

School of Doctoral Studies in Biological Sciences
University of South Bohemia in České Budějovice
Faculty of Science

**Ecological and biogeographical drivers of
Afrotropical Lepidoptera biodiversity**

Ph.D. Thesis

M.Sc. Sylvain Delabye

Supervisor: RNDr. Robert Tropek, Ph.D.

Department of Ecology, Faculty of Science, Charles University, Prague,
& Institute of Entomology, Biology Centre, Czech Academy of Sciences,
České Budějovice

Consultant: Prof. RNDr. Vojtěch Novotný, CSc.

Institute of Entomology, Biology Centre, Czech Academy of Sciences,
České Budějovice, & Faculty of Science, University of South Bohemia,
České Budějovice

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ANNOTATION

The thesis explores the effects of ecological factors at different spatial and temporal scales on biodiversity patterns of butterflies and moths in Afrotropical rainforests and savannahs. Habitat associations of both fruit-feeding butterfly and moth communities were compared in Afrotropical lowland rainforests of Mount Cameroon, Cameroon. In the same time, the impact of natural disturbances (forest elephants) on diversity and structure of butterfly, moth and tree communities at mid-elevation were examined. Then, the effects of combined seasonal dynamics and elevation on different groups of Lepidoptera were evaluated along the complete elevational gradient on Mount Cameroon. Another aspect of this thesis focuses on the relationships between species richness and abundance of moths with environmental productivity on a continent-wide gradient in Southern African savannah ecosystems. Finally, new country records and new species are reported via the contribution of barcoding and traditional morphological identification to the knowledge of butterfly and moth diversity in the Afrotropics.

DECLARATION

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

České Budějovice, 01/02/2021

Sylvain Delabye

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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The thesis is based on the following publications/manuscripts:

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SD analysed data (90% contribution), interpreted results (80%), and led writing of the manuscript (70%).

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A handwritten signature in blue ink, appearing to be 'RT', enclosed within a large, stylized blue loop.

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A handwritten signature in blue ink, appearing to be 'Decaëns', enclosed within a large, stylized blue loop.

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INTRODUCTION

Biodiversity is generally about the number of species in a given area but can also encompass abundance and other related diversity measures (Purvis & Hector, 2000). Biodiversity is not uniformly distributed throughout the world. First works studying spatial patterns of biodiversity showed that it increases from the poles to the equator, from high elevations to low elevations and from islands to continents (Darwin 1839, 1859; von Humboldt, 1849; Wallace 1876, 1878), those patterns being driven by favourable climatic conditions (Wildenow 1805).

Unravelling and describing species distributions and diversity, and comprehending the mechanisms shaping these patterns is still one of the main goals in the current research (Rosenzweig 1995; Waide et al. 1999; Hillebrand 2004; Rangel et al. 2018). Key questions on diversity patterns remain unanswered (Rangel et al. 2018). While ecological research has largely focused on global biodiversity patterns (Rosenzweig 1995; Hillebrand 2004), geographic and temporal gradients in local species richness have long fascinated ecologists (Dobzhansky 1950; Hutchinson 1959; Pianka 1966; MacArthur 1972; Rosenzweig 1995), establishing the importance of spatial and temporal scales on biodiversity patterns (Lomolino 2001). Ecological processes and factors shaping diversity and assemblage of communities have been studied at smaller scale (Ricklefs & Schluter 1993), leading to the concept of metacommunity (Holoymoak et al. 2005), and at landscape or regional scales (Gutzwiller 2002). Comparison of biodiversity at different spatial scales and amongst different studies raised issues regarding biodiversity measurement (see Magurran & McGill 2011 for a review).

Lepidoptera as a biological model

Inaccessibility, time and money limitations, the complexity of habitats and the great number of species make studying all insect species hardly doable in tropical areas (Gardner et al. 2008). Focusing on a single taxon in tropical ecological studies can overcome this bias.

Lepidoptera (butterflies and moths) is one of the major groups of insects in terms of species richness, just behind Hymenoptera, Diptera and Coleoptera (Gaston 1991; van Nieukerken et al. 2011; Forbes et al. 2018). About 160,000 species of Lepidoptera were described, whose ca. 140,000 belong to moths (Footitt & Adler 2009; Kristensen et al. 2007; van Nieukerken et al. 2011), and extrapolative estimates bring their global richness up to 700,000 species (van Nieukerken et al. 2011). High diverse groups of organisms, such as Lepidoptera, are usually considered as potential environmental indicators as they rapidly respond to changes in climate or vegetation (Kitching et al. 2001; Beck et al. 2002; 2006, Bonebrake et al. 2010), and not all groups are affected by the same environmental change (Kremen 1992; New 2004).

Lepidoptera play key roles in ecosystems by their broad range of interactions with other organisms. Most caterpillars are primary consumers, including a wide spectrum of herbivory on trees, shrubs, forbs, grasses, algae, fungi and lichens, but they also include detritivores and carnivores (Powell et al. 1999). Adults feed on other specific resources, such as flower nectar, plant saps, juices of rotten fruits, decaying materials, or are simply unable to feed (Krenn 2010). Lepidoptera are also an important link within foodwebs as hosts for parasitoids, such as Ichneunoidea, Chalcidoidea, and Tachinidae (Forbes et al. 2018), for pathogens (Hawkins et al. 1997), but also as preys for bats, birds, and many other predators (Kalka et al. 2008; ter Hofstede & Ratcliffe 2016; Sam et al. 2017). They play an essential role as pollinators (MacGregor et al. 2015; Ollerton 2017), and most of the species have specialized host associations

with at least a few closely related plants (Novotny et al. 2002; Forister et al. 2015), leading to close evolutionary interactions with their host plants and their predators (Ehrlich & Raven 1964; Agrawal 2007; Krenn 2010; Mikhail et al. 2018). Thus, variation in the structure and diversity of Lepidoptera assemblage can represent of changes at other trophic levels as well. Furthermore, Lepidoptera communities are known to be indicators of habitat change influencing many other taxa. Their diversities are highly correlated with diversity characteristics of other insects, spiders, but also vertebrates and plants (Barlow et al. 2007; Gardner et al., 2008). Thus, Lepidoptera represent an ideal biological model to study various ecological research, such as biodiversity patterns along ecological and biogeographical gradients.

Another advantage of using Lepidoptera as a model are their well-standardised sampling methods. Although some methods focus on caterpillars (Zandt 1994; Raimondo et al. 2009), only adults were studied in this thesis. Amongst the most used methods focusing on adults are transect walks, quantifying relative abundance of individual species (i.e. Pollard technique, Pollard 1977; Nowicki et al. 2008), and the Mark-Release-Recapture method, allowing to precisely quantify population sizes, or to measure their dispersal abilities (Ehrlich 1965; Nowicki et al. 2008). However, these two methods did not serve the purposes of the studies included in the thesis. Instead, bait trapping, light trapping and light catching were extensively used. Bait trapping is commonly used to attract adult butterflies by various food baits, but it also attracts adult moths which are totally neglected in bait-trapping studies (Freitas et al. 2014). Light trapping and catching simply attract moths to light sources. Since the two methodological approaches attract largely different Lepidoptera communities, using both bait and light methods allow to sample a wider species spectrum of the Lepidoptera communities. Their main advantage lies in their efficiency to sample many individuals in a short period of time, offering a relatively good description of the communities (Beck &

Linsenmair, 2006; Freitas et al. 2014). Bait traps can also be set in different layers of vegetation, i.e. canopy and understory, allowing a comparison of communities from different vegetation strata (DeVries et al. 1997). However, using different kinds of baits or light wavelengths attract different species (Langevelde et al. 2011; Freitas et al. 2014), and those methods can be also influenced by environmental and meteorological conditions (moon phases, temperature, precipitation; see Yela and Holyoak 1997 for a review). Nonetheless, protocols involving those methods are easy to standardise which result in strong interpretable datasets for Lepidoptera biodiversity pattern research.

Due to their popularity among naturalists, their relatively well-stabilized taxonomy and their attractive nature, moths and butterflies appear to be an appropriate biological model in order to study diversity patterns of tropical insects.

Patterns of tropical Lepidoptera communities along elevation gradients

Elevation gradients are particularly interesting to study biodiversity patterns, as abiotic conditions, such as temperature, precipitation, moisture rate and soil, vary quickly with elevation (Marrs et al. 1998; Wolf 1993; Begon et al. 2006). Although biodiversity used to be expected to linearly decrease along elevation, numerous recent studies revealed other elevational patterns of biodiversity as well (Rahbek 1995, 2005; McCain & Grytnes 2010).

Regarding tropical Lepidoptera, existing studies originated mainly from the Neotropics (Pyrz & Wojtusiak 2002; Brehm & Fiedler 2003; Brehm et al. 2003, 2005, 2007; Hilt 2005; Hilt & Fiedler 2005; Hilt et al. 2007; Beck & Chey 2008; Fiedler et al. 2008; Pyrcz et al. 2009; Beck et al. 2011; Ignatov et al. 2011; Despland et al. 2012) and southeastern Asia

and Australia (Ashton et al. 2011, 2016a, 2016b; Sam 2011; Bhardwaj et al. 2012; Odell et al. 2016), while Afrotropical mountains were less studied (Axmacher et al. 2004, 2009; Axmacher & Fiedler 2008; Peters et al. 2016). These studies revealed that Lepidoptera species richness patterns along elevation gradients follow four main patterns: a low plateau, a low plateau with a mid-peak, a decrease of species richness with elevation, and a peak of species richness at mid-elevations representing the large majority of the studies (McCain & Grytnes 2010, Beck et al. 2017). Although climatic, biotic, historic, and spatial factors were supposed to explain these patterns (Grytnes & McCain 2007), no single driver can fully explain them (Beck et al. 2017). The decrease of productivity, plant diversity, and available area (species-area relationship), with increase of extreme conditions probably cause the decrease of Lepidoptera species richness along elevation (Lawton et al. 1987). The mid-altitudinal peak could also be caused by the mid-domain effect, a geometric approach which implies an increasing overlap of species ranges at mid-elevation (Colwell et al. 2005, 2016). However, studies on moths did not reveal the effects of the geometric model on the species richness patterns (Brehm et al. 2007; Beck et al. 2017). Then the mid-altitudinal peak could be simply explained by the favourable conditions at middle elevations (averaged temperature), conditions modulated by the mid-domain effect (Colwell et al, 2016).

Temporal dynamics of tropical Lepidoptera communities

The diversity and the short generation time make insects an ideal group for describing seasonality roles on tropical diversity (Janzen 1983). Seasonal aspects are important factors in structuring of insect communities and life history strategies (Wolda 1988; Kishimoto-Yamada & Itioka, 2015). Although seasonality is more pronounced in temperate regions, leading to

a strong phenological synchrony towards the optimal climatic conditions, its role is crucial for many insect species (Wolda 1980, 1988).

Regarding Lepidoptera, in tropical rainforests, annual or biannual peaks of abundance and richness of fruit-feeding butterflies and moths were detected during the drier seasons recording a time delay of three months following the beginning of rainy season(s) (Intachat et al. 2001; DeVries et al., 2012; Grøtan et al. 2012, 2014; Valtonen et al. 2013; Maicher et al. 2018). Other short-term studies also found similar results (Hamer et al. 2005; Aduse-Poku et al. 2012), while Molleman et al. (2006) did not reveal any seasonal pattern during their relatively longer-term monitoring (3 years) in the Afrotropics. Contrastingly, richer and more abundant butterfly communities were detected during wet seasons in Neotropical rainforests, where the seasonality is usually less pronounced (DeVries et al. 1997; DeVries & Walla, 2001; Checa et al. 2014). More humid conditions are associated with resprouting (Hill et al. 2003), when host plants produce new and young leaves and offer ideal sites for oviposition and herbivory, increasing the survival rate of eggs and caterpillars during the wet season (Tauber et al. 1986; DeVries 1997; Valtonen et al. 2013). Moreover, higher temperature and solar radiation rate during the drier seasons extend butterfly activity, contributing to the highest abundance and richness of adults (Ribeiro et al. 2010; Grøtan et al. 2014).

Assessing the processes impacting elevational diversity patterns remain important. With the aim of predicting the consequences of climate change on the diversity patterns, some authors have studied its impact on species elevation ranges (Colwell et al. 2008; Laurance et al. 2011). Upward shifts of Lepidoptera community ranges have been recorded from tropical mountains (Colwell et al. 2009; Chen et al. 2009, 2011a, 2011b). However, the studies have focused on those patterns within a single season or have totally neglected seasonality (Ashton et al. 2016b). As discussed

above, Lepidoptera communities are seasonal. Thus, there is a need to consider their seasonal character in such studies.

Small-scale spatial mechanisms structuring tropical Lepidoptera communities

While environmental productivity and climate are more responsible for structure of communities at large scales, other factors, such as microhabitat characteristics and biotic interactions, are more important at local scale (Cottenie 2005; Benton 2009). Moreover, changes in plant communities often lead to modifications of the vegetation diversity and structure, and therefore in the heterogeneity of the available microhabitats and niches (Lawton 1983; Tews et al. 2004).

Regarding tropical Lepidoptera, their communities are strongly dependant on diversity of plants (Novotný et al. 2002), and environmental changes may favor some host plants, and thus some species of Lepidoptera (Beck et al. 2002; Novotný et al. 2003). Vegetation structure is also linked to Lepidoptera communities. The stratification of vegetation directly causes discret stratification of Lepidoptera communities (DeVries et al. 1997; Aduse-Poku et al. 2012; Roche et al. 2015; Ashton et al. 2016a), and not all groups of Lepidoptera follow a unique pattern of diversity (Fermon et al. 2003, 2005). Such modification of the vegetation characteristics alters the climatic conditions of microhabitats, and generally, light, temperature and humidity are crucial factors structuring Lepidoptera communities. (Spitzer et al. 1997; Beck & Chey 2008; Ribeiro and Freitas 2012).

Since Lepidoptera are strongly sensitive to habitat characteristics, they have been used as relevant indicators of habitat quality, responding to successional processes (Veddeler et al. 2005; Hilt & Fiedler 2006; Nyafwono et al. 2015; Valtonen et al. 2017), to natural disturbances, such

as fire (de Andrade et al. 2017) and tree-fall gaps (Pardouret 2013), and to human disturbances, such as selective logging and farming leading to the habitat fragmentation (Horner-Devine et al. 2003; Bobo et al. 2006; Brito et al. 2014; Filgueiras et al. 2016).

Afrotropical Lepidoptera: poorly understood diversity rich in threatened ecosystems

Tropical ecosystems host tremendous Lepidoptera species richness. Since this hyperdiverse group is a key for fully functional ecosystem, our knowledge of its taxonomy and distribution is an unavoidable condition to study their ecological roles and their diversity patterns. Linnean and Wallacean shortfalls (Brown & Lomolino 1998, Lomolino 2004) are difficult to address in poorly tropical regions such as the Afrotropics (Whittaker et al. 2005). Unfortunately, the knowledge on the Afrotropical Lepidoptera remains unsatisfactory.

The three main areas studied in this thesis, besides involving interesting ecological process, are particularly relevant to show the lack of knowledge on distribution and taxonomy of Lepidoptera. Mount Cameroon and the Gulf of Guinea Highlands belong to the eastern limit of the Guinean Forests of West Africa. This high mountain range stands on the border between the Guinean and the Congolian biogeographic regions and is known to be a biodiversity hotspot with a high endemism rate (Myers et al. 2000; Mittermeier et al. 2011). Unfortunately, it is also critically threatened by high human population densities and human disturbances (e.g. agriculture, logging, poaching) resulting in shrinking and fragmented forests (Oates et al. 2014; Sloan et al. 2014). The diversity of butterflies from Cameroon is relatively well known, a few butterfly species even already known being endemic to Mount Cameroon (Larsen 2005; Sáfián & Tropek 2016; Sáfián et al. 2019). However, our knowledge

on moth diversity is comparatively low (De Prins & De Prins 2021) The numerous new country records (Tropék et al. 2013; Tropék et al. 2015; Maicher et al. 2016; Przybyłowicz et al. 2019) and new described species of moths have been reported the last decade (Yakovlev & Sáfián 2016; Ustjuzhanin et al. 2018), a higher regional species richness of moths is expected. The establishment of the Mount Cameroon National Park in 2009 has substantially improved the conservation and protection of this incredible biodiversity hotspot.

Moth diversity of forests and savannahs of Gabon, belonging to the Congo Basin, has also been targeted by this thesis. The Congo Basin is considered as a Major Tropical Wilderness, which represent important reserves of biodiversity not being dramatically threatened by human activities (Mittermeier et al. 1998; Myers 2000). The Central African forest is the second largest tropical forest area after the Amazon. It is still relatively well-preserved, and its recent shrinkage emphasises the need of conservation and management of this aeras (de Wasseige et al. 2014). While butterfly diversity is also relatively well-known in Gabon (Vande Weghe 2010), there is a general lack of knowledge on the regional diversity of moths.

Finally, Southern Africa hosts a great diversity of habitats, from deserts and grasslands to woodland savannahs. Their dynamic and unstable ecosystems are maintained by regular disturbances, and they generally host a high biodiversity (Murphy et al. 2016). If the pressure from human activities has been historically relatively low in many tropical grassy biomes, this trend is likely to be reversed the next decades (Roxburgh et al. 2010; Searchinger et al. 2015), threatening its unique biodiversity. Paradoxically, because of the high interest of entomologists in South Africa, Southern Africa is probably one of the most studied areas of the Afrotropics. Nevertheless, knowledge on the moth diversity remains unsatisfactory.

Aims of the thesis

In this thesis, the Lepidoptera biodiversity patterns were investigated at different spatial and temporal scales in different Afrotropical regions in order to answer distinct ecological questions.

Comprehension of small-scale ecological mechanisms shaping local communities is important for building up the conservation strategies. If the association of fruit-feeding butterfly communities with forest habitat have been relatively well studied in tropical regions, moth communities were largely neglected. To partly fill this gap, we compared forest habitat associations of both fruit-feeding butterfly and moth communities in the Afrotropical lowland rainforests of Mount Cameroon, Cameroon. The effects of forest openness, forest structure, and plant diversity on both communities have been described for both canopy and understory communities in **Chapter I**. Furthermore, Mount Cameroon is known to hold a small population of megaherbivores (i.e. forest elephants) on its southwestern slopes. Elephants are considered as key ecological engineer species. To evaluate the impact of natural disturbances on diversity and structure of butterfly, moth, and tree communities, we examined these communities at mid-elevation (two altitudes) in elephant disturbed and elephant excluded zones in **Chapter II**.

Besides, biodiversity patterns of Lepidoptera along elevational gradients have been relatively well-studied, although hardly any data originated from the Afrotropical forests. However, the seasonal dynamics of these patterns were not described or even considered in any previous studies. While there is a current increasing need to inquire the effects of climate change on biodiversity, it is however necessary to first understand the short-termed temporal effects related to seasonal cycles. Consequently, in **Chapter III**, we aimed to reveal the effects of seasonal dynamics of different groups of Lepidoptera along the complete elevational gradient of Mount Cameroon.

Furthermore, unravelling the global biodiversity patterns belongs among one of the main goals of the current ecology. Environmental productivity, commonly defined as the amount of biomass produced by primary producers in a given period and area, is considered as one of the main factors affecting local biodiversity. However, the relationship between environmental productivity and species richness of most organisms, including Lepidoptera, is not so simple. Moreover, it is not clear whether this relationship is scale-dependent. In **Chapter IV**, we focused on the relationships between species richness and abundance of moths with environmental productivity on a continent-wide gradient in the Southern African savannah ecosystems.

Finally, the above-mentioned ecological studies were performed in the highly understudied areas where lepidopteran fauna is largely unknown. Our ecological projects brought an interesting and abundant material, and such intensive inventories in poorly sampled areas brought a unnegligible number of unknown species together with new information on species' distribution. Therefore, we examined this exceptional diversity of Lepidoptera from the Afrotropical rainforests and savannahs and showed how barcoding (**Chapter V**) and traditional morphological identification (**Chapters VI, VII and VIII**) could contribute to the knowledge of Lepidoptera diversity in the Afrotropical savannahs and rainforests while reporting new country records. Moreover, in **Chapter VIII**, we emphasized the status of Cameroon as a biodiversity hotspot by describing several new species of many-plumed moths (Alucitidae).

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CHAPTER I

Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon









Delabye, S., Maicher, V., Sáfián, Sz., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Murkwe, M., Šebek, P., & Tropek, R.

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Quantification of light transmitted through the forest canopy on Mount Cameroon with fisheye lens photographs. © S. Delabye

Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon

Sylvain Delabye^{1,2}  | Vincent Maicher^{1,2}  | Szabolcs Sáfán^{2,3} | Jiří Doležal^{2,4}  |
 Jan Altman⁴  | Štěpán Janeček⁵  | Ishmeal N. Kobe⁵  | Mercy Murkwe^{5,6} |
 Pavel Šebek¹  | Robert Tropek^{1,5} 

¹Biology Centre, Institute of Entomology, Czech Academy of Science, Ceske Budejovice, Czechia

²Faculty of Science, University of South Bohemia, Ceske Budejovice, Czechia

³Faculty of Forestry, Institute of Silviculture and Forest Protection, University of West Hungary, Sopron, Hungary

⁴Institute of Botany, Czech Academy of Science, Průhonice, Czechia

⁵Department of Ecology, Faculty of Science, Charles University, Prague, Czechia

⁶Department of Zoology and Animal Physiology, Faculty of Science, University of Buea, Buea, Cameroon

Correspondence

Sylvain Delabye and Robert Tropek, Biology Centre, Czech Academy of Science, Institute of Entomology, Branišovská 31, CZ-37005 Ceske Budejovice, Czechia.
 Emails: sylvain.delabye@gmail.com; robert.tropek@gmail.com

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Abstract

Mechanisms structuring tropical communities are still under-studied, especially in Afrotropical rainforests. Although insect herbivores are considered to depend on plant diversity, we hypothesized that vegetation structure, together with other microhabitat characteristics, can be more important for some insects. Here, we compared habitat associations of fruit-feeding butterflies and moths, two ecologically different groups of Lepidoptera, in three rainforest localities in foothills of Mount Cameroon, West/Central Africa. Based on a comprehensive dataset of 16,040 specimens of 398 species systematically collected by 240 traps at 48 plots (altogether 9.68 ha), we analyzed how plant community composition, habitat openness, and forest structure affect communities of butterflies and moths. We expected different habitat descriptors to predict communities of the two insect groups. Habitats of tropical fruit-feeding moth communities have never been studied before.

In both analyses of species richness and community structure, butterfly communities depended mostly on forest openness. Moth species richness depended on plant diversity and forest openness, whilst the latter substantially influenced their community composition. Additionally, we revealed differences in habitat associations between understory and canopy communities of both groups. Whilst species richness of understory communities was not influenced by any habitat characteristics, it generally followed the general patterns in canopies. By contrast, composition of understory communities followed the general patterns, whilst effects of habitat characteristics on canopy communities were minor for butterflies and none for moths. The differences between such closely related groups of herbivorous insects warn against generalization based on single-taxon studies and highlight the need of community-wide research of tropical rainforests.

Abstract in French is available with online material

KEYWORDS

Afrotropics, community composition, forest structure, insect herbivores, Lepidoptera, plant diversity, tropical ecosystems, vegetation openness

1 | INTRODUCTION

1.1 | Exploring factors responsible for structure of communities belongs among the essential aims of community ecology

The importance of such factors differs 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 large-scale biodiversity patterns, which has resulted in the discovery of some general relationships consistent for different taxa (Gaston, 2000; Hillebrand & Thomas, 2004; Tittensor et al., 2010). Nevertheless, knowledge of the small-scale mechanisms is important for our understanding of the dynamics and structure of local communities (Cottenie, 2005). This is particularly true for the development of local biodiversity conservation strategies. Since the local mechanisms often vary among studied taxa and areas (Siefert et al., 2012; Stein et al., 2014; Tews et al., 2004; Webb & Peart, 1999), more studies are needed, especially from under-studied regions such as the Afrotropics.

Insect herbivores are among the most abundant and species-rich ecological guilds in tropical rainforests, with both top-down and bottom-up effects on the entire ecosystem (Dyer & Letourneau, 1999; Novotný et al., 2010). Their diversity strongly correlates with plant diversity (Basset et al., 2012; Novotný & Basset, 2005; Novotný et al., 2002). 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, 2006). Simultaneously, such a diverse plant community also offers 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 roles of individual components of vegetation structure for communities of tropical herbivorous insects are only scarcely studied.

In tropical rainforests, Lepidoptera communities are highly influenced by species richness and composition of local plant communities (e.g., Novotný, Miller, et al., 2002). The positive correlation between plant and Lepidoptera species richness is commonly described (Brehm et al., 2007; Nyafwono et al., 2014a; Nyafwono et al., 2015; but see opposite results by Axmacher et al., 2004), whilst vegetation structure has also been linked to their community structure (Axmacher et al., 2009). For instance, the stratification of vegetation directly causes discrete vertical stratification of Lepidoptera communities (Aduse-Poku et al., 2012; DeVries & Walla, 2001; Fermon et al., 2005). Simultaneously, canopy openness, specifically an extent of canopy gaps, is another important factor increasing lepidopteran diversity (Hill et al., 2001; Hilt & Fiedler, 2005; Nyafwono et al., 2015; Spitzer et al., 1997), although some species prefer shaded forests. Such vegetation-related characteristics alter for the microclimatic conditions of habitats, especially availability

of light, and varying temperature and humidity, all known to crucially influence the composition of tropical Lepidoptera assemblages (Beck & Chey, 2008; Koh & Sodhi, 2004).

Moths (in this manuscript, we use this term for Heterocera, i.e., macromoths) and butterflies (Rhopalocera) are the best known and species-rich groups of Lepidoptera. Among numerous minor differences, they differ in the day activity of their adults. Despite exceptions in both groups, overwhelming majority of butterfly species are day active, whilst moths represent mostly nocturnal or crepuscular adults. Whilst butterflies often need sunny spots in open forests for behavioral thermoregulation (basking) and other activities (e.g., Dennis, 2010; Spitzer et al., 1997), moths can be expected to be relatively less dependent on the openness of the forest because the adult microhabitats should be less influenced by solar radiation. Therefore, even though their close relatedness and generally similar morphology, these two groups of presumably herbivorous insects can be expected to show differences in use of adult habitats.

However, the relative importance of such habitat characteristics in the structuring of butterfly and moth communities is not fully understood in most tropical rainforest ecosystems. Despite the indisputable 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 (Houlihan et al., 2013; Koh & Sodhi, 2004; Spitzer et al., 1997; Tropek & Konvicka, 2010; Vlašánek et al., 2013) and moths (Axmacher et al., 2009; Beck & Chey, 2008; Brehm et al., 2007; Brehm et al., 2003; Fermon et al., 2005; Hilt & Fiedler, 2005; Rabl et al., 2019). On the contrary, plant community composition predicted butterfly community composition more efficiently than vegetation structure and forest openness in an Afrotropical rainforest in Uganda, although without any 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 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). On the other hand, Axmacher et al., (2009) revealed that moth communities on Mt. Kilimanjaro depended more on the diversity of several most common plant families than on the overall plant diversity. In this study, vegetation structure was shown to be important for moth communities as well, although with substantially less effect than the above-mentioned common plant families. Summing up, whilst vegetation structure was not found to substantially impact tropical moth community composition (with the exception of Mt. Kilimanjaro, Axmacher et al., 2009), it was, together with forest openness, an efficient predictor of the community composition of tropical butterflies (Nyafwono et al., 2014b, 2015; Spitzer et al., 1997).

In this study, we focus on habitat associations of fruit-feeding butterfly and moth communities, a species-rich guild of tropical insects, in rainforests of the largely under-studied Afrotropics. Owing to straightforward and well-standardized sampling methods, butterflies and moths are frequently used as bioindicators in ecological studies (Bonebrake et al., 2010; Braga & Diniz, 2018;

Holloway, 1984). Our intensive sampling in three forest localities in the foothills of Mount Cameroon, together with detailed data on forest composition and structure, allowed a robust analysis of habitat determinants of species richness and community composition of the studied insect groups. Generally, we focused on the relative importance of three main habitat components (plant diversity, forest structure, and forest openness) for both lepidopteran groups. We predicted that according to their different adult activities, butterfly communities would be more influenced by forest openness, whereas moth communities would be better predicted by plant diversity. To our knowledge, we present the first comprehensive study of habitat associations of fruit-feeding moths in any tropical rainforest. Because Lepidoptera communities are known to be vertically stratified, we focused on differences in habitat associations between canopy and understory communities, predicting the forest openness would have less importance for canopy communities because of generally more solar radiation in the higher vegetation strata.

2 | METHODS

2.1 | Study area

Our study was conducted on the southwestern slope of Mount Cameroon (4.1002° N, 9.0503° E), Southwest Region, Cameroon. It is the highest mountain of West/Central Africa (4,095 m asl) and the only active volcano within the Cameroon Volcanic Line. The region has a humid tropical climate with a distinctive dry (late December–February) and wet (June–September) seasons, separated by two transitions (March–May and October–November). The mean annual temperature is $23.3 \pm 0.7^\circ\text{C}$ at 300 m asl (decreasing by ca 0.5°C per 100 altitudinal meters; Fraser et al., 1998) and the mean annual rainfall often surpasses 12,000 mm in the foothills (Maicher et al., 2020), making the southwestern slope of Mount Cameroon one of the rainiest places on the Earth. Its unique climate, relative isolation, and heterogeneity of environments along its elevational gradient make it a biodiversity hotspot for many organisms, including Lepidoptera and plants (Cable & Cheek, 1998; Delabye, Maicher, Sáfián, Doležal, et al., 2020a; Sáfián & Tropek, 2016; Ustjuzhanin et al., 2018).

Our study was carried out in three localities with different tropical forest vegetation, all inside the Mount Cameroon National Park. These study sites were the same as those included in Maicher et al. (2018): the Bamboo Camp (N 04.08990°, E 09.05174°; 350 m asl), a mosaic of primary and secondary lowland forest; the Drink Gari Camp (N 04.10221°, E 09.06304°; 650 m asl), primary dense lowland forest; and the PlanteCam Camp (N 04.11750°, E 09.07094°; 1,100 m asl), an upland forest locally disturbed by elephants which reduces the density of trees and forms clearings dominated by herbs, grasses and ferns. 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. Any non-forest habitats (including large gaps) were avoided during our sampling as we targeted forest Lepidoptera only.

2.2 | Lepidoptera sampling

The sampling of fruit-feeding butterflies and moths (i.e., species with adults feeding on fruits) represented a total of 7,200 trap-days. 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 of 48 sampling plots (see above), five traps were installed (i.e., 80 traps per locality, representing 240 traps altogether); four were exposed in the understory as close to the ground as possible, and one was set in the canopy at $20 (\pm 5)$ m height. Our sampling was repeated during three different seasons: transitions from wet to dry (November/December 2014), and from dry to wet seasons (April 2015), and a high-dry season (January/February 2016). During each season, the traps were exposed for ten consecutive days at the same position within the sampling plots. Every sampling 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. All traps were rebaited every third or fourth day according to weather conditions, the bait was also checked daily and refilled if necessary. For more details on the sampling see also Maicher et al. (2018). Specimens were identified using mainly Larsen (2005) and Vande Weghe (2010) for butterflies, and Seitz (1930) and literature listed in De Prins and De Prins (2020) for moths. Additionally, numerous other resources, together with reference material from numerous collections were used for identification, depending on particular groups. Voucher specimens were deposited in the Nature Education Centre of Jagiellonian University, Kraków, Poland.

2.3 | Habitat characteristics

All 48 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 listed and described in Table 1, most of them were taken from Hořák et al. (2019).

In each plot, for both dead and live trees > 10 cm DBH, height was estimated by an ultrasound instrument system (HAGLOF Vertex IV-GS) and DBH was measured; these values were used for the quantification of 14 characteristics of *forest structure* (Table 1). 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

TABLE 1 Measured descriptors of habitats in three rainforests on Mount Cameroon

| 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 |
| Live tree basal area | LTBA | 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 |
| Dead tree basal area | DTBA | Cumulative area of all dead tree trunks and stems > 10 cm DBH; calculated from measured DBH (m ²) | 2.72–9.34 | 5.19 | 1.49 |
| Stand wood volume | SWV | Calculated from tree height and basal area of all trees (m ³) | 33.12–301.17 | 118.90 | 52.40 |
| Live tree wood volume* | LTWV | Calculated from tree height and basal area of all living trees (m ³) | 0–7.14 | 0.94 | 1.77 |
| Dead tree wood volume* | DTWV | Calculated from tree height and basal area of dead trees (m ³) | 32.54–301.17 | 118.17 | 52.11 |
| Mean Diameter at Breast Height (DBH)* | MnDBH | DBH measured at 1.3 m above ground (cm) | 58.7–200 | 106.26 | 34.01 |
| Maximum Diameter at Breast Height | MxDBH | Maximum DBH from all trees at the plot (cm) | 19.99–34.41 | 25.95 | 3.31 |
| Mean tree height | MnTH | Calculated from estimated heights of individual trees (m) | 17–48 | 33.08 | 6.21 |
| Maximum tree height* | MxTH | Estimated height of the highest tree at plot (m) | 8.61–18.89 | 13.92 | 2.48 |
| Mean Stem Slenderness Index | SSI | Ratio of estimated tree height to measured DBH for each tree, averaged per plot | 0.43–0.90 | 0.64 | 0.11 |
| Forest openness | | | | | |
| Maximum canopy openness | MxCO | Maximum percentage of open sky from beneath a forest canopy determined from hemispherical photographs (%) | 2.24–12.88 | 4.87 | 2.53 |
| Mean canopy openness | MnCO | Mean percentage of open sky from beneath a forest canopy determined from hemispherical photographs (%) | 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 by the same observer (%) | 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 in the soil and not classified as climbers; visually estimated over the entire plot area by the same observer (%) | 10–60 | 40.31 | 14.71 |
| Herb and shrub layer cover | E1 + E2 | Combined cover of herb and shrub layers as described above (%) | 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 direct solar radiation transmitted by the canopy | MxTDr | Maximum amount of direct solar radiation transmitted by the canopy (%) | 3.70–21.43 | 9.16 | 4.46 |

(Continues)

TABLE 1 (Continued)

| Variable | Code | Definition/way of evaluation | Range | Average | SD |
|---|-------|--|------------|---------|-------|
| Mean transmitted direct solar radiation | MnTDr | Mean amount of direct solar radiation transmitted by the canopy (%) | 4.46–41.49 | 14.55 | 8.37 |
| Maximum amount of transmitted diffuse solar radiation | MxTDf | Maximum amount of diffuse solar radiation transmitted by the canopy (%) | 3.57–17.70 | 7.74 | 3.64 |
| Mean transmitted diffuse solar radiation | 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 DCA1 score | TDCA1 | Case scores derived from the tree count produced by a detrended correspondence analysis–Axis 1 | 0.09–1.99 | 1.02 | 0.50 |
| Tree DCA2 score | TDCA2 | ditto–Axis 2 | 0–2.47 | 0.84 | 0.53 |
| Tree DCA3 score | TDCA3 | ditto–Axis 3 | 0–2.49 | 1.66 | 0.38 |
| Tree DCA4 score | TDCA4 | ditto–Axis 4 | 0.83–1.32 | 1.12 | 0.11 |
| Herb DCA1 score | HDCA1 | Case scores derived from the herb count produced by a detrended correspondence analysis–Axis 1 | 0.01–1.94 | 0.69 | 0.39 |
| Herb DCA2 score | HDCA2 | ditto–Axis 2 | 0–3.97 | 1.47 | 1.38 |
| Herb DCA3 score | HDCA3 | ditto–Axis 3 | 0.68–2.75 | 1.45 | 0.47 |
| Herb DCA4 score | HDCA4 | ditto–Axis 4 | 0.61–2.34 | 1.40 | 0.28 |

Abbreviation: SD, standard deviation.

*Indicates variables selected via multivariate Pearson's correlations (Pearson $\rho \leq |0.7|$) and used for the GLMM analyses.

of forest openness were quantified (Table 1). Finally, all trees and herbs were identified to (morpho)species (mostly following Cheek et al., 1996, and Cable & Cheek, 1998; voucher specimens were placed in the Herbarium of Faculty of Science, Palacky University in Olomouc, Czechia), and their species richness, together with ordination scores of tree and herb (incl. plant saplings if in herb shrub layers and identifiable) communities derived from detrended correspondence analyses (DCA, to avoid arch-effect trends in the data, with estimated covers of individual species), composed 10 characteristics of plant diversity (Table 1).

2.4 | Data analyses

In all analyses, butterfly and moth communities were analyzed separately. All analyses were firstly run for the complete dataset, followed by separate analyses of canopy and understory communities.

The focal groups' diversities at individual sampling localities were characterized by observed species richness and bias-corrected Chao1 species richness estimator. Sampling coverage was used as a proxy of sampling completeness (*iNEXT* package, Hsieh et al., 2016). The observed species richness was mostly included within the Chao1 95% confidence intervals (Table 2, Figure S1). Only the observed species

richness (hereinafter referred as species richness) was used for the analyses and interpretations of diversity relationships, as strongly recommended in datasets with high sampling coverages, as in our case (e.g., Beck & Schwanghart, 2010; Brose & Martinez, 2004). For all analyses, catches from all traps per plot (i.e., 4 from understory and/or 1 from canopy) were pooled across all 30 sampling days (i.e., $n = 48$ in all analyses) to avoid non-focal variation and potential noise.

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 particular 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 and Table S1) were included into the models. From the highly inter-correlated variables, we have always selected those which made the most sense for the potential ecological interpretation of relationship with lepidopteran communities, whilst the complete inter-correlation matrix (Table S1) was considered in the results interpretation. The ordination scores (DCA) of tree and herb communities were not included in the GLMMs to avoid a lack of any biological explanation

TABLE 2 Diversity of fruit-feeding butterflies and moths captured in three rainforests on Mount Cameroon

| Locality | Group | Fruit-feeding butterflies | | | | | Fruit-feeding moths | | |
|-----------------|-------|---------------------------|------------------------|------|----------|------|---------------------|---------------------|-----------|
| | | Nymphalidae | | | | | Crambidae | | Erebidae |
| | | Ab/SR | Chao1 (\pm SE) | SC | α | H' | Ab/SR | Chao1 (\pm SE) | Ab/SR |
| Bamboo Camp | C | 1,130/48 | 51.20 (\pm 3.06) | 0.99 | 10.17 | 2.14 | 1/1 | 1 (\pm 0.31) | 222/42 |
| | US | 3,226/78 | 82.05 (\pm 3.60) | 1 | 14.40 | 3.60 | 12/5 | 10.50 (\pm 6.45) | 1,503/74 |
| | All | 4,356/93 | 98.06 (\pm 4.43) | 1 | 16.70 | 3.64 | 13/6 | 15.23 (\pm 9.32) | 1,725/92 |
| Drink Gari Camp | C | 1,962/49 | 85.09 (\pm 25.85) | 0.98 | 10.91 | 2.57 | 2/2 | 2.5 (\pm 1.11) | 267/57 |
| | US | 2,478/84 | 100.89 (\pm 12.72) | 0.99 | 16.80 | 3.53 | 8/4 | 4.88 (\pm 1.92) | 1,265/99 |
| | All | 3,440/96 | 131.99 (\pm 33.40) | 1 | 18.32 | 3.62 | 10/6 | 11.40 (\pm 6.37) | 1,532/125 |
| PlanteCam Camp | C | 441/34 | 131.78 (\pm 111.31) | 0.97 | 8.06 | 2.68 | 1/1 | 1 (\pm 0.31) | 195/56 |
| | US | 2,164/57 | 67.56 (\pm 7.67) | 0.99 | 10.73 | 2.11 | 17/5 | 5.94 (\pm 1.78) | 1,539/91 |
| | All | 2,605/69 | 83.44 (\pm 9.19) | 0.99 | 13.15 | 2.44 | 18/6 | 8.13 (\pm 3.23) | 1,734/109 |

Note: Ab: abundance; SR: observed species richness; SC: sampling coverage; α : Fisher's alpha; H': Shannon index. C: canopy communities, US: understory communities, All: communities from both strata.

of correlation between the analyzed species richness and the plant diversity gradient.

Elevation (i.e., sampling locality) was treated as a random effect factor to filter out their individual differences (e.g., their differing elevation, Maicher et al., 2020), whilst all the tested habitat characteristics were treated as fixed effects to test their effects on species richness of the focal groups. All possible combinations of the pre-selected 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., elevation as the only explanatory variable treated as random factor). The model comparisons were based on the corrected second-order Akaike information criterion (AICc; Anderson & Burnham, 2002; Sugiura, 1978). The most plausible models (Δ AICc < 2) were considered as relevant and are listed in Table 3 (for more details on their statistics, see also Table S2). Simultaneously, the Akaike information criteria weight (w_i) 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., 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 (ter Braak & Šmilauer, 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 the function "downweighting of rare species" was applied (ter Braak & Šmilauer, 2012). Elevation (i.e., sampling locality) was treated as a covariate in order to filter out potential variability related to individual localities (Maicher et al., 2020). Within each group of habitat characteristics, the significant variables were selected by an automatic step-by-step forward selection procedure (Šmilauer & Lepš, 2014), 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 R_a^2 as the measure of variability explained by the particular group of characteristics (conditional effect) or their combinations (marginal effect; Peres-Neto et al., 2006).

3 | RESULTS

After removing butterflies not known to have fruit-feeding adults (24 specimens of Hesperidae) and moths with proboscis-less adults (1 specimen of Lymantriinae), our dataset comprised 10,401 and 5,639 specimens belonging to 111 and 287 (morpho)species of butterflies and moths, respectively. 57 and 97 species of butterflies and moths, respectively, were captured in both strata (Table 2). All the butterflies belonged to the Nymphalidae family, whilst all the moths were from three superfamilies: Geometroidea, Noctuoidea, and Pyraloidea superfamilies (Table 2). Altogether, 3,098 trees > 10 cm DBH of 136 tree species were measured within the 48 sampling plots (Table 1).

3.1 | 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 3). Simultaneously, the null models were almost always (except species richness of all moths and canopy moths, see below) the most plausible ones, or had higher or comparable conditional probability to be the most plausible model according to their w_i . In such cases, we considered such patterns as not relevant and avoided interpretation of the particular relationships of species richness to individual habitat characteristics (these relationships are still listed in Table S2).

| Chao1 (\pm SE) | Geometridae | | Noctuidae | | All Families | | SC | α | H' |
|-----------------------|-------------|----------------------|-----------|----------------------|--------------|-----------------------|------|----------|------|
| | Ab/SR | Chao1 (\pm SE) | Ab/SR | Chao1 (\pm SE) | Ab/SR | Chao1 (\pm SE) | | | |
| 85.90 (\pm 28.22) | 3/3 | 5 (\pm 2.92) | 23/14 | 37.91 (\pm 23.21) | 249/60 | 147.15 (\pm 45.17) | 0.86 | 25.10 | 3.15 |
| 93.52 (\pm 10.21) | 10/9 | 37.80 (\pm 35.68) | 3/3 | 5.00 (\pm 2.92) | 1,528/91 | 138.03 (\pm 19.96) | 0.97 | 21.21 | 2.97 |
| 120.43 (\pm 13.20) | 13/11 | 52.54 (\pm 27.75) | 26/14 | 21.69 (\pm 7.21) | 1,777/123 | 191.71 (\pm 25.03) | 0.97 | 30.02 | 3.25 |
| 94.42 (\pm 20.21) | 30/7 | 16.67 (\pm 9.78) | 76/20 | 22.96 (\pm 3.20) | 375/86 | 136.57 (\pm 21.98) | 0.9 | 34.92 | 3.74 |
| 137.50 (\pm 17.66) | 41/18 | 37.68 (\pm 17.01) | 8/6 | 14.75 (\pm 8.84) | 1,322/127 | 202.05 (\pm 28.66) | 0.96 | 34.62 | 3.51 |
| 179.35 (\pm 22.42) | 71/21 | 44.66 (\pm 19.92) | 84/21 | 27.05 (\pm 6.01) | 1,697/173 | 263.70 (\pm 30.53) | 0.96 | 48.20 | 3.91 |
| 135.67 (\pm 44.23) | 64/20 | 47.73 (\pm 22.82) | 134/22 | 34.41 (\pm 10.61) | 398/100 | 216.05 (\pm 46.17) | 0.86 | 42.93 | 3.86 |
| 119.02 (\pm 13.73) | 172/34 | 66.48 (\pm 26.18) | 38/15 | 28.15 (\pm 12.15) | 1,767/146 | 211.72 (\pm 23.83) | 0.97 | 37.75 | 3.43 |
| 149.48 (\pm 18.03) | 236/38 | 62.40 (\pm 18.53) | 172/25 | 34.94 (\pm 8.32) | 2,165/179 | 252.47 (\pm 24.82) | 0.97 | 46.30 | 3.79 |

The effect of habitat characteristics on species richness of fruit-feeding butterflies was rather marginal and probably related to some other factors (Figure 1, Table 3). The only exception was the relationship of canopy butterfly species richness to the *forest structure* descriptors where the five most plausible models were selected without the null model (Table 3). The positive effect of mean tree height (MnTH) on species richness was included in all of them. According to the individual plausible models, species richness of canopy butterflies was positively related to the number of living trees (LTnb), living trees wood volume (LTWV), or mean DBH (MnDBH), and negatively to dead trees wood volume (DTWV) (Figure 1). Moreover, although the null model was selected among the most plausible *forest openness* models for all butterflies, both its AIC and AIC weight were substantially lower than of the best model (Table 3). We thus considered the positive relationship of all butterfly species richness to herb layer cover (E1) and shrub layer cover (E2), and negative relationships to mean total solar radiation (MnTT) as significant (Figure 1).

All fruit-feeding moth species richness was substantially related to the *forest openness* and *plant diversity* descriptors (Table 3). The *forest openness* models showed a positive relationship to herb layer cover (E1) and the mean tree height (MnTH) (Figure 1). The *plant diversity* models showed a negative relationship of all moths' species richness to tree species richness (TSR), and a positive relationship to herb species richness (HSR) (Figure 1). None of the habitat characteristics groups had a substantial influence on species richness of understory moths, however, the *forest openness* and *plant diversity* descriptors showed substantial relationships to species richness of canopy moths. For *forest openness*, the analyses showed a positive relationship of canopy moth species richness to mean total solar radiation (MnTT) included in all four plausible models (Table 3), as well as to both herb cover (E1) and shrub cover (E2) included in particular plausible models. Lastly,

canopy moth species richness was related positively to herb species richness (HSR), whereas negatively to tree species richness (TSR) (Figure 1).

3.2 | Determinants of community composition

For both all butterfly and understory butterfly communities, *forest openness* showed significant conditional effects on community composition and explained the highest proportions of variability (Figure 2a,b). Its marginal effects were prevalently equally shared with both *forest structure* and *plant diversity* in the former community (Figure 2a), with significant conditional effects. In contrast, for the understory butterfly community, only the *forest structure* variables shared variations with *forest openness* descriptors (Figure 2b), whilst conditional effects of *plant diversity* and *forest structure* were marginally and highly significant, respectively.

However, for the composition of both all and understory moth communities, the *plant diversity* descriptors significantly explained a substantial part of the variation, through both conditional and marginal effects (Figure 2c,d). Both conditional effects of *forest openness* and *forest structure* variables were marginally significant or insignificant, respectively, for both named moth communities.

Finally, whilst the *forest structure* variables significantly affected community composition of butterflies in the canopy, none of the habitat descriptors were important for the composition of canopy moth communities (Table 4).

4 | DISCUSSION

Fruit-feeding butterflies and moths differed in response to their habitats in the studied rainforests of Mount Cameroon, although all three

TABLE 3 Most plausible GLMMs ($\Delta AICc < 2$) explaining species richness of individual groups of fruit-feeding Lepidoptera in three rainforests on Mount Cameroon, as selected

| Community | Forest structure models | Effect | $\Delta AICc$ | w_i | Forest openness models | Effect | $\Delta AICc$ | w_i | Plant diversity models | Effect | $\Delta AICc$ | w_i |
|-------------------------|-------------------------|---------------------|---------------|-------|------------------------|---------------|---------------|-------|------------------------|-----------|---------------|-------|
| All butterflies | <i>Null model</i> | | 0 | 0.36 | ~ E1 + MnTT | E1↑ MnTT↓ | 0 | 0.26 | ~ HSR | HSR↑ | 0 | 0.45 |
| | ~ DTWV | DTWV↑ | 1.21 | 0.17 | ~ E1 | E1↑ | 0.19 | 0.25 | <i>Null model</i> | | 0.85 | 0.29 |
| | ~ LTrnb | LTrnb↑ | 1.42 | 0.17 | ~ E1 + E2 | E1↑ E2↑ | 0.26 | 0.20 | | | | |
| | ~ LTWV | LTWV↑ | 1.54 | 0.15 | ~ E1 + E2 + MnTT | E1↑ E2↑ MnTT↓ | 0.78 | 0.15 | | | | |
| Understorey butterflies | ~ MnTH | MnTH↑ | 1.74 | 0.15 | <i>Null model</i> | | 1.1 | 0.13 | | | | |
| | ~ DTWV | DTWV↑ | 0 | 0.18 | <i>Null model</i> | | 0 | 0.29 | <i>Null model</i> | | 0 | 0.37 |
| | <i>Null model</i> | | 0.61 | 0.13 | ~ E1 | E1↑ | 0.41 | 0.24 | ~ TSR | TSR↑ | 0.62 | 0.27 |
| | ~ DTWV + MnTH | DTWV↑ MnTH↓ | 1.91 | 0.07 | ~ E1 + MnTT | E1↑ MnTT↓ | 1.8 | 0.12 | ~ HSR | HSR↑ | 1 | 0.22 |
| Canopy butterflies | ~ DTWV + LTWV | DTWV↑ LTWV↑ | 1.91 | 0.07 | | | | | ~ TSR + HSR | TSR↑ HSR↑ | 1.95 | 0.14 |
| | ~ MnTH | MnTH↑ | 0 | 0.19 | <i>Null model</i> | | 0 | 0.32 | <i>Null model</i> | | 0 | 0.49 |
| | ~ DTWV + MnTH | DTWV↓ MnTH↑ | 0.74 | 0.13 | ~ E1 | E1↑ | 1.38 | 0.16 | ~ HSR | HSR↑ | 1.48 | 0.23 |
| | ~ LTrnb + MnTH | LTrnb↑ MnTH↑ | 0.87 | 0.13 | ~ MnTT | MnTT↓ | 1.88 | 0.12 | ~ TSR | TSR↓ | 1.91 | 0.19 |
| All moths | ~ LTrnb + DTWV + MnTH | LTrnb↑ DTWV↓ MnTH↑ | 1.73 | 0.08 | ~ E2 | E2↑ | 1.92 | 0.12 | | | | |
| | ~ LTrnb + MnDBH + MnTH | LTrnb↑ MnDBH↑ MnTH↑ | 1.79 | 0.08 | | | | | | | | |
| | <i>Null model</i> | | 0 | 0.17 | ~ E1 | E1↑ | 0 | 0.17 | ~ TSR | TSR↓ | 0 | 0.54 |
| | ~ LTrnb + LTWV + MnDBH | LTrnb↓ LTWV↑ MnDBH↓ | 0.55 | 0.13 | ~ E1 + MnTT | E1↑ MnTT↑ | 1.97 | 0.15 | ~ TSR + HSR | TSR↓ HSR↑ | 1.56 | 0.25 |
| Understorey moths | ~ LTrnb | LTrnb↓ | 1.58 | 0.08 | | | | | | | | |
| | ~ MnDBH | MnDBH↓ | 1.95 | 0.06 | | | | | | | | |
| | <i>Null model</i> | | 0 | 0.17 | <i>Null model</i> | | 0 | 0.30 | <i>Null model</i> | | 0 | 0.46 |
| | ~ MnTH | MnTH↓ | 0.69 | 0.12 | ~ E1 | E1↑ | 0.70 | 0.21 | ~ TSR | TSR↓ | 0.40 | 0.23 |
| Canopy moths | ~ MnDBH | MnDBH↓ | 1.88 | 0.11 | ~ E2 | E2↓ | 1.04 | 0.18 | ~ HSR | HSR↑ | 1.62 | 0.20 |
| | ~ DTWV | DTWV↓ | 0 | 0.17 | ~ MnTT | MnTT↑ | 0 | 0.39 | ~ TSR | TSR↓ | 0 | 0.61 |
| | <i>Null model</i> | | 0.50 | 0.13 | ~ E2 + MnTT | E2↑ MnTT↑ | 1.22 | 0.21 | ~ TSR + HSR | TSR↓ HSR↑ | 1.94 | 0.38 |
| | ~ LTrnb + DTWV + MnTH | LTrnb↓ DTWV↓ MnTH↑ | 0.83 | 0.07 | ~ E1 + MnTT | E1↑ MnTT↑ | 1.46 | 0.19 | | | | |

Note: The models are ranked according to their corrected second-order Akaike information criteria (AICc). Model weights (w_i) are reported, together with positive (↑) or negative (↓) linear effects of each significant habitat characteristics (see Table 1 for their full names and definitions, and Figure 1 for the effects visualization). Individual model details are reported in Table S2.

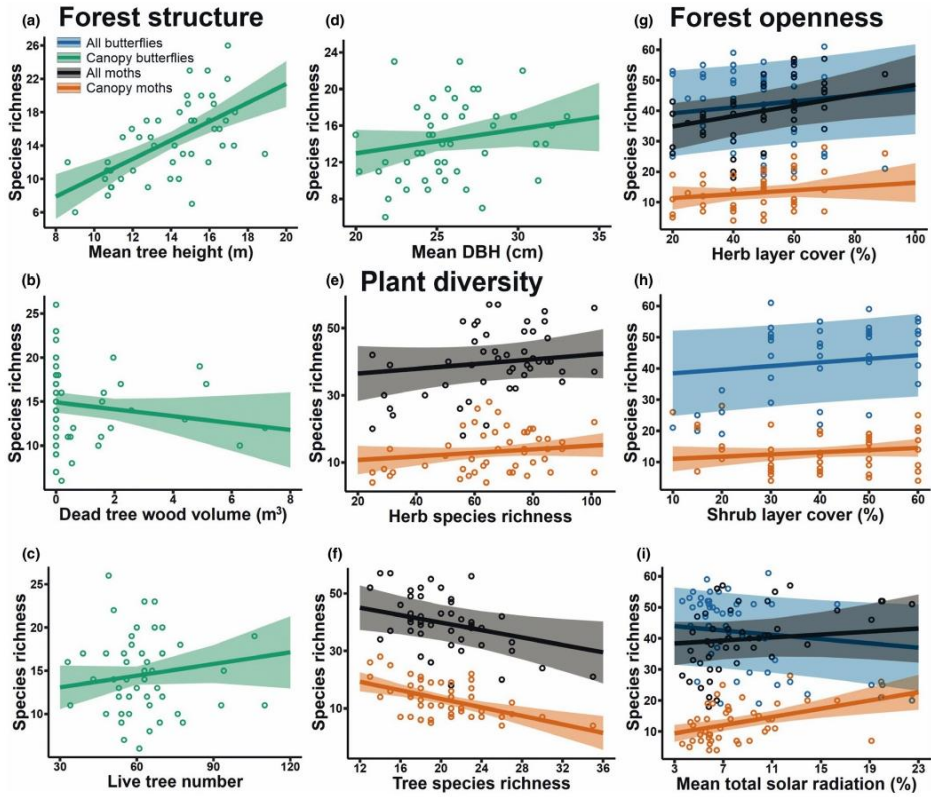


FIGURE 1 Marginal effects of habitat descriptors on species richness of fruit-feeding butterflies and moths in three rainforests on Mount Cameroon. Habitat descriptors are ordered by categories: *forest structure* descriptors: (a) mean tree height, (b) dead tree wood volume, (c) live tree number, and (d) mean DBH; *plant diversity* descriptors: (e) herb species richness, and (f) tree species richness; *forest openness* descriptors: (g) herb layer cover, (h) shrub layer cover, and (i) mean total solar radiation. Shaded areas indicate 95% confidence intervals. Only habitat descriptors from the most plausible GLMMs are visualized. See Table 3 for the models results and Methods for their details

groups of habitat descriptors played a certain role in forming their communities. Whilst both species richness and composition of butterfly communities were affected mainly by the openness of forest and, only to a lesser extent, by the plant diversity and forest structure variables, moth communities were influenced mostly by plant diversity (especially their composition), and only marginally by forest openness and forest structure. Such results confirmed our predictions of differences between these two groups of Lepidoptera, based on particular studies of butterflies (e.g., Nyafwono et al., 2014b; Spitzer et al., 1997; Tropek & Konvička, 2010) and moths (e.g., Axmacher et al., 2009; Beck et al., 2002; Brehm et al., 2003; Rabl et al., 2019) from other tropical regions, although such direct comparative study of the two lepidopteran groups was missing from elsewhere.

The importance of forest openness for rainforest butterflies was not surprising, because many adult tropical butterfly species use sunny spots (i.e., forest gaps, canopy openings, or small light spots under sparse canopy) for basking, nectaring, mating, and oviposition (Spitzer et al., 1997; Tropek & Konvička, 2010; Uehara-Prado et al., 2007; Vlašánek et al., 2013). Similar importance of canopy openness for butterfly community composition has been reported from the understory of the Afrotropical rainforests in Uganda (Nyafwono et al., 2014b, 2015), though these studies revealed also the crucial role of plant diversity for rainforest butterflies. Contrastingly, adult moths are generally not such strongly dependent on solar radiation because of the nocturnal or crepuscular activity of most of their diversity (Ribeiro & Freitas, 2010).

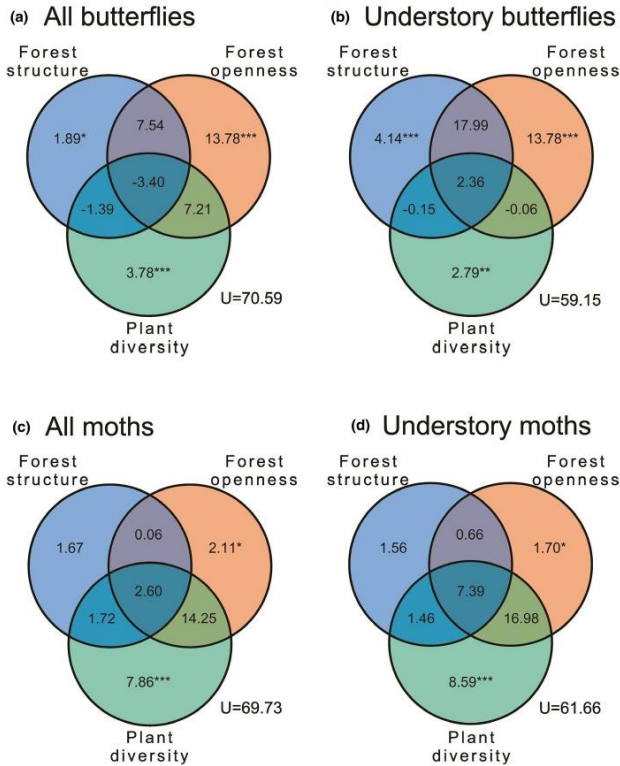


FIGURE 2 Venn diagrams visualizing the partition of explained variation (Ra^2 in %) in community composition of (a) all butterflies, (b) understory butterflies, (c) all moths, and (d) understory moths in three rainforests on Mount Cameroon. U means the unexplained variation. Any negative values of Ra^2 are interpreted as zeros (Šmilauer & Lepš, 2014). The significance values are represented as *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

| Community | Final model | Pseudo-F | p | Ra^2 |
|------------------------|---|----------|-------|--------|
| All butterflies | ~ DTnb + LTBA + MxTdf + E2 + TSR + HSR | 3.9 | 0.001 | 27.2 |
| Understory butterflies | ~ DTnb + MxTH + MnCO + E2 + HSR + TDCA3 | 4.8 | 0.001 | 40.8 |
| Canopy butterflies | ~ SSI | 1.6 | 0.012 | 1.4 |
| All moths | ~ DTBA + TBA + MxTdf + MxTDr + HDCA2 + TSR | 2.3 | 0.001 | 30.3 |
| Understory moths | ~ Tnb + MnDBH + MxTdf + MxLAI + HDCA2 + TDCA1 | 2.7 | 0.001 | 38.3 |
| Canopy moths | No forward-selected variables | - | - | - |

Note: 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 (Ra^2 in %) are reported for individual models. See Table 1 for the habitat descriptors' full names and definitions.

TABLE 4 Results of partial CCAs showing the influence of the habitat descriptors on community composition of individual groups of fruit-feeding Lepidoptera in three rainforests on Mount Cameroon

This could explain the relatively less importance of forest openness for community composition of moths, although it still showed substantial effect on moth species richness together with the plant diversity descriptors.

Although crucial for moth communities, plant diversity had a relatively low effect on fruit-feeding butterflies' community composition and no effect on their species richness. This contradicts the results of several other studies showing plant richness as the main driver

for butterfly communities (e.g., Nyafwono et al., 2014b; Valtonen et al., 2017). The direct dependence of butterfly communities on the local plant communities is indisputable, as caterpillars depend on their foodplants and are relatively highly host-specialized (Forister et al., 2015; Novotný, Miller, et al., 2002). However, the relatively high importance of habitat descriptors not directly related to plant diversity for lepidopteran communities has been shown repeatedly in forests of different tropical areas (Axmacher et al., 2009; DeVries & Walla, 2001; Hill et al., 2001; Hilt & Fiedler, 2005; Nyafwono et al., 2015; Spitzer et al., 1997), although the particular mechanisms were only speculated.

As opposed to fruit-feeding butterflies, the habitat associations of tropical fruit-feeding moths have never yet been reported. However, the crucial role of plant diversity in the increase of moth species richness shown by our data corroborates with some studies of light-attracted communities of other feeding moth guilds. Generally, moth diversity and species composition often closely depended on diversity of plants in tropical forest communities (e.g., Axmacher et al., 2009; Hilt & Fiedler, 2005; Peters et al., 2016). The increase of their species richness with living tree wood volume can be explained by an increase in available niche space or food resources with available leaf area. Moreover, since a majority of moth species feed on woody plants, a larger diversity of tree species is known to support more moth species (e.g., Beck et al., 2002; Brehm et al., 2007), completely opposed to our results. However, Axmacher et al. (2004) found a negative correlation between diversity of Geometridae and dicotyledon plants on Mount Kilimanjaro, although this was the only negative relationship between moth and plant diversities ever reported from any tropical forests to our knowledge. The authors explained it by the young age and the geographical isolation of Mount Kilimanjaro's montane forests (Axmacher et al., 2004). This hypothesis could, however, hardly explain the similar relationship found in the forests in our study area at the transition between the West African rainforests and the Congo basin. Alternatively, fruit-feeding moth communities (as well as fruit-feeding butterflies) depend directly on the availability of fleshy fruits rather than overall tree diversity. Unfortunately, we have no data to test this highly probable hypothesis. Although adult moths are generally not so closely dependent on solar radiation (Ribeiro & Freitas, 2010), temperature has been shown as a better predictor than tree diversity or forest structure along an altitudinal gradient on Borneo (Beck & Chey, 2008) and in South and Central America (Brehm et al., 2007; Brehm et al., 2003).

For both butterflies and moths, we have shown vertically stratified patterns, as the habitat associations of canopy communities largely differed from understory communities. Such vertical stratification of butterfly communities has been observed repeatedly (e.g., DeVries & Walla, 2001; Molleman et al., 2006; Nice et al., 2019). Generally, the combined presence of high numbers of young leaves, sap fluids, nectar and fruits, as well as high abundances of epiphytes and lianas in the rainforest canopy, are likely to attract lepidopteran communities different from species specialized for forest understory (Novotný et al., 2003). In our study, this is particularly noticeable for butterflies, whose canopy communities are influenced only by

forest structure, especially by forest height, density, and the size of living trees. Therefore, the increases in butterfly species richness related to taller, larger and more abundant living trees likely reflect an increase in available microhabitats and resources. Simultaneously, in generally, sunnier canopy the lower importance of forest openness for day-active butterflies can also be expected. On the other hand, we were not able to directly compare lepidopteran abundance and species richness between canopy and understory because of the unbalanced sampling effort. However, both values are known to be generally lower in canopy when compared to understory (DeVries et al., 1999; but see Schulze et al., 2001, for nectar-feeding Lepidoptera).

In conclusion, habitat associations differed between communities of fruit-feeding butterflies and moths in lowland rainforests of Mount Cameroon. The different ecology and habitat use by the two groups related to their different day activity is likely to explain the observed patterns. However, other factors not included in our study, including potential differences in larval and adult food resources between butterflies and moths, could also play a role in the revealed differing patterns. Although our results can hardly be generalized for other geographic areas or for other feeding guilds of Lepidoptera, they evidenced that even groups traditionally seen as ecologically similar can highly differ in their reactions to environmental conditions. Therefore, one must be very careful with any generalizations based on taxonomically restricted results. Nevertheless, a direct explanation of the differences would need experimental approaches, which are still relatively rare in the research of tropical communities. Simultaneously, the studies of habitat associations will probably benefit with implication of some promising new technologies, such as Lidar (e.g., Wallis et al., 2017), in ecological research, resulting in our better understanding of factors responsible for the composition of local communities of insects in tropical forests.

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CONFLICT OF INTEREST

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vhmgqnm> (Delabye, Maicher, Sáfián, Doležal, et al., 2020b).

ORCID

Sylvain Delabye  <https://orcid.org/0000-0003-0911-9721>

Vincent Maicher  <https://orcid.org/0000-0002-9147-3529>

Jiří Doležal  <https://orcid.org/0000-0002-5829-4051>

Jan Altman  <https://orcid.org/0000-0003-4879-5773>

Štěpán Janeček  <https://orcid.org/0000-0003-1285-6490>

Ishmeal N. Kobe  <https://orcid.org/0000-0003-0259-0350>

Pavel Šebek  <https://orcid.org/0000-0003-3341-4771>

Robert Tropek  <https://orcid.org/0000-0001-7499-6259>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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SUPPORTING INFORMATION

TABLE S1. Pearson correlation coefficients of the habitat descriptors for (A) *forest structure*, (B) *forest openness*, (C) *plant diversity*, and (D) habitat descriptors across the groups. The variable selected for the final GLMMs are in **bold** (Pearson $\rho \leq |0.7|$). For details on particular variables, see Table 1.

(A)

| Forest structure | Tnb | LTnb | DTnb | TBA | LTBA | DTBA | SWV | LTWV | DTWV | MnDBH | MxDBH | MnTH | MxTH |
|------------------|-------------|-------|-------------|-------------|-------------|-------------|-------------|-------------|-------|-------|-------|-------------|-------------|
| LTnb | 0.99 | | | | | | | | | | | | |
| DTnb | 0.32 | 0.16 | | | | | | | | | | | |
| TBA | 0.28 | 0.33 | -0.23 | | | | | | | | | | |
| LTBA | 0.17 | 0.25 | -0.35 | 0.98 | | | | | | | | | |
| DTBA | 0.26 | 0.12 | 0.83 | -0.15 | -0.31 | | | | | | | | |
| SWV | -0.02 | 0.04 | -0.32 | 0.88 | 0.90 | -0.25 | | | | | | | |
| LTWV | -0.04 | 0.02 | -0.35 | 0.88 | 0.91 | -0.29 | 1.00 | | | | | | |
| DTWV | 0.06 | -0.07 | 0.72 | -0.21 | -0.33 | 0.81 | -0.16 | -0.20 | | | | | |
| MnDBH | -0.55 | -0.50 | -0.43 | 0.56 | 0.62 | -0.31 | 0.63 | 0.63 | -0.21 | | | | |
| MxDBH | -0.23 | -0.18 | -0.38 | 0.69 | 0.72 | -0.32 | 0.82 | 0.83 | -0.25 | 0.55 | | | |
| MnTH | -0.35 | -0.31 | -0.33 | 0.32 | 0.36 | -0.16 | 0.61 | 0.59 | 0.13 | 0.53 | 0.41 | | |
| MxTH | -0.02 | -0.02 | -0.01 | 0.41 | 0.37 | 0.03 | 0.64 | 0.61 | 0.26 | 0.25 | 0.45 | 0.70 | |
| SSI | -0.06 | -0.04 | -0.12 | 0.09 | 0.08 | 0.01 | 0.37 | 0.35 | 0.27 | -0.01 | 0.25 | 0.81 | 0.70 |

(B)

| Forest openness | MnCO | MxCO | E1 | E2 | E1+E2 | MnLAI | MxLAI | MnTDr | MxTDr | MnTDf | MxTDf | MnTT |
|-----------------|-------------|-------------|-------------|-------|-------|-------------|-------|-------------|-------------|-------------|-------------|-------------|
| MxCO | 0.94 | | | | | | | | | | | |
| E1 | 0.56 | 0.54 | | | | | | | | | | |
| E2 | -0.56 | -0.55 | -0.38 | | | | | | | | | |
| E1+E2 | 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 | TSR |
|-----------------|-------|
| HSR | -0.30 |

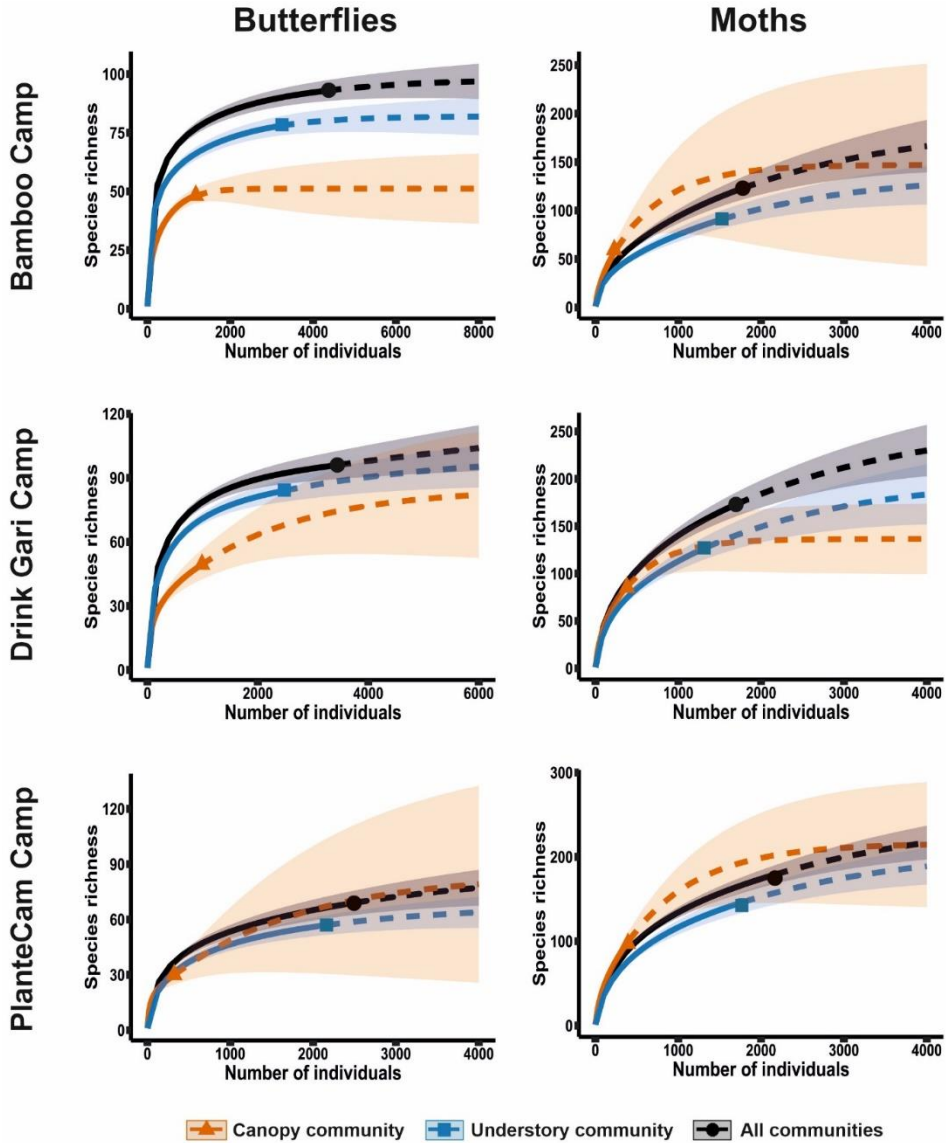
(D)

| Measured descriptors | Tnb | LTnb | DTnb | TBA | LTBA | DTBA | SWV | LTWV | DTWV | MRDBH | MRDBH | MRDBH | MnTH | MnTH | MnTH | 88I | MnCO | MnCO | E1 | E2 | E1+E2 | MnLAI | MnLAI | MnLAI | MnTDr | MnTDr | MnTDr | MnTDr | MnTT | MnTT | | | | |
|----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------------|-------|-------|-------|-----|------|------|----|----|-------|-------|-------|-------|-------|-------|-------|-------|------|------|--|--|--|--|
| MnCO | 0.03 | 0.01 | 0.11 | -0.42 | -0.40 | -0.02 | -0.53 | -0.50 | -0.15 | -0.38 | -0.35 | -0.71 | -0.67 | -0.62 | -0.62 | | | | | | | | | | | | | | | | | | | |
| MnCO | 0.06 | 0.05 | 0.12 | -0.36 | -0.36 | -0.04 | -0.49 | -0.47 | -0.15 | -0.36 | -0.36 | -0.66 | -0.63 | -0.57 | | | | | | | | | | | | | | | | | | | | |
| E1 | 0.06 | 0.05 | 0.06 | -0.32 | -0.26 | -0.12 | -0.30 | -0.29 | -0.05 | -0.33 | -0.27 | -0.35 | -0.39 | -0.26 | | | | | | | | | | | | | | | | | | | | |
| E2 | 0.05 | 0.12 | -0.38 | 0.45 | 0.46 | -0.17 | 0.39 | 0.39 | -0.17 | 0.39 | 0.23 | 0.41 | 0.25 | 0.23 | | | | | | | | | | | | | | | | | | | | |
| E1+E2 | 0.14 | 0.19 | -0.24 | -0.01 | 0.05 | -0.27 | -0.08 | -0.07 | -0.28 | -0.09 | -0.15 | -0.18 | -0.31 | -0.24 | | | | | | | | | | | | | | | | | | | | |
| MnLAI | -0.30 | -0.26 | -0.34 | 0.36 | 0.39 | -0.16 | 0.55 | 0.54 | 0.06 | 0.54 | 0.41 | 0.83 | 0.62 | 0.64 | | | | | | | | | | | | | | | | | | | | |
| MnLAI | -0.29 | -0.25 | -0.27 | 0.35 | 0.38 | -0.10 | 0.44 | 0.44 | 0.05 | 0.54 | 0.33 | 0.63 | 0.43 | 0.42 | | | | | | | | | | | | | | | | | | | | |
| MnTDr | 0.00 | 0.00 | 0.02 | -0.36 | -0.34 | -0.02 | -0.44 | -0.41 | -0.17 | -0.28 | -0.32 | -0.56 | -0.62 | -0.56 | | | | | | | | | | | | | | | | | | | | |
| MnTDr | 0.05 | 0.04 | 0.06 | -0.34 | -0.32 | -0.02 | -0.43 | -0.40 | -0.11 | -0.30 | -0.33 | -0.60 | -0.58 | -0.58 | | | | | | | | | | | | | | | | | | | | |
| MnTDr | 0.01 | 0.00 | 0.03 | -0.38 | -0.35 | -0.07 | -0.47 | -0.44 | -0.20 | -0.32 | -0.32 | -0.64 | -0.65 | -0.59 | | | | | | | | | | | | | | | | | | | | |
| MnTDr | 0.05 | 0.05 | 0.03 | -0.38 | -0.35 | -0.09 | -0.46 | -0.43 | -0.18 | -0.35 | -0.33 | -0.59 | -0.61 | -0.53 | | | | | | | | | | | | | | | | | | | | |
| MnTT | 0.02 | 0.01 | 0.04 | -0.39 | -0.37 | -0.02 | -0.48 | -0.45 | -0.18 | -0.32 | -0.33 | -0.63 | -0.65 | -0.58 | | | | | | | | | | | | | | | | | | | | |
| MnTT | 0.06 | 0.04 | 0.09 | -0.38 | -0.36 | -0.01 | -0.47 | -0.45 | -0.11 | -0.34 | -0.36 | -0.65 | -0.62 | -0.60 | | | | | | | | | | | | | | | | | | | | |
| TnR | 0.24 | 0.20 | 0.25 | 0.17 | 0.14 | 0.25 | 0.20 | 0.19 | 0.33 | -0.06 | 0.01 | 0.26 | 0.50 | 0.43 | | | | | | | | | | | | | | | | | | | | |
| HnR | 0.26 | 0.30 | -0.19 | 0.25 | 0.30 | -0.35 | 0.64 | 0.66 | -0.50 | 0.68 | -0.05 | -0.34 | -0.31 | -0.47 | | | | | | | | | | | | | | | | | | | | |

TABLE S2. Details on the most plausible GLMMs ($\Delta AIC < 2$) explaining species richness of butterflies and moths. Models are ranked according to their 2nd-order Akaike information criterion (AICc). Parameter estimates (coefficients), model weights (w_i), and model total R^2 are reported. For details on particular variables, see Table 1.

| Intercept | Parameter estimates | | | | | | | | | | k | logLik | AICc | $\Delta AICc$ | wi | R^2 | |
|-------------------------------|---------------------|-------|------|-------|------|-------|-------|-------|-------|-------|------|---------|---------|---------------|------|-------|------|
| | LTnb | DTWV | LTWV | MnDBH | MnTH | E1 | E2 | MnTT | T&R | H&R | | | | | | | |
| All butterflies | | | | | | | | | | | | | | | | | |
| 41.96 | | | | | | | | | | | 3 | -155.23 | 317 | 0 | 0.16 | - | |
| 41.46 | | 0.53 | | | | | | | | | 4 | -154.64 | 318.21 | 1.21 | 0.09 | 0.82 | |
| 38.65 | 0.05 | | | | | | | | | | 4 | -154.75 | 318.42 | 1.42 | 0.08 | 0.83 | |
| 39.98 | | | 0.02 | | | | | | | | 4 | -154.81 | 318.54 | 1.54 | 0.08 | 0.80 | |
| 34.03 | | | | 0.57 | | | | | | | 4 | -154.91 | 318.75 | 1.74 | 0.07 | 0.79 | |
| 38.54 | | | | | 0.14 | | | -0.40 | | | 5 | -152.24 | 315.98 | 0 | 0.22 | 0.85 | |
| 37.14 | | | | | 0.10 | | | | | | 4 | -153.58 | 316.1 | 0.19 | 0.2 | 0.85 | |
| 30.53 | | | | | 0.12 | 0.12 | | | | | 5 | -152.37 | 316.17 | 0.26 | 0.19 | 0.86 | |
| 32.67 | | | | | 0.10 | 0.10 | -0.35 | | | | 6 | -151.32 | 316.69 | 0.78 | 0.15 | 0.87 | |
| 41.96 | | | | | | | | | | | 3 | -155.23 | 317 | 1.1 | 0.13 | - | |
| 35.65 | | | | | | | | | | 0.10 | 4 | -153.61 | 316.15 | 0 | 0.45 | 0.86 | |
| 41.96 | | | | | | | | | | | 3 | -155.23 | 317 | 0.85 | 0.29 | 0 | |
| Understory butterflies | | | | | | | | | | | | | | | | | |
| 32.41 | | 0.83 | | | | | | | | | 4 | -152.78 | 314.49 | 0 | 0.18 | 0.78 | |
| 33.19 | | | | | | | | | | | 3 | -154.28 | 315.1 | 0.61 | 0.13 | - | |
| 39.67 | | 0.85 | | | | | -0.52 | | | | 5 | -152.48 | 316.4 | 1.91 | 0.07 | 0.83 | |
| 30.66 | | 0.94 | 0.01 | | | | | | | | 5 | -152.49 | 316.4 | 1.91 | 0.07 | 0.78 | |
| 33.19 | | | | | | | | | | | 3 | -154.28 | 315.1 | 0 | 0.29 | - | |
| 29.46 | | | | | | 0.08 | | | | | 4 | -153.29 | 315.51 | 0.41 | 0.24 | 0.79 | |
| 24.95 | | | | | | 0.10 | 0.08 | | | | 5 | -152.74 | 316.91 | 1.81 | 0.12 | 0.79 | |
| 33.19 | | | | | | | | | | | 3 | -154.28 | 315.1 | 0 | 0.37 | - | |
| 27.49 | | | | | | | | | 0.28 | | 4 | -153.4 | 315.72 | 0.62 | 0.27 | 0.76 | |
| 29.06 | | | | | | | | | | 0.06 | 4 | -153.59 | 316.1 | 1 | 0.22 | 0.78 | |
| 24.18 | | | | | | | | | | 0.26 | 0.06 | 5 | -152.81 | 317.05 | 1.95 | 0.14 | 0.78 |
| Canopy butterflies | | | | | | | | | | | | | | | | | |
| -0.61 | | | | | 1.09 | | | | | | 4 | -129.34 | 267.6 | 0 | 0.19 | 0.39 | |
| -0.76 | | -0.39 | | | 1.13 | | | | | | 5 | -128.46 | 268.34 | 0.74 | 0.13 | 0.40 | |
| -4.62 | 0.05 | | | | 1.17 | | | | | | 5 | -128.52 | 268.47 | 0.87 | 0.13 | 0.40 | |
| -10.72 | 0.07 | | | 0.26 | 1.03 | | | | | | 6 | -127.64 | 269.33 | 1.73 | 0.08 | 0.35 | |
| -4.61 | 0.04 | -0.38 | | | 1.21 | | | | | | 6 | -127.67 | 269.39 | 1.79 | 0.08 | 0.41 | |
| 14.54 | | | | | | | | | | | 3 | -135.01 | 276.57 | 0 | 0.32 | - | |
| 12.64 | | | | | 0.04 | | | | | | 4 | -134.51 | 277.95 | 1.38 | 0.16 | 0.36 | |
| 13.04 | | | | | | 0.04 | | | | | 4 | -134.76 | 278.45 | 1.88 | 0.12 | 0.25 | |
| 15.54 | | | | | | | | -0.12 | | | 4 | -134.78 | 278.49 | 1.92 | 0.12 | 0.25 | |
| 14.54 | | | | | | | | | | | 3 | -135.01 | 276.57 | 0 | 0.49 | - | |
| 12.21 | | | | | | | | | 0.04 | | 4 | -134.96 | 278.05 | 1.48 | 0.23 | 0.36 | |
| 16.62 | | | | | | | | | | -0.10 | 4 | -134.78 | 278.49 | 1.91 | 0.19 | 0.32 | |
| All moths | | | | | | | | | | | | | | | | | |
| 39.71 | | | | | | | | | | | 3 | -167.55 | 341.64 | 0 | 0.17 | - | |
| 79.26 | -0.23 | | 0.07 | -1.30 | | | | | | | 6 | -164.07 | 342.19 | 0.55 | 0.13 | 0.70 | |
| 43.84 | -0.07 | | | | | | | | | | 4 | -167.14 | 343.22 | 1.58 | 0.08 | 0.49 | |
| 46.14 | | | | -0.25 | | | | | | | 4 | -167.33 | 343.59 | 1.95 | 0.06 | 0.44 | |
| 31.39 | | | | | | | | | | | 4 | -164.91 | 338.74 | 0 | 0.35 | 0.51 | |
| 30.45 | | | | | 0.15 | | 0.24 | | | | 5 | -164.64 | 340.72 | 1.97 | 0.15 | 0.52 | |
| 52.8 | | | | | | | | | | -0.65 | 4 | -165.08 | 339.1 | 0 | 0.54 | 0.50 | |
| 48.95 | | | | | | | | | | -0.69 | 0.07 | 5 | -164.62 | 340.66 | 1.56 | 0.25 | 0.55 |
| Understory moths | | | | | | | | | | | | | | | | | |
| 30.04 | | | | | | | | | | | 3 | -163.92 | 334.38 | 0 | 0.17 | - | |
| 49.5 | | | | | | -1.40 | | | | | 4 | -163.07 | 335.07 | 0.69 | 0.12 | 0.39 | |
| 41.36 | | | | -0.44 | | | | | | | 4 | -163.17 | 335.26 | 0.88 | 0.11 | 0.29 | |
| 30.04 | | | | | | | | | | | 3 | -163.92 | 334.38 | 0 | 0.3 | - | |
| 25.44 | | | | | 0.10 | | | | | | 4 | -163.07 | 335.08 | 0.7 | 0.21 | 0.27 | |
| 34.11 | | | | | | | -0.10 | | | | 4 | -163.25 | 335.43 | 1.04 | 0.18 | 0.30 | |
| 30.04 | | | | | | | | | | | 3 | -163.92 | 334.38 | 0 | 0.46 | - | |
| 35.76 | | | | | | | | | -0.28 | | 4 | -163.42 | 335.78 | 1.4 | 0.23 | 0.26 | |
| 25.94 | | | | | | | | | | 0.06 | 4 | -163.54 | 336.01 | 1.62 | 0.2 | 0.25 | |
| Canopy moths | | | | | | | | | | | | | | | | | |
| 13.99 | | -0.88 | | | | | | | | | 4 | -152.46 | 313.84 | 0 | 0.17 | 0.23 | |
| 13.17 | | | | | | | | | | | 3 | -153.9 | 314.35 | 0.5 | 0.13 | - | |
| 16.9 | -0.05 | -0.87 | | | | | | | | | 5 | -152.12 | 315.67 | 1.83 | 0.07 | 0.27 | |
| 21.69 | | -1.04 | | | | -0.54 | | | | | 5 | -152.21 | 315.84 | 1.99 | 0.06 | 0.30 | |
| 7.43 | | | | | | | | | | | 4 | -148.65 | 306.23 | 0 | 0.35 | 0.32 | |
| 3.5 | | | | | | | 0.07 | 0.79 | | | 5 | -145.01 | 309.45 | 1.22 | 0.21 | 0.24 | |
| 5.33 | | | | | | | 0.06 | 0.55 | | | 5 | -148.13 | 309.69 | 1.46 | 0.19 | 0.32 | |
| 28.15 | | | | | | | | | -0.74 | | 4 | -148.55 | 306.03 | 0 | 0.61 | 0.32 | |
| 23.22 | | | | | | | | | | -0.67 | 0.05 | 5 | -147.77 | 306.97 | 0.94 | 0.38 | 0.43 |

FIGURE S1. Individual-based rarefaction curves of species richness of fruit-feeding butterflies and moths in the particular sampling localities in three rainforests of Mount Cameroon with 95% confidence intervals (shaded areas). The solid lines represent the rarefied reference samples, while the dashed lines represent the extrapolated samples.



CHAPTER II

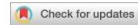
Effects of disturbances by forest elephants on diversity of trees and insects in tropical rainforests on Mount Cameroon

Maicher, V., Delabye, S., Murkwe, M., Doležal, J., Altman, J.,
Kobe, I.N., Desmist, J., Fokam, E.B., Pyrcz, T., & Tropek, R.
(2020).

Scientific Reports, **10**: 21618.



Dead trees and broken logs in the montane forest disturbed by elephants on Mount Cameroon (1,850 a.s.l.). © S. Delabye



OPEN

Effects of disturbances by forest elephants on diversity of trees and insects in tropical rainforests on Mount Cameroon

Vincent Maicher^{1,2,3✉}, Sylvain Delabye^{1,2}, Mercy Murkwe^{4,5}, Jiří Doležal^{2,6}, Jan Altman⁶, Ishmeal N. Kobe⁵, Julie Desmist^{1,7}, Eric B. Fokam⁴, Tomasz Pyrzycz^{8,9} & Robert Tropek^{1,5✉}

Natural disturbances are essential for tropical forests biodiversity. In the Afrotropics, megaherbivores have played a key role before their recent decline. Contrastingly to savanna elephants, forest elephants' impact on ecosystems remains poorly studied. Few decades ago, forests on Mount Cameroon were divided by lava flows, not being crossed by a local population of forest elephants until now. We assessed communities of trees, butterflies and two guilds of moths in the disturbed and undisturbed forests split by the longest lava flow. We surveyed 32 plots, recording 2025 trees of 97 species, and 7853 insects of 437 species. The disturbed forests differed in reduced tree density, height, and high canopy cover, and in increased DBH. Forest elephants' selective browsing and foraging also decreased tree species richness and altered their composition. The elephant disturbance increased butterfly species richness and had various effects on species richness and composition of the insect groups. These changes were likely caused by disturbance-driven alterations of habitats and species composition of trees. Moreover, the abandonment of forests by elephants led to local declines of range-restricted butterflies. The recent declines of forest elephants across the Afrotropics probably caused similar changes in forest biodiversity and should be reflected by conservation actions.

Natural disturbances are key drivers of biodiversity in many terrestrial ecosystems¹, including tropical forests despite their traditional view as highly stable ecosystems^{2,3}. Natural disturbances such as tree falls, fires, landslides, and insect herbivores outbreaks, generally open forest canopy, followed by temporary changes of microclimate and availability of plant resources (e.g., light, water, and soil nutrients)⁴. The consequent changes in plant communities cause cascade effects on higher trophic levels (herbivores, predators, parasites), expanding the impact of disturbances on the entire ecosystem. Such increase of heterogeneity of habitats and species communities substantially contribute to maintaining the overall biodiversity of tropical forest ecosystems^{5,6}.

Megaherbivores, i.e. ≥ 1000 kg herbivorous mammals, used to be among the main causes of such disturbances, before their abundances and diversity seriously dropped in all continents except Africa^{7–9}. Among all megaherbivores, savanna elephants are best known to alter their habitats^{8,10}. Besides their important roles of seed dispersers or nutrient cyclers⁸, they directly impact savanna ecosystems through disturbing vegetation, especially by increasing tree mortality by browsing, trampling, and debarking¹⁰. Such habitat alterations substantially affect diversity of many organism groups¹¹, including insects. Savanna elephants were shown to positively influence diversity of grasshoppers¹² and dragonflies¹³, whilst to have ambiguous effect on diversity of particular butterfly families^{4,13}. Contrarily, too intensive disturbances caused by savanna elephants impact biodiversity negatively^{13,16,17}, similarly to other disturbance types.

¹Institute of Entomology, Biology Centre, Czech Academy of Sciences, Branisovska 31, 37005 Ceske Budejovice, Czech Republic. ²Faculty of Science, University of South Bohemia, Branisovska 1760, 37005 Ceske Budejovice, Czech Republic. ³Nicholas School of the Environment, Duke University, 9 Circuit Dr., Durham, NC 27710, USA. ⁴Department of Zoology and Animal Physiology, Faculty of Science, University of Buea, P.O. Box 63, Buea, Cameroon. ⁵Department of Ecology, Faculty of Science, Charles University, Vinicna 7, 12844 Prague, Czech Republic. ⁶Institute of Botany, Czech Academy of Sciences, Dukelska 135, 37982 Trebon, Czech Republic. ⁷University Paris-Saclay, 15 rue Georges Clemenceau, 91400 Orsay, France. ⁸Institute of Zoology and Biomedical Research, Jagiellonian University, Gronostajowa 9, 30387 Krakow, Poland. ⁹Nature Education Centre of the Jagiellonian University, Gronostajowa 5, 30387 Krakow, Poland. ✉email: vincent.maicher@hotmail.fr; robert.tropek@gmail.com

Although expected already for a few decades¹⁸, effects of forest elephants on biodiversity of Afrotropical forests remain strongly understudied^{10,19}. Despite being smaller (up to 5 tons, in comparison to 7 tons of savanna elephants), forest elephants are expected to affect their habitats by similar mechanisms as their savanna relatives, as recently reviewed by Poulsen et al.¹⁹. They were shown to impact forest tree density and diversity in both negative and positive ways^{19–21}. Besides local opening of forest canopy, they inhibit forest regeneration and maintain small-scaled canopy gaps^{22,23}. However, the consequent cascade effects on forest biodiversity have not been studied yet, although effects of elephant disturbances on other tropical forest organisms can be expected as well^{24,25}. The only existing study of effects of megafauna, including forest elephants, on the Afrotropical forest invertebrates showed that in defaunated forests, termite abundances decreased by orders of magnitude, followed by a significant decrease of invertebrate contribution to litter decomposition²⁶. Such research is urgent especially because of the current steep decline of forest elephants across the Afrotropics (>60% decrease of abundance between 2002 and 2012²⁷), and forest elephants are already extinct in numerous areas, including the protected ones. In such situation, local policy makers and conservationists should be aware of any potential changes in plant and animal communities to initiate more effective conservation planning.

In this study, we bring a direct comparison of a forest structure, and diversity and composition of tree and insect communities in Afrotropical forests with and without forest elephants. Mount Cameroon provides an ideal opportunity for such study by offering a unique 'natural enclosure experiment'. Forests on its southern slope were split by a continuous lava flow after eruptions in 1982 (from ca 2600 m asl., i.e. above the natural timberline, to ca 1400 m asl.) and 1999 (from ca 1550 m asl. to the seashore)²⁸. Probably because of the slow natural succession on this lava flow, local forest elephants do not cross this barrier and stay on its western side close to three crater lakes, the only water sources during the dry seasons²⁸. Such unusual conditions represent a long-term (at least since the last eruption in 1999 in the lower elevations, and since the eruption in 1982 in the upper elevations) enclosure experiment under natural conditions, performed on a much larger scale than any possible artificial enclosure studies. In the disturbed and undisturbed sites, we surveyed forest structure and communities of trees, butterflies, and two ecological guilds of moths. We hypothesized that forest elephants changed the forest structure by opening its canopy, with the consequent changes in composition of all studied groups' communities. We expected decrease of tree diversity by the direct damage by elephants, and related increase of insect diversity caused by the higher habitat heterogeneity. Nevertheless, butterflies and moths differ in their habitat use and requirements. Because butterflies mostly rely on a direct solar radiation for their thermoregulation and other activities, their diversity have been shown to be mostly influenced by forest structure and canopy openness in tropical forests²⁹. On the other hand, moths are relatively less dependent on their habitat structure due to the nocturnal behaviour, and they are more affected by the plant community composition^{29,30}. Therefore, the ambiguous effect can be also hypothesized, as moths more closely depend on tree diversity³¹, whilst butterflies rather benefit from canopy opening³². Finally, we focus on species' distribution ranges in both types of forests, with no a priori hypothesis on the direction of the changes.

Results

In total, 2025 trees were identified to 97 species and 7853 butterflies and moths were identified to 437 species in all sampled forest plots (Supplementary Table S1).

Elephant disturbances and forest structure. The partial-RDA ordination analysis showed significant differences in the forest structure descriptors between the disturbed and undisturbed forests (Fig. 1b). In total, the two main ordination axes explained 18.5% of the adjusted variation (all axes eigenvalues: 0.83; Pseudo-F = 7.8; $p = 0.002$). In the disturbed plots, *tree species richness*, *mean SSL*, *mean height*, *maximum height*, and *higher canopy coverage* were lower. In contrast, *mean DBH* was larger in the disturbed forests (Fig. 1b).

Elephant disturbances and tree diversity. Elephant disturbances affected tree species richness per sampled elevation, as well as per sampled plot. In both upland and montane forests, total tree species richness of the disturbed sites was nearly half in comparison to the undisturbed sites (Fig. 2a; Supplementary Table S1). Tree species richness per plot was significantly affected by disturbance (higher at undisturbed forest plots) and elevation (higher at the upland forests) (Fig. 2b; Table 1). The responses of individual tree families were significantly affected by disturbance and elevation (Pseudo-F: 12.3, p -value: < 0.001, adjusted explained variation: 52.3%; Supplementary Table S2). All tree families but Euphorbiaceae showed higher species richness at undisturbed forests; all families but Rubiaceae had higher species richness in upland forests (Supplementary Fig. S1a).

Tree communities significantly differed in composition between the forests disturbed and undisturbed by elephants according to the partial-CCA (all-axes eigenvalues: 4.55; Pseudo-F = 3.8; $p < 0.001$). The first NMDS axis reflected elevation, whilst the tree communities of the disturbed and undisturbed forests were relatively well-separated along the second axis (Fig. 2c). The ordination diagram also showed relatively higher dissimilarities of tree communities between the disturbed and undisturbed plots at the upland than at the montane forests (Fig. 2c).

Elephant disturbances and insect diversity. The responses of individual insect groups' total species richness per sampling site to elephant disturbances were rather inconsistent among the studied elevations and seasons. Butterflies and fruit-feeding moths showed lower total species richness in the disturbed forests at both elevations during the transition from wet to dry seasons, which became higher or comparable to the undisturbed forests during the transition from dry to wet seasons (Fig. 3a,b; Supplementary Table S1). 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 (Fig. 3c; Supplementary Table S1).

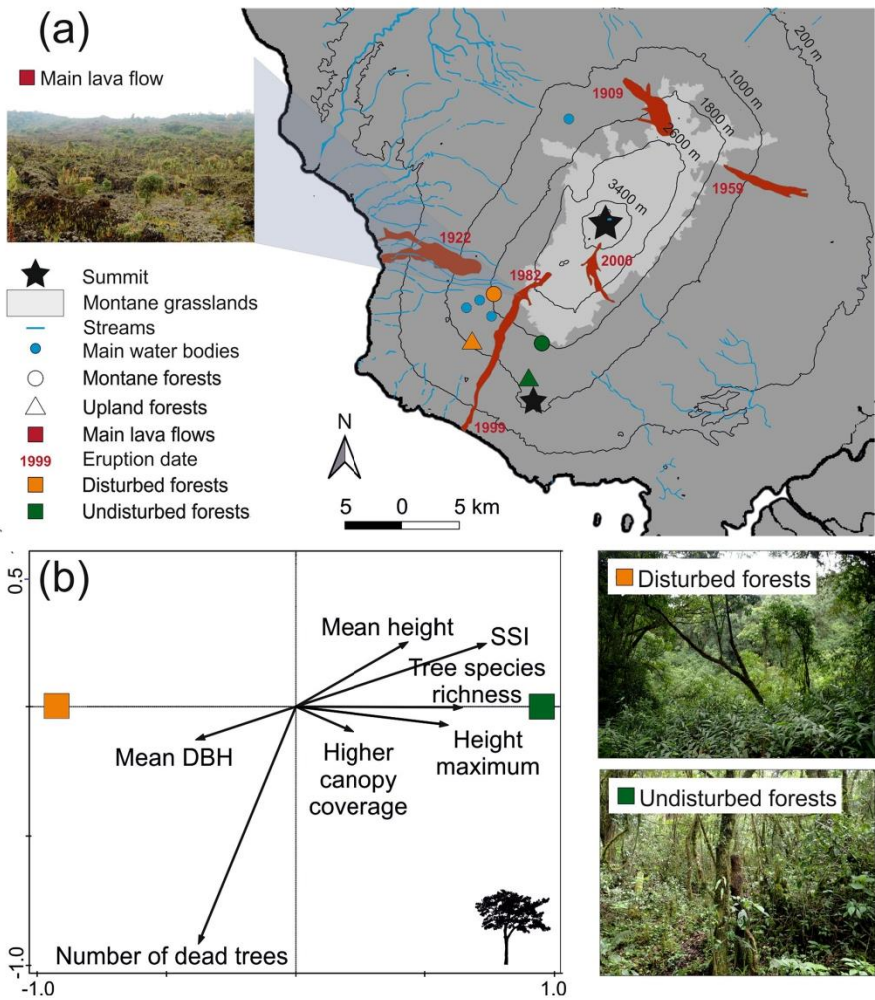


Figure 1. (a) Map of Mount Cameroon with the main lava flows, sampled forests and water resources. The background map was created in QGIS v. 3.10.0 'A Coruña' (<https://qgis.org>) and Corel Draw X7 (<https://www.coreldraw.com>). The pictures of disturbed and undisturbed forests were taken at the studied montane sites. (b) Redundancy analysis diagram visualizing effects of disturbances by elephants on forest structure.

The effects of elephant disturbances on insect species richness per plot also differed among the studied insect groups. The interactions disturbance \times season and disturbance \times elevation were significant for all insect groups (Table 1), indicating complex effects of elephant disturbances on insect species richness. GEEs showed a significant positive effect of elephant disturbances on species richness of butterflies and light-attracted moths (Fig. 3d,f; Table 1). No significant effect of elephant disturbances was detected for fruit-feeding moths (Table 1). Both butterflies and fruit-feeding moths were significantly species richer at the lower altitudes, whilst no significant effect of elevation on light-attracted moths was revealed (Fig. 3d–f; Table 1). Insignificant effects of season were shown

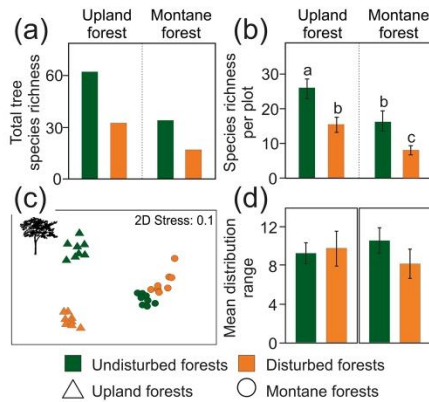


Figure 2. Differences in tree species richness, community composition, and mean distribution range between forests disturbed and undisturbed by elephants. Tree species richness per (a) forest site, and (b) per sampling plot estimated by GEE (estimated means with 95% unconditional confidence intervals). The letters visualize results of the post-hoc pairwise comparisons. (c) NMDS diagrams of the tree community compositions at the sampled forest plots. (d) Mean distribution range of trees per sampling plot estimated by GEE.

| Focal group | Tested variable | Species richness | | | Distribution range | | |
|-----------------------|-------------------------|------------------|---------------|----------------------|--------------------|---------------|----------------------|
| | | df | Wald χ^2 | p-value ^a | df | Wald χ^2 | p-value ^a |
| Trees | Disturbance | 1 | 21.9 | <0.001*** | 1 | 1.4 | 0.23 |
| | Elevation | 1 | 51.9 | <0.001*** | 1 | 0 | 0.86 |
| | Disturbance × Elevation | 1 | 1.3 | 0.25 | 1 | 3.9 | 0.05* |
| Butterflies | Disturbance | 1 | 4.7 | 0.031* | 1 | 9.5 | 0.002** |
| | Season | 1 | 0 | 0.964 | 1 | 67.6 | <0.001*** |
| | Elevation | 1 | 10.2 | 0.001** | 1 | 2.5 | 0.115 |
| | Disturbance × Season | 1 | 7.4 | 0.007** | 1 | 0.2 | 0.654 |
| | Disturbance × Elevation | 1 | 45.1 | <0.001*** | 1 | 7.3 | 0.007** |
| 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* | 1 | 5.1 | 0.024* |
| | Season | 1 | 2.5 | 0.112 | 1 | 0.8 | 0.372 |
| | Elevation | 1 | 2.4 | 0.123 | 1 | 6.9 | 0.009** |
| | Disturbance × Season | 1 | 8.9 | 0.003** | 1 | 0.5 | 0.462 |
| | Disturbance × Elevation | 1 | 67.0 | <0.001*** | 1 | 12.4 | <0.001*** |

Table 1. Results of the GEE models analyzing effects of disturbance, season and elevation on species richness and insects in forests disturbed and undisturbed by elephants on Mount Cameroon. ^a *p < 0.05; **p < 0.01; ***p < 0.001.

for all studied insect groups (Table 1). For butterflies and light-attracted moths, the pairwise post-hoc comparisons of disturbed and undisturbed forests showed that species richness was significantly higher in the disturbed upland forests for both groups, and significantly lower or not significantly different (depending on the sampled season) in the montane forests (Fig. 3d,f). In contrast, fruit-feeding moth species richness was significantly lower in the disturbed forests at both elevations during the transition from wet to dry season, but significantly richer during the transition from dry to wet season (Fig. 3e). The analyses of individual family species richness

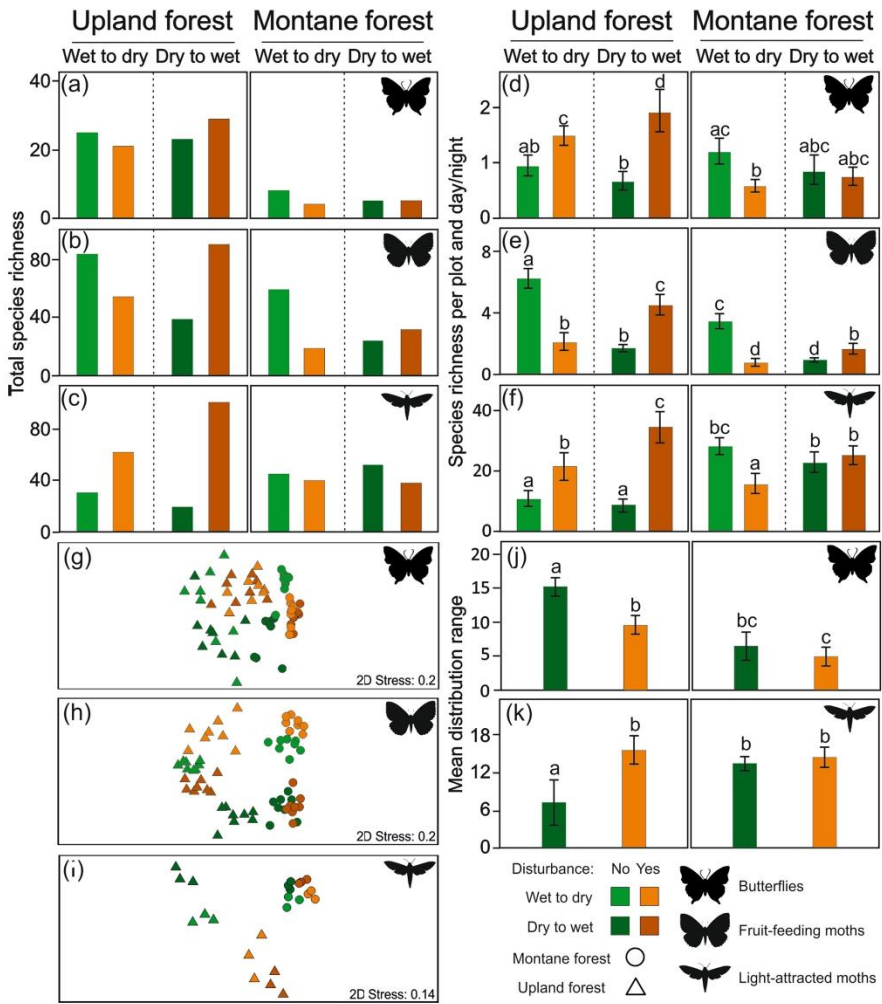


Figure 3. Species richness of insects per sampling site and season (a–c), and sampling plots and day or night (d–f) as estimated by GEEs (estimated means with 95% unconditional confidence intervals are visualized). (g–i) NMDS diagrams of insect community compositions at the sampled forest plots. (j,k) Mean distribution range of insects estimated by GEEs. Letters visualize results of the post-hoc pairwise comparisons.

showed significant effects of the disturbance \times season interaction for butterflies and light-attracted moths (butterflies: Pseudo-F: 12.8, p-value: < 0.001, adjusted explained variation: 36.4%; light-attracted moths: Pseudo-F: 15.8, p-value: < 0.001, adjusted explained variation: 49.1%; Supplementary Table S2). Whilst for butterflies, all families showed consistently higher species richness at disturbed upland forests, most of the analysed families of light-attracted moths had the highest species richness at undisturbed montane forest (Supplementary Fig. S1b,c). The only exceptions were Notodontidae with higher species richness at disturbed upland forest, and Lymantriinae with no apparent trend (Supplementary Fig. S1c).

Elephant disturbances significantly affected species composition of all focal insect groups in partial CCAs (butterflies: all-axes eigenvalue: 2.75; Pseudo-F: 4.6; p-value: <0.001; fruit-feeding moths: all-axes eigenvalue: 5.27; Pseudo-F: 3.2; p-value: <0.001; light-attracted moths: all-axes eigenvalue: 2.96; Pseudo-F: 4.5; p-value: <0.001). For butterflies and fruit-feeding moths, the first NMDS axes can be related to elevation, in contrast to light-attracted moths where elevation can be related to the second NMDS axis (Fig. 3g–i). All groups were well-clustered according to the disturbance type at both elevations. The effect of disturbance was interacting with season and elevation for all groups (Fig. 3g–i). Among all insect groups, light-attracted moths species composition responded to elephant disturbances very similarly to trees, with well-separated upland disturbed and undisturbed forest types and comparatively less heterogeneous montane forest samples (Figs. 2c, 3i).

Elephant disturbances and species' distribution range. Elephant disturbances and elevation showed marginally significant effects of their interaction on distribution range of tree species, although no significant separate effect was detected for them (Table 1). In the undisturbed forests, the mean tree species' distribution range was positively associated with increasing elevation, while negatively associated with increasing elevation in the disturbed forests. However, the pairwise post-hoc comparisons were insignificant (Fig. 2d).

Patterns of distribution range differed between the two analysed insect groups. Butterfly species' distribution range was significantly lower at high elevation and in the disturbed forests (Fig. 3j). Similarly, moths' mean distribution range was significantly affected by elephant disturbances and seasons (Table 1). Nevertheless, pairwise post-hoc comparisons showed that light-attracted moths in the undisturbed upland forest had a significantly lower distribution range than in all other studied forests, which did not significantly differ from each other (Fig. 3k).

Discussion

Our study has shown a strong effect of forest elephants on tropical forest biodiversity. Concordant to our first hypothesis, their long-term absence at the studied forests changed the forest structure. It has led to an increase of forest height, closure of its canopy, and dominance of smaller over large trees. This observed shift in forest structure can be interpreted by a combination of direct and indirect effects driven by forest elephants. Because of their high appetite and large body size, forest elephants surely eliminate some trees²⁵. They directly consume high amount of tree biomass, as well as their fruits and seeds^{33,34}. When struggling through forest, elephants break stems and sometimes even uproot trees, while their repeated trampling denude the forest floor and destroy fallen seeds and saplings²³. Moreover, the direct damages are likely to increase tree susceptibility to pathogens or decomposers, as shown in the previous study of termites²⁶. Although the number of dead trees seemed to poorly characterize the disturbed forests (potentially because of the significantly higher decomposition in elephant-disturbed forests²⁹), the higher tree density in the undisturbed plots supports this hypothesis. Thus, the presence of a few large trees in the plots disturbed by forest elephants can be explained by only a small portion of trees escaping the browsing pressure²³.

Together with altering the forest structure, forest elephants decreased tree species richness and change tree community composition, confirming our second hypothesis. Although forest elephants are generalized herbivores, they prefer particular tree and other plant species³⁴. Thereby, their selective browsing of palatable species affects tree mortality and recruitment, which can explain the observed differences in tree communities between the disturbed and undisturbed forests. Finally, similarly as in savanna, we can reasonably expect different resistance of tree species to repeated disturbances by forest elephants, or differences in their ability to recover from damages³⁵. The revealed higher species richness of Euphorbiaceae trees to the disturbed forest could indicate some resistance to elephant disturbances. Unfortunately, the knowledge of African forest elephants' browsing preferences and/or Afrotropical trees' resistance to disturbances are not enough to decide which effect prevails in the alterations of forest structure by elephants.

The presence of forest elephants impacted all studied herbivorous insect communities as well, although differently for particular insect groups. These can be related to the changes in composition of tree communities and in habitat structure in the disturbed forests. The upland forests disturbed by elephants harboured more species of butterflies and light-attracted moths. This effect was consistent for all butterfly families, although only for notodontid moths. However, all other effects of disturbances differed according to the studied elevation and season, as well as among the insect groups. Many tropical butterflies rely on forests gaps and solar radiation for their thermoregulation³⁶ and oviposition on larval food-plants (mostly herbs³⁷), therefore their diversity decrease after the upland forest elephant's enclosure cannot be surprising. By opening of forest canopy, forest elephants could support quantity and heterogeneity of resources available for butterflies. However, such hypothesis can hardly explain the detected decrease of light-attracted (night flying) moth diversity in the undisturbed upland forests. In fact, diversity of moths has been repeatedly shown to increase with diversity of trees, as the most common food plants for their caterpillars^{38,39}. Therefore, the opposite effect of disturbance by forest elephants can be expected, this was confirmed at least for most light-attracted moth families in the montane forests. Unfortunately, we do not have any other explanation of the positive effect of forest disturbances in the sampled upland forests. Contrastingly, fruit-feeding moths are relatively independent to forest structure²⁹. They can follow the spatiotemporal changes of ripe fruits (adult food) or young sprouts (larval food) more tightly than fruit-feeding butterflies, which could partly explain their seasonally inconsistent reaction to the elephant disturbances. Unfortunately, no data to confirm or reject such hypothesis exist.

In the montane forests, we found no consistent changes of the insects' diversity, as it strongly varied with season and studied insect group. Moreover, the communities of all insect groups were highly homogeneous in both forest types in this high elevation. The montane forests on Mount Cameroon are already relatively open and with limited tree diversity⁴⁰ that additional disturbances by elephants could hardly increase habitat heterogeneity

even for butterflies. Moreover, some tree dominants in the montane forests, such as *Schefflera abyssinica* and *S. mami*, are (semi)deciduous during the dry season which generally open the higher canopy even in the undisturbed forests. Simultaneously, these dominants get typically recruited as epiphytes, later strangling their hosts⁴¹. Therefore, they may more efficiently escape from any elephant effects. We hypothesize that these effects together result in more similarity between the disturbed and undisturbed forests at higher elevations. Last but not least, we have recently revealed a strong seasonal shift in elevational ranges of both butterflies and moths⁴²; the seasonal discrepancies in the effect of disturbance could be related to it. Unfortunately, we do not have any detailed data on this phenomenon from the undisturbed forest plots.

Recently, Poulsen et al.¹⁹ discussed the fate of Afrotropical forests in the future world without forest elephants. The authors hypothesized that their loss would increase understory stem density and change tree species composition. We concur with Poulsen's hypotheses from our data study. Moreover, we have shown that the change of forest structure and composition can have strong cascading effects on other trophic levels, at least in the upland forests. Hawthorne and Parren²¹ demonstrated that the disappearance of forest elephants from several Ghanaian forests did not have any remarkable effect on plant populations at the country level. However, our study has shown that the local consequences of forest elephants' disappearance can be highly significant for trees, as well as for higher trophic levels.

Natural disturbances are important ecological processes increasing habitat heterogeneity^{6,43}. Interestingly, our results showed that some groups of trees and insects may respond positively to the natural disturbances by forest elephants, whilst some others respond negatively. Because many tropical species have highly specific habitat needs^{6,29,44}, homogeneous non-disturbed ecosystems could be impoverished for such open-habitat specialists, whilst the too disturbed ecosystems would lack the close-canopy forest species. Therefore, only the dynamically disturbed ecosystems could harbour the 'complete' local biodiversity. Although more comparative studies are required, forest elephant extinction would accelerate the vegetation succession, enclose the forest canopy, and generally impoverish the habitat heterogeneity in Afrotropical forests. These would be unavoidably followed by changes in tropical forest communities and by declines of range-restricted species that profit from disturbances, as we have shown for some of the herbivorous insects in the upland forests.

In conclusion, our study showed that African forest elephants contribute for maintaining the tropical forest heterogeneity and tree diversity. The elephant-related habitat heterogeneity increased the heterogeneity of available niches and sustain diverse communities of Afrotropical insects. Despite the lack of any data, we can speculate on consequences for biodiversity at other trophic levels. Nevertheless, we have confirmed the African forest elephant as a key-stone species in the Afrotropical forest ecosystems. Altogether, the maintenance of forest elephant populations in Afrotropical forests appears to be necessary to prevent biodiversity declines. Unfortunately, the decline of forest elephant populations in West and Central African tropical forests is alarming, and most probably have already been followed by other species extinctions. It is even highly probable that such processes are already ongoing, although unrecorded in one of the least studied biogeographic areas in the world. Therefore, we urge for more efficient conservation of the remaining populations of forest elephants. Their effects on the entire tropical forest ecosystems must be recognized and incorporated into the management plans of Afrotropical protected areas.

Methods

Study area. Mount Cameroon (South-Western Province, Cameroon) is the highest mountain in West/Central Africa. This active volcano rises from the Gulf of Guinea seashore up to 4095 m asl. Its southwestern slope represents the only complete altitudinal gradient of primary forests from lowland up to the timberline (~2200 m asl.) in the Afrotropics. Belonging to the biodiversity hotspot, Mount Cameroon harbour numerous endemics^{45–47}. With >12,000 mm of yearly precipitation, foothills of Mount Cameroon belong among the globally wettest places⁴². Most precipitation occur during the wet season (June–September; >2000 mm monthly), whilst the dry season (late December–February) usually lacks any strong rains⁴². Since 2009, most of its forests have become protected by the Mount Cameroon National Park.

Volcanism is the strongest natural disturbance on Mount Cameroon with the frequency of eruptions every ten to thirty years. Remarkably, on the studied southwestern slope, two eruptions in 1982 and 1999 created a continuous strip of bare lava rocks (in this study referred as 'the lava flow') interrupting the forests on the southwestern slope from above the timberline down to the seashore (Fig. 1a).

A small population of forest elephants (*Loxodonta cyclotis*) strongly affects forests above ca. 800 m asl. on the southwestern slope^{28,45}. It is highly isolated from the nearest populations of the Korup NP and the Banyang-Mbo Wildlife Sanctuary, as well as from much larger metapopulations in the Congo Basin⁴⁸. It has been estimated to ~130 individuals with a patchy local distribution²⁸. On the southwestern slope, they concentrate around three crater lakes representing the only available water sources during the high dry season, although their local elevational range covers the gradient from lowlands to montane grasslands just above the timberline²⁸. They rarely (if ever) cross the old lava flows, representing natural obstacles dividing forests of the southwestern slope to two blocks with different dynamics. As a result, forests on the western side of the longest lava flow have an open structure, with numerous extensive clearings and 'elephant pastures', whereas eastern forests are characteristic by undisturbed dense canopy (Fig. 1). To our knowledge, the two forest blocks are not influenced by any extensive human activities, nor differ in any significant environmental conditions^{28,45}. Hereafter, we refer the forests west and east from the lava flow as *disturbed* and *undisturbed*, respectively. Effects of forest elephant disturbances on communities of trees and insects were investigated at four localities, two in an upland forest (1100 m asl.), and two in a montane forest (1850 m asl.).

Tree diversity and forest structure. At each of four sampling sites, eight circular plots (20 m radius, ~150 m from each other) were established in high canopy forests (although sparse in the undisturbed sites), any larger clearings were avoided. In the disturbed forest sites, the plots were previously used for a study of elevational diversity patterns^{40,42}. In the undisturbed forest sites, plots were established specifically for this study.

To assess the tree diversity in both disturbed and undisturbed forest plots, all living and dead trees with diameter at breast height (DBH, 1.3 m) ≥ 10 cm were identified to (morpho)species (see⁴⁰ for details). To study impact of elephant disturbances on forest structure, each plot was characterized by twelve descriptors. Besides *tree species richness*, *living* and *dead trees* with DBH ≥ 10 cm were counted. Consequently, DBH and basal area of each tree were measured and averaged per plot (*mean DBH* and *mean basal area*). Height of each tree was estimated and averaged per plot (*mean height*), together with the tallest tree height (*maximum height*) per plot. From these measurements, two additional indices were computed for each tree: stem slenderness index (SSI) was calculated as a ratio between tree height and DBH, and tree volume was estimated from the tree height and basal area⁴⁰. Both measurements were then averaged per plot (*mean SSI* and *mean tree volume*). Finally, following Grote⁵⁰, proxies of shrub, lower canopy, and higher canopy coverages per plot were estimated by summing the DBH of three tree height categories: 0–8 m (shrubs), 8–16 m (lower canopy), > 16 m (higher canopy).

Insect sampling. Butterflies and moths (Lepidoptera) were selected as the focal insect groups because they belong into one of the species richest insect orders, with relatively well-known ecology and taxonomy, and with well-standardized quantitative sampling methods. Moreover, they strongly differ in their habitat use⁵⁹. In conclusion, butterflies⁵¹ and moths⁵² are often used as efficient bioindicators of changes in tropical forest ecosystems, especially useful if both groups are combined in a single study. Within each sampling plot, fruit-feeding lepidopterans were sampled by five bait traps (four in understory and one in canopy per sampling, i.e. 40 traps per sampling site, and 160 traps in total) baited by fermented bananas (see Maicher et al.⁴² for details). All fruit-feeding butterflies and moths (hereinafter referred as *butterflies* and *fruit-feeding moths*) were killed (this is necessary to avoid repetitive counting of the same individuals⁵³) daily for ten consecutive days and identified to (morpho)species.

Additionally, moths were attracted by light at three 'mothing plots' per sampling site, established out of the sampling plots described above. These plots were selected to characterize the local heterogeneity of forest habitats and separated by a few hundred meters from each other. To keep the necessary standardisation, all mothing plots at both types of forest were established in semi-open patches, avoiding both dense forest and larger openings. Moths were attracted by a single light (see Maicher et al.⁴² for details) during each of six complete nights per elevation (i.e., two nights per plot). Six target moth groups (Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae, and Eupterotidae; hereafter referred as *light-attracted moths*) were collected manually, killed, and later identified into (morpho)species. The three lepidopteran datasets (butterflies, and fruit-feeding and light-attracted moths) were extracted from Maicher et al.⁴² for the disturbed forest plots, whilst the described sampling was performed in the undisturbed forest plots specifically for this study. Voucher specimens were deposited in the Nature Education Centre, Jagiellonian University, Kraków, Poland.

To partially cover the seasonality⁵⁴, the insect sampling was repeated during transition from wet to dry season (November/December), and transition from dry to wet season (April/May) in all disturbed and undisturbed forest plots.

Diversity analyses. To check sampling completeness of all focal groups, the sampling coverages were computed to evaluate our data quality using the *iNEXT* package⁵⁵ in R 3.5.1⁵⁶. For all focal groups in all seasons and at all elevations, the sampling coverages were always ≥ 0.84 (mostly even ≥ 0.90), indicating a sufficient coverage of the sampled communities (Supplementary Table S1). Therefore, observed species richness was used in all analyses⁵⁷.

Effects of *disturbance* on species richness were analysed separately for each focal group by Generalized Estimated Equations (GEE) using the *geepack* package⁵⁸. For trees, species richness from individual plots were used as a 'sample' with an independent covariance structure, with *disturbance*, *elevation*, and their interaction treated as explanatory variables. For lepidopterans, because of the temporal pseudo-replicative sampling design, species richness from a sampling day (butterflies and fruit-feeding moths) or night (light-attracted moths) at individual plot was used as a 'sample' with the first-order autoregressive relationship *AR(1)* covariance structure (i.e. repeated measurements design). *Disturbance*, *season*, *elevation*, *disturbance* \times *season*, and *disturbance* \times *elevation* were treated as explanatory variables. All models were conducted with Poisson distribution and log-link function. Pairwise post-hoc comparisons of the estimated marginal means were compared by Wald χ^2 tests. Additionally, species richness of individual families of trees, butterflies, and light-attracted moths were analysed by Redundancy Analyses (RDA), a multivariate analogue of regression, based on the length of gradients in the data⁵⁹. All families with > 5 species were included in three RDA models, separately for the studied groups (the subfamily name Lymantriinae is used, because they are the only group of the hyperdiverse Erebidae family of the light-attracted moths). Fruit-feeding moth families were not analyzed because 83% of their specimens belonged to Erebidae and all other families were therefore minor in the sampled data. Species richness of individual families per plot were used as response variables, whilst interaction of *disturbance* and *elevation* were applied as factorial explanatory variable (for butterflies and light-attracted moths, the temporal variation was treated by adding *season* as a covariate).

Differences in composition of communities between the disturbed and undisturbed forests were analysed by multivariate ordination methods⁵⁹, separately for each focal group. Firstly, the main patterns in species composition of individual plots were visualized by Non-Metric Multidimensional Scaling (NMDS) in Primer-E v6⁶⁰. NMDSs were generated using Bray–Curtis similarity, computed from square-root transformed species

abundances per plot. Subsequently, influence of *disturbance* on community composition of each focal group was tested by constrained partial Canonical Correspondence Analyses (CCA) with log-transformed species' abundances as response variables and *elevation* as covariate⁵⁹. Significance of all partial CCAs were tested by Monte Carlo permutation tests with 9999 permutations.

Finally, differences in the forest structure descriptors between the disturbed and undisturbed forests were analysed by partial Redundancy Analysis (RDA). Prior to the analysis, preliminary checking of the multicollinearity table among the structure descriptors was investigated. Only forest structure descriptors with pairwise collinearity < 0.80, i.e. tree species richness, number of dead trees, mean DBH, mean height, maximum height, mean SSI, and higher canopy coverage, were included in these analyses. Their log-transformed values were used as response variables⁵⁹. RDA was then run with *disturbance* as explanatory variable and *elevation* as covariate, and tested by Monte Carlo permutation test (9999 permutations). All CCAs and RDAs were performed in Canoco 5⁶¹.

Species distribution range. To analyse if the elephant disturbance supports rather range-restricted species or widely distributed generalists, we used numbers of Afrotropical countries with known records of each tree and lepidopteran species as a proxy for their distribution range; we are not aware of any more precise existing dataset covering all studied groups for the generally understudied Afrotropics. Because of the limited knowledge on Afrotropical Lepidoptera, we ranked only butterflies and light-attracted Spingidae and Saturniidae moths (the latter two analysed together and referred as *light-attracted moths*). This distribution data were excerpted from the RAINBIO database for trees⁶², Williams⁶³ for butterflies, and Afromoths.net for moths⁶⁴; all considered as the most comprehensive databases. Two non-native trees (*Persea americana* and *Cecropia peltata*) and three tree species not included in the RAINBIO database and all morphospecies were excluded from these analyses. In total, 73 species of trees and 71 species of insects (50 butterflies and 21 moths) were included in the distribution range analyses.

To consider 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 and their sums were divided by the total number of individuals recorded at each sample. These *mean distribution ranges* per sample were then compared between disturbed and undisturbed forest sites by GEE analyses (with normal distribution; independent covariance structure) following the same model design as for the above-described comparisons of species richness.

Data availability

Data available via the Zenodo repository (<https://doi.org/10.5281/zenodo.4300119>).

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Author contributions

V.M. and R.T. conceived and designed the study, coordinated all its parts, and wrote the manuscript. V.M. performed the statistical analyses. All authors collected the field data and/or processed the collected material, including its identification. All authors critically revised the manuscript and gave the final approval for its publication.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to V.M. or R.T.

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SUPPORTING INFORMATION

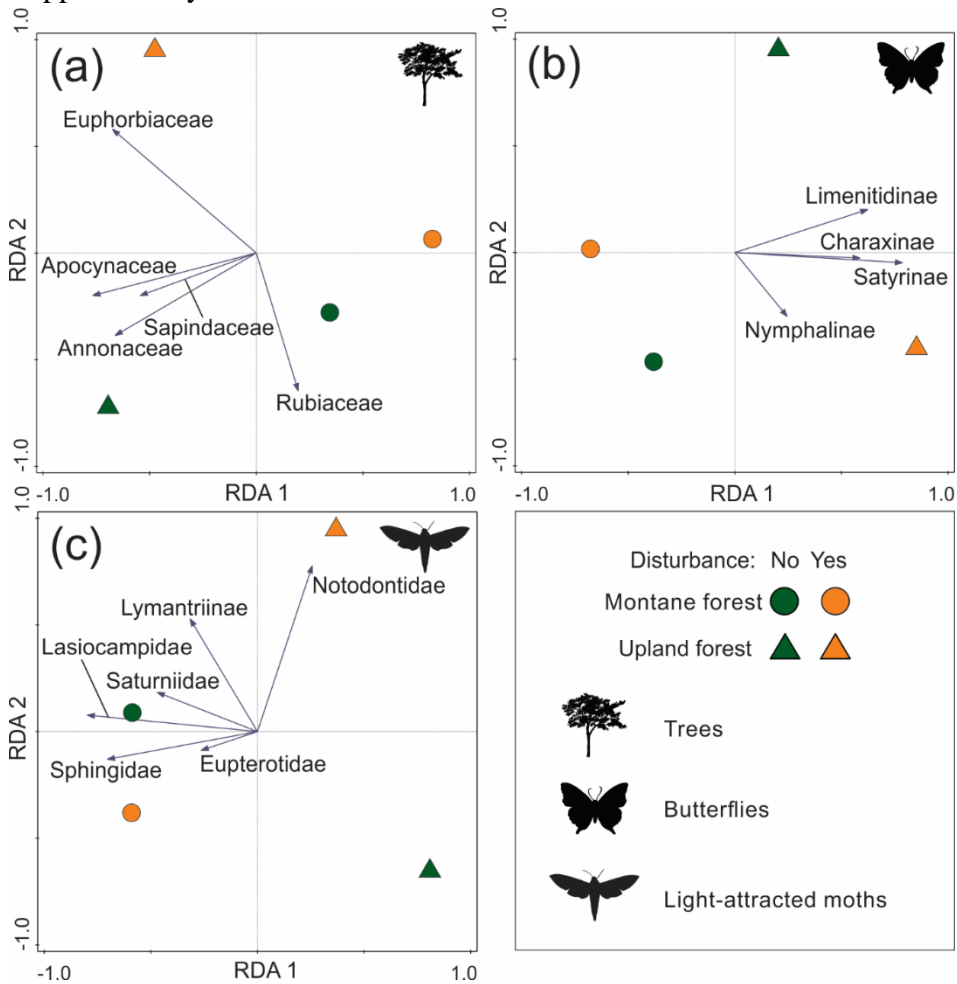
Table S1. Abundances and diversity of trees and insects in forests disturbed and undisturbed by elephants in particular seasons.

| | | Undisturbed forests | | | | Disturbed forest | | | |
|-----------------------|-------------------|---------------------|------------|----------------|------------|------------------|------------|----------------|------------|
| | | 1,100 m a.s.l. | | 1,850 m a.s.l. | | 1,100 m a.s.l. | | 1,850 m a.s.l. | |
| | | 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 | Abundance | 802 | | 438 | | 511 | | 274 | |
| | Species richness | 62 | | 32 | | 32 | | 16 | |
| | Sampling coverage | 0.98 | | 0.99 | | 0.99 | | 0.99 | |
| Butterflies | Abundance | 74 | 67 | 355 | 95 | 255 | 193 | 68 | 119 |
| | Species richness | 25 | 23 | 8 | 5 | 21 | 29 | 4 | 5 |
| | Sampling coverage | 0.88 | 0.85 | 0.99 | 0.99 | 0.97 | 0.95 | 1.00 | 0.99 |
| Fruit-feeding moths | Abundance | 1,806 | 184 | 458 | 93 | 192 | 469 | 101 | 144 |
| | Species richness | 85 | 39 | 60 | 24 | 55 | 92 | 19 | 32 |
| | Sampling coverage | 0.98 | 0.91 | 0.94 | 0.85 | 0.88 | 0.92 | 0.94 | 0.85 |
| Light-attracted moths | Abundance | 326 | 61 | 633 | 473 | 208 | 469 | 383 | 567 |
| | Species richness | 30 | 19 | 45 | 52 | 62 | 101 | 40 | 38 |
| | Sampling coverage | 0.97 | 0.84 | 0.98 | 0.96 | 0.88 | 0.90 | 0.96 | 0.99 |

Table S2. Summary of the redundancy analyzes (RDA) analysing the effect of interaction between *disturbance* by forest elephant and *elevation* for trees, butterflies, and light-attracted moths species richness of families with ≥ 5 species. For butterflies and light-attracted moths, the temporal variation was treated by adding *season* as a covariate. See biplots in Supplementary Fig. S1.

| Statistic | Axis 1 | Axis 2 |
|---|-----------|-----------|
| Trees | | |
| Adjusted explained variation: 52.3% | | |
| Eigenvalues | 0.4 | 0.2 |
| Explained variation (cumulative) | 36.3 | 56.0 |
| Pseudo-canonical correlation | 0.9 | 0.8 |
| Explained fitted variation (cumulative) | 64.0 | 98.4 |
| Butterflies | | |
| Adjusted explained variation: 36.4% | | |
| Eigenvalues | 0.4 | 0.03 |
| Explained variation (cumulative) | 35.9 | 39.3 |
| Pseudo-canonical correlation | 0.9 | 0.5 |
| Explained fitted variation (cumulative) | 91.0 | 99.6 |
| Light-attracted moths | | |
| Adjusted explained variation: 49.1% | | |
| Eigenvalues | 0.3 | 0.2 |
| Explained variation (cumulative) | 29.6 | 47.2 |
| Pseudo-canonical correlation | 0.9 | 0.8 |
| Explained fitted variation (cumulative) | 56.4 | 90.0 5 |

Figure S1. RDA ordination diagrams visualizing the effect of interaction between *disturbance* by elephants and *elevation* for species richness of families of (a) trees, (b) fruit-feeding butterflies, and (c) light-attracted moths. For butterflies and light-attracted moths, the temporal variation was treated by adding season as a covariate. See detailed results in Supplementary Table S2.



CHAPTER III

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

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. (2019).

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Kobe and Pavel on their way to empty traps at the highest elevation (treeline, 2,200 m a.s.l.) of the gradient on Mount Cameroon. © S. Delabye

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

Vincent Maicher^{1,2,3}  | Szabolcs Sáfíán^{2,4} | Mercy Murkwe^{3,5} | Sylvain Delabye^{1,2}  | Łukasz Przybyłowicz⁶  | Pavel Potocký¹  | Ishmeal N. Kobe^{3,5}  | Štěpán Janeček³  | Jan E. J. Mertens³  | Eric B. Fokam⁵  | Tomasz Pyrcz^{7,8}  | Jiří Doležal^{2,9}  | Jan Altman⁹  | David Hořák³  | Konrad Fiedler¹⁰  | Robert Trokek^{1,3} 

¹Biology Centre, Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czechia

²Departments of Zoology, Faculty of Science, University of South Bohemia, Ceske Budejovice, Czechia

³Department of Ecology, Faculty of Science, Charles University, Prague, Czechia

⁴Institute of Silviculture and Forest Protection, Faculty of Forestry, University of West Hungary, Sopron, Hungary

⁵Department of Zoology and Animal Physiology, Faculty of Science, University of Buea, Buea, Cameroon

⁶Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland

⁷Institute of Zoology and Biomedical Research, Jagiellonian University, Krakow, Poland

⁸Nature Education Centre of the Jagiellonian University, Krakow, Poland

⁹Institute of Botany, Czech Academy of Sciences, Trebon, Czechia

¹⁰Department of Botany & Biodiversity Research, University of Vienna, Vienna, Austria

Correspondence

Robert Trokek, Department of Ecology, Faculty of Science, Charles University, Vinicna 7, CZ-12844 Prague, Czechia.
Email: robert.trokek@gmail.com

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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 an 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-catching (126 nights) at seven elevations evenly distributed along the elevational gradient from sea level (30 m a.s.l.) to timberline (2,200 m a.s.l.). Sampling was repeated in three seasons.

Results: 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 five groups, most of them ascending during the dry season. Seasonal shifts of species' elevational ranges were mostly responsible for these diversity pattern shifts along elevation: we found general upward shifts in fruit-feeding butterflies, fruit-feeding moths and Lymantriinae from beginning to end of the dry season. Contrarily, Arctiinae shifted upwards during the wet season. The average seasonal shifts of elevational ranges often exceeded 100 m and were even several times higher for numerous species.

Main conclusions: We report seasonal uphill and downhill shifts of several lepidopteran groups. The reported shifts can be driven by both delay in weather seasonality and shifts in resource availability, causing phenological delay of adult hatching and/or adult migrations. Such shifts may lead to misinterpretations of diversity patterns along elevation if seasonality is ignored. More importantly, considering the surprising extent of seasonal elevational shifts of species, we encourage taking account of such

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natural temporal dynamics while investigating the global climate change impact on communities of Lepidoptera in tropical mountains.

KEYWORDS

Afrotropics, altitude, biodiversity patterns, elevational ranges, elevational shifts, Lepidoptera, phenology, seasonality, spatio-temporal dynamics, tropical rainforest

1 | INTRODUCTION

Research on biodiversity patterns along elevational gradients has crucially contributed to our understanding of species distribution and co-existence (McCain & Grytnes, 2010). Increasingly unfavourable climatic conditions, reduction of habitat area, and constraints in resource diversity and availability have been linked with the diversity decrease in many taxa towards the highest elevations (Forero-Medina, Joppa, & Pimm, 2011; Laurance et al., 2011; McCain & Grytnes, 2010). Simultaneously, species richness of many groups, including Lepidoptera (Beck et al., 2017; Pyrcz & Wojtusiak, 2002; Pyrcz, Wojtusiak, & Garlacz, 2009), peaks at mid-elevations (Colwell et al., 2016; McCain & Grytnes, 2010). Colwell et al. (2016) explained this phenomenon by combined effects of geometric constraints and a unimodal gradient of favourable environmental conditions. However, our understanding of lepidopteran biodiversity organization along elevation is geographically biased. In particular, the large knowledge gap remains in the understudied Afrotropics (Beck et al., 2017), with the only exception of data from Mount Kilimanjaro (Axmacher et al., 2004, 2009; Peters et al., 2016).

Despite the historical concept of 'aseasonal' tropics, tropical insect biodiversity is known to be strongly seasonal (Kishimoto-Yamada & Itioka, 2015; Wolda, 1988). Such 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, Lande, Chacon, & DeVries, 2014; Grøtan, Lande, Engen, Sæther, & DeVries, 2012; Maicher et al., 2018; Valtonen et al., 2013). In contrast, montane insect phenology is crucially driven by seasonal changes of temperature (Bishop, Robertson, van Rensburg, & Parr, 2014; Boulter, Lambkin, & Starick, 2011; Wardhaugh, Stone, & Stork, 2018). Divergent pressures on communities at different elevations might substantially influence the spatial distribution of species diversity along elevation, as well as its temporal dynamics. However, phenological aspects have been ignored in most studies of tropical elevational biodiversity patterns. Most studies have focused on the patterns of biodiversity along tropical elevational gradients within a single season, or have even neglected local seasonality at all. In our opinion, to fully understand the organization of tropical biodiversity, we need to include its temporal aspects.

Biodiversity of tropical mountains has also recently been discussed in terms of the global change (Colwell, Brehm, Cardelús, Gilman, & Longino, 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 (Colwell et al., 2008; Sheldon, Yang, & Tewksbury, 2011). Recently, such upward shifts of lepidopteran elevational ranges related to the global change have been reported from tropical mountains (Chen, Hill, Ohlemüller, Hill, Ohlemüller, Roy, & Thomas, 2011; Chen, Hill, Shiu, et al., 2011; Chen et al., 2009; Laurance et al., 2011). However, these studies consistently neglected the seasonal dynamics of species' ranges since their data were either collected during a single season only or were lumped across seasons (e.g. Ashton et al., 2016; Brehm & Fiedler, 2003). Nevertheless, seasonality is known to strongly affect distribution, abundance and diversity of lepidopteran communities in many tropical ecosystems (Grøtan et al., 2014, 2012; Maicher et al., 2018; Valtonen et al., 2013). 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, the knowledge of natural intra-annual shifts of elevational ranges remains very poor, although crucial for the evaluation of the global change impacts.

Here, we report the first extensive and standardized study of temporal biodiversity patterns of nine lepidopteran groups along an elevational gradient in tropical forest ecosystems. We sampled Mount Cameroon, the only continuously forested gradient from lowland to timberline in the Afrotropics, and thereby produced the second Afrotropical dataset on lepidopteran diversity patterns along elevation. Our main aim was to analyse if the elevational patterns of species richness differ among three different seasons (dry season and both transitions between dry and wet seasons), and if there is any seasonal turnover of communities along elevation. To better understand the inter-seasonal changes, we separated inter-seasonal species turnover at the community level and shifts of individual species' elevational ranges. We expected the latter to represent an important part of the inter-seasonal community differences.

2 | MATERIALS AND METHODS

2.1 | Study sites

All data were collected at seven elevations (Table 1; Figure S1 in Appendix S1; Ferenc et al., 2016, 2018) on southwestern slopes of Mount Cameroon, Southwestern Province, Cameroon, the highest mountain of West/Central Africa (4,095 m a.s.l.) and an important hotspot of biodiversity and endemism for many taxa including Lepidoptera (Ustjuzhanin, Kovtunovich, Sáfián, Maicher, & Tropek,

TABLE 1 Summary of the sampled localities on Mount Cameroon

| Locality | Elevation (m a.s.l.) | Latitude | Longitude | Vegetation type | Sampling periods | | |
|-------------------|----------------------|------------|------------|--|------------------|--------------|--------------|
| | | | | | Wet to dry | Dry | Dry to wet |
| Dikholo Peninsula | 30 m | N 03.9818° | E 09.2625° | Coastal forest | Oct 2017 | Jan 2015 | May 2015 |
| Bamboo Camp | 350 m | N 04.0899° | E 09.0517° | Mosaic of primary and secondary lowland forest | Dec 2014 | Feb 2016 | Apr 2015 |
| Drink Gari | 650 m | N 04.1022° | E 09.0630° | Primary lowland forest | Nov/Dec 2014 | Jan/Feb 2016 | Apr 2015 |
| PlanteCam Camp | 1.100 m | N 04.1175° | E 09.0709° | Upland forest locally disturbed by elephants | Dec 2014 | Jan/Feb 2016 | Apr 2015 |
| Crater Lake | 1.450 m | N 04.1443° | E 09.0717° | Submontane forest locally disturbed by elephants | Nov 2016 | Feb 2017 | Apr/May 2017 |
| Elephant Camp | 1.850 m | N 04.1453° | E 09.0870° | Montane forest locally disturbed by elephants | Nov 2014 | Feb 2017 | Apr 2017 |
| Mann's Spring | 2.200 m | N 04.1428° | E 09.1225° | Montane forest close to the timberline | Nov 2016 | Jan/Feb 2017 | Apr 2017 |

2018). Its southwestern slope offers the only continuous elevational gradient of near-pristine tropical rainforest from lowland (c. 350 m a.s.l.) to the timberline (c. 2,100–2,300 m a.s.l.) on the continent.

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). The well-pronounced seasonality consists of one wet (June–September) and one dry season (late December–February), separated by relatively short transition seasons (Fraser, Hall, & Healey, 1998; Figure 1, Table S1 in Appendix S2). This seasonal cycle is highly regular and predictable and we considered its intra-annual circularity when planning

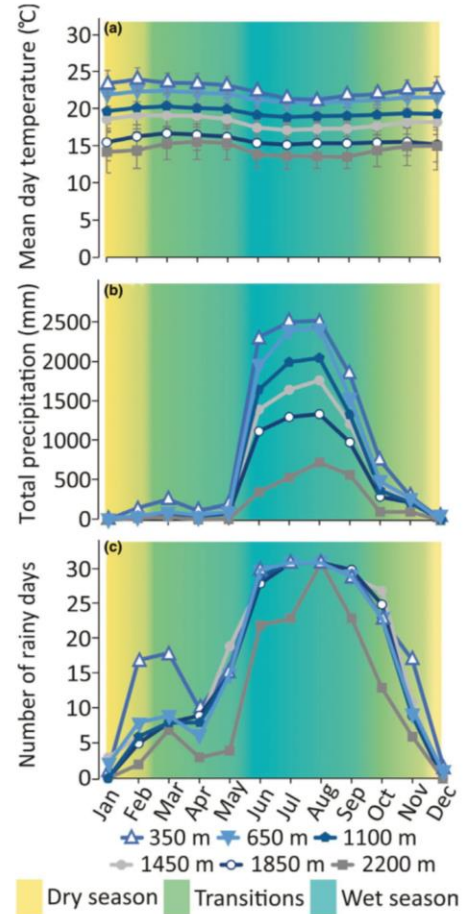


FIGURE 1 Weather on Mount Cameroon. (a) Mean daily temperature, (b) monthly precipitation, and (c) number of rainy days (>2 mm of rainfall)

our sampling schedule. The southwestern slope foothills are among the rainiest places in the world, with annual precipitation often exceeding 10,000 mm (Fraser et al., 1998), with monthly precipitation over 1,500 mm between June and September. Rainfall is rare from November to February, especially at higher elevations (Figure 1, Table S1 in Appendix S2).

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

2.2 | Lepidoptera sampling

At each sampling elevation, lepidopterans were collected following two methods. Fruit-feeding Lepidoptera (hereafter *fruit-feeding butterflies* and *fruit-feeding moths*) were sampled using bait-traps, while seven groups of Lepidoptera (Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae and Eupterotidae) were attracted by light and collected manually. Each elevation was sampled at three distinct seasons: transition from wet to dry season, high dry season and transition from dry to wet season (see Table 1 for sampling periods at particular elevations). No sampling of Lepidoptera was logistically feasible during the high wet season because of Mount Cameroon's extreme weather conditions (Figure 1).

For our sampling, we used the plots already described in Ferenc et al. (2016, 2018). Within each sampling elevation, 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, Csontos, & Winkler, 2011), and baited with fermented mashed bananas. Four traps were installed in understorey and one trap was hung up at 20(±5) m height. The banana bait (c. 0.3 L) was refreshed every day and renewed every 3–5 days, depending on its quality. All traps were exposed for 10 consecutive days per season, during which all trapped lepidopterans were removed and counted daily. Each plot was sampled repeatedly in all three study seasons resulting in 16,800 trapping days (7 elevations × 16 plots × 5 traps × 10 trapping days × 3 seasons).

Moths were also attracted to an energy-saving bulb (type M036, produced by Hadex, Czechia: 4,100 K, 5,300 lm, 105 W, 230 V, 5U) powered by a portable generator. At each elevation, three plots were established a few hundred metres from each other, to partially cover local forest heterogeneity. The focal moth groups were manually collected from dusk till dawn in two nights per plot and season, that is, 126 complete nights altogether (7 elevations × 3 plots × 2 nights × 3 seasons).

Most butterflies and some common bait-trapped moths (especially Calpininae and Erebininae) were identified in the field. All other specimens were dried by silica gel, stored in glassine envelopes, and

later identified to (morpho)species level, based on external morphology and genitalia features using available literature, authors' expertise and several large reference collections. Voucher specimens are stored in the Nature Education Centre (CEP-MZUJ), Jagiellonian University, Krakow, Poland.

2.3 | Weather data

We recorded mean daily temperature, total monthly precipitation and the number of rainy days (defined as >2-mm rainfall per 24 hr) 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 (c. 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.

2.4 | Elevational patterns of species diversity

The nine focal groups (see above) were treated separately in all analyses. Except where specified, 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 coverage was used as a proxy of sampling completeness (*iNEXT* package, Hsieh, Ma, & Chao, 2016).

To test the changes of *species richness with elevation*, generalized linear mixed models (GLMMs, type II Wald χ^2 tests, negative binomial distribution to address overdispersion; *lme4* package, Bates, Mächler, Bolker, & Walker, 2015) were applied. *Elevation* was treated as fixed categorical factor, and *season* and *plot* (nested in elevation) as random intercept factors. For both bait-trapped groups, a sample corresponded to the pooled five trap catches from 10 trapping days at each plot per season; whereas for the light-trapped groups, a sample corresponded to the pooled catches from two sampling nights at each plot per season. Additionally, GLMM models were run separately for understorey and canopy bait-trapped communities. Differences among individual elevations were tested by post-hoc pairwise comparisons of the least square means with Tukey adjustments.

2.5 | 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 random intercept factor. *Species richness* per plot (in 10 sampling days, or 2 sampling nights per season) was fit into negative binomial models to avoid overdispersion.

Simultaneously, 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 transformation 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, 9,999 permutations) with community composition of sampling plots per season as a replicate. For fruit-feeding butterflies and fruit-feeding moths, both GLMM and NMDS models were run also separately for understorey and canopy datasets. Both NMDS and PERMANOVAs were performed in Primer-E v6 with PERMANOVA+ (Clarke & Gorley, 2006).

In the six groups with significant effects of the *elevation* × *season* interaction on species richness (both fruit-feeding groups, Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae), we further focused on the details of their inter-seasonal changes. The local seasonality was considered to follow a circular inter-annual trajectory (i.e. wet and dry seasons predictably follow each other, separated by the transition seasons) independent of the sampling year (e.g. the wet to dry transition is always considered as preceding the dry season in this circularity, although our data may have been sampled later). To determine if the changes are caused rather by species turnover or by shifts of species' elevational ranges, we firstly quantified the proportions of three species categories at each particular elevation and season: (a) *resident species*: those recorded at the same elevation in the previous season as well; (b) *shifted species*: those recorded only at any different elevation(s) in the previous season and (c) *appeared species*: those not recorded in the previous season at all. Singletons per locality and season were excluded from these visualizations.

Finally, we analysed inter-seasonal shifts of species' elevational ranges. We used three measures of elevational range, calculated for each season separately: species' (a) *highest elevation* (uppermost record); (b) *lowest elevation* (lowest record) and (c) *weighted mean elevation* (average of elevations for all individuals of a given species, Menéndez, González-Megías, Jay-Robert, & Marquéz-Ferrando, 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 of its relative isolation from the main transect and thus lower probability of any inter-seasonal migration of specimens.

3 | RESULTS

3.1 | 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 (morpho)species (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 (morpho)species (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 a.s.l. for all groups (350 m a.s.l.: Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae, Figure 2i,m,q,u,y,ac; 650 m a.s.l.: fruit-feeding butterflies, Eupterotidae, Figure 2a,ag; 1,100 m a.s.l.: fruit-feeding moths, Figure 2e), and then steadily declined towards the higher elevations. Elevation also significantly affected *species richness* per plot of all focal groups (Table S1 in Appendix S4), with its peaks at the lower elevations of 350 and 650 m a.s.l. (fruit-feeding butterflies, Arctiinae, Lymantriinae, Notodontidae, Lasiocampidae, Sphingidae, Saturniidae, Eupterotidae, Figure 2c,k,o,s,w,aa,ae,ai; the low-elevation plateau with a mid-peak sensu McCain & Grytnes, 2010) or mid-elevations of 650 and 1,100 m a.s.l. (fruit-feeding moths, Figure 2g; the mid-elevation peak). Above these mid-elevations, *species richness per plot* monotonously decreased with elevation for all groups but Eupterotidae. The lowest elevation was always, except for Eupterotidae, significantly species-poorer than 350 m a.s.l., usually comparably poor as the highest elevations (Figure 2). These patterns stayed relatively consistent for the separate analyses of canopy and understorey bait-trapped communities (Figure S1, Table S2 in Appendix S4).

3.2 | Seasonal changes of weather

Monthly changes of both temperature and precipitation are visualized in Figure 1 and listed in Table S1 in Appendix S2. Both weather measures decreased with elevation and changed with season. While mean daily temperatures did not fluctuate strongly (a few degrees difference between wet and dry seasons), precipitation and the number of rainy days strongly varied with season. Especially in the lowlands, >2 mm of rain fell virtually daily from June to September, exceeding 2,300 mm at 350 m a.s.l. from June to August. Precipitation decreased monotonously with elevation, 350 m was five times rainier than 2,200 m a.s.l. (with monthly precipitation still exceeding 500 mm there during the wet season).

3.3 | Seasonal changes of elevational diversity patterns

Seasonal shifts in *species richness* peaks were consistent per elevation (gamma diversity) and per plot (alpha diversity) for all focal groups. The effect of *elevation* × *season* interactions on *species richness* per plot was significant for fruit-feeding butterflies, fruit-feeding moths, Arctiinae, Lymantriinae and Lasiocampidae,

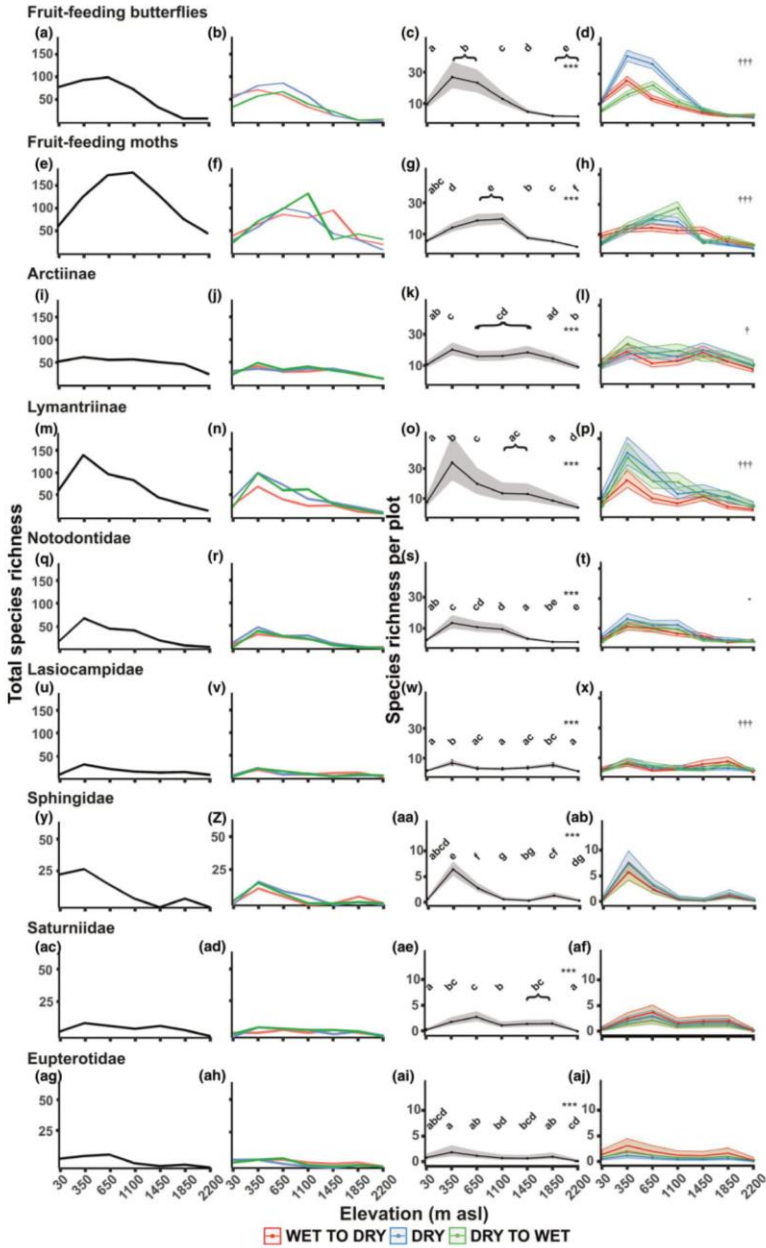


FIGURE 2 Changes of Lepidoptera species richness with elevation and season for individual focal groups on Mount Cameroon. The four columns represent total species richness per elevation, total species richness per elevation and season, GLMM results for species richness per plot and elevation (Table S1 in Appendix S4), and GLMM results per plot, elevation and season (Table S3 in Appendix S4). The latter two columns show means per plot with 95% unconditional confidence intervals; asterisks visualise results of individual tests (effects of elevation in the third column: * $p < .05$; ** $p < .01$; *** $p < .001$; and of elevation \times season interaction in the fourth column: $\bullet p < .01$; $\dagger p < .05$; $\dagger\dagger p < .01$; $\dagger\dagger\dagger p < .001$). Letters visualise results of the post-hoc pairwise comparisons

and marginally insignificant for Notodontidae (Figure 2, Table S3, Table S4 in Appendix S4); only these groups were analysed further. Species richness peaks of fruit-feeding butterflies (Figure 2b,d), fruit-feeding moths (Figure 2h) and Notodontidae (Figure 2r,t) ascended along elevation from the transition from wet to dry to the transition from dry to wet seasons (with the exception of species richness of fruit-feeding moths per elevation with less clear pattern, Figure 2f). On the contrary, Lasiocampidae showed a high-elevation peak at the transition from wet to dry and the mid-lower elevation peak in the other sampled seasons (Figure 2v,x), while species richness of Arctiinae varied locally without any obvious temporal pattern (Figure 2j,l). Although Lymantriinae showed a significant effect of elevation \times season interaction, no seasonal change of the species richness peak was visible (Figure 2n,p). The inter-seasonal shifts of

the butterfly species richness peak were clearly composed by the shifts of species distributions with elevation (Figure 3). The seasonal patterns were highly consistent for canopy and understorey communities of both fruit-feeding groups (Figure S1, Table S5 in Appendix S4). The proportions of *appeared* and *shifted* species of other groups varied among elevations and seasons, although especially in fruit-feeding moths the inter-seasonal community turnover was substantially related to the appearance of new species' adults (Figure 3).

The strong relationship of community composition to the seasons was 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 species-poor lowest (mainly Notodontidae, Sphingidae and Saturniidae) and/or highest (mainly fruit-feeding butterflies, Lasiocampidae, Sphingidae and Eupterotidae) elevation communities (Figure S1 in Appendix S5). These two elevations also differed from the rest of the gradient on the second ordination axes for some groups (Figure S1 in Appendix S5). The PERMANOVAs detected significant, although rather weak, effects of seasonality on the community composition of all focal groups (Table S1 in Appendix S6). Elevation \times season interactions were significant for all groups as well, indicating seasonally different community turnover along elevation (Table S1 in Appendix S6). These patterns remained consistent in separate analyses of canopy and understorey communities of both fruit-feeding groups (Figure S2 in Appendix S5, Table S2 in Appendix S6).

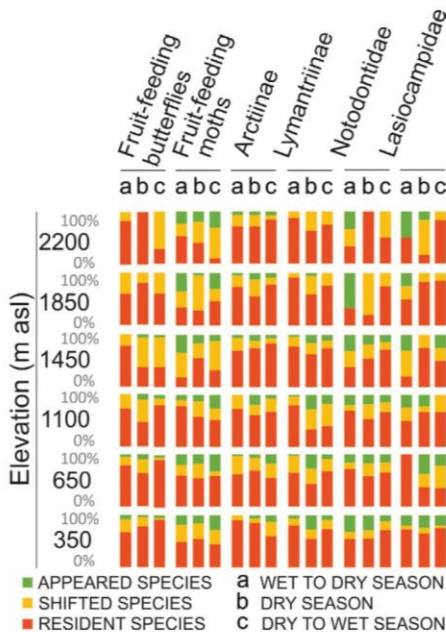


FIGURE 3 Proportions of Lepidoptera species at the studied elevations on Mount Cameroon which already occurred at the same elevation in the previous season (resident species), occurred only at some different elevation in the previous season (shifted species), and did not occur anywhere in the previous season (appeared species). Singletons were excluded

3.4 | Seasonal changes of elevational ranges

Significant seasonal shifts of the used metrics of species' elevational ranges were detected only in communities of fruit-feeding butterflies, fruit-feeding moths, Arctiinae, and Lymantriinae (Figure 4, Table S1 in Appendix S7). During the non-sampled wet season (i.e. between the two sampled transition seasons), *highest elevation* of all named groups but Arctiinae significantly decreased, together with *mean elevation* of fruit-feeding butterflies and fruit-feeding moths. Contrastingly, *lowest elevation* of Arctiinae significantly increased during the same period, while all three metrics did not significantly differ among the other seasons. After the wet season, all elevational range measures continuously shifted upwards for all other groups. These ascents started with the significant increase in *highest elevation* of fruit-feeding butterflies and Lymantriinae at the dry season beginning, followed by the significant increase in *mean elevation* and *lowest elevation* of fruit-feeding 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'

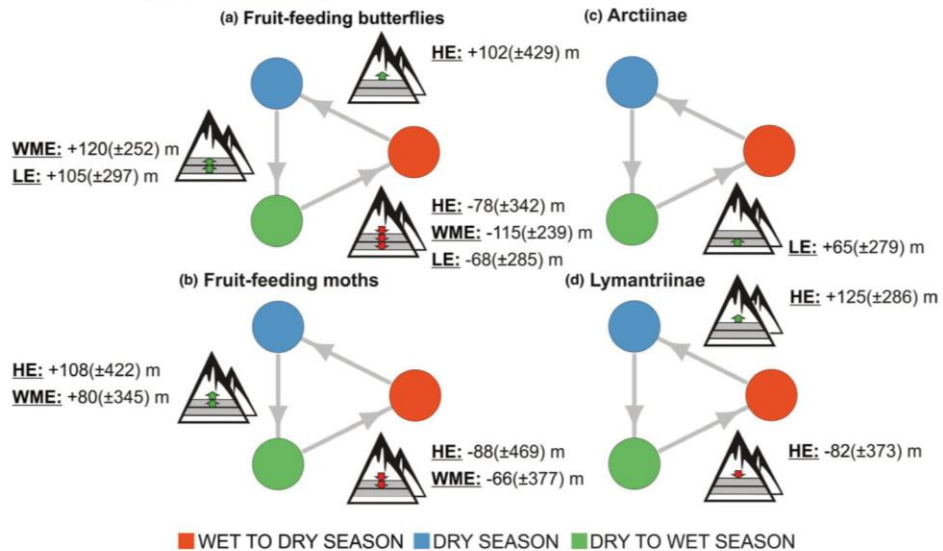


FIGURE 4 Significant inter-seasonal shifts of mean highest elevation (HE), weighted mean elevation (WME), and lowest elevation (LE) of species' ranges for (a) fruit-feeding butterflies, (b) fruit-feeding moths, (c) Arctiinae, and (d) Lymantriinae on Mount Cameroon. The arrows and values (mean with SD) visualise significant shifts (Wilcoxon signed-rank test, Table S1 in Appendix S7) of the individual range measures' shifts

ranges as well (Figure 5). The average values of inter-seasonal shifts of elevational ranges were mostly >100 m a.s.l. for all significant comparisons (Figure 4), and often much higher for individual species' ranges (Figure 5).

4 | DISCUSSION

4.1 | Biodiversity patterns along elevation

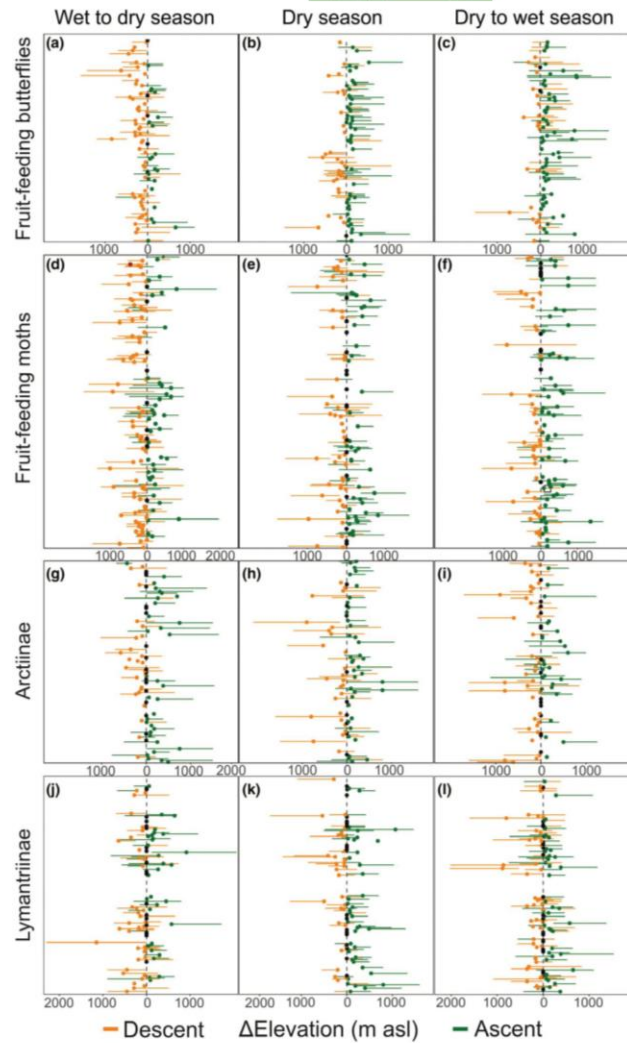
Unsurprisingly, species richness of all sampled groups of butterflies and moths changed along elevation on Mount Cameroon. In concordance with numerous studies of Lepidoptera and other organisms (e.g. Beck et al., 2017; Colwell et al., 2016), highest species richness of most studied lepidopteran groups was detected in lowlands (fruit-feeding 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 a.s.l.; Mongyeh, Philips, Kimbi, & Fokam, 2018) and birds (monotonous decline above 350 m a.s.l.; Ferenc et al., 2016) on Mount Cameroon. The observed patterns are also concordant with the lepidopteran studies on Mount Kilimanjaro, with a monotonous decline of moth diversity above 1,000 m a.s.l. (Axmacher et al., 2004; Peters et al., 2016). Unfortunately, as no lowlands can be sampled on Mount

Kilimanjaro, we cannot state if the described patterns from there are part of the linear diversity decrease along elevation, or rather fit to the mid-elevation peak type (cf. McCain & Grytnes, 2010).

4.2 | Seasonal diversity shifts along elevation

Species richness patterns of most focal groups differed among the sampled seasons. On Mount Cameroon, species richness of most lepidopteran groups in lowland and mid-elevations increased during the dry season and until the transition to the wet season, as already described in Maicher et al. (2018). These latter authors mostly explained this phenology by the locally extreme precipitation during the wet season constraining all life cycle stages, and the consequent emergence of most adults towards the dry season (Maicher et al., 2018). By extending the sampling to the complete rainforest elevational gradient, we have now shown that these increases in species richness differed seasonally among elevations, altogether causing the observed seasonal shifts of diversity peaks. Although we sampled each season only once, available long-term studies of tropical butterfly communities showed that the main seasonal species richness patterns (such as richest and poorest periods) remain relatively constant inter-annually (Grøtan et al., 2014, 2012; Valtonen et al., 2013). However, we admit that temporal replication of particular seasons sampling in different years would be necessary for a more

FIGURE 5 Seasonal shifts of individual species' elevational ranges on Mount Cameroon for the four focal groups of Lepidoptera where at least one significant inter-seasonal shift of the elevational range was detected. Dots represent the weighted mean elevations (see Methods for details), while whiskers represent absolute values of shift of the lowest (left whisker) or highest (right whisker) elevations. Green colour indicates an ascent, and orange colour a descent, of the elevational range measures; black dots are for species with no detected seasonal shift. The changes are related to the previous season in the circular interannual seasonality as defined in Methods



in-depth understanding of the inter-seasonal patterns, as well as to fully control for potential inter-annual dynamics. Nevertheless, our results highlight the necessity of considering seasonal dynamics when interpreting elevational patterns of tropical diversity.

Detailed studies of temporal changes of diversity along tropical elevational gradients are scarce, mostly because of the logistic difficulties of sufficient sampling of each elevation even once. Janzen (1973) showed beetle diversity to decrease in mid-elevations during

the wet season, while he found no seasonal shift of heteropteran diversity in Costa Rica. The only more recent study 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 shifts of beetles abundance or species richness along elevation were observed. This was explained by the short length of the studied elevational gradients (<1,000 m a.s.l.). Nevertheless, as

demonstrated above, the main seasonal shifts of lepidopteran species richness on Mount Cameroon happened below 1,000 m a.s.l.

Any more general conclusions are impeded yet because any comparably comprehensive datasets from the tropics are lacking. However, two studies of seasonal shifts of arthropod diversity on subtropical mountains in southern Africa are consistent with our results; an upward shift of diversity peaks was unveiled in a multiple-year study of ants (Bishop et al., 2014), as well as in a study of spiders (Foord & Dippenaar-Schoeman, 2016). In the latter, a different pattern of the spider diversity shift was detected among the two studied slopes with different precipitation regimes (Foord & Dippenaar-Schoeman, 2016). Additionally, Meyer et al. (2015) revealed seasonal differences in ground-dwelling arthropod communities along an elevational gradient in the subtropical southwestern US but did not further dissect their patterns or drivers. All these studied areas are also characterized by intra-annual cycles of dry and wet seasons similar to our tropical locality.

To our knowledge, the only study on seasonal shifts of individual tropical lepidopteran species along elevation was performed by Janzen (1987) in Costa Rica. He 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) hypothesized 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, Boyle, Cooper, and Chandler (2018) were not supported by any detailed data or evidence, similarly to a report on elevational migration of a tropical wasp *Polistes instabilis* in Costa Rica (Hunt, Brodie, Carithers, Goldstein, & Janzen, 1999). On the other hand, seasonal species' range shifts are known for many species of tropical birds and bats (Hsiung et al., 2018), where they are mostly explained by migrations towards temporarily more suitable conditions.

4.3 | Drivers of the elevational shifts

We found that the phenological patterns of diversity, previously described for six lepidopteran groups in the lowland rainforest of Mount Cameroon (Maicher et al., 2018), change along elevations: the species richest communities occur sooner during the annual cycle at lower elevations, and only later on at the higher sites (Figure 2). We thus hypothesize that the seasonal shifts of both species richness and species' elevational ranges should be related to a phenological delay of some crucial conditions between the beginning and end of the dry season. Unfortunately, we do not have any data from the wet season allowing us to explain the inferred general descent of biodiversity peaks and species' elevational ranges of most focal groups.

Although our data sampling does not allow to distinguish if the described shifts of species' elevational range were caused by a phenologically delayed emergence of adults at higher elevations, or by

a seasonal up- or down-slope migration of individuals, we expect a combination of both drivers behind the described patterns. The temporal changes in weather conditions and availability of resources for both adults and caterpillars might initiate seasonal adult migration (Hsiung et al., 2018; Janzen, 1987). Janzen (1987) suspected a lack of food resources (both nectar flowers for adults and food plant foliage for larvae) during the dry season and the temperature drop during the wet season as the main triggers of the seasonal two-way migration.

4.4 | Implications for global change impact studies

Temporal changes of diversity along tropical elevational gradients have become a widely used approach for studying the global change impacts on biota, despite the above-mentioned insufficient knowledge of their seasonal dynamics (McCain, Szewczyk, & Knight, 2016). The current consensus predicts that the ongoing global climate change will cause uphill shifts of tropical montane species, due to their relatively narrow thermal tolerances (Forero-Medina et al., 2011; Laurance et al., 2011), resulting in subsequent extinctions of mountaintop species (Colwell et al., 2008). Such predictions have recently been supported by observed upward shifts of ranges of tropical frogs (Pounds, Fogden, & Campbell, 1999), birds (Freeman & Class Freeman, 2014) and moths (Chen, Hill, Shiu, et al., 2011; Chen et al., 2009). A recent multi-taxonomical meta-analysis estimated the median rate of uphill shift to be 11 m per decade (Chen, Hill, Ohlemüller, et al., 2011).

Even though insects are a hyper-diverse group of bioindicators, there are only two studies on elevational shifts based on a single dataset from the humid tropics (Chen, Hill, Shiu, et al., 2011; Chen et al., 2009). Their authors resampled the communities of geometrid moths along an 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 specialization of lepidopteran species. The upper elevation species' highest elevational range decreased by 179 m, while 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 and 77 m respectively (Chen, Hill, Shiu, et al., 2011).

However, our study showed that the shifts of individual species' elevational ranges of this extent can also be part of seasonal dynamics. We detected average range shifts of often >100 m (and even several times higher for many species) within natural seasonal changes over just two and half calendar years. Although we accept that any study of long-term changes has its numerous own constraints, we consider the sufficient knowledge of the natural dynamics over shorter time-scales as an essential requirement. Far from doubting the global climate change effects on biodiversity, we urge authors to take into account the seasonal dynamics of both diversity patterns and species' elevational distribution, as exemplified on the tropical mountain in our study. Any sampling shortcut ignoring the main seasonal dynamics might 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, Porporato, & Rodriguez-Iturbe, 2013), we call for 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 on tropical montane biodiversity.

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DATA AVAILABILITY STATEMENT

The datasets supporting this article are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mgqnk98vr>.

ORCID

Vincent Maicher  <https://orcid.org/0000-0002-9147-3529>
 Sylvain Delabye  <https://orcid.org/0000-0003-0911-9721>
 Łukasz Przybyłowicz  <https://orcid.org/0000-0001-5456-9479>
 Pavel Potocký  <https://orcid.org/0000-0002-3744-7282>
 Ishmeal N. Kobe  <https://orcid.org/0000-0003-0259-0350>
 Štěpán Janeček  <https://orcid.org/0000-0003-1285-6490>
 Jan E. J. Mertens  <https://orcid.org/0000-0002-0025-7039>
 Eric B. Fokam  <https://orcid.org/0000-0003-4531-3580>
 Tomasz Pyrz  <https://orcid.org/0000-0003-4822-0670>
 Jiří Doležal  <https://orcid.org/0000-0002-5829-4051>
 Jan Altman  <https://orcid.org/0000-0003-4879-5773>
 David Hořák  <https://orcid.org/0000-0002-8073-1617>
 Konrad Fiedler  <https://orcid.org/0000-0002-4789-3753>
 Robert Tropek  <https://orcid.org/0000-0001-7499-6259>

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**BIOSKETCH**

Insect Community Ecology Group (www.insect-communities.cz; ICEG) is a research group led by R.T. at the Charles University and Biology Centre CAS. It focuses on entomological ecology, including the patterns of biodiversity of Afrotropical Lepidoptera, plant-pollinator interactions in both tropical and temperate ecosystems, and biodiversity restoration at Central European human-affected sites. Since 2014, we have been intensively studying butterflies and moths, as well as pollination networks on Mount Cameroon. Seven co-authors are members of ICEG, including both leading authors.

Author contributions: R.T. and V.M. conceived the ideas. V.M., Sz.S., R.T., M.M., S.D., P.P., I.N.K., Š.J. and J.E.J.M. collected the lepidopteran material. J.D. and J.A. collected the weather data. V.M., Sz.S., Ł.P., P.P., S.D., M.M. and R.T. identified the sampled Lepidoptera. V.M. and R.T. analysed data, interpreted results and led writing. All co-authors participated in the result interpretation and discussion, and in writing the manuscript.

SUPPORTING INFORMATION

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

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SUPPORTING INFORMATION

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

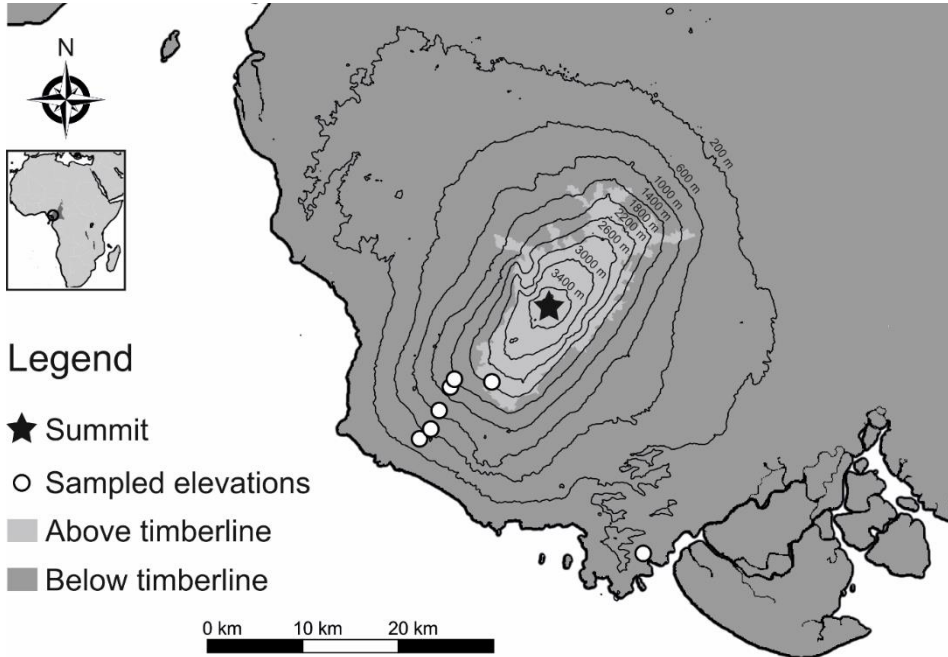


FIGURE S1. Map of Mount Cameroon with the seven sampled elevations.

APPENDIX S2. Details of the collected weather data.

| 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 | 29 | 23 | 10 | 1 | 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 |

TABLE S1. The measured monthly values for mean day temperature (\pm SD), monthly precipitation, and number of rainy days (>2 mm) measured by our dataloggers (see Methods for details) at individual sampled elevations (but the lowest 30 m asl) on Mount Cameroon.

APPENDIX S3. Summary table of the focal groups of Lepidoptera diversity for individual elevations and seasons.

TABLE S1. Diversity of the focal lepidopteran groups for individual elevations and seasons.

| Focal group | Elevation (asl) | Season | Abundance | Species richness | Chao1 (\pm SE) | SC |
|---------------------------|-----------------|------------|-------------|------------------|--------------------------------------|------|
| Fruit-feeding butterflies | 30 m | | 402 | 60 | 66.18 (\pm 4.38) | 0.96 |
| | 350 m | | 792 | 72 | 85.60 (\pm 8.74) | 0.98 |
| | 650 m | | 499 | 60 | 81.00 (\pm12.20) | 0.96 |
| | 1,100 m | Wet to dry | 410 | 34 | 43.43 (\pm 7.25) | 0.97 |
| | 1,450 m | | 738 | 5 | 5.00 (\pm 0.45) | 1 |
| | 1,850 m | | 209 | 5 | 5.00 (\pm 0.00) | 1 |
| | 2,200 m | | 957 | 3 | 3.00 (\pm 0.41) | 1 |
| | 30 m | | 292 | 54 | 69.3 (\pm 9.56) | 0.94 |
| | 350 m | | 3026 | 81 | 87.87 (\pm 5.56) | 1 |
| | 650 m | | 1932 | 87 | 96.43 (\pm7.26) | 0.99 |
| | 1,100 m | Dry | 1831 | 58 | 65.33 (\pm 5.67) | 0.99 |
| | 1,450 m | | 1520 | 16 | 18.50 (\pm 3.15) | 1 |
| | 1,850 m | | 505 | 5 | 5.00 (\pm 0.22) | 1 |
| | 2,200 m | | 32 | 2 | 2.00 (\pm 0.00) | 1 |
| | 30 m | | 120 | 34 | 52.2 (\pm 13.14) | 0.88 |
| | 350 m | | 538 | 58 | 63.05 (\pm 3.78) | 0.97 |
| | 650 m | | 1021 | 68 | 81.91 (\pm8.68) | 0.98 |
| | 1,100 m | Dry to wet | 376 | 41 | 76.00 (\pm 25.59) | 0.96 |
| | 1,450 m | | 706 | 24 | 29.00 (\pm 6.63) | 0.99 |
| | 1,850 m | | 255 | 5 | 8.00 (\pm 4.38) | 0.99 |
| | 2,200 m | | 1123 | 7 | 13.00 (\pm 7.07) | 1 |
| Fruit-feeding moths | 30 m | | 899 | 39 | 115.0 (\pm 50.2) | 0.98 |
| | 350 m | | 406 | 65 | 93.1 (\pm 14.6) | 0.93 |
| | 650 m | | 443 | 86 | 145.0 (\pm26.2) | 0.91 |
| | 1,100 m | Wet to dry | 390 | 78 | 131.1 (\pm 25.3) | 0.91 |
| | 1,450 m | | 248 | 95 | 131.6 (\pm 15.1) | 0.83 |
| | 1,850 m | | 156 | 31 | 54.0 (\pm 16.4) | 0.9 |
| | 2,200 m | | 68 | 20 | 28.0 (\pm 7.6) | 0.85 |
| | 30 m | | 79 | 29 | 41.0 (\pm 9.2) | 0.82 |
| | 350 m | | 484 | 57 | 96.6 (\pm 22.0) | 0.95 |
| | 650 m | | 618 | 100 | 174.2 (\pm30.1) | 0.92 |
| | 1,100 m | Dry | 739 | 89 | 135.6 (\pm 21.2) | 0.95 |
| | 1,450 m | | 139 | 43 | 97.2 (\pm 32.7) | 0.83 |
| | 1,850 m | | 69 | 30 | 46.0 (\pm 11.0) | 0.76 |
| | 2,200 m | | 8 | 8 | 14.5 (\pm 8.1) | 0.28 |

| | | | | | | |
|-----------|---------|------------|--|-------------|------------|---|
| | | | | | | |
| | 30 m | | | 152 | 23 | 40.3 (± 15.0) 0.93 |
| | 350 m | | | 887 | 71 | 160.0 (± 44.8) 0.96 |
| | 650 m | | | 636 | 96 | 144.9 (± 20.5) 0.94 |
| | 1,100 m | Dry to wet | | 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 |
| | | | | | | |
| | 30 m | | | 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 | Wet to dry | | 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 | | | 566 | 29 | 33.1 (± 4.8) 0.99 |
| Arctiinae | 1,100 m | Dry | | 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 | | | 145 | 23 | 25.5 (± 2.7) 0.96 |
| | 350 m | | | 697 | 49 | 54.0 (± 4.4) 0.99 |
| | 650 m | | | 429 | 34 | 54.3 (± 70.9) 0.97 |
| | 1,100 m | Dry to wet | | 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 |
| | | | | | | |
| | 30 m | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 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 | | | 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 | Wet to dry | | 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 | | | 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 | Dry | | 139 | 41 | 61.1 (± 12.6) 0.87 |
| | 1,450 m | | | 195 | 32 | |

| | | | | | | |
|----------------------|---------|------------|------------|-----------|----------------------|------|
| | 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 |
| | 30 m | | 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 | Wet to dry | 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 | | 49 | 13 | 44.3 (±38.7) | 0.84 |
| | 350 m | | 147 | 48 | 60.6 (±7.6) | 0.87 |
| | 650 m | | 158 | 29 | 52.8 (±20) | 0.92 |
| Notodontidae | 1,100 m | Dry | 157 | 30 | 85.8 (±49.5) | 0.90 |
| | 1,450 m | | 39 | 11 | 23.1 (±16.7) | 0.87 |
| | 1,850 m | | 42 | 7 | 12.6 (±6.9) | 0.91 |
| | 2,200 m | | 129 | 1 | 1.0 (±0.0) | 1.00 |
| | 30 m | | 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 | Dry to wet | 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 |
| | 30 m | | 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 | Wet to dry | 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 |
| Laslocampidae | 30 m | | 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 | Dry | 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 | | 16 | 6 | 10.2 (±6.8) | 0.84 |

| | | | | | | |
|--------------------|---------|------------|------------|-----------|---------------------|------|
| | 30 m | | 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 | Dry to wet | 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 |
| | 30 m | | 20 | 1 | 1.0 (±0.0) | 1 |
| | 350 m | | 93 | 12 | 13.2 (±1.8) | 0.96 |
| | 650 m | | 21 | 6 | 16.0 (±10.1) | 0.77 |
| | 1,100 m | Wet to dry | 0 | 0 | - | - |
| | 1,450 m | | 3 | 1 | 1.0 (±0.0) | 1 |
| | 1,850 m | | 21 | 6 | 12.0 (±7.0) | 0.82 |
| | 2,200 m | | 2 | 1 | 1.0 (±0.0) | 1 |
| | 30 m | | 0 | 0 | - | - |
| | 350 m | | 137 | 17 | 19.5 (±3.1) | 0.96 |
| | 650 m | | 114 | 10 | 25.0 (±13.5) | 0.95 |
| Sphingidae | 1,100 m | Dry | 11 | 6 | 9.0 (±4.1) | 0.65 |
| | 1,450 m | | 0 | 0 | - | - |
| | 1,850 m | | 19 | 2 | 2.0 (±0.0) | 1 |
| | 2,200 m | | 0 | 0 | - | - |
| | 30 m | | 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 | Dry to wet | 1 | 1 | 1.0 (±0.0) | 1 |
| | 1,450 m | | 1 | 1 | 1.0 (±0.0) | 1 |
| | 1,850 m | | 10 | 2 | 2.0 (±0.3) | 1 |
| | 2,200 m | | 5 | 1 | 1.0 (±0.0) | 1 |
| | 30 m | | 4 | 3 | 3.5 (±1.2) | 0.63 |
| | 350 m | | 8 | 3 | 3.0 (±0.4) | 1 |
| | 650 m | | 27 | 5 | 6.0 (±2.2) | 0.93 |
| | 1,100 m | Wet to dry | 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 |
| Saturniidae | 30 m | | 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 | Dry | 16 | 5 | 8.0 (±4.4) | 0.82 |
| | 1,450 m | | 14 | 2 | 2.0 (±0.0) | 1 |
| | 1,850 m | | 22 | 4 | 5.0 (±2.2) | 0.92 |
| | 2,200 m | | 1 | 1 | 1.0 (±0.0) | 1 |

| | | | | | | |
|---------------------|---------|------------|-----------|----------|-------------------------------------|------|
| | 30 m | | 4 | 2 | 2.0 (± 0.3) | 1 |
| | 350 m | | 16 | 7 | 7.3 (± 0.9) | 0.89 |
| | 650 m | | 55 | 6 | 7.0 (± 2.2) | 0.98 |
| | 1,100 m | Dry to wet | 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 |
| | 2,200 m | | 0 | 0 | - | - |
| | 30 m | | 6 | 4 | 4.8 (± 1.6) | 0.78 |
| | 350 m | | 23 | 6 | 6.2 (± 0.7) | 0.98 |
| | 650 m | | 14 | 6 | 13.4 (± 10.8) | 0.72 |
| | 1,100 m | Wet to dry | 18 | 4 | 4.0 (± 0.5) | 1.00 |
| | 1,450 m | | 52 | 3 | 3.4 (± 1.3) | 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 |
| Eupterotidae | 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) | 0.78 |
| | 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.

TABLE S1. Results of the generalised mixed-effect models (GLMM) with elevation as fixed effect factor, and season and plot nested in elevation as random effect factors. The type II Wald χ^2 tests were applied for the models testing, while the “delta” method (Barton, 2018) was applied for the marginal R^2 calculations.

| Focal group | χ^2 | df | p-value | Marginal R^2 |
|---------------------------|----------------------------|-----------|----------------|----------------------------------|
| Fruit-feeding 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 generalised mixed-effect models (GLMM) carried out separately for fruit-feeding butterflies and moths collected in canopy and understory. Elevation was treated as fixed effect factor, and season and plot nested in elevation as random effect factors. The type II Wald χ^2 tests were applied for the models testing, while the “delta” method (Barton, 2018) was applied for the marginal R^2 calculations.

| Focal group | χ^2 | df | p-value | Marginal R^2 |
|----------------------------------|----------------------------|-----------|----------------|----------------------------------|
| Fruit-feeding butterflies | | | | |
| Canopy | 432.6 | 6 | <0.01 | 0.62 |
| Understory | 1137.8 | 6 | <0.01 | 0.85 |
| Fruit-feeding moths | | | | |
| Canopy | 153.8 | 6 | <0.01 | 0.33 |
| Understory | 481.9 | 6 | <0.01 | 0.75 |

TABLE S3. Results of the generalised mixed-effect models (GLMM) with elevation, season, and their interaction as fixed effect factors, and plot nested in elevation as random effect factor. The type II Wald χ^2 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 | χ^2 | df | p-value | Marginal R^2 |
|---------------------------|--------------------|----------|----|---------|----------------|
| 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 | n.s. | |
| | Elevation * Season | 30.3 | 12 | <0.01 | |
| Sphingidae | Elevation | 175.1 | 6 | <0.01 | 0.53 |
| | Season | 3.0 | 2 | n.s. | |
| | 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. | |

| Variables | Fruit-feeding butterflies | | Fruit-feeding moths | | Acanthinae | | Lymantrinae | | Noctonidae | | Lasiocampidae | | Sphingidae | | Saturnidae | | Eupteridae | |
|------------------------|---------------------------|------|---------------------|------|------------|------|-------------|------|------------|------|---------------|------|------------|------|------------|------|------------|------|
| | Estim | SE | Estim | SE | Estim | SE | Estim | SE | Estim | SE | Estim | SE | Estim | SE | Estim | SE | Estim | SE |
| 30 m / W-D (Intercept) | 2.50 | 0.07 | 2.19 | 0.10 | 2.44 | 0.11 | 2.03 | 0.15 | 1.22 | 0.22 | 0.85 | 0.25 | -0.67 | 0.34 | -1.40 | 0.41 | 0.30 | 0.26 |
| 300 m / W-D | 0.75 | 0.09 | 0.42 | 0.13 | 0.51 | 0.15 | 1.12 | 0.19 | 1.19 | 0.25 | 0.97 | 0.30 | 2.42 | 0.34 | 1.76 | 0.42 | 0.81 | 0.30 |
| 650 m / W-D | 0.11 | 0.10 | 0.48 | 0.13 | -0.01 | 0.16 | 0.32 | 0.21 | 1.10 | 0.25 | 0.07 | 0.40 | 1.54 | 0.36 | 2.16 | 0.41 | 0.36 | 0.33 |
| 1,100 m / W-D | -0.36 | 0.11 | 0.34 | 0.13 | 0.12 | 0.16 | -0.09 | 0.23 | 0.70 | 0.27 | 0.00 | 0.37 | -0.11 | 0.46 | 1.34 | 0.44 | -0.13 | 0.37 |
| 1,450 m / W-D | -1.13 | 0.14 | 0.34 | 0.13 | 0.47 | 0.15 | 0.45 | 0.21 | 0.39 | 0.28 | 0.92 | 0.30 | -0.62 | 0.60 | 1.54 | 0.43 | -0.21 | 0.37 |
| 1,850 m / W-D | -1.90 | 0.20 | -0.49 | 0.15 | 0.09 | 0.16 | -0.49 | 0.23 | -1.04 | 0.45 | 1.15 | 0.28 | 0.79 | 0.39 | 1.58 | 0.43 | 0.17 | 0.34 |
| 2,200 m / W-D | -1.75 | 0.18 | -1.31 | 0.19 | -0.47 | 0.19 | -0.84 | 0.26 | -0.82 | 0.41 | -0.85 | 0.58 | -0.62 | 0.60 | -1.10 | 0.79 | -1.67 | 0.63 |
| 30 m / Dry | -0.03 | 0.10 | -0.88 | 0.16 | -0.12 | 0.15 | 0.43 | 0.17 | 0.20 | 0.28 | -0.15 | 0.38 | 0.25 | 0.18 | 0.30 | 0.20 | -1.01 | 0.24 |
| 30 m / D-W | -0.77 | 0.12 | -0.74 | 0.16 | -0.09 | 0.14 | 0.00 | 0.20 | -0.71 | 0.48 | -0.67 | 0.48 | -1.00 | 0.19 | 0.54 | 0.19 | -0.54 | 0.21 |
| 300 m / Dry | 0.52 | 0.11 | 0.84 | 0.20 | 0.01 | 0.20 | 0.18 | 0.20 | 0.20 | 0.32 | 0.30 | 0.44 | | | | | | |
| 650 m / Dry | 1.02 | 0.12 | 1.21 | 0.19 | 0.68 | 0.21 | 0.62 | 0.22 | -0.01 | 0.33 | 0.39 | 0.65 | | | | | | |
| 1,100 m / Dry | 0.89 | 0.14 | 1.25 | 0.19 | 0.31 | 0.21 | 0.27 | 0.26 | 0.44 | 0.34 | 0.47 | 0.51 | | | | | | |
| 1,450 m / Dry | 0.43 | 0.18 | 0.04 | 0.21 | 0.21 | 0.20 | -0.17 | 0.24 | -0.56 | 0.40 | -0.63 | 0.48 | | | | | | |
| 1,850 m / Dry | 0.24 | 0.26 | 0.34 | 0.25 | 0.33 | 0.22 | 0.40 | 0.26 | 0.60 | 0.53 | -0.69 | 0.47 | | | | | | |
| 2,200 m / Dry | -0.79 | 0.31 | -0.71 | 0.42 | 0.41 | 0.25 | 0.18 | 0.30 | -0.61 | 0.59 | 1.07 | 0.71 | | | | | | |
| 300 m / D-W | 0.32 | 0.14 | 0.83 | 0.19 | 0.33 | 0.19 | 0.52 | 0.22 | 0.90 | 0.51 | 0.82 | 0.53 | | | | | | |
| 650 m / D-W | 1.28 | 0.15 | 1.11 | 0.19 | 0.66 | 0.20 | 0.79 | 0.24 | 0.75 | 0.51 | 1.25 | 0.60 | | | | | | |
| 1,100 m / D-W | 1.08 | 0.16 | 1.53 | 0.19 | 0.51 | 0.20 | 1.19 | 0.26 | 1.02 | 0.53 | 0.80 | 0.62 | | | | | | |
| 1,450 m / D-W | 1.25 | 0.19 | -0.29 | 0.21 | -0.05 | 0.20 | 0.03 | 0.27 | 0.02 | 0.57 | -0.41 | 0.69 | | | | | | |
| 1,850 m / D-W | 0.84 | 0.28 | 1.00 | 0.22 | 0.28 | 0.21 | 0.91 | 0.27 | 0.84 | 0.70 | 0.41 | 0.52 | | | | | | |
| 2,200 m / D-W | 0.98 | 0.25 | 0.86 | 0.28 | 0.42 | 0.25 | 0.51 | 0.32 | 0.49 | 0.71 | 1.65 | 0.80 | | | | | | |

TABLE S4. The GLMMs fixed effect coefficients for the individual groups of variables (Estim: models estimates; SE: standard error).

*When the interaction was not significant, i.e. the effect of season was not consistent across all elevations, only the overall effects of season was shown.

TABLE S5. Results of the generalised mixed-effect models (GLMM) carried out separately for fruit-feeding butterflies and moths collected in canopy and understory, with elevation, season, and their interaction as fixed effect factors, and plot nested in elevation as random effect factor. The type II Wald χ^2 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 | χ^2 | df | p-value | Marginal R^2 |
|----------------------------------|--------------------|----------|----|---------|----------------|
| Fruit-feeding butterflies | | | | | |
| Canopy | Elevation | 386.6 | 6 | <0.01 | 0.70 |
| | Season | 49.6 | 2 | <0.01 | |
| | Elevation * Season | 56.2 | 12 | <0.01 | |
| Understory | Elevation | 1189.5 | 6 | <0.01 | 0.88 |
| | Season | 352.8 | 2 | <0.01 | |
| | Elevation * Season | 219.9 | 12 | <0.01 | |
| Fruit-feeding moths | | | | | |
| Canopy | Elevation | 139.8 | 6 | <0.01 | 0.55 |
| | Season | 3.3 | 2 | n.s. | |
| | Elevation * Season | 54.2 | 12 | <0.01 | |
| Understory | Elevation | 478.7 | 6 | <0.01 | 0.86 |
| | Season | 40.1 | 2 | <0.01 | |
| | Elevation * Season | 210.1 | 12 | <0.01 | |

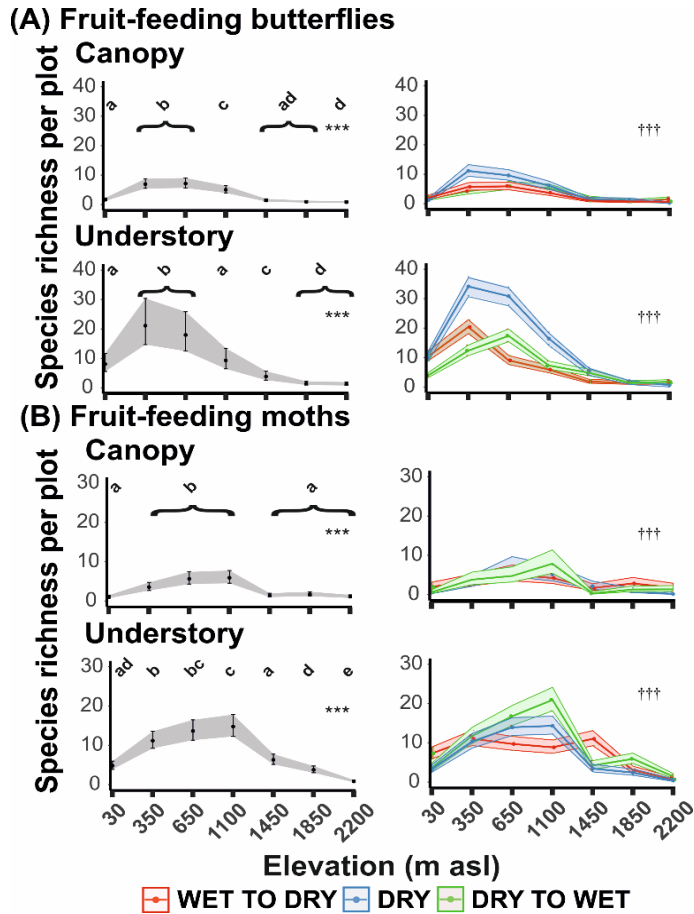


FIGURE S1. Changes of the fruit-feeding Lepidoptera species richness along elevation and season, analysed separately for understory and canopy strata on Mount Cameroon. The two columns represent visualisation of the GLMM results for species richness per plot and elevation (Table S2 in Appendix S4), and GLMM results per plot, elevation and season (Table S5 in Appendix S4). Means per plot with 95% unconditional confidence intervals are visualised; asterisks visualise significance of individual tests (effects of elevation in the third column: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; and of elevation \times season interaction 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.

REFERENCE

Barton, K. (2018). MuMIn: multi-model inference, R package version 1.40.4. <http://r-forge.r-project.org/projects/mumin/>

APPENDIX S5. Nonmetric multidimensional scaling (NMDS) two-dimensional plots of individual focal group.

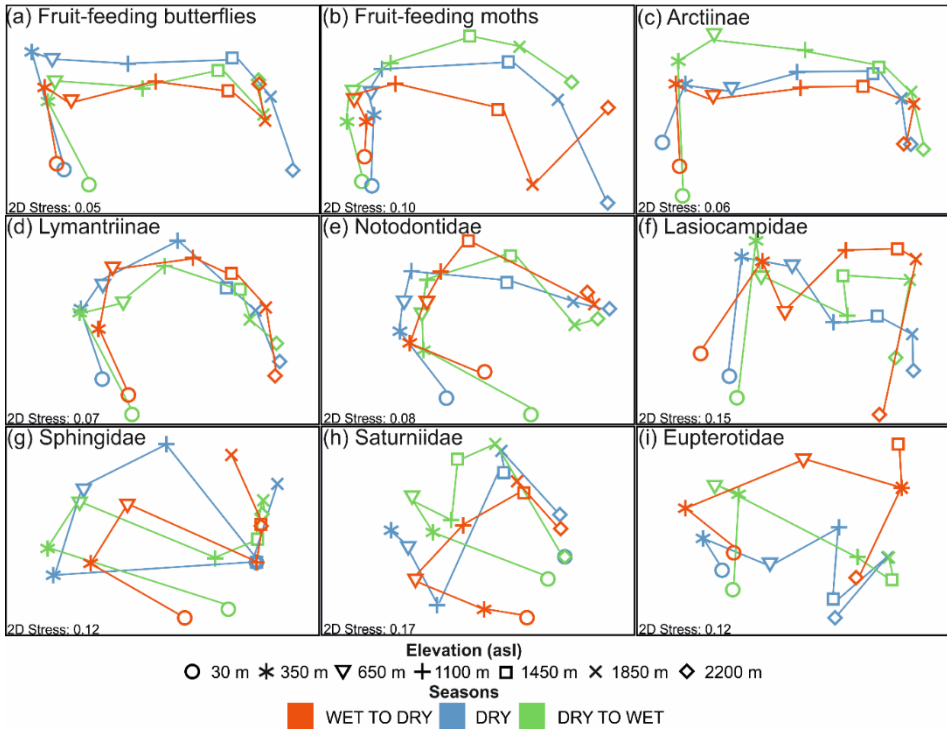


FIGURE S1. Nonmetric multidimensional scaling (NMDS) two-dimensional plots of bait-trapped (a) fruit-feeding butterflies and (b) fruit-feeding moths; and light-attracted (c) Arctiinae, (d) Lymantriinae, (e) Notodontidae, (f) Lasiocampidae, (g) Sphingidae, (h) Saturniidae, and (i) Eupterotidae collected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

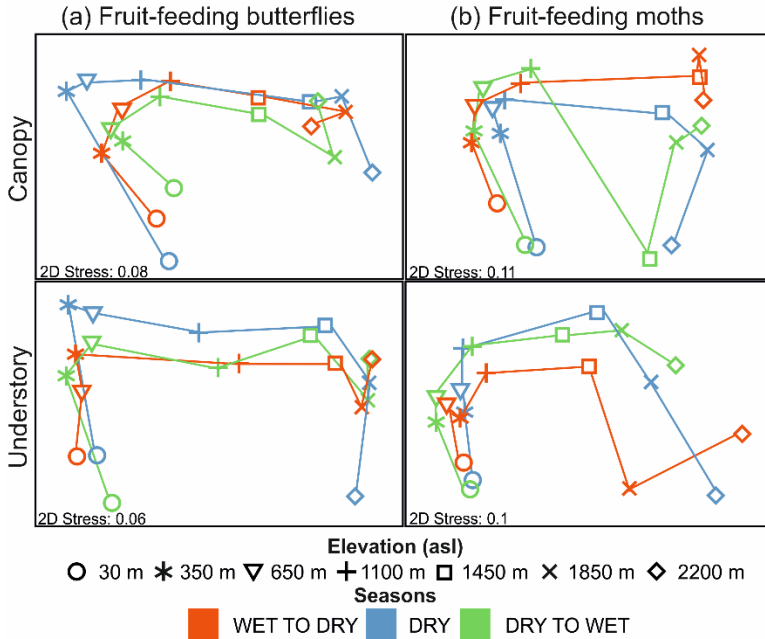


FIGURE S2. Nonmetric multidimensional scaling (NMDS) two-dimensional plots of bait-trapped (a) fruit-feeding butterflies and (b) fruit-feeding moths collected in both canopy (upper charts) and understory (lower charts) on Mount Cameroon. Ordinations are based on matrices calculated with the Bray-Curtis similarity index of square root transformed data. The low stress values indicate a high goodness-of-fit of the ordinations.

APPENDIX S6. Results of PERMANOVAs of the differences in community composition of individual focal groups of Lepidoptera.

TABLE S1. Results of sequential PERMANOVAs carried out for all focal groups of Lepidoptera on Mount Cameroon.

| Taxon | Source | df | Sums of square | Pseudo-F | p |
|----------------------------------|--------------------|-----|----------------|----------|-------|
| Fruit-feeding 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 | | |

TABLE S2. Results of sequential PERMANOVAs carried out separately for fruit-feeding butterflies and moths collected in canopy and understory on Mount Cameroon.

| Taxon | Source | df | Sums of square | Pseudo-F | p |
|----------------------------------|--------------------|-----|----------------|----------|-------|
| Fruit-feeding butterflies | | | | | |
| Canopy | Elevation | 6 | 274,420 | 38.36 | <0.01 |
| | Season | 2 | 34,043 | 14.27 | <0.01 |
| | Elevation x Season | 12 | 92,566 | 6.47 | <0.01 |
| | Residuals | 315 | 375,570 | | |
| Understory | Elevation | 6 | 534,520 | 93.908 | <0.01 |
| | Season | 2 | 34,655 | 18.265 | <0.01 |
| | Elevation x Season | 12 | 136,240 | 11.968 | <0.01 |
| | Residuals | 315 | 298,830 | | |
| Fruit-feeding moths | | | | | |
| Canopy | Elevation | 6 | 122,200 | 12.255 | <0.01 |
| | Season | 2 | 19,791 | 5.9542 | <0.01 |
| | Elevation x Season | 12 | 65,665 | 3.2926 | <0.01 |
| | Residuals | 315 | 523,500 | | |
| Understory | Elevation | 6 | 360,050 | 37.995 | <0.01 |
| | Season | 2 | 58,404 | 18.49 | <0.01 |
| | Elevation x Season | 12 | 163,310 | 8.6167 | <0.01 |
| | Residuals | 315 | 497,500 | | |

APPENDIX S7. Detailed results of the Wilcoxon signed-rank tests of seasonal shifts of species' elevational ranges.

| Range measures | Season* | Value | Fruit-feeding butterflies | Fruit-feeding moths | Arctiinae | Lymantriinae | Notodontidae | Lasiocampidae | Sphingidae | Saturniidae | Eupterotidae |
|------------------------|------------|------------|---------------------------|---------------------|---------------|------------------|--------------|---------------|-------------|-------------|--------------|
| Highest altitude | W-D to Dry | | 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 | V; p-value | 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 | | 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 | V; p-value | 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 | | 84.0; 0.162 | 722.5; 0.800 | 98.5; 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 | V; p-value | 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 |

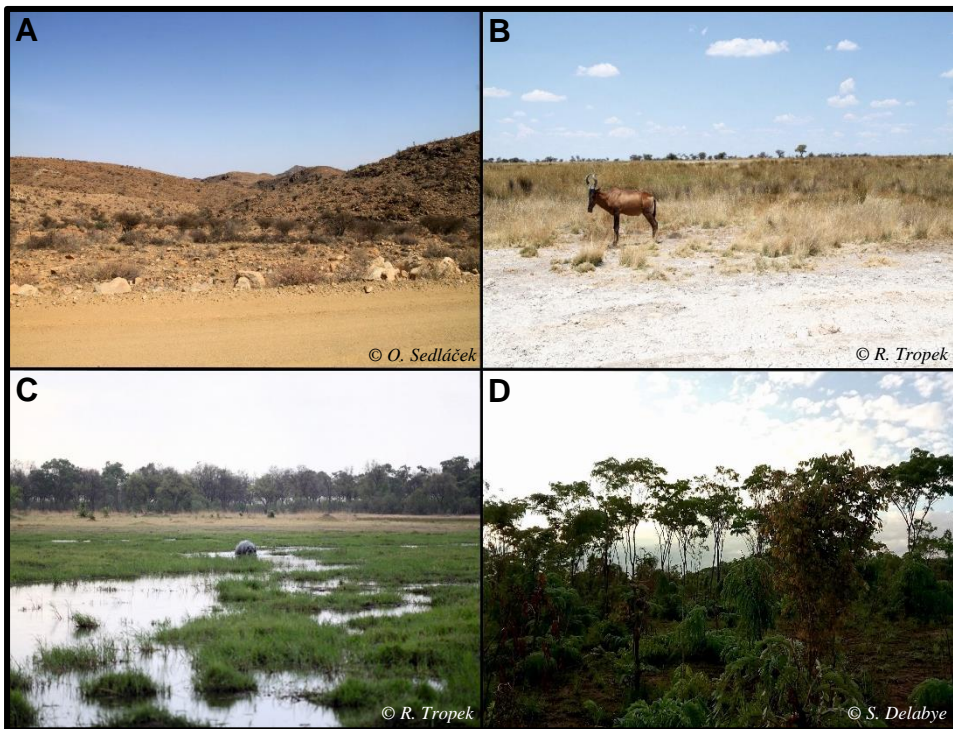
TABLE S1. Detailed results of the Wilcoxon signed-rank tests of the changes of the three measures of species' elevational ranges for all focal groups of Lepidoptera on Mount Cameroon. The first number gives the V-statistic, while the second number represents the p-value (W-D: Transition from wet to dry season; Dry: Full-dry season; D-W: Transition from dry to wet season; + <0.06; * p <0.05; ** p <0.01; *** p <0.001).

CHAPTER IV

Patterns of moth diversity along a continent-wide environmental productivity gradient in south African savannahs

Delabye, S., Storch, D., Sedláček, O., Albrecht, T., Hořák, D.,
Maicher, V., Tószögyová, A. & Tropek, R.

Manuscript



Four sites where moths were sampled along the productivity gradient. From the lowest to the highest productivity sites: A) Namibgrems, B) Etosha, C) Bwabwata and D) Chizarira.

Patterns of moth diversity along a continent-wide environmental productivity gradient in south African savannahs

Sylvain Delabye^{1,2,3,*}, David Storch^{1,4}, Ondřej Sedláček¹, Tomáš Albrecht^{1,5}, David Hořák¹, Vincent Maicher^{1,2,6}, Anna Tószögyová^{1,4}, Robert Tropek^{1,2,*}

1 Departments of Ecology and Zoology, Faculty of Science, Charles University, Viničná 7, 12844 Prague, Czechia

2 Institute of Entomology, Biology Centre, Czech Academy of Sciences, Branišovská 31, 37005 České Budějovice, Czechia

3 Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, 37005 České Budějovice, Czechia

4 Center for Theoretical Study, Charles University, Prague and the Czech Academy of Sciences, Jilská 1, 11000 Praha, Czech Republic

5 Institute of Vertebrate Biology, the Czech Academy of Sciences, Studenec 122, 67502 Koněšín, Czech Republic

6 Nicholas School of the Environment, Duke University, 9 Circuit Dr., Durham, NC 27710, USA

** Corresponding authors: sylvain.delabye@gmail.com (Sylvain Delabye); robert.tropek@gmail.com (Robert Tropek)*

ABSTRACT

Unravelling global biodiversity patterns is one of the main goals of current ecology. Environmental productivity, commonly defined as the amount of biomass produced by primary producers within a given period and area, is considered to belong among the main factors affecting local biodiversity. However, reliable data on the relationship between productivity and species richness of most organisms, including Lepidoptera, are largely missing. Moreover, this relationship seems to be scale dependent. We present moth biodiversity patterns along a continent-wide gradient of environmental productivity in southern African savannah ecosystems, at

local and regional spatial scales. Moths (Heterocera) were sampled along a gradient of environmental productivity (quantified by Normalized Difference Vegetation Index – NDVI) from the Namib Desert to woody savannahs of the valley of Zambezi. By standardised light trapping, we collected moths at 120 sampling plots within 12 localities along the gradient, resulting in 12,372 specimens of ca. 487 (morpho)species. The relationship between species richness of most of the focal groups and environmental productivity was positively exponential at both local and regional scales. Moreover, the absence of a relationship between abundance and environmental productivity emphasized the number of individuals as an irrelevant factor for shaping species richness patterns of moths. The role of environment productivity in structuring of the moth diversity patterns may be explained by the direct and indirect effects of climatic covariates, such as temperature and water availability.

KEYWORDS

Abundance, Afrotropics, Heterocera, insect, large-scale patterns, light trapping, Lepidoptera, NDVI, primary productivity, savannah ecosystems.

INTRODUCTION

Environmental productivity, defined as the rate of biomass production by a given ecosystem, ranks among the most studied ecological factors responsible for the global patterns of biodiversity (Waide et al. 1999; Mittelbach et al. 2001; Gaston 2000; but see Storch 2012). It determines availability of various resources, which should drive intensity of interspecific competition (Grime 1973), and consequently limit the

maximum number of coexisting species (Hutchinson 1959; Wright 1983; Hurlbert & Stegen 2014; Huston 2014).

However, the relationship of species diversity to environmental productivity has been insufficiently studied and therefore remains highly questionable (Mittelbach et al. 2001; Gillman & Wright 2006; Adler et al. 2011; Fraser et al. 2015). Mainly, this relationship has been showed as highly variable across geographic scales. Environmental productivity (or its surrogates; see Šímová & Storch 2017) usually shows a positive linear correlation with species richness at large (continent-wide or global) spatial scales (e.g. Wright 1983; Waide et al. 1999; Hawkins et al. 2003; Gillman & Wright 2006; Field et al. 2009). Nevertheless, several studies validated a unimodal relationship (diversity first increases and then declines with increasing environmental productivity) at local scales (Leibold 1999; Dodson et al. 2000; Chase & Leibold 2002). Too high eutrophication of the ecosystem at higher productive sites can cause a decrease in species richness by reducing species dissimilarity between habitats or by the presence of a few competitive species of a few competitive species in communities. Nevertheless, such unimodal patterns were reported even in some large-scaled studies, often in aquatic systems (Guo & Berry 1998; Mittelbach et al. 2001),

The More Individuals Hypothesis (MIH) has been suggested to explain the positive linear relationship of species richness to environmental productivity. It expects that environmental productivity limits the number of species either through limiting the number of individuals (Wright 1983; Srivastava & Lawton 1998) or the total niche space (Schemske 2002). Although several studies found that species richness has often been positively related to available energy, the number of individuals, diversity patterns do not seem to be mediated by the number of individuals (Currie et al. 2004; Šímová et al. 2011, 2013; Storch 2012). The MIH stays a strongly limited hypothesis at local scales, and most often

its formulation even differs between authors (Šímová & Storch 2017; Storch et al. 2018).

The patterns of animal species richness along gradients of environmental productivity vary among taxonomic groups, particularly in relation to the differences in thermal physiology between endotherms and ectotherms (Wiens 2007; Wiens et al. 2009, 2010; Buckley et al. 2012), as predicted by the Metabolic Theory (Brown et al. 2004). Corroboratively, species richness of endotherms was revealed positively correlated with primary productivity, whilst species richness of ectotherms corresponded more with temperature (Buckley & Jetz 2010; Buckley et al. 2012).

Based on vertebrate diversity patterns, environmental productivity has also been suggested as a potential driver of insect diversity and abundance (Lightfoot & Whitford 1991; Wenninger & Inouye 2008). However, the lack of studies on this relationship are scarce. Moreover, the impacts of environmental productivity were often studied along latitudinal and elevational gradients. At a global scale, insect species richness is known to be highest in the tropics and to decrease towards the poles (Wallace 1878; Kusnezov 1957; Kaspari et al. 2004; Schuldt et al. 2018), although the pattern is reversed for ichneumon wasps (Janzen 1981), aphids (Dixon et al. 1987) and sawflies (Kouki et al. 1994). Along elevational gradients, the midpeak patterns of richness for moths were best explained by area-integrated productivity, although the relationship remained relatively weak (Beck et al. 2011; Levanoni et al. 2011). Because latitude and elevation broadly covary with productivity, energy, insolation and thermal seasonality, it is difficult to separate the possible effects of productivity on those insect diversity patterns. When environmental productivity is not studied along elevational or latitudinal gradients, either a significant positive linear relationship (Bailey et al. 2004; Seto et al. 2004), or a weak positive linear relationship or no significant relationships were found for butterflies (Kerr et al. 2001), ants (Kaspari et al. 2004) and damselflies (Brasil et al. 2019) at local and regional scales. Regarding the

insect beta diversity patterns, the relationship with environmental productivity has not been studied along a latitudinal- or elevation-independent gradient. However, the scale dependence of the productivity-diversity relationship implies a positive relationship between environmental productivity and beta diversity, as found for butterflies in a temperate region along a latitudinal gradient (Andrew et al. 2011). Similarly, little evidence for a relationship between environmental productivity and insect abundance was found (Srivastava & Lawton 1998), while a positive decelerating function of abundance was found at local, regional, and continental scales in ant communities (Kaspari et al. 2000).

In the Afrotropics, only the patterns of sphingid moth richness has been studied at a continental scale, evaluating environmental productivity as one of the many factors, with a strong positive relationship with species richness (Ballesteros-Mejia et al. 2013). Nevertheless, this study did not work with the field data, but with modelled species distribution. This highlights how poorly insect diversity patterns and productivity relationships were studied in the Afrotropics, and particularly in Afrotropical grassy biomes (Murphy et al. 2016; Delabye et al. 2020).

In this study, we focus on patterns of diversity and abundance of adult moths along a continent-wide gradient of environmental productivity in southern African savannahs, at local and regional scales. Moths are a diverse group of commonly used bioindicators (Braga & Diniz 2018), with an important position in ecosystem foodwebs, including herbivory, food for many animals, or pollination. Therefore, their communities should be closely related to the availability of energy and other related resources in the ecosystems. We focused on the following questions: (1) Do relationships between species richness and productivity differ at both local (alpha diversity) and regional (gamma diversity) scales? (2) If so, how beta diversity varies along the environmental gradient? (3) How abundance is related to environmental productivity at both scales? We expected a positive linear relationship of species richness at both scales. If the

productivity–diversity relationship is scale-dependent, then the difference in species composition among sites within regions should increase with productivity. We also predicted a positive decelerating relationship between the number of individuals and productivity.

MATERIALS AND METHODS

All fieldwork was conducted along a continent-wide gradient of environmental productivity in southern Africa, from the deserts in western Namibia, through semideserts and open savannahs in Namibia and Botswana, to productive woodland savannahs in northwestern Zimbabwe. Along this productivity gradient, we sampled moth communities at 12 sites in open and semi-open natural habitats (Fig. 1; Table 1).

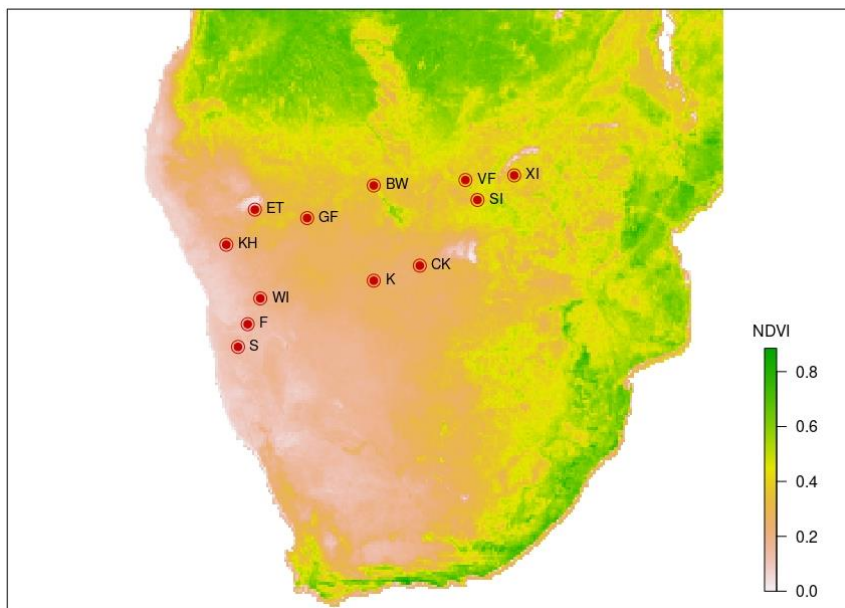


Fig. 1. Studied sites in southern Africa sampled for moth communities along the gradient of environmental productivity. Spatial distribution of mean NDVI in the beginning of vegetation season (October to December) is visualised. Site codes are reported in Table 1.

| Site (code) | Elevation (m a.s.l.) | Latitude | Longitude | Vegetation type | Maximum NDVI | Mean NDVI | Minimum NDVI | Mean Vegetation Cover (%) | < 30 cm vegetation layer cover (%) | < 2 m vegetation layer cover (%) | < 5 m vegetation layer cover (%) | > 5 m vegetation layer cover (%) |
|-----------------------|----------------------|------------|------------|---|--------------|-----------|--------------|---------------------------|------------------------------------|----------------------------------|----------------------------------|----------------------------------|
| Soususvlei (S) | 760 | S 24.5427° | E 15.7894° | Namib Desert with very rare vegetation | 0.111924 | 0.108621 | 0.103822 | 14.6 | 9.9 | 4.1 | 0.5 | 0.0 |
| Namibgreens (F) | 1790 | S 23.6429° | E 16.2786° | Namib Escarpment Woodland: dry savannas and shrubby areas with scattered trees | 0.144751 | 0.141666 | 0.138290 | 16.8 | 6.8 | 5.3 | 4.7 | 0.0 |
| Khorixas (KH) | 1040 | S 20.3386° | E 15.2145° | Angolian Mopane Woodland: mosaic of <i>Acacia</i> and mopane woodlands | 0.186351 | 0.173242 | 0.15926 | 45.7 | 2.8 | 22.3 | 17.7 | 2.9 |
| Windhoek (WI) | 1800 | S 22.6082° | E 16.7727° | Namib Escarpment Woodland: dry savannas and shrubby areas with scattered trees | 0.227593 | 0.196426 | 0.171894 | 46.9 | 26.0 | 16.2 | 4.7 | 0.0 |
| Etosha (ET) | 1120 | S 19.0507° | E 16.5408° | Angolian Mopane Woodland: mosaic of <i>Acacia</i> and mopane woodlands | 0.283652 | 0.241193 | 0.201848 | 99.7 | 39.4 | 32.7 | 21.6 | 0.0 |
| Thakadu (K) | 1120 | S 21.8666° | E 21.6969° | Kalahari Xeric Savanna: dry open savannas, with scattered trees | 0.297891 | 0.248134 | 0.204659 | 106.0 | 35.5 | 49.5 | 20.5 | 0.5 |
| Central Kalahari (CK) | 980 | S 21.2881° | E 23.7162° | Kalahari <i>Acacia</i> Woodland: mosaics of <i>Vochellia</i> , <i>Baikiea</i> and mopane woodlands, and small-leaved savannas | 0.348738 | 0.258567 | 0.191219 | 87.7 | 26.0 | 33.5 | 23.5 | 4.7 |
| Grootfontein (GF) | 1220 | S 19.3456° | E 18.812° | Kalahari <i>Acacia</i> Woodland: mosaics of <i>Vochellia</i> , <i>Baikiea</i> and mopane woodlands, and small-leaved savannas | 0.355407 | 0.288392 | 0.226441 | 133.2 | 55.0 | 45.0 | 27.5 | 5.7 |
| Bwabwata (BW) | 1030 | S 18.0917° | E 21.6863° | Zambesian <i>Baikiea</i> Woodlands: mosaic of mopane and <i>Baikiea</i> woodlands, and secondary grasslands | 0.445946 | 0.354166 | 0.268880 | 114.6 | 39.5 | 40.3 | 12.5 | 22.3 |
| Hwange (SI) | 1020 | S 18.6991° | E 26.1919° | Zambesian and Mopane Woodlands: mosaic of miombo and mopane woodlands, and shrubby savannas | 0.546752 | 0.408974 | 0.273454 | 106.1 | 42.3 | 35.5 | 18.0 | 10.3 |
| Victoria Falls (VF) | 920 | S 17.8716° | E 25.7213° | Zambesian and Mopane Woodlands: mosaic of mopane and <i>Baikiea</i> woodlands, and secondary grasslands | 0.543068 | 0.422227 | 0.306561 | 123.8 | 49.0 | 41.5 | 25.2 | 8.1 |
| Chizarira (XI) | 1010 | S 17.7010° | E 27.8546° | Zambesian and Mopane Woodlands: mosaic of mopane and <i>Baikiea</i> woodlands, and secondary grasslands | 0.569224 | 0.437890 | 0.314471 | 124.2 | 45.2 | 27.2 | 32.0 | 15.1 |

Table 1. Summary of the sampling sites with their elevation, GPS coordinates, description of the vegetation type, maximum, mean and minimum NDVI values and individual vegetation layer coverages (visually estimated). NDVI values and vegetation layer coverages were averaged over the 10 plots for each site.

At each sampling site, 10 plots were placed at least 1 km apart from each other, forming a 10 km-transect, or two perpendicular transects in some sites. Nocturnal moths were collected using portable light traps (made by Hutor NGO, Hradec Kralove, Czechia, with 48 LED lights arranged into two strips, prevailing UV light spectrum – 400 nm, 400 lm; run by a 12 V battery). All sampling was conducted in the beginning of the vegetation season, i.e. November and December. All captured moths were euthanised by ammonium carbonate placed in a small mesh bag in each trap. A light trap was exposed for a night (from dusk till dawn) at each sampling plot. Moth specimens were immediately sorted out in the field, dried by silicagel, and stored in paper envelopes. All individuals of the target moth groups (Noctuoidea: Erebidae, Eutellidae, Noctuidae, Notodontidae; Bombycoidea *s.l.*: Eupterotidae, Lasiocampidae, Saturniidae, Sphingidae; Zygaenoidea: Limacodidae) were later mounted, identified to species or morphospecies by combining morphological characters and genitalia dissections, and counted. Specimens of Geometroidea were counted but not identified, therefore this superfamily was used only for analyses of abundances but not for analyses of species richness. Vouchers were deposited in the Nature Education Centre of the Jagiellonian University in Krakow, Poland.

Environmental productivity of each site was characterised by the normalized difference vegetation index (NDVI; Rouse et al. 1974) for quantifying remotely sensed vegetation greenness (Tucker et al. 1985). It is a widely accepted proxy for environmental productivity, commonly applied in many studies at different spatial scales in order to predict species richness (Šímová & Storch 2017). We used the NDVI values produced by an extended 8-km Advanced Very High Resolution Radiometer (AVHRR; Tucker et al. 2005). We used the average of monthly maximum NDVI from the beginning of the vegetation season in the studied region (i.e. from October to December) from years 1982–2004 (Tucker et al. 2005). Each sampling plot was characterised by three characteristics of environmental

productivity (maximum NDVI, minimum NDVI, mean NDVI) of its 8-km grid cell. Moreover, to partly describe the habitat complexity, individual vegetation layer coverages were visually estimated at each plot during the light traps setting, the values were averaged over the 10 sampled plots for each site (Table 1). Finally, values of each characteristic were averaged for the 10 plots of each site. We tested collinearity among all described characteristics. Because virtually all characteristics were intercorrelated (Pearson $\rho \leq |0.5|$; Table S1), we selected mean NDVI as the only proxy for environmental productivity in our analyses.

Data analyses

We analysed the relationship of moth diversity with environmental productivity in R 4.0.3 (R Core Team 2020). All analyses were firstly run for the complete datasets (i.e. all moths for abundances, and all moths but Geometroidea for diversity indices), followed by separate analyses of particular moth groups to reveal potential different patterns between them. Based on numbers of sampled species and specimens, we analysed separately superfamilies Bombycoidea and Noctuoidea. Because families Erebiidae and Noctuidae (both belonging to Noctuoidea) were substantially abundant in our material, and they are common focal groups for numerous diversity studies, we ran additional separate analyses for them as well.

We tested the relationship to environmental productivity for alpha diversity (calculated as a mean number of species sampled at individual plots in each sampling site), gamma diversity (expressed as a number of species sampled at all plots in each site), beta diversity (calculated as gamma diversity divided by alpha diversity for each site) and abundance (expressed as a number of all specimens sampled across all plots in each site). Because we hypothesised the exponential relationships of these response variables to environmental productivity, we log-transformed

($x+1$) them prior to analyses. We tested relationships of all four diversity metrics of moth communities to mean NDVI by linear models (after visual checking for the normal distribution in our data). Linear and unimodal functions were fit in separate models.

For significant linear relationships (exponential relationships when log-transformed), we compared the fit of log-transformed and non-transformed species richness to check the validity of the exponential relationships. To compare the inter-group relationships to primary productivity, we compared slopes of their linear models using the *smatr* package (Warton et al. 2012).

RESULTS

In total, 12,372 individuals of the focal moth groups were captured. Among these, 9,048 individuals were identified to 487 species or morphospecies within families (Noctuoidea: Erebidae, Eutellidae, Noctuidae, Notodontidae; Bombycoidea *s.l.*: Eupterotidae, Lasiocampidae, Saturniidae, Sphingidae; Zygaenoidea: Limacodidae; Table 2, Table S2), while 3,324 specimens of Geometroidea were counted without further identification.

All studied groups showed significant positive linear or exponential relationships of alpha and gamma diversities to mean NDVI, while the unimodal relationships were never significant for alpha and gamma diversities (Table 3, Fig. 2). For alpha diversity, the coefficients of determination were slightly higher when species richness was log-transformed and were greater than 60% for all families (without Geometroidea), and for Bombycoidea, Noctuoidea, and Erebidae, suggesting an exponential relationship between mean NDVI and alpha diversity. Only Noctuidae showed a lower coefficient of determination

| Focal group | All families | | | All families + Geometridae | | | Bombycoidea s.l. | | | Noctuoidea | | | Erebidae | | | Eupterotidae | | | |
|------------------|--------------|-------|------|----------------------------|-------|-------|------------------|-----------|-------|------------|------|-----------|----------|-------|------|--------------|-------|-------|------|
| | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta |
| Soussusviei | 10 | 1.9 | 5.3 | 47 | 3 | 0.1 | 10.0 | 1 | 9 | 1.8 | 5.0 | 46 | 3 | 0.8 | 3.8 | 23 | 0 | 0 | 0 |
| Namibgrens | 45 | 9.7 | 4.6 | 1331 | 201 | 2 | 0.3 | 6.7 | 41 | 9.2 | 4.5 | 1324 | 13 | 3.1 | 4.2 | 57 | 0 | 0 | 0 |
| Khorixas | 45 | 9 | 5.0 | 382 | 56 | 2 | 0.2 | 10.0 | 2 | 4.3 | 8.8 | 49 | 380 | 11 | 1.6 | 6.9 | 20 | 0 | 0 |
| Windhoek | 32 | 7 | 4.6 | 389 | 37 | 3 | 0.4 | 7.5 | 4 | 28 | 6.5 | 4.3 | 384 | 11 | 3.2 | 3.4 | 195 | 1 | 0.2 |
| Etosha | 39 | 9.2 | 4.2 | 710 | 166 | 0 | 0 | - | 0 | 39 | 9.2 | 4.2 | 710 | 13 | 2.8 | 4.6 | 50 | 0 | 0 |
| Thekadu | 50 | 10.1 | 5.0 | 350 | 54 | 6 | 1.5 | 4.0 | 27 | 44 | 8.6 | 5.1 | 323 | 11 | 3.1 | 3.5 | 64 | 1 | 0.2 |
| Central Kalahari | 74 | 18.4 | 4.0 | 589 | 43 | 8 | 2.5 | 3.2 | 54 | 66 | 15.9 | 4.2 | 515 | 19 | 4.3 | 4.4 | 89 | 0 | 0 |
| Grootfontein | 85 | 21.3 | 4.0 | 1337 | 1741 | 15 | 4.9 | 3.1 | 161 | 70 | 16.4 | 4.3 | 1176 | 16 | 4.4 | 3.6 | 686 | 0 | 0 |
| Bwabwata | 92 | 23 | 4.0 | 762 | 220 | 19 | 4.8 | 4.0 | 149 | 71 | 17.9 | 4.0 | 610 | 30 | 8 | 3.8 | 389 | 1 | 0.4 |
| Hwange | 145 | 36 | 4.0 | 994 | 238 | 9 | 3.3 | 2.7 | 124 | 125 | 27.8 | 4.5 | 669 | 49 | 9.6 | 5.1 | 249 | 2 | 1.5 |
| Victoria Falls | 179 | 44.8 | 4.0 | 1757 | 425 | 15 | 4.1 | 3.7 | 63 | 152 | 36.5 | 4.2 | 1574 | 71 | 16.1 | 4.4 | 340 | 3 | 0.9 |
| Chitizarra | 99 | 19.2 | 5.2 | 410 | 140 | 11 | 3.7 | 3.0 | 98 | 80 | 13.4 | 6.0 | 203 | 35 | 6.2 | 5.6 | 102 | 3 | 1.3 |

| Focal group | Euliellidae | | | Lasiocampidae | | | Limaecoidae | | | Noctuidae | | | Notodontidae | | | Saturniidae | | | Sphingidae | | |
|------------------|-------------|-------|------|---------------|-------|-------|-------------|-----------|-------|-----------|------|-----------|--------------|-------|------|-------------|-------|-------|------------|--|--|
| | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | Abundance | Gamma | Alpha | Beta | | |
| Soussusviei | 0 | 0 | 0 | 1 | 0.1 | 1 | 0.1 | 1 | 0 | 0 | 0 | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Namibgrens | 0 | 0 | 0 | 2 | 0.3 | 5 | 0.2 | 2 | 28 | 6.1 | 4.6 | 1267 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Khorixas | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 32 | 7.2 | 4.4 | 360 | 0 | 0 | 0 | 1 | 0.1 | 1 | 1 | | |
| Windhoek | 0 | 0 | 0 | 2 | 0.2 | 2 | 1 | 0.1 | 17 | 3.3 | 5.2 | 199 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Etosha | 1 | 1 | 348 | 0 | 0 | 0 | 0 | 0 | 25 | 5.4 | 4.6 | 312 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | | |
| Thekadu | 0 | 0 | 0 | 2 | 0.9 | 18 | 0 | 0 | 32 | 5.3 | 6.0 | 254 | 1 | 0.2 | 5 | 1 | 0.1 | 1 | 2 | | |
| Central Kalahari | 0 | 0 | 0 | 4 | 1.5 | 37 | 0 | 0 | 47 | 11.6 | 4.1 | 448 | 0 | 0 | 0 | 1 | 0.1 | 1 | 3 | | |
| Grootfontein | 1 | 0.1 | 1 | 6 | 2.1 | 94 | 0 | 0 | 50 | 10.8 | 4.6 | 325 | 3 | 1.1 | 154 | 1 | 0.2 | 2 | 8 | | |
| Bwabwata | 1 | 0.1 | 1 | 7 | 1.5 | 47 | 2 | 0.3 | 3 | 39 | 9.7 | 4.0 | 209 | 1 | 0.1 | 1 | 4 | 1 | 26 | | |
| Hwange | 0 | 0 | 0 | 2 | 0.3 | 3 | 11 | 4.9 | 201 | 73 | 17.4 | 4.2 | 406 | 3 | 0.8 | 14 | 1 | 0.2 | 2 | | |
| Victoria Falls | 0 | 0 | 0 | 5 | 1.1 | 11 | 12 | 4.2 | 120 | 72 | 17.6 | 4.1 | 1121 | 9 | 2.8 | 113 | 2 | 0.2 | 2 | | |
| Chitizarra | 0 | 0 | 0 | 5 | 1.6 | 60 | 8 | 2.1 | 109 | 35 | 4.7 | 7.4 | 62 | 10 | 2.5 | 39 | 1 | 0.4 | 5 | | |

Table 2. Diversity (gamma, alpha and beta diversities, and abundance) of the focal lepidopteran groups at each individual sites.

(39%) with the linear relationship. For gamma diversity, both coefficients of determination for log-transformed and non-transformed species richness were comparable. Only Erebidae showed a better fit with the log-transformed data (82% vs 69%) (Table 3). The test for a common slope between the different groups did not show any difference from the common slope (for alpha diversity: likelihood ratio = 0.98, $p = 0.91$, $df = 4$; for gamma diversity: likelihood ratio = 1.78, $p = 0.78$, $df = 4$).

Beta diversity did not show any significant relationship with mean NDVI, except for Bombycoidea with beta diversity significantly linearly correlated with mean NDVI (Table 3). Only Bombycoidea, Geometroidea, and Noctuidae showed significantly positive linear relationships of their abundances to mean NDVI (Table 3, Fig. 3). The correlations were weaker for Geometroidea and Noctuidae (37 and 28% of explained variation, respectively), while the abundance of Bombycoidea correlated better with mean NDVI (57%). No significant unimodal relationships were detected. When a common slope between the individual groups is tested, the slopes of individual groups did not significantly differ from their common slope (likelihood ratio = 2.41, $p = 0.30$, $df = 2$).

| Response variable transformation | Alpha diversity | | | | Gamma diversity | | | | Beta diversity | | | | Abundance | |
|----------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| | Linear | | Unimodal | | Linear | | Unimodal | | Linear | | Unimodal | | Linear | Unimodal |
| | non-transformed | log-transformed | Log-transformed | log-transformed | Non-transformed | log-transformed | log-transformed | log-transformed | log-transformed | log-transformed | log-transformed | log-transformed | log-transformed | log-transformed |
| All families | 0.68*** | 0.71*** | 0.76 | 0.75*** | 0.76*** | 0.75*** | 0.77 | 0.12 | 0.35 | 0.19 | 0.26 | 0.20 | 0.29 | |
| All families + Geometroidea | - | - | - | - | - | - | - | - | - | - | - | 0.28* | 0.34 | |
| Geometroidea | - | - | - | - | - | - | - | - | - | - | - | 0.57** | 0.56 | |
| Bombycoidea s.l. | 0.63** | 0.67*** | 0.66 | 0.51** | 0.54** | 0.51** | 0.47 | 0.62** | 0.73 | 0.03 | 0.15 | 0.08 | 0.40 | |
| Noctuoidea | 0.60** | 0.65*** | 0.69 | 0.71*** | 0.72*** | 0.71*** | 0.73 | -0.10 | 0.08 | 0.37* | 0.40 | -0.08 | -0.05 | |
| Erebidae | 0.63** | 0.79*** | 0.77 | 0.82*** | 0.69*** | 0.82*** | 0.80 | -0.07 | -0.11 | -0.08 | -0.05 | -0.08 | -0.05 | |
| Noctuidae | 0.39* | 0.37* | 0.45 | 0.51** | 0.54** | 0.51** | 0.60 | -0.10 | -0.02 | -0.08 | -0.05 | -0.08 | -0.05 | |

Table 3. Coefficients of determination (adjusted R^2) between diversity indexes (alpha diversity, gamma diversity, beta diversity, abundance) and NDVI mean for each focal group of moths. Values in bold indicate: * $p \leq 0.05$; ** $p \leq 0.01$, *** $p \leq 0.001$.

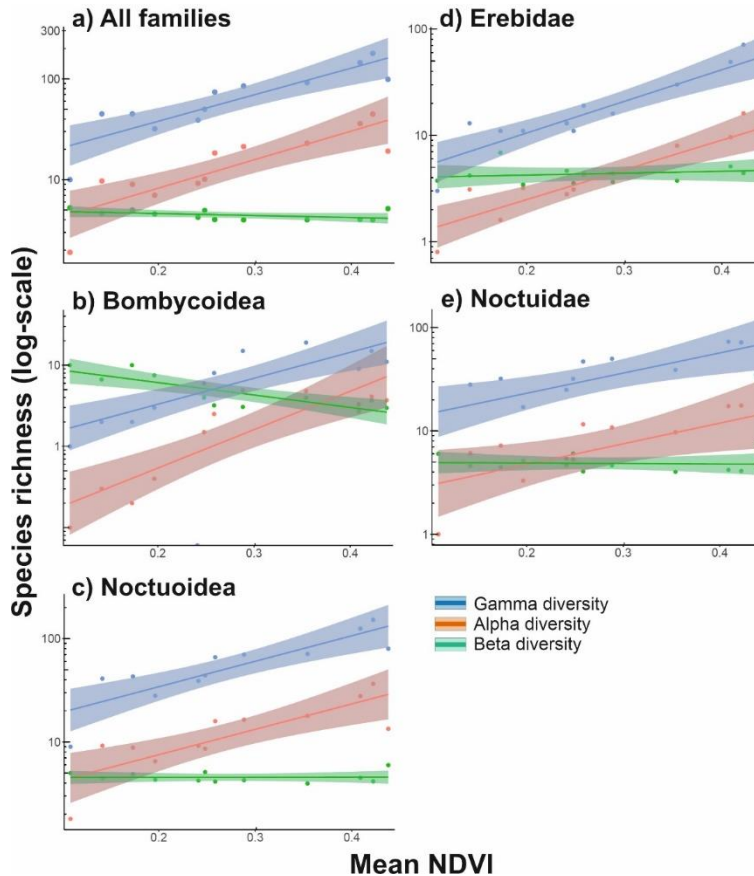


Fig. 2. Effects of the mean NDVI on the species richness (alpha and gamma diversities) of the focal groups of moths sampled along the environmental productivity gradient. Only the groups of moths, whose relationships between alpha and/or gamma diversities and the mean NDVI were significant, are visualized: a) all families, b) Bombycoidea *s.l.*, c) Noctuoidea, d) Erebidae, and e) Noctuidae. Shaded areas indicate 95% confidence intervals. The adjusted R^2 and p-values are reported in Table 3.

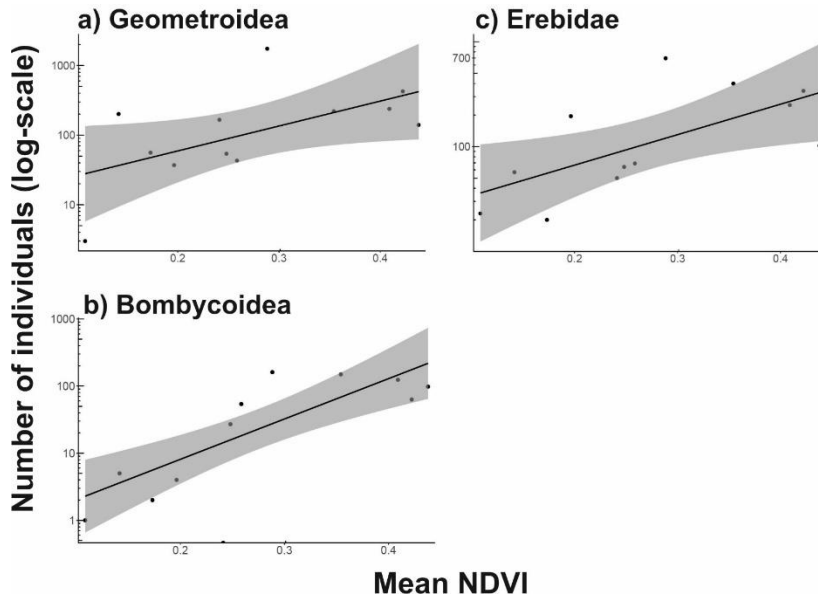


Fig. 3. Effects of the mean NDVI on abundances of the focal groups of moths sampled along the environmental gradient. Only the groups of moths, whose relationships were significant, are visualized: a) Geometroidea, b) Bombycoidea *s.l.*, c) Erebidae. Shaded areas indicate 95% confidence intervals. The adjusted R^2 and p-values are reported in Table 3.

DISCUSSION

Moth species richness patterns were highly consistent among the individual focal groups: there was an exponential growth of species richness at local (alpha diversity) and regional (gamma diversity) scales along the environmental productivity gradient, rejecting our hypothesis. This result differed from other studies on insect species richness, which found significant (Bailey et al. 2004; Seto et al. 2004) or weak positive linear relationships or no relationships (Kerr et al. 2001; Kaspari et al. 2004; Levanoni et al. 2011; Brasil et al. 2019) at local and regional scales. Several hypotheses focusing on the quantity and variability of energy and resource availability could explain the increasing species richness of moths with environmental productivity at local and regional scales. Species richness of moths, as herbivores, depends on availability of food generated through the primary productivity of plants. This refers to the productivity hypothesis which stated that energy limits species richness through the trophic cascades: higher primary productivity generates higher biomass and can also cause the high plant diversity (Wright 1983). This also leads to a higher complexity in the vegetation structure, offering more microhabitats and resources for moths (Lawton 1983, Tews 2004). However, the productivity-diversity relationships of herbaceous vegetation are variable (Adler et al. 2011; Fraser et al. 2015), and it was admitted that herbaceous vegetation biomass production is a poor predictor of herb diversity (Šimová et al. 2013).

On the other hand, plant diversity can be rather limited by solar energy and water availability (Wright 1983; Mittelbach et al. 2001), which would act indirectly on moth diversity. This energy hypothesis stated that energy availability drives and maintain the species richness gradients: sites with higher energy flow (e.g. evapotranspiration) host more species (Wright 1983). Climatic conditions, such as temperature and precipitation, are covariates of environmental productivity and they have been shown to

be a better predictor of insect species richness at local and regional scales than the primary productivity itself (Kaspari et al. 2004; Brasil et al. 2019). Sites with higher precipitation and evapotranspiration generally host more species (O'Brien 1998). The environmental productivity gradient studied here is also a gradient of temperature and water availability (Davies 2011). Water is a typical limiting factor for plant growth in arid and grassy ecosystems, increasing plant biomass (Whitford et al. 1995), offering moths protection from desiccation, favorable microclimatic conditions, and water for their metabolism (Lightfoot & Whitford, 1991). As ectotherms, moths are sensitive to the temperature their environment. They may acquire less energy for their metabolism in sites with lower temperature, limiting their activity. Temperature has also a positive effect on metabolic rates of insects, leading to generation time shortening, and accelerate the species diversification (Allen et al. 2007). Besides, the climate seasonality or climate heterogeneity (in space and time) seem to be the main driver of damselflies species richness in Brazilian savannahs, as it generates greater niche and resource variability (Brasil et al. 2019). In small geographic ranges, within tropical biomes, a greater diversity was observed in heterogeneous climatic sites (Vieira et al. 2018). Unfortunately, as we do not have any seasonal climatic data, we cannot extrapolate this result to moth communities in this study.

In our study, environmental productivity was not related to any significant patterns of abundance for most of the focal groups, and the significant relationships (Geometroidea, Bombycoidea *s.l.*, and Erebidae) were relatively weak. This contradicts our expectations: a positive (decelerating) relationship between abundance and environmental productivity, as found by Kaspari et al. (2000) for ant communities. This result has disproved the more individual hypothesis, in which environmental productivity limits the number of species through the number of individuals (Wright 1983; Srivastava and Lawton 1998). This hypothesis suggested that the higher energy availability supports more

individuals, which consequently generates communities with more species with large and viable populations sizes (Šímová et al. 2011) and decreasing extinction probabilities (Evans et al. 2005). Similarly, weak or no relationships have been also found between abundance and environmental productivity, and species richness and abundance, in several ectotherm taxa, including butterflies (Currie et al. 2004). This hypothesis involves many problems in its definition and quantification of the energy availability (see Storch et al. (2018) for a review). Moreover, insect abundance can greatly vary at a given temporal scale (both intra and interannual variability) and can mislead the role of abundance in insect diversity patterns (Vagle & McCain 2020). As explained previously, temperature and water availability may be better predictors of insect abundance (Buckley et al. 2012).

CONCLUSION

Our study shown that environmental productivity structures exponential growth of species richness patterns of Afrotropical moth communities in savannahs at both local and regional scales. Covariates of environmental productivity, such as temperature and water availability, are likely drive those patterns. However, no significant patterns of moth abundance were found for the entire communities, suggesting that abundance do not limit species richness of moth communities in African savannahs. It also indicates that generally, insect abundances are not robust estimates of insect diversity patterns. Future research is also needed to ascertain the degree to which our results can be generalised to other taxa in African savannahs, especially at other trophic levels.

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SUPPLEMENTARY INFORMATION

Table S1. Pearson correlation coefficients of the habitat descriptors characterized at each site. The variables are considered collinear if Pearson $\rho \leq |0.5|$ (**in bold**). For details on particular variables, see Table 1.

| | Maximum NDVI | Mean NDVI | Minimum NDVI | Mean vegetation Cover | < 30 cm vegetation layer cover (%) | < 2 m vegetation layer cover (%) | < 5 m vegetation layer cover (%) |
|------------------------------------|--------------|-----------|--------------|-----------------------|------------------------------------|----------------------------------|----------------------------------|
| Mean NDVI | 1.00 | | | | | | |
| Minimum NDVI | 0.98 | 0.99 | | | | | |
| Mean vegetation Cover | 0.85 | 0.86 | 0.88 | | | | |
| < 30 cm vegetation layer cover (%) | 0.80 | 0.81 | 0.83 | 0.93 | | | |
| < 2 m vegetation layer cover (%) | 0.64 | 0.65 | 0.67 | 0.90 | 0.78 | | |
| < 5 m vegetation layer cover (%) | 0.70 | 0.70 | 0.72 | 0.84 | 0.69 | 0.73 | |
| >5 m vegetation layer cover (%) | 0.75 | 0.76 | 0.76 | 0.60 | 0.50 | 0.40 | 0.35 |

Table S2. Summary of species richness and abundance of the focal groups of moths sampled along the environmental productivity gradient.

| Groups | Species richness | Abundance |
|------------------------------------|-------------------------|------------------|
| All families | 487 | 9048 |
| All families + Geometroidea | - | 12372 |
| Geometroidea | - | 3324 |
| Bombycoidea <i>s.l.</i> | 44 | 688 |
| Noctuoidea | 424 | 7924 |
| Erebidae | 153 | 2264 |
| Eupterotidae | 5 | 134 |
| Eutellidae | 1 | 350 |
| Lasiocampidae | 20 | 278 |
| Limacodidae | 19 | 436 |
| Noctuidae | 251 | 4984 |
| Notodontidae | 19 | 326 |
| Saturniidae | 8 | 40 |
| Sphingidae | 11 | 236 |

CHAPTER V

Characterization and comparison of poorly known moth communities through DNA barcoding in two Afrotropical environments in Gabon

Delabye, S., Rougerie, R., Bayendi, S., Andeime-Eyene, M., Zakharov, E. V., deWaard, J.R., Hebert, P.D.N., Kamgang, R., Le Gall, P., Lopez-Vaamonde, C., Mavoungou, J.-F., Moussavou, G., Moulin, N., Oslisly, R., Rahola, N., Sebag, D., & Decaëns, T. (2019).

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Mosaic of savannah and forest galleries in Lopé National Park. © S. Delabye

Characterization and comparison of poorly known moth communities through DNA barcoding in two Afrotropical environments in Gabon¹

Sylvain Delabye, Rodolphe Rougerie, Sandrine Bayendi, Myriam Andeime-Eyene, Evgeny V. Zakharov, Jeremy R. deWaard, Paul D.N. Hebert, Roger Kamgang, Philippe Le Gall, Carlos Lopez-Vaamonde, Jacques-François Mavoungou, Ghislain Moussavou, Nicolas Moulin, Richard Oslisly, Nil Rahola, David Sebag, and Thibaud Decaëns

Abstract: Biodiversity research in tropical ecosystems—popularized as the most diverse habitats on Earth—often neglects invertebrates, yet invertebrates represent the bulk of local species richness. Insect communities in particular remain strongly impeded by both Linnaean and Wallacean shortfalls, and identifying species often remains a formidable challenge inhibiting the use of these organisms as indicators for ecological and conservation studies. Here we use DNA barcoding as an alternative to the traditional taxonomic approach for characterizing and comparing the diversity of moth communities in two different ecosystems in Gabon. Though sampling remains very incomplete, as evidenced by the high proportion (59%) of species represented by singletons, our results reveal an outstanding diversity. With about 3500 specimens sequenced and representing 1385 BINs (Barcode Index Numbers, used as a proxy to species) in 23 families, the diversity of moths in the two sites sampled is higher than the current number of species listed for the entire country, highlighting the huge gap in biodiversity knowledge for this country. Both seasonal and spatial turnovers are strikingly high (18.3% of BINs shared between seasons, and 13.3% between sites) and draw attention to the need to account for these when running regional surveys. Our results also highlight the richness and singularity of savannah environments and emphasize the status of Central African ecosystems as hotspots of biodiversity.

Key words: community ecology, DNA barcodes, Lepidoptera, taxonomic deficit, tropical Africa.

Résumé : La recherche sur la biodiversité dans les écosystèmes tropicaux — présentés comme les habitats les plus riches en biodiversité sur la Terre — néglige souvent les invertébrés qui constituent pourtant la part la plus importante de cette richesse en espèces. Les communautés d'insectes en particulier sont particulièrement affectées par les lacunes de connaissances, tant d'un point de vue taxonomique (le déficit Linnéen) que du point de vue de notre compréhension de la distribution des espèces (le déficit Wallacéen), de telle manière que l'identification des espèces demeure un défi considérable, limitant l'utilisation de ces organismes comme indicateurs dans le cadre d'études d'écologie et de conservation. Dans ce travail, les auteurs utilisent

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S. Delabye.* Faculty of Science, University of South Bohemia in České Budějovice, Branišovská 1760, 37005, České Budějovice, Czech Republic; Biology Center, Institute of Entomology, The Czech Academy of Science, Branišovská 31, 37005, České Budějovice, Czech Republic.

R. Rougerie.*† Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE, 57 rue Cuvier, CP 50, 75005 Paris, France.

S. Bayendi and M. Andeime-Eyene. Institut de Recherches Agronomique et Forestière (IRAF-CENAREST), Libreville, Gabon.

E.V. Zakharov, J.R. deWaard, and P.D.N. Hebert. Centre for Biodiversity Genomics, Biodiversity Institute of Ontario, University of Guelph, Guelph, ON N1G 2W1, Canada.

R. Kamgang[†] and P. Le Gall.[†] Laboratoire Evolution, Génomes, Comportement, Ecologie (EGCE UMR 247, IRD-CNRS-Université Paris-Sud), Avenue de la Terrasse, Bâtiment 13, Boite Postale 1, 91198 Gif sur Yvette, France.

C. Lopez-Vaamonde.[†] INRA, UR633, Zoologie Forestière, F-45075 Orléans, France; Institut de Recherche sur la Biologie de l'Insecte, UMR 7261 CNRS, Université de Tours, UFR Sciences et Techniques, Tours, France.

J.-F. Mavoungou. Institut de Recherches en Ecologie Tropicale (IRET-CENAREST), Libreville, Gabon; Département de Biologie, Faculté des Sciences, Université des Sciences et Techniques de Masuku, BP 943, Franceville, Gabon.

G. Moussavou.[†] Institut de Recherches en Ecologie Tropicale (IRET-CENAREST), Libreville, Gabon.

N. Moulin.[†] Nicolas Moulin Entomologiste, 82 route de l'École, 76680 Montérolier, France.

R. Oslisly.[†] Agence Nationale des Parcs Nationaux (ANPN), BP 20379, Libreville, Gabon; Laboratoire Patrimoines Locaux et Gouvernance (PALOC) UMR 208, IRD-MNHN, 57 rue Cuvier - Case Postale 26, 75231 Paris cedex 05, France.

N. Rahola.[†] International Centre for Medical Research (CIRMF), Franceville, Gabon.

D. Sebag.[†] Normandie Université, UNIROUEN, UNICAEN, CNRS, M2C UMR 6143, Place Emile Blondel - Bâtiment IRESE A, 76821 Mont Saint Aignan Cedex, France.

T. Decaëns.[†] Centre d'Ecologie Fonctionnelle et Evolutive (CEFE UMR 5175, CNRS-Université de Montpellier-Université Paul-Valéry Montpellier-EPHE), 1919 Route de Mende, F-34293 Montpellier, France.

Corresponding author: Thibaud Decaëns (email: thibaud.decaens@cefe.cnrs.fr).

*Contributed equally to the paper.

[†]Members of the ECOTROP team. The remaining members of this team, and their affiliations, are given in Appendix A.

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les codes-barres ADN comme alternative à l'approche taxonomique conventionnelle pour caractériser et comparer la diversité des communautés de papillons de nuit au sein de deux écosystèmes contrastés au Gabon. Bien que l'échantillonnage demeure très incomplet, comme en témoigne la grande proportion (59 %) d'espèces présentes sous forme de singleton, les résultats révèlent une diversité extraordinaire. Avec ses 3500 spécimens séquencés, lesquels englobent 1385 BIN (« Barcode Index Number », assimilés à des espèces) au sein de 23 familles, la diversité des papillons de nuit au sein des deux sites échantillonnés est plus élevée que le nombre total d'espèces jusqu'alors répertoriées pour le pays entier. Ceci souligne les lacunes énormes en matière de connaissance de la biodiversité de ce pays. Le taux de remplacement des espèces, tant saisonnier que spatial, est étonnamment élevé (18,3 % des BIN partagés entre saisons, 13,3 % entre les deux sites), ce qui indique la nécessité d'en tenir compte lors de la réalisation d'inventaires régionaux. Ces résultats soulignent également la richesse et la singularité des savanes et font ressortir le fait que les écosystèmes de l'Afrique Centrale constituent des zones extrêmement riches en biodiversité.

Mots-clés : écologie des communautés, codes-barres ADN, lépidoptères, déficit taxonomique, Afrique tropicale.

Introduction

Tropical ecosystems host unrivalled species richness (Kier et al. 2005; Myers 1984; Myers et al. 2000), a fact that has long captivated public attention and raised concerns about the way to conserve this immense biodiversity (Wilson 1988). Understanding of tropical biodiversity has historically been biased toward the largest organisms such as angiosperms and vertebrates (May 2011), leaving considerable gaps in our knowledge of hyperdiverse groups of smaller animals, especially arthropods. These organisms are nevertheless key to ecosystem functioning (Erwin 1983; Zhang 2011) and the shortfalls in our taxonomic, biogeographic, and ecological knowledge are strong impediments against the integration of these organisms in conservation and management strategies (Miller and Rogo 2002; Whittaker et al. 2005). Because the few studies addressing this topic predict high extinction numbers for insects (Fonseca 2009; Stork and Habel 2014), it is urgent to lift “the curse of ignorance” (Diniz-Filho et al. 2010) by developing multi-scale studies on insect diversity that benefit from the technological revolution of the “genomic era” (Godfray 2006; Wilson 2003) and its recent developments in biodiversity sciences (Hebert et al. 2003a).

The Afrotropical region is one of the Major Tropical Wilderness Areas on earth (Myers 1990; Wilson 2002), i.e., a large and highly diverse area that has seen little impact from human activities until recently (i.e., <5 inhab. km⁻² and >75% of the original vegetation still present) (Mittermeier et al. 1998). However, recent estimates indicate that annual net deforestation of African tropical rainforests, although less dramatic than in Latin America or Southeast Asia, approached 0.3 million ha/year for the 2000–2010 decade (Achard et al. 2014), which could have led to dramatic biodiversity loss. As many as 100 000 insect species have been reported from the area, but Miller and Rogo (2002) suggest that species richness could exceed 600 000 species. In Gabon, a central-African country which is still covered by 80% of tropical rainforests, insect inventories have only considered butterflies (vande Weghe 2010), a few groups with limited number of species such as Mantodea (Roy 1973; Moulin 2018), Lucanidae (Maes and Pauly 1998), or Apoidea (Pauly 1998), and groups with specific economical and (or) agronomical importance such as Pseudococcidea (Hemiptera) and their parasitoids (Boussienguet et al. 1991). A few studies have also targeted terrestrial arthropod assemblages along human disturbance gradients (Basset et al. 2004, 2008).

Several authors emphasized the potential of using highly diverse groups, such as Lepidoptera, as environmental indicators (Axmacher et al. 2004a, 2004b; Beck et al. 2013; Kitching et al. 2000; Ricketts et al. 2001). They are indeed key herbivores and an important link within foodwebs as prey or as hosts for parasitoids. Variation in the diversity and structure of lepidopteran communities is thus likely to be representative of changes at other

trophic levels. For instance, lepidopteran species depend on their host plant species (or a few closely related plants), and in turn they play a fundamental role as pollinators; this connects them closely to plant community structure and composition (Ehrlich and Raven 1964; Novotny et al. 2002b). On the other hand, trophic cascades in food webs are likely to link both host plant and primary consumer assemblages to associated higher trophic levels of predators and parasitoids. Surprisingly however, only a few studies have examined this group in the Afrotropics. The taxonomic deficit and the high number of species that occur in those environments are certainly important causes for this deficit, because they impede reliable inventories and the description of community patterns. In a recent study based on a substantial sampling effort in Papua New Guinea (over 30 000 specimens collected over several years), Ashton et al. (2015) found that no asymptote was reached by species accumulation curves. These authors, however, also suggested that more limited sampling could be efficient in highlighting differences in the diversity and composition of moth communities among distant localities.

In this study, we use DNA barcodes to document and compare communities of moths in two differing ecosystems of Gabon. Several recent studies have demonstrated the effectiveness of DNA barcoding—a tool for species identification based on a short standardized DNA fragment (Hebert et al. 2003b)—in documenting species diversity of lepidopteran communities in regions where species assemblages are very diverse and when many species are undescribed (Janzen et al. 2009; Lamarre et al. 2016; Lees et al. 2014; Zenker et al. 2016). With this approach we aim at evaluating the sampling effort required to produce relevant census of these communities, to document seasonal variation in community composition, and if species-turnover (β -diversity) as revealed from our data are reflecting significant differences in richness and composition that can be linked to the different habitats sampled. Finally, we discuss the contribution of our study to the current knowledge of moth diversity in Gabon and in the Afrotropical region, with special reference to information compiled in AfroMoths, an online database of Afrotropical moth species (De Prins and De Prins 2017).

Material and methods

Study sites

Moths were collected at two locations (named Lopé 2 and Ipassa) in the province of Ogooué-Ivindo, Gabon (Figs. 1 and 2):

The Lopé 2 site is situated in the northern part of Lopé National Park, about 12 km south from Lopé village and the Dr. Alphonse Mackanga Missandzou Training Centre (CEDAMM, Wildlife Conservation Society; coordinates: 0°13'9.699"S, 11°35'5.6394"E; altitude: 300 m). Vegetation comprises a mosaic of forest and shrub savannah (Fig. 2A). Shrub savannah is dominated by Poaceae and Cyperaceae like *Anadelphia arrecta*, *Andropogon pseudapricus*, *Schizachyrium platyphyllum*, *Hyparrhenia diplandra*, or *Ctenium newtoni* and by a shrub layer with *Crossopteryx febrifuga* and *Nautclea latifolia* (White

Fig. 1. Location of the study sites. Dark grey areas represent National Parks in Gabon. The Ipassa site is located near Ivindo.

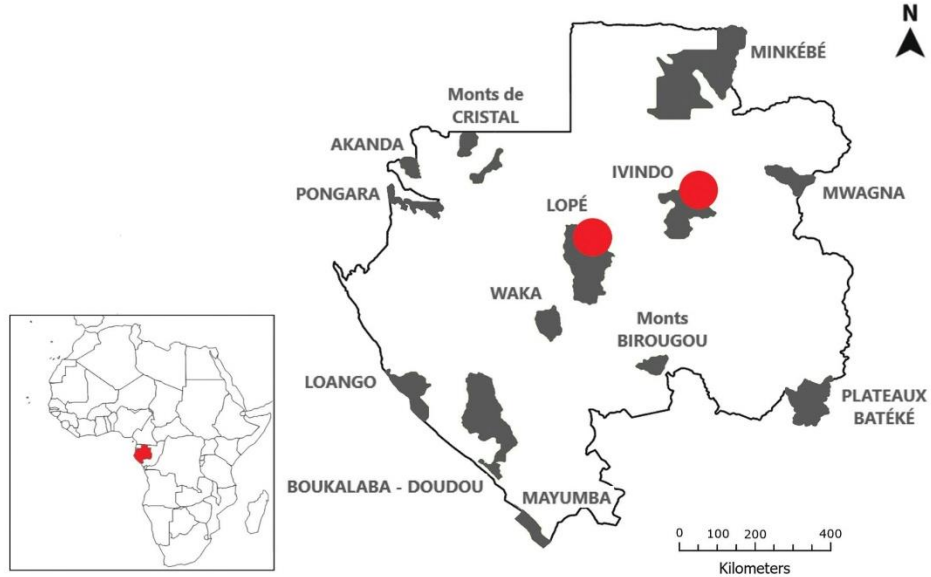
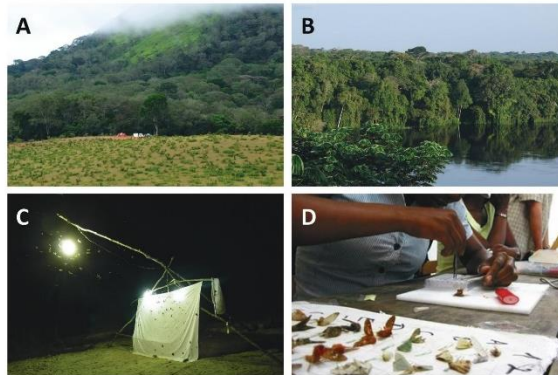


Fig. 2. Photos of the two study sites and sampling methods: (A) View of the savannah–forest patchwork in Lopé National Park, showing the position of the light trap (Lopé 2, November 2009); (B) Rainforests at Ipassa research station at the edge of the Ivindo River (November 2009); (C) Light trapping at Lopé 2 in March 2011; (D) Tissue sampling for DNA barcoding during the ECOTROP field class in March 2011.



and Abernethy 1997). Forest patches are mainly secondary to mature okoumé rainforests, the dominant forest type in western Gabon, dominated by *Aucoumea klaineana* ("okoumé"), *Lophira alata*, *Desbordesia glaucescens*, *Scyphocephalum ochochoa*, *Dacryodes buttneri*, *Santiria trimera*, *Sindoropsis le-testui*, and *Uapaca guineensis* (Ben Yahmed and Pourtier 2004; White and Abernethy 1997).

The Ipassa research station (Institut de Recherches en Ecologie Tropicale) is situated in the northern part of Ivindo National Park, 12 km from the city of Makokou (coordinates: 0°30'38.1456"N, 12°48'1.2594"E; altitude: 500 m). The site is mainly surrounded by mature Guineo-Congolese rainforest showing both Atlantic and continental influences (Doumenge et al. 2004; Nicolas 1977; White

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1983), with *Baphia leptobotrys* and *Milletia laurentii* dominating the tree cover, as well as *Scorodophoeus zenkeri*, *Plagiostyles africana*, *Dichostemma glaucescens*, *Santiria trimera*, *Polyalthia suaveolens*, and *Poncovia pedicellaris* (Fig. 2B).

The two sites are 160 km apart and share a similar seasonal cycle typical of the equatorial transition zone, with short (January–February) and long (June–September) dry seasons. The average monthly temperature is 24 °C with a mean annual precipitation of 1500 mm at Lopé and 1700 mm at Ipassa.

Moth sampling

Sampling was conducted at both sites in November 2009 and at Lopé 2 in February–March 2011 during a field class organized in the Lopé National Park (ECOTROP field class; <http://davidsebagafira.free.fr/BlogScienceAfrica/ECOTROP/ECOTROP.html>). We used a standard light trap technique consisting of a 250 W UV (mercury vapor) bulb placed 4–5 m above the ground to attract insects (Figs. 2A and 2C). Two low voltage lamps (80 W) were positioned on both sides of a vertical white sheet positioned below the UV bulb. Specimens were collected during dark-moon phases from dusk to dawn (18:00–06:00, local time) to collect species with varying flight times (Lamarre et al. 2015). Overall, four collecting nights were carried out at each site in 2009 (10–14 November at Lopé 2 and 14–18 November at Ipassa), and three additional nights at the end of the short dry season at Lopé 2 in 2011 (27 February, 1 March, and 4 March). Our sampling design was therefore relevant to compare observed communities between sites from the samples collected during the rainy season in 2009, and to investigate seasonal turnover at Lopé 2.

Our study focuses on macro-moths, i.e., moths whose wingspan were >1 cm, which includes the nocturnal part of Macrolepidoptera as well as larger representative of non-macrolepidopteran families (so-called Microlepidoptera), and excludes the smaller species of other families of Macrolepidoptera. Each night, we sampled specimens of as many species of macro-moths as could be distinguished morphologically when collecting. Moths were killed using a cyanide jar or by an injection of ammonia into the thorax for larger species, and were placed in glassine envelopes marked with a code unique to each sampling event. Specimens are currently deposited in the Museum national d'Histoire Naturelle in Paris, where they are available for further taxonomic study.

DNA barcoding and taxonomic assignments

The day after collecting, specimens were sorted into morphospecies, i.e., groups of specimens that were readily distinguishable from their external morphology. A maximum of four specimens per morphospecies and per collecting night were then selected for molecular analyses. A small piece of tissue (generally a complete leg or its tarsus for the largest species) was sampled for each of them (Fig. 2D). DNA extraction was carried out at the Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph following a standard automated protocol (Ivanova et al. 2006; Hajibabaei et al. 2005). Tissue lysis occurred in 50 μ L of lysis buffer and proteinase K (0.02 mg/ μ L) incubated at 56 °C overnight. A 658 bp segment of the 5' region of the COI mitochondrial gene used as a standard DNA barcode was amplified through PCR using the primer pair LepF1/LepR1 (Hebert et al. 2004). Samples failing to amplify after this first PCR pass were re-processed using the primer sets LepF1/MLepR1 and MLepF1/LepR1 that target 307 and 407 bp overlapping fragments, respectively (Hajibabaei et al. 2006). A standard PCR reaction protocol was used for all PCR amplifications and products were checked on a 2% E-gel 96 Agarose (Invitrogen). Un-purified PCR amplicons were sequenced in both directions using the same primers as those used for the initial amplification, and following standard CCDB protocols (<http://ccdb.ca/resources/>) (Hajibabaei et al. 2005). Trimming of primers, sequence editing,

and contig assembly were carried out at CCDB using CodonCode software (CodonCode Corporation, Centerville, MA, USA). All sequences were aligned and inspected for frame-shifts and stop codons for removal of editing errors and possible pseudogenes, and then uploaded in the Barcode of Life Data systems (BOLD, Ratnasingham and Hebert 2007). All records—including specimen and sequence data—can be accessed publicly in BOLD and GenBank, and were assembled within BOLD dataset DS-LOPELEPI.

Species identification of specimens using either DNA barcodes or morphology could not be achieved for all the specimens, because of the incompleteness of the current DNA barcode library for the region, and because of the lack of taxonomic expertise for many of the moths collected. Also, the use of provisional morphospecies was intractable considering the large number of specimens and the need for a thorough processing of individuals (spreading of wings, genitalia dissections) for a reliable assessment of observed species diversity (Zenker et al. 2016). As a consequence, we used DNA barcodes to delineate molecular taxonomic units (MOTUs) as a proxy for species. More specifically, we used Barcode Index Numbers (BINs) derived from the automated MOTU delineation tool implemented in BOLD (Ratnasingham and Hebert 2013), and which have already been used to consistently approximate species in Lepidoptera (Hautmann et al. 2013; Kekkonen and Hebert 2014). In two families, Saturniidae and Sphingidae, species were carefully identified (by R.R. and T.D.) on the basis of morphology and the results were used to test their correspondence with BINs.

A “reverse taxonomy” approach (Markmann and Tautz 2005) using DNA barcode results coupled with the BOLD identification tool, as well as the topology of the NJ tree, failed to produce species identification for most of our query sequences. However, we were able to provide a family-level identification for the majority of individuals analyzed using either their general morphology or DNA barcode analysis. For this second approach, the richness of the BOLD DNA barcode library, with records for more than 100 000 species of Lepidoptera, proved very useful using a simple query for best close matches in the database. Instead of applying a threshold to generate family (or occasionally subfamily and genus) assignment, we verified the proposed assignments by comparing images and, where relevant, by examining the specimens and confirming the proposed taxon on the basis of its morphology.

Community data analyses

The α -diversity at each site was assessed by plotting rarefaction curves and their extrapolations for both species richness and sample coverage (i.e., a measure of sample completeness that estimates the proportion of the total number of individuals in a community that belong to the species represented in the sample), using specimen numbers as a measure of sampling intensity. These analyses were carried out using the iNEXT package (Hsieh et al. 2014) for R 3.0.2 (R Development Core Team 2004). We then used the vegan package (Oksanen et al. 2013) to calculate several diversity indices: observed richness (defined as the total number of observed BINs at a given sampling site or on a given date), Chao1, ACE and second order jackknife diversity estimators, and Fisher α -diversity index. We also used iNEXT to calculate the number of species observed given a constant level of sampling coverage, and vegan for the estimation of species richness rarefied to a constant level of sampling intensity (i.e., a constant number of specimens collected). We finally used fisherfit, prestonfit, and prestonfistr functions of vegan to plot rank-abundance diagrams and fit Fisher's logseries, Preston's lognormal, and truncated log-normal models to abundance data for each sampling site.

To assess β -diversity among sampling sites (for samples collected in 2009) and seasons (at Lopé 2 site only), we calculated an

Table 1. Number of individuals and number of BINs collected for different families and subfamilies of macro-moths at the two study sites and for two seasons at Lopé 2, and number of species listed in the AfroMoths online database (De Prins and De Prins 2017) for the same families and subfamilies.

| | Ipassa (WS) | | Lopé (WS) | | Lopé (DS) | | Lopé | | Total | | AfroMoths* |
|-------------------------|--------------------|-------------|--------------------|-------------|--------------------|-------------|--------------------|-------------|--------------------|-------------|----------------|
| | No. of individuals | No. of BINs | No. of individuals | No. of BINs | No. of individuals | No. of BINs | No. of individuals | No. of BINs | No. of individuals | No. of BINs | No. of species |
| Bombycidae | 2 | 2 | — | — | — | — | — | — | 2 | 2 | 0 |
| Brahmaeidae | 2 | 1 | 2 | 1 | — | — | 2 | 1 | 4 | 1 | 0 |
| Cossidae | 6 | 5 | 5 | 4 | 8 | 4 | 13 | 8 | 19 | 11 | 1 |
| Crambidae | 17 | 14 | 73 | 31 | 19 | 16 | 92 | 43 | 109 | 52 | 9 |
| Drepanidae | 6 | 4 | — | — | 1 | 1 | 1 | 1 | 7 | 5 | 9 |
| Erebidae (Arctiinae) | 198 | 71 | 131 | 41 | 75 | 37 | 206 | 65 | 404 | 113 | 103 |
| Erebidae (Erebinae) | 75 | 38 | 71 | 24 | 47 | 34 | 118 | 46 | 193 | 72 | 42 |
| Erebidae (Lymantriinae) | 220 | 103 | 47 | 32 | 79 | 54 | 126 | 73 | 346 | 164 | 117 |
| Other Erebidae | 61 | 33 | 102 | 18 | 22 | 18 | 124 | 32 | 185 | 60 | 97 |
| Eriocottidae | — | — | 2 | 2 | — | — | 2 | 2 | 2 | 2 | 2 |
| Eupterotidae | 13 | 10 | 22 | 3 | 5 | 3 | 27 | 5 | 40 | 15 | 32 |
| Euteliidae | — | — | 1 | 1 | 4 | 2 | 5 | 2 | 5 | 2 | 5 |
| Geometridae | 293 | 153 | 130 | 63 | 117 | 62 | 247 | 107 | 540 | 220 | 175 |
| Lasiocampidae | 88 | 55 | 80 | 42 | 74 | 36 | 154 | 61 | 242 | 101 | 68 |
| Lecithoceridae | — | — | 1 | 1 | 2 | 1 | 3 | 2 | 3 | 2 | 0 |
| Limacodidae | 31 | 15 | 20 | 14 | 8 | 7 | 28 | 18 | 59 | 30 | 25 |
| Noctuidae | 199 | 125 | 103 | 66 | 95 | 69 | 198 | 124 | 397 | 224 | 69 |
| Nolidae | — | — | 2 | 2 | — | — | 2 | 2 | 2 | 2 | 22 |
| Notodontidae | 155 | 77 | 72 | 31 | 45 | 27 | 117 | 49 | 272 | 104 | 180 |
| Psychidae | 1 | 1 | 2 | 2 | 6 | 4 | 8 | 4 | 9 | 5 | 8 |
| Pyralidae | 65 | 29 | 82 | 37 | 25 | 18 | 107 | 49 | 172 | 70 | 6 |
| Saturniidae | 62 | 32 | 79 | 31 | 36 | 9 | 115 | 33 | 177 | 43 | 110 |
| Sphingidae | 98 | 44 | 58 | 28 | 111 | 40 | 169 | 47 | 267 | 66 | 124 |
| Thyrididae | 4 | 4 | 18 | 1 | — | — | 18 | 1 | 22 | 5 | 34 |
| Tineidae | — | — | 2 | 1 | — | — | 2 | 1 | 2 | 1 | 3 |
| Tortricidae | 5 | 4 | — | — | 1 | 1 | 1 | 1 | 6 | 5 | 9 |
| Uraniidae | — | — | 1 | 1 | — | — | 1 | 1 | 1 | 1 | 1 |
| Zygaenidae | 1 | 1 | — | — | — | — | 0 | — | 1 | 1 | 7 |
| Not identified | 2 | 2 | 4 | 4 | — | — | 4 | 4 | 6 | 6 | — |
| Total | 1604 | 823 | 1110 | 481 | 780 | 443 | 1890 | 782 | 3494 | 1385 | 1258 |

Note: WS, wet season; DS, dry season.

*Apr.18th, 2017 (subspecies removed).

average Sørensen's index of dissimilarity using the package *vegan* (Oksanen et al. 2013):

$$\beta_{BC} = (b + c)/(2a + b + c)$$

where *a* is the number of species (here BINs) shared between two sites B and C, and *b* and *c* are the numbers of unique BINs for sites B and C.

We used the *betapart* package to decompose β -diversity into two components (Baselga 2010): nestedness (i.e., when the composition of communities with a smaller species number is a subset of a richer community), which reflects non-random processes of species loss, and spatial turnover, which results from species replacement as a consequence of environmental sorting or spatial and historical constraints (Qian et al. 2005; Ulrich et al. 2009; Wright and Reeves 1992). Analyses of β -diversity were carried out with and without singletons (i.e., BINs represented by a single specimen in the dataset), as their inclusion can lead to overestimation of β -diversity.

Results

Species richness at the regional scale

We obtained 3494 (97.7%) sequences from the 3576 specimens selected for DNA barcoding. These sequences included representatives of 1385 BINs representing 23 families of Lepidoptera

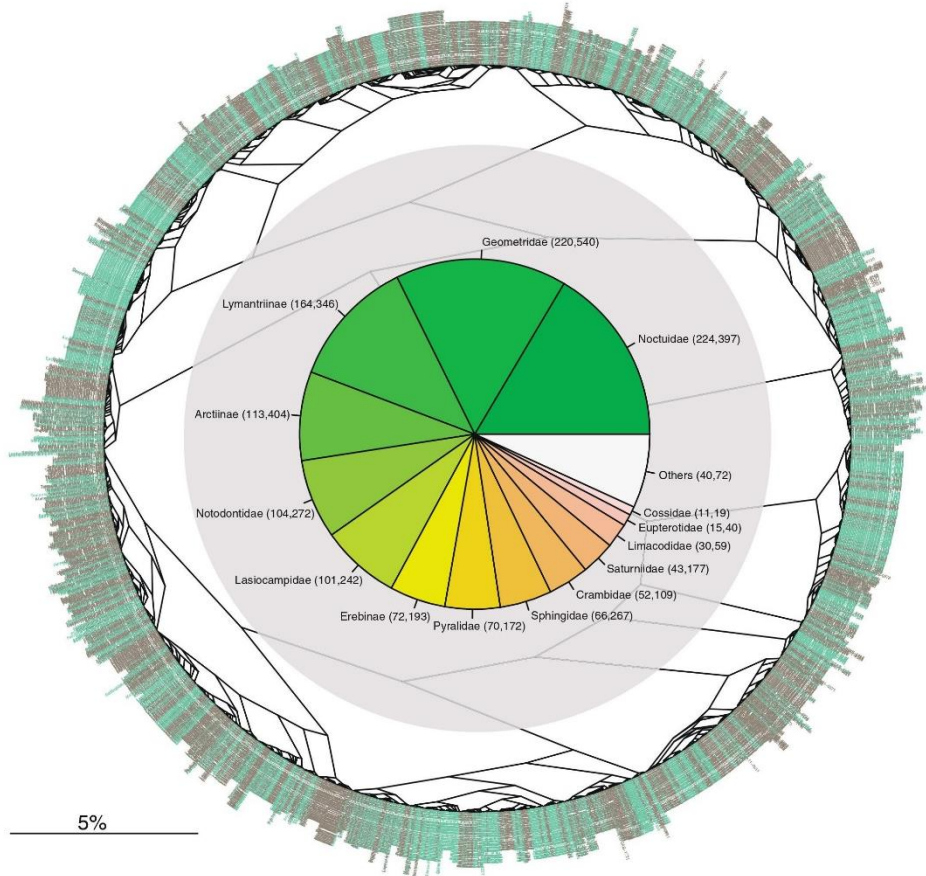
(Table 1; Fig. 3), and only six specimens (6 BINs) could not be identified to family level. Noctuidae, Erebidae, and Geometridae represented about one third of the BINs and sampled individuals (Fig. 3), whereas 10 other families were each represented by less than 10 specimens. More than half of the BINs (796 in total, 59%) were represented by a single individual in our data set (i.e., singleton).

Morphological examination of specimens in the families Saturniidae (177) and Sphingidae (267) led to the distinction of 42 and 63 species, respectively, of which only two (in family Saturniidae) could not be identified to species and were given provisional names (*Orthogonioptilum* mgab_RR01 and *Dogioia* mgab_RR01). The correspondence between morphologically assigned species and BINs was nearly perfect: 42 species versus 43 BINs in Saturniidae (98%) and 63 versus 66 in Sphingidae (95%) (see DNA barcode NJ trees in the Supplementary data File S1² and File S2²). In other families, 112 species (representing 121 BINs) were formally identified by taxonomic experts (see acknowledgments) or through DNA barcode matches in BOLD. Overall, with Saturniidae and Sphingidae included, these species represent about 16% of all BINs (230/1385).

Comparison between the number of BINs observed in our study and the list of recognized species and subspecies for Gabon, as derived from AfroMoths (De Prins and De Prins 2017), revealed the strong taxonomic deficit and the lack of exploration (i.e., bio-

²Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/gen-2018-0063>.

Fig. 3. Diversity and composition of the macro-moth sample at the two study locations (Lopé 2 and Ipassa): the circular phylogram represents the results of a Neighbor-Joining analysis in BOLD of 3494 COI sequences clustering into 1385 BINs; barcodes obtained for specimens from Ipassa are in green and those from Lopé 2 in grey. The pie chart represents the relative contribution (ordered) of the different families and subfamilies (for Erebiidae) of moths collected in the two sites; numbers within brackets indicate the number of BINs and number of specimens sampled, respectively.

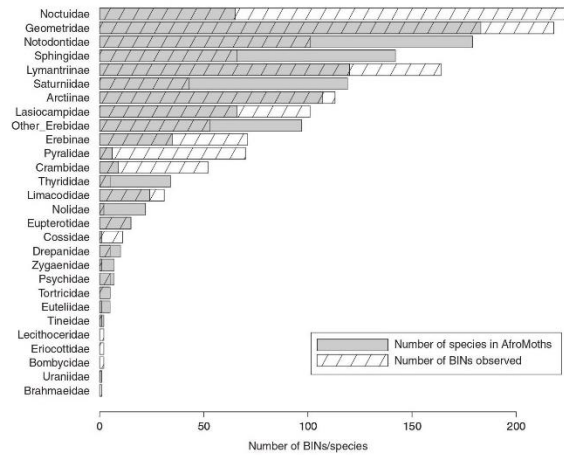


diversity surveys, collecting activities) that characterizes moth diversity in the Afrotropics (Fig. 4). AfroMoths is based on the survey of 7355 published sources for the whole Afrotropical region (as of 8 August 2017) and the authors' own studies. It lists 1301 moth species and subspecies for Gabon, belonging to 36 families. Our survey, limited to macro-moths collected during only 11 nights at two sites, revealed 1385 BINs in just 25 families. Three families (Bombycidae, Brahmaeidae, and Lecithoceridae) detected in our study lack published records for Gabon in AfroMoths. For 10 of the 22 other families, the number of BINs recorded in our study exceeded the number of known species (Fig. 4). Large differences

were observed for Cossidae (1 species in AfroMoths vs. 11 BINs), Crambidae (9 vs. 52), Erebiidae (309 vs. 369), Geometridae (184 vs. 220), Lasiocampidae (68 vs. 101), Noctuidae (71 vs. 224), and Pyralidae (6 vs. 70), which may represent the most understudied families or those yet incompletely surveyed in AfroMoths.

In the few families that are well studied for this region, we collected approximately half the known number of species (48.2%, $sd = 6.9$, $N = 4$), including Saturniidae (43 BINs versus 110 species listed in AfroMoths, 39%), Eupterotidae (15 vs. 32, 47%), Sphingidae (66 vs. 124, 53%), and Lasiocampidae (101 vs. 188 as listed by P. Basquin, personal communication, 54%).

Fig. 4. Comparisons between the number of BINs observed in this study for 28 families and subfamilies of macro-moths (dashed bars) and the number of species reported from Gabon in the AfroMoths online database (grey bars; De Prins and De Prins 2017).



Species richness and diversity patterns between sampling sites

Our survey revealed a total of 823 BINs (1604 specimens analyzed) and 782 BINs (1890 specimens analyzed) at the Ipassa and Lopé 2 sites, respectively (Table 1; Fig. 3). Sampling resulted in a high proportion of singletons at both sites (64% and 59% of BINs at Ipassa and Lopé 2, respectively); 57% of all BINs when combining the two sites, and the distributions of BIN abundance are a strong fit to a log-series model (File S3²). While observed richness was similar between the sites, we collected fewer BINs at Lopé 2, despite collecting three additional nights in this site during the dry season.

For comparison of the two sites, we only considered specimens collected during the wet season when sampling efforts were identical. The four collecting nights at each site resulted in the capture of 1604 and 1110 specimens, which belonged to 823 and 481 BINs for Ipassa and Lopé 2, respectively (Table 2). Richness estimators indicate that species richness ranged between 1250 and 1850 species at Ipassa and between 700 and 1200 species at Lopé 2. Rarefaction curves clearly show a higher richness at Ipassa (Fig. 5A), while sampling coverage rate was slightly higher at Lopé 2 (73% vs. 68% at Ipassa) (Table 2; Figs. 5B and 5C). Overall, the moth communities at both sites showed a similar relative abundance of the different families, both in terms of specimen numbers and BINs, although observed richness in the most diverse families was consistently higher at Ipassa, with the exception of Crambidae and Pyralidae, which had more BINs at Lopé 2 (Table 1).

Comparison of BINs collected during the wet season at Lopé 2 and Ipassa revealed only 158 BINs shared by the two sites, 13.8% of the total number analyzed. Sørensen's index of β -diversity calculated between the two sites was 0.76 for the whole dataset and 0.42 after singletons were removed (Table 3). In both cases, β -diversity was mainly explained by spatial turnover (71.0% and 67.6%, respectively) and to a lesser extent by nestedness (29.0% and 32.4%).

Seasonal changes in moth assemblages at Lopé 2

We generated DNA barcodes for 1110 and 780 specimens from Lopé 2 during the rainy and the dry seasons, respectively. Observed richness during the wet season was slightly higher (478 BINs versus 441 BINs during the dry season), but this trend

was reversed after rarefying richness to a constant sampling effort or a constant sampling coverage. Rarefaction curves and diversity estimators were also quite similar, the latter ranging between 650 and 1100 for both seasons (Fig. 5).

During the dry season, we collected moths belonging to 17 families versus 21 families during the wet season. Seven families were not shared between the two sampling seasons, but all were represented by few BINs (maximum 2) and individuals (maximum 2), excepting one BIN in the family Thyrididae for which 18 specimens were collected in the wet season. Overall, the diversity for each family was similar for the two sampling periods (Table 1) with a few exceptions: the Crambidae (31 vs. 16 BINs), Pyralidae (37 vs. 18), and Saturniidae (31 vs. 9), which were all more diverse during the wet season, and the Sphingidae (40 vs. 28) that was more diverse during the dry season. Out of a total of 782 BINs, 144 (i.e., 18.5%) were found during both the rainy and the dry seasons. Sørensen's index of dissimilarity between seasons was 0.69, largely explained by temporal turnover (95.4%), but it dropped to 0.23 and was evenly explained by turnover and nestedness after removing singletons from the data set (Table 3).

Discussion

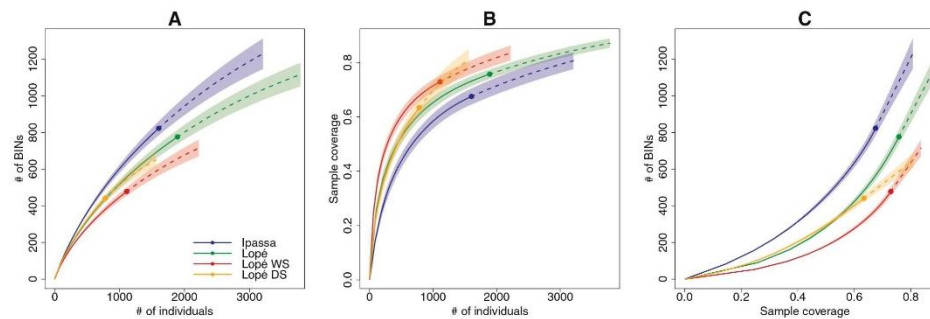
DNA barcodes for the study of moth diversity in the tropics

Overall, we documented in our study a number of molecular units (BINs) that was higher than the total number of species listed for the country in AfroMoths, including three families not documented so far (De Prins and De Prins 2017). Considering the relatively shallow geographical range and temporal extent of our study, this result highlights the weakness of the current knowledge of moth diversity in the Afrotropics, despite the remarkable efforts by De Prins and De Prins (2017) to synthesize and centralize this knowledge in AfroMoths. Our results clearly highlight the value of DNA barcoding for producing a rapid and accurate census of moth diversity in a poorly studied tropical region. Because this approach facilitates comparisons between sampling campaigns through barcode matches (as exemplified here between sites, but it can also be applied between countries as currently in progress with a similar campaign in Central African Republic), its system-

Table 2. Summary of macro-moth data sets collected at the two study sites and for two seasons at Lopé 2 (numbers in parentheses represent the 95% confidence intervals based on a bootstrap method with 200 replications).

| | Ipassa (WS) | Lopé (WS) | Lopé (DS) | Lopé |
|---|------------------------|------------------------|-----------------------|------------------------|
| No. of individuals collected | 1604 | 1110 | 780 | 1890 |
| Observed richness | 823 | 481 | 443 | 782 |
| Proportion of singletons (%) | 63.85 | 63.61 | 64.93 | 59.31 |
| Sampling coverage (%) | 67.32 (± 2.95) | 72.44 (± 2.27) | 63.14 (± 3.02) | 75.54 (± 1.77) |
| Richness at constant sampling coverage of 50% | 469.2 (± 13.8) | 197.6 (± 7.0) | 313.7 (± 12.9) | 330.4 (± 7.6) |
| Richness at constant sampling intensity of 1000 individuals | 599.1 (± 8.9) | 449.9 (± 4.4) | 511.4 (± 25.6) | 521.5 (± 9.5) |
| Chao1 estimated richness | 1837.0 (± 130.6) | 1011.6 (± 107.9) | 869.5 (± 70.9) | 1513.4 (± 96.5) |
| ACE estimated richness | 1849.4 (± 27.6) | 1120.6 (± 20.7) | 1054.4 (± 22.9) | 1629.5 (± 26.2) |
| First order jackknife estimated richness | 1269.2 (± 286.2) | 728.5 (± 169.7) | 663.7 (± 166.9) | 1211.4 (± 197.0) |
| Fisher alpha | 678.3 (± 36.5) | 318.2 (± 21.0) | 419.3 (± 32.3) | 491.5 (± 25.0) |

Note: WS, wet season; DS, dry season.

Fig. 5. Individual-, sample-, and coverage-based rarefaction and extrapolation curves for the two study sites and for two seasons at Lopé 2 (DS, dry season; WS, wet season): (A) Size-based rarefaction and extrapolation curves; (B) Sample coverage plotted against the number of individuals; (C) Coverage-based rarefaction and extrapolation (rarefaction curves are represented in solid lines, extrapolation curves in dashed lines; shaded areas represent a 95% confidence intervals based on a bootstrap method with 200 replications).**Table 3.** Comparison of macro-moth species assemblages between the two study sites and for two seasons at Lopé 2 showing the Sørensen index of dissimilarity (with singletons removed or not from the dataset) and its partitioning into geographical/seasonal turnover and nestedness.

| | Sørensen | Turnover (%) | Nestedness (%) |
|-----------------------------|----------|--------------|----------------|
| Ipassa vs. Lopé 2 | 0.75 | 70.97 | 29.03 |
| Same without singletons | 0.40 | 67.57 | 32.43 |
| Wet vs. dry season (Lopé 2) | 0.69 | 95.39 | 4.61 |
| Same without singletons | 0.23 | 54.76 | 45.24 |

atic implementation would represent a powerful mean to address both the Linnean and Wallacean shortfalls (Lomolino 2004), i.e., the inadequacies in taxonomic and distributional knowledge that characterise most invertebrate taxa in poorly studied regions such as the Congo basin (Whittaker et al. 2005).

In our study, the large number of BINs without taxonomic assignment at species level (1155 out of 1385) corresponds both to already known species not yet documented in the BOLD libraries and to species that are new to science. The number and proportion of the latter remains unclear and further study by expert taxonomists of the specimens collected is needed, as well as continued efforts to populate DNA barcode reference libraries. In addition, the inflation of species numbers in many families may reflect an incomplete census of Gabonese records in past studies, a considerable task initiated in Afromoths, but certainly suffering from the absence of recent dedicated efforts to synthesize lepidopteran diversity data for this country. The bombycid *Amusaron*

kolga (Druce, 1887) and brahmaeid *Dactylocera lucina* (Drury, 1782) for instance represent new records for their respective families in Gabon, but they are species known to occur in neighbouring countries of the Congo basin (De Prins and De Prins 2017). In Lasiocampidae, the number of species listed in AfroMoths (68) is identical to the number of species reported from an independent literature survey by a specialist of this family on the African continent (P. Basquin, personal communication). Furthermore, this same taxonomic authority (unpublished results) has recorded approximately 188 Gabonese lasiocampid species in natural history collections worldwide, which clearly demonstrates how insufficient the published data are for this family at the regional scale and is consistent with the number of BINs (101) reported in our study.

The very close fit we found between species names and BINs in the families Saturniidae and Sphingidae supports previous assessments of BINs as good proxies for species in Lepidoptera where empirical studies (e.g., Hausmann et al. 2013) revealed only few occurrences of discrepancies between morphologically identified and molecular species (for instance one species divided in two or more BINs, or multiple species merged within a single BIN; see Ratnasingham and Hebert 2013). Within the two families thoroughly investigated here, mismatches between BINs and species are cases where supposedly well-defined morphological species appeared to be split into two or three distinct BINs. These require further study using an integrative approach and may represent cases of cryptic species, i.e., species that cannot be distinguished from morphological characters, or that present subtle morphological and (or) ecological traits previously ascribed to intra-specific variation or thought to be insignificant for species-level

recognition (Janzen et al. 2009, 2012; Rougerie et al. 2014). Alternatively, these BIN “splits” may also cause an overestimation of species diversity if they represent cases of pseudogene amplification (although this is considered unlikely here because of the absence of indels, stop codons, or unusual amino acid substitutions), insufficient sampling of genetic variation biasing BIN assignments, or *Wolbachia* infections isolating lineages within species (Smith et al. 2008). Geographical structure of populations in poorly mobile species could also cause strong genetic structure that may inflate the number of BINs per species, but we consider this unlikely in the present study because of the small geographical distance between sampled sites, the absence of geographical barriers, and the generally high vagility of moth species. DNA barcoding has revealed many cases of cryptic diversity in Lepidoptera since its broad integration in the taxonomic toolbox of lepidopteran taxonomists (e.g., Vaglia et al. 2008; Rougerie et al. 2012, 2014) and we consider it is very likely that speciose and less studied families such as Erebiidae, Geometridae, and Noctuidae will also reveal many such cases, leading to an increase of species numbers in these groups compared to available checklists only based on morphologically recognized species.

Moth diversity at Ivindo and Lopé National Parks

Among the 1385 BINs found in our samples, 796 (i.e., 58% of the total) were represented by a single specimen, which is a high singleton proportion compared to the average of 32% found by Coddington et al. (2009) in a review of tropical arthropod studies. There are little or no biological explanations for the high proportion of rare species usually found in tropical insect surveys (Novotný and Basset 2000). Rather, this pattern can be attributed to undersampling of highly diverse communities (Coddington et al. 2009), suggesting that caution should be taken when interpreting the observed patterns of community composition and structure. It also suggests that the estimates of species richness derived from our results probably represent a low estimation of the actual diversity of these ecosystems. Both rarefaction curves and sampling coverage indices (Fig. 5; Table 2) support this idea, suggesting that at least twice the number of collected species may occur in the study area.

We found only a few studies that assessed moth local richness in tropical rainforest or savannah ecosystems and that can be readily compared with our own results. Ashton et al. (2015) sampled 791 to 2795 species and produced Chao1 estimates ranging from 1478 to 3666 among three rainforest locations in Malaysia. In Costa Rica, Janzen et al. (2009) published a census of 2349 species using a DNA barcode-based assessment of macro-moth assemblages in the Area de Conservación Guanacaste (see also Janzen and Hallwachs 2016). On the other hand, Hawes et al. (2009) reported 98 species of Arctiinae (Erebidae), 43 of Saturniidae, and 5 of Sphingidae in a primary forest area of Brazilian Amazonia, which is well below our findings in the present study. Variations in the number of species observed among studies are however difficult to interpret, because they can both reflect real differences in species diversity, but can also be biased by differences in sampling efforts and (or) sampling performed in different seasons. In fact, the moth sampling by Ashton et al. (2015) and Hawes et al. (2009) was done through 264 and 30 collecting nights per study site, respectively, while the survey of Janzen et al. (2009) was conducted over decades and involved additional sampling methods (in particular, the mass rearing of caterpillars). Comparing the results obtained in different studies and with different sampling intensity requires standardization through rarefaction procedure (Gotelli and Colwell 2001). Applying this approach to the data from Ashton et al. (2015) produces a result different from what can be directly deduced from observed richness (A. Nakamura, L.A. Ashton, R.L. Kitching, personal communication). For instance, species numbers in their Malaysian sites ranged from 290 to 475 after standardization to a constant sampling effort of

1000 individuals, and from 100 to 270 at a constant sampling coverage of 50%, which was lower to what we found in our two study sites (Table 2). This suggests that Central African rainforests may represent an important hotspot for moth diversity.

Variation in moth diversity and composition among study sites

Our analyses of moth assemblages during the rainy season in the rainforest of Ipassa and the savannah-forest landscape of Lopé 2 unveiled significant differences in both species diversity and composition. As expected from differences in vegetation coverage, the observed and estimated richness were both higher at Ipassa. Plant diversity is indeed higher in the rainforest landscape of Ipassa than in the shrubland savannahs and peaty marshes that dominate the landscapes of the northern part of Lopé National Park (White and Abernethy 1997). In addition, despite presenting a comparable structure, forests at Ipassa are more humid and present higher tree diversity when compared with the gallery forests of Lopé 2. These features presumably offer a broader diversity of ecological niches in terms of trophic resources and microhabitats, in particular via the important diversity of epiphytes and lianas (Ben Yahmed and Pourtier 2004).

Difference in species assemblage composition among sites was high, with only 13.3% of BINs found in both. This high β -diversity was mainly attributed to spatial turnover, meaning that under-sampling may only weakly account for this variation. This is in contrast with other studies that reported relatively low β -diversity of insect herbivores in comparable tropical rainforest habitats (Basset et al. 2012; Novotný et al. 2007). This also concurs with other studies having reported high species turnovers among sites as long as these comprised enough variability in vegetation types (Beck and Vun Khen 2007; Odegaard 2006). In fact, contrasted composition of dominant forest tree species among our study sites may have selected for different assemblages of herbivorous species, as leaf-chewing insects are usually specialized on a single genus of host plants (Novotný et al. 2002a, 2002b). Similarly, the presence of herbaceous ecosystems and secondary forests at Lopé 2 may have also driven the presence of specific species assemblages associated with these open habitats. The high diversity of Crambidae and Pyralidae observed at this site compared to Ipassa could for instance be linked to species preferences within these groups for herbaceous host-plants (Kitching et al. 2000).

Even if additional sampling is necessary to confirm this finding, these preliminary results suggest that landscapes dominated by a savannah-forest patchwork may host substantial levels of herbivore insect diversity with a high compositional specificity at species level compared to typical tropical rainforests. This argues in favor of a better consideration of savannah ecosystems in both global estimates and conservation strategies of insect biodiversity.

Seasonal variation of moth assemblages

At Lopé 2 we found little difference in species richness of moth assemblages collected during the rainy and the dry seasons. In contrast, BINs compositions clearly differed from one season to the other, with only 18.3% of the BINs collected being observed in both seasons, and this temporal β -diversity being clearly explained by seasonal turnover rather than by nestedness (Table 3). Composition may simply be influenced by the level of vegetation development during the seasonal cycle, which is well known to influence the phenology of lepidopteran species, or by different climatic preferences linked to the feeding and (or) reproductive activity of the moths.

From a methodological point of view, these results highlight the importance of standardizing the period of sampling to provide fully comparable results among different localities. They also suggest the need of sampling different seasons to obtain a reliable inventory of species at a given study site, as the assemblages observed at the rainy season (the usually preferred period for moth

collecting) clearly do not provide a representative overview of the actual species composition of the focal community.

Conclusion

Our study highlights the usefulness of utilizing DNA barcodes for performing rapid analyses of taxonomic diversity and composition of moth assemblages in poorly studied areas. It also stresses the need to accelerate biodiversity inventories in those areas that have been insufficiently explored regarding moths and other poorly studied invertebrates. Central Africa clearly is one of those areas and our results represent the first robust assessment of moth diversity in Gabonese forests and savannahs, highlighting a strongly understudied fauna. The material collected and the DNA barcode library released with this study are thus important contributions and we expect that they will serve the development of knowledge on the diversity and distribution of African moths. In general, studies combining molecular data and traditional taxonomic expertise are critically needed to better document invertebrate communities in tropical areas, especially in the regions where anthropogenic pressures are high and where species extinctions remain unaccounted for because species simply remain undocumented.

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Appendix A

Table A1. List of ECOTROP team members not already listed as authors on the manuscript.

| Names | Contact |
|-------------------------------|---|
| Emilie Arlette Apinda Legnouo | CENAREST, IRET, Libreville, Gabon. Email: ea.apindalegnouo@yahoo.fr |
| Diego Ayala | MIVEGEC, IRD, CRMF, Franceville, Gabon. Email: diego.ayala@ird.fr |
| Marlucia Bonifacio Martins | Museu Paraense Emilio Goeldi, Belem, Para, Brazil. Email: marlucia@museu-goeldi.br |
| Laurent Bremond | ISEM, Université de Montpellier, EPHE, IRD, CNRS, Montpellier, France. Email: laurent.bremond@umontpellier.fr |
| Barabara Evrard | Normandie Univ, UNIROUEN, UNICAEN, CETAPS 76000 Rouen, France. Email: barbara.evrard@univ-rouen.fr |
| Damien Femenias | Normandie Univ, UNIROUEN, UNICAEN, CETAPS 76000 Rouen, France. Email: Damien.Femenias@univ-rouen.fr |
| Flore Koumba Pambo | CENAREST, IRAF, Libreville, Gabon. Email: csar_cenarest@yahoo.fr |
| Boris Makanga | CENAREST, IRET, Libreville, Gabon. Email: makanga.boris@gmail.com |
| Mike Makaya Mvoubou | Université des Sciences et Techniques de Masuku, Franceville, Gabon. Email: makayamvoubou@yahoo.fr |
| Elise Mazeyrac | WCS-Gabon, La Lopé, Gabon. Email: elise.mazeyrac@ntymail.com |
| Judicaël Obame Nkoghe | CIRMF, Franceville, Gabon. Email: judicael.obame@live.fr |
| Marjolaine Okanga-Guay | LAGRAC, Université Omar Bongo, Libreville, Gabon. Email: m_okanga_guay@yahoo.fr |
| Didier Orevouno | Ecole Nationale des Eaux et Forêts, Libreville, Gabon. Email: orevouno2001@yahoo.fr |
| Johan Oszwald | LETG, CNRS, Université Rennes 2, Rennes, France. Email: johan.oszwald@univ-rennes2.fr |
| Christophe Paupy | MIVEGEC, IRD, CNRS, Université de Montpellier, Montpellier, France. Email: christophe.paupy@ird.fr |
| Olivia Scholtz | WCS-Gabon, Libreville, Gabon. Email: Olivia_scholtz@hotmail.com |
| Maurice Tindo | Université de Douala, Cameroun. Email: tindodouala@yahoo.com |
| Michel Veuille | ISYEB, CNRS, MNHN, UPMC, EPHE, Paris, France. Email: veuille@mnhn.fr |

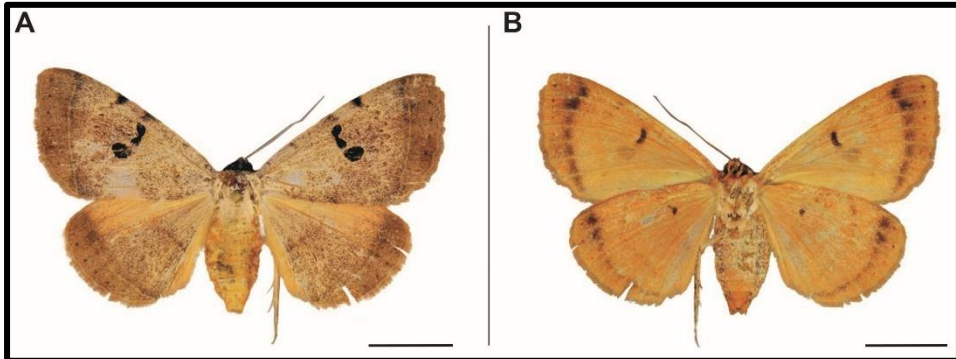
Note: The ECOTROP team is a multidisciplinary and international consortium of university teachers and researchers working together at organizing field classes in the domain of environmental and ecological research in the tropics. From 2011 to 2014, they coordinated four successive editions of a training course in biodiversity assessment in the North of the Lope National Park in Gabon, producing some of the results included in this paper.

CHAPTER VI

New records of six moth (Lepidoptera: Erebidae, Lasiocampidae) species in south African countries, with comments on their distribution

Delabye, S., Sedláček, O., Maicher, V., & Tropek, R. (2020).

Biodiversity Data Journal, **8**: e59339.



Dorsal (A) and ventral (B) view of Hypopyra africana (Kirby, 1896), new country record in Zimbabwe. © P. Potocký



New records of six moth (Lepidoptera: Erebidae, Lasiocampidae) species in south African countries, with comments on their distribution

Sylvain Delabye^{‡,§,¶}, Ondřej Sedláček[‡], Vincent Maicher^{‡,¶,¶}, Robert Tropek^{‡,¶}

[‡] Institute of Entomology, Biology Centre, Czech Academy of Sciences, Branišovská 31, 37005, České Budějovice, Czech Republic

[§] Faculty of Science, University of South Bohemia, Branišovská 1760, 37005, České Budějovice, Czech Republic

[¶] Department of Ecology, Faculty of Science, Charles University, Viničná 7, 12944, Prague, Czech Republic

^{¶¶} Nicholas School of the Environment, Duke University, 9 Circuit Dr., NC 27710, Durham, United States of America

Corresponding author: Sylvain Delabye (sylvain.delabye@gmail.com).

Robert Tropek (robert.tropek@gmail.com)

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Abstract

Background

Southern Africa hosts a high diversity of ecosystems and habitats with a tremendous diversity of Lepidoptera. Although it is one of the most studied parts of the Afrotropics, the knowledge on diversity and distribution of south African moth fauna remains insufficient. To partly fill this gap, we surveyed macromoths by automatic light traps in five localities in two relatively less sampled south African countries.

New information

We reported six species and one genus (*Remigioides*) of moths which had not yet been recorded in Namibia or Zimbabwe. Although none of these records broadened the known distribution of individual species to a new biogeographical region, they still fill important

gaps in their distributions. The known distributional ranges of two species have been substantially extended, although they are still within the same biogeographical regions: ca. 800 km southwards for *Remigioides remigina* (Mabille, 1884) and ca. 600 km westwards for *Haplopacha cinerea* Aurivillius, 1905.

Keywords

Afrotropics, faunistic report, light trapping, savannahs, southern African region, Zambezi region

Introduction

The south African countries offer a wide variety of biomes, from deserts and grasslands to woodland savannahs. Some of them are considered to be biodiversity hotspots, such as the Succulent Karoo, the Cape Floristic Province and the Maputaland-Pondoland-Albany (Myers et al. 2000, Mittermeier et al. 2004). Besides these unique ecosystems, most of southern Africa is covered by open and woodland savannahs belonging to two distinct bioregions: the Southern African region and the Zambezi region (Linder et al. 2012). For some taxa (including many groups of plants, mammals and birds), parts of these savannahs are known to harbour a species richness similar to Afrotropical rainforests (Murphy et al. 2016).

However, knowledge on the diversity and distribution of macromoths (Lepidoptera: Macroheterocera, hereinafter referred as *moths*) in these regions is uneven. Due to the long tradition of entomological research, the moth fauna of South Africa is relatively well known, with ca. 7,300 taxa identified in De Prins and De Prins (2020). In comparison, the neighbouring countries of Namibia and Zimbabwe are only represented by ca. 1,500 and 3,000 moth taxa, respectively, in the same database.

Our recent sampling of moths in savannahs of Namibia and Zimbabwe resulted in more than 12,000 trapped individuals. Amongst these, we identified six moth species recorded for the first time in one or the other of the two countries. Here, we present the sampled material of these six species, with remarks on their general distribution and their reported expansion.

Materials and methods

All reported moth specimens were collected in five localities in Namibia and Zimbabwe (Figs 1, 2, Table 1) in 2016 and 2017. The nomenclature for biogeographical region follows Linder et al. (2012). Vegetation units are based on Burgess et al. (2004), Sayre et al. 2013, Heppner (1991) and Hacker (2019) (Table 1).

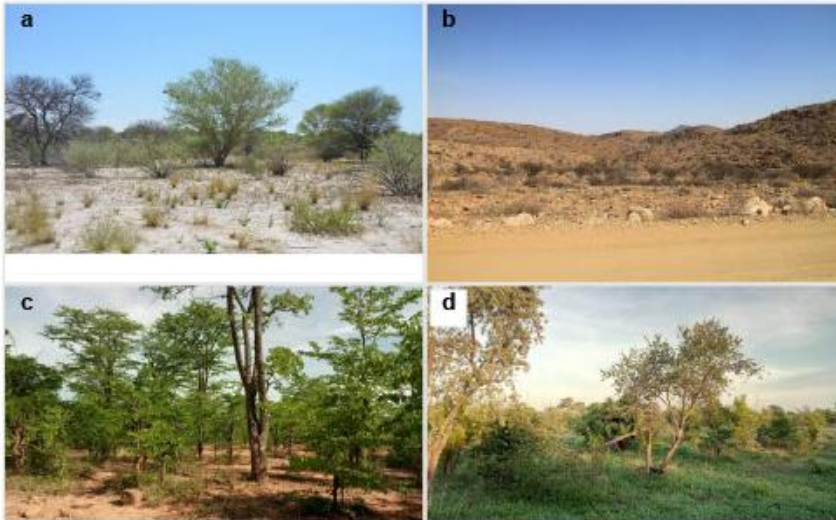


Figure 2.

Selected sampled habitats.

a: Mosaics of *Vachellia* woodland, mixed with *mopane* (*Colophospermum mopane*) and *Baikiaea* and microphyllous savannahs (Grootfontein). [doi](#)

b: Dry savannahs and shrubs with scattered trees (Namibgrens). [doi](#)

c: Mosaic of miombo woodland, savannahs and shrubs and *mopane* (*C. mopane*) woodlands (Hwange). [doi](#)

d: Mosaic of *mopane* (*C. mopane*) woodland, grasslands and *Baikiaea plurijuga* forests (Bwabwata National Park, Victoria Falls). [doi](#)

All moths were attracted by light. The traps consisted of a two-sided strip of 48 LEDs emitting UV light and powered by 12V batteries placed at the intersection of three plexiglass panels placed on top of a plastic bucket. Attracted specimens were anaesthetised by ammonium hydrogen carbonate. More than 12,000 individuals were trapped. Nine families were focused on (i.e. Erebidae, Eutellidae, Noctuidae, Notodontidae, Eupterotidae, Lasiocampidae, Saturniidae, Sphingidae and Limacodidae) and, after removing non-focused groups (mainly Geometridae), our dataset comprised 9,048 specimens belonging to 488 species or morphospecies, based mostly on external morphology using various available literature, including numerous online resources. Genitalia dissection was done when needed and the exhaustive collection in the Nature Education Centre (Krakow, Poland) was consulted for confirmation of some species identification. From this material, six reliably identified species appeared to be new country records; these are included in this report.

Nomenclature and distribution of the reported species were based on the AfroMoths online database (De Prins and De Prins 2020), on the Global Biodiversity Information Facility data infrastructure (GBIF.org 2020), on the LepiMAP database (LepiMAP 2014) and on the

Barcoding of Life Data System (Ratnasingham and Hebert 2007). The voucher material is deposited in the Nature Education Centre of Jagiellonian University in Krakow, Poland.

Taxon treatments

Plecoptera sarcistis Hampson, 1910

Nomenclature

Erebidae, Anobinae

Materials

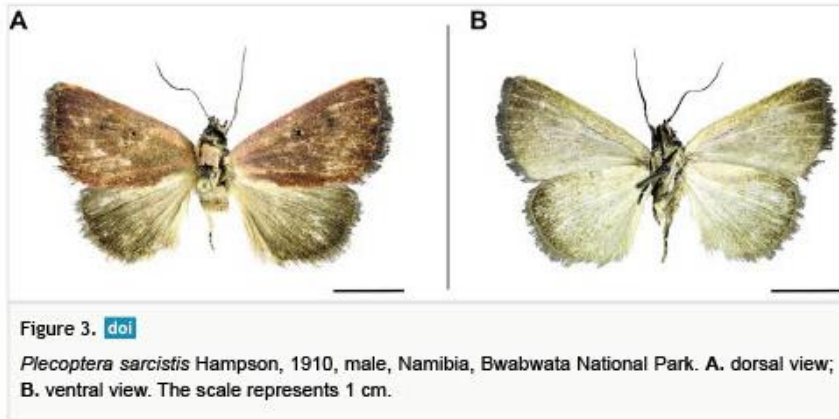
- a. scientificName: *Plecoptera sarcistis* Hampson, 1910; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,018 m; decimalLatitude: -18.1170; decimalLongitude: 21.6797; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 1; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Plecoptera sarcistis* Hampson, 1910; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,042 m; decimalLatitude: -18.0688; decimalLongitude: 21.6702; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 2; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Plecoptera sarcistis* Hampson, 1910; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,044 m; decimalLatitude: -18.0592; decimalLongitude: 21.6872; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 1; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Plecoptera sarcistis* Hampson, 1910; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,051 m; decimalLatitude: -18.0545; decimalLongitude: 21.6954; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 2; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Plecoptera sarcistis* Hampson, 1910; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,047 m; decimalLatitude: -18.0498; decimalLongitude: 21.7035; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 7; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Description

The identification was based on Hampson (1910).

Distribution

This species is recorded for the first time in Namibia. All reported specimens were collected in the Bwabwata National Park belonging to the Zambezi biogeographical region. In this region, the species was already known from Zimbabwe and Zambia and it was also already recorded in the neighbouring Southern African region. Therefore, its distribution in north-eastern Namibia could be expected (Fig. 3).



Hypopyra africana (Kirby, 1896)

Nomenclature

Erebidae, Erebinae

Materials

- a. scientificName: *Hypopyra africana* (Kirby, 1896); continent: Africa; country: Zimbabwe; stateProvince: Matabeleland North; locality: Victoria Falls; verbatimElevation: 927 m; decimalLatitude: -17.9018; decimalLongitude: 25.7634; samplingProtocol: Light-trapping; eventDate: 14/12/2017; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Hypopyra africana* (Kirby, 1896); continent: Africa; country: Zimbabwe; stateProvince: Matabeleland North; locality: Victoria Falls; verbatimElevation: 969 m; decimalLatitude: -17.9099; decimalLongitude: 25.7487; samplingProtocol: Light-trapping; eventDate: 14/12/2017; individualCount: 1; sex: female; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Hypopyra africana* (Kirby, 1896); continent: Africa; country: Zimbabwe; stateProvince: Matabeleland North; locality: Victoria Falls; verbatimElevation: 908 m; decimalLatitude: -17.8281; decimalLongitude: 25.6568; samplingProtocol: Light-trapping;

eventDate: 13/12/2017; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO
 UR|http://grbio.org/cool/8t1f-g2z6; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- d. scientificName: *Hypopyra africana* (Kirby, 1896); continent: Africa; country: Zimbabwe; stateProvince: Matabeleland North; locality: Victoria Falls; verbatimElevation: 909 m; decimalLatitude: -17.8416; decimalLongitude: 25.6446; samplingProtocol: Light-trapping; eventDate: 13/12/2017; individualCount: 1; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO
 UR|http://grbio.org/cool/8t1f-g2z6; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Description

The identification of this species was based on photograph of the type specimen in De Prins and De Prins (2020) and comparison with the original description in Kirby (1896).

Distribution

Our records expand the known distribution of the species to Zimbabwe. *Hypopyra africana* was previously reported from the Somalian (Kenya), Zambezan and Southern African regions, including countries bordering with Zimbabwe (Botswana, Namibia, South Africa, Zambia). All six reported specimens were found near Victoria Falls and partially fill the gap in our knowledge of the distribution of this species (Fig. 4).

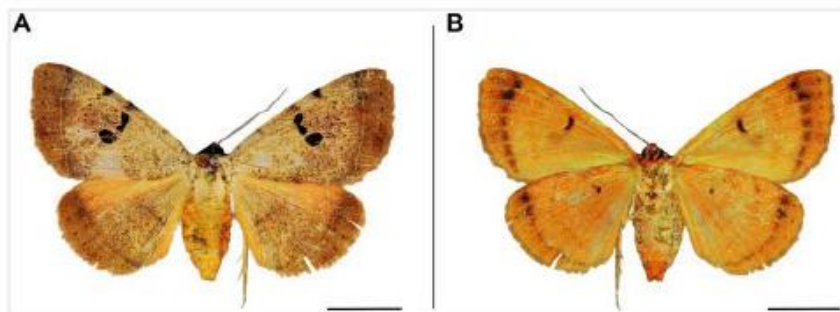


Figure 4. [doi](#)
Hypopyra africana (Kirby, 1896), female, Zimbabwe, Victoria Falls. A. dorsal view; B. ventral view. The scale represents 1 cm.

Remigiodes remigina (Mabille, 1884)

Nomenclature

Erebidae, Erebinae

Materials

- a. scientificName: *Remigiodes remigina* (Mabille, 1884); continent: Africa; country: Zimbabwe; stateProvince: Matabeleland North; locality: Hwange; verbatimElevation: 1,033 m; decimalLatitude: -18.7051; decimalLongitude: 26.2039; samplingProtocol: Light-trapping; eventDate: 13/12/2017; individualCount: 3; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Remigiodes remigina* (Mabille, 1884); continent: Africa; country: Zimbabwe; stateProvince: Matabeleland North; locality: Hwange; verbatimElevation: 1,014 m; decimalLatitude: -18.6954; decimalLongitude: 26.1880; samplingProtocol: Light-trapping; eventDate: 13/12/2017; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Description

The detailed diagnosis made by Hacker (2016) enabled identification of this species.

Distribution

Our four captured individuals represent the first record of *R. remigina* in Zimbabwe. It is also the first record of *Remigiodes* in the country. This widespread species was already known from the Guinean (Togo, Nigeria), Congolian (Democratic Republic of Congo), Somalian (Ethiopia, Somalia and Kenya) and Zambezian (Tanzania) biogeographic regions and from Madagascar. Our record extended its known continental distribution range by ca. 800 km southwards (Fig. 5).

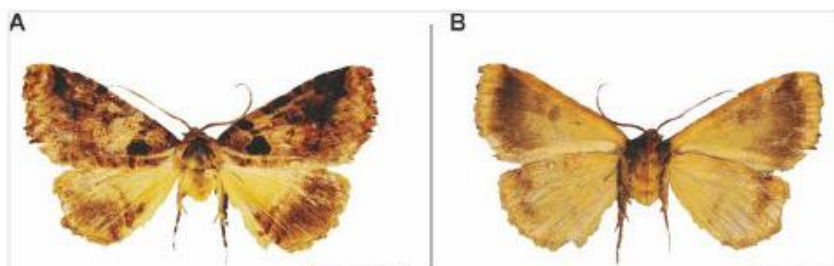


Figure 5. [doi](#)

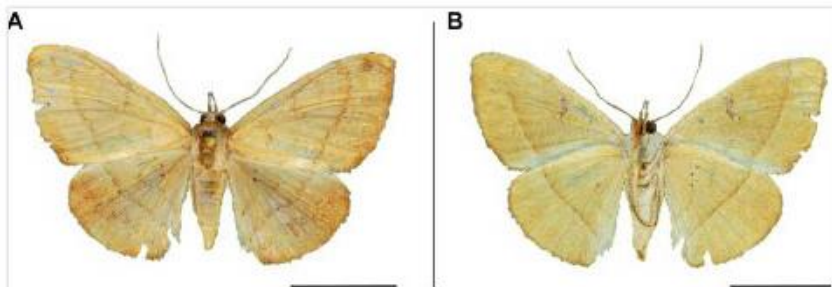
Remigiodes remigina (Mabille, 1884), male, Zimbabwe, Hwange. A. dorsal view; B. ventral view. The scale represents 1 cm.

Taviodes subjecta* (Walker, 1865)*Nomenclature**

Erebidae, Pangraptinae

Materials

- a. scientificName: *Taviodes subjecta* (Walker, 1865); continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,042 m; decimalLatitude: -18.0688; decimalLongitude: 21.6702; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 1; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URIhttp://grbio.org/cool/8t1f-g2z6; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Taviodes subjecta* (Walker, 1865); continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,044 m; decimalLatitude: -18.0642; decimalLongitude: 21.6784; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 1; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URIhttp://grbio.org/cool/8t1f-g2z6; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Taviodes subjecta* (Walker, 1865); continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,044 m; decimalLatitude: -18.0592; decimalLongitude: 21.6872; samplingProtocol: Light-trapping; eventDate: 20/11/2016; individualCount: 1; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URIhttp://grbio.org/cool/8t1f-g2z6; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Figure 6. [doi](#)

Taviodes subjecta (Walker, 1865), male, Namibia, Bwabwata National Park. A. dorsal view; B. ventral view. The scale represents 1 cm.

Description

The identification of this species was based on Pinhey (1975).

Distribution

We report this species for the first time in Namibia. It was already known from several countries in the Congolian (Democratic Republic of Congo), Somalian (Kenya), Zambezan and Southern African biogeographic regions, including South Africa, Zimbabwe and Zambia, all bordering with Namibia (Pinhey 1975). All three specimens were collected in the Bwabwata National Park, in the Zambezan region (Fig. 6).

Haplopacha cinerea Aurivillius, 1905

Nomenclature

Lasiocampidae, Lasiocampinae

Materials

- a. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,026 m; decimalLatitude: -18.1118; decimalLongitude: 21.6717; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,018 m; decimalLatitude: -18.1170; decimalLongitude: 21.6797; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 8; sex: 2 females, 6 males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,009 m; decimalLatitude: -18.1237; decimalLongitude: 21.6862; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,025 m; decimalLatitude: -18.1308; decimalLongitude: 21.6923; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,017 m; decimalLatitude: -18.1375; decimalLongitude: 21.6990; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID:

GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- f. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Khomas Region; locality: Namibgrens; verbatimElevation: 1,769 m; decimalLatitude: -23.6517; decimalLongitude: 16.2934; samplingProtocol: Light-trapping; eventDate: 4/11/2016; individualCount: 1; sex: female; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Otjozondjupa Region; locality: Grootfontein; verbatimElevation: 1,210 m; decimalLatitude: -19.2951; decimalLongitude: 18.7968; samplingProtocol: Light-trapping; eventDate: 15/11/2016; individualCount: 3; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Haplopacha cinerea* Aurivillius, 1905; continent: Africa; country: Namibia; stateProvince: Otjozondjupa Region; locality: Grootfontein; verbatimElevation: 1,219 m; decimalLatitude: -19.3909; decimalLongitude: 18.8282; samplingProtocol: Light-trapping; eventDate: 16/11/2016; individualCount: 1; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI<http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

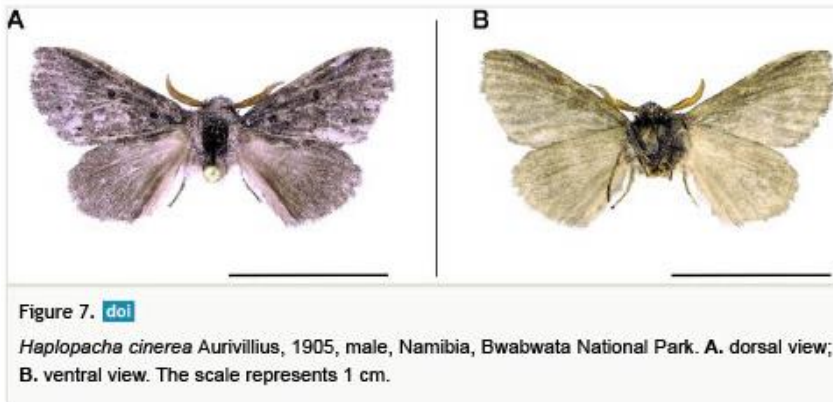


Figure 7. [doi](#)

Haplopacha cinerea Aurivillius, 1905, male, Namibia, Bwabwata National Park. A. dorsal view; B. ventral view. The scale represents 1 cm.

Description

The genitalia dissection and the diagnosis of this species made by Dupont et al. (2016) enabled identification of our specimens.

Distribution

Our specimens represented the first record of this species in Namibia. We collected them in the Zambezi (Bwabwata National Park) and Southern African (Namibgrens, Grootfontein) regions. This species was previously reported from these two

biogeographical regions only, with records from numerous countries from Tanzania to South Africa. In South Africa, the species was known only from the north-eastern parts of the country (Dupont et al. 2016). Hence, our records substantially extended its known distribution range westwards (Fig. 7).

Laeliopsis punctuligera Aurivillius, 1911

Nomenclature

Lasiocampidae, Lasiocampinae

Material

- a. scientificName: *Laeliopsis punctuligera* Aurivillius, 1911; continent: Africa; country: Namibia; stateProvince: Kavango East; locality: Bwabwata National Park; verbatimElevation: 1,018 m; decimalLatitude: -18.1170; decimalLongitude: 21.6797; samplingProtocol: Light-trapping; eventDate: 18/11/2016; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2019; type: PhysicalObject; institutionID: GRBIO URI/http://grbio.org/cool/8t1f-g2z6; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Description

The identification of this species was based on Pinhey (1975).

Distribution

Our single specimen is the first record of this species in Namibia. It was collected in the Bwabwata National Park, belonging to the Zambezi biogeographical region. The species was previously known from only this region, including from Zambia and Zimbabwe bordering with Namibia. Therefore, extension of its distribution into the Caprivi Strip in north-eastern Namibia is not surprising (Fig. 8).

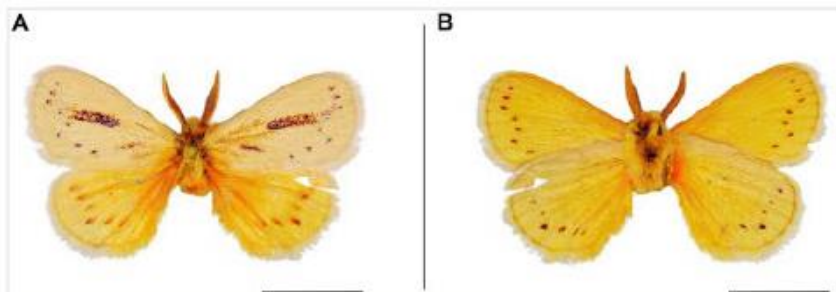


Figure 8. [doi](#)

Laeliopsis punctuligera Aurivillius, 1911, male, Namibia, Bwabwata National Park. A. dorsal view; B. ventral view. The scale represents 1 cm.

Discussion

We presented records of six species of moths (*Plecoptera sarcistis*, *Hypopyra africana*, *Remigiodes remigina*, *Taviodes subjecta*, *Haplopacha cinerea* and *Laeliopsis punctuligera*) newly reported to occur in one or the other of the two sampled countries. Altogether, we reported four species so far not recorded in Namibia and two species so far not recorded in Zimbabwe. Additionally, the genus *Remigiodes* was reported for the first time in Zimbabwe.

All of these species could have been expected in the reported countries because they were previously known to occur in either the Southern African or Zambezi region, whilst four species (except *R. remigina* and *L. punctuligera*) occur in both. All but *R. remigina* were already reported from one or several adjacent countries.

Even though most of the presented new country records could have been expected, at least two of our findings substantially extend the species' known distribution. The nearest known distribution of *R. remigina* prior to our study was from the Democratic Republic of the Congo. Therefore, our records extend its known distribution by ca. 800 km southwards, although still within the Zambezi geographic region. *Haplopacha cinerea* was previously known from both studied regions. Still, our records from central Namibia extended its known distribution by ca. 600 km westwards.

We consider the presented new country reports as additional evidence of the insufficient knowledge of moth diversity in the Afrotropics. Although the result of a relatively non-intensive sampling effort, our records did increase the number of moth taxa recorded in both countries. Since those records either extend the known distribution of particular species or fill gaps in their continuous distribution, we consider reporting of moth records even from such non-intensive sampling as interesting and highly important for improving our knowledge of diversity and distribution of south African moths.

Acknowledgements

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Author contributions

All authors collected the materials. SD prepared part of the material for identification and identified all reported specimens. SD and RT wrote the manuscript, which was later commented upon and approved by all co-authors.

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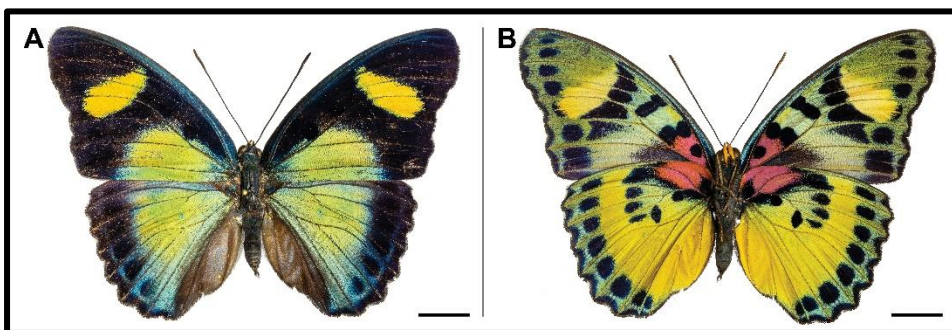
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CHAPTER VII

First records of 31 species of butterflies and moths (Lepidoptera) in Cameroon, with remarks on their elevational ranges

Delabye, S., Maicher, V., Sáfíán, Sz., Potocký, P., Mertens, J.E.J., Przybyłowicz, Ł., Murkwe, M., Kobe, I.N., Fokam, E.B., Janeček, Š., & Tropek, R. (2020).

Biodiversity Data Journal, **8**: e50543.



Dorsal (A) and ventral (B) view of Euphaedra temeraria Hecq, 2007, new country record in Cameroon. © J.E.J. Mertens



First records of 31 species of butterflies and moths (Lepidoptera) in Cameroon, with remarks on their elevational ranges

Sylvain Delabye^{‡,§}, Vincent Maicher^{‡,‖}, Szabolcs Sáfán^{§,¶}, Pavel Potocký[‡], Jan E.J. Mertens^{‡,¶}, Łukasz Przybyłowicz[¶], Mercy Murkwe[¶], Ishmeal N. Kobel, Eric B. Fokam[¶], Štěpán Janeček[‡], Robert Tropek^{‡,‖}

[‡] Biology Centre, Czech Academy of Science, Institute of Entomology, Branisovska 31, CZ-37005 Ceske Budejovice, Czech Republic

[§] Faculty of Science, University of South Bohemia, Branisovska 1760, CZ-37005 Ceske Budejovice, Czech Republic

[‖] Department of Ecology, Faculty of Science, Charles University, Vinicna 7, CZ-12844 Prague, Czech Republic

[¶] Institute of Silviculture and Forest Protection, Faculty of Forestry, University of West Hungary, Bajcsy-Zsilinszky utca 4, H-9400 Sopron, Hungary

[#] Biodiversity Inventory for Conservation NPO (BINCO), Walmersumstraat 44, 3380 Glabbeek, Belgium

[◦] Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, PL-31-016 Krakow, Poland

[«] Department of Zoology and Animal Physiology, Faculty of Science, University of Buea, P.O. Box 83, Buea, Cameroon

Corresponding author: Sylvain Delabye (sylvain.delabye@gmail.com).

Robert Tropek (robert.tropek@gmail.com)

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<https://doi.org/10.3897/BDJ.8.e50543>

Abstract

Background

The biodiversity of West and Central Africa is understudied, including butterflies and moths (Lepidoptera). Cameroon, through its position in between few biogeographic regions and diversity of habitats, is an important hotspot of lepidopteran diversity. However, the country also ranks low when it comes to local biodiversity knowledge. During our long-term ecological projects in the Cameroonian part of the Gulf of Guinea Highlands, we collected rich material of butterflies and moths, including a number of interesting faunistic records.

New information

In this study, we report 31 species of butterflies and moths which have not yet been recorded in Cameroon. These species comprised eight new genera records for the country. In many cases, our records represented an important extension of the species' known distribution, including ten species whose distribution ranges extended into the Guinean biogeographic region. We also comment on the species' elevational distribution ranges on Mount Cameroon where most of our records originated. Additionally, we confirm the presence of a butterfly *Telchinia encedena*, after more than a century since its first and so far its only record in Cameroon.

Keywords

Afrotropics, bait-trapping, Bamenda Highlands, faunistics, light-trapping, Mount Cameroon

Introduction

West and Central Sub-Saharan Africa belong to the areas with the lowest knowledge on regional biodiversity on the continent. Although almost 3,000 taxa of moths (De Prins and De Prins 2019) and almost 1,600 taxa of butterflies (Williams 2018) have been reported from Cameroon so far, much higher diversity of these groups can be expected, considering the country's high habitat heterogeneity. The Gulf of Guinea Highlands is an important montane range on the borders of Nigeria and Cameroon (i.e. at the edge of the Guinean and Congolian biogeographic regions). It represents the only large montane area in the region and is recognised as a biodiversity hotspot with high endemism for numerous taxa (Myers et al. 2000), including butterflies and moths (Larsen 2005, Ustjuzhanin et al. 2018). However, the biodiversity of this montane range is still relatively unexplored and comprehensive studies of Lepidoptera are still under-represented.

Several recent ecological studies on lepidopteran communities in the Gulf of Guinea Highlands (e.g. Tropek and Konvička 2010, Maicher et al. 2018, Maicher et al. 2020) collected an extensive number of butterflies and moths, including several newly described species (e.g. Yakovlev and Sáfián 2016, Ustjuzhanin et al. 2018, Sáfián and Tropek 2016, Sáfián et al. 2019), as well as new country records already published during earlier stages of the projects (e.g. Tropek et al. 2013, Tropek et al. 2015, Maicher et al. 2016, Ustjuzhanin et al. 2018, Przybyłowicz et al. 2019b). The large amount of collected material still holds new species of general faunistic or taxonomic interest. In this study, we report 31 species of butterflies and moths recorded in Cameroon for the first time. In some cases, these records significantly extended the species' known geographical ranges. These are supplemented by a rediscovery of a butterfly species in Cameroon after more than a century.

Materials and methods

All reported butterfly and moth specimens were collected between 2008 and 2017 in Cameroon (Fig. 1).

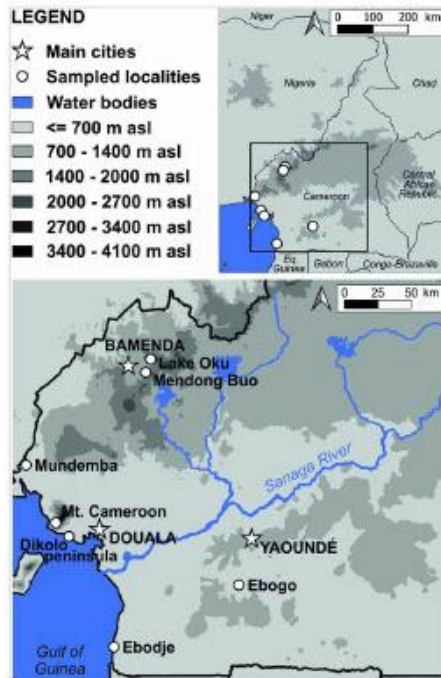


Figure 1. [doi](#)

Map of Cameroon with the study sites and the Sanaga river considered as a border between the Guinean and Congolian biogeographic regions.

Nine sampled localities lie in the Mount Cameroon region, Fako Division, Southwest Region, Cameroon. Seven of these localities are on the south-western slope of Mount Cameroon inside the Mount Cameroon National Park, in tropical rainforests at different elevations. These represent mosaics of primary and secondary lowland forests (Bamboo Camp, 350 m a.s.l.; Drink Gari camp, 650 m a.s.l.), through upland (PlanteCam camp, 1,100 m a.s.l.) and submontane (Crater Lake camp, 1,450 m a.s.l.) forests locally disturbed by elephants, to montane forests (Elephant Camp, 1,850 m a.s.l.; Mapanja camp, 1,850 m a.s.l.; Mann's Spring, 2,200 m a.s.l.) (Fig. 2b, c, d, e). The two remaining localities in the Mount Cameroon region are situated in a coastal forest (Fig. 2a) of the Bimbia-Bonadikombo Community Forest (Dikolo Peninsula camp, 30 m a.s.l.; Ferenc et al. 2018) and in a heavily disturbed lowland forest on a lower hill with a cell tower close to the Chop Farm junction, Bimbia village (Radio Hill, 220 m a.s.l.).



Figure 2.

Selected study sites in Cameroon.

a: Coastal forest in the Bimbia-Bonadikombo Community Forest, Dikolo Peninsula (30 m a.s.l.). [doi](#)

b: Primary lowland forest, Drink Gari, Mount Cameroon (650 m a.s.l.). [doi](#)

c: Upland forest locally disturbed by elephants, PlanteCam Camp, Mount Cameroon (1,100 m a.s.l.). [doi](#)

d: Montane forest, Mapanja camp, Mount Cameroon (1,850 m a.s.l.) [doi](#)

e: Montane forest close to the timberline, Mann's Spring, Mount Cameroon (2,200 m a.s.l.). [doi](#)

f: Mosaic of montane forest remnants and open habitats in Mendong Buo (2,200 m a.s.l.). [doi](#)

The other two localities are situated in the Bamenda Highlands, Northwest Region, Cameroon. Mendong Buo, ca. 5 km south-east of Big Babanki, represents a mosaic of montane forest remnants, forest clearings dominated by *Pteridium aquilinum*, submontane grasslands maintained by cattle grazing and species-rich scrub vegetation along streams

(Tropek and Konvička 2010; Fig. 2f). Lake Oku represents a primary montane forest along the crater lake shore, on the southern slopes of Mount Oku.

The last three localities are in disturbed lowland forests across the country. Mundemba represents heavily disturbed secondary regrowth south of Mundemba, close to the Korup NP, Southwest Region. Ebogo is a disturbed lowland rainforest in the Ebogo Ecotouristic Site, ca. 80 km south of Yaounde, Centre Region. Lastly, close to Ebodje, South Region, butterflies were recorded in a secondary lowland forest.

All moths were attracted to light (see Maicher et al. 2020 for the detailed protocol). Butterflies were collected by traps baited with fermented mashed bananas (*Euphaedra temeraria*, see Maicher et al. 2020 for details) or by a butterfly net (all other butterfly species).

Nomenclature and distribution of the reported species were based on the AfroMoths online database (De Prins and De Prins 2019) for moths and on Williams (2018) for butterflies. The biogeographic regions nomenclature follows Linder et al. (2012). The voucher material is deposited in the Nature Education Centre of the Jagiellonian University in Kraków, Poland and in the Biology Centre, Czech Academy of Sciences, České Budějovice, Czechia.

Taxon treatments

Anapisa holobrunnea (Talbot, 1932)

Nomenclature

Erebidae, Arctiinae

Material

- a. scientificName: *Anapisa holobrunnea* (Talbot, 1932); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 13/10/2017; habitat: Coastal forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

A. holobrunnea was previously reported from Ghana and Guinea only (Przybyłowicz and Bąkowski 2011) and, therefore, it was considered as an endemic to the western part of the Guinean subregion. Our record has enlarged its known range to over 1,000 km to the east. It has also evidenced the species' presence in the eastern part of the Guinean region. In the Mount Cameroon region, the single individual was collected in the lowest locality (30 m a.s.l.) (Fig. 3).

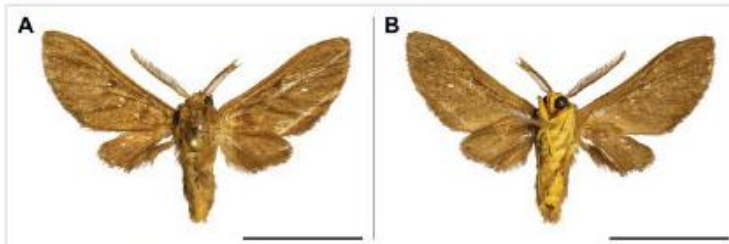


Figure 3. [doi](#)

Anapisa holobrunnea Tams, 1932. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Anapisa metarctioides (Hampson, 1907)

Nomenclature

Erebidae, Arctiinae

Materials

- a. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 13/12/2014; habitat: Upland forest locally disturbed by elephants; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 13/04/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 01/02/2016; habitat: Upland forest locally disturbed by elephants; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 24/11/2016; habitat: Submontane forest locally disturbed by elephants; individualCount: 10; sex: males; lifeStage: adult;

- identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 20/02/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 8; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 28/04/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 4; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 21/11/2014; habitat: Montane forest locally disturbed by elephants; individualCount: 7; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 20/02/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 12; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- i. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 22/04/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 9; sex: 8 males, 1 female; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- j. scientificName: *Anapisa metarctioides* (Hampson, 1907); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mann's Spring, Mount Cameroon; verbatimElevation: 2,200 m; decimalLatitude: 04.1428; decimalLongitude: 09.1225; samplingProtocol: Light catching; eventDate: 09/11/2016; habitat: Montane forest close to the timberline; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Kenya, Uganda, Rwanda and the Democratic Republic of Congo. Our record on Mount Cameroon has extended its western distribution and has evidenced the species from the Guinean biogeographic region. On Mount Cameroon, it is restricted to above 1,100 m a.s.l. (Fig. 4).

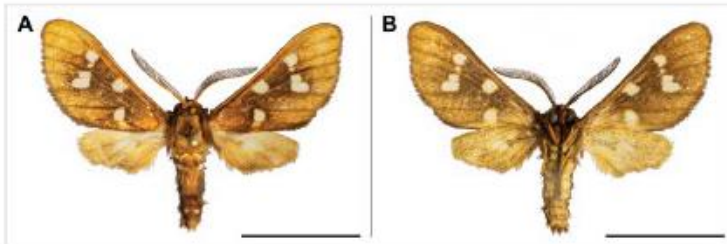


Figure 4. [doi](#)

Anapisa metarctioides (Hampson, 1907). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Archithosia makomensis (Strand, 1912)

Nomenclature

Erebidae, Arctiinae

Materials

- a. scientificName: *Archithosia makomensis* (Strand, 1912); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 26/04/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Balacra compsa* (Jordan, 1904); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 26/04/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Balacra compsa* (Jordan, 1904); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 20/11/2014; habitat: Montane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy:

Lukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- d. scientificName: *Balacra compsa* (Jordan, 1904); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 20/04/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Lukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Ghana, Nigeria and Equatorial Guinea. Hence, its distribution in Cameroon was thus expected, although never reported before. The only specimen was caught in montane forest (1,850 m a.s.l.) (Fig. 5).

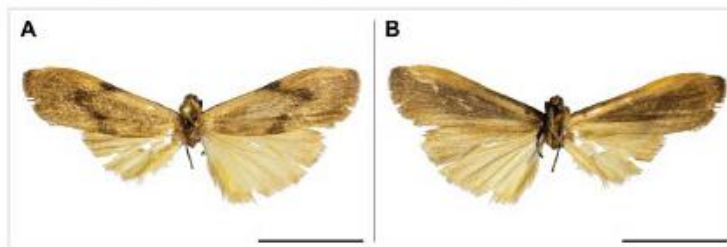


Figure 5. [doi](#)

Archithosia makomensis (Strand, 1912). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Balacra compsa (Jordan, 1904)

Nomenclature

Erebidae, Arctiinae

Materials

- a. scientificName: *Balacra compsa* (Jordan, 1904); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 26/04/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Lukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Balacra compsa* (Jordan, 1904); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 20/11/2014; habitat: Montane forest locally

disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- c. scientificName: *Balacra compsa* (Jordan, 1904); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 20/04/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was previously known from the Congolian and Shaba biogeographic regions (Przybyłowicz 2013). Our record extended its distribution to the Guinean biogeographic region. We collected it only in submontane and montane forests (1,450 and 1,850 m a.s.l.) (Fig. 6).

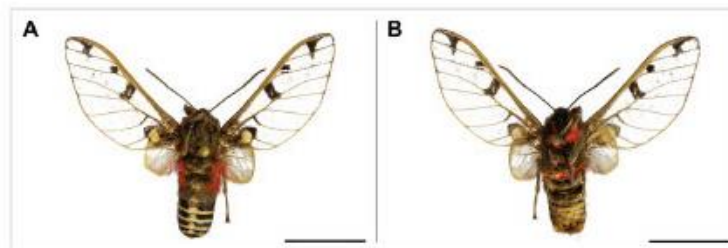


Figure 6. [doi](https://doi.org/10.1111/1365-3113.12111)
Balacra compsa (Jordan, 1904). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Daphaenisca inexpectata (Durante & Zangrilli, 2016)

Nomenclature

Erebidae, Arctiinae

Materials

- a. scientificName: *Daphaenisca inexpectata* (Durante & Zangrilli, 2016); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 16/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 14; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- b. scientificName: *Daphaenisca inexpectata* (Durante & Zangrilli, 2016); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 26; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Daphaenisca inexpectata* (Durante & Zangrilli, 2016); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 08/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 9; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Daphaenisca inexpectata* (Durante & Zangrilli, 2016); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 28/11/2014; habitat: Primary lowland forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Daphaenisca inexpectata* (Durante & Zangrilli, 2016); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 15/04/2015; habitat: Primary lowland forest; individualCount: 6; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Daphaenisca inexpectata* (Durante & Zangrilli, 2016); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 09/02/2016; habitat: Primary lowland forest; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was recently described from Gabon and considered as endemic to the country. Our record extended its known distribution to Cameroon, as well as to the Guinean biogeographic region. On Mount Cameroon, our records came from lowland forests only (350 and 650 m a.s.l.) (Fig. 7).

- Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Hippurarcia judith* Kiriakoff, 1959; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 20/02/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Ghana and Democratic Republic of Congo (Przybyłowicz and Bąkowski 2011). Our record confirmed its probable occurrence across the Afrotropical rainforest zone by partially filling the distributional gap. On Mount Cameroon, it was recorded from lowland to submontane forests (650 and 1,450 m a.s.l.) (Fig. 8).

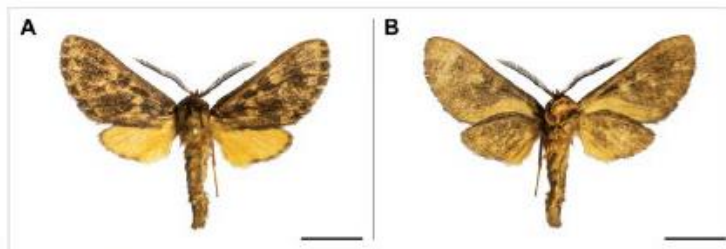


Figure 8. [doi](#)
Hippurarcia judith Kiriakoff, 1959. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Ligulosia costimaculata (Aurivillius, 1910)

Nomenclature

Erebidae, Arctiinae

Materials

- a. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 09/02/2016; habitat: Primary lowland forest; individualCount: 1; sex: female; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- b. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 24/11/2016; habitat: Submontane forest locally disturbed by elephants; individualCount: 55; sex: 54 males, 1 female; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 20/02/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 15; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 26/04/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 15; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 21/11/2014; habitat: Montane forest locally disturbed by elephants; individualCount: 4; sex: 3 males, 1 female; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 20/02/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 32; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 23/04/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 83; sex: males; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mann's Spring, Mount Cameroon; verbatimElevation: 2,200 m; decimalLatitude: 04.1428; decimalLongitude: 09.1225; samplingProtocol: Light catching; eventDate: 08/11/2016; habitat: Montane forest close to

- the timberline; individualCount: 9; sex: females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- i. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mann's Spring, Mount Cameroon; verbatimElevation: 2,200 m; decimalLatitude: 04.1428; decimalLongitude: 09.1225; samplingProtocol: Light catching; eventDate: 01/02/2017; habitat: Montane forest close to the timberline; individualCount: 46; sex: females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- j. scientificName: *Ligulosia costimaculata* (Aurivillius, 1910); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mann's Spring, Mount Cameroon; verbatimElevation: 2,200 m; decimalLatitude: 04.1428; decimalLongitude: 09.1225; samplingProtocol: Light catching; eventDate: 18/04/2017; habitat: Montane forest close to the timberline; individualCount: 64; sex: females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was reported from montane regions of Central (Democratic Republic of Congo) and Eastern (Kenya and Tanzania) Africa. Our record thus extended its known range to the Guinean biogeographic region. It was also the first record of *Ligulosia* genus in Cameroon. On Mount Cameroon, it has a relatively broad elevational distribution range (650–2,200 m a.s.l.), although most specimens were recorded at the higher elevations (Fig. 9).

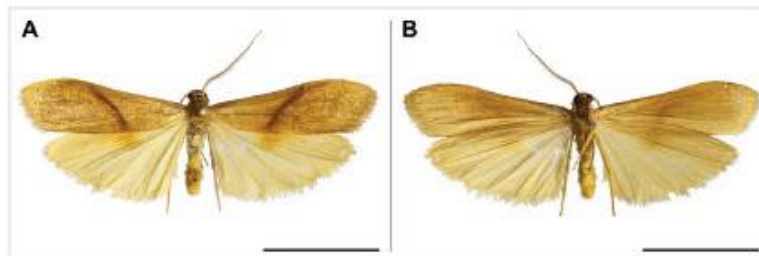


Figure 9. [doi](#)

Ligulosia costimaculata (Aurivillius, 1910). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Palaeugoa spurrelli* (Hampson, 1914)*Nomenclature**

Erebidae, Arctiinae

Materials

- a. scientificName: *Palaeugoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 09/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 10; sex: 3 males, 7 females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Palaeugoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 28; sex: 16 males, 12 females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Palaeugoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 17/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 4; sex: 3 males, 1 female; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Palaeugoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 04/02/2016; habitat: Primary lowland forest; individualCount: 71; sex: 33 males, 38 females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Palaeugoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Primary lowland forest; individualCount: 14; sex: 12 males, 2 females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Palaeugoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 06/12/2014; habitat: Primary lowland forest;

- individualCount: 10; sex: 9 males, 1 female; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Palaeogoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 30/01/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 5; sex: 3 males, 2 females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Palaeogoa spurrelli* (Hampson, 1914); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 18/12/2014; habitat: Upland forest locally disturbed by elephants; individualCount: 2; sex: females; lifeStage: adult; identifiedBy: Łukasz Przybyłowicz; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

P. spurrelli was reported only from Ghana and Kenya. Such scattered known distribution implies poor knowledge of the distributional range of the species. This is also the first record of the *Palaeogoa* genus in Cameroon. The two records from Mount Cameroon were made in lowland and upland forests (from 350 to 1,100 m a.s.l.) (Fig. 10).

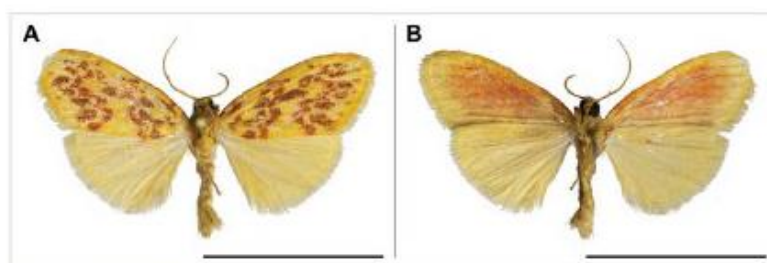


Figure 10. [doi](#)

Palaeogoa spurrelli (Hampson, 1914). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Calligraphidia opulenta (Möschler, 1887)

Nomenclature

Erebidae, Calpinae

Material

- a. scientificName: *Calligraphidia opulenta* (Möschler, 1887); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mapanja Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1157; decimalLongitude: 09.1315; samplingProtocol: Light catching; eventDate: 10/05/2017; habitat: Montane forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://qrbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Gabon and Ghana only. This is also the first record of the *Calligraphidia* genus in Cameroon. The only specimen from Mount Cameroon was collected in montane forest (1,850 m a.s.l.) (Fig. 11).

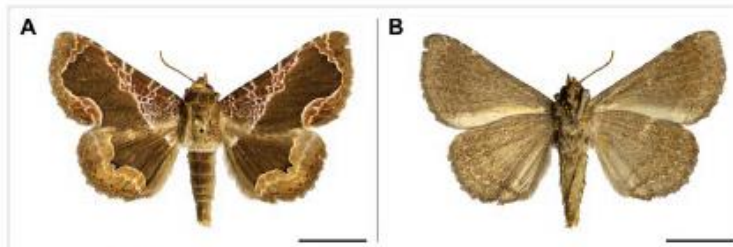


Figure 11. [doi](#)
Calligraphidia opulenta (Möschler, 1887). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Uripao albizonata Hampson, 1926

Nomenclature

Erebidae, Calpinae

Material

- a. scientificName: *Uripao albizonata* Hampson, 1926; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mapanja Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1157; decimalLongitude: 09.1315; samplingProtocol: Light catching; eventDate: 15/05/2017; habitat: Montane forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye;

dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>;
institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Gabon and Sierra Leone only. This record confirmed its broader distribution. This is also the first record of the *Uripao* genus in Cameroon. On Mount Cameroon, our only record came from the montane forests (1,850 m a.s.l.) (Fig. 12).

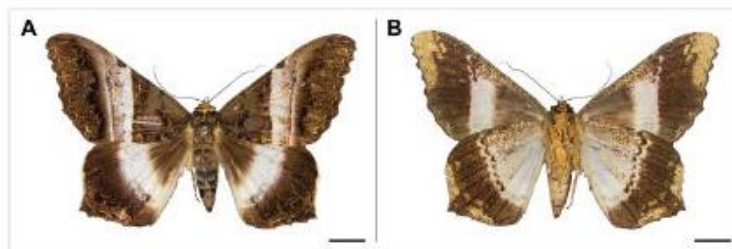


Figure 12. [doi](#)

Uripao albizonata Hampson, 1926. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Dasychira punctifera (Walker, 1858)

Nomenclature

Erebidae, Lymantriinae

Materials

- a. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 11/10/2017; habitat: Coastal forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 13/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon;

verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 9; sex: 8 males, 1 female; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- d. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 10/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 9; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 17/12/2014; habitat: Primary lowland forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 22/04/2015; habitat: Primary lowland forest; individualCount: 3; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 05/02/2016; habitat: Primary lowland forest; individualCount: 9; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 17/12/2014; habitat: Upland forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- i. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 07/04/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 4; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- j. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 31/01/2016; habitat: Upland forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- k. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 28/11/2016; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- l. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 19/02/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- m. scientificName: *Dasychira punctifera* (Walker, 1858); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 19/02/2017; habitat: Montane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

D. punctifera was known from several countries across Central and Eastern Africa (but none bordering with Cameroon), but also in Côte d'Ivoire and South Africa. In the Mount Cameroon region, it has a very broad elevational range from 30 m to 1,850 m a.s.l. (Fig. 13).

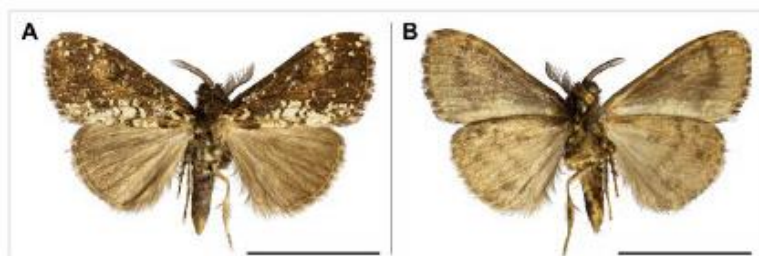


Figure 13. [doi](#)

Dasychira punctifera (Walker, 1858). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Euproctis ceramozona* Collenette, 1931*Nomenclature**

Erebidae, Lymantriinae

Materials

- a. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 15/01/2016; habitat: Coastal forest; individualCount: 1; sex: female; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 15/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 3; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 09/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 24; sex: 21 males, 3 females; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 17/04/2015; habitat: Primary lowland forest; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 05/02/2016; habitat: Primary lowland forest;

individualCount: 12; sex: 10 males, 2 females; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- g. scientificName: *Euproctis ceramozona* Collenette, 1931; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 09/04/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Ghana and Nigeria. Our record broadened its known distribution eastwards. In the Mount Cameroon region, we recorded it in all sampled lowland and upland forests up to 1,100 m a.s.l. (Fig. 14).

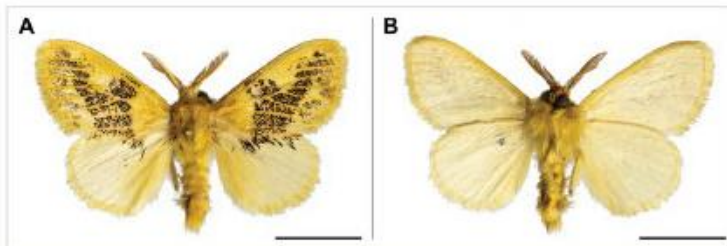


Figure 14. [doi](#)
Euproctis ceramozona Collenette, 1931. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Lomadonta saturata Swinhoe, 1904

Nomenclature

Erebidae, Lymantriinae

Materials

- a. scientificName: *Lomadonta saturata* Swinhoe, 1904; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 22/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Lomadonta saturata* Swinhoe, 1904; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon;

verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 10/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- c. scientificName: *Lomadonta saturata* Swinhoe, 1904; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 16/04/2015; habitat: Primary lowland forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Lomadonta saturata* Swinhoe, 1904; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 05/02/2016; habitat: Primary lowland forest; individualCount: 5; sex: 4 males, 1 female; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Lomadonta saturata* Swinhoe, 1904; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 01/02/2016; habitat: Upland forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Mimopacha tripunctata* (Aurivillius, 1905); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 24/11/2016; habitat: Submontane forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Mimopacha tripunctata* (Aurivillius, 1905); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 18/11/2014; habitat: Montane forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Mimopacha tripunctata* (Aurivillius, 1905); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mapanja Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1157; decimalLongitude: 09.1315; samplingProtocol: Light catching; eventDate: 24/10/2017; habitat: Montane forest; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was considered as endemic to Nigeria; we extended its known distribution eastwards. On Mount Cameroon, it was collected in forests from 350 to 1,100 m a.s.l. (Fig. 15).

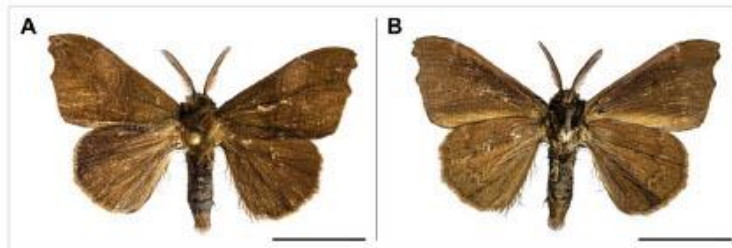


Figure 15. [doi](#)

Lomadonta saturata Swinhoe, 1904. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Orgyia basalis (Walker, 1855)

Nomenclature

Erebidae, Lymantriinae

Materials

- a. scientificName: *Orgyia basalis* (Walker, 1855); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 15/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Orgyia basalis* (Walker, 1855); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 3; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Orgyia basalis* (Walker, 1855); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 09/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 9; sex: 8 males, 1 female; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject;

institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- d. scientificName: *Orgyia basalis* (Walker, 1855); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 14/11/2015; habitat: Primary lowland forest; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Orgyia basalis* (Walker, 1855); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 04/02/2016; habitat: Primary lowland forest; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Orgyia basalis* (Walker, 1855); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 13/04/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was previously recorded only in Sierra Leone and Zimbabwe; our record thus partly filled the wide gap in its distribution. It is also the first record of the *Orgyia* genus in Cameroon. On Mount Cameroon, it was recorded in lowland and upland forests ranges from 350 to 1,100 m a.s.l. (Fig. 16).

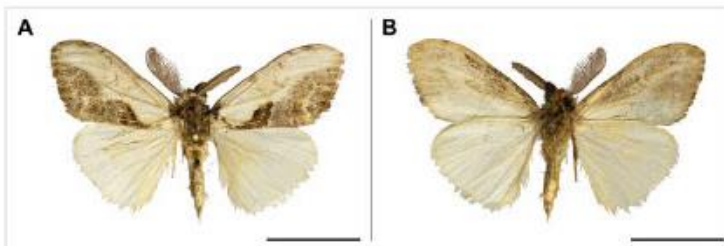


Figure 16. [doi](#)

Orgyia basalis (Walker, 1855). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Pirga ubangiana* Schultze, 1934*Nomenclature**

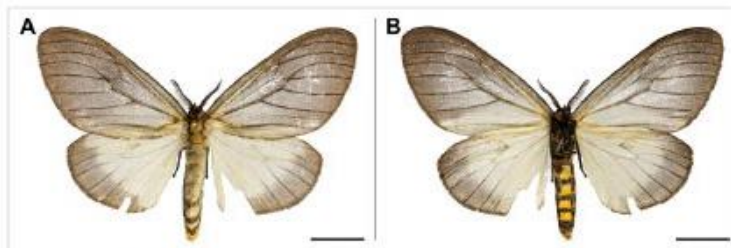
Erebidae, Lymantriinae

Materials

- a. scientificName: *Pirga ubangiana* Schultze, 1934; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 2; sex: females; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Pirga ubangiana* Schultze, 1934; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 03/02/2016; habitat: Primary lowland forest; individualCount: 2; sex: females; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known only from Uganda and Central African Republic. Our Cameroonian record thus broadened its distribution range westwards to the Guinean biogeographic region. On Mount Cameroon, it was collected in lowland forests at 350 and 650 m a.s.l. (Fig. 17).

Figure 17. [doi](#)

Pirga ubangiana Schultze, 1934. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Rhyopteryx rubripunctata* (Weymer, 1892)*Nomenclature**

Erebidae, Lymantriinae

Materials

- a. scientificName: *Rhyopteryx rubripunctata* (Weymer, 1892); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 14/01/2016; habitat: Coastal forest; individualCount: 6; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Rhyopteryx rubripunctata* (Weymer, 1892); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 19/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Rhyopteryx rubripunctata* (Weymer, 1892); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 17/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Rhyopteryx rubripunctata* (Weymer, 1892); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 09/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 17; sex: females; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Rhyopteryx rubripunctata* (Weymer, 1892); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 09/02/2017; habitat: Primary lowland forest; individualCount: 1; sex: males; lifeStage: adult; identifiedBy: Sylvain Delabye; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from the Democratic Republic of Congo, Tanzania and South Africa. Our record in Cameroon is thus the westernmost for the species and extended its distribution to the Guinean biogeographic region. In the Mount Cameroon region, it was recorded in all studied lowland forests up to 650 m a.s.l. (Fig. 18).

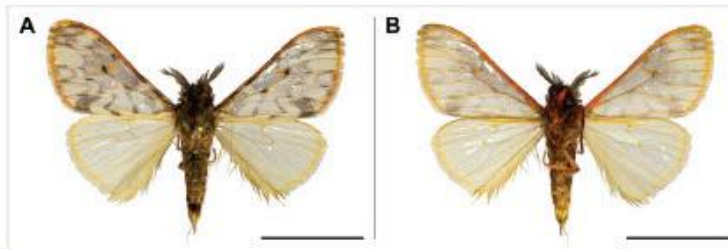


Figure 18. [doi](#)

Rhypopteryx rubripunctata (Weymer, 1892). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Stenoglene plagiatus (Aurivillius, 1911)

Nomenclature

Eupterotidae, Janinae

Material

- a. scientificName: *Stenoglene plagiatus* (Aurivillius, 1911); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 17/01/2016; habitat: Coastal forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

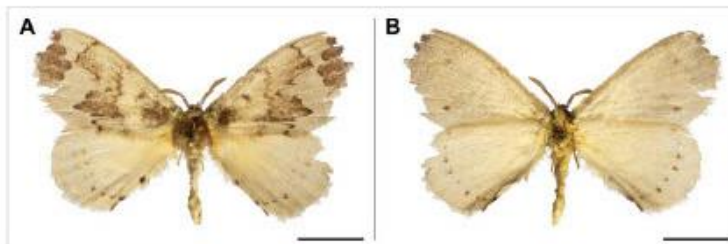


Figure 19. [doi](#)

Stenoglene plagiatus (Aurivillius, 1911). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Distribution

The known distribution of this species already included the Guinean (Ghana) and Congolian (Gabon, Central African Republic and Democratic Republic of Congo) biogeographic regions. The only specimen was collected in coastal forest at 30 m a.s.l. (Fig. 19).

Hypotrabala castanea Holland, 1893

Nomenclature

Lasiocampidae, Lasiocampinae

Materials

- a. scientificName: *Hypotrabala castanea* Holland, 1893; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 10/10/2017; habitat: Coastal forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Hypotrabala castanea* Holland, 1893; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 18/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was reported from Ghana, Nigeria and Gabon. It is also the first record of *Hypotrabala* genus in Cameroon. In the Mount Cameroon region, it was collected in lowland forests up to 350 m a.s.l. (Fig. 20).

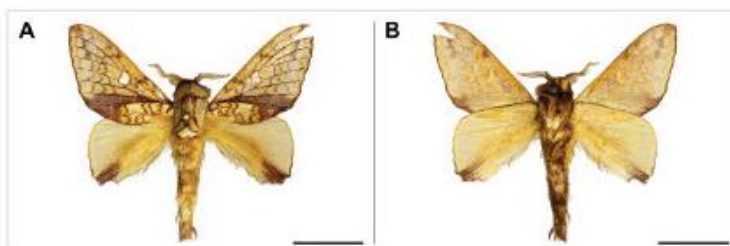


Figure 20. [doi](https://doi.org/10.1111/1365-3113.12111)
Hypotrabala castanea Holland, 1893. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Mimopacha tripunctata* (Aurivillius, 1905)*Nomenclature**

Lasiocampidae, Lasiocampinae

Materials

- a. scientificName: *Mimopacha tripunctata* (Aurivillius, 1905); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 24/11/2016; habitat: Submontane forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://qrbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Mimopacha tripunctata* (Aurivillius, 1905); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Elephant Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1453; decimalLongitude: 09.0870; samplingProtocol: Light catching; eventDate: 18/11/2014; habitat: Montane forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://qrbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Mimopacha tripunctata* (Aurivillius, 1905); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mapanja Camp, Mount Cameroon; verbatimElevation: 1,850 m; decimalLatitude: 04.1157; decimalLongitude: 09.1315; samplingProtocol: Light catching; eventDate: 24/10/2017; habitat: Montane forest; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://qrbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

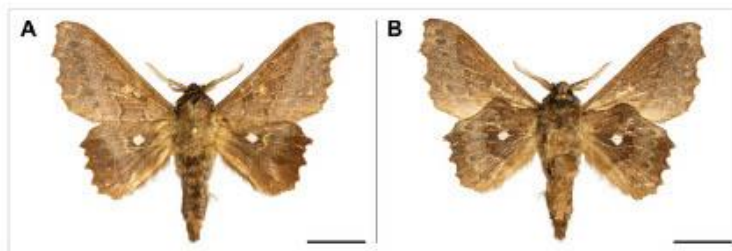


Figure 21. [doi](https://doi.org/10.1111/1365-3113.12111)
Mimopacha tripunctata (Aurivillius, 1905). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Distribution

This species was known from the Guinean (Côte d'Ivoire and Nigeria) and Zambebian (Kenya, Tanzania and Uganda) biogeographic regions, with a large distribution gap in

the Congolian biogeographic region. On Mount Cameroon, it was recorded in the submontane and montane forests between 1,450 and 1,850 m a.s.l. (Fig. 21).

Pachytrina gilharta Zolotuhin & Gurbovich

Nomenclature

Lasiocampidae, Lasiocampinae

Materials

- a. scientificName: *Pachytrina gilharta* Zolotuhin & Gurbovich, 2009; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 16/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Pachytrina gilharta* Zolotuhin & Gurbovich, 2009; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 23/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Pachytrina gilharta* Zolotuhin & Gurbovich, 2009; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 06/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Pachytrina gilharta* Zolotuhin & Gurbovich, 2009; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 23/04/2015; habitat: Primary lowland forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was already known from several countries in the Guinean and Congolian biogeographic regions, including Nigeria, Gabon and Congo bordering Cameroon. On Mount Cameroon, it was recorded in lowland forests at 350 and 650 m a.s.l. (Fig. 22).

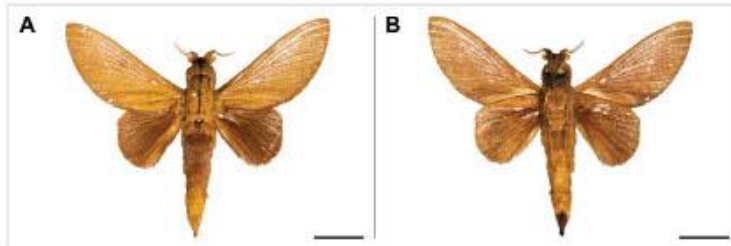


Figure 22. [doi](#)

Pachytrina gliharta Zolotuhin & Gurkovich, 2009. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Archinadata aurivilliusi (Kiriakoff, 1954)

Nomenclature

Notodontidae, Notodontinae

Materials

- a. scientificName: *Archinadata aurivilliusi* (Kiriakoff, 1954); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 23/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Archinadata aurivilliusi* (Kiriakoff, 1954); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 17/04/2015; habitat: Primary lowland forest; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from the Guinean (Côte d'Ivoire) and Congolian (Gabon, Democratic Republic of Congo and Rwanda) biogeographic regions. It is also the first record of the *Archinadata* genus in Cameroon. On Mount Cameroon, it was recorded in the lowland forests at 350 and 650 m a.s.l. (Fig. 23).

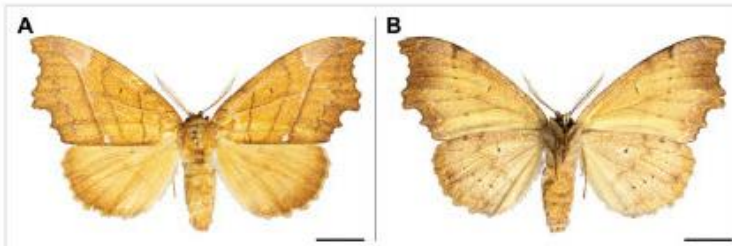


Figure 23. [doi](#)

Archinadata aurivilliusi (Kiriakoff, 1954). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

***Brachychira punctulata* Kiriakoff, 1966**

Nomenclature

Notodontidae, Notodontinae

Materials

- a. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 16/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 14; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 22/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 08/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 7; sex: 6 males, 1 female; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 05/02/2016; habitat: Primary lowland forest;

- individualCount: 20; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 09/12/2014; habitat: Primary lowland forest; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- f. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 20/04/2015; habitat: Primary lowland forest; individualCount: 7; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- g. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 11/04/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 5; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- h. scientificName: *Brachychira punctulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 01/02/2016; habitat: Upland forest locally disturbed by elephants; individualCount: 4; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

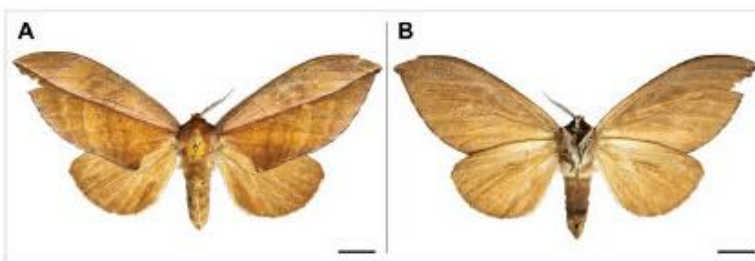


Figure 24. [doi](#)

Brachychira punctulata Kiriakoff, 1966. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Distribution

This species was considered endemic to Gabon. Our record in Cameroon extended its distribution range into the Guinean biogeographic region. On Mount Cameroon, it occurred in lowland and upland forests between 350 and 1,100 m a.s.l. (Fig. 24).

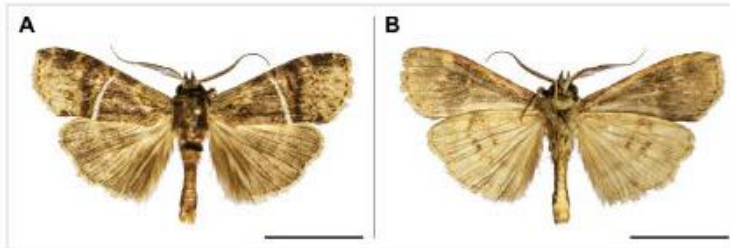
Gargettoscrancia albolineata (Strand, 1912)

Nomenclature

Notodontidae, Notodontinae

Materials

- a. scientificName: *Gargettoscrancia albolineata* (Strand, 1912); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 17/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Gargettoscrancia albolineata* (Strand, 1912); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 22/04/2015; habitat: Primary lowland forest; individualCount: 1; sex: female; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Gargettoscrancia albolineata* (Strand, 1912); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709; samplingProtocol: Light catching; eventDate: 13/04/2015; habitat: Upland forest locally disturbed by elephants; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- d. scientificName: *Gargettoscrancia albolineata* (Strand, 1912); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 17/02/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Figure 25. [doi](#)

Gargettoscrancia albolineata (Strand, 1912). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Distribution

This species was known from the Guinean (Ivory Coast) and Congolian (Equatorial Guinea and the Democratic Republic of the Congo) biogeographic regions. It is also the first record of the *Gargettoscrancia* genus in Cameroon. On Mount Cameroon, it was collected in lowland (350 m a.s.l.) to submontane (1,450 m a.s.l.) forests (Fig. 25).

Pseudobarobata denticulata Kiriakoff, 1966

Nomenclature

Notodontidae, Notodontinae

Materials

- a. scientificName: *Pseudobarobata denticulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Light catching; eventDate: 14/01/2016; habitat: Coastal forest; individualCount: 1; sex: female; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Pseudobarobata denticulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 13/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Pseudobarobata denticulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 21/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 4; sex: males; lifeStage: adult;

identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord:

PreservedSpecimen

- d. scientificName: *Pseudobarobata denticulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 11/02/2016; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- e. scientificName: *Pseudobarobata denticulata* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Light catching; eventDate: 20/11/2016; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Gabon, Central African Republic and Tanzania. Our record from Cameroon thus broadened its known distribution westwards, as well as into the Guinean biogeographic region. In the Mount Cameroon region, it was collected in lowland forests (30 and 350 m a.s.l.), although one specimen was recorded in submontane forest (1,450 m a.s.l.) (Fig. 26).

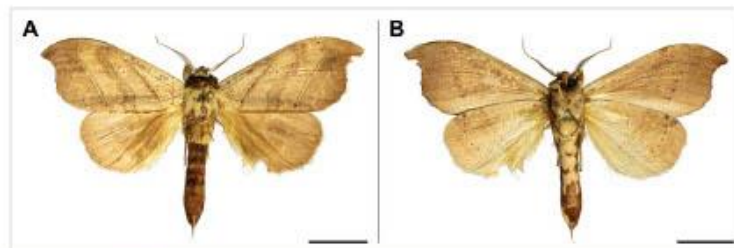


Figure 26. [doi](#)
Pseudobarobata denticulata Kiriakoff, 1966. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Pseudobarobata integra* Kiriakoff, 1966*Nomenclature**

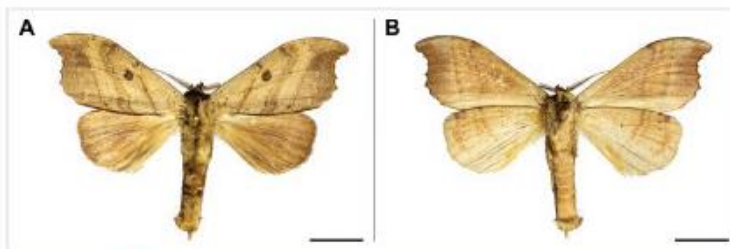
Notodontidae, Notodontinae

Materials

- a. scientificName: *Pseudobarobata integra* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Light catching; eventDate: 12/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 2; sex: males; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Pseudobarobata integra* Kiriakoff, 1966; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Light catching; eventDate: 27/11/2014; habitat: Primary lowland forest; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Vincent Maicher; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was reported from the Congolian biogeographic region only (Central African Republic and Gabon). Our record extended its known distribution to the Guinean biogeographic region. On Mount Cameroon, it was recorded in lowland forests at 350 and 650 m a.s.l. (Fig. 27).

Figure 27. [doi](#)

Pseudobarobata integra Kiriakoff, 1966. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Borbo borbonica* (Boisduval, 1833)*Nomenclature**

Hesperiidae, Hesperinae

Materials

- a. scientificName: *Borbo borbonica* (Boisduval, 1833); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Butterfly net; eventDate: 30/12/2014; habitat: Coastal forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfian; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Borbo borbonica* (Boisduval, 1833); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Crater Lake, Mount Cameroon; verbatimElevation: 1,450 m; decimalLatitude: 04.1443; decimalLongitude: 09.0717; samplingProtocol: Butterfly net; eventDate: 26/04/2017; habitat: Submontane forest locally disturbed by elephants; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfian; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

The nominotypical subspecies is relatively common in the Guinean biogeographic zone (most countries along the seashore between Mauritania and Nigeria) and from the Southern African region and Madagascar. Our Cameroonian record thus extended its distribution to the easternmost edge of the Guinean biogeographic zone. In the Mount Cameroon region, it was recorded from coastal (30 m a.s.l.) and submontane forests (1,450 m a.s.l.) (Fig. 28).

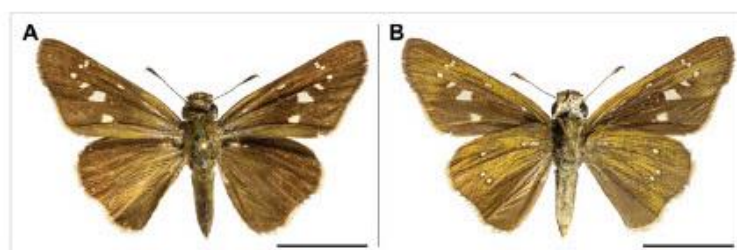


Figure 28. [doi](#)

Borbo borbonica (Boisduval, 1833). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Meza mabiliei* (Holland, 1893)*Nomenclature**

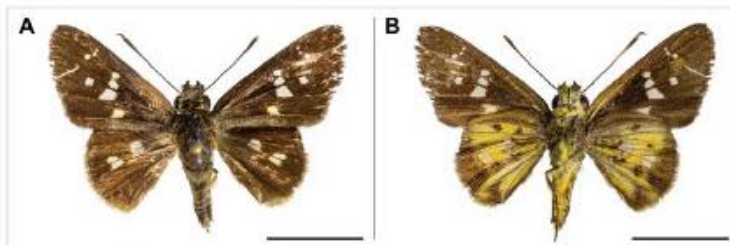
Hesperiidae, Hesperinae

Materials

- a. scientificName: *Meza mabiliei* (Holland, 1893); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Dikolo Peninsula, Bimbia-Bonadikombo Community Forest; verbatimElevation: 30 m; decimalLatitude: 03.9818; decimalLongitude: 09.2625; samplingProtocol: Butterfly net; eventDate: 09/05/2015; habitat: Coastal forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfán | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Meza mabiliei* (Holland, 1893); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Radio Hill, Bimbia village; verbatimElevation: 220 m; decimalLatitude: 03.9666; decimalLongitude: 09.2411; samplingProtocol: Butterfly net; eventDate: 30/12/2014; habitat: Hilltop with disturbed lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfán | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known to be widely distributed in the Guinean biogeographic region (most countries from Guinea to Nigeria) and in Gabon. In the Mount Cameroon region, it was collected in the two lowest localities (30 and 220 m a.s.l.) (Fig. 29).

Figure 29. [doi](#)

Meza mabiliei (Holland, 1893). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Acraea macaria* (Faricius, 1793)*Nomenclature**

Nymphalidae, Heliconiinae

Materials

- a. scientificName: *Acraea macaria* (Faricius, 1793); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Butterfly net; eventDate: 01/12/2014; habitat: Primary lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfián | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Acraea macaria* (Faricius, 1793); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Butterfly net; eventDate: 26/04/2015; habitat: Lowland forest disturbed by historical selective logging; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfián | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

A. macaria was known from the western part of the Guinean biogeographic region only (most countries along the seashore between Senegal and Ghana). Our record from Cameroon therefore extended its distribution for over 1,000 km westwards to the easternmost edge of the Guinean biogeographic region. In the Mount Cameroon region, it was collected in the two lowest localities (30 and 220 m a.s.l.).

Telchinia encedana* (Pierre, 1976)*Nomenclature**

Nymphalidae, Heliconiinae

Material

- a. scientificName: *Telchinia encedana* (Pierre, 1976); continent: Africa; country: Cameroon; stateProvince: Northwest Region; locality: Mendong Buo, Big Babanki, Bamenda Highlands; verbatimElevation: 2,200 m; decimalLatitude: 06.0921; decimalLongitude: 10.2987; samplingProtocol: Butterfly net; eventDate: 30/11/2016; habitat: Mosaic of mountain forest remnants, forest clearings dominated by *Pteridium aquilinum*, submontane grasslands maintained by cattle grazing and species-rich scrub vegetation along streams; individualCount: 1; sex: male; lifeStage: adult; identifiedBy: Robert Tropek; dateIdentified: 2017; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This relatively widespread species was recorded from numerous countries of the Guinean (from Senegal to Cameroon) and Congolian (Democratic Republic of the Congo) biogeographic regions, but also from the Ethiopian, Somalian, Zambezan and Shaba regions. In Cameroon, its only record was published by Aurivillius (1905) more than a century ago, from the Adamawa Province. Our recent record therefore confirmed its presence in the country and extended the species' distribution range to the Northwest Province (Fig. 30).

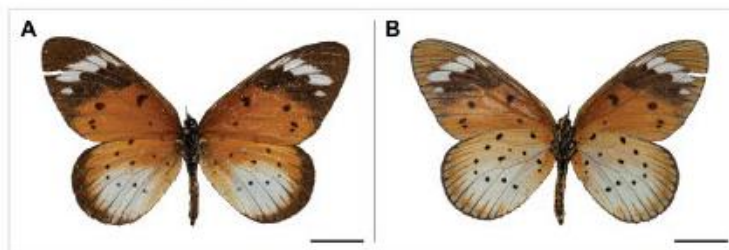


Figure 30. [doi](#)
Telchinia encedana (Pierre, 1976). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Euphaedra temeraria Hecq, 2007

Nomenclature

Nymphalidae, Limenitidinae

Materials

- a. scientificName: *Euphaedra temeraria* Hecq, 2007; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Bamboo Camp, Mount Cameroon; verbatimElevation: 350 m; decimalLatitude: 04.0899; decimalLongitude: 09.0517; samplingProtocol: Bait trap; eventDate: 07/12/2014; habitat: Lowland forest disturbed by historical selective logging; individualCount: 72; lifeStage: adult; identifiedBy: Szabolcs Sáfián; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Euphaedra temeraria* Hecq, 2007; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Drink Gari, Mount Cameroon; verbatimElevation: 650 m; decimalLatitude: 04.1022; decimalLongitude: 09.0630; samplingProtocol: Bait trap; eventDate: 02/12/2014; habitat: Primary lowland forest; individualCount: 53; lifeStage: adult; identifiedBy: Szabolcs Sáfián; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- c. scientificName: *Euphaedra temeraria* Hecq, 2007; continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: PlanteCam Camp, Mount Cameroon; verbatimElevation: 1,100 m; decimalLatitude: 04.1175; decimalLongitude: 09.0709;

samplingProtocol: Bait trap; eventDate: 14/12/2014; habitat: Upland forest locally disturbed by elephants; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfian; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

Distribution

This species was known from Equatorial Guinea and Gabon, both in the Congolian biogeographic region. Our record thus extended its distribution range northwards and evidenced its occurrence in the Guinean biogeographic region. On Mount Cameroon, it was collected mostly in the lowland forests at 350 and 650 m a.s.l.; one specimen was caught also in the upland forest at 1,100 m a.s.l. (Fig. 31).

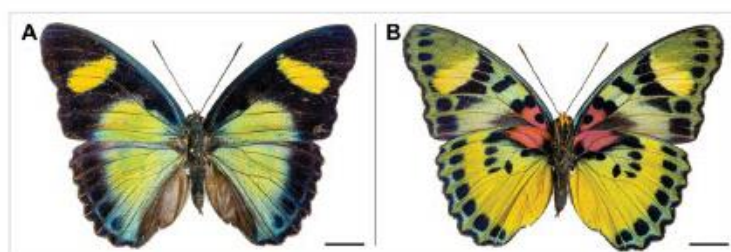


Figure 31. [doi](#)
Euphaedra temeraria Hecq, 2007. A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Neptis metella (Doubleday, [1850])

Nomenclature

Nymphalidae, Limenitidinae

Materials

- a. scientificName: *Neptis metella* (Doubleday, [1850]); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Radio Hill, Bimbilla village; verbatimElevation: 220 m; decimalLatitude: 03.9666; decimalLongitude: 09.2411; samplingProtocol: Butterfly net; eventDate: 31/12/2014; habitat: Hilltop with disturbed lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfian | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Neptis metella* (Doubleday, [1850]); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Radio Hill, Bimbilla village; verbatimElevation: 220 m; decimalLatitude: 03.9666; decimalLongitude: 09.2411; samplingProtocol: Butterfly net; eventDate: 08/01/2015; habitat: Hilltop with disturbed lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfian | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/8t1f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen

- c. scientificName: *Neptis metella* (Doubleday, [1850]); continent: Africa; country: Cameroon; stateProvince: Northwest Region; locality: Lake Oku, Mount Oku; verbatimElevation: 2,200 m; decimalLatitude: 06.1924; decimalLongitude: 10.4616; samplingProtocol: Butterfly net; eventDate: 24/12/2009; habitat: Montane forest; individualCount: 1; lifeStage: adult; identifiedBy: Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/06zb-203s>; institutionCode: IECA; basisOfRecord: PreservedSpecimen
- d. scientificName: *Neptis metella* (Doubleday, [1850]); continent: Africa; country: Cameroon; stateProvince: Centre Region; locality: Ebogo Forest; verbatimElevation: 660 m; decimalLatitude: 03.3880; decimalLongitude: 11.4700; samplingProtocol: Butterfly net; eventDate: 04/01/2012; habitat: Disturbed lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/06zb-203s>; institutionCode: IECA; basisOfRecord: PreservedSpecimen

Distribution

This species was previously known from the Guinean (from Guinea to Nigeria), Shaba, Zambezian and Sudanian biogeographic regions. Our record in Cameroon partly filled the gap in its known distribution. It was known as a relatively common species in many disturbed lowland forests in the surrounding countries (Larsen 2005), thus its occurrence in Cameroon is not surprising. Three of the four reported specimens were collected in disturbed lowland forests (220 and 660 m a.s.l.), corresponding to the known species' habitats (Larsen 2005). On the other hand, its occurrence at 2,200 m a.s.l. has evidenced the species as a habitat generalist (Fig. 32).

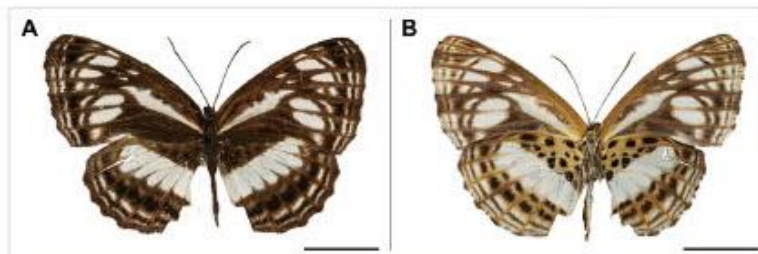


Figure 32. [doi](#)
Neptis metella (Doubleday, [1850]). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Eurema floricola leonis (Butler, 1886)

Nomenclature

Pieridae, Coliadinae

Materials

- a. scientificName: *Eurema floricola leonis* (Butler, 1886); taxonRank: subspecies; scientificNameAuthorship: (Butler, 1886); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Radio Hill, Bimbria village; verbatimElevation: 220 m; decimalLatitude: 03.9666; decimalLongitude: 09.2411; samplingProtocol: Butterfly net; eventDate: 09/05/2015; habitat: Hilltop with disturbed lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Szabolcs Sáfíán | Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/81f-g2z6>; institutionCode: ZMJU; basisOfRecord: PreservedSpecimen
- b. scientificName: *Eurema floricola leonis* (Butler, 1886); taxonRank: subspecies; scientificNameAuthorship: (Butler, 1886); continent: Africa; country: Cameroon; stateProvince: Southwest Region; locality: Mundemba; verbatimElevation: 20 m; decimalLatitude: 04.9300; decimalLongitude: 08.8540; samplingProtocol: Butterfly net; eventDate: 02/01/2010; habitat: Disturbed secondary regrowths; individualCount: 1; lifeStage: adult; identifiedBy: Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/06zb-203s>; institutionCode: IECA; basisOfRecord: PreservedSpecimen
- c. scientificName: *Eurema floricola leonis* (Butler, 1886); taxonRank: subspecies; scientificNameAuthorship: (Butler, 1886); continent: Africa; country: Cameroon; stateProvince: Centre Region; locality: Ebogo Forest; verbatimElevation: 660 m; decimalLatitude: 03.3880; decimalLongitude: 11.4700; samplingProtocol: Butterfly net; eventDate: 12/01/2008; habitat: Disturbed lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/06zb-203s>; institutionCode: IECA; basisOfRecord: PreservedSpecimen
- d. scientificName: *Eurema floricola leonis* (Butler, 1886); taxonRank: subspecies; scientificNameAuthorship: (Butler, 1886); continent: Africa; country: Cameroon; stateProvince: South Region; locality: Ebodje; verbatimElevation: 20 m; decimalLatitude: 02.5720; decimalLongitude: 09.8320; samplingProtocol: Butterfly net; eventDate: 17/12/2011; habitat: Secondary lowland forest; individualCount: 1; lifeStage: adult; identifiedBy: Robert Tropek; dateIdentified: 2015; type: PhysicalObject; institutionID: <http://grbio.org/cool/06zb-203s>; institutionCode: IECA; basisOfRecord: PreservedSpecimen

Distribution

This species was recorded from West Africa (from Guinea-Bissau to Nigeria) to Central (Democratic Republic of the Congo) and Eastern Africa. Especially because it was already known from the Cross River State in Nigeria (Larsen 2005), its occurrence in Cameroon could be expected. We collected four specimens, each in a different disturbed lowland forest (from 20 to 660 m a.s.l.), therefore the species seems to be widespread, but locally scarce in Cameroon. This fully corresponds with T. Larsen's experience with this species in Nigeria (Larsen 2005) (Fig. 33).

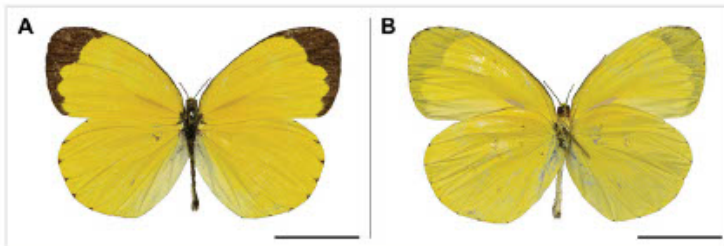


Figure 33. [doi](#)

Eurema floricola leonis (Butler, 1886). A. dorsal view; B. ventral view. The scale bar represents 1 cm.

Discussion

Altogether, the Lepidoptera species included in this study comprise 31 species and 8 genera new for the entomofauna of Cameroon, as well as a butterfly *T. encedana* that had not been recorded for more than a century in Cameroon. With the records from this study, the known diversity in Cameroon now surpasses 3,000 taxa for moths (species and subspecies combined; De Prins and De Prins 2019), whilst it approximates 1,600 taxa for butterflies (Williams 2018).

Of the 31 species new for Cameroon, four are known from the Guinean biogeographic region only (De Prins and De Prins 2019, Williams 2018). Therefore, our records did not change their endemic status, although this study extended their distribution to the easternmost border of the Guinean region (including an extension of ca. 1,000 km for *A. holobrunnea* and *A. macaria*). Another ten of the listed species had been previously recorded in the Congolian region only. From these, our records have extended distribution of *Euphaedra temeraria* northwards, while the other species' distributions have been extended eastwards (De Prins and De Prins 2019, Williams 2018). Mainly, we have evidenced these ten species to occur in the Guinean biogeographic region, although only at its edge. This broadening of the easternmost, westernmost or northernmost limits of the numerous species distribution shows the importance of Cameroon (with special emphasis on Mount Cameroon) as the 'crossroads' between the Guinean and the Congolian biogeographic regions. It also reinforces Mount Cameroon as a biodiversity hotspot area (Myers et al. 2000, Ustjuzhanin et al. 2018).

Several other species records included in this report are not surprising since they more or less expectedly fill gaps in their known distribution. Most expectedly, we recorded twelve species (such as *A. makomensis* and *S. plagiatus*) already known from the countries bordering Cameroon or some other nearby countries in the Guinean and Congolian regions (De Prins and De Prins 2019). Six other species (such as *P. spurrelli* and *M. tripunctata*) were known to have a more scattered distribution amongst West, East and South Africa, but in countries more distant from Cameroon, forming a relatively large gap in their known distribution. Aside from the species with azonal distribution (such as the

montane species), such large gaps rather imply lack of knowledge on the species occurrence (cf. Maicher et al. 2016). Our records in Cameroon have confirmed such suggestion by the partial filling of these distribution gaps. The record of the widespread *T. encedana* more than 100 years after its first and only record in Cameroon is also a perfect illustration of this general lack of knowledge on the Cameroonian (and Afrotropical) biodiversity of Lepidoptera. This was already pointed out by Tropek et al. (2013) and Tropek et al. (2015) for butterflies and by Maicher et al. (2016) for moths.

Considering the elevational ranges of the reported species, 19 reported lepidopteran species were exclusively collected in lowland and upland forests (between 30 and 1,100 m a.s.l.) on Mount Cameroon, while records of five moth species were restricted to submontane and montane forests (between 1,450 and 2,100 m a.s.l.). Consequently, given that the local lepidopteran diversity is known to be higher at lower elevations (differing amongst the lepidopteran groups but always up to 1,100 m a.s.l.; Maicher et al. 2020), it appears that the knowledge gap seems proportionally comparable between the lower and higher elevations on the mountain. Although knowledge on precise elevational ranges of Afrotropical moths is highly limited, all five high-elevation species were previously reported from countries with montane ranges. These species are also the ones with the known azonal distributions which can be related to their affiliation to (sub)montane habitats rather than the severe lack of knowledge on their actual distribution. The remaining seven species have been recorded in both lowland and montane forests on Mount Cameroon.

In conclusion, our report of numerous butterfly and moth species and genera, previously not known to occur in Cameroon, highlights the relatively poor knowledge on the local and regional diversity of Afrotropical Lepidoptera. Moreover, some of these records represent a substantial extension of the individual species' known distribution. Altogether, we encourage the collection and publishing of similar faunistic data on lepidopteran occurrence from the Afrotropical countries.

Acknowledgements

We are grateful to Francis E. Luma, Eliška Chmelová, Petra Janečková, Zuzana Musilová, Ernest Vunan Amohlon and numerous other colleagues and field assistants for their help in the field; the Mount Cameroon National Park staff for their support; and Tomasz Pycz and his team at the Nature Education Centre, Jagiellonian University, Krakow, Poland, for setting and curating our Lepidoptera material; Karolina Fok and Magdalena Kawalkowska for taking pictures of *Daphaenisca inexpectata*. Our sampling was permitted by the Ministries of the Republic of Cameroon for Forestry and Wildlife and for Scientific Research and Innovation. Our projects were funded by the Czech Science Foundation (20-16499S), Charles University (PRIMUS/17/SCI/8 and UNCE204069), University of South Bohemia (GAJU030/2016/P and 152/2016/P) and Institute of Entomology, BC CAS (RVO: 60077344).

Author contributions

SD, VM, SzS, PP, JEJM, MM, INK, ŠJ and RT collected the materials. SD, VM, SzS, ŁP, MM and RT identified the sampled specimens. JEJM photographed the specimens. SD and RT led the manuscript writing and all co-authors participated in the manuscript writing and approved its submission.

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CHAPTER VIII

Even hotter hotspot: description of seven new species of many-plumed moths (Lepidoptera, Alucitidae) from Mount Cameroon

Ustjuzhanin, P., Kovtunovich, V., Maicher, V., Sáfián, Sz.,
Delabye, S., Streltsov, A., & Tropek, R. (2020).

Zookeys, **935**: 103-119.



Paratype of Alucita bokwango Ustjuzhanin Kovtunovich, 2020, one of the new described species collected on Mount Cameroon. © S. Reshetnikov

Even hotter hotspot: description of seven new species of many-plumed moths (Lepidoptera, Alucitidae) from Mount Cameroon

Peter Ustjuzhanin^{1,2}, Vasily Kovtunovich³, Vincent Maicher^{4,5,6}, Szabolcs Sáfán^{5,7}, Sylvain Delabye^{4,5}, Alexander Streltsov⁸, Robert Tropolik^{4,6}

1 Altai State University, Lenina 61, Barnaul, RU-656049, Russia **2** Biological Institute, Tomsk State University, Lenina Prospekt 36, Tomsk 634050, Russia **3** Moscow Society of Nature Explorers, Bolshaya Nikitskaya 2, Moscow, RU-125009, Russia **4** Institute of Entomology, Biology Centre of the Czech Academy of Sciences, Branišovská 31, CZ-37005 České Budějovice, Czech Republic **5** Faculty of Science, University of South Bohemia, Branišovská 1760, CZ-37005 České Budějovice, Czech Republic **6** Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12844 Prague, Czech Republic **7** Institute of Silviculture and Forest Protection, University of Sopron, Bajcsy-Zsilinszky u. 4. H-9945 Sopron, Hungary **8** Herzen State Pedagogical University of Russia, 48, Moika Emb., Saint-Petersburg, 191186, Russia

Corresponding author: Robert Tropolik (robert.tropolik@gmail.com)

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Abstract

Mount Cameroon, SW Cameroon, has already been described as a unique hotspot of the many-plumed moth (Lepidoptera, Alucitidae), with their local diversity unrivalled in the entire Afrotropics. We confirm its importance with description of seven new species: *Alucita bakwari* Ustjuzhanin & Kovtunovich, **sp. nov.**, *Alucita jana* Ustjuzhanin & Kovtunovich, **sp. nov.**, *Alucita bakingili* Ustjuzhanin & Kovtunovich, **sp. nov.**, *Alucita tatjana* Ustjuzhanin & Kovtunovich, **sp. nov.**, *Alucita zuza* Ustjuzhanin & Kovtunovich, **sp. nov.**, *Alucita deja* Ustjuzhanin & Kovtunovich, **sp. nov.**, and *Alucita bokwango* Ustjuzhanin & Kovtunovich, **sp. nov.** These descriptions have raised the known local diversity of many-plumed moth species on Mount Cameroon to 22, i.e., over a quarter of the known Afrotropical biodiversity of this group. This study also emphasises the great conservation importance of the area.

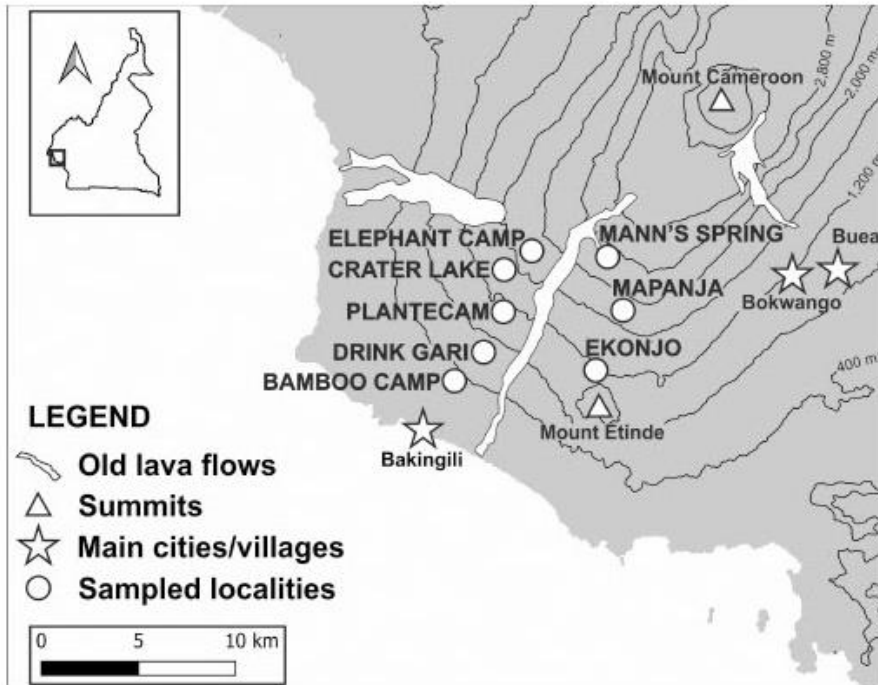


Figure 1. Map of the Mount Cameroon region with the sampling localities.

(2018). Each permanent preparation received a unique code under which it is searchable in the collections where they are stored; the relevant numbers are listed in captions of the genitalia figures.

Sampling localities

All sampling localities (Fig. 1) are listed below; the localities not included in Ustjuzhanin et al. (2018) are marked with *:

Bamboo Camp. Bamboo Camp (350 m a.s.l.), Mount Cameroon (SW slope), 4.0879°N, 9.0505°E; a lowland rainforest with historical disturbances from selective logging.

***Crater Lake.** Crater Lake camp (1450 m a.s.l.), Mount Cameroon (SW slope), 4.1443°N, 9.0717°E; a submontane rainforest locally disturbed by forest elephants.

Drink Gari. Drink Gari camp (650 m a.s.l.; also known as “Drinking Gari”), Mount Cameroon (SW slope), 4.1014°N, 9.0610°E; a lowland rainforest with canopy layer presumed to be closed.

***Ekonjo.** Ekonjo camp (1150 m a.s.l.), Mount Cameroon (S slope), 4.0881°N, 9.1168°E; an upland closed-canopy rainforest.

Elephant Camp. Elephant Camp (1850 m a.s.l.), Mount Cameroon (SW slope), 4.1170°N, 9.0729°E; a montane forest with a sparse canopy layer as a consequence of natural disturbances by forest elephants.

***Mann's Spring.** Mann's Spring camp (2200 m a.s.l.), Mount Cameroon (SW slope), 4.1428°N, 9.1225°E; a montane forest at the natural timberline.

***Mapanja.** Mapanja camp (1850 m a.s.l.), Mount Cameroon (S slope), 4.1157°N, 9.1315°E; a montane forest with canopy layer presumed to be closed.

PlanteCam. PlanteCam camp (1100 m a.s.l.; also misspelled as "Planticamp"), Mount Cameroon (SW slope), 4.1175°N, E9.0709°E; an upland rainforest in the transition between the lowland and montane zones, with a sparse canopy layer as a consequence of natural disturbances by forest elephants.

Species descriptions

Alucita bakweri Ustjuzhanin & Kovtunovich, sp. nov.

<http://zoobank.org/4CCBE08C-2366-40FF-B52F-D7B3D60DF816>

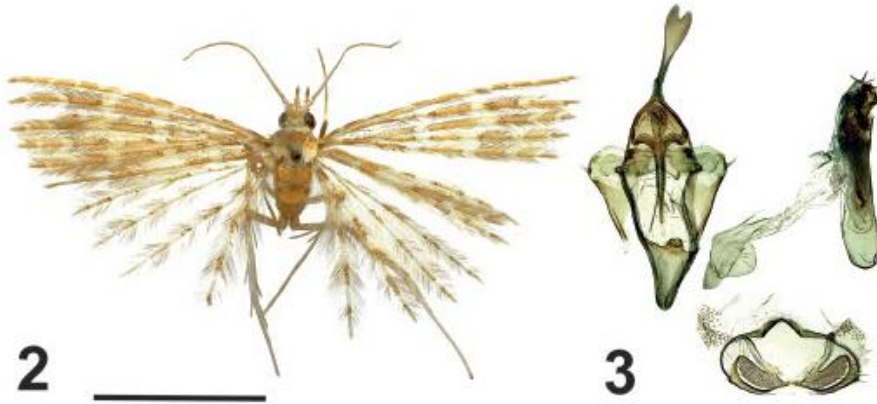
Figs 2, 3

Type material. *Holotype* • 1 male, (NECJU 201901) Cameroon, PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 11–18.XII.2014, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek.

Diagnosis. In the yellowish colour of its wings, this species resembles *Alucita ferruginea* Walsingham, 1881, *Alucita balioxantha* (Meyrick, 1921), and *Alucita compsoxantha* (Meyrick, 1924), from which it differs in the structure of male genitalia. Genitalia of the new species differ from *A. balioxantha* by a thin sharp gnathos, prolonged saccus, and short, wide and wing-like valvae (Fig. 19). *Alucita balioxantha* gnathos is wider, with a blunt and round top, the saccus is archlike and not prolonged, and valvae are thin and lancet-like. In the shape of the uncus and gnathos of the male genitalia, *A. bakweri* is similar to *A. ferruginea*, from which it differs in having an elongated, narrowing saccus without the distinct notch on its outer edge. Additionally, unlike *A. ferruginea*, *A. bakweri* has clusters of small acicular cornuti apically on the aedaeagus. Moreover, its valvae are short, wide and wing-like, with a bundle of thin needle-like cornuti in its apical part. Whilst male genitalia of the new species have a forked uncus and comparatively short aedaeagus, *A. compsoxantha* has a simple short uncus and a very long aedaeagus.

External characters. Wingspan 18 mm. Head with white scales, thorax and tegulae yellowish-brown. Labial palpus yellow, thin, straight, twice as long as longitudinal eye diameter. Third segment discrete, directed forward, median part framed by brown lines, apically pale and sharp. Antenna white, basally thickened. Wings yellowish-brown, with four white transverse lines. Wings basally darkened with brown scales. Abdomen yellowish-brown. Hind leg pale yellow.

Male genitalia. Uncus long, distally widened, apically with triangle notch. Gnathos narrow, apically tapered, in length equal to uncus. Gnathos arms short, thick,



Figures 2, 3. *Alucita bakweri* Ustjuzhanin & Kovtunovich, sp. nov. **2** adult male, Holotype, NECJU **3** male genitalia, Holotype, preparation slide no. 201901. Scale bar: 5 mm.

smoothly bent inwards. Valves short, wide, wing-shaped, apically with bundle of fine acicular setae. Anellus arms wide, short. Saccus elongated, narrow triangular. Aedeagus almost straight, with an elongated uncinat cornutus in middle, groups of fine acicular cornuti distally, and narrow sharp cornuti sticking out apically.

Distribution. Cameroon.

Flight period. December.

Etymology. We name the species after the Bakweri people, the main ethnic group of the Mount Cameroon region. Without the priceless assistance of numerous local people our project would not be possible. We hope such dedication will encourage protection of the species' habitats.

***Alucita jana* Ustjuzhanin & Kovtunovich, sp. nov.**

<http://zoobank.org/2EE6AAB9-8CCB-4123-B957-786B6776CB92>

Figs 4, 5

Type material. *Holotype* • male, (NECJU 201902) Cameroon, PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 09–14.IV.2015, lgt. V. Maicher, Sz. Sáfián, S. Jančec, R. Tropek. *Paratypes* • 1 male, (CUK), Ekonjo, 1150 m a.s.l., Mount Cameroon (SW slope), 4.0881°N, 9.1168°E, 24.X.2017, lgt. V. Maicher, P. Potocký, S. Delabye • 1 male, (CUK), Mapanja camp, 1850 m a.s.l., Mount Cameroon (SW slope), 4.1157°N, 9.1315°E, 25.X.2017, V. Maicher, P. Potocký, S. Delabye.

Diagnosis. The new species is similar in the shape of the uncus and valves of the male genitalia to *Alucita tessarata* (Meyrick, 1918) (Fig. 20), but it differs in the apically narrow gnathos and the presence of a group of fine acicular cornuti in the aedeagus. *Alucita jana* also differs from *A. tessarata* in the wing colouration.



Figures 4, 5. *Alucita jana* Ustjuzhanin & Kovtunovich, sp. nov. **4** adult male, Holotype, NEJCU **5** male genitalia, Holotype, preparation slide no. 201902. Scale bar: 5 mm.

External characters. Wingspan 15 mm. Head, thorax and tegulae with brown appressed scales. Labial palpus wide, short, 1.5 longer than longitudinal eye diameter, slightly bent upwards, brown scaled inside and outside. Third segment discrete, apically sharp. Antenna yellowish-brown. Wings yellowish-brown, distinctive pale brown band medially. Forewings show a dark brown postmedial band. Forewing basally with dark brown scales, hindwing basally light. Distally, alternating portions of brown and yellowish scales. Fringe of wings yellow, with alternating portions of brown hairs. Hind leg pale yellow.

Male genitalia. Uncus long, apically slightly widened. Gnathos long, distally widened, apically slightly tapered, equal to uncus in length. Valve short, finger-like, membranous. Anellus arms narrow, long, apically slightly widened. Saccus with oval outer edge. Aedeagus straight, basally widened, apically with a group of fine acicular cornuti.

Distribution. Cameroon.

Flight period. April, October.

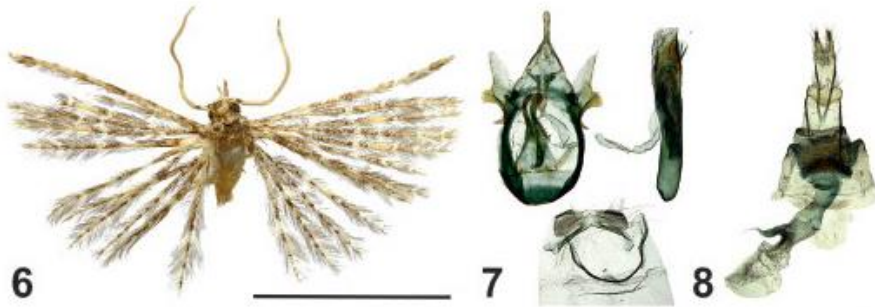
Etymology. The species name is a noun in apposition in honour to Robert Tropek's mother, Jana Tropková.

***Alucita bakingili* Ustjuzhanin & Kovtunovich, sp. nov.**

<http://zoobank.org/C1503460-2901-4437-BFA7-49D660E2462F>

Figs 6–8

Type material. *Holotype* • male (NECJU 201903) Cameroon, Bamboo Camp, 350 m a.s.l., Mount Cameroon (SW slope), 4.0879°N, 9.0505°E, 12–20.XII.2014, lgt. V. Maicher, Sz. Sáfíán, S. Janeček, R. Tropek. *Paratypes* • 1 male (CUK), same data as the holotype • 1 female (NECJU 201908), same data as the holotype • 1 male, (CUK), PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 29.I.-07.II.2016, lgt. V. Maicher, Sz. Sáfíán, R. Tropek.



Figures 6–8. *Alucita bakingili* Ustjuzhanin & Kovtunovich, sp. nov. **6** adult male, Holotype, NEJCU **7** male genitalia, Holotype, preparation slide no. 201903 **8** female genitalia, Paratype, preparation slide no. 201908. Scale bar: 5 mm.

Diagnosis. The new species resembles *Alucita fokami* Ustjuzhanin & Kovtunovich, 2018 in external appearance but it substantially differs in both male and female genitalia (for genitalia of *A. fokami*, see Ustjuzhanin et al. 2018). *Alucita bakingili* is similar to *Alucita seychellensis* (T.B. Fletcher, 1910) in male genitalia (illustrated in Ustjuzhanin and Kovtunovich 2016), specifically in the sclerotized process on the sacculus. *Alucita bakingili* also differs from *A. seychellensis* in its wide gnathos, the narrow triangular valves and the short narrow uncus. In the female genitalia, the new species is similar to *Alucita rhapsica* (Meyrick, 1920) (Fig. 21), from which it differs in its rectangular lamina postvaginalis and in the longer and narrower ductus.

External characters. Wingspan 12–15 mm, holotype 12 mm. Head, thorax and tegulae with dark grey scales and an admixture of white scales. Labial palpus grey outside, white inside, 1.5 times longer than longitudinal eye diameter, directed forward. Third segment short, apically slightly sharpened. Antenna pale grey, distinct dark elongated spot basally just beyond scape. Wings mottled, yellowish-grey, medially with a poorly expressed yellowish-brown band. Alternating portions of grey and white scales shaped as elongated strokes, spots and points on lobe of all wings. Fringe with alternating portions of grey and white hairs. Hind leg pale yellow.

Male genitalia. Uncus short, straight, slightly widened apically. Gnathos wide, sharply narrowing apically, a little longer than uncus. Valve short, narrow triangular, membranous. Sacculus with membranous process containing a large sclerotized uncinuate process in lower part. Anellus arms very long, basally wide, medially narrowing, apically widened and slightly bent. Saccus with oval outer edge. Aedeagus long, straight, with two robust cornute in this medial part.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses thin, straight. Anterior apophyses also thin, straight, equal in length to posterior apophyses. Lamina postvaginalis sclerotized, wide, rectangular, with blunt angular lateral projections. Antrum corrugated, wide, short. Ductus wide, medially swollen. Ductus seminalis short,

well expressed. Bursa copulatrix small, oval, with robust elongated comb-shaped signum located basally and reaching base of ductus seminalis.

Distribution. Cameroon.

Flight period. December to February.

Etymology. The species is named after Bakingili, a village at the southern foothills of Mount Cameroon, in which area it was collected. Numerous people from the village helped our project as field assistants and by many other ways, and therefore the community was crucial for its success. The Bakingili people are also necessary for protection of the species' natural area.

***Alucita tatjana* Ustjuzhanin & Kovtunovich, sp. nov.**

<http://zoobank.org/2CCDE55D-7D9C-413C-A5B0-42833DE8F770>

Figs 9, 10

Type material. *Holotype* • female, (NECJU 201904) Cameroon, PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 09–14.IV.2015, V. Maicher, Sz. Sáfián, S. Janeček, R. Tropek; *Paratype* • 1 female, (CUK), Ekonjo, 1150 m a.s.l., Mount Cameroon (S slope), 4.0881°N, 9.1168°E, 24.X.2017, lgt. V. Maicher, P. Potocký, S. Delabye.

Diagnosis. The new species resembles *Alucita mischenini* Ustjuzhanin & Kovtunovich, 2018 in the light colour of its wings and the wide medial band, but it differs in its larger size (21 mm vs. 12–15 mm wingspan). Additionally, the position and shape of dark markings in the basal and distal portions of the wings differentiates *A. tatjana* from *A. mischenini* whose forewings bear extensive brown areas in the basal portions and almost continuous dark brown marks covering the distal halves of the first two forewing lobes (Ustjuzhanin et al. 2018). Additionally, forewings of the new species differ from *A. mischenini* by the continuation of the brown medial band through most of the length of the second forewing lobe. In female genitalia, *A. tatjana* is similar to *A. compositoxantha* Meyrick, 1924 (Fig. 22), especially in the shape of the antrum and the absence of any signa in the bursa copulatrix. However, *A. tatjana* differs in its shorter and wider ductus and substantially shorter anterior and posterior apophyses. These species also differ in the colouration of their wings.

External characters. Wingspan 21 mm. Head, thorax and tegulae with appressed white scales. Labial palpus twice as long as longitudinal eye diameter, white, with a brown band of the third segment, thin, apically tapered, sharp. Antenna white. Scape extended and flattened. Wings white with well-expressed wide median band, brown on forewing and almost black on hindwing. Subterminal band narrower, consisting of brown spots of scales, intermittently traced throughout all lobes. First forewing lobe apically brown. Second forewing lobe with brown colouration continuous between median band and subterminal band. Forewing basally white with well-expressed dark brown fringes near the base of the cleft between the second and third lobes. Hindwing basally white with scattered dark brown scales and a prominent dark brown marking across base of second to sixth lobes. Hind leg pale yellow (although not so apparent in Fig. 9).



Figures 9, 10. *Alucita tatjana* Ustjuzhanin & Kovtunovich, sp. nov. **9** adult female, Holotype, NECJU **10** female genitalia, Holotype, preparation slide no. 201904. Scale bar: 5 mm.

Female genitalia. Papilla analis narrow, elongated. Posterior and anterior apophyses thick, straight. Anterior apophyses equal in length to posterior apophyses. Antrum wide, goblet-like. Ductus short, expanded in median part around junction with ductus seminalis, and corrugated at junction with bursa copulatrix. Bursa copulatrix small, oval, without signa.

Distribution. Cameroon.

Flight period. April, October.

Etymology. The species is a noun in apposition in honour to Petr Ustjuzhanin's sister, Tatjana Ustjuzhanina.

***Alucita zuza* Ustjuzhanin & Kovtunovich, sp. nov.**

<http://zoobank.org/3EFBC3D5-E44D-4F58-A1D4-3E5D049D58E3>

Figs 11, 12

Type material. *Holotype* • 1 male, (NECJU 201905) Cameroon, Drink Gari, 650 m a.s.l., Mount Cameroon (SW slope), 4.1014°N, 9.0610°E, 11–23.IV.2015, lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Tropek; *Paratypes* • 1 male, (CUK), same data as the holotype • 1 male (CUK), PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 29.I–07.II.2016, lgt. V. Maicher, Sz. Sáfián, R. Tropek • 1 male (CUK), Drink Gari, 650 m a.s.l., Mount Cameroon (SW slope), 4.1014°N, 9.061°E, 20.XI–10.XII.2014, lgt. V. Maicher, Sz. Sáfián, R. Tropek.

Diagnosis. In its male genitalia, the new species shares the elongated saccus and absence of valves with *A. fokami* (illustrated in Ustjuzhanin et al. 2018), but it differs in the narrow uncus which is not expanded apically, and in the absence of a long needle-like cornutus in the aedeagus.



Figures 11, 12. *Alucita zuza* Ustjuzhanin & Kovtunovich, sp. nov. **11** adult male, Holotype, NEJCU **12** male genitalia, Holotype, preparation slide no. 201905. Scale bar: 5 mm.

External characters. Wingspan 12 mm. Head white, with two brown spots between antennae. Thorax and tegulae white. Labial palpus straight, 1.5 times as long as longitudinal eye diameter, with alternating white and dark bands on each segment. Third segment short, not tapered apically. Antenna yellow, with small dark brown spots basally, just above scape. Wings mottled in their dark parts. Forewing darker than hindwing, with predominance of dark brown spots and strokes, while these spots and strokes are less expressed on the hindwing, with predominance of pale-yellow portions. Wings basally white, although locally darkened with dark brown scales. Fringe with alternating portions of light and brown hairs. Hind leg pale yellow.

Male genitalia. Uncus straight, finger-like, of even width. Gnathos and its arms wide, short. Valves absent. Anellus arms short, narrow, arched, apically sharp. Saccus very long, narrow, elongated, slightly expanded medially. Aedeagus straight, medially with two small, spinous cornuti (not apparent on Fig. 12).

Distribution. Cameroon.

Flight period. November till February, April.

Etymology. The species name is a noun in apposition. It was named in honour of the ichthyologist Zuzana Musilová, Robert Tropek's wife.

***Alucita deja* Ustjuzhanin & Kovtunovich, sp. nov.**

<http://zoobank.org/9C094272-0A16-4CEA-AB05-CD4E3C04D27B>

Figs 13–15

Type material. *Holotype* • male (NEJCU 201906), Cameroon, Bamboo Camp, 350 m a.s.l., Mount Cameroon (SW slope), 4.0879°N, 9.0505°E, 20.XII.2014, lgt. V. Maicher, Sz. Sáfián, Š. Jancček, R. Tropek. *Paratypes* • 1 female (CUK), PlanteCam,



Figures 13–15. *Alucita deja* Ustjuzhanin & Kovtunovich, sp. nov. **13** adult female, Paratype, NEJCU **14** male genitalia, Holotype, preparation slide no. 201906 **15** female genitalia, Paratype, preparation slide no. 201909. Scale bar: 5 mm.

1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 11–18.XII.2014, lgt. V. Maicher, Sz. Sáfián, Š. Jančėk, R. Tropek • 1 female (NEJCU 201909), Plant-cCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 11–23. IV.2015, lgt. V. Maicher, Sz. Sáfián, Š. Jančėk, R. Tropek.

Diagnosis. *Alucita deja* differs from other *Alucita* species by the distinctive white mirrors on its abdomen. The new species' male genitalia are similar to *A. janeceki* Ustjuzhanin & Kovtunovich, 2018 in the absence of valves and the shape of the saccus (illustrated in Ustjuzhanin et al. 2018), but *A. deja* differs in the smoothly rounded apex of its uncus, the apically sharp anellus arms, jagged acicular cornuti in the aedeagus, and the wing colouration.

External characters. Female wingspan 15 mm, male wingspan 13 mm. Head with pure-white appressed scales. Thorax and tegulae also pure white anteriorly, sharply contrasting with dark brown posterior portions. Labial palpus short, 1.5 times as long as longitudinal eye diameter. Third segment short, not tapered apically. Antenna brown. Scape pure white. Wings and fringes dark brown. First lobe of forewing with white band around 1/3, narrow white band around 3/5 and yellowish-brown band edged with white around 4/5. Several irregular fine white cross-lines across all other lobes and fringes of both wings. Hind leg yellowish-brown. Fourth, sixth and last tergites of abdomen with mirrors of pure-white scales. Abdomen completely pure-white ventrally.

Male genitalia. Uncus straight, long, of even width. Gnathos short, wide, apically expanded. Valves not developed. Anellus arms straight, apically sharp. Saccus shaped as elongated oval, with small notch at apex. Aedeagus robust, slightly shorter than entire genital structure, with jagged acicular cornuti from its medial part to apex.

Female genitalia. Papilla analis narrow, elongated. Posterior apophyses thin, straight, shorter than anterior apophyses. Antrum wide, sclerotized, shaped as truncated tube with extended ostium. Outer edge of ostium jagged. Ductus wide and corrugated at its confluence to antrum and bursa copulatrix. Ductus seminalis short, bag-like, membranous, departing from confluence of ductus to antrum. Bursa copulatrix of irregular oval shape with elongated protrusion at apex.

Distribution. Cameroon.



Figures 16–18. *Alucita bokwango* Ustjuzhanin & Kovtunovich, sp. nov. **16** adult male, Paratype, NECJU **17** male genitalia, Holotype, preparation slide no. 201907 **18** female genitalia, Paratype, preparation slide no. 201910. Scale bar: 5 mm.

Flight period. April, December.

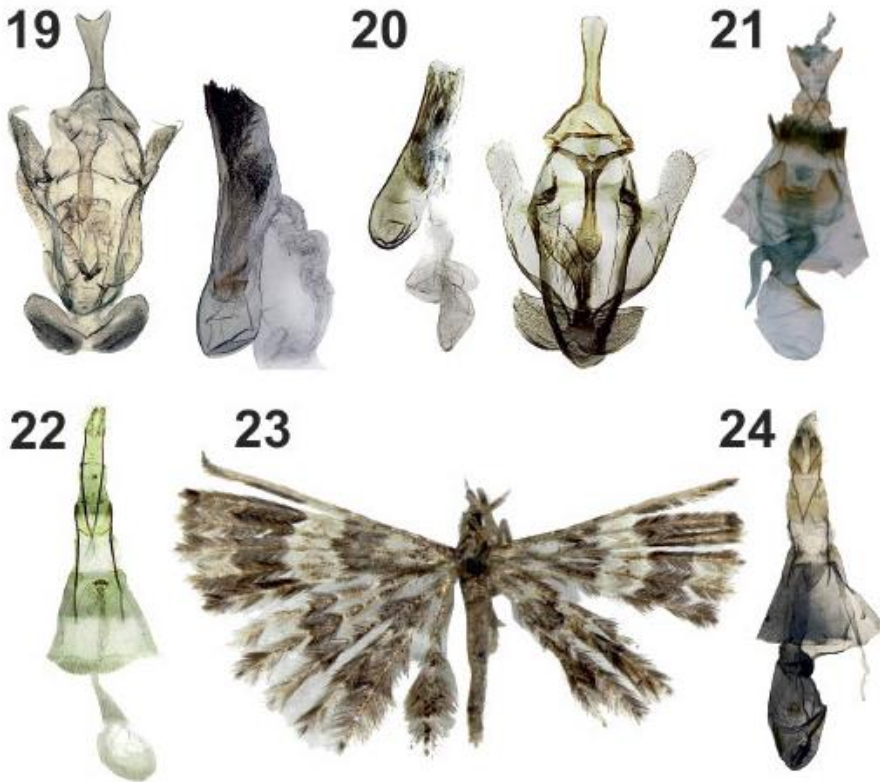
Etymology. The species name is a noun in apposition in honour of the limnologist and cyanobacteria specialist, Andreja Kust, a dear soulmate of Vincent Maicher.

***Alucita bokwango* Ustjuzhanin & Kovtunovich, sp. nov.**

<http://zoobank.org/C84BA8AD-3588-494F-86C8-55DEA44AC841>

Figs 16–18

Type material. *Holotype* • male (NECJU 201907), Cameroon, Elephant Camp, 1850 m a.s.l., Mount Cameroon (SW slope), 4.1170°N, 9.0729°E, 19–24.XI.2014, lgt. V. Maicher, Sz. Sáfián, Š. Jančėek, R. Tropek. *Paratypes* • 1 female, (NECJU 201910), + 16 ex., (NECJU, CUK), same data as holotype • 1 male, (CUK), PlanteCam, 1100 m a.s.l., Mount Cameroon (SW slope), 4.1175°N, 9.0709°E, 06–15.II.2016, lgt. V. Maicher, Sz. Sáfián, R. Tropek • 2 ex., (CUK, NECJU), PlanteCam, 1100 m a.s.l., 4.1175°N, 9.0709°E, 11–18.XII.2014, lgt. V. Maicher, Sz. Sáfián, Š. Jančėek, R. Tropek • 1 male (CUK), Crater Lake, 1500 m a.s.l., Mount Cameroon (SW slope), 4.1443°N, 9.0717°E, 11–21.II.2016, lgt. P. Potocký, Sz. Sáfián, J. Mertens, Š. Jančėek, R. Tropek • 1 male (CUK), Elephant Camp, 1850 m a.s.l., Mount Cameroon (SW slope), 4.1170°N, 9.0729°E, 17–22.II.2017, lgt. P. Potocký, Sz. Sáfián, J. Mertens, Š. Jančėek, R. Tropek • 1 male (NECJU), Mann's Spring, 2200 m a.s.l., Mount Cameroon (SW slope), 4.1428°N, 9.1225°E, 16–21.IV.2017, lgt. V. Maicher, P. Potocký, S. Delabye • 1 male (CUK), Crater Lake, 1500 m a.s.l., Mount Cameroon (SW slope), 4.1443°N, 9.0717°E, 23–29.IV.2017, lgt. V. Maicher, P. Potocký, S. Delabye • 8 ex., (NECJU, CUK), Elephant Camp, 1850 m a.s.l., Mount Cameroon (SW slope), 4.1170°N, 9.0729°E, 18–26.IV.2017, lgt. V. Maicher, P. Potocký, S. Delabye • 5 ex. (CUK, NECJU), Mapanja, 1850 m a.s.l., Mount Cameroon (S slope), 4.1157°N, 9.1315°E, 05–14.V.2017, lgt. V. Maicher, P. Potocký, S. Delabye • 6 ex. (CUK, NECJU), Mapanja, 1850 m a.s.l., Mount Cameroon (SW slope), 4.1157°N, 9.1315°E, 23–28.X.2017, lgt. V. Maicher, P. Potocký, S. Delabye.



Figures 19–24. Comparative illustrations of other *Alucita* species mentioned in the new species' diagnoses **19** *A. baliosantha* (Meyrick, 1921), type, male genitalia **20** *A. tessarata* (Meyrick, 1918), type, male genitalia **21** *A. rhapsica* (Meyrick, 1920), female genitalia **22** *A. compsoxantha* (Meyrick, 1924), type, female genitalia **23** *A. chloracta* (Meyrick, 1908), type, adult female **24** *A. chloracta*, type, female genitalia.

Diagnosis. The new species resembles *Alucita chloracta* (Meyrick, 1908) in its external characters and the structure of the male genitalia. Genitalia of *A. bokwango* differs from *A. chloracta* in the needle-like apex of the uncus and the oval apical expansions of the valvae, whilst the uncus of *A. chloracta* is noticeably widened apically with a notch and valvae have a rounded apex. In its female genitalia, *A. bokwango* differs from *A. chloracta* (Fig. 24) in the short narrow ductus, wide funnel-shaped antrum and absence of a plaque-like signum in the bursa copulatrix. The wing colouration of *A. bokwango* is more contrasted than in *A. chloracta* (Fig. 23), and the new species is also substantially larger (23–25 mm vs. 15–16 mm wingspan).

External characters. Wingspan 23–25 mm. Head, thorax, tegulae and abdomen all dark brown. Labial palpus yellowish-brown, three times as long as longitudinal eye diameter, directed forward. Third segment thin, apically tapered. Antenna pale brown, with small dark brown spots basally, just above scape. Wings brown, outer edge slightly

lighter. Medial band on all wings whitish, almost transparent, interspersed with brown portions of hairs on lobes fringe. Hind leg yellow.

Male genitalia. Uncus thin, long, needle-shaped. Gnathos equal to uncus in length, apically sharp. Valves long, membranous, smoothly forming an oval apically. Anellus arms straight, narrow, equal to gnathos in their length. Saccus oval. Aedeagus robust, thick, almost equal in length to genital structure without uncus, two spinous cornuti distally.

Female genitalia. Papilla analis oval, wide throughout length. Posterior apophyses slightly shorter than anterior, thick and slightly undulated. Antrum wide, funnel-like. Ductus short, thin, membranous. Bursa copulatrix large, oval, with two large, lanceolate signa (although not clearly apparent in Fig. 18).

Distribution. Cameroon.

Flight period. October–May

Etymology. The species is named after Bokwango, a village on the eastern slope of Mount Cameroon where our project established its main base and where we made a lot of good friends. Many of the species records were also made in forests belonging to the village. Last but not least, most of our field assistants and other helpers came from Bokwango and we are thankful to all of them for the success of the project. We strongly believe this dedication will also help protect the unique biodiversity of the region.

Note. 18 specimens from Elephant Camp, 19–24.XI.2014, and two specimens from PlanteCam, 11–18.XII.2014, (all lgt. V. Maicher, Sz. Sáfián, Š. Janeček, R. Trepk), were erroneously indicated as *A. chloracta* by Ustjuzhanin et al. (2018). The other *A. chloracta* specimens referred by Ustjuzhanin et al. (2018) from Bamboo Camp, Drink Gari and PlanteCam were identified correctly.

Discussion

With the seven newly described *Alucita* species, the known diversity of many-plumed moths on Mount Cameroon has been increased to 22 species (Table 1). Altogether, 19 of these species were collected in the single locality, PlanteCam (Table 1), but the general diversity patterns will be analysed only once the complete *Alucita* material from our collections is processed. This comprises more than a quarter of the known Afrotropical diversity of many-plumed moths. At most, only a few species of the group are known from other localities in the region (Ustjuzhanin et al. 2018; De Prins and De Prins 2019). Although microlepidopteran diversity in the Guineo-Congolian forest zone remains largely unknown, discoveries of multiple undescribed species of many-plumed moths from a single locality is unexpected (Ustjuzhanin et al. 2018).

Mount Cameroon is known to harbour high diversity in many groups, including Lepidoptera (e.g., Ballesteros-Mejia et al. 2013; Maicher et al. 2016; Przybyłowicz et al. 2019; Delabye et al. 2020). This is usually explained as a result of the combination of its position at the border between the Guinean and Congolian biogeographic regions, its diversity of habitats along the elevational and precipitation gradients,

Table 1. Summary of all specimens of *Alucita* moths sampled on Mount Cameroon in this study and by Ustjuzhanin et al. (2018).

| Sampling locality | Altitude | | | | | | | | | | | | | | | | | | | | | | |
|--------------------|----------|--------------------|----------------------|-------------------|-------------------|--------------------|---------------------|--------------------|----------------|--------------------|------------------|----------------|--------------------|------------------|-----------------------|--------------------|----------------------|----------------------|----------------|---------------------|-------------------|-----------------|-----------------|
| | | <i>A. acalypta</i> | <i>A. bakingslii</i> | <i>A. bakweri</i> | <i>A. besongi</i> | <i>A. bokwango</i> | <i>A. chloracta</i> | <i>A. coffeina</i> | <i>A. deya</i> | <i>A. exobarii</i> | <i>A. fobami</i> | <i>A. jana</i> | <i>A. jancecki</i> | <i>A. lidiya</i> | <i>A. longipennis</i> | <i>A. ludmilla</i> | <i>A. megapbimus</i> | <i>A. mischenini</i> | <i>A. olga</i> | <i>A. spicifera</i> | <i>A. tatjana</i> | <i>A. zinoi</i> | <i>A. zizca</i> |
| Bimbia-Bonadikombo | 30 m | | | | | | | | | | | | | | | | 1 | | | | | | |
| Bamboo Camp | 350 m | 1 | 3 | 3 | | 7 | 1 | 2 | 2 | | 2 | 1 | | 2 | 6 | | 4 | | | | | | |
| Drink Gari | 650 m | | | | | 1 | | | 1 | | 1 | 1 | | 1 | 3 | | | | | | | | 3 |
| PlanteCam | 1100 m | | 1 | 1 | 3 | 3 | 1 | 2 | 2 | 1 | 1 | | 2 | 1 | 1 | 5 | 2 | 1 | 1 | 1 | 1 | 1 | 1 |
| Ekonjo | 1150 m | | | | | | | | | | | 1 | | | | | | | | | 1 | | |
| Crater Lake | 1450 m | | | | | 2 | | | | | | | | | | | | | | | | | |
| Elephant Camp | 1850 m | | | | | 27 | | | | | | | | | 7 | | | | | 7 | | | |
| Mapanja | 1850 m | | | | | 11 | | | | | | 1 | | | | | | | | | | | |
| Mann's Spring | 2200 m | | | | | 1 | | | | | | | | | | | | | | | | | |

and its isolated “sky island” character (Ustjuzhanin et al. 2018). Nevertheless, even such unique combination of conditions can hardly explain why Mount Cameroon so strongly outnumbers all other Afrotropical localities in the species richness of its many-plumed moths. Of the known 22 *Alucita* species, 16 have been described from the site and have not yet been found anywhere else. Although it is highly expected that some of these will be distributed more widely, several of the newly described species are distinctive and unmistakable in their appearance. These are unlikely to have been overlooked in collections. Therefore, we expect that most of this many-plumed moth diversity is endemic to the study area. Several other potentially endemic species of moths (e.g., Yakovlev and Sáfián 2016; De Prins and De Prins 2019; Przybyłowicz et al. 2019;) and butterflies (e.g., Larsen 2005; Sáfián and Tropek, 2016; Sáfián et al. 2019) are already known from Mount Cameroon. Nevertheless, the real character of the endemism within Alucitidae on Mount Cameroon, as well as the mechanisms underlying the group’s speciation (or even local radiation), will need more detailed research.

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Summary

The aim of the thesis was to explore how the selected ecological and biogeographical factors might influence and structure Lepidoptera community structure in the generally understudied Afrotropical systems (rainforests and savannahs).

The first two chapters focused on the effects of small-scale spatial mechanisms on butterfly and moth communities. To our knowledge, they came as the first comprehensive studies of habitat use by fruit-feeding moths in any tropical area. In **Chapter I**, we focused on habitat associations of fruit-feeding butterflies and moths in Afrotropical rainforests in the foothills of Mount Cameroon. Mainly, we tested our hypothesis that whilst moths are affected mostly by the plant community composition, forest openness and structure is more crucial for the communities of butterflies. This brought the direct and well-standardized comparison of the two closely related groups of herbivorous insects with partly different habitat use. We showed that the butterfly communities depended mostly on forest openness. Moth species richness depended more on plant diversity and forest openness, whereas their community composition was mainly influenced by forest openness. Moreover, canopy and understory communities differed in their patterns, the latter not being influenced by any habitat characteristics, while canopy communities tended to follow the general patterns. The revealed strong differences in factors responsible for forming of the two closely related insect groups can potentially influence community ecology in tropical ecosystems, as it warns against too strong generalizations based on single taxon studies. The study also highlighted the need to study and sample both canopy and understory strata.

In **Chapter II**, we investigated the effects of natural disturbances made by forest elephants on Lepidoptera and tree communities on Mount Cameroon. As seen in Chapter I, moths and butterflies differ in their habitat requirements and use. An opening of the forest canopy was expected to change the composition of the communities. We surveyed insect and tree communities at mid-elevation (two altitudes) during two different seasons in forests impacted by forest elephants and in untouched forests. The forest structure was modified by elephants, leading to less dense forest with generally higher trees and an open canopy. Despite being generalized herbivores, elephants are selective browsers of palatable species, leading to a decrease in tree species richness and changes in tree community composition. This had indirect effects on Lepidoptera communities. Butterflies are more dependent on solar radiation, explaining the higher diversity of butterflies in the disturbed areas. On the other hand, moths are more dependent on plant diversity, and the decrease of plant diversity by elephants impacted negatively their communities. This work provided evidence that forest elephants are the key ecological engineer species, similarly to savannah elephants, as they strongly impact both vegetation and Lepidoptera communities. In Central Africa, elephant forest populations are decreasing at an important rate, and the impacts of such a small dense population of elephants on Mount Cameroon raise conservation concerns and issues.

In **Chapter III**, we focused on shifts of species richness patterns, seasonal turnover, and seasonal shifts of species' elevational ranges along the elevation gradient on Mount Cameroon. Butterflies and moths were sampled at seven elevations during three different seasons. While we revealed a mid-elevation peak of species richness for almost all groups of Lepidoptera, confirming the most common biodiversity pattern along the elevational gradient, this chapter is novel in demonstrating seasonal up- and downhill shifts for six out of the nine studied Lepidopteran groups, shifts so far not reported from any tropical mountains. This study is an

important contribution to research on tropical biodiversity and elevational ranges, in the context of assessing the impacts of the global climatic change. We brought strong evidence that the seasonal dynamics of local communities need to be included in studies on tropical biodiversity, along elevational gradients. Moreover, regarding the habitat use and associations of Lepidoptera communities studied in the **Chapters I and II**, it would be interesting to describe the niche conservatism and niche breadth of the Lepidoptera communities along the elevational gradient of Mount Cameroon. The high-elevation species could use the more diverse environment, i.e. be more generalised, because their niches are more constrained by abiotic factors than interspecific competition. Such hypothesis should be tested in the future.

In **Chapter IV**, since the effects of environmental productivity on insect diversity patterns is understudied, we checked relationships between species richness and abundance of moths with environmental productivity at both local and regional scales in southern African savannah ecosystems. Moths were sampled at 12 sites, at the beginning of the rainy season, and along an environmental productivity gradient not depending on latitudes and elevations. While we expected a positive linear relationship of species richness at both scales, we revealed a pattern with an exponential growth of moth species richness at both scales along the gradient, indicating, through temperature and water availability, the indirect effects of environmental productivity on moth communities in African savannahs. However, although we also predicted a positive relationship between the number of individuals and environmental productivity, we shown no significant relationships, suggesting that abundance does not limit the species richness of moth communities, and implying that insect abundance is not a strong estimate of insect diversity patterns. Comparative studies on other trophic levels on such continent-wide gradients of environmental productivity would be interesting to test, especially on insect predators, in

order to reveal whether environmental productivity structure similar patterns of diversity, as expected by the productivity hypothesis.

Chapters V till VIII emphasise that the exceptional diversity and distribution of Afrotropical Lepidoptera is still largely unexplored. Using DNA barcoding enabled to describe the taxonomic diversity and composition of Lepidoptera assemblages, and to confirm its low knowledge in the Central Africa (**Chapter V**). The high amount of new country records found in our samples shows our general lack of knowledge on Afrotropical Lepidoptera (**Chapters VI and VII**). Moreover, the area appeared to be the newly discovered hotspot for many-plumed moths (**Chapter VIII**).

Conclusion

The several studies included in this thesis reported several ecological and taxonomical aspects of Lepidoptera communities in the Afrotropics. Some ecological gradients, such as elevation and productivity, and their effects on biodiversity patterns have been studied here. Studying these ecological gradients offered the opportunity to reveal how small and large spatial and temporal scale mechanisms structure insect communities and their diversity patterns. It is remarkable to notice that their spatial and temporal mechanisms remain far from being totally understood and deserve more attention. Moreover, since temperature is thought to be one of the most important factors affecting insect abundance, distribution, and survival, understanding those mechanisms seem to be even more important in order to predict insect community changes in the context of the global climate. Furthermore, identifying areas with the high species richness, vulnerable groups of species, or endemic species, is needed for land management and conservation. The few examples of the Afrotropical studies in this thesis showed how unique they are in terms of biodiversity, climate, and habitats.

CURRICULUM VITAE

Sylvain Delabye

Ph.D. candidate, Department of Ecology, Faculty of Science, University of South Bohemia in České Budějovice, Czechia

<http://www.insect-communities.cz/team/sylvain-delabye/>

e-mail: sylvain.delabye@gmail.com

Phone: +420 723 328 695

ORCID ID: 0000-0003-0911-9721

Born: Barentin, France, November 15, 1990

Languages: French (native), English

EDUCATION

April 2016 – present: Ph.D. candidate at the University of South Bohemia, Ceske Budejovice, Czechia. Thesis: *Ecological and biogeographical drivers of Afrotropical Lepidoptera biodiversity*

September 2012 – June 2014: M.Sc. in Environment, Soils, Water and Biodiversity, Biodiversity Option, University of Rouen, France – With High Honours.

- First year thesis: **Bryophyte, fungi and lichen biodiversity in response to forest management ending and other forest management variables** – supervised by Frédéric Gosselin (National Research Institute of Science and Technology for Environment and Agriculture - Nogent-sur-Vernisson, BIODIVERSITY Team)
- Second year thesis: **Barcoding of moth communities in two contrasted Afrotropical environments in Lopé and Ivindo National Parks, Gabon** – supervised by Thibaud Decaëns (Ecology Laboratory, Biodiversity Study and Understanding – University of Rouen)

September 2010 – 2012: B.Sc. in Life, Earth and Environment Sciences - Ecology and Biology Organisms, University of Rouen, France – With Honours. Thesis: **Entomology education and realization of a mainland France Coleoptera reference collection** – supervised by Nicolas Moulin (“Nicolas Moulin Entomologiste” Business)

September 2008 – June 2010: Classe Préparatoire aux Grandes Ecoles: two-year undergraduate intensive program in Biology, Chemistry, Physics and Earth Sciences (BCPST), Pierre Corneille Secondary School, Rouen, France

EMPLOYMENTS

2016 – present: Ph.D. student, Institute of Entomology, **Biology Centre, Czech Academy of Sciences**, České Budějovice, Czechia.

2018 – present: Technician, Department of Ecology, **Faculty of Science, Charles University**, Prague, Czechia.

CURRENT RESEARCH INTERESTS

Biodiversity, ecology, biogeography, taxonomy and natural history of Afrotropical moths and butterflies

Biodiversity patterns along environmental gradients

MAIN FIELD RESEARCH

2014: **Gabon**. Research on barcoding of moth communities in Lopé National Park. ECOTROP field class. 2 weeks.

Since 2016: **Cameroon**. Research on diversity of Lepidoptera along an elevational gradient of Mount Cameroon; research on the influence of forest remnants characteristics on moth communities in a fragmented landscape of the Bamenda Highlands. 3 expeditions, 5 months together. Co-leader of two expeditions.

Since 2016: **Czechia**. Collecting data on pollinator ecology in fragmented wet meadow landscapes (Železné hory) and along an elevational gradient (Krkonoše), on diversity of moths in previously burnt forests (České Švýcarsko), and on biodiversity of several groups of arthropods along a gradient of disturbance intensity (Brdy Mts.). Several short field trips, 2 months together.

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

2018: **Madagascar**. Survey of Lepidoptera in the Ranomafana National Park. 1 week.

Since 2018: **Republic of South Africa**, Kruger NP – research on dynamics of biodiversity in African savannah (field technician for entomological parts), 4 expeditions, 3 months together. Leader of one expedition.

STUDY STAYS

Since 2016: **Poland**. Zoological Museum of the Jagiellonian University. Sorting and identification of moths; close collaboration with the team of Dr. Tomasz Pyrcz. 6 visits, 3 months together.

RESEARCH GRANTS

2020: Travel Grant Programme of the Biology Centre, Czech Academy of Science: attendance at the 18th Savanna Science Network Meeting, 2020, Skukuza, South Africa.

PUBLICATIONS

As of January 2021: 20 citations in Google Scholar

Delabye, S., Maicher, V., Sáfián, Sz., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Murkwe, M., Šebek, P., & Tropek, R. (2020) Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon. *Biotropica*, in press.

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Delabye S., Rougerie, R., Bayendi, S., Andeime-Eyene, M., Zakharov, E.V., deWaard, J.R., Hebert, P.D.N., Kamgang, R., Le Gall, P., Lopez-Vaamonde, C., Mavoungou, J.-F., Moussavou, G., Moulin, N., Oslisly, R., Rahola, N., Sebag, D., & Decaëns, T. (2019) Characterization and comparison of poorly known moth communities through DNA barcoding in two Afrotropical environments in Gabon. *Genome*, **62**: 96-107.

TEACHING AND SUPERVISING OF STUDENTS

Co-supervision of one B.Sc. thesis:

- **Jaroslav Kajínek**: Importance of seasonal rivers for biodiversity of moths in African savannahs (2019 – ongoing, University of South Bohemia, České Budějovice)

Co-supervision of international research interns:

- **Julie Desmist**: Diversity of Afrotropical and Central European moths. Volunteering internship, Université Paris-Saclay, France (2 months stay, summer 2018; together with Vincent Maicher)
- **Léna Jégo**: Diversity of macromoths: from sampling to identification. Erasmus Practical Traineeship, ENSAIA, Nancy, France (2 months stay, summer 2019)

COMMUNICATIONS

Delabye, S., Maicher, V., Sedláček, O., Potocký, P., Albrecht, T., Ferenc, M., Hořák, D., Storch, D., Tropek, R. Diversity patterns of moth communities along a productivity gradient in Southern African savannas. *Talk*. **18th Savanna Science Network Meeting, 2020, Skukuza, South Africa.**

Delabye, S., Maicher, V., Sedláček, O., Potocký, P., Albrecht, T., Ferenc, M., Storch, D., Tropek, R. Diversity patterns of moth communities along a productivity gradient in Southern Africa – Preliminary results. *Poster*. **Czech Society for Ecology Conference 2019, Olomouc, Czech Republic.**

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- Delabye, S., Maicher, V., Sáfián, S., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Šebek, P., Tropek, R. Influence of forest structure and vegetation composition on communities of Afrotropical fruit-feeding butterflies and moths – Preliminary results. *Talk. Afrotropical Lepidoptera Network meeting 2017, Krakow, Poland.*
- Delabye, S., Maicher, V., Sáfián, S., Doležal, J., Altman, J., Janeček, Š., Kobe, I.N., Šebek, P., Tropek, R. Influence of forest structure and vegetation composition on communities of Afrotropical fruit-feeding butterflies and moths. *Poster. Czech Society for Ecology Conference 2017, Prague, Czech Republic.*
- Delabye, S., Decaëns, T., Bayendi, S., Ntie, S., Le Gall, P., Lopez Vaamonde, C., Moulin, N., Sebag, D., Rougerie, R., The ECOTROP TEAM. Using DNA barcoding as a tool to describe moth community patterns in Lopé and Ivindo National Parks, Gabon. *Talk. Forum Herbulot 2014, Annaberg-Buchholz, Germany.*

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sylvain.delabye@gmail.com

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University of South Bohemia in České Budějovice

Faculty of Science

Branišovská 1760

CZ-37005 České Budějovice, Czech Republic

Phone: +420 387 776 201

www.prf.jcu.cz, e-mail: sekret-fpr@prf.jcu.cz