Lymantriinae	Elevation	6	79,694	6.45	<0.01
	Season	2	10,331	2.51	<0.01
	Elevation x Season	12	29,592	1.20	0.05
	Residuals	42	86,450		
Notodontidae	Elevation	6	33,383	5.63	<0.01
	Season	2	6,804	3.44	<0.01
	Elevation x Season	12	107,960	9.10	<0.01
	Residuals	42	41,495		
Lasiocampidae	Elevation	6	30,997	4.56	<0.01
	Season	2	4,574	2.02	<0.01
	Elevation x Season	12	91,285	6.72	<0.01
	Residuals	42	47,552		
Sphingidae	Elevation	6	80,462	23.15	<0.01
	Season	2	3,653	3.15	<0.01
	Elevation x Season	12	17,918	2.58	<0.01
	Residuals	42	24,333		
Saturniidae	Elevation	6	58,927	13.60	<0.01
	Season	2	9,955	6.89	<0.01
	Elevation x Season	12	24,091	2.78	<0.01
	Residuals	42	30,341		
Eupterotidae	Elevation	6	36,850	7.30	<0.01
	Season	2	11,992	7.13	<0.01
	Elevation x Season	12	23,040	2.28	<0.01
	Residuals	42	35,323		

Appendix S6. Detailed results of the Wilcoxon signed-rank tests.

Table S1. Detailed results of the Wilcoxon signed-rank tests of the changes of the three measures of altitudinal ranges on all the focal groups. First number give the V-statistic while the second number represent the p-value (W-D: Transition from wet to dry season; Dry: Full-dry season; D-W: Transition from dry to wet season; $^{+}$ <0.06; * p <0.05; ** p <0.01; *** p <0.001).

Range measures	Season*	Value	Fruit-feeding butterflies	Fruit-feeding moths	Arctiinae	Lymantriinae	Notodontidae	Lasiocampidae	Sphingidae	Saturniidae	Eupterotidae
Highest altitude	W-D to Dry	V; p-value	465.0; 0.038*	1053.5; 0.600	309.5; 0.843	175.5; <0.001***	102.5; 0.662	26.5; 0.673	17.5; 0.611	1.5; 0.586	8.0; 0.345
	Dry to D-W		468.5; 0.800	550.5; 0.007***	301.0; 0.492	1086.0; 0.591	107.5; 0.343	12.0; 0.212	22.0; 0.619	5.0; 0.572	7.5; 1.000
	D-W to W-D		498.5; 0.059+	1821.0; 0.004***	227.0; 0.149	597.0; 0.011*	59.5; 0.676	51.0; 0.717	10.0; 0.583	2.0; 0.345	10.0; 0.583
Weighted mean altitude	W-D to Dry	V; p-value	1418.0; 0.300	2337.5; 0.800	694.0; 0.07	1096.0; 0.163	276.0; 0.720	61.5; 0.950	19.0; 0.944	16.0; 0.813	5.0; 0.295
	Dry to D-W		699.5; <0.001***	1822.5; 0.010**	1390.5; 0.068	2460.5; 0.504	233.0; 1.000	74.0; 0.409	23.0; 0.529	18.0; 0.636	18.0; 0.578
	D-W to W-D		2347.5; <0.001***	4382.5; 0.020*	768.5; 0.102	1489.5; 0.446	283.0; 0.304	117.0; 0.667	15.0; 0.402	5.0; 0.078	28.0; 0.183
Lowest altitude	W-D to Dry	V; p-value	84.0; 0.162	722.5; 0.800	98.5.0; 0.902	302.0; 0.064	69.0; 0.620	10.0; 1.000	1.5; 1.000	4.0; 0.789	1.5; 0.134
	Dry to D-W		57.0; 0.003***	656.0; 0.200	253.0; 0.443	487.5; 0.457	30.5; 0.794	20.5; 0.310	5.0; 1.000	6.0; 0.784	13.5; 0.136
	D-W to W-D		265.0; 0.054+	1717.0; 0.100	47.0; 0.030*	135.0; 0.073	46.0; 0.420	28.5; 0.718	3.0; 0.371	3.0; 0.581	1.5; 1.000



Holotype of Alucita longipenis Ustjuzhanin & Kovtunovich, 2018*, one of the newly discovered species along the Mt. Cameroon altitudinal gradient. This male specimen was caught in the montane forest around the Elephant camp (ca., 1,850 m asl.) © S. Mischenin*

CHAPTER VI

A newly discovered biodiversity hotspot of many-plumed moths in the Mount Cameroon area: first report on species diversity, with description of nine new species (Lepidoptera, Alucitidae)

Ustjuzhanin, P., Kovtunovich, V., Sáfián, Sz., Maicher, V., & Tropek, R. (2018).
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A newly discovered biodiversity hotspot of many-plumed moths in the Mount Cameroon area: first report on species diversity, with description of nine new species (Lepidoptera, Alucitidae)

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Abstract

Fifteen species of many-plumed moths are recorded from the Mount Cameroon area, SW Cameroon, West Africa. Nine species: *Alucita longipenis* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. lidiya* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. ludmila* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. escobari* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. mischenini* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. fokami* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. janeceki* Ustjuzhanin & Kovtunovich, **sp. n.,** *A. besongi* Ustjuzhanin & Kovtunovich, **sp. n.,** and *A. olga* Ustjuzhanin & Kovtunovich, **sp. n.,** are described as new for science. Four species are recorded as new from Cameroon: *A. acalyptra*, *A. chloracta*, *A. coffeina,* and *A. spicifera*. By these records, the Mount Cameroon area has become the richest known Afrotropical locality for the Alucitidae, highlighting its tremendous value for biodiversity conservation.

Keywords

Alucitidae, biodiversity, Cameroon, many-plumed moths, Mount Cameroon, new species, new records, tropical rainforest

Introduction

Many-plumed moths (Alucitidae) differ from other Lepidoptera by the structure of their wings, which are each split into six lobes, with the exception of the oriental genus *Triscaedecia* Hampson, 1905, which has seven-lobed hind wings. These moths are active at night, and relatively well attracted to light. Most of their diversity is currently known from the Palearctic region, where their caterpillars usually live concealed in plant tissue, some make leafmines, others feed in flowers and buds of various species in the honeysuckle family (Caprifoliaceae). However, the biology of the African many-plumed moths is virtually unstudied.

The taxonomy and distribution of the many-plumed moths are seriously understudied in the Afrotropical Region, despite recent publications of material originating from South Africa, Zimbabwe, and Malawi (Ustjuzhanin and Kovtunovich 2011, 2016). Altogether, 58 species are known from all of the Afrotropics (De Prins and De Prins 2018). Most of the previously described species originate from southern and eastern Africa (Meyrick 1908, 1911, 1913, 1920, Hering 1917, Viette 1958), whereas only 12 species were known to occur in the Guineo-Congolian forest zone, virtually each of them from a few records only (De Prins and De Prins 2018). Nevertheless, this region includes two of the recognised biodiversity hotspots of Africa (Myers et al. 2000) and is thus also expected to harbour many more species of Alucitidae. This is reflected in recent unpublished collections by Sz. Sáfián, who collected several species in Ghana and Liberia.

Since 2014, the last three authors have been coordinating an extensive study of the biodiversity of Lepidoptera on Mount Cameroon, Southwest Province, Cameroon. Its aim was to survey butterfly and moth communities in different altitudinal forest zones on the south-western slopes of the mountain. Originally, Alucitidae were not included in the target groups (which are mainly various groups of Bombycoidea, Noctuoidea, and Geometroidea), but during the first collecting hours, the authors realised how species-rich the family appeared in the study area. Consequently, all Alucitidae specimens were systematically collected during each sampling night. The collected material was sent to the first two authors for identification and further taxonomic work. This paper presents the first results of the study, including descriptions of nine new species, a staggering increase in the known species of Alucitidae from West Africa.

Materials and methods

Abbreviations

NHM	Natural History Museum, London, UK.
CUK	personal collections of P. Ustjuzhanin and V. Kovtunovich, Novosibirsk and Moscow, Russia.
NECJU	Nature Education Centre, Jagiellonian University, Kraków, Poland.

MNHN	Muséum national d'Histoire naturelle, Paris, France.
TMSA	Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa.
ZMHB	Museum für Naturkunde, Berlin, Germany.
ZISP	Zoological museum of St. Petersburg, Russia.

Sampling localities

All the presented material was sampled in rainforests of the Mount Cameroon National Park and in the littoral forest of the nearby Bimbia-Bonadikombo Community Forest, both lying in the Southwest Province, Cameroon (Fig. 1). This paper presents data from the first two field expeditions, when mostly the lower altitudinal zones were sampled, with the exception of mountain forests around the Elephant Camp. The two reported field trips comprised sampling in a transition from wet to dry seasons (November/December 2014 – Bamboo Camp, Drinking Gari Camp, Elephant Camp, PlanteCam), a full dry season (December 2014/January 2015 – Bimbia-Bonadikombo), and a transition from dry to wet seasons (April/May 2015 – Bamboo Camp, Drinking Gari Camp, Bimbia-Bonadikombo, PlanteCam). All the sampled localities are listed here:

Bamboo Camp – Bamboo Camp (350 m a.s.l.), Mount Cameroon (SW slope), N4.08791°, E9.05051°; a lowland forest with historical disturbances by selective logging.
Bimbia-Bonadikombo – Mexico Camp (30 m a.s.l.), Bimbia-Bonadikombo Community Forest, N3.98183°, E9.26250°; a littoral forest in the formally non-intervention part of the Community forest, but with intensive current logging (Ferenc et al. in press)
Drinking Gari – Drinking Gari Camp (650 m a.s.l.), Mount Cameroon (SW slope), N4.10144°, E9.06100°; a lowland forest with a presumably closed canopy layer.
Elephant Camp – Elephant Camp (1850 m a.s.l.), Mount Cameroon (SW slope), N4.11700°, E9.07292°; a montane forest with a highly sparse canopy layer, as a consequence of intensive natural disturbances by forest elephants.
PlanteCam – PlanteCam Camp (1100 m a.s.l.; also misspelled as "Planticamp"), Mount Cameroon (SW slope), N4.11750°, E9.07094°; an upland forest in the transition between lowland and montane zones, its canopy layer is substantially opened by natural disturbances by forest elephants.

Sampling methods

In each of the above-listed localities, three sampling plots were established to partially cover the heterogeneity of local forest habitats. In each plot, moths were collected during two full nights (from dusk till dawn) in each sampled season. All specimens were captured at an artificial light (a single energy saving bulb: 4100 K, 5300 lm,

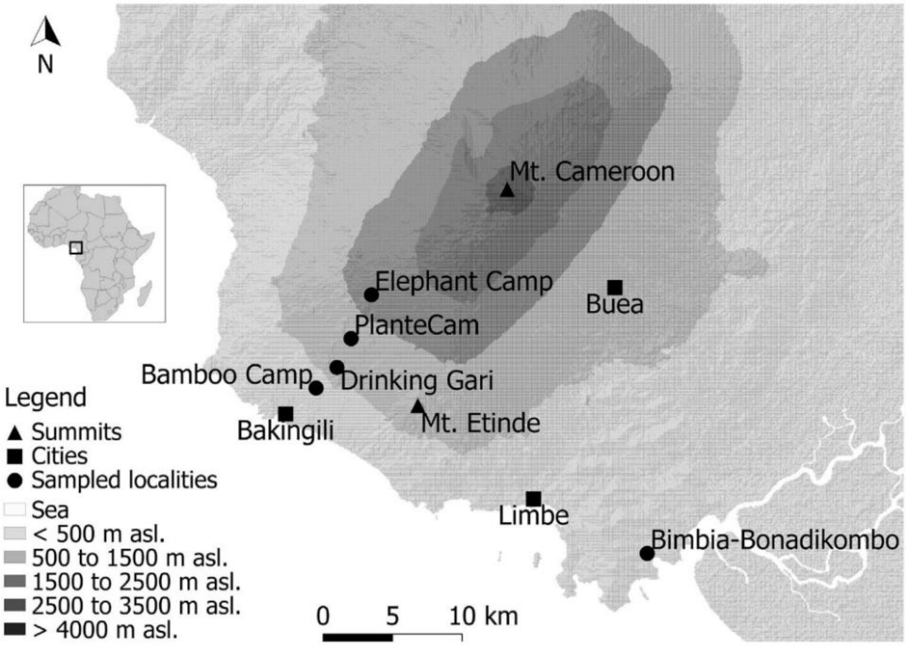


Figure 1. Map of the study area and localities.

105 W, 5 U), powered by a portable generator. The bulb was set in the centre of two perpendicularly placed white sheets (1.5 × 1.5 × 1.8 m, the cloth type B, produced by Entosphinx, Czechia). Specimens were killed by ammonia vapours and either pinned in situ or temporarily stored in glassine envelopes, all dried by silica gel. Later, all specimens were properly mounted in the lab.

Genitalia preparations

The preparation of genitalia slides is necessary for the identification of Alucitidae. Normally, abdomens were boiled in a 10–15% solution of potassium hydroxide until semi-transparent. After this, they were rinsed in water thoroughly for the preparation of permanent slides. On the mount, genitalia were put in a small drop of Euparal after being dehydrated in 100% ethanol. The mounts were then covered with a cover glass. In case the genitalia structures were not well sclerotised, they were stained with Chlorazol Black for greater contrast. Permanent preparations were dried for at least two weeks before being studied. Each permanent preparation received its unique code under which it is searchable in the collections where they are stored; the relevant numbers are also mentioned in captions of the genitalia figures.

Results

Recorded species

Altogether 15 species of Alucitidae were recorded on Mount Cameroon during the reported two field expeditions: nine of them proved to be new for science, and four others were new country records for Cameroon (marked with *), only two had been recorded previously. The morphological terminology follows Zagulajev (1986). The distribution of individual species follows the Afromoths database (De Prins and De Prins 2018).

**Alucita acalyptra* (Meyrick, 1913)

Orneodes acalyptra Meyrick, 1913: 269. Type locality: Barberton, Republic of South Africa. Holotype: male, TMSA, examined by the authors.

Material examined. Bamboo Camp, 1 female, (CUK), 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the mottled grey colour of the wings with contrast zigzag bands, this species is close to *A. agassizi* Ustjuzhanin & Kovtunovich, 2018. In the male genitalia, the shape of the phallus and the lanceolate uncus are similar to *A. hemicyclus* (Hering, 1917), but it differs by the blunt gnathos and the basally narrow valves.

Distribution. Malawi, Republic of South Africa, Cameroon.

**Alucita chloracta* (Meyrick, 1908)

Orneodes chloracta Meyrick, 1908: 507. Type locality: Benin. Holotype: female, BMNH, examined by the authors.

Material examined. PlanteCam, 5 ex., (CUK, NECJU), 11–18.XII.2014; **Elephant Camp,** 18 ex., 19–24.XI.2014; **Bamboo Camp,** 7 ex., (CUK, NECJU), 17–23.IV.2015; **Drinking Gari,** 1 male, (CUK), 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the female genitalia, the shape of the bursa copulatrix and the round signum, resemble those of *A. entoprocta* (Hering, 1917), from which it differs by the wide ductus, the narrow antrum, and by the wings pattern.

Distribution. Benin, Cameroon.

**Alucita coffeina* (Viette, 1958)

Orneodes coffeina Viette, 1958: 457. Type locality: Oubangui-Chari, Boukoko, [Central African Republic]. Holotype: female, MNHN, examined by the authors.

Material examined. PlanteCam, 1 male, (CUK), 11–18.XII.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The bright orange wings with dark, almost black bases and the large size (about 20 mm), are unique for this species. In the male genitalia, the blunt apex of the uncus and the narrow anellus arms, are close to *A. crococyma* (Meyrick, 1937), from which it differs by the short triangular valves, the narrow gnathos and the needle-like clusters of cornuti in the distal part of the phallus.

Distribution. Central African Republic, Cameroon.

Alucita megaphimus (Hering, 1917)

Orneodes megaphimus Hering, 1917: 191. Type locality: Cameroon. Holotype: male, ZMHB, examined by the authors.

Material examined. Bamboo Camp, 6 ex., (CUK, NECJU), 17–23.IV.2015; **PlanteCam**, 5 ex., (CUK, NECJU), 09–14.IV.2015; **Drinking Gari**, 3 ex., (CUK, NECJU), 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the mottled colour of the wings with zigzag white bands, the species is similar to *A. seychellensis* (Fletcher, 1910), but differs by the larger size and the elongated fore wings. In the male genitalia, it differs from *A. seychellensis* by the notch at the apex of the uncus, more narrow valves, and robust serrated saccular processes.

Distribution. Cameroon.

**Alucita spicifera* (Meyrick, 1911)

Orneodes spicifera Meyrick, 1911: 221. Type locality: Pretoria, Republic of South Africa. Holotype: male, TMSA, examined by the authors.

Material examined. PlanteCam, 1 male, (NECJU), 11–18.XII.2014, 4 males, (CUK, NECJU), 09–14.IV.2015; **Elephant Camp**, 7 males, (CUK, NECJU), 19–24.XI.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the male genitalia, the species is close to the Palaearctic species of *Alucita*. In particular, in its crown-shaped uncus, narrow membranous valves and long anellus arms, the species is similar to *A. cinnerethella* (Amsel, 1935), known from Iran, Turkey and Israel. However, it is distinctive in the shorter phallus, in the widened, almost round apex of the gnathos, and also in the wing colour.

Distribution. Republic of South Africa, Malawi, Tanzania, Cameroon.

Alucita zinovievi Kovtunovich & Ustjuzhanin, 2016

Alucita zinovievi Kovtunovich & Ustjuzhanin, 2016: 299. Type locality: PlanteCam, Moutn Cameroon, Cameroon. Type: male, ZISP, examined by the authors.

Material examined. PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), N4.1175000°, E9.0709440°, 11–18.XII.2014. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the male genitalia, the shape of the uncus, gnathos, and phallus, this species is similar to *A. aarviki* Ustjuzhanin & Kovtunovich, 2016. These species differ from each other by the wider valves, long anellus arms and cornuti. The new species is also distinctive in the wing colour: in *A. aarviki* the wings are yellow with white transverse bands, while in *A. zinovievi*, the wings are white with wide dark brown bands (Kovtunovich and Ustjuzhanin 2016).

Distribution. Cameroon.

Alucita longipenis Ustjuzhanin & Kovtunovich, sp. n.

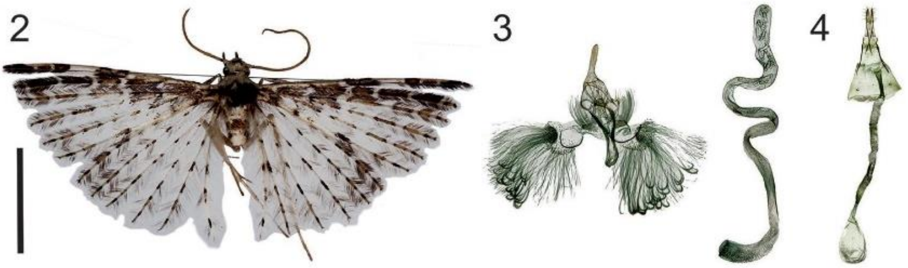
http://zoobank.org/0C5D41E9-38EE-4A7C-BB72-56855C9066D7

Figs 2–4

Type material. Holotype, male, (NECJU 201801) **CAMEROON**, **Elephant Camp**, 1850 m a.s.l., Mount Cameroon (SW slope), N4.11700°, E9.07292°, 19–24.XI.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 4 males, 2 females (NECJU, CUK) same data as holotype; 1 male (CUK), **PlanteCam**, 09–14.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the wings' colour and the male genital structure, the new species is unique, with no analogues among known African Alucitidae. The phallus length, disproportionate in relation to the entire genital structure, distinguishes this species from all the known species of this family.

External characters. Head with white spiky hairs, thorax, and tegula white with portions of brown strokes. Labial palpus thin, straight, 2 × longer than longitudinal eye diameter; brown on the outside, white on the inside. Third segment thin, narrow, tapered to apex. Antenna white, scape laterally thickened. Wingspan 18–23 mm, of holotype 22 mm. Wings white, with patches of brown strokes and spots. Small, dark brown rectangular spot in basal part of first lobe of fore wing. Larger, pale brown elongated spot with triangle cut in middle part of lobe. Alternating white, pale brown, and dark brown patches in the distal part of the first lobe. Apical part darkened with black scales. Dark brown elongated patches separated by narrow white bands on second lobe. Alternating brown and white elongated portions of scales on other four lobes of fore wing. Lobes of hind wing white, with patches of elongated brown strokes and spots. Fringe on wing pale, between first and second lobe of fore wing fringe with portions of dark brown scales. Abdomen white, with small spots of dark brown scales. Hind leg pale yellow.



Figures 2–4. *Alucita longipenis* Ustjuzhanin & Kovtunovich, sp. n. **2** Adult male, Holotype, NECJU **3** Male genitalia, Holotype, NECJU, preparation slide no. 201801 **4** Female genitalia, Paratype, NECJU, preparation slide no. 201810. Scale bar: 5 mm.

Male genitalia. Uncus long, equally wide along entire length. Gnathos longer than uncus, sharply thickened at end. Gnathos arms narrow, tapered to apices. Valva reduced, poorly expressed. Anellus arms long, narrow, slightly widened at apices. Saccus very long, elongated, smoothly curved in distal part. Phallus extremely long: 5 × longer than the entire genital structure, sharp arched bands in middle part, without cornuti.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses straight, thin, long. Anterior apophyses equal in length to posterior apophyses, but slightly thicker and undulated. Antrum narrow, tubulate, length almost equal to posterior apophyses. Ductus corrugated, thin, very long: 4 × longer than antrum. Bursa copulatrix small, oval, barely exceeds length of antrum, without signa.

Distribution. Cameroon.

Flight period. April, November.

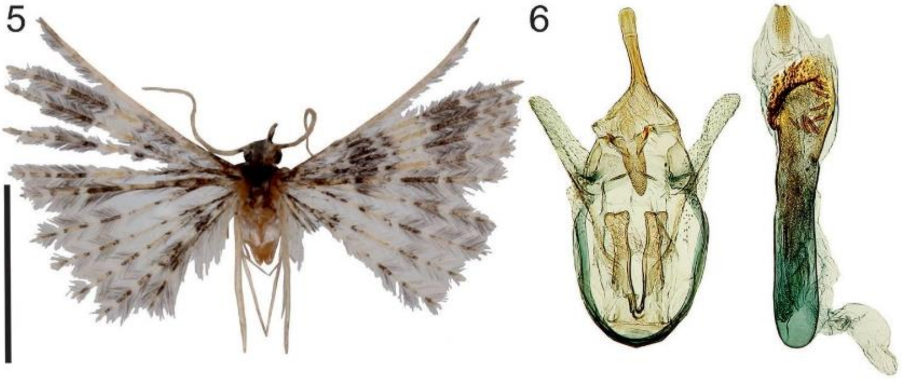
Etymology. The species is named after the morphological peculiarity of the phallus; the species name is a noun in apposition.

Alucita lidiya Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/0149F089-D5B7-47BD-BF49-B8A5FAF14FC1
Figs 5–6

Type material. Holotype, male, (NECJU 201802) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male (CUK), **Drinking Gari**, 11–23.IV.2015; 2 males (NECJU, CUK), **PlanteCam**, 09–14.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled pattern of the wings and position of the bands of the new species is similar to *A. chloracta* (Meyrick, 1908). These species differ from each other by the pale yellow median band in *A. lidiya*, while in *A. chloracta* the band is brown. *A. lidiya* has paler hind wings, without saturated dark grey portions of fringe, as in *A. chloracta.* Male genitalia of the new species also have some similarity to *A. chloracta*,



Figures 5–6. *Alucita lidiya* Ustjuzhanin & Kovtunovich, sp. n. **5** Adult male, Holotype, NECJU **6** Male genitalia, Holotype, NECJU, preparation slide no. 201802. Scale bar: 5 mm.

but there are significant differences in the shape of the narrow valva, the wide gnathos and the wide anellus arms of *A. lidiya*; while in *A. chloracta* the valva is significantly wider and rounded distally, the gnathos is thin, and the anellus arms are narrow.

External characters. Head, thorax and tegula with dark grey clinging hairs. Labial palpus dark grey, short, slightly longer than longitudinal eye diameter. Third segment thin, short, white, tapered to apex. Antenna pale grey. Wingspan 14–15 mm, of holotype 14 mm. Wing greyish brown. Base of fore and hind wing coloured with dark brown scales. Wide pale yellow band in median part, wide dark brown band in distal part of wing. Fringe on wing with alternating portions of pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus quite long, narrow, slightly widened distally. Gnathos short, wide, shorter than uncus. Gnathos arms thin, undulate, widened to apices. Valva narrow, quite long, poorly sclerotised. Anellus arms long, wide, equal to valva in length. Phallus short, almost straight, group of various cornuti in the distal part: fine needle-shaped and large, with serrated edges.

Distribution. Cameroon.

Flight period. April.

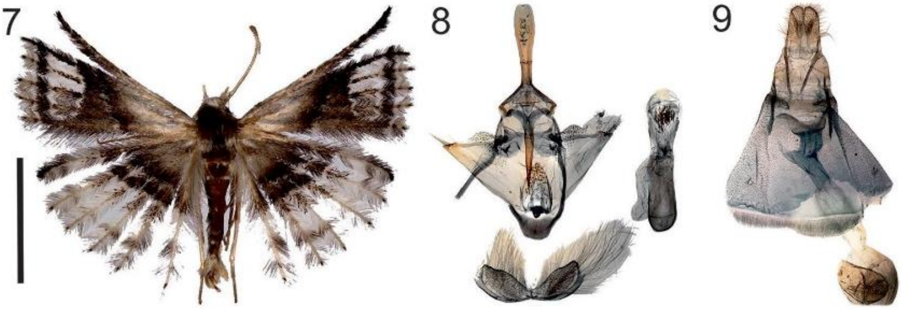
Etymology. The species name is a noun in apposition in honour of Lidiya Bezverkhova.

Alucita ludmila Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/6B6DA5D1-494E-47E5-A362-9DB51258D5EC

Figs 7–9

Type material. Holotype, male, (NECJU 201803) **CAMEROON**, **Bamboo Camp** (350 m a.s.l.), Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015.



Figures 7–9. *Alucita ludmila* Ustjuzhanin & Kovtunovich, sp. n. **7** Adult male, Holotype, NECJU **8** Male genitalia, Holotype, NECJU, preparation slide no. 201803 **9** Female genitalia, Paratype, CUK, preparation slide no. 451. Scale bar: 5 mm.

V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male (NECJU), **Bamboo Camp,** 12–20.XII.2014; 1 male (CUK), **PlanteCam,** 11–18.XII.2014; 1 male (CUK), **Drinking Gari**, 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek; 1 male (NHM), **NIGERIA**, **Forest Sapobc** (?), 17.IV.1976, M.A. Comes; 1 male (NHM), **NIGERIA**, **Gambari Forest**, Oyo State, 2.X.1976, M.A. Comes; 1 male (NHM), **NIGERIA**, **Gambari Forest**, Oyo State, 8.X.1977, J. Riley; 1 female (NHM), **NIGERIA**, **Port Harcourt**, Rivers, 2.VI.1958, B.J. MacNutly; 1 male (NHM), **NIGERIA**, Crin, 30.VII.1976, M.A. Comes; 1 female (CUK), **GHANA**, **Bunso Arboretum**, Eastern Region, 16–18.XI.2011, Sz. Sáfián, F. Pühringer.

Diagnosis. In the wing colour, this new species is unique among the African Alucitidae. In the male genitalia structure, the wing-shaped valva and shape of the phallus are similar to *A. aarviki* Ustjuzhanin & Kovtunovich, 2016, but it differs from that by the shape of the uncus, the tapered apices of the valva, the narrow arms of the anellus and the cluster of needle-shaped cornuti in the distal part of the phallus.

External characters. Head, thorax, and tegula with greyish white clinging hairs. Labial palpus greyish white, almost 2 × longer than longitudinal eye diameter. Third segment thin, short, white, tapered to apex. Antenna pale brown. Wingspan 16–23mm, of holotype 17 mm. Wing colour greyish white. Base of wing pale grey, wide brownish grey band in median part. Well pronounced pale elongated patch, framed by dark brown band in distal part. Portions of dark brown hairs in distal part of hind wing. Fringe on wing with alternating portions of pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus long, paddle-like, with even edge of apex. Gnathos longer than uncus, narrow, tapered to apex. Gnathos arms short, wide. Valva wing-like, triangle, long needle-shaped bristles in apical part. Anellus arms short, narrow. Saccus short, with even outer edge. Phallus quite short, almost straight, cluster of small needle-shaped cornuti in distal part.

Female genitalia. Papilla analis wide, elongated. Posterior apophyses straight, short, slightly longer than the papilla analis. Anterior apophyses thicker than posterior ones, equal to them in length. Ostium wide, cupped. Antrum tubulate, short, wide, sclerotised, almost equal to length of posterior apophyses. Ductus wide at confluence to antrum, twice as wide as antrum, ductus seminalis short. Bursa copulatrix round, without signa.

Distribution. Cameroon, Nigeria, Ghana.

Flight period. From April to December.

Etymology. The species name is a noun in apposition in honour of the first author's wife, Ludmila Ustjuzhanina.

Alucita escobari Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/D1CF050D-CB13-4283-87C2-5DE4D082E730
Figs 10–12

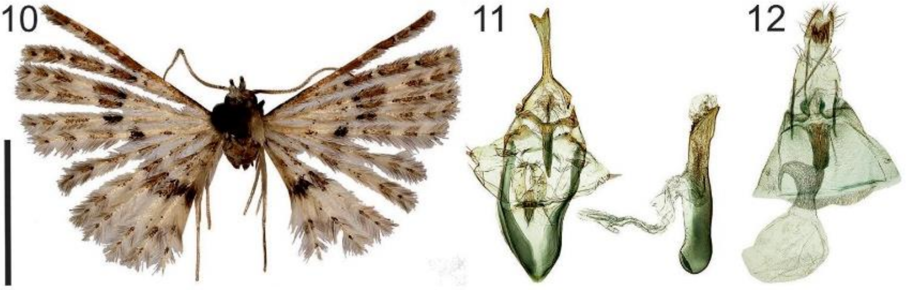
Type material. Holotype, male, (NECJU 201804) **CAMEROON**, PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), N4.11750°, E9.07094°, 11–18.XII. 2014. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 female (CUK), same data as holotype; 2 males (NECJU, CUK), **Bamboo Camp,** 12–20.XII.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled colour and the median arched band on the wings of the new species is similar to *A. mischenini*. The new species is distinguished by the brown spot of scales on the sixth lobe of the fore wing, declining from the correct arc and shifting towards the basal part of the lobe. In the male genital structure, the uncus with the apical triangle cut and the phallus obliquely cut at apex of the new species are similar to *A. balioxantha* Meyrick, 1921. These species differ from each other by the valva in the shape of a wide-triangle valva, the elongated saccus, and the tapered gnathos in *A. escobari.*

External characters. Head with white spiky hairs, thorax, and tegula white. Labial palpus quite wide, short, 1.5 × longer than longitudinal eye diameter, slightly bent upwards, painted with brown scales inside and outside. Third segment short, white on apex. Antenna yellowish brown, scape thickened. Wingspan 14–16 mm, of holotype 15.5 mm. Wing yellowish brown. Transverse brown arched band well expressed in median part of both wings. On sixth lobe of fore wing, patch of scales declining from correct arc and shifting towards basal part of lobe. Wing base pale, interspersed with small brown scales. Alternating brown and white elongated portions of scales in distal part of fore wing. Fringe on wing yellow with rare portions of brown hairs. Hind leg yellow.

Male genitalia. Uncus long, widened distally, triangle cut apically. Gnathos slightly shorter than uncus, thick, tapered to apex. Gnathos arms short, thick, smoothly bent inwards. Valva short, wide-triangle, apically with bunch of thin needle-shaped bristles. Anellus arms wide, slightly shorter than gnathos, slightly bent inwards, narrowed apically. Saccus elongated, narrow-triangle, sharp outer edge. Phallus almost straight, apex obliquely cut, small needle-shaped cornuti medially and distally.

Female genitalia. Papilla analis narrow, triangle. Posterior apophyses straight, long, thin. Anterior apophyses thicker than posterior, equal to them in length. An-



Figures 10–12. *Alucita escobari* Ustjuzhanin & Kovtunovich, sp. n. **10** Adult male, Holotype, NECJU **11** Male genitalia, Holotype, NECJU, preparation slide no. 201804 **12** Female genitalia, Paratype, CUK, preparation slide no. 452. Scale bar: 5 mm.

trum tubulate, sclerotised, length equal to posterior apophyses. Ductus wide at confluence with antrum, twice as wide as antrum, ductus seminalis short. Bursa copulatrix round, without signa.

Distribution. Cameroon.

Flight period. December.

Etymology. The authors name the species in recognition of Francis Luma Ewome, locally well known as 'Escobar', a very well trained guide on Mount Cameroon. Over the years, he became instrumental in organising and implementing the field expeditions, and also became a good friend to the last three authors of this paper. It could be stated that the research would have been extremely difficult without the selfless help of Escobar.

Alucita mischenini Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/ACC44B4D-76B6-4364-86CB-90BA6665C3B6
Figs 13–14

Type material. Holotype, male, (NECJU 201805) **CAMEROON**, **Bimbia-Bonadikombo**, 30 m a.s.l., Mexico Camp, Bimbia-Bonadikombo Community Forest, N3.98183°, E9.26250°, 07–12.V.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes:** 2 males (NECJU, CUK), **PlanteCam**, 11–18.XII.2014, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled colour and the transverse arched band on the wings of *A. mischenini* are similar to *A. escobari*. These species differ from each other by the brown spot of scales on the sixth lobe of the fore wing, declining from the arc to the distal part of the lobe. In the male genital structure, the shape of the valva and the phallus is also similar to *A. escobari*. These species differ from each other by the shape of the uncus, the longer gnathos, the saccus wide in the base, and narrower, longer anellus arms in *A. mischenini*.

External characters. Head, thorax and tegula with white clinging scales. Labial palpus short, 1.5 × longer than longitudinal eye diameter, directed forward, white on

Figures 13–14. *Alucita mischenini* Ustjuzhanin & Kovtunovich, sp. n. **13** Adult male, Holotype, NECJU **14** Male genitalia, Holotype, NECJU, preparation slide no. 201805. Scale bar: 5 mm.

inside, coloured with small brown scales on outside. Third segment short, middle part framed in narrow brown band, apex tapered. Antenna yellow. Wingspan 12–15 mm, of holotype 12 mm. Wing mottled, median transverse band of brown elongated spots of scales developed on first five lobes of fore wing. Similar spot on sixth lobe, declining from band and shifted to distal part of lobe. Median transverse band on hind wing forms correct arc. Small dark brown scales in basal part of fore and hind wing. Alternating portions of brown and yellow scales in distal part. Fringe on wing yellow, with alternating rare portions of brown hairs. Hind leg white.

Male genitalia. Uncus long, basally narrow, distally wide, with poorly expressed cut at apex. Gnathos significantly longer than uncus, narrow, tapered to apex. Gnathos arms short, thick, smoothly bent inwards. Median process between gnathos arms well developed. Valva wing-like, short, wide. Anellus arms long, slightly shorter and noticeably wider than gnathos. Saccus short, basally wide, small oval cut on outer edge. Phallus short, slightly bent in middle, distally with small needle-shaped cornuti.

Distribution. Cameroon.

Flight period. May, December.

Etymology. The species is named after the Novosibirsk biologist and naturalist Sergei Ivanovich Mischenin.

Alucita fokami Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/A61D9EE8-F9A8-4A57-97AA-F21CAC659328

Figs 15–17

Type material. Holotype, male, (NECJU 201806) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 female (NECJU), same data

Figures 15–17. *Alucita fokami* Ustjuzhanin & Kovtunovich, sp. n. **15** Adult male, Holotype, NECJU **16** Male genitalia, Holotype, NECJU, preparation slide no. 201806 **17** Female genitalia, Paratype, NECJU, preparation slide no. 201811. Scale bar: 5 mm.

as holotype; 1 male (CUK), **PlanteCam,** 11–18.XII. 2014; 2 males, 1 female (NECJU, CUK), **Drinking Gari,** 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled colour of the wings and the median arched band on the fore wing in *A. fokami.* is similar to *A. escobari*. *A. fokami* is characterised by the absence of such a band on the hind wings and by the base of the wings darkened with brown scales. In the male genitalia, the absence of the valva in the new species is similar to *A. janeceki.* These species differ from each other by the long needle-shaped cornutus, narrow elongated saccus, and the shape of the uncus in *A. fokami.*

External characters. Head with pale yellow spiky hairs, thorax and tegula pale brown. Labial palpus yellow-brown, 1.5 × longer than eye diameter. Antenna yellow. Wingspan 12–13 mm, of holotype 12 mm. Wing yellowish brown with three white transverse bands. Wing base darkened with brown scales. Fringe on wing yellow. Hind leg white.

Male genitalia. Uncus basally narrow, distally wide, apex with small oval cut. Gnathos short, 3 × smaller than uncus, narrow, slightly tapered to apex. Gnathos arms thick, long, undulate, apically tapered. Median process between gnathos arms well developed. No valva. Anellus arms very short, in shape of wide lobes, equal to gnathos in length. Saccus narrow, elongated, exceeds length of uncus with tegumen. Phallus short, almost straight, distally with long needle-shaped cornutus exceeding total length of phallus.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses very long, slightly undulated. Anterior apophyses straight, long, slightly shorter than posterior apophyses. Antrum narrow, short. Ductus long, corrugated, with well-expressed longitudinal cords. Ductus narrow at confluence to bursa copulatrix. Ductus seminalis short, wide. Bursa copulatrix oval, small, equal to papilla analis, without signa.

Distribution. Cameroon.

Flight period. April, December.

Etymology. The authors name this species in recognition of Dr. Eric Bertrand Fokam, the current head of the Department of Zoology and Animal Physiology, University of Buea. Eric is a renowned ecologist and a keen field scientist. He has not only been an active collaborator during the field research on Mount Cameroon, but has also brought up a new generation of young Cameroonians to continue the scientific work on insects and other animal groups in Cameroon.

Alucita janeceki Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/2753F767-627A-4882-B138-E8DB95800AE7
Figs 18–20

Type material. Holotype, male, (NECJU 201807) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male, 1 female (NECJU, CUK), same data as holotype; 1 male (CUK), **Drinking Gari,** 11–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The wings colour and the absence of the valva in the male genitalia of the new species is similar to *A. fokami*. In the male genitalia, *A. janeceki* is characterised by the oval saccus, the long uncus slightly tapered to apex, the long and wide phallus without a large needle-shaped cornutus. In the female genitalia, the new species is characterised by the oval bursa copulatrix with the ductus seminalis inside, and by the very long posterior apophyses.

External characters. Head, thorax and tegula yellowish white, interspersed with fine brown scales. Labial palpus white, 2 × longer than eye diameter, slightly bent upwards. Third segment thin, tapered to apex. Antenna pale brown. Wingspan 10–12 mm, of holotype 12 mm. Wing greyish white. Wing base darkened with brown scales. Well expressed elongated brown strokes separated by yellowish portions on first lobe. Apical part of lobe brown, sharp. Second and other lobes repeat the pattern of first but with less contrast. Fringe on wing with alternating pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus very long, distally wide, apically slightly tapered. Gnathos not expressed. Valva reduced. Anellus arms straight, wide, twice as short as uncus. Saccus oval. Phallus long and wide, 1.5 × longer than uncus, almost straight, medially and distally with clusters of small spiny cornuti.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses very long, thin. Anterior apophyses straight, very long, equal to posterior apophyses. Antrum short, V-shaped. Ductus wide, corrugated, with longitudinal cords and clusters of small signa. Ductus seminalis inside bursa copulatrix, long, distally widened. Bursa copulatrix big, oval, with impregnation of small spiny signa.

Distribution. Cameroon.

Flight period. April.

Etymology. The species is named after Dr. Štěpán Janeček, an experienced botanist who accompanied all our field expeditions and crucially helped us with many things, including the collection of a substantial part of the presented specimens.

Figures 18–20. *Alucita janeceki* Ustjuzhanin & Kovtunovich, sp. n. **18** Adult male, Holotype, NECJU **19** Male genitalia, Holotype, NECJU, preparation slide no. 201807 **20** Female genitalia, Paratype, CUK, preparation slide no. 453. Scale bar: 5 mm.

Alucita besongi Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/2753F767-627A-4882-B138-E8DB95800AE7
Figs 21–23

Type material. Holotype, male, (NECJU 201808) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17–23.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 2 females (NECJU, CUK), same data as holotype.

Diagnosis. The yellowish brown wings and the small size of the new species are similar to *A. certifica* Meyrick, 1909. These species differ from each other by the absence of the wide pale-brown band in the median portion of the fore wing in *A. besongi*. In the male genitalia, the shape of the uncus and the gnathos of the new species have some similarities to those of *A. acalyptra* Meyrick, 1913; these species differ from each other by the elongated saccus, the peculiar shape of the valva and the phallus with large needle-shaped cornuti in *A. besongi*.

External characters. Head, thorax, and tegula with white clinging scales. Labial palpus white, interspersed with small brown scales, 2 × longer than longitudinal eye diameter, bent upwards. Third segment thin, framed with narrow brown band at base. Antenna yellow. Wingspan 8–10 mm, of holotype 9 mm. Wing yellowish brown. Wing base interspersed with small brown scales. White longitudinal strokes separated by pale brown portions well expressed on first lobe. Poorly noticeable series of white bands from wing base to apical area. Fringe on wing yellowish brown. Hind leg pale yellow.

Male genitalia. Uncus long, distally wide, apically slightly tapered. Gnathos narrow, long, tapered to apex. Valva basally wide, then smoothly narrowing. Anellus arms straight, long. Saccus elongated, oval. Phallus thick, long, almost twice as long as entire genital structure, with cluster of large spiny cornuti.

Figures 21–23. *Alucita besongi* Ustjuzhanin & Kovtunovich, sp. n. **21** Adult male, Holotype, NECJU. **22** Male genitalia, Holotype, NECJU, preparation slide no. 201808. **23** Female genitalia, Paratype, NECJU, preparation slide no. 201812. Scale bar: 5 mm.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses long, thin. Anterior apophyses straight, equal to posterior apophyses. Antrum short, V-shaped. Ductus short, corrugated, with longitudinal cords, smoothly turning into bursa copulatrix. Ductus seminalis inside bursa copulatrix. Bursa big, oval, with long ribbon-like signa and impregnation of small spiny signa.

Distribution. Cameroon.

Flight period. April.

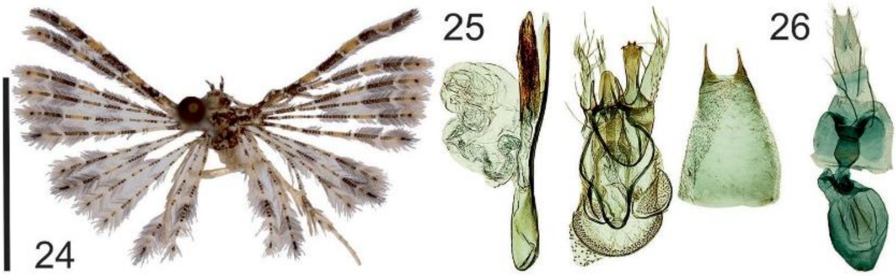
Etymology. The species is named after Simon B. Besong, the current main conservator of the Mount Cameroon National Park, who helped our research by various means of support.

Alucita olga Ustjuzhanin & Kovtunovich, sp. n.

http://zoobank.org/461C9B8A-5BF5-46B9-9A1A-CB04F656358A
Figs 24–26

Type material. Holotype, male, (NECJU 201809) **CAMEROON**, **Bamboo Camp**, 350 m a.s.l., Mount Cameroon (SW slope), N4.08791°, E9.05051°, 17.-23.IV.2015. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek. **Paratypes**: 1 male, 2 females (NECJU, CUK), same data as holotype; 1 male (CUK), **PlanteCam,** 09–14.IV.2015, V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. The mottled yellowish brown wings of the new species have some similarity to *A. lidiya*, but these species differ from each other by the narrow medial band and the dark-brown spots in the apical parts of the lobes in *A. olga*. In the male genitalia, the shapes of the uncus, saccus and phallus of *A. olga* are similar to *A. spicifera* Meyrick, 1911. These species differ from each other by the wide, oval gnathos and the short valva not widened distally, in *A. olga*, and by the gnathos and valva widened at the apices in *A. spicifera*.



Figures 24–26. *Alucita olga* Ustjuzhanin & Kovtunovich, sp. n. **24** Adult male, Holotype, NECJU **25** Male genitalia, Holotype, NECJU, preparation slide no. 201809 **26** Female genitalia, Paratype, NECJU, preparation slide no. 201813. Scale bar: 5 mm.

External characters. Head, thorax and tegula with brown-yellow clinging scales. Labial palpus spotty, with alternating white and black scales, 2 × longer than longitudinal eye diameter, bent upwards. Third segment long, thin, tapered to apex. Antenna yellow, interspersed with dark brown scales. Wingspan 10–11 mm, of holotype 11 mm. Wing mottled, yellowish brown. Wing base coloured with dark brown scales. First lobe of fore wing with well-expressed orange elongated spots, alternating with dark brown elongated spots separated by white bands. Alternation of orange and dark brown spots on other lobes of both wings. Apical area of all lobes ends with dark brown spot. Fringe on wing yellowish brown, with alternating portions of pale and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus medially narrow, distally widened, apex with four claw-like processes forming a kind of rake. Gnathos wide, oval. Gnathos arms straight, narrow, apically tapered. Valva quite wide, short, membranous, poorly sclerotised. Anellus arms long, wide. Saccus slightly elongated, oval. Phallus narrow, elongated, longer than entire genital structure, with one well-expressed narrow long cornutus and cluster of small needle-shaped cornuti distally.

Female genitalia. Papilla analis elongated, narrow triangle. Posterior apophyses thin, straight. Anterior apophyses thin, slightly longer than posterior apophyses. Antrum wide, funnel-shaped, sclerotised. Ductus wide, short, narrow at confluence to bursa copulatrix. Ductus seminalis short, wide. Bursa copulatrix big, oval, with two narrow longitudinal ribbon-like signa, impregnation of many small spines inside the whole bursa.

Distribution. Cameroon.

Flight period. April.

Etymology. The species name is a noun in apposition in honour of Olga Birichevskaya.

Discussion

Our report, although covering just the first part of the sampled material, has revealed that the Mount Cameroon area is the richest known locality for Alucitidae in the whole Afrotropical Region. To the best of our knowledge, maximally only a few species are known from elsewhere in the region; they are met extremely rarely and very locally in other biogeographic areas as well. Partly, this is an artefact of incomplete sampling and relatively less attention to the group during many biodiversity surveys. On the other hand, Alucitidae were specifically focused by various lepidopterists in many places in the Afrotropics in the recent years, never resulting in such rich local biodiversity. By its 15 reported species, Mount Cameroon outnumbers all the other localities in biodiversity of many-plumed moths. The Mount Cameroon area is known to host an exceptional diversity of some other groups of organisms, including Lepidoptera (Ballesteros-Mejia et al. 2013, Maicher et al. 2016, Ferenc et al. in press). Its tremendous biodiversity is considered to be the result of its location on the border between the West African Forests and the Congolese Basin, combining species pools of both these species-rich regions, together with its own endemics (Myers et al. 2000, Maicher et al. 2016). Moreover, its complete altitudinal forest gradient from seashore to timberline comprises a few steep gradients of environmental conditions known to support high species richness.

Our results have also highlighted the poor knowledge of Lepidoptera of the studied region, despite its high importance for biodiversity and its conservation. This paper increased the known Cameroonian fauna of Alucitidae from three (De Prins and De Prins 2018) to 16 species. The nine new species of *Alucita* described in this study can be supplemented by numerous recent descriptions of new species from various lepidopteran groups (e.g., Przybyłowicz 2013, Yakovlev and Sáfián 2016, Sáfián and Tropek 2016). Moreover, our lack of knowledge is further evidenced by the faunistic importance of some of our findings. Three species reported as new for the country had their nearest known localities thousands of kilometers away, in different biogeographic regions. A comparable pattern has already been reported in Erebidae by Maicher et al. (2016). It is highly unlikely that Mount Cameroon would be a refugium for so many species of Lepidoptera occurring in different Afrotropical areas. We thus rather hypothesise that at least some of the mentioned species have a more continuous distribution area, but are just insufficiently explored.

Acknowledgements

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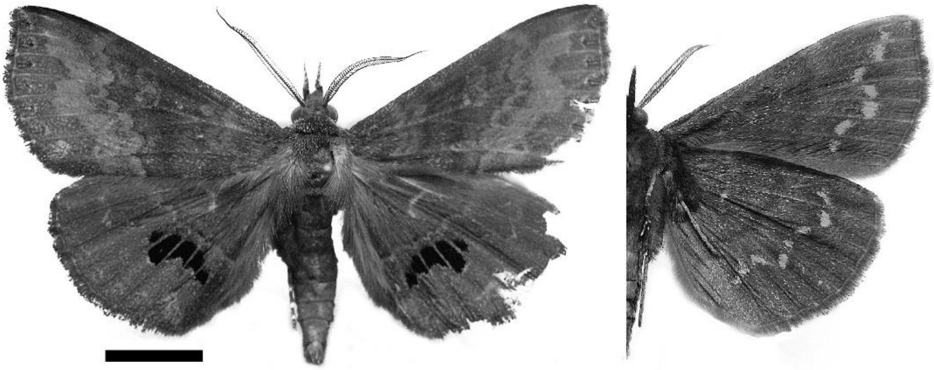
Supplementary material 1

Table of localities

Authors: Peter Ustjuzhanin, Vasily Kovtunovich, Szabolcs Sáfián, Vincent Maicher, Robert Tropek

Data type: occurence

Link: https://doi.org/10.3897/zookeys.777.24729.suppl1



So far, Deinypena lathetica Holland, 1894 *has been known from Gabon only © V. Maicher*

CHAPTER VII

Two genera and nineteen species of fruit-feeding erebid moths (Lepidoptera: Erebidae) recorded in Cameroon for the first time

Maicher, V., Sáfián, Sz., Ishmeal, K.N., Murkwe, M.,
Kimbeng, T.J., Janeček, Š., & Tropek, R. (2016).
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TWO GENERA AND NINETEEN SPECIES OF FRUIT-FEEDING EREBID MOTHS (LEPIDOPTERA: EREBIDAE) RECORDED IN CAMEROON FOR THE FIRST TIME[1]

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ABSTRACT: During our surveys of fruit-feeding Lepidoptera at the Mount Cameroon National Park and the Bimbia Bonadikombo Community Forest (both southwestern Cameroon) we recorded nineteen species of Erebidae moths not previously reported from Cameroon. Simultaneously, we provide the first records of genera *Ametropalpis* and *Lacera* from the country.

KEY WORDS: Erebinae, Calpinae, Hypeninae, Macroheterocera, Mount Cameroon, the Gulf of Guinea Highlands, Africa, frugivorous insects, distribution

INTRODUCTION

Cameroon lies on the border between the West African and Central African biogeographic regions, one of the areas of highest species diversity in the world (Bergl et al., 2007). The forests of Mt. Cameroon, lying west of the Sanaga River and thus belonging to the West African forests (Larsen, 2005), are recognized as an important hotspot of biodiversity and endemism of many organisms, including Lepidoptera (Myers et al., 2000; Larsen, 2005). On the other hand, despite its high conservation value, this region suffers from a lack of entomological surveys, including even basic faunistic data on many groups of moths.

Erebidae is a hyperdiverse family of moths (Lepidoptera: Macroheterocera) with more than 24,500 described species (Zahiri et al., 2011). In contrast to its high diversity and potential negative impacts of some species on agriculture, the Erebidae faunal diversity and distribution patterns remain poorly understood in the Afrotropics, especially for subfamilies covered by our paper (i.e., Erebinae, Calpinae, Hypeninae). Since 2014 we have intensively sampled communities of fruit-feeding Lepidoptera on the forested slopes of Mt. Cameroon. Erebids, containing many species with fruit-feeding adults, constitute a substantial part of all captured Lepidoptera specimens. Here, we report several species identified in the

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material sampled between November 2014 and January 2015 and not previously recorded in Cameroon.

METHODS

All erebid specimens listed in this paper were captured by intensive bait trapping at three different elevations (ca. 350, 650, and 1100 m a.s.l.) of the southwestern slope of Mt. Cameroon and in the Bimbia Bonadikombo Community Forest on the coast (see Table 1 for sampling area coordinates). At each elevation, five traps (modified IKEA PS Fångst hanging storage, height 85 cm, diameter 30 cm; first modified and used by Sáfián et al., 2011) were exposed in each of the sixteen 50 m plots (i.e., 80 traps per elevation). Within each plot, four traps were installed in the understory, with the entrance placed as close to the ground as possible, and one trap in the canopy layer about 20 m (±5 m) above the ground. The traps were baited with fermented mashed bananas refreshed each 3-5 days according to the bait condition. All the traps were checked and emptied every day for a 10-day sampling session. All trapped moth specimens were dried by silica gel and kept for later identification. All the specimens are currently stored in the Institute of Entomology, Biology Centre, České Budějovice, Czech Republic. Voucher specimens of each species will be later deposited also in the Zoological Museum of the Jagiellonian University, Krakow, Poland. For identification we used various available literature and online sources, and collections of the Bavarian State Collection of Zoology in Munich and the Zoological Museum of the Jagiellonian University in Krakow. Nomenclature and distribution of individual species follow the AfroMoth online database (De Prins and De Prins, 2016) reviewing currently more than 5,600 published sources and thus being by far the most comprehensive source of information on Afrotropical moths.

Table 1. Overview of the sampled localities (MC: Mt. Cameroon; BBCF: the Bimbia Bonadikombo Community Forest).

Locality	Coordinates		Altitude	Habitats
Mexico camp, BBCF	N 03.98183°	E 09.26250°	0 m	Disturbed lowland rainforest
Bamboo camp, MC	N 04.08990°	E 09.05174°	350 m	Disturbed lowland rainforest
Drinking Gari camp, MC	N 04.10221°	E 09.06304°	650 m	Lowland rainforest
PlantiCam camp, MC	N 04.11750°	E 09.07094°	1100 m	Open-canopy upland rainforest

RESULTS

In total, we identified 19 species of erebid moths never previously reported from Cameroon, including two never reported genera. Nine are also new records in the West African biogeographic region. The details on the individual sampling sites are listed in Table 1.

Erebidae: Erebinae

Achaea ezea (Cramer, 1779)
1 ♂, Bimbia Bonadikombo Community Forest, Mexico camp, 05.I.2015; 1 ♂, Mt. Cameroon, Drinking Gari camp, 27.XI.2014.
This is a West/Central African species recorded from several countries from Gambia in the west to the Democratic Republic of Congo (DRC) and Congo in the east and Equatorial Guinea and Gabon in the south.

Achaea finita (Guenée, 1852)
1 ♀, Mt. Cameroon, Bamboo camp, 05.XII.2014; 1 ♂, Mt. Cameroon, Drinking Gari camp, 02.XII.2014.
This widespread species is known from many countries across Sub-Saharan Africa, including countries bordering with Cameroon (Nigeria and DRC).

Achaea indicabilis Walker, 1858
1 ♂, Mt. Cameroon, Drinking Gari camp, 02.XII.2014.
A. indicabilis is known from West (Sierra Leone, Ghana, São Tomé & Principe) and Central (DRC) Africa.

Achaea mormoides Walker, 1858
2 ♀♀, Bimbia Bonadikombo Community Forest, Mexico camp, 01-07.I.2015; 2 ♀♀, Mt. Cameroon, Bamboo camp, 06-10.XII.2014.
A. mormoides is a relatively widespread species known from various countries of Sub-Saharan Africa, including several countries bordering Cameroon (DRC, Equatorial Guinea, Nigeria).

Ercheia subsignata (Walker, 1865)
1 ♀, Mt. Cameroon, Bamboo camp, 04.XII.2014; 1 ♂, 5 ♀♀, Mt. Cameroon, Drinking Gari camp, 29.XI.2014-06.XII.2014; 1 ♂, 7 ♀♀, Mt. Cameroon, PlantiCam camp, 09-15.XII.2014.
This widespread species is known from many countries across Sub-Saharan Africa, including those bordering Cameroon (Nigeria and DRC).

Euminucia conflua Hampson, 1913
1 ♂, Mt. Cameroon, Drinking Gari camp, 02.XII.2014; 1 ♂, Mt. Cameroon, PlantiCam camp, 11.XII.2014.
This relatively uncommon West African species has so far been known from Ghana and Nigeria only. Our record extends its known distribution to the east.

Pseudoarcte melanis (Mabille, 1890)
1 ♂, 8 ♀♀, Bimbia Bonadikombo Community Forest, Mexico camp, 01-09.I.2015; 20 ♀♀, Mt. Cameroon, Bamboo camp, 04-12.XII.2014; 11 ♀♀, Mt. Cameroon, Drinking Gari camp, 28.XI.2014-05.XII.2014; 4 ♀♀, Mt. Cameroon, PlantiCam camp, 11-16.XII.2014.
This species occurs from Ivory Coast to Uganda, although it has never been recorded from Cameroon.

Thyas metaphaea (Hampson, 1913)
2 ♀♀, Mt. Cameroon, Drinking Gari camp, 29.XI.2014-01.XII.2014.
T. metaphaea has so far been recorded from Ghana, Nigeria and DRC.

Erebidae: Calpinae

Deinypena lathetica Holland, 1894
10 ♂♂, 8 ♀♀, Mt. Cameroon, Bamboo camp, 04-09.XII.2014; 3 ♂♂, 2 ♀♀, Mt. Cameroon, Drinking Gari camp, 27-29.XI.2014.
This species has been so far considered as an endemic to Gabon. This is thus its first record from the West African biogeographic region.

Deinypena marginepunctata Holland, 1894
1 ♀, Mt. Cameroon, Bamboo camp, 04.XII.2014.
So far, this species has been reported from DRC and Gabon only, and we thus extend its distribution into the West African biogeographic region.

Deinypena lacista Holland, 1894
6 ♂♂, 18 ♀♀, Mt. Cameroon, Bamboo camp, 04-13.XII.2014.
This species has been so far known from the Central African region (Central African Republic, DRC, Equatorial Guinea). This is its first record from West Africa.

Gonioscia piperita (Holland, 1894)
6 ♂♂, 2 ♀♀, Mt. Cameroon, Bamboo camp, 04-12.XII.2014.
G. piperita has been so far considered to be endemic to Gabon. We extend its known distribution to the West African biogeographic region.

Hesperochroa multiscripta (Holland, 1894)
2 ♂♂, 14 ♀♀, Mt. Cameroon, Bamboo camp, 04-12.XII.2014; 1 ♂, 4 ♀♀, Mt. Cameroon, Drinking Gari camp, 28.XI.2014-04.XII.2014; 6 ♀♀, Mt. Cameroon, PlantiCam camp, 10-14.XII.2014.
This species has been so far known from Central Africa (DRC, Gabon), and this is its first record from the West African biogeographic region.

Lacera alope (Cramer, 1790)
1 ♀, Mt. Cameroon, PlantiCam camp, 09.XII.2014.
A widespread species, with a distribution ranging to East and South-East Asia, and New Guinea. Pinhey (1975) suggested that the African counterpart could be a separate species but so far no taxonomic decision has been made. It is known from the eastern part of Africa to South Africa and DRC. This is thus the species' westernmost known record extending its range to the West African biogeographic region, as well as the first record of the genus *Lacera* in Cameroon.

Miniodes phaeosoma Hampson, 1913
2 ♂♂, Mt. Cameroon, Bamboo camp, 10.XII.2014.
M. phaeosoma was previously known from several West African countries (Sierra Leone, Ghana, Nigeria) and DRC.

Ogovia tavetensis Holland, 1892
1 ♂, Mt. Cameroon, Bamboo camp, 10.XII.2014; 3 ♂♂, Mt. Cameroon, Planti Cam camp, 10-17.XII.2014.
This species was previously known from East/Central Africa only (DRC, Tanzania, Zimbabwe), but by this westernmost record we extend its known distribution to the West African biogeographic region.

Pseudotolna eximia (Holland, 1894)
3 ♂♂, 3 ♀♀, Mt. Cameroon, Bamboo camp, 05-11.XII.2014; 1 ♂, 3 ♀♀, Mt. Cameroon, Drinking Gari camp, 05-06.XII.2014; 3 ♂♂, 9 ♀♀, Mt. Cameroon, PlantiCam camp, 10-16.XII.2014.
The known distribution of this species is quite patchy in West (Sierra Leone, Ghana) and Central (DRC, Equatorial Guinea) Africa.

Serrodes trispila (Mabille, 1890)
1 ♂, Mt. Cameroon, Drinking Gari camp, 30.XI.2014.
This species occurs in several countries of southern and eastern Africa, and also in Congo and São Tomé & Principé. We extend its known distribution to the West African biogeographic region.

Erebidae: Hypeninae

Ametropalpis vidua (Holland, 1894)
1 ♂, Mt. Cameroon, Drinking Gari camp, 30.XI.2014; 3 ♂♂, Mt. Cameroon, PlantiCam camp, 09-10.XII.2014.
A. vidua was previously known from Gabon and Uganda only. This is thus the first record of the genus from the West African geographic region. The genus *Ametropalpis* has not previously been recorded from Cameroon.

DISCUSSION

Our findings of the relatively high number of so far unrecorded erebid species in a quite small area confirm the poor knowledge of the group in Cameroon. The majority of the reported species were already known from the neighboring countries and their distribution in Cameroon thus could be expected, although the lack of extensive faunistic research of Erebidae has prevented their detection. Considering the family's high diversity in the Afrotropics together with a general lack of recent comprehensive studies of the group from the whole region, we suppose that more species of biogeographic interest are present in Cameroon and adjoining countries. Extending the known distribution of the nine reported species to the West African biogeographic region provides further evidence of high biogeographical importance of the Mt. Cameroon area. The first results of our study also reveal a high potential of using fruit-baited net traps for sampling of fruit-feeding moths. These traps are quite often used for various studies of butterflies (e.g., Sáfián et al., 2011; Aduse-Poku et al., 2012; Van Swaay et al., 2015), but the captured moths are generally ignored. Following the initial results of our sampling, we appeal to lepidopterists studying fruit-feeding butterflies to pay more attention to captured moths.

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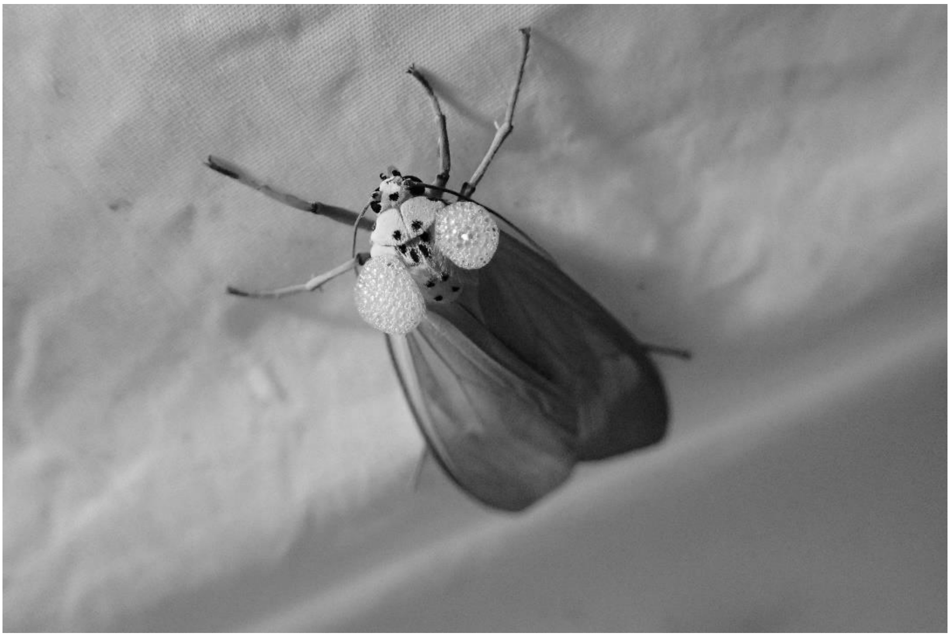

Amerila femina (Berio, 1935)*, endemic from Mt. Cameroon, excretes alkaloid chemical defense from its thorax. The adult was recorded in the montane forest around the Elephant camp (ca., 1,850 m asl.) © S. Delabye*

CHAPTER VIII

Amerila (Lepidoptera: Erebidae: Arctiinae) of Cameroon: faunistic and taxonomic summary, and first illustration of female genitalia

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Submitted manuscript

ABTRACT

Amerila is one of the most studied Afrotropical genera of Arctiinae. However, based on a regionally constrained sample of specimens from Mount Cameroon, we show how superficial our knowledge on these tiger moths is. Among six collected *Amerila* species, *A. femina*'s female is described here for the first time, and *A. mulleri* and *A. roseomarginata* had never been recorded before in the country. Moreover, novel biological data are presented, including individual species' elevational ranges. Finally, female reproductive organs of the genus are illustrated here for the first time. The value of such regional studies is highlighted, with some remarks on necessary requirements of such small-scaled field sampling.

INTRODUCTION

Amerila Walker, 1855 is a diverse genus of tiger moths (Erebidae: Arctiinae: Amerilini) with approximately 60 described species distributed in the Old-World tropics (Häuser, 1993). More than half of them inhabit Sub-Saharan Africa, including its offshore islands such as Aldabra in the Seychelles archipelago (Fryer, 1912), Mauritius (Cramer, 1781), Madagascar (de Toulgoët, 1978; Häuser & Boppré, 1997), Comoros (de Toulgoët, 1978), Zanzibar (Bartel, 1903; Holland, 1896) in the Indian Ocean, Principe (Aurivillius, 1910; Berio, 1935), and Bioko (Aurivillius, 1925) in the Gulf of Guinea in the Atlantic Ocean. The genus was traditionally included in the tribe Arctiini based on its superficial similarity to some other tropical genera (e.g., *Rhodogastria*, *Caryatis*). However, modern phylogenetical studies based on genetic data provided the unexpected evidence that *Amerila* rather constitutes a sister group to the Syntomini+Arctiini clade formally accepted as the tribe Amerilini (Zahiri *et al.*, 2012; Zaspel *et al.*, 2014; Zenker *et al.*, 2017).

Although the *Amerila* genus is among the best-known Afrotropical tiger moths, interest of both collectors and scientists is still limited, despite the relatively large size and attractive coloration of the genus members. The milestone regarding the knowledge on the taxonomy and distribution of the African species is the monograph by Häuser & Boppré (1997), preceded by the world catalogue of the species-group names (Häuser, 1993). The only later contribution to the alpha taxonomy of the genus is Kühne (2008), containing photographs of male genitalia of the morphologically similar species *A. luteibarba* (Hampson, 1901) and *A. affinis* (Rothschild, 1910), depicting the specific characteristics of both taxa deeper than in Häuser & Boppré (1997). A few remaining recent publications mainly focused on presenting new distributional records for a few species only (Dubatolov, 2009; Hacker, 2016; Baron *et al.*, 2017).

The reproductive organs of both *Amerila* sexes are rather insufficiently studied. The descriptions of most of the taxa in Häuser & Boppré (1997) contained only drawings of male genitalia with separately illustrated morphological details of vesica, uncus and valva. In contrast, no female genitalia have ever been illustrated. Similarly, Kühne (2008) illustrated male genitalia of *A. luteibarba* and *A. affinis* only, whereas the catalogue of African tiger moths (Goodger & Watson, 1995) illustrates only male genitalia of an Asian species, *A. astreus* (Drury, 1773). In summary, to our knowledge, no comprehensive description nor illustration of any African *Amerila* female reproductive organs has ever been published.

Cameroon lies on the border between the Guinean, and Congolian and Sudanian biogeographic regions (Linder *et al.*, 2012). Hence it hosts fauna elements of all three regions, together with numerous endemic species of Lepidoptera (Heppner, 1991; Larsen, 2005; Joannou & Krüger, 2009; Yakovlev, 2015; Sáfián & Tropek, 2016). Moreover, the country offers a large spectrum of biotopes, ranging from tropical lowland rainforests in the south to dry savannahs and Sahel in the north, additionally enriched by the only substantial areas of high mountains in the region. As a result, Cameroon is considered as one of the most species-rich areas in Africa for a wide range of taxa, including moths (Heppner, 1991; Ballesteros-Mejia *et al.*, 2013). However, despite its high biodiversity and biogeographic importance, Cameroonian moth fauna have still been insufficiently studied. Most of our recent knowledge on the local moth fauna is based on wider catalogues and on biogeographical studies of a few emblematic groups such as Saturniids and Sphingids (e.g., Darge, 1995, 2003; Kitching & Cadiou, 2000; Ballesteros-Mejia *et al.*, 2013), or a study of ecological patterns of larger lepidopteran taxa (Maicher *et al.*, 2018). Most recent publications on other groups are restricted to rather scarce faunistic records or species descriptions (e.g., Tropek *et al.*, 2015; Maicher *et al.*, 2016; Ustjuzhanin *et al.*, 2018). Even such a large and relatively colorful group as tiger moths lacks any comprehensive inventory. The only species list of the Cameroonian Arctiinae can be compiled from the African catalogue (Goodger & Watson, 1995), and no detailed work on any tiger moth groups, including *Amerila*, exists from the country.

In this paper, we summarize the available data on all species of *Amerila* ever recorded from Cameroon, supplemented by our recent extensive collections from Mount Cameroon, bringing new country records of two additional species. We also use the recently collected material to briefly discuss the morphological variation of a few selected species. Additionally, for the first time we describe and illustrate the morphology of female reproductive organs of a few representatives of the genus, together with a description of the so far unknown female of *A. femina*. Finally, we correct the misleading interpretation of *A. syntomina* as published in the monograph by Häuser & Boppré (1997) based on examination of the type specimen and other newly collected material.

MATERIALS AND METHODS

We summarized all published records of the genus from Cameroon, using mainly Häuser & Boppré (1997) and the AfroMoths web page (De Prins & De Prins, 2018). All original references cited in the AfroMoths have been checked to ensure correct information.

Most of the newly collected material discussed in this paper originates from the southwestern slopes of Mount Cameroon, South-West Province, where R. Tropek, V. Maicher, and Sz. Sáfián, together with Štěpán Janeček, Pavel Potocký, Sylvain Delabye, Jan Mertens and other colleagues, have been studying changes of Lepidoptera communities along the altitudinal gradient since 2014. Here, we present specimens collected during seven field expeditions (November/December 2014, April/May 2015, January/February and November/December 2016, January/February, March and October 2017) in eight sampling sites:

Bamboo Camp: N 4.0879°, E 9.0505°; 350 m asl., lowland rainforest with historical disturbances by selective logging;
Drink Gari camp: N 4.1014°, E 9.0610°; 650 m asl., lowland rainforest with a presumably closed canopy;
Ekonjo: N 4.0921°, E 9.1156°; 1800 m asl., upland rainforest with a presumably closed canopy
Crater Lake: N 4.1443° E 9.0717°; 1450 m asl., upland rainforest locally disturbed by elephants;
Elephant Camp: N 4.1453°, E 9.0870°; 1850 m asl., montane forest locally disturbed by elephants;
Mapanja: N 4.1191°, E 9.1284°; 1800 m asl., montane forest of a presumably closed canopy;
Mann's Spring camp: N 4.1428°, E 9.1226°; 2200 m asl., montane forest close to the natural timberline;
PlanteCam camp (also misspelled as Planty camp): N 4.1175°, E 9.0709°; 1100 m asl., upland forest locally disturbed by elephants.

During these expeditions, we sampled also in another site (Bimbia-Bonadikombo Community Forest, N 3.9818°, E 9.2625°, 30 m asl.) following the same protocol, but no *Amerila* specimen was recorded there. Our sampling implied several full nights of an active catching of all Arctiinae attracted by light (a single energy-saving bulb: 4100 K, 5300 lm, 105 W, 5U), supplemented with an intensive bait-trapping by fermented mashed bananas (for more details on the sampling protocol, see Maicher *et al.* 2018) around each camp. A single specimen collected in the Dom forest, North-West Province, Cameroon (1850–2100 m asl., N 6.3570°, E 10.6088°, mosaic of montane forests and open habitats), by the last author was added. Voucher specimens are deposited in the Nature Education Centre of Jagiellonian University, Krakow, Poland.

The terminology for the genitalia morphology description is based on Kôda (1987). Wing and body measurements (in millimeters) were taken using a digital caliper. The forewing length was measured along the costa from the wing base to the apex of the terminal fringe scales. Photographs of specimens were taken using a Canon EOS 40D digital SLR camera. Genitalia photographs were taken with a Nikon SMZ binocular microscope. For each species, weighted mean elevation (i.e., the average of elevations for all individuals of a given species, Menéndez *et al.*, 2014) was calculated, and together with the highest and lowest record also visualized in Fig. 1.

RESULTS

During the present surveys on Mount Cameroon, 143 specimens of six *Amerila* species were collected. All six species were attracted by light. *Amerila femina, A. luteibarba*, and *A. niveivitrea* were also captured by bait traps. The sampled material includes a so far unknown female of *A. femina*, specimens of *A. mulleri,* and a specimen of *A. roseomarginata* never recorded in Cameroon, as well as a male of *A. syntomina* which had already been reported from the country but without any locality specification. Together with this material, 13 *Amerila* species are currently known from Cameroon.

Checklist of Cameroonian *Amerila*

Species with further remarks are marked with ‘*’, new country records with ‘**’.

Amerila brunnea (Hampson, 1901)
**Amerila femina* (Berio, 1935)
Amerila fennia (Druce, 1887)
Amerila leucoptera (Hampson, 1901)
* *Amerila luteibarba* (Hampson, 1901)
** *Amerila mulleri* (Häuser and Boppré, 1997)

Amerila nigroapicalis (Aurivillius, 1899)
* *Amerila niveivitrea* (Bartel, 1903)
Amerila puella rothi (Rothschild, 1910)
** *Amerila roseomarginata* (Rothschild, 1910)
* *Amerila syntomina* (Butler, 1787)
Amerila vidua (Cramer, 1780)
Amerila vitrea Plötz, 1880

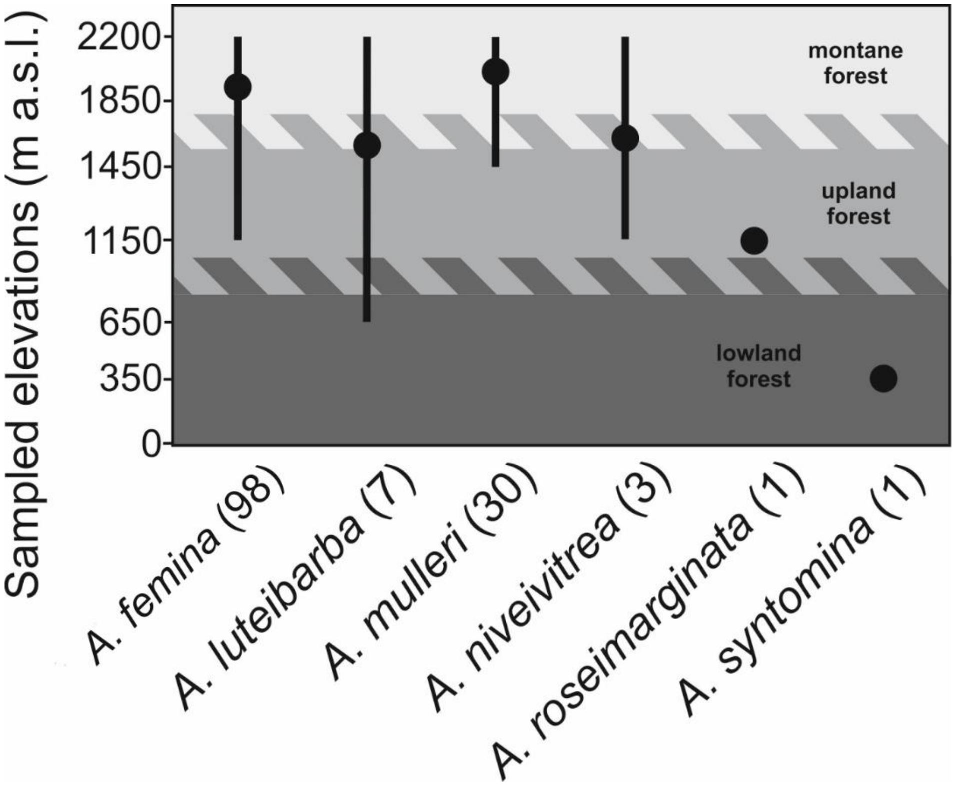

Fig 1. Elevational distribution of *Amerila* species on Mount Cameroon. The weighted mean elevation of individual species (black dot), together with their lowest and highest records, are visualized. After species names, numbers of collected specimens are stated.

Specimen data, descriptions, and annotations on selected species

Amerila femina (Berio, 1935) (Figs 2–6, 16–17, 25)

Material (98 specimens). 1♂ Mount Cameroon (SW slope), 18.xi.2014, Elephant camp (1850 m asl.), N 4.1453°, E 9.0870°, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek; 1♂ as above but 19.xi.2014; 2♂♂ as above but 24.xi.2014; 1♂ as above but 25.xi.2014; 1♂ as above but 20.iv.2017, lgt. V. Maicher, P. Potocký, S. Delabye; 8♂2♀♀ as above but 25.iv.2017; 1♀ as above but Ekonjo sector, 21.x.2017, Ekonjo camp (1150 m asl.), N 4°0921, E 9°1156, lgt. V. Maicher, S. Delabye; 1♂ as above but 6.xi.2016, Mann’s Spring (2200 m asl.), N 4.1428°, E 9.1226°, lgt. V. Maicher, Š. Janeček, R. Tropek; 2♂♂ as above but 7.xi.2016; 1♂ as above but 9.xi.2016; 1♂ as above but 28.i.2017, lgt. P. Potocký, R. Tropek, J. Mertens, Š. Janeček; 2♂♂1♀ as above but 17.iv.2017, lgt. V. Maicher, P. Potocký, S. Delabye; 6♂♂6♀♀ as above but 18.iv.2017; 1♂10♀♀ as above but 19.iv.2017; 3♂♂1♀ as above but 20.iv.2017; 5♂♂ as above but 21.iv.2017; 4♂♂ as above but 19.iv.2017, lgt. V. Maicher, P. Potocký, S. Delabye; 2♀♀ as above but Mapanja sector, 11.v.2017, Mapanja camp (1800 m asl.), N 4.1191°, E 9.1284°, lgt. V. Maicher, S. Delabye; 1♂ as above but 12.v.2017; 3♀♀ as above but 13.v.2017; 7♂♂6♀♀ as above but 14.v.2017; 1♂ as above but 15.v.2017; 2♀♀ as above but 22.x.2017; 1♂3♀♀ as above but 23.x.2017; 1♂3♀♀ as above but 25.x.2017; 2♂♂2♀♀ as above but 28.x.2017; 2♂♂ as above but 29.x.2017 (all above attracted by light); 1♀ as above but 9.iv.2015, PlanteCam camp (1100 m asl.), N 4.1175°, E 9.0709° (bait-trapped).

Distribution. Until now, the species was known only from two males collected on Mount Cameroon: the first one in Buea, 800–1200 m, 21.iv.1902 (Berio, 1935), and the second one labelled as Mount Cameroon, 4.iv.1958 (Häuser & Boppré, 1997). According to the elevation indicated on the labels of both previously and newly collected specimens, the species occurs between 800 and 2200 m asl., and seems to be restricted to submontane and montane forest (Fig. 1).

Male genitalia. Illustrated in Häuser and Boppré (1997). The specimen examined by us bears an inwardly curved (not straight) process of valva (Figs 16-17).

Description of female. ***Head.*** Frons and vertex pinkish rusty, each with a single central black spot; frons additionally with a pair of lateral, minute black spots near the eye margin; labial palps upcurved, rounded terminally, segment III half the length of the segment II, basal portion of each segment pink, terminal black with the segment III half black; scapus pink with black scales at its inner surface; flagellum filiform, uniformly ochraceous.

Thorax. Pale pinkish rusty above, slightly more intensively pink below, with minute blackish blotches at the base of fore and mid coxa; patagium with two distinct blackish blotches; tegula with two well defined black dots: one basoventral and one anterior; mesothorax with a blackish pattern: three pairs of parallel, subdorsal blotches, an additional pair of basolateral blotches partly covered by tegulae; foreleg: coxa pale rusty, with a blackish blotch on its ventroproximal surface, femur dorsally intensive pinkish, ventrally pale rusty with a blackish dot terminally, tibia and tarsus dorsally pale rusty, ventrally pinkish; epiphysis more than 1/3 the length of tibia; middle and hindleg similar in the pattern and coloration, but hind tibia provided with two pairs of spines.

Abdomen. Dorsal segments with the gradually changing coloration from pale rusty to pinkish towards the termination, ventral segments monochromatically pale rusty; the blackish pattern consists of a series of six distinctive blotches at the lateral margin of each tergite and a series of small dots located between sternite and tergite just below each spiracle.

Forewing. Length 24–29 mm; upperside pale ochreous-brown; central area from the base to the postdiscal region semitransparent except for the densely scaled discal vein; the base of the radial veins with two black dots. Underside similar in the pattern and coloration but without the basal black dots.

Hindwing. Extensively semitransparent; upperside pinkish to pale ochreous depending on particular specimen; the coloration towards the margin gradually more intensive. Underside similar in pattern and coloration.

Female genitalia (Fig. 25). Papillae anales large, subsquare, terminally covered with dense setae; a pair of elongate membranous lobes ventrally, anteriorly from an oviduct; apophyses anteriores short, thick, “thorn” like; apophyses posteriores slender, one and half times as long as apophyses anteriores; dorsal and ventral pheromone glands reduced; sternum VIII weakly sclerotized, posteriorly evenly emarginated, medially deeply divided by a wide longitudinal slit; ostium bursae wide, membranous; antrum short, membranous; ductus bursae straight, moderately elongate with the ventral wall membranous and dorsal wall sclerotized; corpus bursae oval, membranous, densely plicate with a prominent funnel shaped sclerotization; ductus seminalis slender, originating in the anterolateral portion of corpus bursae.

Remarks. The intensity of the pinkish suffusion of the head, thorax, hindwing and abdomen may vary substantially among specimens both in males (Figs 2–4) and females (Figs 5–6). In both sexes, the pink and pale ochraceous specimens are frequently encountered with all intermediate color forms. There are no detected differences between the color morphs in respect to male and female genitalia. The description of female is based on the examination of twenty specimens. The forewing length of forty studied males varies between 25–30 mm. The females were captured by both light catching and bait trapping.

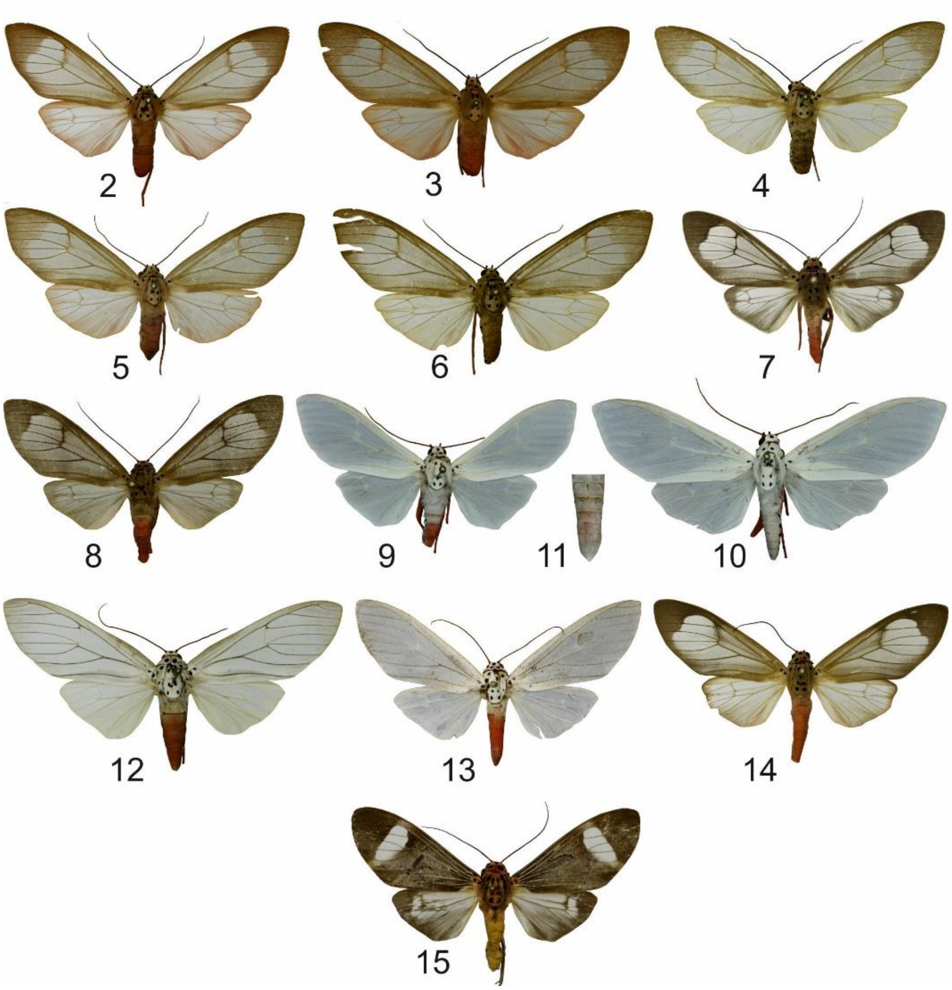

Fig. 2–15. *Amerila* habitus; **2** *A. femina* ♂ pink form; **3** *A. femina* ♂ intermediate form; **4** *A. femina* ♂ brown form; **5** *A. femina* ♀ pink form; **6** *A. femina* ♀ brown form; **7** *A. luteibarba* ♂, **8** *A. luteibarba* ♀; **9** *A. mulleri* ♂; **10** *A. mulleri* ♀ with typical white abdomen; **11** *A. mulleri* ♀ with rare pinkish abdomen; **12** *A. niveivitrea* ♂; **13** *A. niveivitrea* ♀; **14** *A. roseomarginata* ♀; **15** *A. syntomina* ♂.

Amerila luteibarba (Hampson, 1901) (Figs 7–8, 18–19, 26)

Material (7 specimens). 1♂ Mount Cameroon (SW slope), 27.xi.2016, Crater Lake (1500 m asl.), N 4.1443°, E 9.0717°, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek; 1♂ as above but 23.xi.2014, Elephant camp (1850 m asl.), N 4.1453°, E 9.0870°; 1♂ as above but 7.xi.2016, Mann's Spring (2200 m asl.), N 4.1428°, E 9.1226°; 1♂ as above but 9.xi.2016; 1♀ as above but 13.iv.2015, PlanteCam camp (1100 m asl.), N 4.1175°, E 9.0709°; 1♂ as above but 14.iv.2015 (all above attracted by light); 1♂ as above but 30.xi.2014, Drink Gari camp (650 m asl.), N 4.1014°, E 9.0610° (bait-trapped).

Distribution. One of the most widespread species of the genus, although restricted to the Guineo-Congolian forest zone. Known from Sierra Leone to west Kenya (Kakamega Forest) and northwest Tanzania. On Mount Cameroon, it was collected from 650 m asl. up to the timberline (Fig. 1).

Male genitalia (Figs 18–19). Morphology of the studied specimen does not differ from those presented in Häuser & Boppré (1997).

Female genitalia (Fig. 26). Papillae anales subsquare, terminally covered with sparse setae; a pair of minute but distinctive membranous lobes ventrally, anteriorly from oviduct; apophyses anteriores moderate length, thick, "thorn" like; apophyses posteriores narrower, twice as long as apophyses anteriores, slightly flattened at apex; dorsal and ventral pheromone glands reduced; sternum VIII sclerotized, posteriorly evenly emarginated, divided medially by the membranous longitudinal concavity; ostium bursae wide, membranous; ductus bursae very short, membranous; corpus bursae oval, membranous, densely plicate; signum in the form of weakly expressed, sclerotized zone in the laterodistal portion of corpus bursae, additionally a pair of weakly sclerotized, narrow, elongate, parallel structures located on the opposite wall of corpus bursae; ductus seminalis slender, with wide entering, originating at the middle of corpus bursae.

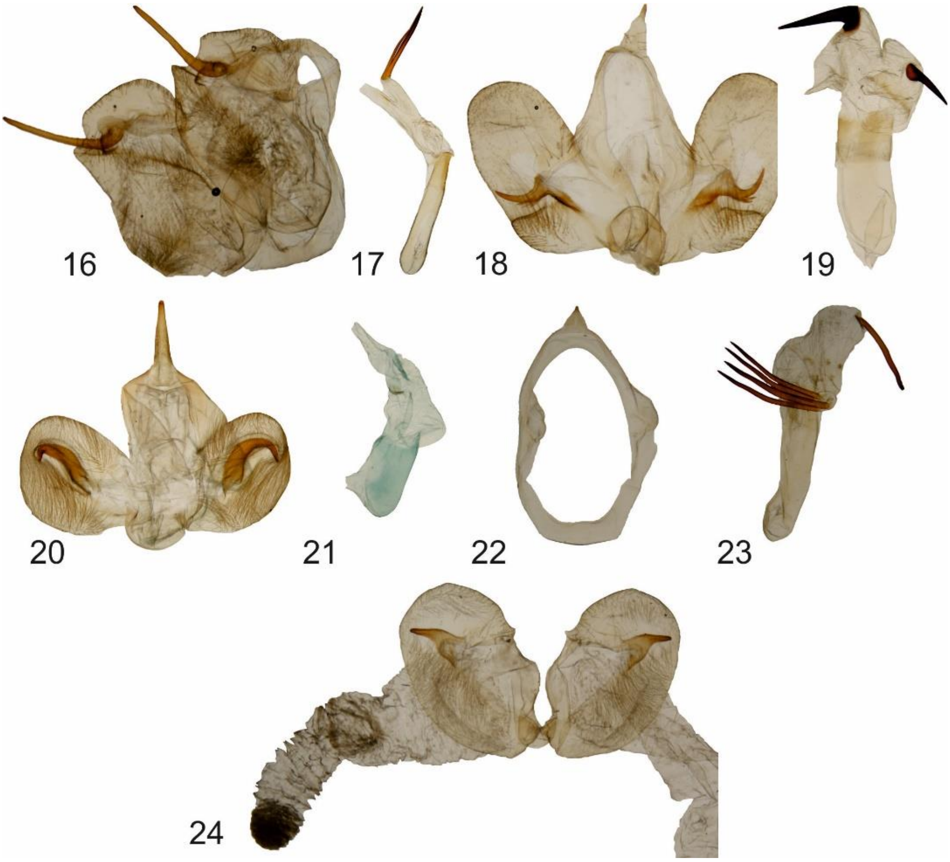

Fig. 16-24. Male genitalia of *Amerila* species; **16** *A. femina*; **17** aedeagus; **18** *A. luteibarba*; **19** aedeagus; **20** *A. mulleri*; **21** aedeagus; **22** *A. syntomina* tegumen; **23** aedeagus; **24** valva.

***Amerila mulleri* (Häuser & Boppré, 1997) (Figs 9–11, 20–21, 27)**

Material (30 specimens). 1♀ Mount Cameroon (SW slope), 25.xi.2016, Crater Lake (1500 m asl.), N 4.1443°, E 9.0717°, lgt. V. Maicher, Sz.

Sáfián, Š. Janeček, R. Tropek; 1♀ as above but 27.xi.2016; 1♂, 1♀ as above but 24.xi.2014, Elephant camp (1850 m asl.), N 4.1453°, E 9.0870°; 1♀ as above but 20.iv.2017, lgt. V. Maicher, P. Potocký, S. Delabye; 2♀♀ as above but 6.xi.2016, Mann’s Spring (2200 m asl.), N 4.1428°, E 9.1226°, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek; 2♂♂7♀♀ as above but 7.xi.2016; 1♀ as above but 8.xi.2016; 2♂♂2♀♀ as above but 9.xi.2016; 1♀ as above but 11.xi.2016; 1♂ as above but 18.iv.2017, lgt. V. Maicher, P. Potocký, S. Delabye; 1♀ as above but 19.iv.2017; 1♂ Mapanja sector; 14.x.2017, Mapanja camp (1800 m asl.), N 4.1191°, E 9.1284°, lgt. V. Maicher, S. Delabye; 1♂ as above but 23.x.2017; 1♂ as above but 29.x.2017; 2♂♂1♀ as above but 26.x.2017 (all above attracted by light).

Distribution. The species range is probably underestimated due to the small number of available records. The species has earlier been recorded in several Eastern and Southern African localities. The northwesternmost locality is Ituri-Nioka near Albert Lake (northeast Democratic Republic of Congo). The new localities in Cameroon indicate that the species’ distribution in tropical Africa is substantially wider than was known before (by approximately 2300 km to the west). As several males and females were collected on Mount Cameroon over the four years of our sampling, there are no doubts about the existence of a stable population of *A. mulleri*. On Mount Cameroon it was collected from 1450 up to the timberline, occurring mainly in the montane forest (Fig. 1).

Male genitalia. Morphology of the studied male (Fig. 20) shows some differences compared with the drawings published by Häuser & Boppré (1997), especially concerning the aedeagus structure. The length of aedeagus (Fig. 21) can be smaller than its double width while the drawing suggests it is much longer. The vesica bears medially a small plate-like sclerotization, as written in the original description of species but invisible on the illustration (Häuser & Boppré, 1997).

Female genitalia (Fig. 27). Papillae anales subsquare, terminally covered with sparse setae, bearing a pair of indistinctive membranous protuberances ventrally, anteriorly from oviduct; apophyses anteriores moderate length, thick, slightly sinuose; apophyses posteriores narrower, almost three times as long as the apophyses anteriores; dorsal and ventral pheromone glands reduced; sternum VIII moderately sclerotized in the form of a pair of small, flat, subsquare protrusions; ostium bursae wide, membranous; ductus bursae much shorter than corpus bursae, membranous with a distinct dilation at 1/3 of its length; corpus bursae oval, membranous, moderately plicate, without any trace of sclerotizations; ductus seminalis originating at the anterolateral portion of the corpus bursae, with very wide, gradually tapering opening.

Remarks. The morphological description of male provided in Häuser & Boppré (1997) requires some corrections based on the examined specimens. The information claiming forewing veins to be dark is misleading and can be misinterpreted by readers. In fact, the veins of older specimens usually look dark, because the scales are worn off; but the scales of younger specimens could be removed also accidentally during their spreading in the laboratory. Actually, the dark coloration comes from the chitin sclerotization of veins. Such a trait, although easily visible in the lighter species, should not be treated as diagnostic feature. In fact, the entire wing of the undisturbed specimens is always covered by white scales (Fig. 9-10).

Another mistake concerns the number of dark dots on tegula referred to regarding most species in Häuser & Boppré (1997). The authors recognized only the anterior and posterior dots, omitting the additional, often prominent dot located in many species basoventrally between the ventral margin of patagium and the base of forewing. Taking this into consideration, *A. mulleri* possesses two well defined black dots on tegula: basoventral and anterior.

The relatively high number of available females in our material (17 specimens) allowed revealing of a so far unknown phenotypic variation in the coloration of abdominal tergites. The typical and commonest form was entirely white (Fig. 10), while part of the specimens (three in our material) differed by a pinkish suffusion in the distal half of abdomen (Fig. 11). These forms do not differ in their genitalia morphology.

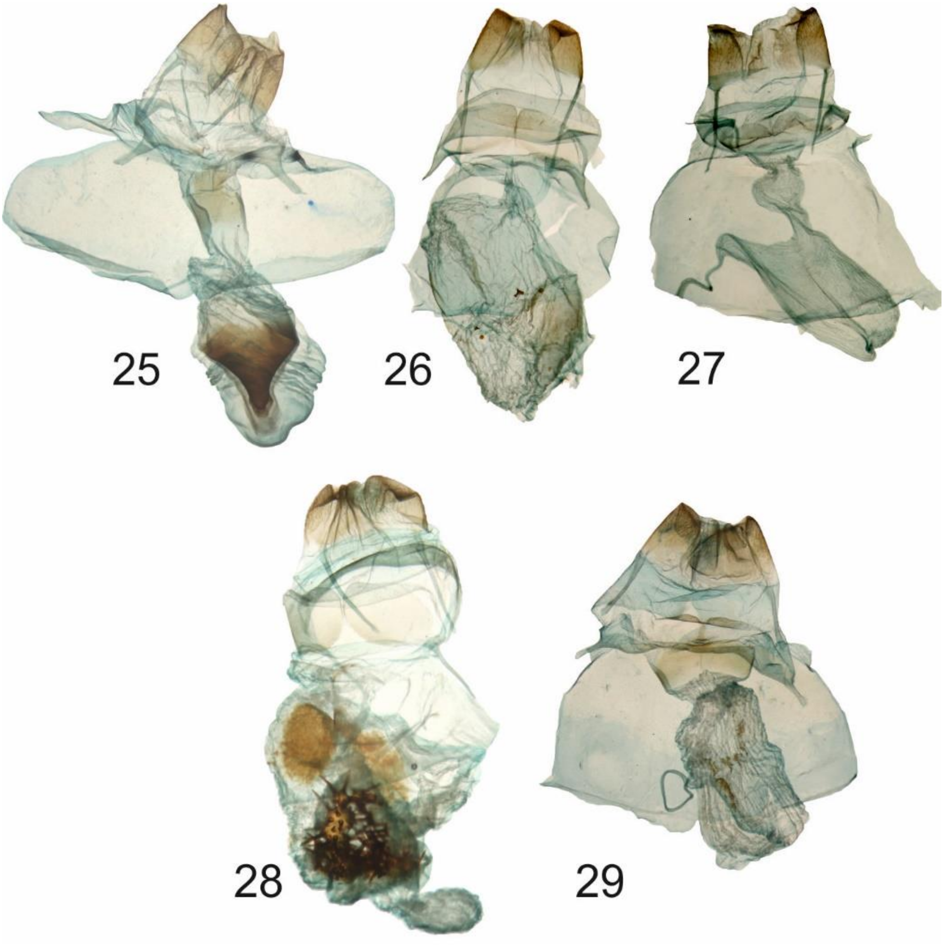

Fig. 25-29. Female genitalia of *Amerila* species; **25** *A. femina*; **26** *A. luteibarba*; **27** *A. mulleri*; **28** *A. niveivitrea*; **29** *A. roseomarginata*.

Amerila niveivitrea (Bartel, 1903) (Figs 12–13, 28)

Material (3 specimens). 1♀ Dom Forest, NW Province, 28-29.xi.2011, 1850-2100 m asl., N 6.3570°, E 10.6088°, lgt. R. Tropek, P. Jansta, D. Lestina; 1♂ Mount Cameroon (SW slope), 6.xi.2016, Mann's Spring (2200 m asl.), N 4.1428°, E 9.1226°, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek (the latter two attracted by light); 1♀ as above but 10.iv.2015, PlanteCam camp (1100 m asl.), N 4.1175°, E 9.0709° (bait-trapped).

Distribution. One of the most widespread *Amerila* species, known from 14 countries in sub-Saharan Africa. In Cameroon, it was recorded from Southwest and Northwest Provinces. On Mount Cameroon, *A. niveivitrea* was recorded only between 1100 and 2200 m asl. (Fig. 1).

Female genitalia (Fig. 28). Papillae anales subsquare, terminally covered with dense setae; a pair of elongated membranous protuberances ventrally, anteriorly from the oviduct; protuberances distinctly wide and shallow proximally, then gradually tapering and more conspicuous distally; apophyses anteriores moderate length, straight, not triangular; apophyses posteriores of the same width, 50 percent longer than the apophyses anteriores; dorsal and ventral pheromone glands reduced; sternum VIII moderately sclerotized with a pair of small, rounded protrusions raised towards the median line of the body; ostium bursae wide, sclerotized; ductus bursae much shorter than its width, membranous; corpus bursae forming an irregular, ovoid, densely plicate pouch with several small, spiny, heavily sclerotized signa; single, elongate near the origin of the ductus seminalis and several minute sclerotizations forming an irregular line in the proximal section of corpus bursae; ductus seminalis narrow, originating from the slightly convex medio-lateral portion of the corpus bursae.

Remarks. Female genitalia were briefly described in Häuser & Boppré (1997) for the first time but have not been illustrated anywhere yet.

Amerila roseomarginata **(Rothschild, 1910) (Figs 14, 29)**

Material (1 specimen). 1 ♂ Mount Cameroon (SW slope), 1.ii.2016, PlanteCam camp (1,100 m asl.), N 4.1175°, E 9.0709°, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek (attracted by light).

Distribution. Very common species frequently collected across equatorial Africa. It is sparsely distributed from the Ivory Coast to the eastern regions of Kenya and Tanzania with some gaps most probably caused by the insufficient faunistic exploration in many countries. The present record (Fig. 14) is the first one for Cameroon, suggesting that the species might have a continuous range in tropical Africa. On Mount Cameroon, only a single specimen was collected at 1150 m asl. (Fig. 1).

Female genitalia (Fig. 29). Papillae anales subsquare, terminally covered with sparse setae; separated ventrally by a pair of elongated membranous protuberances, anteriorly from the oviduct; apophyses anteriores moderate length, straight; apophyses posteriores narrower, one-third longer than apophyses anteriores; dorsal and ventral pheromone glands reduced; sternum VIII sclerotized, forming a pair of prominent, flat, subsquare protrusions; ostium bursae wide, membranous; ductus bursae much shorter than its width, membranous; corpus bursae forming an irregular pouch with two sclerotized, flat surfaces in the proximal section and extensive irregular signum bursae with numerous, sharp, elongate spines in the distal section, terminating in a small, papilla-like appendix bursae; ductus seminalis narrow, arising from the anteromedian portion of the bursa.

Remarks. Female genitalia have neither been described nor illustrated before. The species identity of the collected specimen is confirmed by the key characters of imago provided by Häuser & Boppré (1997).

Amerila syntomina (Butler, 1787) (Figs 15, 22-24)

Material (1 specimen). 1 ♂ Mount Cameroon (SW slope), 17.iv.2015, Bamboo camp (350 m asl.), N 4.0879°, E 9.0505°, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek (attracted by light).

Distribution. The species is known from the Afrotropical forests from Guinea through the Congo-Guinean basin to Tanzania, but the real distribution is still dubious due to the mistake by Häuser & Boppré (1997) discussed below. Mount Cameroon is the only known locality in Cameroon, we collected a single specimen at 350 m asl. (Fig. 1).

Male genitalia. Tegumen (Fig. 23) narrow, pedunculus broadened, directed posteriorly; uncus very small, triangular, pointed apically, not longer than the dorsal part of tegumen; vinculum long, slender; saccus reduced; valva (Fig. 22) large, ovoid, its outer surface with the long, protrudable, tube-like coremata, its inner surface with a horn-like sclerotized process slightly curved and apically pointed, not reaching the outer margin of valva; phallus (Fig. 24) straight, weakly sclerotized; vesica shorter than the phallus with four large, elongate, basally not fused, sharply pointed cornuti in the basal zone and additionally a single, similarly long but apically rounded cornutus in its terminal section.

Remarks. Previously, *A. syntomina* was reported from Cameroon only by Gaede (1926), without any locality or other specific data.

The illustrations of male genitalia provided by Häuser & Boppré (1997: plate 13) are incorrect. Examination of the primary types of both A.

syntomina and *A. syntomina rubondoi* by the third author (GyML) revealed that these taxa represent two distinct species. Häuser & Boppré (1997) did not examine the type of *A. syntomina* and they mistakenly assumed that ssp. rubondoi has identical male genitalia to the nominotypical subspecies. Consequently, the illustrated genitalia did not belong to *A. syntomina*, but to rubondoi. We illustrate the male genitalia of *A. syntomina* for the first time (Figs. 22 and 23), they are identical to that of this taxon lectotype (housed at the NHMUK). As the complete taxonomic revision of the *A. syntomina* species group exceeds the scope of this paper, the revision clarifying taxonomy of the species group will be prepared as a separate publication in the near future.

DISCUSSION

The present study highlights the need of further investigations of the genus *Amerila*, despite being considered among the most studied Afrotropical tiger moths. By our recent material, the number of species recorded from Cameroon has been raised from 11 to 13. Additionally, we described the unknown female of *A. femina*, which is considered endemic for Mount Cameroon, and illustrated and described the female of *A. niveivitrea* in more detail.

The different color forms identified morphologically as endemic *A. femina* represent a single taxon to our knowledge, such phenotypic variation was not distinguishable from the only two previously collected males so far available in collections. The newly collected material unveiled the surprising coloration variability ranging from the completely vivid pinkish hindwings overflowing most of the abdomen, to uniformly ochraceous specimens that are devoid of any trace of the pinkish scales. Specimens with an intermediate colouration were found as well.

We also confirmed the unique faunistic character of Mount Cameroon already noted in some previous lepidopterological studies (e.g., Maicher *et* *al.*, 2016; Sáfián & Tropek, 2016; Ustjuzhanin *et al.*, 2018). In this aspect, we consider the additional specimens of the endemic *A. femina* of special importance. We have unveiled that most of the *Amerila* species recorded on Mount Cameroon occur in forests of higher elevations, including the endemic *A. femina*. Their diversity pattern thus differs from the mid-elevation peak of tiger moth diversity described from the mountain (Maicher *et al.*, under review). Simultaneously, it is also another undeniable argument for protection of the upper elevations of the mountain.

Furthermore, our results proved that local surveys of Lepidoptera diversity can be of a substantial scientific value, especially in such understudied region as the Afrotropics. However, it should be emphasized that such field sampling must follow some basic requirements: a) The material has to be properly collected, stored, and curated to enable wide range of studies (e.g., morphological, genetical, or ecological). b) The sampling should cover complete diversity and enough abundance of the selected target group(s) to obtain a substantial number of specimens necessary for more detailed studies. c) The field sampling should include a comprehensive range of available conditions in both small (local habitats) and large (elevations) scales, and/or seasons (cf., Maicher *et al.*, 2018 for Mount Cameroonian moths) to obtain substantially representative and variable samples of the target group from the focal area.

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A local paradox: A protection panel installed by the Cameroonian Ministry of Forestry stands right next to an illegal logging site in the sampled Bimbia-Bonadikombo coastal forest (ca., 30 m asl.) © V. Maicher

CHAPTER IX

Something is missing at the bottom: Importance of coastal rainforests for conservation of trees, birds and butterflies in the Mount Cameroon area

Ferenc, M., Sedláček, O., Tropek, R., Albrecht, T., Altman, J., Doležal, J., Janeček, Š., Maicher, V., Motombi, F.N., Murkwe, M., Sáfián, Sz., & Hořák, D. (2018).
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SHORT COMMUNICATION

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Something is missing at the bottom: Importance of coastal rainforests for conservation of trees, birds and butterflies in the Mount Cameroon area

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1 | INTRODUCTION

The Guinean Forest of West Africa is a biodiversity hot spot (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) and comprises the Mount Cameroon National Park (MCNP) with its high diversity of endemic animal and plant species (Ayonghe, 2012; psmnr-swr.org; WWF, 2010). The highest richness of plant, reptile, mammal or bird species is found in low elevation forests (Ayonghe, 2012; Cable & Cheek, 1998; Ferenc et al., 2016; Gonwouo et al., 2007), but MCNP protects habitats only above ca. 300 m a.s.l. (psmnr-swr.org), because primary coastal forests are not included within its area. The only largest remnant of littoral forest in the whole region is the Bimbia Bonadikombo community forest (BB forest) lying approximately 15–20 km apart. By its 3,735 ha, it covers diverse habitats, such as coastal forest, freshwater swamp forest and mangroves (Ayonghe, 2012), and is structurally exceptionally heterogeneous. To our knowledge, its biodiversity is rather poorly known and any regional comparison is completely missing. The insufficient knowledge contrasts with the fact that these lowland habitats are highly threatened by destruction and they hosted the most plant species currently considered as possibly extinct (Cable & Cheek, 1998).

Therefore, we asked (i) whether the high diversity of vegetation types in BB forest corresponds with high species richness of trees, birds and fruit-feeding butterflies. At least in lowland rainforests, vegetation structure, rather than tree species richness, seems to be important for both birds (Ferger, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014; Jankowski et al., 2013) and fruit-feeding butterflies (Nyafwono, Valtonen, Nyeko, Owiny, & Roininen, 2015). Therefore, we do not expect a close match in species richness patterns for the three taxa. (ii) Whether there is a match in total vegetation volume and the detected abundance of birds and fruit-feeding butterflies as resource availability is expected to increase with vegetation biomass (Janzen, 1973). (iii) What proportion of tree, bird and fruit-feeding butterfly species is unique to BB forest. To answer these questions, we compared the biodiversity of the three groups in BB forest with two lowland localities within MCNP.

2 | MATERIALS AND METHODS

This study was performed at the foothills of Mount Cameroon, Southwest Province, Cameroon. Three lowland localities were sampled: (i) littoral forests of the Bimbia Bonadikombo area (BB forest —30 m a.s.l.; GPS: 3°58′43″N, 9°15′54″E); (ii) Bamboo Camp (BC—350 m; GPS: 4°5′36″N, 9°3′5″E) and Drinking Gari (DG —650 m a.s.l.; GPS: 4°6′6″N, 9°3′47″E) at the SW slope of Mt. Cameroon. The latter two are inside a large forest block within the MCNP, while BB forest is located on the seashore and is separated by approximately 15–20 km of various altered habitats ranging from urban areas, plantations and pockets of community forest to secondary growth.

At each locality, we established 16 plots (i.e. 48 altogether across the three localities) located 150 m apart from each other. Tree, bird and fruit-feeding butterfly communities were sampled at the same permanent circular plots—within a radius of 20 m for trees and butterflies, and 50 m for birds. Between 2011 and 2015, all trees (living and dead) exceeding 10 cm DBH were tagged, identified to species (ca. 98% of individuals) or genus level. Tree height and basal area were recorded and tree volume calculated as the product of these two variables. Subsequently, tree volume was summed across all individuals at each locality. Bird sampling was conducted during mornings (6–10 a.m.) in the beginning of dry season (BB forest: December 2015; BC: November/December 2011; and DG: November 2013) using the point count method (Bibby, Burgess, Hill, & Mustoe, 2000). All forest birds seen or heard within a 15-min period were recorded on three different days at each plot. The maximum abundance of each species at a sampling plot was recorded (Ferenc et al., 2016). Fruit-feeding butterflies were sampled in three different seasons between 2014 and 2016 (transition from wet to dry: November/December, high dry: January/February and transition from dry to wet: May/April) by hanging net traps (modified IKEA PS Fångst hanging storage devices: height 75 cm and diameter 23 cm; (Sáfián, Csontos, & Winkler, 2011)) baited by mashed fermented bananas. At each plot, four traps were set in the understory and a single trap in the canopy layer (i.e. 5 traps/plot, 80 traps/locality). During each season, all traps were exposed for ten consecutive days, and all captured butterfly specimens were removed, identified and counted every day. Butterfly specimens from all five traps and 30 sampling days per plot were pooled, with all nonspecialized fruit-feeders excluded. Differences in species richness of sampling plots among the three study localities (BB forest, BC and DG) were tested using the nonparametric Kruskal–Wallis test in R (R Core Team, 2017).

3 | RESULTS AND DISCUSSION

We recorded 113 tree species in BB forest, 101 species at BC and 71 species at DG (Figure 1). The richest tree community thus reflects the diversity of vegetation types in BB forest (Ayonghe, 2012). In contrast, for birds and fruit-feeding butterflies, BB forest was the poorest, BC was intermediate and DG was the richest with 71, 76 and 90 species of birds and 77, 93 and 99 of fruit-feeding butterfly species, respectively (Figure 1). Significant differences in species richness among the three locations were revealed also at the sampling plot level (Figure 2). In BB forest, BC and DG, respectively, we recorded per plot on average 32, 24 and 18 tree species (Figure 2a); 29, 24 and 36 bird species (Figure 2b); and 22, 52 and 48 fruit-feeding butterfly species (Figure 2c). These patterns confirmed our expectation that richer bird and fruit-feeding butterfly communities are not necessarily associated with rich tree communities (Ferger et al., 2014; Jankowski et al., 2013; Nyafwono et al., 2015).

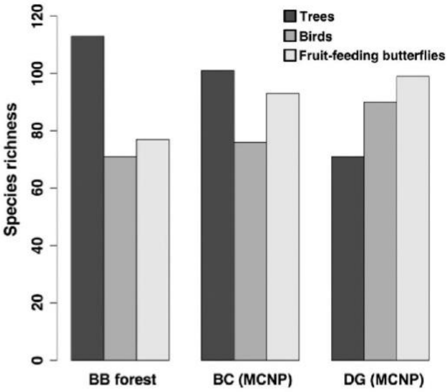

FIGURE 1 Total tree, bird and fruit-feeding butterfly species richness (BB forest = Bimbia Bonadikombo community forest; BC = Bamboo Camp; DG = Drinking Gari; and MCNP = Mount Cameroon National Park)

One of the explanations of the relatively lower avian richness in BB forest and BC can be that both are located at the edge of primary forest and thus might be negatively influenced by forest fragmentation and habitat alteration (Dranzoa, 1998; Owiunji & Plumptre, 1998). Both BB forest and BC have degraded or transformed habitats in their vicinity, while DG is fully enclosed in a large forest tract (Bussmann, 2006; Cable & Cheek, 1998; Proctor, Edwards, Payton, & Nagy, 2007). On the other hand, fruit-feeding butterflies' total species richness is low only in BB forest, while BC and DG are comparable. Habitat-specialized butterflies in BB forest may suffer from a lack of suitable habitats in the landscape, which can cause population declines and some species might be already locally extinct (Brown & Kodric-Brown, 1977; Hanski, 1998; Koh, Sodhi, & Brook, 2004). Alternatively, composition or structural characteristics of vegetation in BB forest might simply lead to less diverse bird and fruit-feeding butterfly communities. Unfortunately, it is impossible to tease apart these scenarios as any larger patch of coastal forest is not available for comparison in the region due to habitat destruction (Cable & Cheek, 1998; Din, Saenger, Jules, Siegried, & Basco, 2008).

Nevertheless, the impoverishment of butterfly communities was confirmed by their low abundances in BB forest (816 individuals) in

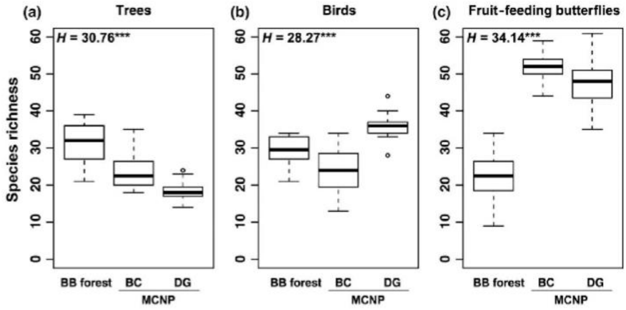

FIGURE 2 Species richness of trees, birds and fruit-feeding butterflies on sampling plots (BB forest = Bimbia Bonadikombo community forest; BC = Bamboo Camp; DG = Drinking Gari; and MCNP = Mount Cameroon National Park). Kruskal–Wallis test results are shown in the insets (***$p < .001$)

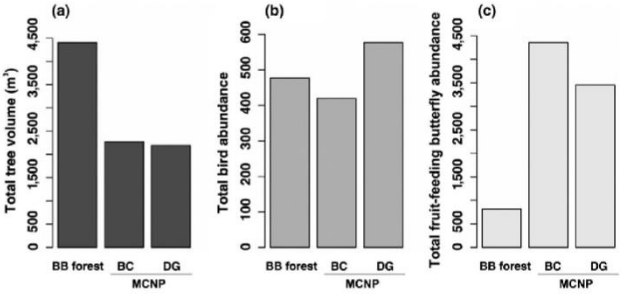

FIGURE 3 Total tree volume and total abundances of birds and fruit-feeding butterflies (BB forest = Bimbia Bonadikombo community forest; BC = Bamboo Camp; DG = Drinking Gari; and MCNP = Mount Cameroon National Park)

comparison with BC (4,356 individuals) and DG (3,452 individuals) located in MCNP (Figure 3c). This pattern strongly contrasted with birds, where the differences in total abundances among locations were much smaller (Figure 3b). The highest total abundance was recorded at DG (577 individuals), followed by BB forest (478 individuals) and the lowest at BC (420 individuals). Moreover, the total abundance patterns of both taxa contrasted with patterns of total tree volume that was approximately twice as high in BB forest (ca. 4,400 m^3) as at BC and DG (both ca. 2,200 m^3; Figure 3a). Contrary to our expectation, the total tree volume was not reflected in the abundance patterns of birds and fruit-feeding butterflies. Possibly, it is not a good proxy variable for resource availability for these taxa and they might react to more specific vegetation properties, for example species composition or vertical configuration (Ferger et al., 2014; Jankowski et al., 2013; Nyafwono et al., 2015). Alternatively, birds and fruit-feeding butterflies can be affected by habitat alterations more rapidly compared to trees. Butterflies are generally considered more sensitive to habitat changes due to faster generation cycles and resource use than plants or some vertebrates (New, 1997).

Despite the relatively lower biodiversity of birds and fruit-feeding butterflies in BB forest compared to BC and DG, these communities are unique with many species not recorded in MCNP: 35% of tree (66 of 190), 12% of bird (14 of 116) and 13% of fruit-feeding butterfly species (16 of 120) were recorded only in BB forest in our study (Table 1). Moreover, a substantial part of the recorded species had relatively higher density estimates in BB forest. Out of the shared species between BB forest and the two pooled MCNP localities, the density estimates of 64% (29 of 45) of tree, 58% (33 of 57) of bird and 22% (13 of 60) of fruit-feeding butterfly species were higher in BB forest (Table 1). Therefore, many of these populations might become threatened, especially the less mobile ones, if BB forest becomes degraded.

TABLE 1 Total species richness of trees, birds and fruit-feeding butterflies recorded at the three study localities; percentage of shared species between the Bimbia Bonadikombo community forest (BB forest) and Mount Cameroon National Park (MCNP); and percentage of shared species with higher density estimates in BB forest than at two lowland localities within MCNP

Taxon	Total species richness at all localities	Percentage of spp. unique to BB forest (%)	Percentage of shared spp. with higher density estimates in BB forest (%)
Trees	190	35	64
Birds	116	12	58
Fruit-feeding butterflies	120	13	22

Despite BB forest has a community forest status, various human interventions are indeed a severe threat to its biodiversity (Ayonghe, 2012; Din et al., 2008; Minang, 2007; Ngalim & Terence, 2016; Nuesiri, 2010, 2015). During our fieldwork, we repeatedly observed intensive logging even in the study area that was selected within an area proclaimed as noninterventional (Ngalim & Terence, 2016). After our sampling, some of the study plots were completely cleared and the logging is still proceeding. Considering that BB forest is the last larger and not entirely degraded coastal forest in the region, the current pace and trajectory of its habitat destruction will most probably cause regional extinctions of numerous species not occurring in the lowland forest of MCNP. Taking into account the relatively efficient facilities of forest protection of the nearby national park, we propose a much closer collaboration between the MCNP and BB forest instead of their current complete separation. Due to endemism of many species (Cable & Cheek, 1998), BB forest should be considered as a unique and essential locality for biodiversity conservation of global importance, instead of its current status of an unsustainably exploited MCNP buffer zone.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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The Crater Lake (ca., 1,450 m asl.) is an important water reserve for the local fauna during the high-dry season on the Southwestern slope © F. "Escobar" Luma

CHAPTER X

Summary of results & Conclusion

~ · SUMMARY · ~

Different aspects of butterfly and moth biodiversity on Mount Cameroon have been explored in this thesis. First, the study of the impacts of the extreme seasonality occurring on the southwestern slope has been shown to strongly affect butterfly and moth phenology in the lowland forest. Generally, we detected that individual groups of Lepidoptera responded differently to seasonality, some being richer during the high-dry season and others during the late dry season. Moreover, the strong turnover of several Lepidoptera groups among seasons suggests a high seasonal specialization of local communities (**Chapter II**).

Extending the investigation of seasonal patterns of biodiversity along the full elevational range had surprising outcomes. We reported a seasonal uphill and downhill shift of several Lepidoptera groups, so far not reported from tropical mountains. Although it is unclear what could be the drivers of such seasonal shifts, they are proposed to be caused by a delay in weather seasonality response of the populations at higher elevations and/or by shifts in resources availability, causing delay of adult hatching or triggering individual migrations. While investigating the impact of climate change on Lepidoptera species along elevational ranges, we strongly recommend future authors to consider the seasonal dynamic of local communities as well (**Chapter V**).

The study of habitat association of both butterflies and moths highlighted the importance of small-scale mechanisms for shaping the dynamics and structure of their local communities. We showed that both butterflies and moths responded relatively similarly to several habitat descriptors. Surprisingly, both groups were sensitive to parameters linked to the canopy openness and to a lesser extent to plant diversity. Overall, several mechanisms such as larval host-plant specificity, sensitivity to microclimatic conditions, and habitat heterogeneity are proposed to be the

main factors affecting butterfly and moth spatial distribution on Mount Cameroon (**Chapter III**).

Comparing both disturbed and undisturbed forests by forest elephants on Mount Cameroon raised conservation issues. While forest elephants are disappearing at an alarming rate in Central Africa, it appeared that the small population of Mount Cameroon is dense enough to have a strong impact on both vegetation and Lepidoptera communities at mid-elevation. The high species richness and unique diversity of butterflies and moths found in the disturbed forests suggest that forest elephants are keystone ecological engineers in tropical rainforests, raising further concerns about their current disappearance from extensive areas in Central Africa (**Chapter IV**).

Lepidoptera diversity of Mount Cameroon has proven to be largely unexplored by the remarkable amount of new species that we collected. Particularly, Mount Cameroon have been raised as a new hotspot of diversity of *Alucita* (**Chapter VI**), so far unmatch in the whole Afrotropics. Our general lack of knowledge on the local Lepidoptera is further evidenced by the high amount of new country records found in our samples (**Chapter VII**) as well as the discovery of a new female and several new country records of a supposedly well-known moth genera (**Chapter VIII**). From this observation, it is more than likely that hundreds of taxonomic novelties remain to be described in Mount Cameroon.

It is undeniable that the creation of the Mount Cameroon National Park in 2009 had greatly contributed to protect its remarkable biodiversity. Despite the fact that the human population density surrounding the mountain is high, large portions of the Mount Cameroon forests remain currently untouched. However, the absence of coastal forest within the limit of the park is regrettable. While the last large patch of coastal forest gathers a unique diversity of trees, birds, butterflies, and cover a high range of rare habitats, its current community forest status appeared to be inefficient and should be reevaluated (**Chapter IX**).

~ · CONCLUSION · ~

This thesis contributed to tackle various aspects of Lepidoptera biodiversity from an understudied tropical area. While reporting the impacts of the unique climate of Mount Cameroon on Lepidoptera phenology in the lowland forest and along the full elevational range, as well as detailing the habitat association of butterflies and moths in both naturally disturbed and undisturbed forests, the extent of the ecological questions tackled is wide and deserved to be further studied. Further research plans might include the sampling of different slopes, as well as the investigation of the montane grasslands above the tree line. Because of its high elevational range, its volcanism, and its unique climate and biodiversity, Mount Cameroon has proven to be an ideal location to study a vast array of questions related to tropical ecology.

Part of the Lepidoptera and botanist teams pose for the camera in the Drink Gari camp (ca., 650 m asl.), at the end of the second expedition in May 2015 © Š. Janeček

CHAPTER XII

Curriculum vitae

VINCENT MAICHER

http://www.insect-communities.cz/team/vincent-maicher/

Date and place of birth: 8th December 1988 in Reims, France
e-mail: vincent.maicher@hotmail.fr
Phone: +420 723638784

EDUCATION

2014 - present: **Ph.D. in Entomology.** Faculty of Science, University of South Bohemia, Czechia. Thesis: *Biodiversity patterns of butterflies and moths on Mount Cameroon*.

2011 - 2013: M.Sc. in **Ecology, Biodiversity and Evolution**, National Museum of Natural History, Paris, France.
Master 2 thesis: National Museum of Natural History, Paris. Habitat and demographic parameters of the endangered vulture *Neophron percnopterus*.
Master 1 thesis: University Pierre and Marie Curie, Paris. Evolutionary origin of a new phenotype in the North African ant *Cataglyphis bombycina*.

2009 - 2011: B.Sc. in **Biology of Organisms**, University of Rennes 1, France.

EMPLOYMENT

2014 - present: Ph.D. student. Institute of Entomology, **Biology Centre, Czech Academy of Sciences**, České Budějovice, Czechia.

2014 - 2018: Technician. Department of Zoology, **Faculty of Science, University of South Bohemia**, České Budějovice, Czechia.

2013: employed by the French **League for Bird Protection** (LPO) for the monitoring of two endangered vulture species in the Occidental Pyrénées region, France.

CURRENT RESEARCH INTERESTS

Ecology, evolution, and natural history of Afrotropical Lepidoptera
Taxonomy and biogeography of Macro-Lepidoptera families in West Africa
Pollination biology in Afromontane ecosystems

AWARDS

2018: Best Ph.D. student publication of the year. For: Maicher V. *et al.* (2018). Flying between raindrops: Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon. *Ecology and Evolution*, **8**, 12761-12772.

2018: Best presentation award - PhD seminar. Department of Zoology, PřF JU.

2017: Best presentation award - PhD seminar. Department of Zoology, PřF JU.

SCIENTIFIC EXPERIENCE

Since 2014: **Cameroon**. Research on diversity of Lepidoptera along an elevational gradient of Mount Cameroon. 14 months, seven expeditions. Served as leader for two expeditions.

Since 2014: **Poland**. Zoological Museum of the Jagiellonian University, regular visits, 3 months.

Since 2014: **Germany**. Bavarian State Collection of Zoology, Munich, regular visits, 2 months.

2018: **Austria**. University of Vienna. Data processing. 2 months.

2017: **Zimbabwe.** Research on diversity of Lepidoptera along a productivity gradient. 2 weeks.

2017: **Czechia.** Research on diversity of pollinators in fragmented wet meadow landscapes. 1 month.

2017: **Madagascar.** Lepidoptera monitoring in Ranomafana National Park. 10 days.

2014: **Hungary**. Lepidoptera monitoring with the Hungarian Natural Heritage Trust in Sopron. 2 weeks.

RESEARCH GRANTS AND FELLOWSHIPS

Principal investigator

2016-2017 – Elephants as a keystone in forming and maintaining of tropical biodiversity – a study of moths in Mt. Cameroon, Grant Agency of the University of South Bohemia (GAJU 030/2016/P).

Collaborating Researcher

2014-2018 – Centre for Tropical Ecology, Czech Science Foundation (PI: prof. Vojtěch Novotný).

Others

2018 - International mobility support, USB, Přf. University of Vienna, 2 months.

2018 - International mobility support, BC CAS: IBERA, Madagascar, workshop, 10 days.

PUBLICATIONS

As of March 2019: 27 citations in Google Scholar

Maicher, V., Sáfián, Sz., Murkwe, M., Przybyłowicz, Ł., Janeček, Š., Fokam, E.B., Pyrcz, T., & Tropek, R. (2018). Flying between raindrops: Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon. *Ecology and Evolution*, **8**, 12761-12772.

Ustjuzhanin, P., Kovtunovich, V., Sáfián, Sz., **Maicher, V.**, & Tropek, R. (2018). A newly discovered biodiversity hotspot of many-plumed moths (Lepidoptera, Alucitidae) in the Mount Cameroon area: first report on species diversity, with description of nine new species. *Zookeys*, **777**, 119-139.

Ferenc, M. *et al.* (including **Maicher, V.**) (2018). Something is missing at the bottom: Importance of coastal rainforests for conservation of trees, birds and butterflies in the Mount Cameroon area. *African Journal of Ecology*, **56**(3), 679-683.

Mertens, J., Tropek, R., Dzekashu, F., **Maicher, V.**, Fokam, E., & Janeček, Š. (2018). Communities of flower visitors of *Uvariopsis dioica* (Annonaceae) in lowland forests of Mt. Cameroon, with notes on its potential pollinators. *African Journal of Ecology*, **56**(1), 146-152.

Maicher, V., Sáfián, Sz., Ishmeal, K.N., Murkwe, M., Kimbeng, T.J., Janeček, Š., & Tropek, R. (2016). Two genera and nineteen species of fruit-feeding erebid moths (Lepidoptera: Erebidae) recorded in Cameroon for the first time. *Entomological News*, **126**, 64-70.

Molet, M., **Maicher, V.**, & Peeters, C. (2014). Bigger helpers in the ant *Cataglyphis bombycina*: increased worker polymorphism or novel soldier caste? *PLoS ONE*, **9**, e84929.

PUBLICATIONS SUBMITTED AND IN PREPARATION

Przybyłowicz, Ł., **Maicher, V.**, Laszlo, G., Sáfián, Sz., & Tropek, R. *Amerila* (Lepidoptera: Erebidae: Arctiinae) of Cameroon: faunistic and taxonomic summary, and first illustration of female genitalia. *Submitted February 2019 (Zootaxa)*.

Maicher, V., Sáfián, Sz., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., Kobe, I.N., Janeček, Š., Mertens, J.E.J., Fokam, E.B., Pyrcz, T., Doležal, J., Altman, J., Hořák, D., Fiedler, K., & Tropek, R. Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *Major revision upon acceptance (Journal of Biogeography)*.

Maicher, V., Delabye, S., Murkwe, M., Kobe, I.N., Doležal, J., Altman, J., Desmist, J., Fokam, E.B., Pyrcz, T., & Tropek, R. Does rainforest biodiversity stand on the shoulders of giants? Effect of disturbances by forest elephants on trees and insects on Mount Cameroon. *In prep.*

Delabye, S., **Maicher, V.**, Sáfián, Sz., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Murkwe, M., Šebek, P., & Tropek, R. Response of butterfly and moth communities to habitat structure in lowland rainforests of Mount Cameroon. *In prep.*

TEACHING AND SUPERVISING OF STUDENTS

2016: (co)supervision of Charles University Bachelor's field course: *Field course in Ecology*.

2015 - present: (co)supervision of two Masters' internships. Both graduated.

ORAL PRESENTATIONS

Maicher, V. *et al.* Seasonal shifts of biodiversity patterns and species' elevation ranges of Lepidoptera along a complete rainforest elevational gradient on Mt. Cameroon. *Zoo dný 2019*. Brno, Czechia.

Maicher, V. *et al.* Seasonality of lepidopteran communities in lowland forests of Mt. Cameroon. *African Lepidoptera Workshop 2018*. Ranomafana, Madagascar.

Maicher, V. *et al.* Seasonality of lepidopteran communities in lowland forests of Mt. Cameroon. *African Lepidoptera Workshop 2017*. Krakow, Poland.

Maicher, V. *et al.* Afrotropical biodiversity of macromoths. *Lepidopterologické kolokvium IX (2014)*. Prague, Czechia.

Maicher, V. *et al.* Biodiversity patterns of Lepidoptera along an altitudinal gradient of Mt. Cameroon. *Invited talk for Master's students of the University of Buea* (2014), Cameroon.

POSTERS

Maicher, V. *et al.* African forest elephant disturbances maintain Lepidoptera biodiversity in the Mount Cameroon National Park, Cameroon. *5th International Global Biodiversity Conservation Conference*. Book of abstract. 25th-26th September 2018, Prague, Czechia.

Maicher, V. *et al.* Patterns of butterflies and moths (Lepidoptera) communities along a complete Afrotropical forest gradient – results from the elevations of the gradient. *53rd annual meeting of the ATBC*. Book of abstract. 19th-23rd June 2016, Montpellier, France.

Maicher, V. *et al.* Biodiversity of Afrotropical butterflies and moths along an altitudinal gradient of Mt. Cameroon - the project introduction. *5th Conference of the Czech Society for Ecology*. Book of abstract. České Budějovice, Czechia.

LANGUAGES

French (native), **English** (TOEFL 2017: C1 oral, B2 writing), **Spanish** (B1), **Czech** (A1), **Croatian** (A1).

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The cover picture of *Euphaedra permixtum* is used with the generous authorisation of Jan Mertens

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