SPATIAL AND TEMPORAL DISTRIBUTION OF BUTTERFLIES ACROSS AN ELEVATION GRADIENT IN NYUNGWE NATIONAL PARK; RWANDA

by

Jean de Dieu UWIZELIMANA

(From Rwanda)

Accepted dissertation for the partial fulfillment of the requirements for a

Doctor of Natural Sciences

Fachbereich 3: Mathematik/ Naturwisssenschaften

Universität Koblenz-Landau

Reviewer:

Prof. Dr. Thomas Wagner

Prof. Dr. Donat Nsabimana

Examiner:

Prof. Dr. Bernhard Köppen

Prof. Dr. Thomas Wagner

Prof. Dr. Donat Nsabimana

Date of the oral examination: 24 November 2022

Table of Contents

Summary

Tropical rainforests are the most important terrestrial ecosystems for biodiversity conservation. Biodiversity studies have been conducted within these forest ecosystems but there is still a knowledge gap in some taxa such as insects in some not yet or underexplored regions such as the Afrotropical high mountain regions. For example, although butterflies are well documented among insects, there is still a lack of information about their diversity and distribution in underexplored Afrotropical montane biodiversity hotspot forests of the Albertine Rift (AR) region. Nyungwe National Park (NNP) in Rwanda is part of those biodiversity hotspot forests within the AR and little is known about its insect communities including butterflies, good indicators of climate change, and forest ecosystem health. That park is of high conservation importance in central Africa due to its hosted high biodiversity including AR endemics. This thesis documented the diversity and distribution of butterflies in NNP and the main goal was to avail baseline data on butterfly species distribution in Nyungwe National Park and Cyamudongo adjacent forest fragment in Rwanda, for future use in monitoring climate change-driven shifts and the effects of forest fragmentation on biodiversity of Nyungwe. Butterflies were collected seasonally using fruit-baited traps for those feeding on fruits as adults and a hand net for nectar and pollen feeders along elevational transects spanning from 1700 m up to 2950 m of altitude. Two hundred forty-two species including 28 endemics to the AR were documented from 4289 collected specimens. Species richness and abundance declined with increasing elevation and higher seasonal occurrence was observed during the dry season. Among the recorded species, eighteen were selected to serve as potential local climate change indicators in NNP. As this was the preliminary study on the spatial and temporal distribution of butterflies in Nyungwe, further studies could be

conducted to add more species and allow a depth understanding of the ecology of Nyungwe butterflies.

Zusammenfassung

Tropische Regenwälder sind wichtige terrestrische Ökosysteme für den Erhalt der Biodiversität. Trotz einiger Studien innerhalb dieser Waldökosysteme, gibt immer noch eine Wissenslücke bei einigen Taxa, vor allem bei Insekten. Obwohl Schmetterlinge unter Insekten gut dokumentiert sind, gibt es selbst hier einen Mangel an Informationen über ihre Diversität und Verbreitung in wenig erforschten afrotropischen montanen Biodiversitäts-Hotspot-Wäldern der Region Albertine Rift (AR). Der Nyungwe-Nationalpark (NNP) in Ruanda ist Teil dieser Biodiversitäts-Hotspot-Wälder innerhalb des AR. Dieser Park ist in Zentralafrika aufgrund seiner hohen Biodiversität, einschließlich endemischer AR, von großer Bedeutung für den Naturschutz.

Diese Dissertation dokumentierte die Vielfalt und Verbreitung von Schmetterlingen in NNP und das Hauptziel war es, Basisdaten zu deren Verbreitung im Nyungwe-Nationalpark und im angrenzenden Waldfragment Cyamudongo zu erfassen. Diese können zukünftig bei der Studien zum Klimawandel und zum Einfluss der Waldfragmentierung auf die Biodiversität von Nyungwe genutzt werden. Schmetterlinge wurden saisonal mit Fruchtköderfallen, sofern sich die Imagines von Früchten ernährten, und einem Handnetz für Nektar- und Pollenfresser entlang von Höhentransekten gesammelt, die sich von 1700 bis 2950 Metern erstreckten. Zweihundertzweiundvierzig Arten, darunter 28 Endemiten der AR, wurden anhand von 4289 gesammelten Exemplaren dokumentiert. Der Artenreichtum nahm mit zunehmender Höhe ab. Während der Trockenzeit wurde ein höheres saisonales Vorkommen beobachtet. Unter den erfassten Arten wurden achtzehn ausgewählt, um als potenzielle lokale Indikatoren für den Klimawandel in NNP zu dienen. Da dies die erste umfassende Studie zur räumlichen und zeitlichen Verteilung von Schmetterlingen in Nyungwe war, werden Folgeuntersuchungen sicherlich weitere Arten zu Tage fördern.

Chapter 1 **General Introduction**

Tropical rainforests are important terrestrial ecosystems for biodiversity conservation all over the world because they host a high number of plant and animal species than any other terrestrial region (Ghazoul, 2010). However, there is still a knowledge gap in some taxa such as insects in some underexplored regions such as the Afrotropical mountain ecosystems (Primack & Corlett, 2006). For example, although butterflies are well documented among insects, there is still a lack of information about their diversity and distribution in some underexplored Afrotropical montane forests of the Albertine Rift (AR) region, a biodiversity hotspot (Liseki & Vane-Wright, 2018; Plumptre et al., 2007). These mountains are of the great importance for biodiversity conservation as they host a large number of species including endemics and threatened species throughout their different elevation vegetation strata (Körner, 2004; Rahbek et al., 2019; Spehn et al., 2011) and thus, serve as suitable ecosystems to monitor climate change effects through species elevation range shifts (Forister et al., 2010; Halsch et al., 2021; Laurance et al., 2011).

Nyungwe tropical montane rainforest in Rwanda is among the underexplored biodiversity hotspot within the AR. This forest is of great importance for the conservation of biodiversity in Africa as it is the largest montane forest and hosting a high number of species and endemism in central Africa (Plumptre et al., 2002, 2007). Some biodiversity research has been conducted in the park but it appears from the literature that emphasis was made on plant diversity (Dhetchuvi & Fischer, 2006; Fischer & Ackermann, 2019; Fischer & Killmann, 2008; Senyanzobe et al., 2020) and ecophysiology (Manishimwe et al., 2022; Mujawamariya et al., 2018), Lichens (Bock et al., 2007; Fischer et al., 2017; Killmann & Fischer, 2007; Sérusiaux et al., 2006), vertebrates mostly primates (Fashing et al., 2007; Fimbel et al., 2001;

Gross-Camp & Kaplin, 2011; Kaplin, 2001; Matthews et al., 2019; Moore et al., 2018) and birds (Neate-Clegg et al., 2020; Rurangwa et al., 2020) while little is known on invertebrates (Boxnick et al., 2015; Ngirinshuti et al., 2019; Tedrow et al., 2014) including butterflies among insects (Plumptre et al., 2007; Vingerhoedt & Vande Weghe, 2011).

In addition to their aesthetic value, consumption as caterpillars, their potential as good inspiration models in arts, and cultural significance in some African societies (Van Huis, 2019), butterflies have been found to serve as good models for environmental change studies and the monitoring of forest ecosystem health due to their quick reaction to any changing environment and thus alerting conservationists to take immediate actions (Kremen, 1992; Maleque et al., 2009; Nyafwono et al., 2014; Oloya et al., 2021). Moreover, some tropical butterfly species feed exclusively on rotting fruits (Molleman et al., 2005), while others visit flowers for pollen and nectar feeding (Beck & Fiedler, 2009; Mertens et al., 2021) which makes them excellent pollinators of forest flowering plants (Balducci et al., 2019; Barrios et al., 2016; Sáfián, 2021).

Although research has been conducted on Afrotropical butterflies' ecology (Cordeiro, 2017; Larsen, 2008; Sáfián, & Larsen, 2009; Molleman et al., 2006; Nyafwono et al., 2014; Oloya et al., 2021; Roche et al., 2015; Valtonen et al., 2013) limited research has been conducted on Afrotropical mountain ecosystems (Maicher et al., 2019) and currently, there is none documentation on the ecology of butterflies of Nyungwe National Park. Butterfly studies across mountain ecosystems have documented either a species decline (Leingärtner et al., 2014; Molina-Martinez et al., 2013; Pires et al., 2020; Sanchez-Rodriguez & Baz, 1995) or an increase in species richness (Cómbita et al., 2022) and diversity (Pyrcz et al., 2009) with elevation while in others a pic of species richness is observed at mid-elevation altitude

(Despland et al., 2012; Mertens et al., 2021). In addition to the influence of altitude, butterflies' distribution has been found to correlate with environmental factors such as temperature and humidity at different vegetation types throughout the elevation gradient (Bhardwaj et al., 2012; Maleque et al., 2009). Moreover, seasonal variation was found to have an impact on species occurrence within tropical butterflies with more occurrence during the dry season (Austin et al., 1996; Maicher et al., 2018; Mertens et al., 2021).

Global warming due to climate change is reported among the major threats to biodiversity (Laurance et al., 2011; Nunez et al., 2019; Xu et al., 2009) including Lepidoptera (Crossley et al., 2021; Halsch et al., 2021) and studies have documented a species elevation range shift within mountainous ecosystems (Chen et al., 2011; Forister et al., 2010; Sheldon et al., 2011; Wilson et al., 2007). Furthermore, models predicted more vulnerability to bottom specialist and top dwelling mountain species as there is no possibility for these top montane species to shift their home range and this would lead to the extirpation and/ or extinction risk of some species before even they are known to science (Mccain & Colwell, 2011; Ponce-Reyes et al., 2017; Rödder et al., 2021).

In addition to the effects of climate change, in some regions with high human population density, species also are negatively affected by habitat fragmentation due to various anthropogenic activities (Hansen et al., 2020; Hill et al., 2011; Lewis et al., 2015; Wilson et al., 2009). Like other forests within the Albertine rift region (Ayebare et al., 2018), Nyungwe National Park has undergone fragmentation around a hundred years ago due to human activities including gold mining, agriculture, and human settlements, and comprises currently Nyungwe's main forest block and Cyamudongo forest fragment located at around 10 km from Nyungwe main forest block but protected as part of Nyungwe National Park since 2004

(Fischer & Killmann, 2008). Since the break up, there was no documentation on the effects of isolation on the biodiversity of the park and it is not known whether there is a biodiversity loss or not due to forest fragmentation. Similar to Nyungwe main forest, a few research conducted in Cyamudongo emphasized on plants (Fischer & Killmann, 2008; Nsanzurwimo, 2021) and a small endangered chimpanzee (*Pan troglodytes schweinfurthii*) population (Moore et al., 2018) while a little is known about insects including butterflies. Hence, a study on butterfly diversity and distribution was undertaken in Nyungwe National Park (NNP) for the first time to increase the knowledge of its biodiversity and avail baseline data for future use in monitoring climate change-driven shifts and the effects of fragmentation on the biodiversity of Nyungwe. The specific objectives were respectively to i) Identify butterfly species inhabiting NNP, including climate data and distribution across an elevation gradient, ii) Identify butterflies with a narrow range of distribution which could serve as future climate change indicators, iii) Assess the effect of seasonal variation on the elevation distribution of butterfly species in NNP, and iv) Assess the effect of forest fragmentation on butterflies of NNP.

Sampling was conducted in Nyungwe main forest block and Cyamudongo forest fragment from late September 2019 until early September 2020 during three seasons: rain season (Sept –December 2019), short dry season (Jan-March 2020), and dry season (June-ealy Sept 2020) occurring respectively in both habitats. Butterflies were sampled using fruit-baited traps for fruit feeding species (Hughes et al., 1998) and a hand net for nectar and pollen feeders along elevation transects spanning from 1700 m up to 2950 m of altitude covering the three (Low, Middle, High) elevation forest zones of Nyungwe National Park. For each collected specimen, vegetation type, altitude, microclimate temperature, and humidity under which the butterfly species was active were recorded. Baited traps were set at every 25 m of elevation and hunged either side of the trail and a hand net was used to collect every butterfly encountered within 5 m width while walking along the trail (Basset et al., 2011; Pollard, 1977). The total length of the sampled trails was around 45 km walking distance. Collected individuals were identified using morphological traits and genitalia dissection. A preliminary butterfly species checklist was established and species distribution patterns were analyzed from all collected data and findings are presented in a format of papers in section 2 below.

Chapter 2 **Papers**

This thesis is organized in chapters of the published papers. So far, three papers were published and one manuscript is under revision.

I. Uwizelimana, J. d. D., Nsabimana, D. & Wagner, T. (2021). A preliminary butterfly checklist (Lepidoptera: Papilionoidea) for Cyamudongo tropical forest fragment, Rwanda. Metamorphosis 32: 93–103. DOI: https://dx.doi.org/10.4314/met.v32i1.15

II. Uwizelimana, J. d. D., Nsabimana, D. & Wagner, T. (2022). Diversity and distribution of Fruit- feeding butterflies (Lepidoptera: Nymphalidae) in Nyungwe National Park, Rwanda. African Journal of Ecology 00: 1– 12. https://doi.org/10.1111/aje.12997

III. Uwizelimana, J. d. D. (2022). The butterflies of Nyungwe National Park, Rwanda (Lepidoptera: Rhopalocera, Papilionoidea). Entomologische Zeitschrift 132 (2):67–79.

IV. Uwizelimana, J. d. D., Nsabimana, D. & Wagner, T. (Submitted to Biotropica). Altitudinal distribution of butterflies (Lepidoptera: Papilionoidea) in Nyungwe National Park, Rwanda.

2.1 A butterfly species checklist for Cyamudongo tropical forest fragment

METAMORPHOSIS

LEPIDOPTERISTS' SOCIETY OF AFRICA

Volume 32: 93–103

ISSN 1018 6490 (PRINT)
ISSN 2307–5031 (ONLINE)

A preliminary butterfly checklist (Lepidoptera: Papilionoidea) for Cyamudongo tropical forest fragment, Rwanda

Published online: 22 December 2021

*Jean de Dieu Uwizelimana[1,2], Donat Nsabimana[3], Thomas Wagner[1]

[1]Universität Koblenz-Landau, Institut für Integrierte Naturwissenschaften, Biologie, Universitätsstr. 1, 56070 Koblenz, Germany.

[2]University of Rwanda, College of Science and Technology, Biology Department, KN 67 Street Nyarugenge, PO Box 3900 Kigali, Rwanda.

[3]University of Rwanda, College of Agriculture, Animal Sciences and Veterinary Medicine, School of Forestry, Biodiversity and Conservation, PO Box 117 Butare, Rwanda.

Email (corresponding author*): juwizelimana@gmail.com

Abstract: This study provides a preliminary checklist of butterfly species occurring in the Cyamudongo tropical forest fragment, Rwanda. A survey of butterflies was conducted seasonally from October 2019 to August 2020. Butterflies were collected for identification using butterfly nets and fruit-baited traps along trails within Cyamudongo forest. One hundred and sixty-two butterfly species were recorded in the Cyamudongo forest, including thirteen species that are endemic to the Albertine Rift. This preliminary checklist serves as baseline data for conservationists including park managers and researchers concerned with butterfly conservation.

Key words: Forest fragmentation, butterfly, species checklist, Albertine Rift, Cyamudongo forest

Citation: Uwizelimana, J., Nsabimana, D., Wagner, T. A preliminary butterfly checklist (Lepidoptera: Papilionoidea) for Cyamudongo tropical forest fragment, Rwanda. *Metamorphosis* **32**: 93–103.
DOI: https://dx.doi.org/10.4314/met.v32i1.15

INTRODUCTION

Human activities, including agriculture, are the main drivers of natural habitat fragmentation including tropical rain forests (Lewis *et al.*, 2015), which are terrestrial biodiversity hotspots throughout the world (Ghazoul, 2010). With increasing human population demands, models predict an increase of tropical forest fragmentation with time (Taubert *et al.*, 2018) which negatively impacts resident biodiversity including the butterfly population. For example, large body size butterflies were found to be more vulnerable to extinction due to forest fragmentation (Shahabuddin & Ponte 2005), and predictive models have shown limitations in expansion range for some butterfly species within fragmented forests (Wilson *et al.*, 2009).

Some of the remaining Afrotropical forest fragments are under protection due to their cultural value or conservation significance (Bossart *et al.*, 2006). Cyamudongo forest is among the protected forest fragments due to its high significance for the conservation of biodiversity within the Albertine Rift (AR) region, a biodiversity hotspot. Historically, this fragment was connected to the Nyungwe main forest and was disconnected around 100 years ago due to agriculture and human settlements. Since the break up the fragment has become very isolated, managed as a forest reserve, and was gazetted as part of Nyungwe National Park since 2004 (Fischer & Killmann, 2008). Cyamudongo forest is located around 10 km from the Nyungwe main forest and consists of a dense forest with a few clearings. It hosts a rich biodiversity including species endemic to the Albertine Rift (Plumptre *et al.*, 2007). However, it appears from the literature that the few studies conducted in the Cyamudongo forest concentrated on plant diversity and taxonomy (Fischer *et al.*, 2003; Fischer & Killmann, 2008) or on primates such as endangered chimpanzees (Moore *et al.*, 2018), but little is known about invertebrates including butterflies.

Butterflies as a biodiversity component of forest ecosystems play an important role in plant pollination (Winfree *et al.*, 2011; Barrios *et al.*, 2016; Majewska *et al.*, 2018; Sáfián, 2021) and have been largely used as bioindicators of environmental change and forest restoration and management (Kremen, 1992; Maleque *et al.*, 2009; Nyafwono *et al.*, 2014; Oloya *et al.*, 2021). While some butterfly surveys have been conducted in protected areas within countries neighbouring Rwanda (e.g. Ducarme, 2018; Forbes, 2018), no butterfly survey has been conducted in the Cyamudongo forest fragment to provide baseline information on its butterfly population. This fragment is currently an island in an anthropogenic dominated landscape that might serve as a refugium for diverse species including butterflies from the surrounding matrix (Bossart *et al.*, 2006), and thus contribute to the preservation of butterflies. Knowledge of the butterfly diversity in the Cyamudongo fragment would be an aid to effectively manage this fragment and ensure the protection of its biodiversity. This motivated a preliminary survey of butterfly species inhabiting the fragment. In addition, the authors wanted to make a

Received: 2 September 2021
Published: 22 December 2021

collection for educational purposes and provide baseline data for future research on butterflies in the region.

MATERIALS AND METHODS

Study site

This study was conducted in Cyamudongo forest (Fig. 1), a submontane forest fragment located in the south-western part of Rwanda (02°33.12′ S, 28°59.49′ E) with an area of c. 400 ha (Mvunabandi *et al.*, 2015) and altitude between 1500–2140 m a.m.s.l. Cyamudongo tropical rainforest fragment is part of Nyungwe National Park since 2004 (Fischer & Killmann, 2008) and hosts a primate population of chimpanzees, Olive baboons, L' Hoest monkeys, Mona monkeys, and bird species, including the Great Blue Turaco among many others. The fragment also hosts a variety of plants including species endemic to the Albertine Rift region such as *Impatiens* spp., and some locally endemic plant species such as *Polystachya bruechertiae* and *Gastrodia rwandensis* are only found there (Fischer *et al.*, 2003; Fischer & Killmann, 2008). Cyamudongo is an income tourist site for Rwanda, especially through its endangered charismatic chimpanzee population. From a nearby meteorology station located in the Nyakabuye sector, the annual rainfall was 1668 mm in 2019. Major threats to the Cyamudongo forest include firewood collection, fodder collection for cattle, and encroachment of agricultural lands.

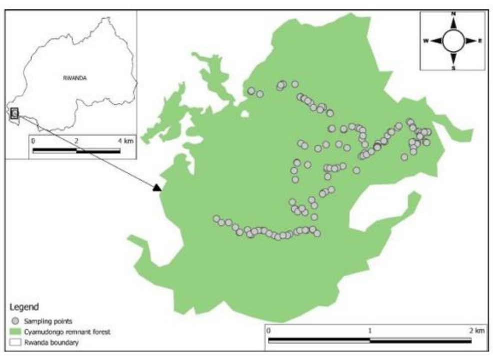


Figure 1 – Map of Cyamudongo forest fragment with butterfly sampling points.

Sampling methods

Sampling of butterflies in Cyamudongo was conducted from October to December 2019, January and March 2020, and August 2020. These periods correspond to the rainy season, short dry season, and dry season, respectively in this area. Butterflies were collected along tourist trails due to the hazardous terrain within the forest, using butterfly nets either in flight, resting, feeding on flowers or animal excrement, or mud puddling. The trails were walked for the purpose of a checklist survey (Royer *et al.*, 1998) rather than a Pollard monitoring walk (Pollard, 1977) which is commonly used for quantitative monitoring of butterfly population change over time rather than conducting preliminary inventories. Three trails with a total length of 4.6 km on foot were accessible for butterfly sampling within the Cyamudongo forest. Depending on the trail's accessibility, butterflies were collected by two collectors within 5 m of width along the trail walk and much effort was put into collecting every butterfly encountered along the trail. In addition, 48 nymphalid species (Appendix) were recorded using traps baited with fermented bananas along the same trails.

Depending on weather conditions, sampling took place on sunny days from 9 am until 5 pm, the period when most butterflies were active. For each collected butterfly, GPS coordinates were recorded. Photographs were also taken where possible especially for butterflies observed puddling, drinking, or feeding on decaying materials such as carnivore dung. Each trail was walked two consecutive days per season making six days per season in total to cover the three trails within the forest. All collected specimens were stored in envelopes for later identification. Species identification of collected specimens used available literature about the region (Kielland, 1990; Carder and Tindimubona, 2002; Larsen, 2005a,b; Woodhall, 2005; Vande Weghe, 2010; Martins & Collins, 2016; Liseki & Vane-Wright, 2018; Williams, 2021) and websites such as Dominique Bernaud's "Le site des Acraea" (http://www.acraea.com/) and African Butterfly Database (ABDB) (https://www.abdb-africa.org/). The expertise of local experts in the region was also sought for species confirmation. A checklist of all butterfly species occurring in Cyamudongo tropical forest fragment is provided. The butterfly classification follows Williams (2015), Dhungel & Wahlberg (2018) and Espeland *et al.* (2018). Collected specimens will be maintained in the Centre of Excellence and Biodiversity at the University of Rwanda.

RESULTS

One hundred and sixty-two species, 6 families, and 20 subfamilies were recorded in the Cyamudongo forest fragment. Nymphalid species were dominant while only one riodinid species was recorded. A checklist including thirteen butterfly species endemic to the Albertine Rift (AR) is provided in the Appendix. The AR endemics are *Charaxes mafuga, Cymothoe collarti, Euphaedra margueriteae, E. barnsi, E. phosphor, Euriphene amicia excelsior, Belenois victoria, Mylothris polychroma, M. ruandana, Bicyclus matuta, B. neustetteri, B. persimilis* and *Gnophodes grogani* (Davenport, 2002)

DISCUSSION

This survey recorded more Nymphalidae species than Lycaenidae (the most species-rich African butterfly family) (Larsen, 2005b). This dominance of the Nymphalidae in the Cyamudongo forest is similar to the eastern forests of the Democratic Republic of Congo, a neighbouring country (Ducarme, 2018). However, the low number of recorded Lycaenidae and Hesperiidae might be due to their small size and some being canopy dwellers, which makes them difficult to observe (Vande Weghe, 2010) in the dense forest. As in another inventory conducted in a lowland forest in Tanzania (Mtui *et al.*, 2019), the riodionids were least abundant in the Cyamudongo fragment. This group represents less than one per cent of all described African butterfly species, while the subfamilies Limenitidinae and Heliconiinae dominate among the Nymphalidae and this explains their dominance among the recorded subfamilies in Cyamudongo forest (see Appendix). This butterfly survey was the first in Cyamudongo and was conducted within a short time. Thus, a long-term standardised monitoring programme should be established by park managers to add more species to the list. With respect to biodiversity conservation, butterfly inventory studies should be conducted in other protected forest fragments of Rwanda. Such inventories should also be conducted in fragments outside protected areas to assess whether they might accommodate species with urgent protection needs.

ACKNOWLEDGEMENTS

We thank the Rwanda Development Board (RDB) for their authorisation to conduct this research in the Cyamudongo forest fragment, and Baranyeretse Laurent, Simon Muhayimana, and Thacien Hagenimana for their help during data collection. We are also grateful to the Centre of Excellence in Biodiversity and Natural Resources management for technical assistance during fieldwork, and the Rwanda Meteorology Agency for providing meteorological data for the Cyamudongo forest. Gaël Ruboneka Vande Weghe and Szabolcs Sáfián are thanked for their help in butterfly species identification.

LITERATURE CITED

BARRIOS, B., PENA, S.R., SALAS, A. & KOPTUR, S. 2016. Butterflies visit more frequently, but bees are better pollinators: The importance of mouthpart dimensions in effective pollen removal and deposition. *AoB Plants*. https://doi.org/10.1093/aobpla/plw001.

BOSSART, J.L., OPUNI-FRIMPONG, E., KUUDAAR, S. & NKRUMAH, E. 2006. Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. *Biodiversity and Conservation* **15**: 333–359. https://doi.org/10.1007/s10531-005-2574-6.

CARDER, N. & TINDIMUBONA, L. 2002. *Butterflies of Uganda: A field guide to butterflies and silk moths from the collection of the Uganda society*. Uganda Society.

DAVENPORT, T.R.B. 2002. *Endemic butterflies of the Albertine Rift-an annotated checklist*.

DHUNGEL, B. & WAHLBERG, N. 2018 'Molecular systematics of the subfamily Limenitidinae (Lepidoptera: Nymphalidae). *PeerJ* **6**: e4311. https://doi.org/10.7717/peerj.4311.

DUCARME, R. 2018. The butterflies (Lepidoptera: Papilionoidea) of the north-easthern Democratic Republic of Congo. *Metamorphosis* **29**: 23–37.

ESPELAND, M., BREINHOLT, J., WILLMOTT, K.R., WARREN, A.D., VILA, R., TOUSSAINT, E.F.A., MAUNSELL, S.C., ADUSE-POKU, K., TALAVERA, G., EASTWOOD, R., JARZYNA, M.A., GURALNICK, R., LOHMAN, D.J., PIERCE, N.E. & KAWAHARA, A.Y. 2018. A comprehensive and dated phylogenomic analysis of butterflies. *Current Biology* **28**: 1 –9.

FISCHER, E., DHETCHUVI, J.B. & NTAGANDA, C. 2003. A New Species of Impatiens (Balsaminaceae) from Nyungwe Forest , Rwanda. *Systematics and Geography of Plants*. **73(1)**: 91–95. https://www.jstor.org/stable/3668483.

FISCHER, E. & KILLMANN, D. 2008. *Illustrated field guide to the plants of Nyungwe National Park, Rwanda*. 1st Edition. Koblenz geographical colloquia, Series biogeographical monographs 1.

FORBES, S. 2018. The butterflies (Lepidoptera: Papilionidae) of Semuliki National Park, western Uganda. *Metamorphosis* **29**: 14–21.

GHAZOUL, J. 2010. *Tropical rain forest ecology, diversity, and conservation*. Oxford University Press.

KIELLAND, J. 1990. Butterflies of Tanzania. Hill House publishers, London.

KREMEN, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2(2)**: 203–217.

LARSEN, T.B. 2005a. *Butterflies of West Africa Plate volume*. Apollo Books, Sternstrup. 270 pp.

LARSEN, T.B. 2005b. *Butterflies of West Africa Text volume*. Apollo Books, Sternstrup. 595 pp.

LEWIS, S.L., EDWARDS, D.P. & GALBRAITH, D. 2015. Increasing human dominance of tropical forests. *Science* **349(6250)**: 827–832.

LISEKI, S.D. & VANE-WRIGHT, R.I. 2018. Butterflies (Lepidoptera: Papilionoidea) of mount kilimanjaro: Nymphalidae subfamily helconiinae. *Journal of Natural History* **52(39–40)**: 2511–2552. https://doi.org/10.1080/00222933.2018.1539780.

MAJEWSKA, A.A., SIMS, S., WENGER, S.J., DAVIS, A.K. & ALTIZER, S. 2018. Do characteristics of pollinator-friendly gardens predict the diversity, abundance, and reproduction of butterflies? *Insect Conservation and Diversity*. https://doi.org/10.1111/icad.12286.

MALEQUE, A.M., MAETO, K. & ISHII, H.T. 2009. Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Applied Entomology and Zoology* **44(1)**: 1–11. https://doi.org/10.1303/aez.2009.1.

MARTINS, D.J. & COLLINS, S. 2016. *Pocket Guide Butterflies of East Africa*. Struik Nature. 144 pp.

MOORE, J.K., MULINDAHABI, F., GATORANO, G., NIYIGABA, P., NDIKUBWIMANA, I., CIPOLLETTA, C. & MASOZERA, M.K. 2018. Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda. *American Journal of Physical Anthropology* **80**: e22897. https://doi.org/10.1002/ajp.22897.

MTUI, D., CONGDON, C., BAMPTON, I., KALENGA, P. & LEONARD, H. 2019. Altitudinal Distribution and Monthly Occurrence of Butterflies in the Kihansi Gorge Forest , Tanzania , with a Checklist of Species. *Tanzania Journal of Science* **45(4)**: 543–558.

MVUNABANDI, D., VAN DUREN, I. & WANG, T. 2015. Eastern Chimpanzee's habitat fragmentation in Nyungwe National Park (NNP), Rwanda, pp.1-16. In: *Proceedings of GeoTech Rwanda, Kigali*. https://www.geotechrwanda2015.com/wp-content/uploads.

NYAFWONO, M., VALTONEN, A., NYEKO, P. & ROININEN, H. 2014. Fruit-feeding butterfly communities as indicators of forest restoration in an Afro-tropical rainforest. *Biological Conservation* **174***:* 75–83. https://doi.org/10.1016/j.biocon.2014.03.022.

OLOYA, J., MALINGA, G. M., NYAFWONO, M., AKITE, P., NAKADAI, R., HOLM, S. & VALTONEN, A. 2021. Recovery of fruit-feeding butterfly communities in Budongo Forest Reserve after anthropogenic disturbance. *Forest Ecology and Management* **491**: 119087. https://doi.org/10.1016/j.foreco.2021.119087.

PLUMPTRE, A.J., DAVENPORT, T.R.B., BEHANGANA, M., KITYO, R., EILU, G., SSEGAWA, P., EWANGO, C., MEIRTE, D., KAHINDO, C., HERREMANS, M., PETERHANS, J.K., PILGRIM, J.D., WILSON, M., LANGUY, M. & MOYER, D. 2007. The biodiversity of the Albertine Rift. *Biological Conservation* **134**: 178–194. https://doi.org/10.1016/j.biocon.2006.08.021.

POLLARD, E. 1977. A method for assessing changes in the abundance of butterflies. *Biological Conservation* **12**: 115–134. https://doi.org/10.1016/0006-3207(77)90065-9.

ROYER, R.A., AUSTIN, J.E. & NEWTON, W.E. 1998. Checklist and "Pollard Walk" butterfly survey methods on public lands. *The American Midland Naturalist* **140**: 358–371.

SÁFIÁN, S. 2021. The highly invasive Siam Weed, *Chromolaena odorata* (L.) King and Robinson (Asteraceae), as a seasonal prime nectar source for butterflies (Lepidoptera: Papilionoidea) and other insects (Insecta: Lepidoptera, Hymenoptera, Coleoptera) in West Africa. *Metamorphosis* **32**: 49–57. https://dx.doi.org/10.4314/met.v32i1.10.

SHAHABUDDIN, G. & PONTE, C. A. 2005. Frugivorous butterfly species in tropical forest fragments: Correlates of vulnerability to extinction. *Biodiversity and Conservation* **14(5)**: 1137–1152. https://doi.org/10.1007/s10531-004-7842-3.

TAUBERT, F., FISCHER, R., GROENEVELD, J., LEHMANN, S., MÜLLER, M.S., RÖDIG, E., WIEGAND, T.& HUTH, A. 2018. Global patterns of tropical forest fragmentation. *Nature* **554**: 519–522. https://doi.org/10.1038/nature25508.

VANDE WEGHE, G.R. 2010. *Papillons du Gabon*. Wildlife Conservation Society.

WILLIAMS, M.C. 2015. Classification of the Afrotropical butterflies to generic level. *Metamorphosis* **26**: 102–108.

WILLIAMS, M. C. 2021. Butterflies and Skippers of the Afrotropical Region. www.metamorphosis.org.za/?p=articles&s=atb.

WILSON, R.J., DAVIES, Z.G. & THOMAS, C.D. 2009. Modelling the effect of habitat fragmentation on range expansion in a butterfly. In: *Proceedings of the Royal Society B: Biological Sciences* **276**: 1421–1427. https://doi.org/10.1098/rspb.2008.0724.

WINFREE, R., BARTOMEUS, I. & CARIVEAU, D.P. 2011. Native pollinators in anthropogenic habitats. *Annual Review of Ecology, Evolution, and Systematics*. **42**: 1–22. https://doi.org/10.1146/annurev-ecolsys-102710-145042.

WOODHALL, S. 2005. *Field Guide to Butterflies of South Africa*. Struik Nature.

APPENDIX – Preliminary checklist of butterfly species and their seasonal occurrence in Cyamudongo tropical forest fragment. Species with (*) were recorded by both butterfly net and fruit-baited traps, and species with (**) were only recorded by fruit baited traps. DS = Dry season, RS = Rain season, SDS = Short dry season.

TAXON	DS	RS	SDS	ALL
FAMILY HESPERIIDAE Latreille, 1809				
Subfamily Coeliadinae Evans, 1937				
Genus *Coeliades* Hübner, [1818]				
Coeliades forestan forestan (Stoll, [1782])	X			1
Subtotals for the subfamily Coeliadinae	**1**	**0**	**0**	**1**
Subfamily Hesperiinae Latreille, 1809				
Tribe Ceratrichiini Grishin, 2019				
Genus *Ceratrichia* Butler, 1870				
Ceratrichia semlikensis Joicey & Talbot, 1921	X	X	X	1
Genus Pardaleodes Butler, 1870				
Pardaleodes tibullus torensis Bethune-Baker, 1906	X	X	X	1
Tribe Hesperiini Latreille, 1809				
Genus *Gorgyra* Holland, 1896				
Gorgyra aretina (Hewitson, 1878)			X	1
Genus *Paracleros* Berger, 1978				
Paracleros biguttulus (Mabille, 1889)	X			1
Genus *Platylesches* Holland, 1896				
Platylesches galesa (Hewitson, 1877)		X		1
Tribe Baorini Doherty, 1886				
Genus *Torbenlarsenia* Kemal & Koçak, 2020				
Torbenlarsenia perobscura (Druce, 1912)	X			1
Subtotals for the subfamily Hesperiinae	**4**	**3**	**3**	**6**
Subfamily Tagiadinae Mabille, 1878				
Tribe Tagiadini Mabille, 1878				
Genus *Eagris* Guenée, 1862				
Eagris lucetia (Hewitson, 1875)		X	X	1
Eagris tigris kayonza Evans, 1956	X			1
Eagris subalbida aurivillii (Neustetter, 1927)		X		1
Genus *Tagiades* Hübner, 1819				
Tagiades flesus (Fabricius, 1781)	X			1
Genus *Netrobalane* Mabille, 1903				
Netrobalane canopus (Trimen, 1864)	X			1
Tribe Celaenorrhinini Swinhoe, 1912				
Genus *Celaenorrhinus* Hübner, 1819				
Celaenorrhinus mediostictus mediostictus Libert, 2014			X	1
Genus *Apallaga* Strand, 1911				
Apallaga kivuensis (Joicey & Talbot, 1921)		X		1
Apallaga rwandae Libert, 2014	X	X	X	1
Genus *Eretis* Mabille, 1891				
Eretis buamba Evans, 1937			X	1
Eretis mitiana Evans, 1937	X			1
Genus *Sarangesa* Moore, 1881				
Sarangesa haplopa Swinhoe, 1907		X		1
Subtotals for the subfamily Tagiadinae	**5**	**5**	**4**	**11**
FAMILY LYCAENIDAE Leach, 1815				
Subfamily Miletinae				

Tribe Spalgini Toxopeus, 1929				
Genus *Spalgis* Moore, 1879				
Spalgis lemolea lemolea Druce, 1890	X			1
Subtotals for the subfamily Miletinae	**1**	**0**	**0**	**1**
Subfamily Aphnaeinae Distant, 1884				
Genus *Lipaphnaeus* Aurivillius, 1916				
Lipaphnaeus aderna pan (Talbot, 1935)	X			1
Subtotals for the subfamily Aphnaeinae	**1**	**0**	**0**	**1**
Subfamily Polyommatinae				
Tribe Lycaenesthini Toxopeus, 1929				
Genus *Anthene* Doubleday, 1847				
Anthene larydas (Cramer, [1780])		X	X	1
Anthene ligures ligures (Hewitson, 1874)	X	X	X	1
Tribe Polyommatini Swainson, 1827				
Subtribe incertae sedis				
Genus *Azanus* Moore, 1881				
Azanus mirza (Plötz, 1880)	X			1
Genus *Cacyreus* Butler, 1897				
Cacyreus lingeus (Stoll, [1782])	X			1
Genus *Tuxentius* Larsen, 1982				
Tuxentius margaritaceus (Sharpe, 1892)	X	X	X	1
Genus *Uranothauma* Butler, 1895				
Uranothauma falkensteini (Dewitz, 1879)	X	X		1
Uranothauma heritsia intermedia (Tite, 1958)	X			1
Genus *Zizeeria* Chapman, 1910				
Zizeeria knysna knysna (Trimen, 1862)	X			1
Subtotals for the subfamily Polyommatinae	**7**	**4**	**3**	**8**
Subfamily Theclinae Swainson, 1830				
Tribe Hypolycaenini Swinhoe, 1910				
Genus *Hypolycaena* Felder, 1862				
Hypolycaena hatita ugandae Sharpe, 1904	X	X	X	1
Hypolycaena liara liara Druce, 1890		X	X	1
Tribe Deudorigini Doherty, 1886				
Genus *Deudorix* Hewitson, [1863]				
Deudorix kayonza (Stempffer, 1956)	X			1
Genus *Pilodeudorix* Druce, 1891				
Pilodeudorix azurea azurea (Stempffer, 1964)	X			1
Subtotals for the subfamily Theclinae	**3**	**2**	**2**	**4**
FAMILY NYMPHALIDAE Rafinesque, 1815				
Subfamily Biblidinae Boisduval, 1833				
Tribe Biblidini Boisduval, 1833				
Genus *Ariadne* Horsfield, [1829]				
**Ariadne pagenstecheri* (Suffert, 1904)	X	X	X	1
Genus *Eurytela* Boisduval, 1833				
**Eurytela dryope angulata* Aurivillius, [1899]	X			1
**Eurytela hiarbas hiarbas* (Drury, 1782)	X	X	X	1
Genus *Neptidopsis* Aurivillius, [1899]				
Neptidopsis ophione nucleata Grünberg, 1911	X	X	X	1
Tribe Epicaliini Guenée, 1865				
Genus *Sevenia* Koçak, 1996				

**Sevenia boisduvali omissa* (Rothschild, 1918)	X	X	X	**1**
**Sevenia garega* (Karsch, 1892)	X	X		**1**
Subtotals for the subfamily Biblidinae	**6**	**5**	**4**	**6**
Subfamily Charaxinae Guenée, 1865				
Tribe Charaxini Guenée, 1865				
Genus *Charaxes* Ochsenheimer, 1816				
**Charaxes acuminatus kigezia* van Someren, 1963		X	X	**1**
**Charaxes ameliae ameliae* Doumet, 1861			X	**1**
**Charaxes anticlea adusta* Rothschild, 1900	X	X	X	**1**
**Charaxes brutus alcyone* Stoneham, 1943	X	X		**1**
**Charaxes candiope* (Godart, [1824])	X	X		**1**
**Charaxes etesipe* (Godart, [1824])	X			**1**
**Charaxes eudoxus lequeuxi* Plantrou, 1982	X			**1**
**Charaxes mafuga* van Someren, 1969	X	X		**1**
**Charaxes mafugensis* Jackson, 1956			X	**1**
***Charaxes numenes aequatoralis* van Someren, 1972	X		X	**1**
**Charaxes pleione delvauxi* Turlin, 1987	X	X	X	**1**
**Charaxes pollux pollux* (Cramer, 1775)	X			**1**
**Charaxes tiridates tiridatinus* Röber, 1936			X	**1**
Subtotals for the subfamily Charaxinae	**9**	**6**	**7**	**13**
Subfamily Cyrestinae Guenée, 1865				
Genus *Cyrestis* Boisduval, 1832				
Cyrestis camillus camillus (Fabricius, 1781)	X	X	X	**1**
Subtotals for the subfamily Cyrestinae	**1**	**1**	**1**	**1**
Subfamily Danainae Boisduval, 1833				
Tribe Danaini Boisduval, 1833				
Genus *Tirumala* Moore, 1880				
Tirumala formosa mercedonia (Karsch, 1894)	X	X	X	**1**
Subtribe Amaurina Le Cerf, 1922				
Genus *Amauris* Hübner, 1816				
Amauris inferna grogani Sharpe, 1901	X	X		**1**
Amauris niavius niavius (Linnaeus, 1758)	X	X		**1**
Subtotals for the subfamily Danainae	**3**	**3**	**1**	**3**
Subfamily Heliconiinae Swainson, 1822				
Tribe Acraeini Boisduval, 1833				
Subtribe Acraeina Boisduval, 1833				
Genus *Acraea* Fabricius, 1807				
Acraea aganice montana (Butler, 1888)	X	X		**1**
Acraea asboloplintha Karsh, 1894	X	X	X	**1**
Acraea cerasa cerita Sharpe, 1906	X			**1**
Acraea egina egina (Cramer, 1775)		X	X	**1**
Acraea eltringhami Joicey & Talbot, 1921		X		**1**
Acraea kinduana Pierre, 1979			X	**1**
Acraea kivuensis kivuensis (Joicy & Tabot, 1927)	X	X		**1**
Acraea parageum parageum (Grose-Smith, 1900)	X	X		**1**
Acraea quadricolor (Rogenhofer, 1891)			X	**1**
Acraea quirina (Fabricius, 1781)	X			**1**
Subtribe Actinotina Henning, 1992				
Genus *Telchinia* Hübner, [1819]				
Telchinia alicia Sharpe, 1890		X		**1**

Telchinia bonasia (Fabricius, 1775)	X	X	X	**1**
Telchinia cinerea (Neave, 1904)	X		X	**1**
Telchinia disjuncta (Grose-Smith, 1898)	X	X	X	**1**
Telchinia jodutta iodutta (Fabricius, 1793)		X		**1**
Telchinia kalinzu (Carpenter, 1936)	X			**1**
Telchinia lycoa (Godart, [1819])	X	X		**1**
Telchinia ntebiae ntebiae (Sharpe, 1897)	X			**1**
Telchinia oreas oreas (Sharpe, 1891)	X	X		**1**
Telchinia orestia (Hewitson, 1874)	X	X	X	**1**
Telchinia parrhasia servona (Godart, [1819])		X		**1**
Telchinia penelope penelope (Staudinger, 1896)	X	X	X	**1**
Telchinia pentapolis pentapolis (Ward, 1871)		X		**1**
Telchinia pharsalus (Ward, 1871)	X	X	X	**1**
Telchinia sotikensis sotikensis (Sharpe, 1892)	X	X		**1**
Telchinia toruna (Grose-Smith, 1900)	X	X	X	**1**
Telchinia uvui uvui (Grose-Smith, 1890)		X	X	**1**
Tribe Vagrantini Pinratana & Eliot, 1996				
Genus *Lachnoptera* Doubleday, [1847]				
Lachnoptera anticlia (Hübner, [1819])	X			**1**
Genus *Phalanta* Horsfield, 1829				
Phalanta eurytis eurytis (Doubleday, [1847])	X	X	X	**1**
Subtotals for the subfamily Heliconiinae	**20**	**21**	**13**	**29**
Subfamily Limenitidinae Behr, 1864				
Tribe Cymothoini Dhungel & Wahlberg, 2018				
Genus *Cymothoe* Hübner, 1819				
Cymothoe collarti werneri Beaurain, 1984	X	X	X	**1**
**Cymothoe herminia johnstoni* (Butler, 1902)	X	X	X	**1**
Genus Harma Doubleday, 1848				
**Harma theobene superna* (Fox, 1968)	X	X	X	**1**
Tribe Adoliadini Doubleday, 1845				
Subtribe Bebearina Hemming, 1960				
Genus *Evena* Westwood, [1850]				
**Evena crithea* (Drury, 1773)	X	X	X	**1**
Genus *Pseudathyma* Staudinger, 1891				
Pseudathyma plutonica plutonica Butler, 1902	X			**1**
Genus *Euphaedra* Hübner, 1819				
**Euphaedra barnsi* Joicey & Talbot, 1922	X			**1**
**Euphaedra harpalyce dowsetti* Hecq, 1990		X	X	**1**
Euphaedra margueriteae Hecq, 1978		X		**1**
Euphaedra medon fraudata van Someren, 1935	X	X	X	**1**
Euphaedra phosphor Joicey & Talbot, 1921		X	X	**1**
Genus *Euriphene* Boisduval, 1847				
**Euriphene butleri remota* Hecq, 1994	X	X	X	**1**
**Euriphene amicia excelsior* (Rebel, 1911)	X	X	X	**1**
Genus *Euryphura* Staudinger, 1891				
Euryphura chalcis chalcis (Felder & Felder, 1860)	X			**1**
Genus *Aterica* Boisduval, 1833				
**Aterica galene extensa* Heron, 1909	X	X	X	**1**
Genus *Bebearia* Hemming, 1960				
**Bebearia sophus monforti* Hecq, 1990	X	X	X	**1**

Tribe Neptini Newman, 1870				
Genus *Neptis* Fabricius, 1807				
Neptis agouale Pierre-Baltus, 1978	X	X	X	**1**
Neptis cf. *quintilla* Mabille, 1890	X	X	X	**1**
Neptis nemetes nemetes Hewitson, [1868]	X			**1**
Neptis nicoteles Hewitson, 1874	X			**1**
Neptis occidentalis Rothschild, 1918	X	X	X	**1**
Neptis ochracea ochreata Gaede, 1915		X		**1**
Neptis saclava marpessa Hopffer, 1855	X	X		**1**
Tribe Pseudacraeini Dhungel & Wahlberg, 2018				
Genus *Pseudacraea* Westwood, 1850				
Pseudacraea dolomena kayonza Jackson, 1956			X	**1**
**Pseudacraea eurytus eurytus* (Linnaeus, 1758)	X			**1**
**Pseudacraea lucretia protracta* (Butler, 1874)	X	X	X	**1**
Subtotals for the subfamily Limenitidinae	**20**	**18**	**16**	**25**
Subfamily Libytheinae Boisduval, 1833				
Genus *Libythea* Fabricius, 1807				
Libythea labdaca Westwood, [1851]		X		**1**
Subtotals for the subfamily Libytheinae	**0**	**1**	**0**	**1**
Subfamily Nymphalinae Rafinesque, 1815				
Tribe Junoniini Reuter, 1896				
Genus *Hypolimnas* Hübner, 1819				
Hypolimnas anthedon anthedon (Doubleday, 1845)	X		X	**1**
Genus *Junonia* Hübner, 1819				
**Junonia gregorii* Butler, 1896	X	X	X	**1**
Junonia terea tereoides (Butler, 1901)	X			**1**
Genus *Precis* Hübner, 1819				
Precis rauana silvicola Schultze, 1916	X	X	X	**1**
Precis sinuata hecqui Berger, 1981	X			**1**
Genus *Protogoniomorpha* Wallengren, 1857				
**Protogoniomorpha parhassus* (Drury, 1782)	X	X	X	**1**
Protogoniomorpha temora temora (Felder & Felder, [1867])	X	X	X	**1**
Genus *Salamis* Boisduval, 1833				
Salamis cacta cacta (Fabricius, 1793)		X		**1**
Tribe incertae sedis				
Genus *Kallimoides* Shirôzu & Nakanishi, 1984				
**Kallimoides rumia rattrayi* (Sharpe, 1904)	X	X	X	**1**
Genus *Vanessula* Dewitz, 1887				
**Vanessula milca latifasciata* Joicey & Talbot, 1928	X	X	X	**1**
Tribe Nymphalini Swainson, 1827				
Genus *Vanessa* Fabricius, 1807				
**Vanessa dimorphica dimorphica* (Howarth, 1966)	X			**1**
Genus *Antanartia* Rothschild & Jordan, 1903				
* *Antanartia schaeneia dubia* Howarth, 1966	X	X		**1**
Subtotals for the subfamily Nymphalinae	**11**	**8**	**7**	**12**
Subfamily Satyrinae Boisduval, 1833				
Tribe Melanitini Reuter, 1896				
Genus *Gnophodes* Doubleday, 1849				
**Gnophodes grogani* Sharpe, 1901	X	X		**1**
Genus *Melanitis* Fabricius, 1807				

**Melanitis leda* Westwood [1851]	X			**1**
Tribe Satyrini Boisduval, 1833				
Subtribe Mycalesina Reuter, 1896				
Genus *Bicyclus* Kirby, 1871				
***Bicyclus* cf. *smithi* (Aurivillius, [1899])	X	X	X	**1**
**Bicyclus dentata* (Sharpe, 1898)	X	X		**1**
**Bicyclus jefferyi* Fox, 1963	X			**1**
**Bicyclus mandanes* Hewitson, 1873		X		**1**
**Bicyclus matuta matuta* (Karsch, 1894)		X		**1**
**Bicyclus mesogena ugandae* (Riley, 1926)	X			**1**
**Bicyclus neustetteri* (Rebel, 1914)		X		**1**
**Bicyclus persimilis* (Joicey & Talbot, 1921)		X	X	**1**
***Bicyclus safitza safitza* (Westwood, [1850])			X	**1**
***Bicyclus sandace* (Hewitson, [1877])	X			**1**
**Bicyclus sophrosyne sophrosyne* (Plötz, 1880)	X	X	X	**1**
***Bicyclus vulgaris* (Butler, 1868)	X			**1**
Subtotals for the subfamily Satyrinae	**9**	**8**	**4**	**14**
FAMILY PAPILIONIDAE Latreille, 1802				
Subfamily Papilioninae Latreille, 1802				
Tribe Leptocircini Kirby, 1896				
Genus *Graphium* Scopoli, 1777				
Graphium policenes policenes (Cramer, [1775])	X	X	X	**1**
Tribe Papilionini Latreille, [1802]				
Genus *Papilio* Linnaeus, 1758				
Papilio chrapkowskoides Storace, [1952]	X	X		**1**
Papilio dardanus dardanus Brown, 1776	X		X	**1**
Papilio echerioides joiceyi Gabriel, 1945	X	X		**1**
Papilio jacksoni ruandana Le Cerf, 1924	X	X	X	**1**
Papilio mackinnoni mackinnoni Sharpe, 1891	X	X		**1**
Papilio nireus nireus Linnaeus, 1758	X	X	X	**1**
Papilio phorcas congoanus Rothschild, 1896	X	X	X	**1**
Subtotals for the family Papilionidae	**8**	**7**	**5**	**8**
FAMILY PIERIDAE Swainson, 1820				
Subfamily Coliadinae Swainson, 1821				
Genus *Terias* Swainson, [1821]				
Terias desjardinsii regularis Butler, 1876	X			**1**
Terias floricola leonis Butler, 1886	X			**1**
Terias hapale Mabille, 1882		X	X	**1**
Terias hecabe solifera Butler, 1875	X		X	**1**
Terias senegalensis Boisduval, 1836	X	X	X	**1**
Subtotals for the subfamily Coliadinae	**4**	**2**	**3**	**5**
Subfamily Pierinae Swainson, 1820				
Tribe Pierini Swainson, 1820				
Subtribe Appiadina Kuzsenov, 1921				
Genus *Appias* Hübner, 1819				
Appias sabina sabina (Felder & Felder, [1865])	X			**1**
Subtribe Aporiina Chapman, 1895				
Genus *Belenois* Hübner, 1819				
Belenois raffrayi extendens (Joicey & Talbot, 1927)	X		X	**1**
Belenois victoria schoutedeni Berger, 1953	X	X	X	**1**

Belenois zochalia agrippinides (Holland, 1896)		X		**1**
Genus *Mylothris* Hübner, 1819				
Mylothris agathina richlora Suffert, 1904	X			**1**
Mylothris kiwuensis kiwuensis Grünberg, 1910	X		X	**1**
Mylothris nagichota rwandensis Warren-Gash, 2020		X	X	**1**
Mylothris polychroma Berger, 1981		X	X	**1**
Mylothris ruandana ruandana Strand, 1909	X			**1**
Tribe Nepheroniini Braby, 2014				
Genus *Nepheronia* Butler, 1870				
Nepheronia argia argia (Fabricius, 1775)	X	X	X	**1**
Tribe Teracolini Reuter, 1896				
Genus *Colotis* Hübner, 1819				
Colotis elgonensis basilewskyi Berger, 1956	X		X	**1**
Tribe Leptosiaini Braby, 2014				
Genus *Leptosia* Hübner, 1818				
Leptosia nupta pseudonupta Bernardi, 1959	X	X	X	**1**
Subtotals for the subfamily Pierinae	**9**	**6**	**8**	**12**
FAMILY RIODINIDAE Grote, 1895				
Subfamily Nemeobiinae Bates, 1868				
Tribe Abisarini Stichel, 1928				
Subtribe Abisarina Stichel, 1928				
Genus *Afriodinia* d'Abrera, 2009				
Afriodinia neavei neavei (Riley, 1932)	X	X	X	**1**
Subtotals for the family Riodinidae	**1**	**1**	**1**	**1**
OVERALL TOTALS	**123**	**99**	**82**	**162**

2.2 Distribution patterns of Fruit- feeding butterflies in Nyungwe National Park

Received: 19 August 2021 | Revised: 30 November 2021 | Accepted: 24 February 2022

DOI: 10.1111/aje.12997

ARTICLE

African Journal of Ecology WILEY

Diversity and distribution of Fruit-feeding butterflies (Lepidoptera: Nymphalidae) in Nyungwe National Park, Rwanda

Jean de Dieu Uwizelimana[1,2] | Donat Nsabimana[3] | Thomas Wagner[1]

[1]Institut für Integrierte Naturwissenschaften, Biologie, Universität Koblenz-Landau, Koblenz, Germany

[2]College of Science and Technology, Biology Department, University of Rwanda, Kigali-Rwanda, Rwanda

[3]College of Agriculture, Animal Sciences and Veterinary Medicine, School of Forestry, Biodiversity and Conservation, University of Rwanda, Butare-Rwanda, Rwanda

Correspondence
Jean de Dieu Uwizelimana, College of Science and Technology, Biology Department, University of Rwanda, KN 67 Street, P o Box 3900, Kigali-Rwanda, Rwanda.
Email: juwizelimana@gmail.com

Abstract

Tropical rainforests including high mountains are the most diverse terrestrial ecosystems. The ecology of tropical insects has been documented, but there is still a knowledge gap on insect diversity within certain underexplored regions such as the Afrotropical Mountains. A study was conducted in Nyungwe National Park, Rwanda, an Afromontane tropical rainforest and a biodiversity hotspot. The aims of the study were to assess (1) the fruit-feeding butterfly species and their distribution across an elevation gradient in Nyungwe; (2) the elevation distribution range of each fruit-feeding butterfly species; and (3) the effect of seasonal variation on fruit-feeding butterflies' distribution across an elevation gradient in Nyungwe National Park. Stratified seasonal sampling was conducted using fruit-baited traps along an elevation gradient spanning from 1700 to 2950 m of altitude. Fifty-six species including 10 Albertine Rift endemics were recorded, and 77% of the recorded species range between 1700 and 2100 m of altitude. Higher species richness and abundance were recorded during the dry season and decreased with increasing elevation. This study contributed to the knowledge of Nyungwe butterflies' diversity and provided baseline data for use in future monitoring of climate change effects in high mountain tropical rainforests within the Albertine Rift region.

KEYWORDS
bioindicator, climate change, distribution range, elevation, fruit-feeding butterfly, Nyungwe National Park

Résumé

Les forêts tropicales humides, y compris les hautes montagnes, font partie des écosystèmes terrestres les plus diversifiés. L'écologie des insectes tropicaux a été documentée, mais il existe encore un manque d'information sur la diversité des insectes dans certaines régions sous-explorées telles que les montagnes afrotropicales. Une étude a été menée dans le Parc National de Nyungwe, au Rwanda, une forêt tropicale humide afromontagnarde et un point chaud de la biodiv ersité. Les objectifs de l'étude étaient d'évaluer: (a) les espèces de papillons fruitiers et leur répartition sur un gradient altitudinal à Nyungwe; (b) la gamme de distribution d'élévation de chaque espèce de papillon fruitier; et (c) l'effet de la variation saisonnière sur la distribution des papillons fruitiers sur un gradient altitudinal dans le Parc National de Nyungwe. Un échantillonnage saisonnier stratifié a été effectué à l'aide de pièges à fruits le long d'un gradient altitudinal allant de 1700 m à 2950 m d'altitude. Cinquante-six espèces dont dix endémiques du Rift Albertin ont été recensées, et 77% des espèces recensées se situent entre 1700 m et 2100 m d'altitude. Une richesse et une abondance d'espèces plus élevées ont été enregistrées pendant la saison sèche et ont diminué avec l'augmentation de l'altitude. Cette étude a contribué à la connaissance de la diversité des papillons de Nyungwe et a fourni des données de base à utiliser pour le suivi des effets du changement climatique dans les forêts tropicales humides de haute montagne dans la région du Rift Albertin.

1 | INTRODUCTION

Tropical rainforests including high mountain ecosystems are known for their rich biodiversity compared with other ecosystems. However, although most of the vertebrates have been described and named, insects are still poorly known in tropical regions (Primack & Corlett, 2006). Butterflies are among the well-documented insects all over the world, but when compared to temperate regions, little is known about the ecology of tropical butterflies (Bonebrake et al., 2010). Moreover, within the tropics, little is known for example about fruit-feeding butterflies' distribution and ecology in Afrotropical regions (Aduse-Poku et al., 2012; Maicher et al., 2019; Molleman et al., 2006; Oloya et al., 2021; Valtonen et al., 2013), compared with Neotropics (Beirão et al., 2021; DeVries et al., 2012; DeVries & Walla, 2001; Morina-Martínez et al., 2013; dos Santos et al., 2017; Whitworth et al., 2016). It appears from the literature that studies on Afrotropical fruit-feeding butterflies' diversity have been conducted in low lands (Bobo et al., 2006; Molleman et al., 2006; Nkongolo & Bapeamoni, 2018; Nyafwono et al., 2014; Roche et al., 2015), but few have been conducted in high mountain tropical ecosystems, (Maicher et al., 2019) although these mountains are biodiversity-rich due to their diverse habitat types across elevation gradient (Spehn et al., 2011).

Butterflies have been used as environmental indicators due to their rapid response to any change within their habitat and thus can alert conservationists that something disturbing their natural habitat is happening (Kremen, 1992; Maleque et al., 2009). They are also valuable as habitat quality indicators (Maes & Dyck, 2005; Syaripuddin et al., 2015; Wood & Gillman, 1998) and their distribution has been largely found to be influenced by altitude, temperature, precipitation, habitat quality and vegetation type (Maleque et al., 2009; Storch et al., 2003). Moreover, seasonal variation has been found to have an impact on butterfly occurrence in a given ecosystem. In some ecosystems, butterfly species richness and abundance peak a few months after the beginning of the rain (Valtonen et al., 2013), while in others, more abundant butterflies occur during the dry season (Sagwe et al., 2015).

More generally, climate change or variability is expected to negatively affect biodiversity (Chen et al., 2011; Sheldon et al., 2011; Williams et al., 2003), especially in high elevation ecosystems by species altitudinal range shifts and some species extirpations and/or extinctions (Evangelista et al., 2016; Forister et al., 2010; Hodkinson, 2005; Mccain & Colwell, 2011; Xu et al., 2009). Under global warming, models predict strong negative impacts on species with narrow vertical distributions within mountain ecosystems (Hansen et al., 2001; La Sorte & Jetz, 2010). However, it appears from the literature that little is known about insect species distribution including butterflies in some tropical mountain biodiversity hotspot regions of the African continent such as the Albertine Rift (AR) (Kasangaki et al., 2012; Liseki & Vane-Wright, 2018; Plumptre et al., 2007). Hence, a study to document butterflies as potential climate indicators in the AR region would not only increase our understanding of the natural history of the area but also provide baseline data for future monitoring efforts for potential ecosystem changes within the region. Such information can be used to develop more effective management strategies to conserve the rich biodiversity of the region, particularly in light of climate change.

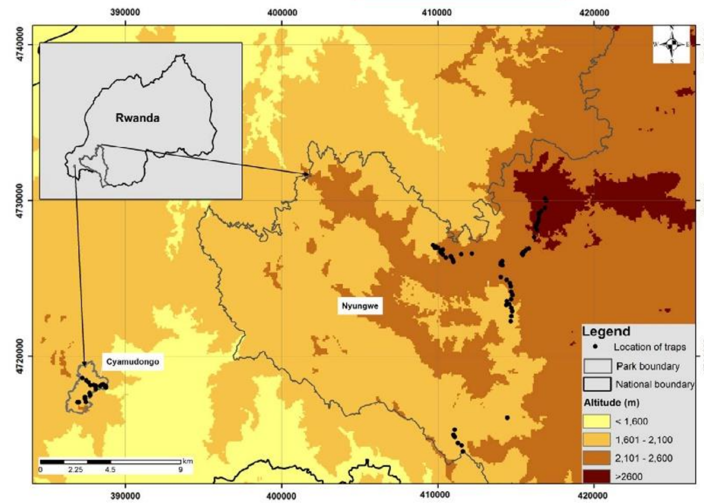
Rwanda comprises important parts of the Albertine Rift (AR) region and little research have been conducted on insects within its high mountain protected ecosystems including Nyungwe National Park (NNP), a biodiversity hotspot (Tedrow et al., 2014). There have been no studies documenting the effect of elevation on butterfly species distribution in the high mountain forests of Rwanda. The fruit-feeding butterflies were selected among other Lepidoptera because they are easy to trap particularly in inaccessible steep mountains of Nyungwe, and their identification is easy compared with other butterfly groups (Liseki & Vane-Wright, 2016; Molleman et al., 2006). The specific objectives of the study were to assess (1) fruit-feeding butterfly species and their distribution across an elevation gradient; (2) the elevation distribution range of each fruit-feeding butterfly species across an elevation gradient; and (3) the effect of season variation on the distribution of fruit-feeding butterfly species across an elevation gradient in Nyungwe National Park, Rwanda.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted at Nyungwe National Park (NNP), Rwanda. NNP is located in the southwestern part of Rwanda (2°15′–2°55′ S, 29°00′–29°30′ E; Figure 1), one of the Afrotropical montane

FIGURE 1 Map of Nyungwe National Park with butterfly traps location



protected areas within the AR, and a biodiversity hotspot. NNP is ranked among the most important conservation areas in the AR with high numbers of species including endemics (Plumptre et al., 2002, 2007). Encompassing approximately 1013 km^2, it ranges in elevation from 1600 to 2950 m with a mean annual rainfall of 1744 mm. It hosts at least 285 bird species, 26 of which are endemic to the AR and 13 species of primates including the endangered chimpanzee population. The vegetation of NNP is mostly made of primary and secondary forest types and a few marshlands (Fashing et al., 2007), due to past anthropogenic disturbances including mining activities. Three distinct altitudinal forest zones are observable in Nyungwe: low montane forest zone (from 1600 to 2100 m), middle montane forest zone (from 2100 to 2600 m) and upper montane forest zone (from 2600 up to 2950 m) respectively. The lower montane forest zone is well developed from Bweyeye to Pindura with a tree layer reaching up to 40 m height, the middle montane forest zone well developed at Uwinka, and the upper montane forest with many ferns at Mount Bigugu compared with others (Fischer & Killmann, 2008). Cyamudongo forest (Figure 1), located on the western side of NNP is a forest fragment ranging between 1500 and 2140 m of altitude with about 300 ha and was disconnected from the Nyungwe main forest by agricultural activities about 100 years ago but protected as part of the NNP since 2004 (Fischer & Killmann, 2008). Like Nyungwe main forest, the Cyamudongo forest fragment has faced diverse anthropogenic disturbances and is currently made of primary and secondary forest types.

2.2 | Butterfly sampling methods

Butterfly sampling was conducted in both Nyungwe main forest and Cyamudongo fragment. Due to the topography of the site, which is very steep and not easy to walk on, existing tourist trails within three elevation forest zones were used to sample fruit-feeding butterflies using fruit-baited traps (Austin & Riley, 1995; Devries et al., 1997, 1999; Hughes et al., 1998) type of East African hanging traps (Rydon, 1964).

Depending on site accessibility, butterfly sampling was conducted along with tourist trails from 1700 up to 2950 m of altitude in Nyungwe main forest and from 1700 to 2040 m within the Cyamudongo forest fragment. A sampling point was set at every 25 m of elevation, and 96 elevation sampling points in total were established (Table 1). Each sampling site was made of one accessible trail except at Cyamudongo where two trails (one from 1700 to 2040 m and another from 1750 to 2000 m of altitude) were accessible for butterfly sampling.

At each elevation sampling point, three baited traps were set: two on either side of the trail hanging between one to two metres from the ground and another hanging at least five metres height from the ground suspended to a tree branch with a means of the attached cord. The attached cord allowed the easy lowering of a trap to the ground while checking caught specimens. Along sampling trails, vegetation type and canopy cover were recorded to characterise the microhabitat within which traps were set in. Vegetation type was recorded as follows: Primary or secondary forest type, Ferns opening and Marshlands. Primary and secondary forest types were distinguished by tree species characteristics of each forest type (Fischer & Killmann, 2008) and a microhabitat with submerged water was recorded as marshland. Canopy cover was measured using a forest spherical densitometer (Lemon, 1956), and for the purpose of the analysis was classified as follows: open 0%–50% of closure; semi-open 50%–75%, and closed from 75% to 100% of closure. In addition to vegetation type and canopy cover, GPS coordinates were also recorded at each elevation sampling point.

Butterfly sampling was conducted in three different seasons and elevation sampling points were labelled so that the sampling was repeated at the same location. Sampling was conducted from October to December 2019, January to late March 2020 and June to August 2020 which correspond to the rainy season, short dry season and dry season, respectively, in Nyungwe National Park. Butterfly sampling was conducted once for each season and traps were set for four consecutive days at each elevation sampling point, which make 1152 trap-days: 96 (elevation sampling points) × 3 (number of traps at each elevation sampling point) × 4 (days of traps exposition) per season and a total of 3456 trap-days (96 × 3 × 4 × 3) for the whole three-season sampling periods.

Bait was made of a mixture of fermented bananas, pineapple, sugar and honey and was prepared a week in advance and renewed with fresh bananas a day before its usage. This protocol was followed throughout the completely sampling period because studies have shown that a little old bait attracts more fruit-feeding butterflies (Austin & Riley, 1995). A bait in a trap was renewed after 2 days depending on the level of its consumption or denaturation, mostly by rain or eaten by squirrels and/ or primates.

Due to a long walking distance to reach sampling sites within the forest, traps were visited once a day, and caught specimens were collected and stored in glassine envelopes for later identification, and the establishment of a collection at the Center of Excellence in Biodiversity at the University of Rwanda. Collected specimens were identified to morpho-species level using available literature (Carder & Tindimubona, 2002; Kielland, 1990; Larsen, 2005a, 2005b; Liseki & Vane-Wright, 2016; Martins & Collins, 2016; Vande Weghe, 2010; Woodhall, 2005) and an online encyclopaedia of Afrotropical butterflies and skippers (https://www.metamorphosis.org.za/?p=articles&s=atb). Butterfly experts in the region were also consulted for species confirmation. All collected voucher specimens will serve to establish a collection at the Center of Excellence in Biodiversity at the University of Rwanda.

TABLE 1 Description of sampled sites with a total of sampled elevation points in each site

Site	Elevation range	Elevation strata	Sampling points
Bigugu	2375–2950	Middle, High	24
Pindura	1900–2350	Low, Middle	19
Uwinka	1975–2444	Low, Middle	19
Bweyeye	1700–1875	Low	8
Cyamudongo	1700–2040	Low	26
Total			96

2.3 | Data analysis

All collected data were recorded in an excel sheet and analysed to assess the diversity and distribution patterns of fruit-feeding butterflies in Nyungwe National Park. Only fruit-feeding butterfly species were considered for analysis and recorded facultative species such as *Amauris*, *Neptis*, *Acraea* and *Issoria* genera were excluded because their data will be published elsewhere. Biodiversity Professional software version 2 (McAleece et al., 1997) was used to calculate biodiversity indices such as Shannon index and evenness (Magurran, 1988) to characterise butterfly species diversity within sampled sites. Species accumulation curve (Gotelli & Colwell, 2011) was performed to assess the species richness and sampling completeness, and Bray–Curtis cluster analysis was used to assess the similarity between three elevation forest zones within different sampled seasons. A regression model was performed to test a relationship between butterfly species distribution and altitude in NNP. An estimator of predictor, Akaike information criteria (AIC) was used to test the best fit model, and a quadratic regression was tested the best fit model ($F = 3.2336$ df = 3, $p = 0.02546$, df = 10, AIC = 579.7391) over a simple linear regression (df = 7, AIC = 583.8273). The best fit model is one with a small AIC.

The elevation distribution range of each species across an elevation gradient in Nyungwe National Park was reported as the minimum and maximum elevation where the species was recorded during the period of the study. We used non-metric multidimensional scaling (NMDS), Bray–Curtis distance square root transformation to represent butterfly communities among sampled sites between Cyamudongo fragment and Nyungwe main forest. An NMDS ordination graph of sampled sites was performed with stress equal to 0.1. A permutational multivariate analysis of variance (PERMANOVA) test was used to test the significant difference of butterfly communities

TABLE 2 Recorded fruit-feeding butterfly specimens and species across sampled sites in Nyungwe National Park

	Fragment	Nyungwe main forest					
Subfamily	Cyamudongo	Bi	Bwe	Pi	Uwi	Total specimens	Species number
Biblidinae	56		6	4	1	67	5
Charaxinae	119	8	129	70	57	383	19
Limenitidinae	47			1	1	49	11
Nymphalinae	49	27	19	30	13	138	6
Satyrinae	339	42	59	89	49	578	15
Total	610	605				1225	56

Abbreviations: Bi, Bigugu; Bwe, Bweyeye; Pi, Pindura; Uwi, Uwinka.

between Cyamudongo and the Nyungwe main forest at $p > 0.05$. Statistical tests were performed using R studio version 4.0.4 (R Core Team, 2021).

3 | RESULTS

For all collected specimens, 1215 individuals with 56 species were recorded, and Charaxinae and Satyrinae groups were dominant (Table 2). These two groups were abundant in primary forest type, Satyrinae within closed canopy and Charaxes open canopy during the period of the study (Table 3).

Of the 56 recorded species, 85.71% (48) of the total species were recorded in Cyamudongo forest fragment and 66.07% (37) within Nyungwe main forest. 51.78% (29) of the total species were shared between Cyamudongo fragment and Nyungwe main forest. Nineteen species were unique to Cyamudongo fragment while eight were for the Nyungwe main forest (Appendix 1). The recorded taxa include endemic AR highland forest species such as *Bicyclus aurivillii*, *B. matuta*, *B. neustetteri*, *B. persimilis*, *Gnophodes grogani* among Satyrinae; *Charaxes nyungwensis*, *C. zoolina mafugensis*, *C. opinatus* among Charaxinae; *Euriphene excelsior* and *Euphaedra barnsi* among Limenitidinae (Davenport, 2002). A performed species accumulation curve for all recorded specimens did not reach an asymptote, which shows an incomplete sampling (Figure 2).

Higher diversity, species richness and abundance were recorded in low elevation forest zone for overall species (Table 4) and the rain season was less species-rich than the dry season and short dry season. Some species were recorded in all three seasons while others were found in one or two seasons. It is the case for example with *Vanessa dimorphica* and *V. schaeneia* which were recorded during all sampling seasons across all elevation forest zones, while within the higher elevation forest zone, the species *Charaxes acuminatus* was only recorded during the rainy season (Appendix 1). However, overall results show a decrease of both butterfly species richness and abundance with increasing altitude in three different seasons (Figure 3). A dendrogram of a performed Bray–Curtis cluster analysis showed more similarity between low and middle elevation forest zones in terms of butterfly species composition (Figure 4). Cyamudongo fragment was species-rich and diversified (Appendix 1). An NMDS ordination of sampled sites within different seasons showed distinct butterfly communities between the Cyamudongo forest fragment and Nyungwe main forest (Figure 5), and a PERMANOVA test showed a significant difference between butterfly communities in two habitats ($F = 2.5267$, $df = 1$, $p = 0.024$).

Majority of the recorded frugivorous butterfly species (76.79%) range between 1700 and 2100 m of altitude, which corresponds to the low elevation forest zone of NNP. A few species such as *Vanessa dimorphica*, *V. schaeneia* and *Charaxes acuminatus* have a large range of elevation distribution. Genus *Vanessa* ranges from 1700 up to 2950 m of altitude, while *Charaxes acuminatus* ranges from 1700 to 2800 m of altitude.

4 | DISCUSSION

4.1 | Species distribution patterns across the elevation gradient in NNP

This study documented higher abundance, species richness and diversity of fruit-feeding butterflies in the low elevation forest zone of Nyungwe National Park, which decline with increasing elevation. This distribution pattern is consistent with dung beetles distribution across an elevation gradient in NNP (Muhirwa et al., 2018). A similar study in the high Mountain of Cameroon has found the same findings as this study, with a peak of fruit-feeding butterfly species at low elevation (Maicher et al., 2019). However, we cannot know if it is really the same distribution pattern, as there is no low elevation stratum (<100 m of altitude) in Nyungwe for comparison to Mount Cameroon. But generally, butterfly distribution in Nyungwe National Park might be influenced by altitude, temperature and forest vegetation structure like in most mountain ecosystems (Bhardwaj et al., 2012; Maleque et al., 2009; Storch et al., 2003).

Most frugivorous butterfly studies have been conducted in Afrotropical low lands (Aduse-Poku et al., 2012; Bossart et al., 2006; Kasangaki et al., 2012; Molleman et al., 2006; Nkongolo &

TABLE 3 Relative abundance (percentage) of recorded frugivorous butterfly species (56 = 100%) per vegetation types and canopy cover in Nyungwe National Park

	Vegetation type				Canopy cover		
Subfamily	Ferns	Marshland	Primary forest	Secondary forest	Closed	Open	Semi open
Biblidinae			5	4	5	4	5
Charaxinae	2	1	17	11	13	18	11
Limenitidinae			8	8	9	6	2
Nymphalinae	2		5	5	5	4	2
Satyrinae	3		13	13	13	11	12
Species richness	7	1	48	41	45	43	32
Relative abundance (%)	12.5	1.79	85.71	73.21	80.36	76.8	57.14

Bapeamoni, 2018; Nyafwono et al., 2014; Roche et al., 2015). Only a few have addressed the issue of altitude on fruit-feeding butterfly diversity and distribution (Maicher et al., 2019). However, there are a few similar studies conducted on Lepidoptera in East African high mountain forests with comparable findings. For example, Axmacher et al. (2004) have documented a decrease of moth species richness with elevation at Mount Kilimanjaro, Tanzania. Moreover, other similar studies conducted across the world have found similar results to Nyungwe. For example, Morina-Martínez et al. (2013), have documented a decrease in butterfly species richness with elevation in high lands of Southern Mexico and another decline of butterfly species richness with elevation was documented in a Mediterranean mountain central Spain (Sanchez-Rodriguez & Baz, 1995). Apart from studies carried out on butterflies, various studies on arthropods have documented a decline of species richness with elevation. For example, Gebert et al. (2020) have documented a decline of dung beetle species richness with elevation at Mount Kilimanjaro and another decline of dung beetles abundance along with an elevation gradient has been reported in a Brazilian tropical mountain ecosystem (Flinte et al., 2011).

Vanessa dimorphica, *V. schaeneia* and *Charaxes acuminatus* have a large elevation distribution range in Nyungwe National Park. This is common for the Genus *Vanessa* like in other mountainous regions (Benítez et al., 2019; Ian, 2017). *Charaxes acuminatus* is believed to occur up to 2700 m at Mount Kilimanjaro (Liseki & Vane-Wright, 2016) among the highest Afrotropical ecosystems. It is probably normal to record it at 2800 m of altitude in Nyungwe National Park.

The diversity and abundance of fruit-feeding butterfly species in primary forests with closed canopy is quite similar in many African forests within the Albertine Rift, where more species are found in closed forests, while a smaller number of species occurs in marshlands (Kasangaki et al., 2012). The observed *Charaxes* abundance in open canopy should be explained by the fact that, in addition to fermented bait attraction, *Charaxes* have a high long-distance dispersal ability to locate their food within their natural habitat (Molleman et al., 2005), and this should have allowed catching more specimens foraging

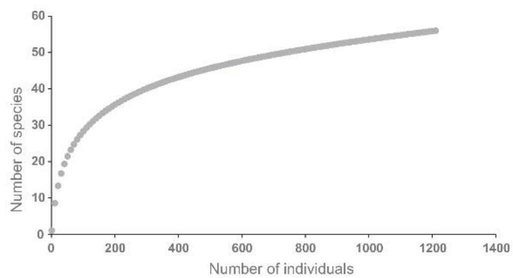


FIGURE 2 Species accumulation curve for all collected fruit-feeding butterflies in Nyungwe National Park

TABLE 4 Overall distribution of fruit-feeding butterfly species in three elevation forest zones and seasonality in NNP

	Elevation forest zone			Season		
	High	Low	Middle	Dry season	Rain season	Short dry season
Number of individuals	58	998	159	726	165	324
Species richness	4	53	21	42	30	37
Shannon index	0.46	1.359	1.068	1.289	1.286	1.316
Evenness	0.764	0.788	0.808	0.794	0.87	0.839

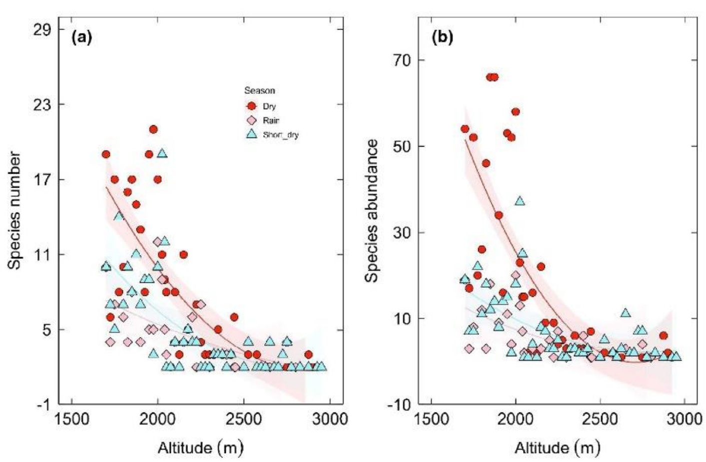


FIGURE 3 Fruit-feeding butterfly species richness (a) and abundance (b) in relation to altitude and seasonality in NNP. The line represents the fitted model, shaded area confidence interval at 95%

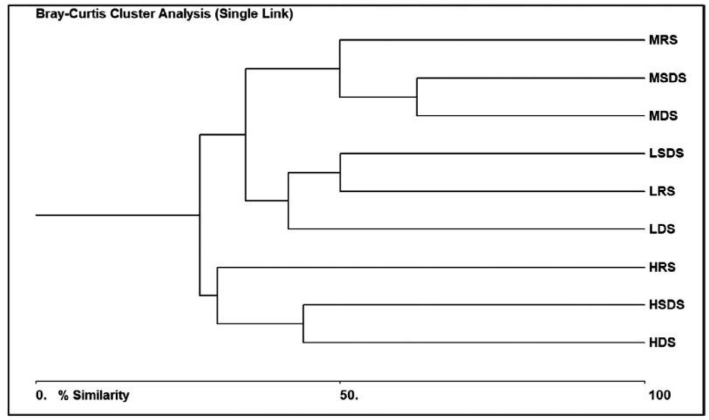


FIGURE 4 Dendrogram showing similarity between three elevation forest zones of NNP with regard to seasonality. HDS, high dry season; HRS, high rain season; HSDS, high short dry season; LDS, low dry season; LRS, low rain season; LSDS, low short dry season; MDS, middle dry season; MRS, middle rain season; MSDS, middle short dry season

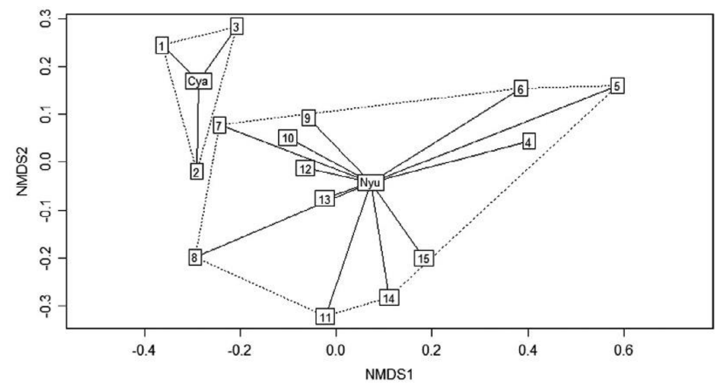


FIGURE 5 Non-metric multidimensional scaling ordination of butterfly communities within sampled sites at Nyungwe National Park, Rwanda. Cya, Cyamudongo fragment; Nyu, Nyungwe main forest; 1, Cyamudongo dry season; 2, Cyamudongo rain season; 3, Cyamudongo short dry season; 4, Bigugu dry season; 5, Bigugu rain season; 6, Bigugu short dry season; 7, Bweyeye dry season; 8, Bweyeye rain season; 9, Bweyeye short dry season; 10, Pindura dry season; 11, Pindura rain season; 12, Pindura short dry season; 13, Uwinka dry season; 14, Uwinka rain season; 15, Uwinka short dry season

throughout the forest. In addition to that, tree branches along tourist trails are regularly cut and this clearing creates openings on the forest understorey. Thus, *Charaxes* would easily fly from canopy forests and visit ground openings (DeVries, 1988; Fermon et al., 2003).

4.2 | Effect of season variation on distribution of fruit-feeding butterflies in NNP

The high abundance and species richness of fruit-feeding butterflies found in Nyungwe during the dry season is similar to the findings at Mount Cameroon (Maicher et al., 2019). Moreover, another study conducted in the highlands of Kenya has also documented more butterfly species in a dry season than rain season (Sagwe et al., 2015). Apart from the Afrotropical regions, dos Santos et al. (2017) have documented more butterfly species richness and abundance between dry and wet seasons in Brazil. Rainy season might probably affect negatively Lepidoptera life, especially their dispersal and egg-laying activity (Maicher et al., 2018) and that would help to explain the rainy season-low abundance and species richness in NNP. However, in Neotropical regions (Beirão et al., 2021; DeVries & Walla, 2001) and in some semi-arid tropical ecosystems (Nobre et al., 2012), the rainy seasons show more abundance for fruit-feeding butterflies, especially canopy species than the dry seasons. Hence, a study on vertical stratification of Nyungwe butterflies including canopy species would help clearly assess the effect of seasonality on the distribution of fruit-feeding butterflies in the Nyungwe mountain forest.

The abundance of fruit-feeding butterflies during the dry season may be due to the food availability, as the dry season corresponds to the fruiting season of most trees in NNP (Sun et al., 1996). A species accumulation curve showed a sampling incompleteness, and with regard to seasonality, the few species recorded in Nyungwe

National Park might be due to season fluctuation (author personal observation). During the sampling period, it was almost raining every day, sometimes it rained the whole day, and due to a long distance, we had to walk to check traps, so some of the specimens may have escaped especially during the rainy season before traps checking started. Hence, a long-term seasonal sampling programme would document more species and help better understand the effect of seasonality on the altitudinal distribution of butterflies in Nyungwe National Park.

4.3 | Cyamudongo fragment versus the main forest of Nyungwe National Park

Cyamudongo fragment was species-rich, diversified than Nyungwe main forest, and shows a strong difference in butterfly assemblage. This is a surprising result. However, despite the reported negative effect of fragmentation on biological diversity (Solé et al., 2004), studies have shown resistance of African forest butterflies to extinction for more than 100 years in some forest remnants (Larsen, 2008). Regardless of fragmentation, larger isolated forest fragments were also found still to maintain a diversity of species (Bossart et al., 2006). Moreover, a study in Kenya has shown the persistence of some forest butterfly species in the fragmented forests, and some species occur only within the fragments (Rogo & Odulaja, 2001). This is consistent with our result here whereby some species were recorded only in Cyamudongo fragment, not in Nyungwe main forest, and vice versa. Apart from similar findings within the tropics, studies also outside the tropics have documented no effect of fragmentation on butterflies within fragmented landscapes. For example, Uehara-Prado et al., (2007) has documented no effect of fragmentation on frugivorous butterflies within a subtropical fragmented forest landscape in Brazil.

The butterfly diversity at Cyamudongo fragment, currently considered as an island in agriculture dominated landscape, should be explained by two hypotheses: on one hand, maybe after fragmentation, species from the surroundings should have used Cyamudongo as a refugia place as far as anthropogenic activities including forest conversion into agriculture increased with time. Unfortunately, we cannot know whether there is a species decline and/ or extinction due to fragmentation. No other study has been conducted before in that fragment. Thus, this study serves as baseline data for comparison with future studies. On the contrary, species richness at Cyamudongo should be due to differences in altitude and sampling effort. Two trails were accessible in Cyamudongo, which may have increased the chances of getting more butterfly specimens. Nevertheless, it is still not understandable because Nyungwe main forest has more diversified habitat types than Cyamudongo and in addition, more traps were set in Nyungwe main forest, which could have caught more species. A study on non-fruit-feeding butterfly groups should be conducted to assess whether the observed distribution pattern would be the same or not.

This study was the first to document the spatial and temporal distribution of fruit-feeding butterflies in the Nyungwe tropical montane rainforest. The study has provided baseline data to researchers for further studies. Conservationists including park managers need to establish a scheme for future monitoring of climate change effects on Nyungwe biodiversity locally and the Albertine rift region in general. Changes in altitudinal ranges are anticipated as a result of warmer temperatures. A similar study should be extended to other butterfly groups in order to have complete baseline data on the ecology of all butterfly groups of Nyungwe and their distribution along the elevation gradient as has been in Mount Kilimanjaro (Liseki & Vane-Wright, 2011, 2013, 2014, 2016, 2018).

ACKNOWLEDGEMENTS

We thank Rwanda Development Board (RDB)-Conservation and tourism department for their authorisation to conduct this research in Nyungwe National Park. Our thanks go to Nyungwe National Park rangers for their help during fieldwork and field assistants Baranyeretse Laurent, Simon Muhayimana and Thacien Hagenimana. We thank also the Center of Excellence in Biodiversity and Natural Resources management for technical assistance during fieldwork. Thanks to Gaël Ruboneka Vande Weghe for his help in butterfly species identification, Eric Dusenge Mirindi and Tobias Frenzel (Mohr) for help in statistical analysis; Joseph Tuyishimire for GIS assistance and Eberhard Fischer and Dorothee Killmann for valuable information on the vegetation of Nyungwe National Park. Finally, we thank Ian Gordon to provide constructive comments on the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict interest that could have influenced the work reported in this paper.

AUTHOR CONTRIBUTIONS

Jean de Dieu Uwizelimana contributed to writing—original draft, conceptualisation, methodology and formal analysis. Donat Nsabimana contributed to supervision and writing—review and editing, Thomas Wagner contributed to supervision, conceptualisation, methodology and writing—review and editing.

DATA AVAILABILITY STATEMENT

Data related to this paper are available at the Dryad repository: https://doi.org/10.5061/dryad.s7h44j18h

ORCID

Jean de Dieu Uwizelimana https://orcid.org/0000-0002-0790-0162

REFERENCES

Aduse-Poku, K., William, O., Oppong, S. K., Larsen, T., Ofori-Boateng, C., & Molleman, F. (2012). Spatial and temporal variation in butterfly biodiversity in a West African forest: Lessons for establishing efficient rapid monitoring programmes. *African Journal of Ecology*, *50*(3), 326–334. https://doi.org/10.1111/j.1365-2028.2012.01328.x

Austin, G. T., & Riley, T. J. (1995). Portable bait traps for the study of butterflies. *Tropical Lepidoptera*, *6*(1), 5–9. Retrieved from https://tropl ep.org/TLR/6-1-part1/pdf003.pdf

Axmacher, J. C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K., & Fiedler, K. (2004). Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, *10*(4), 293–302. https://doi.org/10.1111/j.1366-9516.2004.00101.x

Beirão, M. V., Neves, F. S., & Fernandes, G. W. (2021). Climate and plant structure determine the spatiotemporal butterfly distribution on a tropical mountain. *Biotropica*, *53*, 191–200. https://doi.org/10.1111/btp.12860

Benítez, H. A., Villalobos-Leiva, A., Ordenes, R., & Cruz-Jofré, F. (2019). Elevational record of Vanessa carye (Hübner 1812) (Lepidoptera Nymphalidae) in the northern Chilean Altiplano Highlands. *Nota Lepidopterologica*, *42*, 157–162. https://doi.org/10.3897/nl.42.38549

Bhardwaj, M., Uniyal, V. P., Sanyal, A. K., & Singh, A. P. (2012). Butterfly communities along an elevational gradient in the tons valley, Western Himalayas: Implications of rapid assessment for insect conservation. *Journal of Asia-Pacific Entomology*, *15*, 207–217. https://doi.org/10.1016/j.aspen.2011.12.003

Bobo, K. S., Waltert, M., Fermon, H., Njokagbor, J., & Mühlenberg, M. (2006). From forest to farmland: Butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. *Journal of Insect Conservation*, *10*, 29–42. https://doi.org/10.1007/s10841-005-8564-x

Bonebrake, T. C., Ponisio, L. C., Boggs, C. L., & Ehrlich, P. R. (2010). More than just indicators: A review of tropical butterfly ecology and conservation. *Biological Conservation*, *143*(8), 1831–1841. https://doi.org/10.1016/j.biocon.2010.04.044

Bossart, J. L., Opuni-Frimpong, E., Kuudaar, S., & Nkrumah, E. (2006). Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. *Biodiversity and Conservation*, *15*, 333–359. https://doi.org/10.1007/s10531-005-2574-6

Carder, N., & Tindimubona, L. (2002). *Butterflies of Uganda: A field guide to butterflies and silk moths from the collection of the Uganda society*. The Society.

Chen, I.-C., Hill, J. K., Shiu, H.-J., Holloway, J. D., Benedick, S., Chey, V. K., Barlow, H. S., & Thomas, C. D. (2011). Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography*, *20*(1), 34–45. https://doi.org/10.1111/j.1466-8238.2010.00594.x

Davenport, T. R. B. (2002). *Endemic butterflies of the Albertine Rift – An annotated checklist*. Wildlife Conservation Society.

DeVries, P. J. (1988). Stratification of fruit-feeding nymphalid butterflies in a Costa Rican rainforest. *Journal of Research on the Lepidoptera*, *26*(1–4), 98–108.

DeVries, P. J., Alexander, L. G., Chacon, I. A., & Fordyce, J. A. (2012). Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *Journal of Animal Ecology*, *81*, 472–482. https://doi.org/10.1111/j.1365-2656.2011.01922.x

Devries, P. J., Murray, D., & Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a hit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society*, *62*, 343–364.

DeVries, P. J., & Walla, T. R. (2001). Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnean Society*, *74*, 1–15. https://doi.org/10.1006/bij1.2001.0571

DeVries, P. J., Walla, T. R., & Greeney, H. F. (1999). Species diversity in spatial and temporal dimensions of hit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society*, *68*, 333–353. Retrieved from http://www.idealibrary.com

dos Santos, J. P., Iserhard, C. A., Carreira, J. Y. O., & Freitas, A. V. L. (2017). Monitoring fruit-feeding butterfly assemblages in two vertical strata in seasonal Atlantic Forest: Temporal species turnover is lower in the canopy. *Journal of Tropical Ecology*, *33*, 345–355. https://doi.org/10.1017/S0266467417000323

Evangelista, A., Frate, L., Carranza, M. L., Attorre, F., Pelino, G., & Stanisci, A. (2016). Changes in composition, ecology and structure of high-mountain vegetation: A re-visitation study over 42 years. *AoB PLANTS*, *8*, 1–11. https://doi.org/10.1093/aobpla/plw004

Fashing, P. J., Mulindahabi, F., Gakima, J. B., Masozera, M., Mununura, I., Plumptre, A. J., & Nguyen, N. (2007). Activity and ranging patterns of colobus angolensis ruwenzorii in Nyungwe forest, Rwanda: Possible costs of large group size. *International Journal of Primatology*, *28*(3), 529–550. https://doi.org/10.1007/s10764-006-9095-3

Fermon, H., Waltert, M., & Mühlenberg, M. (2003). Movement and vertical stratification of fruit-feeding butterflies in a managed West African rainforest. *Journal of Insect Conservation*, *7*, 7–19.

Fischer, E., & Killmann, D. (2008). Koblenz geographical colloquia, Series biogeographical monographs 1. *Illustrated field guide to the plants of Nyungwe National Park, Rwanda* (1st ed., pp. 1). University of Koblenz-Landau.

Flinte, V., de Freitas, S., de Macedo, M. V., & Monteiro, R. F. (2011). Altitudinal and temporal distribution of Plagiometriona Spaeth, 1899 (Coleoptera, Chrysomelidae, Cassidinae) in a tropical forest in southeast Brazil. *ZooKeys*, *157*, 15–31. https://doi.org/10.3897/zookeys.157.1179

Forister, M. L., McCall, A. C., Sanders, N. J., Fordyce, J. A., Thorne, J. H., O'Brien, J., Waetjen, D. P., & Shapiro, A. M. (2010). Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(5), 2088–2092. https://doi.org/10.1073/pnas.0909686107

Gebert, F., Peters, M. K., Dewenter, I. S., & Moretto, P. (2020). Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. *Journal of Biogeography*, *47*, 371–381. https://doi.org/10.1111/jbi.13710

Gotelli, N. J., & Colwell, R. K. (2011). Estimating species richness. In A. E. Magurran, & B. J. McGill (Eds.), *Biological diversity: Frontiers in measurement and assessment*. Oxford University Press.

Hansen, A. J., Neilson, R. P., Dale, V. H., Flather, C. H., Iverson, L. R., Currie, D. J., & Bartlein, P. J. (2001). Global change in forests: Responses of species, communities, and biomes. *BioScience*, *51*(9), 765–779.

Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Review*, *80*, 489–513. https://doi.org/10.1017/S1464793105006767

Hughes, J. B., Daily, G. C., & Ehrlich, P. R. (1998). Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Revista de Biologia Tropical*, *46*(3), 697–704. https://doi.org/10.15517/rbt.v46i3.20199

Ian, C. S. (2017). Further observations on Lepidoptera larval host plants in the Lowveld, Mpumalanga Province, South Africa. *Metamorphosis*, *28*, 22–25.

Kasangaki, P., Akol, A. M., & Basuta, G. I. (2012). Butterfly species richness in selected west Albertine rift forests. *International Journal of Zoology*, *2012*, 1–7, https://doi.org/10.1155/2012/578706

Kielland, J. (1990). *Butterflies of Tanzania*. Hill House publishers.

Kremen, C. (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications*, *2*(2), 203–217. Retrieved from https://doi.org/10.2307/1941776

La Sorte, F. A., & Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings Royal*

Society London B, 277(1699), 3401–3410. https://doi.org/10.1098/rspb.2010.0612

Larsen, T. B. (2005a). *Butterflies of West Africa plate volume*. Apollo Books.

Larsen, T. B. (2005b). *Butterflies of West Africa text volume*. Apollo Books.

Larsen, T. B. (2008). Forest butterflies in West Africa have resisted extinction ... so far (Lepidoptera: Papilionoidea and Hesperioidea). *Biodiversity and Conservation*, *17*, 2833–2847. https://doi.org/10.1007/s10531-008-9399-z

Lemon, P. E. (1956). A spherical densiometer for estimating forest overstory density. *Forest Science*, *2*, 314–320.

Liseki, S. D., & Vane-Wright, R. I. (2011). Butterflies (Lepidoptera: Papilionoidea) of mount Kilimanjaro: Introduction and family papilionidae. *Journal of Natural History*, *45*(37–38), 2375–2396. https://doi.org/10.1080/00222933.2011.596635

Liseki, S. D., & Vane-Wright, R. I. (2013). Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: Family Pieridae, subfamily Pierinae. *Journal of Natural History*, *48*(25-26), 1543–1583. https://doi.org/10.1080/00222933.2014.886343

Liseki, S. D., & Vane-Wright, R. I. (2014). Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: Family Pieridae, subfamily Pierinae. *Journal of Natural History*, *48*(25–26), 1543–1583. https://doi.org/10.1080/00222933.2014.886343

Liseki, S. D., & Vane-Wright, R. I. (2016). Butterflies (Lepidoptera: Papilionoidea) of mount Kilimanjaro: Nymphalidae subfamilies Libytheinae, Danainae, Satyrinae and Charaxinae. *Journal of Natural History*, *50*(13–14), 865–904. https://doi.org/10.1080/00222933.2015.1091106

Liseki, S. D., & Vane-Wright, R. I. (2018). Butterflies (Lepidoptera: Papilionoidea) of mount Kilimanjaro: Nymphalidae subfamily Helconiinae. *Journal of Natural History*, *52*(39–40), 2511–2552. https://doi.org/10.1080/00222933.2018.1539780

Maes, D., & Dyck, H. V. (2005). Habitat quality and biodiversity indicator performances of a threatened butterfly versus a multispecies group for wet heathlands in Belgium. *Biological Conservation*, *123*, 177–187. https://doi.org/10.1016/j.biocon.2004.11.005

Magurran, A. E. (1988). *Ecological diversity and its measurement*. Princeton University Press.

Maicher, V., Janeček, Š., Sáfián, S., Murkwe, M., Przybyłowicz, Ł., Fokam, E. B., & Tropek, R. (2018). Flying between raindrops: Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon. *Ecology and Evolution*, *8*, 12761–12772. https://doi.org/10.1002/ece3.4704

Maicher, V., Sáfián, S., 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). Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *Journal of Biogeography*, *47*(2), 342–354. https://doi.org/10.1111/jbi.13740

Maleque, A. M., Maeto, K., & Ishii, H. T. (2009). Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Applied Entomology and Zoology*, *44*(1), 1–11. https://doi.org/10.1303/aez.2009.1

Martins, D. J., & Collins, S. (2016). *Pocket guide butterflies of East Africa*. Struk Nature.

McAleece, N., Gage, J. D., Lambshead, J., & Patterson, G. L. J. (1997). *Biodiversity professional*. The Natural History Museum & The Scottish Association for Marine Science.

Mccain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, *14*, 1236–1245. https://doi.org/10.1111/j.1461-0248.2011.01695.x

Molleman, F., Kop, A., Brakefield, P. M., DeVries, P. J., & Zwaan, B. J. (2006). Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodiversity and Conservation*, *15*, 107–121. https://doi.org/10.1007/s10531-004-3955-y

Molleman, F., van Alphen, M. E., Brakefield, P. M., & Zwaan, B. J. (2005). Preferences and food quality of fruit-feeding butterflies in Kibale forest, Uganda. *Biotropica*, *37*(4), 657–663.

Morina-Martínez, A., León-Cortés, J. L., & Regan, H. M. (2013). Climatic and geometric constraints as driving factors of butterfly species richness along a Neotropical elevational gradient. *Journal of Insect Conservation*, *17*, 1169–1180. https://doi.org/10.1007/s10841-013-9598-0

Muhirwa, F., Maniragaba, A., & Kaplin, B. A. (2018). Dung beetle distribution, abundance, and diversity along an elevation gradient in Nyungwe National Park, Rwanda: A preliminary survey. *Journal of Entomology and Zoology Studies*, *6*(2), 2637–2640.

Nkongolo, N. V., & Bapeamoni, F. (2018). The effect of land use type on butterfly diversity at Masako forest reserve, Kisangani, democratic republic of Congo. *International Journal of Biodiversity and Conservation*, *10*(3), 131–144. https://doi.org/10.5897/IJBC2017.1160

Nobre, C. E. B., Iannuzzi, L., & Schlindwein, C. (2012). Seasonality of fruit-feeding butterflies (Lepidoptera, Nymphalidae) in a Brazilian semi-arid area. *International Scholarly Research Network Zoology*, *2012*, 1–8. https://doi.org/10.5402/2012/268159

Nyafwono, M., Valtonen, A., Nyeko, P., & Roininen, H. (2014). Fruit-feeding butterfly communities as indicators of forest restoration in an Afro-tropical rainforest. *Biological Conservation*, *174*, 75–83. https://doi.org/10.1016/j.biocon.2014.03.022

Oloya, J., Malinga, G. M., Nyafwono, M., Akite, P., Nakadai, R., Holm, S., & Valtonen, A. (2021). Recovery of fruit-feeding butterfly communities in Budongo forest reserve after anthropogenic disturbance. *Forest Ecology and Management*, *491*, 119087. https://doi.org/10.1016/j.foreco.2021.119087

Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J. K., Pilgrim, J. D., Wilson, M., Languy, M., & Moyer, D. (2007). The biodiversity of the Albertine rift. *Biological Conservation*, *134*, 178–194. https://doi.org/10.1016/j.biocon.2006.08.021

Plumptre, A. J., Masozera, M., Fashing, P. J., McNeilage, A., Ewango, C., Kaplin, B. A., & Liengola, I. (2002). *Biodiversity surveys of the Nyungwe forest reserve in S.W.Rwanda*. WCS Working Paper no. 19. Retrieved from http://www.wcs.org/science/

Primack, R., & Corlett, R. (2006). *Tropical rain forests, an ecological and biogeographical comparison.* , 2nd edn. Blackwell Publishing.

R Core Team, (2021). *A language and environment for statistical computing*. R foundation for statistical Computing.

Roche, K. N., Piorkowski, J. M., Sanyaolu, R. A., & Cordeiro, N. J. (2015). Vertical distribution of fruit-feeding butterflies with evidence of sex-specific differences in a Tanzanian forest. *African Journal of Ecology*, *53*, 480–486. https://doi.org/10.1111/aje.12234

Rogo, L., & Odulaja, A. (2001). Butterfly populations in two forest fragments at the Kenya coast. *African Journal of Ecology*, *39*, 266–275. https://doi.org/10.1046/j.1365-2028.2001.00313.x

Rydon, A. (1964). Notes on the use of butterfly traps in East Africa. *Journal of the Lepidopterists' Society*, *18*(1), 51–58.

Sagwe, R. N., Muya, S. M., & Maranga, R. (2015). Effects of land use patterns on the diversity and conservation status of butterflies in Kisii highlands, Kenya. *Journal of Insect Conservation*, *19*, 1119–1127. https://doi.org/10.1007/s10841-015-9826-x

Sanchez-Rodriguez, J. F., & Baz, A. (1995). The effects of elevation on the butterfly communities of a mediterranean mountain, sierra de Javalambre, central spain. *Journal of the Lepidopterists' Society*, *49*(3), 192–207. Retrieved from http://biostor.org/reference/115911

Sheldon, K. S., Yang, S., & Tewksbury, J. J. (2011). Climate change and community disassembly: Impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, *14*, 1191–1200. https://doi.org/10.1111/j.1461-0248.2011.01689.x

Solé, R. V., Alonso, D., & Saldaña, J. (2004). Habitat fragmentation and biodiversity collapse in neutral communities. *Ecological Complexity*, *1*, 65–75. https://doi.org/10.1016/j.ecocom.2003.12.003

Spehn, E. M., Rudmann-Maurer, K., & Körner, C. (2011). Mountain biodiversity. *Plant Ecology and Diversity*, *4*(4), 301–302. https://doi.org/10.1080/17550874.2012.698660

Storch, D., Konvicka, M., Benes, J., Martinkova, J., & Gaston, K. J. (2003). Distribution patterns in butterflies and birds of the Czech Republic: Separating effects of habitat and geographical position. *Journal of Biogeography*, *30*, 1195–1205.

Sun, C., Kaplin, B. A., Kristensen, K. A., Munyaligoga, V., Mvukiyumwami, J., Kajondo, K. K., & Moermond, T. C. (1996). Tree phenology in a tropical Montane forest in Rwanda. *Biotropica*, *28*(4b), 668–681. Retrieved from http://www.jstor.org/stable/2389053. https://doi.org/10.2307/2389053

Syaripuddin, K., Sing, K., & Wilson, J. (2015). Comparison of butterflies, bats and beetles as bioindicators based on four key criteria and DNA barcodes. *Tropical Conservation Science*, *8*(1), 138–149. https://doi.org/10.1177/194008291500800112

Tedrow, R., Nathan, K., Richard, N., & Svenson, G. J. (2014). A new species of Dystacta Saussure, 1871 from Nyungwe National Park, Rwanda (Insecta, Mantodea, Dystactinae). *ZooKeys*, *410*, 1–21. https://doi.org/10.3897/zookeys.410.7053

Uehara-Prado, M., Brown, K. S., & Freitas, A. V. L. (2007). Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: Comparison between a fragmented and a continuous landscape. *Global Ecology and Biogeography*, *16*, 43–54. https://doi.org/10.1111/j.1466-8238.2006.00267.x

Valtonen, A., Molleman, F., Chapman, C. A., Carey, J. R., Ayres, M. P., & Roininen, H. (2013). Tropical phenology: Bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage. *Ecosphere*, *4*(3), 36.

Vande Weghe, G. R. (2010). *Papillons du Gabon*. Wildlife Conservation Society.

Whitworth, A., Villacampa, J., Brown, A., Huarcaya, R. P., Downie, R., & MacLeod, R. (2016). Past human disturbance effects upon biodiversity are greatest in the canopy; A case study on rainforest butterflies. *PLoS One*, *11*(3), e0150520. https://doi.org/10.1371/journal.pone.0150520

Williams, S. E., Bolitho, E. E., & Fox, S. (2003). Climate change in Australian tropical rainforests: An impending environmental catastrophe. *Proceedings Royal Society London B*, *270*, 1887–1892. https://doi.org/10.1098/rspb.2003.2464

Wood, B., & Gillman, M. P. (1998). The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. *Biodiversity and Conservation*, *7*, 597–616. https://doi.org/10.1023/A:1008800317279

Woodhall, S. (2005). *Field guide to butterflies of South Africa*. Struik Nature.

Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., & Wilkes, A. (2009). The melting Himalayas: Cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology*, *23*(3), 520–530. https://doi.org/10.1111/j.1523-1739.2009.01237.x

How to cite this article: Uwizelimana, J. D. D., Nsabimana, D., & Wagner, T. (2022). Diversity and distribution of Fruit-feeding butterflies (Lepidoptera: Nymphalidae) in Nyungwe National Park, Rwanda. *African Journal of Ecology*, *00*, 1–12. https://doi.org/10.1111/aje.12997

APPENDIX 1

SPECIES LIST AND INDIVIDUAL NUMBERS OF FRUIT-FEEDING BUTTERFLIES RECORDED IN NYUNGWE NATIONAL PARK, SEASONALITY AND THEIR ELEVATION DISTRIBUTION RANGE. SPECIES IN BOLD ARE ENDEMICS TO THE ALBERTINE RIFT REGION. DS, DRY SEASON; RS, RAIN SEASON; SDS, SHORT DRY SEASON

	Fragment			Main forest			
Species	DS	RS	SDS	DS	RS	SDS	Elevation range
Ariadne pagenstecheri (Suffert, 1904)	9	1	1	1		2	1725–2225
Aterica galene extensa Heron, 1909	2	2					1700–1950
Bebearia sophus monforti Hecq, 1990	2						1975
Bicyclus aurivillii kivuensis (Joicey & Talbot, 1924)				3	5	30	2500–2875
Bicyclus cf. smithi (Aurivillius, [1899])	49	33	18	3		3	1700–2200
Bicyclus dentata (Sharpe, 1898)	17	3	4	28	8	14	1700–2275
Bicyclus jefferyi Fox, 1963	34			5	2	2	1700–1975
Bicyclus mandanes Hewitson, 1873	4						1700–1925
***Bicyclus matuta matuta* (Karsch, 1894)**		1		31	8	15	1825–2425
Bicyclus mesogena ugandae (Riley, 1926)	10	2	2	17	3	5	1750–2250
***Bicyclus neustetteri* (Rebel, 1914)**		1		8	8	8	1900–2525
***Bicyclus persimilis* (Joicey & Talbot, 1921)**	18	3	2	1	1		1750–2050
Bicyclus safitza safitza (Westwood, [1850])			1				1775
Bicyclus sandace (Hewitson, 1877)	6						1750
Bicyclus sophrosyne sophrosyne (Plötz, 1880)		6					1950
Bicyclus vulgaris (Butler, 1868)	3						1700–1850

Species	Fragment			Main forest			Elevation range
	DS	RS	SDS	DS	RS	SDS	
Evena crithea (Drury, 1773)	1			1			1950–1975
Charaxes acuminatus kigezia van Someren, 1963	4	1	4	32	7	24	1700–2800
Charaxes ameliae ameliae Doumet, 1861			1				2040
Charaxes brutus alcyone Stoneham, 1943	13	4	2	33	7	10	1700–2325
Charaxes candiope (Godart, [1824])	21	10	21	52	4	18	1700–2350
Charaxes druceanus obscura Rebel, 1914					1		2250
Charaxes etesipe (Godart, [1824])	1						1750
Charaxes eudoxus lequeuxi Plantrou, 1982	1			8	1		1700–2150
Charaxes eupale (Drury, 1782)				1			1700
Charaxes imperialis werneri Turlin, 1989				22	5	2	1700–2225
***Charaxes nyungwensis* Vingerhoedt & Vandeweghe 2011**	1		1			1	1850–2025
Charaxes numenes aequatoralis van Someren, 1972)	2		3			1	1850–2000
***Charaxes opinatus* Heron, 1909**				1			2225
Charaxes pleione delvauxi Turlin, 1987		1		2	1	3	1700–2025
Charaxes pollux pollux (Cramer, 1775)	1	1	4				1775–2040
Charaxes saturnus Butler, 1866				1			1700
Charaxes tiridates tiridatinus Röber, 1936	5	3	12	4	5		1700–2150
Charaxes varanes vologeses (Mabille, 1876)				1			1750
Charaxes xiphares burgessi van Son, 1953				5	1	1	2000–2025
***Charaxes mafugensis* Jackson, 1956**		1	1	6	2	2	1700–2444
Cymothoe herminia johnstoni (Butler, 1902)			16				1700–2040
***Euphaedra barnsi* Joicey & Talbot, 1922**			1				2025
Euphaedra harpalyce dowsetti Hecq, 1990			1				1875
Euriphene butleri remota Hecq, 1994			1				2025
***Euriphene excelsior* (Rebel, 1911)**		2			1		200–2200
Eurytela dryope angulata Aurivillius, [1899]	1			1			1825–1975
Eurytela hiarbas hiarbas (Drury, 1782)	7		11			1	1700–2040
***Gnophodes grogani* Sharpe, 1901**	3			3			1825–2050
Harma theobene superna (Fox, 1968)			8				1700–2040
Junonia gregorii Butler, 1896			1				2025
Kallimoides rumia rattrayi (Sharpe, 1904)	5	3	1	1			1700–1850
Melanitis leda (Westwood, [1851])	119			26	1	1	1700–2250
Protogoniomorpha parhassus (Drury, 1782)	3						1875
Pseudacraea eurytus eurytus (Linnaeus, 1758)			1				1700
Pseudacraea lucretia protracta (Butler, 1874)		5	5				1700–2025
Sevenia boisduvali omissa (Rothschild, 1918)	8	1	2	2	1		1700–2100
Sevenia garega (Karsch, 1892)	9	6		3			1800–2025
Vanessa dimorphica dimorphica (Howarth, 1966)	8		3	17	1	22	1800–2925
Antanartia schaeneia dubia Howarth, 1966	11	2	11	29		18	1725–2950
Vanessula milca latifasciata Joicey & Talbot, 1928)			1			1	1700–2025
Shannon diversity index	1.29			1.25			
Evenness	0.77			0.8			
Species richness	48			37			

2.3 A preliminary species checklist of butterflies of Nyungwe National Park

The butterflies of Nyungwe National Park, Rwanda (Lepidoptera: Rhopalocera, Papilionoidea)

● JEAN DE DIEU UWIZELIMANA

Abstract. An inventory of butterflies of Nyungwe National Park, Rwanda was conducted from late September 2019 to early September 2020 with the aim of establishing a first preliminary list of butterfly species occurring in the park. Butterfly sampling was conducted seasonally and specimens were collected using butterfly hand net, fermented bananas traps, and opportunistic sampling. A total of 242 species including 28 Albertine rift endemics were recorded and the dry season was the most species-rich among the sampled seasons. Given that the butterfly sampling was incomplete, an extended sampling period is recommended to add more species to the list.

Zusammenfassung. Eine Erfassung der Tagfalter im Nyungwe National Park, Rwanda wurde von September 2019 bis September 2020 durchgeführt. Hiermit sollte eine vorläufige Liste der Arten aus dem Nationalpark erstellt warden. Die Tagfalter wurde zur Trocken- und Regenzeit durch Handfang (Schmetterlingsnetz) und Köderfallen mit faulendem Obst entlang von Transketen erfasst, welche die gesamte Höhenspanne des Waldes berücksichtigen. Die Erfassung erfolgten im geschlossenen Nyungwe NP sowie im etwa zehn Kilometer südwestlich liegenden, isolierten Fragment des Cyamudongo Forest. Zudem erfolgten einige Nachweise zufällig. Insgesamt konnten 242 Arten, darunter 28 endemische Arten des Albertine Rift nachgewiesen werden, mit der höchsten Diversität in der Trockenzeit. Trotz der, zumal für temperate Gebiete, sehr hohen Artenzahl, dürfte dass bei Weitem nicht der Gesamtbestand der Tagfalter sein und weitere Untersuchungen sind hier angeraten.

Key words. Biodiversity, butterfly, inventory, rainforest, seasonality, Nyungwe National Park, Rwanda, Albertine Rift, Afrotropical Region.

Introduction

Tropical rainforests including Afrotropical regions are considered as sinks of terrestrial biodiversity worldwide and this has led to their protection as either National Parks and /or forest reserves. In some Afrotropical regions such as Rwanda, rainforests are still threatened with the increase of the human population which mostly depend on them for their subsistence (MAY 1995). This overexploitation constitutes a major threat to the biodiversity of these forests and among the mitigation measures; the government has placed some remaining rainforests under National Parks status to protect the inhabiting biodiversity. It is in that regard Nyungwe forest in Rwanda, which was guarded as a forest reserve since 1933 gained a protection status as a National Park since 2004 to strengthen the preservation of its biodiversity which was threatened by anthropogenic activities including gold mining and extension of agricultural lands (PLUMPTRE et al. 2002, FISCHER & KILLMANN 2008). However, good management and monitoring of the park should rely on knowledge of its hosted biodiversity because we have to protect what we know.

Although Nyungwe is ranked among the most species-rich park in both the number of species and endemism within the Albertine Rift region, it appears from the literature that its biodiversity is still unknown. The only available biodiversity inventory conducted within the park made an emphasis on plants and vertebrates while invertebrates including insects are still poorly known (PLUMPTRE et al. 2002, 2007). In addition, most of the research carried out at Nyungwe has focused on plants (FISCHER & KILLMANN 2008, NYIRAMBANGUTSE et al. 2017, MUJAWAMARIYA et al. 2018, MANISHIMWE et al. 2022), vertebrates such as primates (GROSS-CAMP et al. 2009, GROSS-CAMP & KAPLIN 2011, MOORE et al. 2018), and birds (RURANGWA et al. 2020, 2021) and little has been conducted on insects (TEDROW et al. 2014). However, the insect communities including butterflies are key to the forest ecosystems functioning as they play a big role in plant pollination (BARRIOS et al. 2016, SÁFIÁN 2021) and serve as food for most insectivorous vertebrates such as birds. In addition to their aesthetic value and their role as biodiversity components of the forest ecosystem, butterflies have been also found to be good models for environmental and forest ecosystem change monitoring (KREMEN 1992, NYAFWONO et al. 2014, OLOYA et al. 2021).

Compared to neighbouring countries within the East Africa region little is known about butterfly diversity in Nyungwe National Park. For example, much is known about butterfly diversity in some tropical rainforests of Uganda (BARON et al. 2017, FORBES 2018, CARDER & TINDIMUBONA 2002), Tanzania (KIELLAND 1990, MTUI et al. 2019; LISEKI & VANE-WRIGHT 2011, 2013, 2014, 2016, 2018), Eastern region of the Republic of Congo (DUCARME 2018) and Kenya (LARSEN 1991, KÜHNE et al. 2004). According to Nyungwe management authorities, some individual butterfly surveys have been conducted in Nyungwe mostly by foreign experts but currently, there is no available compiled list for butterfly species of the park. Hence, a preliminary inventory of the butterflies of Nyungwe would provide baseline information on the butterfly diversity of the park on which would base their protection and management policies. Thus, an inventory of butterflies of Nyungwe National Park

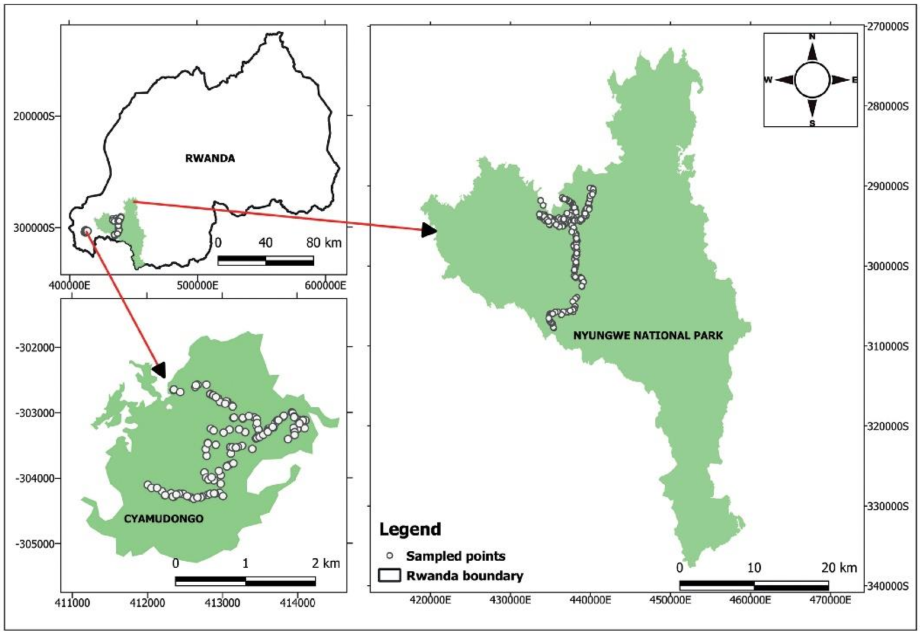


Fig. 1. A map of Nyungwe National Park and Cyamudongo adjacent forest fragment with butterfly sampling points.

was undertaken to establish a preliminary list of butterfly species occurring in the park (Uwizelimana et al. 2021, 2022). This inventory is also part of creating the first butterfly reference collection at the University of Rwanda to serve for teaching and research.

Material and methods

Study site

The butterflies' inventory was conducted in Nyungwe National Park (NNP) and Cyamudongo adjacent remnant forest, Rwanda (Fig. 1). Nyungwe National Park is located in the south-west of Rwanda (2°15'–2°55'S/29°00'–29°30'E), Africa. This park is a 1013 km² montane tropical rainforest with an altitude spanning from 1600 up to 2950 m (Figs 5, 6) within the Albertine Rift (AR), a biodiversity hotspot. The Nyungwe tropical montane forest is among the most Afrotropical rainforests of importance due to its hosted biodiversity including endemic species to AR. It hosts more than 260 tree species, 280 bird species of which 26 are AR endemics, 13 primates species including the endangered population of Chimpanzee (*Pan troglodytes schweinfurthii*), owl-faced guenons (*Cercopithecus hamlyni*), and Angolan black and white colobus monkeys (*Colobus angolensis ruwenzorii*) (Plumptre et al. 2002, 2007). NNP comprises Nyungwe main forest block and Cyamudongo adjacent forest fragment. Cyamudongo forest fragment (2°33.12'S/28°59.49'E) with around (400 km²) and elevation spanning from 1500 up to around 2140 m is located at ten kilometres from Nyungwe main forest block and was disconnected to Nyungwe around 100 years due to agriculture, and protected as part of Nyungwe National Park since 2004 (Fischer & Killmann 2008). The mean annual rainfall in Nyungwe spans from 1500 to 2500 mm, while the mean average temperature ranges from 10.9 to 19.6°C (Sun et al. 1996, Seimon 2012; Nyirambangutse et al. 2017, Mujawamariya et al. 2018).

Butterfly sampling

Butterfly sampling was conducted from late September 2019 to early September 2020. Sampling was conducted in both Nyungwe main forest block and Cyamudongo adjacent remnant forest (Fig. 1) using butterfly hand net (Fig. 8) and fruit-baited traps (Fig. 7; Austin & Riley 1995, Molleman et al. 2006, Devries et al. 2012) along existing tourist trails. These trails were used because the site is very steep and not easy to walk on to design random standard sampling transects. Much effort was made to catch every butterfly individual encountered within five metres width along the trail walk (Pollard 1977). Traps baited with fermented bananas and pineapples were set on either side of the trail at each 25 m elevation interval and were hanged at least one metre from the forest ground understorey. A few

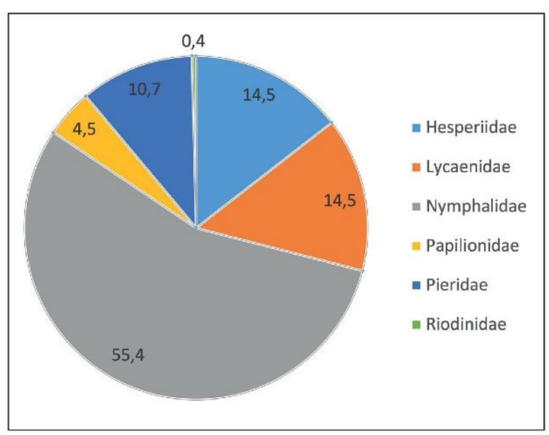


Fig. 2. Proportion (%, n = 242) of recorded butterfly species within their respective families in Nyungwe National Park, Rwanda.

opportunistic samplings were also conducted out of the trails where possible like around waterfalls to maximize the chance of recording the majority of species occurring in NNP. The total walked trails were around 40 km in Nyungwe main forest block and four kilometres in Cyamudongo forest fragment. Sampling was conducted in three seasons occurring in Nyungwe which correspond respectively to rain season (September to December 2019), short dry season (January to March 2020), and dry season (June to early September 2020). Sampling was governed by the sun and started in the morning with the sunrise, and ended in the afternoon with the sunset depending on the weather of the day, shade, and site accessibility. Butterflies were sampled four consecutive days each season and collected specimens were stored in envelopes and labelled for later identification. GPS coordinates were also recorded for each collected specimen. Identification of collected specimens was performed using identification keys, field guide books, and other relevant available literature on Afrotropical butterflies (LARSEN 1991, 2005A, 2005B; MARTINS & COLLINS 2016, VAN DE WEGHE 2010, KIELLARD 1990, WOODHALL 2005; LISEKI & VANE-WRIGHT 2011, 2013, 2014, 2015, 2018). Lepidopterist experts in the region were consulted for species confirmation. All collected specimens were brought to the University of Rwanda to establish the first butterfly collection within the zoological collection at the Center of Excellence in Biodiversity and Natural Resource Management (CoEB).

Data analysis

For all collected specimens a proportion of each butterfly family among the recorded species was computed by taking the species number in each family divided by the total number of species recorded throughout the whole survey. Individuals-species accumulation curve (GOTELLI & COLWELL 2011) was performed to assess the level of sampling completeness. Biodiversity professional version two was used to assess the similarity in species composition among the sampled seasons.

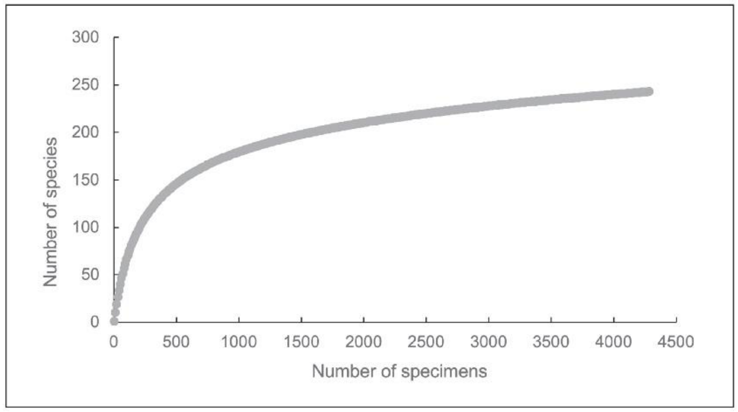


Fig. 3. Individuals-species accumulation curve of the recorded butterfly species in Nyungwe National Park, Rwanda.

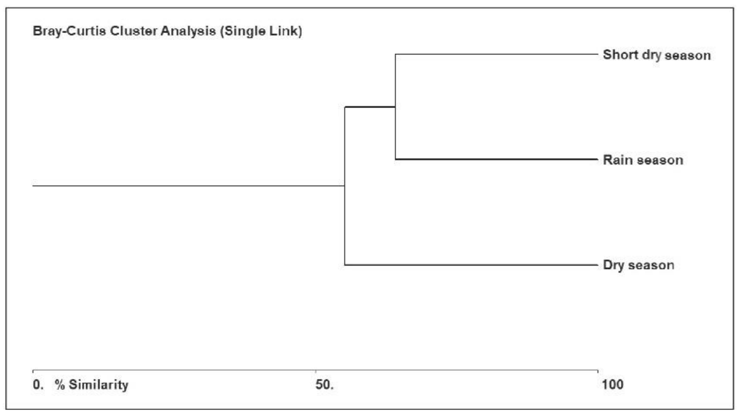


Fig. 4. Cluster analysis dendrogram showing similarities between seasons in terms of butterfly species composition in Nyungwe National Park.

Figs 5, 6. Nyungwe landscape views. **5.** To the top of Mt Bigugu (2950 m). **6.** Middle elevation cloud forest stratum of Nyungwe National Park (Pindura 2370 m).

Tab. 1. A list of butterfly species recorded in Nyungwe National Park, the site from which they were collected, and the method by which each species was collected. Cya: Cyamudongo, Nyu: Nyungwe main forest block. Species with (*) are endemic to the Albertine Rift.

Taxon	Cya	Nyu	Net	Trap
HESPERIIDAE				
Coeliadinae				
Coeliades forestan forestan (Stoll, [1782])	X		X	
Hesperiinae				
Borbo borbonica borbonica (Boisduval, 1833)		X	X	
Borbo fatuellus fatuellus (Hopffer, 1855)		X	X	
Ceratrichia semlikensis Joicey & Talbot, 1921	X	X	X	
Chondrolepis cynthia Evans, 1936*		X	X	
Gegenes niso (Linnaeus, 1764)		X	X	
Gorgyra aretina (Hewitson, 1878)	X		X	
Gorgyra bibulus Riley, 1929		X	X	
Paracleros biguttulus (Mabille, 1889)	X		X	
Pardaleodes tibullus torensis Bethune-Baker, 1906	X	X	X	
Pelopidas mathias (Fabricius, 1798)		X	X	
Platylesches cf. moritili (Wallengren, 1857)		X	X	
Platylesches galesa (Hewitson, 1877)	X		X	
Platylesches rasta Evans, 1937		X	X	
Semalea pulvina (Plötz, 1879)		X	X	
Semalea sextilis (Plötz, 1886)		X	X	
Torbenlarsenia perobscura (Druce, 1912)	X		X	
Heteropterinae				
Metisella midas midas (Butler, 1894)		X	X	
Metisella orientalis orientalis (Aurivillius, [1925])		X	X	
Pyrginae				
Apallaga kivuensis (Joicey & Talbot, 1921)	X	X	X	
Apallaga rwandae Libert, 2014*	X	X	X	
Bettonula bettoni (Butler, 1902)		X	X	
Celaenorrhinus mediostictus mediostictus Libert, 2014	X	X	X	
Celaenorrhinus proxima (Mabille, 1877)		X	X	
Tagiadinae				
Eagris lucetia (Hewitson, 1875)	X	X	X	
Eagris subalbida aurivillii (Neustetter, 1927)	X		X	
Eagris tigris kayonza Evans, 1956	X		X	
Eretis buamba Evans, 1937	X		X	
Eretis herewardi herewardi Riley, 1921		X	X	
Eretis lugens (Rogenhofer, 1891)		X	X	
Eretis mitiana Evans, 1937	X	X	X	
Netrobalane canopus (Trimen, 1864)	X		X	
Sarangesa haplopa Swinhoe, 1907	X	X	X	
Spialia ploetzi ploetzi (Aurivillius, 1891)		X	X	
Tagiades flesus (Fabricius, 1781)	X		X	
LYCAENIDAE				
Aphnaeinae				
Aphnaeus orcas (Drury, 1782)		X	X	
Lipaphnaeus aderna pan (Talbot, 1935)	X		X	
Miletinae				
Spalgis lemolea lemolea Druce, 1890	X		X	
Polyommatinae				
Anthene definita definita (Butler, 1899)		X	X	
Anthene hobleyi kigezi Stempffer, 1961		X	X	
Anthene larydas (Cramer, [1780])	X	X	X	
Anthene ligures ligures (Hewitson, 1874)	X	X	X	
Azanus mirza (Plötz, 1880)	X	X	X	
Cacyreus lingeus (Stoll, [1782])	X	X	X	
Cacyreus palemon (Stoll, [1782])		X	X	
Euchrysops malathana (Boisduval, 1833)		X	X	
Harpendyreus kisaba (Joicey & Talbot, 1921)*		X	X	
Harpendyreus marungensis wollastoni (Bethune-Baker, 1926)		X	X	
Lampides boeticus (Linnaeus, 1767)		X	X	
Leptotes babaulti (Stempffer, 1935)		X	X	
Leptotes pirithous (Linnaeus, 1767)		X	X	
Phlyaria cyara tenuimarginata (Grünberg, 1908)		X	X	
Thermoniphas albocoerulea Stempffer, 1956*		X	X	
Tuxentius margaritaceus (Sharpe, 1892)	X	X	X	
Uranothauma delatorum Heron, 1909		X	X	
Uranothauma falkensteini (Dewitz, 1879)	X	X	X	
Uranothauma heritsia intermedia (Tite, 1958)	X	X	X	
Uranothauma lunifer (Rebel, 1914)*		X	X	
Uranothauma nubifer (Trimen, 1895)		X	X	
Zizeeria knysna knysna (Trimen, 1862)	X	X	X	
Theclinae				
Deudorix antalus (Hopffer, 1855)		X	X	
Deudorix kayonza (Stempffer, 1956)	X	X	X	
Hypolycaena hatita ugandae Sharpe, 1904	X	X	X	
Hypolycaena jacksoni Bethune-Baker, 1906		X	X	
Hypolycaena liara liara Druce, 1890	X	X	X	
Iolaus jamesoni (Druce, 1891)		X	X	
Iolaus pseudopollux Stempffer, 1962*		X	X	
Pilodeudorix ankoleensis (Stempffer, 1953)*		X	X	
Pilodeudorix azurea azurea (Stempffer, 1964)	X		X	
Pilodeudorix zela (Hewitson, 1869)		X	X	
NYMPHALIDAE				
Biblidinae				
Ariadne pagenstecheri (Suffert, 1904)	X	X	X	X
Eurytela dryope angulata Aurivillius, [1899]	X	X	X	X
Eurytela hiarbas hiarbas (Drury, 1782)	X	X	X	X
Neptidopsis ophione nucleata Grünberg, 1911	X	X	X	
Sevenia boisduvali omissa (Rothschild, 1918)	X	X	X	X
Sevenia garega (Karsch, 1892)	X	X	X	X
Sevenia occidentalium occidentalium (Mabille, 1876)		X	X	

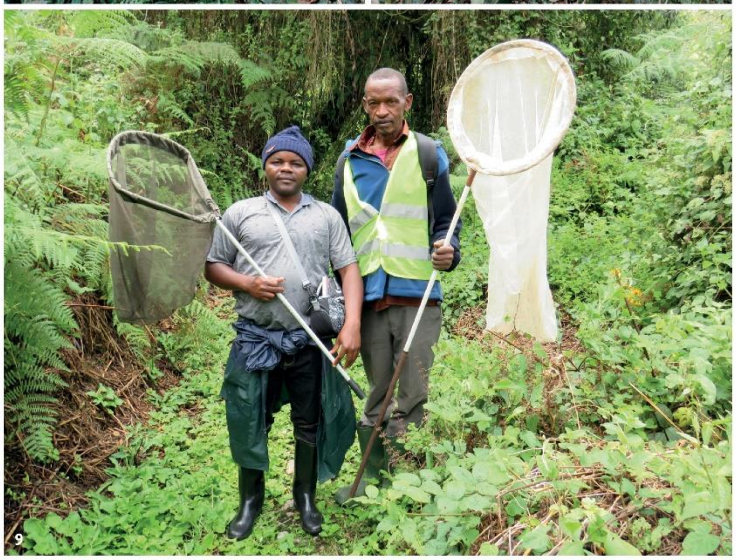
Taxon	Cya	Nyu	Net	Trap
Charaxinae				
Charaxes acuminatus kigezia van Someren, 1963	X	X	X	X
Charaxes ameliae ameliae Doumet, 1861	X		X	X
Charaxes anticlea adusta Rothschild, 1900	X	X	X	X
Charaxes brutus alcyone Stoneham, 1943	X	X	X	X
Charaxes candiope (Godart, [1824])	X	X	X	X
Charaxes cf. etheocles (Cramer, 1777)		X	X	
Charaxes druceanus obscura Rebel, 1914		X	X	X
Charaxes etesipe (Godart, [1824])	X		X	X
Charaxes eudoxus lequeuxi Plantrou, 1982	X	X	X	X
Charaxes eupale (Drury, 1782)		X	X	X
Charaxes imperialis werneri Turlin, 1989		X	X	X
Charaxes mafuga van Someren, 1969*	X	X	X	X
Charaxes mafugensis Jackson, 1956	X	X	X	X
Charaxes numenes aequatoralis van Someren, 1972	X	X	X	X
Charaxes opinatus Heron, 1909*		X	X	X
Charaxes pleione delvauxi Turlin, 1987	X	X	X	X
Charaxes pollux pollux (Cramer, 1775)	X		X	X
Charaxes saturnus Butler, 1866		X	X	X
Charaxes tiridates tiridatinus Röber, 1936	X	X	X	X
Charaxes varanes vologeses (Mabille, 1876)		X		X
Charaxes xiphares burgessi van Son, 1953		X		X
Cyrestinae				
Cyrestis camillus camillus (Fabricius, 1781)	X		X	
Danainae				
Amauris albimaculata magnimacula Rebel, 1914		X	X	
Amauris elliotii elliotii Butler, 1895		X	X	
Amauris hecate Hecate (Butler, 1866)		X	X	
Amauris inferna grogani Sharpe, 1901	X	X	X	X
Amauris niavius niavius (Linnaeus, 1758)	X		X	
Amauris tartarea Mabille, 1876		X	X	
Danaus chrysippus aegyptius (Schreber, 1759)		X	X	
Tirumala formosa mercedonia (Karsch, 1894)	X		X	
Heliconiinae				
Acraea aganice montana (Butler, 1888)	X	X	X	
Acraea asboloplintha Karsch, 1894	X	X	X	
Acraea cerasa cerita Sharpe, 1906	X	X	X	
Acraea egina egina (Cramer, 1775)	X	X	X	
Acraea eltringhami Joicey & Talbot, 1921	X	X	X	
Acraea hamata Joicey & Talbot, 1922*		X	X	
Acraea kinduana Pierre, 1979	X		X	
Acraea kivuensis kivuensis (Joicey & Talbot, 1927)	X		X	
Acraea parageum parageum (Grose-Smith, 1900)	X		X	
Acraea quadricolor (Rogenhofer, 1891)	X	X	X	
Acraea quirina (Fabricius, 1781)	X		X	

Taxon	Cya	Nyu	Net	Trap
Issoria baumanni baumanni (Rebel & Rogenhofer, 1894)		X	X	X
Lachnoptera anticlia (Hübner, [1819])	X	X	X	
Phalanta eurytis eurytis (Doubleday, [1847])	X	X	X	
Telchinia alicia (Sharpe, 1890)	X		X	
Telchinia amicitiae (Heron, 1909)*		X	X	
Telchinia ansorgei (Grose-Smith, 1898)		X	X	
Telchinia bonasia (Fabricius, 1775)	X	X	X	
Telchinia cinerea (Neave, 1904)	X	X	X	
Telchinia disjuncta (Grose-Smith, 1898)	X	X	X	
Telchinia jodutta iodutta (Fabricius, 1793)	X		X	
Telchinia kalinzu (Carpenter, 1936)	X	X	X	
Telchinia lycoa (Godart, [1819])	X	X	X	
Telchinia melanoxantha (Sharpe, 1891)		X	X	
Telchinia ntebiae ntebiae (Sharpe, 1897)	X	X	X	
Telchinia oreas oreas (Sharpe, 1891)	X	X	X	
Telchinia orestia (Hewitson, 1874)	X	X	X	
Telchinia parrhasia servona (Godart, [1819])	X	X	X	
Telchinia penelope penelope (Staudinger, 1896)	X	X	X	
Telchinia pentapolis pentapolis (Ward, 1871)	X	X	X	
Telchinia pharsalus Ward, 1871	X		X	
Telchinia sotikensis sotikensis (Sharpe, 1892)	X	X	X	
Telchinia toruna (Grose-Smith, 1900)	X	X	X	
Telchinia uvui uvui (Grose-Smith, 1890)	X	X	X	X
Limenitidinae				
Aterica galene extensa (Heron, 1909)	X		X	X
Bebearia dowsetti Hecq, 1990		X	X	
Bebearia sophus monforti Hecq, 1990	X	X	X	X
Cymothoe collarti werneri Beaurain, 1984*	X	X	X	
Cymothoe heliada (Hewitson, 1874)		X	X	
Cymothoe herminia johnstoni (Butler, 1902)	X		X	X
Euphaedra barnsi Joicey & Talbot, 1922*	X	X	X	X
Euphaedra harpalyce dowsetti Hecq, 1990	X	X	X	X
Euphaedra margueriteae Hecq, 1978*	X		X	
Euphaedra medon fraudata van Someren, 1935	X		X	
Euphaedra phosphor Joicey & Talbot, 1921*	X		X	
Euriphene amicia excelsior (Rebel, 1911)*	X	X	X	X
Euriphene butleri remota Hecq, 1994	X	X	X	X
Euryphura chalcis chalcis (Felder & Felder, 1860)	X	X	X	
Evena crithea (Drury, 1773)	X	X	X	X
Hamanumida daedalus (Fabricius, 1775)		X	X	
Harma theobene superna (Fox, 1968)	X	X	X	X
Neptis agouale Pierre-Baltus, 1978	X	X	X	X
Neptis cf. quintilla Mabille, 1890	X	X	X	X
Neptis exaleuca Karsch, 1894		X	X	
Neptis nemetes nemetes Hewitson, [1868]	X	X	X	

Taxon	Cya	Nyu	Net	Trap
Neptis nicoteles HEWITSON, 1874	X		X	
Neptis occidentalis occidentalis ROTHSCHILD, 1918	X	X	X	
Neptis ochracea ochreata GAEDE, 1915	X	X	X	X
Neptis saclava marpessa HOPFFER, 1855	X	X	X	
Neptis serena serena OVERLAET, 1955		X		X
Pseudacraea deludens terrena JACKSON, 1956		X	X	
Pseudacraea dolomena kayonza JACKSON, 1956	X	X	X	
Pseudacraea eurytus eurytus (LINNAEUS, 1758)	X		X	X
Pseudacraea lucretia protracta (BUTLER, 1874)	X	X	X	X
Pseudathyma plutonica plutonica BUTLER, 1902	X	X	X	
Libytheinae				
Libythea labdaca WESTWOOD, [1851]	X	X	X	
Nymphalinae				
Antanartia schaeneia dubia HOWARTH, 1966	X	X	X	X
Hypolimnas anthedon anthedon (DOUBLEDAY, 1845)	X	X	X	
Junonia gregorii BUTLER, 1896	X	X	X	X
Junonia terea tereoides (BUTLER, 1901)	X	X	X	
Kallimoides rumia rattrayi (SHARPE, 1904)	X	X	X	X
Precis octavia sesamus TRIMEN, 1883		X	X	
Precis rauana silvicola SCHULTZE, 1916	X	X	X	
Precis sinuata hecqui BERGER, 1981	X	X	X	
Precis tugela pyriformis (BUTLER, 1896)		X	X	
Protogoniomorpha parhassus (DRURY, 1782)	X	X	X	X
Protogoniomorpha temora temora (FELDER & FELDER, [1867])	X	X	X	
Salamis cacta cacta (FABRICIUS, 1793)	X		X	
Vanessa cardui (LINNAEUS, 1758)		X	X	
Vanessa dimorphica dimorphica HOWARTH, 1966	X	X	X	X
Vanessula milca latifasciata JOICEY & TALBOT, 1928	X	X	X	X
Satyrinae				
Bicyclus aurivillii kivuensis (JOICEY & TALBOT, 1924)*		X	X	X
Bicyclus cf. *smithi* (AURIVILLIUS, 1899)	X			X
Bicyclus dentata (SHARPE, 1898)	X	X		X
Bicyclus jefferyi FOX, 1963	X	X	X	X
Bicyclus mandanes HEWITSON, 1873	X		X	X
Bicyclus matuta matuta (KARSCH, 1894)*	X	X	X	X
Bicyclus mesogena ugandae (RILEY, 1926)	X	X	X	X
Bicyclus neustetteri (REBEL, 1914)*	X	X	X	X
Bicyclus persimilis (JOICEY & TALBOT, 1921)*	X	X	X	X
Bicyclus safitza safitza (WESTWOOD, 1850)	X			X
Bicyclus sandace (HEWITSON, 1877)	X			X
Bicyclus sophrosyne sophrosyne (PLÖTZ, 1880)	X	X	X	X
Bicyclus vulgaris (BUTLER, 1868)	X			X
Gnophodes grogani SHARPE, 1901*	X	X	X	X
Melanitis leda Westwood [1851]	X	X	X	X

Taxon	Cya	Nyu	Net	Trap
Ypthima albida albida BUTLER, 1888		X	X	
PAPILIONIDAE				
Papilioninae				
Graphium policenes policenes (CRAMER, [1775])	X		X	
Papilio chrapkowskoides STORACE, 1952	X	X	X	
Papilio dardanus dardanus BROWN, 1776	X	X	X	
Papilio demodocus demodocus ESPER, [1798]		X	X	
Papilio echerioides joiceyi GABRIEL, 1945	X	X	X	
Papilio hesperus Hesperus WESTWOOD, 1843		X	X	
Papilio jacksoni ruandana LE CERF, 1924	X	X	X	
Papilio leucotaenia ROTHSCHILD, 1908*		X	X	
Papilio mackinnoni mackinnoni SHARPE, 1891	X	X	X	
Papilio nireus nireus LINNAEUS, 1758	X		X	
Papilio phorcas congoanus ROTHSCHILD, 1896	X	X	X	
PIERIDAE SWAINSON, 1820				
Coliadinae				
Catopsilia florella (FABRICIUS, 1775)		X	X	
Colias electo pseudohacate BERGER, 1940		X	X	
Terias brigitta brigitta (STOLL, [1780])		X	X	
Terias desjardinsii regularis BUTLER, 1876	X	X	X	
Terias floricola leonis BUTLER, 1886	X	X	X	
Terias hapale MABILLE, 1882	X	X	X	
Terias hecabe solifera BUTLER, 1875	X	X	X	
Terias mandarinula HOLLAND, 1892		X	X	
Terias senegalensis BOISDUVAL, 1836	X	X	X	
Pierinae				
Appias sabina sabina (FELDER & FELDER, [1865])	X	X	X	
Belenois aurota (FABRICIUS, 1793)		X	X	
Belenois raffrayi extendens (JOICEY & TALBOT, 1927)	X	X	X	
Belenois victoria schoutedeni BERGER, 1953*	X	X	X	
Belenois zochalia agrippinides (HOLLAND, 1896)	X	X	X	
Colotis elgonensis basilewskyi BERGER, 1956	X	X	X	
Leptosia nupta pseudonupta BERNARDI, 1959	X	X	X	
Mylothris agathina richlora SUFFERT, 1904	X	X	X	
Mylothris croceus croceus BUTLER, 1896*		X	X	
Mylothris interposita mafuga BERGER, 1981*		X	X	
Mylothris jacksoni jacksoni SHARPE, 1891		X	X	
Mylothris kiwuensis kiwuensis GRÜNBERG, 1910	X	X	X	
Mylothris marginea JOICEY & TALBOT, 1925		X	X	
Mylothris nagichota rwandensis WARREN-GASH, 2020	X	X	X	
Mylothris polychroma BERGER, 1981*	X	X	X	
Mylothris ruandana ruandana STRAND, 1909*	X	X	X	
Nepheronia argia argia (FABRICIUS, 1775)	X	X	X	
RIODINIDAE GROTE, 1895				
Nemeobiinae				
Afriodinia neavei neavei (RILEY, 1932)	X	X	X	




Figs 7–10. Methods conducted and people involved. **7.** Jean de Dieu Uwizelimana setting butterfly fruit-baited trap. **8.** He is handling caught *Charaxes* specimen in Nyungwe National Park. **9.** With field assistant Laurent Baranyeretse. **10.** Laurent Baranyeretse, Simon Muhayimana, Marc Schendzielorz, Jean de Dieu Uwizelimana, and Thomas Wagner (left to right), southernmost point of Bweyeye transect at the border to Burundi in front of Ruhwa river bridge.

Figs 11–18. Examples of Nyungwe butterflies I. **11.** *Tirumala formosa mercedonia* (Karsch, 1894). **12.** *Amauris hecate hecate* (Butler, 1866). **13.** *Amauris niavius niavius* (Linnaeus, 1758). **14.** *Amauris elliotii elliotii* Butler, 1895. **15.** *Amauris tartarea* Mabille, 1876. **16.** *Danaus chrysippus aegyptius* (Schreber, 1759). **17.** *Mylothris agathina* Cramer, 1779. **18.** *Hypolimnas anthedon anthedon* (Doubleday, 1845).

Figs 19–26. Examples of Nyungwe butterflies II. **19.** *Bebearia sophus* monforti Hecq, 1990. **20.** *Euriphene butleri remota* Hecq, 1994. **21.** *Euriphene excelsior* Rebel 1911. **22.** *Euphaedra margueriteae* Hecq, 1978. **23.** *Cyrestis camillus camillus* (Fabricius, 1781). **24.** *Precis sinuata hecqui* Berger, 1981. **25.** *Protogoniomorpha temora temora* (Felder & Felder, [1867]). **26.** *Nepheronia argia argia* (Fabricius, 1775).


11
12
13
14
15
16
17
18

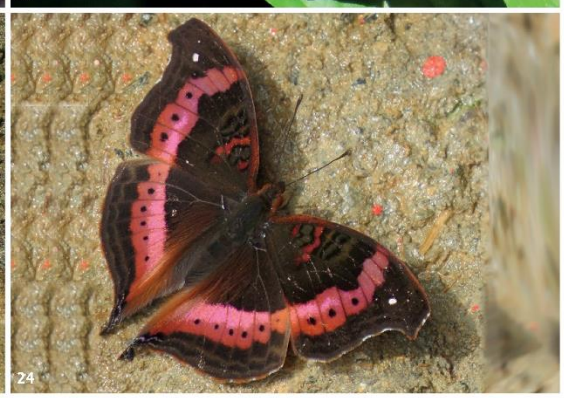

19


20


21


22


23


24


25


26

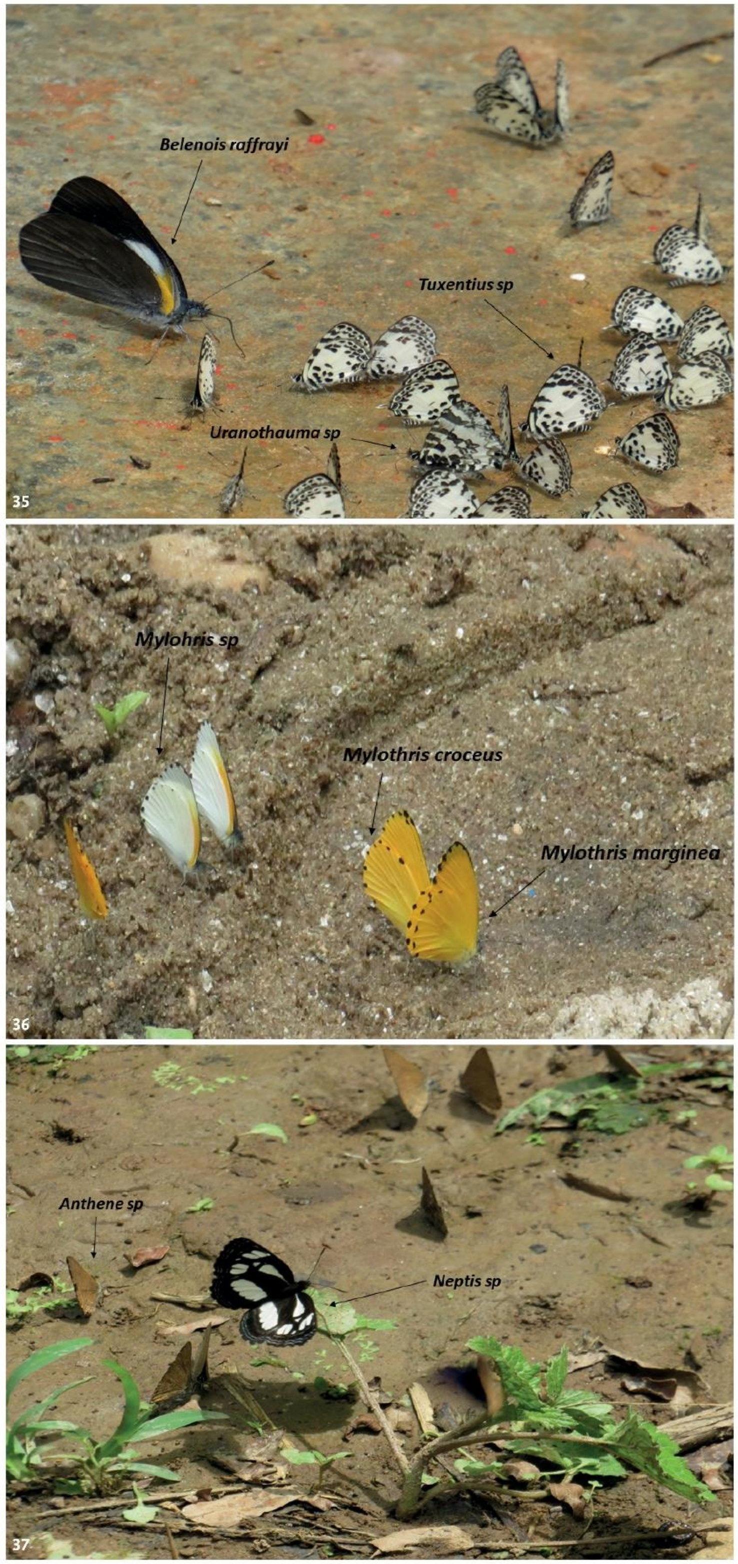

27
28
29
30
31
32
33
34

A Chi-square test was used to test a significant difference in species composition between different sampled seasons at P > 0.05. A species checklist of the butterflies occurring in Nyungwe National Park was compiled. The classification into butterfly taxa in the list follows Wiliams 2015, Dhungel & Wahlberg 2018, and Espeland et al. 2018.

Results

The inventory recorded 242 butterfly species including 28 species that are endemic to the Albertine rift region from a total of 4289 individuals collected (Tab. 1). These endemics are *Acraea hamata, Apallaga rwandae, Belenois victoria, Bicyclus aurivillii, Bicyclus matuta, Bicyclus neustetteri, Bicyclus persimilis, Charaxes mafuga, Charaxes opinatus, Chondrolepis cynthia, Cymothoe collarti, Euphaedra barnsi, Euphaedra margueriteae, Euphaedra phosphor, Euriphene excelsior, Gnophodes grogani, Harpendyreus kisaba, Hypolycaena hatita ugandae, Iolaus pseudopollux, Mylothris croceus, Mylothris interposita mafuga, Mylothris polychroma, Mylothris ruandana, Papilio leucotaenia, Pilodeudorix ankoleensis, Telchinia amicitiae, Thermoniphas albocoerulea,* and *Uranothauma lunifer* (Davenport 2002).

Of the total recorded species, Nymphalids were dominant; follow Hesperiids and Lycaenids (Fig. 2) and some species were common to both Cyamudongo fragment and Nyungwe main forest block while some others were unique to either the fragment or Nyungwe main forest block (Tab. 1). A performed individuals-species



Figs 27–34. Examples of Nyungwe butterflies III. **27.** *Charaxes etesipe* (Godart, [1824]). **28.** *Charaxes numenes aequatoralis* van Someren, 1972. **29.** *Charaxes candiope* (Godart, [1824]). **30.** *Bicyclus aurivillii kivuensis* (Joicey & Talbot, 1924). **31.** *Bicyclus mandanes* Hewitson, 1873. **32.** *Acraea pharsalus* Ward, 1871. **33.** *Harma theobene* Doubleday, [1848]. **34.** *Papilio mackinnoni mackinnoni* Sharpe, 1891, feeding on carnivore dungs.

Figs 35–37. Butterflies mud puddling in Nyungwe National Park (all photographs: J. d. Dieu Uwizelimana).

accumulation curve (Fig. 3) did not reach a plateau, which shows an incomplete sampling. More butterfly species were recorded during the dry season but the short dry season and rain season showed more similarity than the dry season (Fig. 4) and a statistical test showed a significant difference in species composition between the three seasons ($N = 4292$, $X^2 = 1224$, $Df = 484$, $P = 0{,}0001$).

Discussion

The inventory of butterflies of NNP documented 242 butterfly species with the dominance of the Nymphalids group. This finding is similar to the inventories conducted within neighbouring countries of Rwanda. For example, Ducarme 2018 documented a dominance of Nymphalids within the North-Eastern rainforests of the Democratic Republic of Congo, and the same Nymphalids dominance was recorded in a lowland forest ecosystem in Tanzania East of Rwanda (Mtui et al. 2019). Moreover, a similar dominance of Nymphalids has been documented in Kakamega tropical rainforest, Kenya (Kühne et al. 2004). Furthermore, a similar dominance of Nymphalids has been reported by some butterfly inventory studies conducted in other tropical rainforests (Austin et al. 1996, Raguso & Gloster 1993).

The dominance of Nymphalids in NNP should partly be due to the influence of sampling techniques. The majority of this group are fruit feeders as adults and a large number have been captured in fruit-baited traps while a few numbers have been caught by hand net (see Tab. 1). This is for example the case of *Charaxes* and Satyrinae, which were the most attracted by fermented bananas. Hence, they were more caught within traps compared to other groups only recorded with a hand net, and for which their observation was most of the time not easy in inaccessible terrain of Nyungwe forest. Hesperids and Lycaenidae came to second place after Nymphalids while these two groups are the most dominant among the Afrotropical butterflies (Larsen 2005b). Maybe less abundance of these groups is due to their small size, which makes them difficult to observe on the field, especially in the hazardous mountain terrain of Nyungwe. This inaccessibility should also justify the incompleteness of sampling. Thus, maybe a further extended sampling period would add more species to the list including probably some rare and / or localised species.

Nyungwe National Park is ranked the second to host a big number of butterfly species endemic to the Albertine Rift region with 21 species among the 117 species recorded for the whole AR region (Plumptre et al. 2003) and our survey added seven more endemics to the list making a total of 28 butterfly species. However, due to the incompleteness of our sampling, we believe that further extended inventory would possibly add more endemic species to the list.

Some species were unique to either Cyamudongo fragment or Nyungwe main forest block while some others were common to both habitats. Because this study is the first conducted in the park, we cannot attribute the difference in species composition between the two habitats to the forest fragmentation which dated around 100 years ago (Fischer & Killmann 2008), and further studies using for example molecular analysis can be conducted on common species to both habitats to assess whether due to isolation, there is a difference in their genome composition (Williams et al. 2003). Thus, this study should serve as a starting point for future studies to assess the effect of forest fragmentation and habitat loss on butterflies of the Nyungwe National Park.

Acknowledgements. I thank the Rwanda Development Board (RDB) to allow us to conduct this research in Nyungwe National Park. Thanks to Nyungwe Park rangers and field assistants Laurent Baranyeretse, Thacien Hagenimana, and Simon Muhayimana for their help during data collection. I am also grateful to Gaël Ruboneka Vande Weghe, Szabolcs Sáfián, and Steve Collins for their help in species identification. I thank Thomas Wagner and Donat Nsabimana for many discussions and their supervision for this study, which is my PhD-project under the cooperation between Germany Academic Exchange Service (DAAD) and the Government of Rwanda.

References

Austin, G. T., Hadad, N. M., Méndes, C., Sisk, T. D., Murphy, D. D., Launer, A. E. & Ehrlich, P. R. 1996. Annotated checklist of the Butterflies of the Tikal National Park area of Guatemala. *Tropical Lepidoptera* **7** (1): 21–37. Retrieved from http://journals.fcla.edu/troplep/article/view/90056

Austin, G. T. & Riley, T. J. 1995. Portable bait traps for the study of butterflies. *Tropical Lepidoptera* **6** (1): 5–9. Retrieved from https://troplep.org/TLR/6-1-part1/pdf003.pdf

Baron, T., Akite, P., Barnett, M., collins, S. C., Dobson, J., Fric, Z. F. & Ward, P. 2017. The second Afrotropical Lepidoptera Workshop in Uganda – A Contribution to the Lepidoptera Fauna of Kibale National Park and the Mpanga Forest Reserve. *Entomologische Zeitschrift-Schwanfeld* **127** (2): 65–104.

Barrios, B., Pena, S. R., Salas, A. & Koptur, S. 2016. Butterflies visit more frequently, but bees are better pollinators: The importance of mouthpart dimensions in effective pollen removal and deposition. *AoB PLANTS*. https://doi.org/10.1093/aobpla/plw001

Carder, N. & Tindimubona, L. 2002. *Butterflies of Uganda: a field guide to butterflies and silk moths from the collection of the Uganda Society*. The Society.

Davenport, T. R. B. 2002. *Endemic butterflies of the Albertine Rift-an annotated checklist*. Wildlife Conservation Society, Mbeya, Tanzania.

DeVries, P. J., Alexander, L. G., Chacon, I. A. & Fordyce, J. A. 2012. Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *Journal of Animal Ecology* **81**: 472–482. https://doi.org/10.1111/j.1365-2656.2011.01922.x

Dhungel, B. & Wahlberg, N. 2018. Molecular systematics of the subfamily Limenitidinae (Lepidoptera: Nymphalidae). *PeerJ* **6**: e4311. https://doi.org/10.7717/peerj.4311

Ducarme, R. 2018. The butterflies (Lepidoptera: Papilionoidea) of the north-easthern Democratic Republic of Congo. *Metamorphosis* **29**: 23–37.

Espeland, M., Breinholt, J., Willmott, K. R., Warren, A. D., Vila, R., Toussaint, E. F. A. & Kawahara, A. Y. 2018. A Comprehensive and Dated Phylogenomic Analysis of Butterflies. *Current Biology* **28**: 770–778. https://doi.org/10.1016/j.cub.2018.01.061

Fischer, E. & killmann, D. 2008. *Illustrated field guide to the plants of Nyungwe National Rwanda Rwanda* (1st editio). Koblenz geographical colloquia, Series biogeographical monographs 1.University of Koblenz-Landau.

Forbes, S. 2018. The butterflies (Lepidoptera: Papilionidae) of Semuliki National Park, western Uganda. *Metamorphosis* **29**: 14–21. Retrieved from http://metamorphosis.org.za/articlesPDF/1459/2018.05.21 Metamorphosis 29_14-21 Forbes.pdf

Gotelli, N. J. & Colwell, R. K. 2011. Estimating species ricness. In A. E. Magurran & B. J. McGill (Eds.), *Biological diversity: Frontiers in measurement and assessment*. Oxford University Press.

Gross-camp, N. D. & Kaplin, B. A. 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica* **37** (6): 578–586. https://doi.org/10.1016/j.actao.2011.04.003

Gross-camp, N. D., Masozera, M. & Kaplin, B. A. 2009. Chimpanzee seed dispersal quantity in a tropical montane forest of Rwanda. *American Journal of Primatology* **71** (11): 901–911. https://doi.org/10.1002/ajp.20727

Kielland, J. 1990. *Butterflies of Tanzania*. Hill House publishers , London.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* **2** (2): 203–217. Retrieved from http://www.jstor.org/stable/1941776

Kühne, L., Collins, S. C. & Kinuthia, W. 2004.

Check-list of the butterflies of the Kakamega Forest Nature Reserve in western Kenya (Lepidoptera: Hesperioidea, Papilionoidea). *Nachrichten Der Entomologische Verei Apollo* **25** (4): 161–174.

Larsen, T. B. 1991. *The butterflies of Kenya and their natural history*. New York: Oxford University Press Inc.

Larsen, T. B. 2005a. *Butterflies of West Africa Plate volume*. Stenstrup: Apollo Books.

Larsen, T. B. 2005b. *Butterflies of West Africa Text volume*. Stenstrup: Apollo Books.

Liseki, S. D. & Vane-wright, R. I. 2011. Butterflies (Lepidoptera: Papilionoidea) of mount kilimanjaro: Introduction and family papilionidae. *Journal of Natural History* **45** (37–38): 2375–2396. https://doi.org/10.1080/00222933.2011.596635

Liseki, S. D. & Vane-wright, R. I. 2013. Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: family Pieridae, subfamily Pierinae. *Journal of Natural History*. https://doi.org/10.1080/00222933.2014.886343

Liseki, S. D. & Vane-wright, R. I. 2013. Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: family Pieridae, subfamily Pierinae. *Journal of Natural History* **48** (25–26): 1543–1583. https://doi.org/10.1080/00222933.2014.886343

Liseki, S. D. & Vane-Wright, R. I. (2016). Butterflies (Lepidoptera: Papilionoidea) of mount Kilimanjaro: Nymphalidae subfamilies Libytheinae, Danainae, Satyrinae and Charaxinae. *Journal of Natural History* **50** (13–14): 865–904. https://doi.org/10.1080/00222933.2015.1091106

Liseki, S. D. & Vane-wright, R. I. 2018. Butterflies (Lepidoptera: Papilionoidea) of mount kilimanjaro: Nymphalidae subfamily helconiinae. *Journal of Natural History* **52** (39–40): 2511–2552. https://doi.org/10.1080/00222933.2018.1539780

Manishimwe, A., Ntirugulirwa, B., Zibera, E., Nyirambangutse, B., Mujawamariya, M., Dusenge, M. E., … & Wallin, G. 2022. Warming Responses of Leaf Morphology Are Highly Variable among Tropical Tree Species. *Forests* **13**: 219. https://doi.org/https://doi.org/10.3390/f13020219

Martins, D. J. & Collins, S. 2016. *Pocket Guide Butterflies of East Africa*. Struk Nature.

May, J. F. 1995. Policies on population, land use, and environment in Rwanda. *Population and Environment* **16** (4): 321–334. https://doi.org/10.1007/BF02208117

Molleman, F., Kop, A., Brakefield, P. M., Devries, P. J. & Zwaan, B. J. 2006. Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodiversity and Conservation* **15**: 107–121. https://doi.org/10.1007/s10531-004-3955-y

Moore, J. F., Mulindahabi, F., Gatorano, G., Masozera, M. K. & Jennifer moore, C. F. 2018. Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (Pan troglodytes schweinfurthii) in Nyungwe National Park, Rwanda. *American Journal of Physical Anthropology* **80**: e22897. https://doi.org/10.1002/ajp.22897

Mtui, D., Congdon, C., Bampton, I., Kalenga, P. & Leonard, H. 2019. Altitudinal Distribution and Monthly Occurrence of Butterflies in the Kihansi Gorge Forest , Tanzania , with a Checklist of Species. *Tanzania Journal of Science* **45** (4): 543–558.

Mujawamariya, M., Manishimwe, A., Ntirugulirwa, B., Zibera, E., Ganszky, D., Bahati, E. N., … & Uddling, J. 2018. Climate sensitivity of tropical trees along an elevation gradient in rwanda. *Forests* **9**: (647). https://doi.org/10.3390/f9100647

Nyafwono, M., Valtonen, A., Nyeko, P. & Roininen, H. 2014. Fruit-feeding butterfly communities as indicators of forest restoration in an Afro-tropical rainforest. *Biological Conservation* **174**: 75–83. https://doi.org/10.1016/j.biocon.2014.03.022

Nyirambangutse, B., Zibera, E., Uwizeye, F. K., Nsabimana, D., Bizuru, E., Pleijel, H., … & Wallin, G. 2017. Carbon stocks and dynamics at different successional stages in an Afromontane tropical forest. *Biogeosciences* **14** (5): 1285–1303. https://doi.org/10.5194/bg-14-1285-2017

Oloya, J., Malinga, G. M., Nyafwono, M., Akite, P., Nakadai, R., Holm, S. & Valtonen, A. 2021. Recovery of fruit-feeding butterfly communities in Budongo Forest Reserve after anthropogenic disturbance. *Forest Ecology and Management* **491**: 119087. https://doi.org/10.1016/j.foreco.2021.119087

Plumptre, A. J., Behangana, M., Ndomba, E., Davenport, T., Kahindo, C., Kityo, R., … & Owiunji, I. 2003. *The biodiversity of the Albertine Rift. Albertine Rift technical reports no. 3*.

Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., … & Moyer, D. 2007. The biodiversity of the Albertine Rift. *Biological Conservation* **134**: 178–194. https://doi.org/10.1016/j.biocon.2006.08.021

Plumptre, A. J., Masozera, M., Fashing, P. J., Mcneilage, A., Ewango, C., Kaplin, B. A. & Liengola, I. 2002. *Biodiversity surveys of the Nyungwe forest reserve in S.W.Rwanda. WCS working paper no. 19*. Retrieved from http://www.wcs.org/science/

Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. *Biological Conservation* **12**: 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Raguso, R. A & Gloster, O. 1993. Preliminary Checklist and Field Observations of the Butterflies of the Maquipucuna Field Station (Pichincha Province, Ecuador). *Journal of Research on the Lepidoptera* **32**: 135–161.

Rurangwa, M. L., Aguirre-gutiérrez, J., Matthews, T. J., Niyigaba, P., Wayman, J. P., Tobias, J. A. & Whittaker, R. J. 2021. Effects of land-use change on avian taxonomic, functional and phylogenetic diversity in a tropical montane rainforest. *Diversity and Distributions* **27**: 1732–1746. https://doi.org/10.1111/ddi.13364

Rurangwa, M. L., Matthews, T. J., Niyigaba, P., Tobias, J. A. & Whittaker, R. J. 2020. Assessing tropical forest restoration after fire using birds as indicators: An afrotropical case study. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2020.118765

Sáfián, S. 2021. The highly invasive Siam Weed, Chromolaena odorata (L.) King and Robinson (Asteraceae), as a seasonal prime nectar source for butterflies (Lepidoptera: Papilionoidea) and other insects (Insecta: Lepidoptera, Hymenoptera, Coleoptera) in West Africa. *Metamorphosis* **32**: 49–57.

Seimon, A. 2012. *Climatology and Potential Climate Change Impacts in the Nyungwe Forest National Park, Rwanda*. New York, USA. Retrieved from http://www.albertinerift.org/challenges/climatechange/tabid/7525/default.aspx

Sun, C., Kaplin, B. A., Kristensen, K. A., Munyaligoga, V., Mvukiyumwami, J., Kajondo, K. K. & Moermond, T. C. 1996. Tree Phenology in a Tropical Montane Forest in Rwanda. *Biotropica* **28** (4b): 668–681. Retrieved from http://www.jstor.org/stable/2389053

Tedrow, R., Nathan, K., Richard, N. & Svenson, G. J. 2014. A new species of Dystacta Saussure, 1871 from Nyungwe National Park , Rwanda (Insecta , Mantodea, Dystactinae). *ZooKeys* **410**: 1–21. https://doi.org/10.3897/zookeys.410.7053

Uwizelimana, J. de D., Nsabimana, D. & Wagner, Th. 2021. A preliminary butterfly checklist (Lepidoptera: Papilionoidea) for Cyamudongo tropical forest fragment, Rwanda. *Metamorphosis* **32**: 85–95. DOI: https://dx.doi.org/10.4314/met.v32i1.15

Uwizelimana, J. de D., Nsabimana, D. & Wagner, Th. 2022. Diversity and distribution of Fruit-feeding butterflies (Lepidoptera: Nymphalidae) in Nyungwe National Park, Rwanda. *African Journal of Ecology* **60** (2): 1–12. DOI: 10.1111/aje.12997.

Vande Weghe, G. R. 2010. *Papillons du Gabon*. Wildlife Conservation Society.

Williams, B. L., Brawn, J. D. & Paige, K. N. 2003. Landscape scale genetic effects of habitat fragmentation on a high gene flow species: Speyeria idalia (Nymphalidae). *Molecular Ecology* **12**: 11–20.

Williams, M. C. 2015. Classification of the Afrotropical butterflies to generic level. *Metamorphosis* **26**: 102–108.

Woodhall, S. 2005. *Field guide to butterflies of South Africa*. Struik Nature.

● Jean de Dieu Uwizelimana,
Universität Koblenz-Landau, Institut für Integrierte Naturwissenschaften, Biologie, Universitätsstr. 1, 56070 Koblenz, Germany & University of Rwanda, College of Science and Technology, Biology Department, KN 67 Street Nyarugenge, PO Box 3900 Kigali, Rwanda;
E-Mail: juwizelimana@gmail.com

2.4 Effect of altitude and seasonal variation on butterflies distribution in NNP

Note by the author: This chapter is based on the following journal publication. Due to copyright issues, the text of the chapter was replaced by the reference information. Thus, the interested reader is kindly asked to read the published paper via the following reference:

Uwizelimana, J. d. D., Nsabimana, D. & Wagner, T. (Submitted to Biotropica). Altitudinal distribution of butterflies (Lepidoptera: Papilionoidea) in Nyungwe National Park, Rwanda.

Abstract

Although the ecology and distribution of tropical rainforest butterflies are among the best-documented insect groups, there is still a knowledge gap on butterfly diversity in some not yet or underexplored tropical regions such as the Afrotropical high montane ecosystems. These ecosystems are important for biodiversity conservation due to various vegetation types along their altitudinal gradients and their status as refugia for threatened and endemic species. Here we present a study conducted on the altitudinal distribution of butterflies in Nyungwe National Park (NNP), Rwanda. The study aimed at answering the following questions: (a) Which butterfly species occur in Nyungwe National Park? (b) What is the altitudinal distribution range and minimum microclimatic conditions for the occurrence of each species? (c) Which species are likely to be most valuable as indicators of climate change? Butterfly sampling was conducted seasonally along an altitudinal trail using a butterfly net, and air temperature and relative humidity at which each butterfly was collected were recorded. A total of 199 species, including 24 species endemic to the Albertine Rift, were found to occur in NNP, and both species richness and abundance declined with altitude. The highest species richness and abundance were recorded during the dry season, with the greatest record at around 26˚C air temperature and 58% humidity. The study provided baseline data including 18 species for potential use in climate change monitoring and future butterfly research.

Chapter 3 **General discussion**

As more discussion is provided in each of the published papers and the current manuscript, in this section, I will highlight major findings related to the research objectives. Indeed, two hundred forty- two butterfly species including eighteen selected as potential climate change indicators were documented in Nyungwe National Park. More species were recorded during the dry season and species richness declined with increasing elevation. Of the recorded species, Nymphalids were dominant and this is similar to neighbouring tropical rainforests of Rwanda (Ducarme, 2018; Forbes, 2018; Mtui et al., 2019) and other rainforests throughout tropical regions (Austin et al., 1996; Saikia, Kalita, & Saikia, 2010). Furthermore, a similar dominance of the Nymphalids group was documented in a semi-green tropical forest in Bangladesh (Hasan et al., 2018) and at Himalaya , the world highest mountain ecosystem (Joshi & Arya, 2007). The dominance of Nymphalids in Nyungwe should be due to the use of fruit-baited traps which probably attracted more individuals, especially the canopy high moving species such as Charaxes (Habel et al., 2022) than the ones caught by hand net (See Paper III) on one hand, and by the tree phenology on the other hand. The fruiting season of most trees in Nyungwe occurs during the dry season which should also explain their high dry season occurrence (Sun et al., 1996).

Similar to other findings within large African rainforest fragments (Bossart et al., 2006), Nyungwe’s main forest was more species-rich than the Cyamudongo fragment (see Paper III). In addition to the difference in size, we think the species richness of Nyungwe should also be due to the difference in elevation with the elevational different vegetation types offering more heterogeneous ecological niches for different butterfly species colonization than Cyamudongo low land forest. Although some studies have shown no effect of fragmentation on tropical butterflies (Larsen, 2008; Uehara-Prado et al., 2007), due to the small size of the Cyamudongo forest we don't know whether there has been a species decline or loss because this is the first study conducted in the site. Thus, further studies using molecular techniques should assess whether the common species between Nyungwe's main forest and the Cyamudongo fragment have undergone a genomic material change (Fountain et al., 2016) which could lead either to species extinction or speciation within the fragment. Such information would be useful to establish conservation policies such as the establishment of the corridor to allow gene flow between butterfly populations of the two habitats. Given that during the dry season, the Cyamudongo fragment gets more dried probably due to increased edge effects (Murcia, 1995) compared to Nyungwe main forest, and even some of the streams within the fragment dry up (Personal observation), maybe that dryness affects negatively some adult butterfly species due to food scarcity and forces them to migrate to Nyungwe main forest block as some butterfly species have the ability to migrate long-distance around 4000 km (Stefanescu et al., 2016). Hence further studies could then investigate this in the future.

A decrease in butterfly species richness with increasing altitude is concordant with dung beetles (Muhirwa et al., 2018) and land snails distribution in Nyungwe National Park (Boxnick et al., 2015). Unfortunately, there is no other similar study on butterflies conducted within the Albertine rift mountain ecosystems for direct comparison. However similar findings have been documented in some other Afrotropical montane forests although they differ in the sampled elevation habitats (Maicher et al., 2019) and within some other tropical forests (Molina-Martinez et al., 2013). Moreover, other similar studies outside tropical regions have also documented a species decline of fruit-feeding butterflies (Beirão et al.,

2021) and Hesperids (Carneiro et al., 2014) with increasing elevation in mountain ecosytems of Brasil and Himalaya mountain ecosystems (Acharya & Vijayan, 2015). Apart from butterflies, similar altitudinal distribution trends to the butterflies of Nyungwe were documented for other flying insects within tropical forests such as moths at Mt Kilimanjaro (Axmacher et al., 2004) and fruit flies in Papua new Guinea (Finnie et al., 2021). Although there is no available information on the altitudinal distribution of potential host plant species in Nyungwe, we believe that, in addition to environmental factors, the butterfly species decline should also be due to host plant food sources declining with increasing altitude because a study in Itobwe, a nearby mountain forest in the Democratic Republic of Congo showed a woody species richness decline with increasing elevation (Cirimwami et al. 2019). A study on the altitudinal distribution of butterfly host plants would clarify the observed butterfly distribution pattern in Nyungwe National Park.

Butterfly species diversity, richness, and abundance in Nyungwe National Park exhibited seasonal variation (Paper II, IV). Similar findings were documented at Mt Cameroon (Maicher et al., 2018; Mertens et al., 2021) and in a neigbouring tropical forest of Uganda with a great number of butterfly species recorded during the dry season (Valtonen et al., 2013). Moreover, a similar abundance of butterfly species during the dry season was documented in Guatemala’s tropical rainforest (Austin et al., 1996). This seasonal pattern of butterflies of Nyungwe highlights the necessity of taking into account seasonal variation while conducting preliminary biodiversity studies in underexplored ecosystems. It is also very useful for species management and /or monitoring by conservationists and researchers for future studies, especially those targeting individual species such as those that are endemic to the region. Knowledge of their seasonality would help in planning when to observe the targeted species such as the AR endemics and/ or potential climate change indicators. However, because this study was conducted in a short time and seasonality studies require more extended time; further studies could be conducted either by the park management authority or by independent researchers to confirm the observed seasonal pattern in Nyungwe National Park.

Chapter 4 **Acknowledgements**

I would like to thank first Prof Thomas Wagner and Prof Donat Nsabimana for the supervision of this thesis, and Prof Fischer Eberhard for his help to establish my first contact with Thomas Wagner as supervisor. In addition to my thesis supervision, Thomas Wagner made me discover the biodiversity within different ecosystems of Germany through excursions and even visits to Zoos including marine aquariums where I saw a Dolphin among many other marine species for the first time. It was a pleasure to have him as supervisor and conservationist. Thank you very much for your social life and for everything.

I thank all people who contributed to my education from my childhood until the present. Thank you parents for your endless love and to offer me whatever you were able. You made me the man I am now.

My thanks go to Rwanda Development Board for their authorization to conduct this research in Nyungwe National Park and to Innocent Ndikubwimana and his team in charge of research and monitoring in NNP for their assistance with logistics during fieldwork. Park rangers and field assistants Laurent Baranyetse, Simon Muhayimana, and Thacien Hagenimana are thanked for their endless effort to collect butterflies in the challenging terrain of the Nyungwe and the stress due to Covid-19 that occurred during data collection phase. There are many stories to tell about this and thank you for not having abandoned me alone in the forest during that very difficult time.

I thank also my wife Bernadette Mahoro Uwihoreye and my sons Kundwa Ihirwe Elie Bright and Rugwiro Aimé Doran for their support from the beginning to the end of this research. Thanks to Dr. Killmann Dorothee for a valuable book on plants of Nyungwe National Park and Siegmar Seidel for his help in finding accommodation during my stay in Koblenz.

I am very grateful to Gaël R.Vande Weghe, Szabolcs Sáfián, Steve Collins for their expertise and help in species identification, Dusenge Mirind Eric for his help in statical analysis, Joseph Tuyishimire for GIS assistance, Prof Beth Kaplin for her help in proposal writing and Dr. Ian Gordon and Richard I. Vane-Wright for constructive comments on manuscripts.

Thanks to colleagues Tobias Frenzel, Ange Raharivololoniaina, Ronny Richter, Daronja Terense, and the biology staff in Koblenz with whom we shared a good time in the Department of Biology. It was a pleasure working with you.

Finally, I thank the Government of Rwanda for its cooperation with the German Academic Service Exchange (DAAD) under which my Ph.D. was organized, and to everybody who contributed in one way or another to the achievement of this study.

May God bless you all!

Chapter 5 **References**

Acharya, B. K., & Vijayan, L. (2015). Butterfly diversity along the elevation gradient of Eastern Himalaya, India. *Ecological Research*, *30*, 909–919. https://doi.org/10.1007/s11284-015-1292-0

Aduse-Poku, K., William, O., Oppong, S. K., Larsen, T., Ofori-Boateng, C., & Molleman, F. (2012). Spatial and temporal variation in butterfly biodiversity in a West African forest: Lessons for establishing efficient rapid monitoring programmes. *African Journal of Ecology*, *50*(3), 326–334. https://doi.org/10.1111/j.1365-2028.2012.01328.x

Austin, G. T., Hadad, N. M., Méndez, C., Sisk, T. D., Murphy, D. D., Launer, A. E., & Ehrlich, P. R. (1996). Annotated checklist of the Butterflies of the Tikal National Park area of Guatemala. *Tropical Lepidoptera*, *7*(1), 21–37. Retrieved from http://journals.fcla.edu/troplep/article/view/90056

Axmacher, J. C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K., & Fiedler, K. (2004). Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, *10*(4), 293–302. https://doi.org/10.1111/j.1366-9516.2004.00101.x

Ayebare, S., Plumptre, A. J., Kujirakwinja, D., & Segan, D. (2018). Conservation of the endemic species of the Albertine Rift under future climate change. *Biological Conservation*, *220*, 67–75. https://doi.org/10.1016/j.biocon.2018.02.001

Balducci, M. G., Van der Niet, T., & Johnson, S. D. (2019). Butterfly pollination of Bonatea cassidea (Orchidaceae): Solving a puzzle from the Darwin era. *South African*

Journal of Botany, *123*, 308–316. https://doi.org/10.1016/j.sajb.2019.03.030

Barrios, B., Pena, S. R., Salas, A., & Koptur, S. (2016). Butterflies visit more frequently, but bees are better pollinators: The importance of mouthpart dimensions in effective pollen removal and deposition. *AoB PLANTS*, *8*, plw001. https://doi.org/10.1093/aobpla/plw001

Basset, Y., Eastwood, R., Sam, L., Lohman, D. J., Novotny, V., Treuer, T., … Osorio-Arenas, M. A. (2011). Comparison of rainforest butterfly assemblages across three biogeographical regions using standardized protocols. *The Journal of Research on the Lepidoptera*, *44*, 17–28.

Beck, J., & Fiedler, K. (2009). Adult life spans of butterflies (Lepidoptera: Papilionoidea + Hesperioidea): Broadscale contingencies with adult and larval traits in multi-species comparisons. *Biological Journal of the Linnean Society*, *96*, 166–184. https://doi.org/10.1111/j.1095-8312.2008.01102.x

Beirão, M. V., Neves, F. S., & Fernandes, G. W. (2021). Climate and plant structure determine the spatiotemporal butterfly distribution on a tropical mountain. *Biotropica*, *53*, 191–200. https://doi.org/10.1111/btp.12860

Bhardwaj, M., Uniyal, V. P., Sanyal, A. K., & Singh, A. P. (2012). Butterfly communities along an elevational gradient in the Tons valley, Western Himalayas: Implications of rapid assessment for insect conservation. *Journal of Asia-Pacific Entomology*, *15*, 207–217. https://doi.org/10.1016/j.aspen.2011.12.003

Bock, C., Hauck, M., & Fischer, E. (2007). The lichen flora of Rwanda: an annotated checklist. *Willdenowia*, *37*(2), 563. https://doi.org/10.3372/wi.37.37216

Bossart, J. L., Opuni-Frimpong, E., Kuudaar, S., & Nkrumah, E. (2006). Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. *Biodiversity and Conservation*, *15*, 333–359. https://doi.org/10.1007/s10531-005-2574-6

Boxnick, A., Apio, A., Wronski, T., & Hausdorf, B. (2015). *Diversity patterns of the terrestrial snail fauna of Nyungwe Forest National Park (Rwanda), a Pleistocene refugium in the heart of Africa*. Retrieved from https://academic.oup.com/biolinnean/article/114/2/363/2415907

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Carder, N., & Tindimubona, L. (2002). *Butterflies of Uganda:A field guide to butterflies and silk moths from the collection of the Uganda society*. Uganda society.

Carignan, V., & Villard, M. (2002). Selecting indicator species to monitor ecological integrity: A review. *Environmental Monitoring and Assessment*, *78*, 45–61. Retrieved from https://link.springer.com/content/pdf/10.1023/A:1016136723584.pdf

Carneiro, E., Mielke, O., Casagrande, M., & Fiedler, K. (2014). Skipper Richness (Hesperiidae) Along Elevational Gradients in Brazilian Atlantic Forest. *Neotropical Entomology*, *43*, 27–28. https://doi.org/10.1007/s13744-013-0175-8

Chao, A., & Chiu, C.-H. (2016). Species Richness : Estimation and Comparison. *Wiley*

StatsRef: Statistics Reference Online, 1–26. https://doi.org/10.1002/0471667196.ess5051

Chen, I.-C., Hill, J. K., Shiu, H.-J., Holloway, J. D., Benedick, S., Chey, V. K., … Thomas, C. D. (2011). Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. *Global Ecology and Biogeography*, *20*(1), 34–45. https://doi.org/10.1111/j.1466-8238.2010.00594.x

Cómbita, J. L., Giraldo, C. E., & Escobar, F. (2022). Environmental variation associated with topography explains butterfly diversity along a tropical elevation gradient. *Biotropica*, *54*, 146–156. https://doi.org/10.1111/btp.13040

Cordeiro, N. J. (2017). Geographical Consistency in Vertical Stratification Preferences of Butterfly Species in Eastern Africa. *African Entomology*, *25*(2), 550–553. https://doi.org/10.4001/003.025.0550

Crossley, M. S., Smith, O. M., Berry, L. L., Phillips-Cosio, R., Glassberg, J., Holman, K. M., … Snyder, W. E. (2021). Recent climate change is creating hotspots of butterfly increase and decline across North America. *Global Change Biology*, *27*, 2702–2714. https://doi.org/10.1111/gcb.15582

De Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, *119*, 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x

Despland, E., Humire, R., & Martín, S. (2012). Species richness and phenology of butterflies along an altitude gradient in the desert of Northern Chile. *Arctic, Antarctic,* *and Alpine Research*, *44*(4), 423–431. https://doi.org/10.1657/1938-4246-44.4.423

DeVries, P. J., Alexander, L. G., Chacon, I. A., & Fordyce, J. A. (2012). Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *Journal of Animal Ecology*, *81*, 472–482. https://doi.org/10.1111/j.1365-2656.2011.01922.x

Dhetchuvi, J. B., & Fischer, E. (2006). A New Species of Aframomum (Zingiberaceae) from Nyungwe National Park / Rwanda. *Systematics and Geography of Plants*, *76*, 241–245.

Dhungel, B., & Wahlberg, N. (2018). Molecular systematics of the subfamily Limenitidinae (Lepidoptera: Nymphalidae). *PeerJ*, *6*, e4311. https://doi.org/10.7717/peerj.4311

Ducarme, R. (2018). The butterflies (Lepidoptera: Papilionoidea) of the north-easthern Democratic Republic of Congo. *Metamorphosis*, *29*, 23–37.

Espeland, M., Breinholt, J., Willmott, K. R., Warren, A. D., Vila, R., Toussaint, E. F. A., … Kawahara, A. Y. (2018). A Comprehensive and Dated Phylogenomic Analysis of Butterflies. *Current Biology*, *28*, 770–778. https://doi.org/10.1016/j.cub.2018.01.061

Fashing, P. J., Mulindahabi, F., Gakima, J. B., Masozera, M., Mununura, I., Plumptre, A. J., & Nguyen, N. (2007). Activity and ranging patterns of Colobus angolensis ruwenzorii in Nyungwe forest, Rwanda: Possible costs of large group size. *International Journal of Primatology*, *28*(3), 529–550. https://doi.org/10.1007/s10764-006-9095-3

Fimbel, C., Vedder, A., Dierenfeld, E., & Mulindahabi, F. (2001). An ecological basis for large group size in Colobus angolensis in the Nyungwe Forest, Rwanda. *African Journal of Ecology*, *39*, 83–92. https://doi.org/10.1046/j.1365-2028.2001.00276.x

Finnie, S., Sam, K., Leponce, M., Basset, Y., Drew, D., Schutze, M. K., … Novotny, V. (2021). Assemblages of fruit flies (Diptera: Tephritidae) along an elevational gradient in the rainforests of Papua New Guinea. *Insect Conservation and Diversity*, *14*, 348–355. https://doi.org/10.1111/icad.12456

Fischer, E., & Ackermann, M. (2019). A new species of Kniphofia (Asphodelaceae) from nyungwe national park, Rwanda. *Phytotaxa*, *391*(1), 39–56. https://doi.org/10.11646/phytotaxa.391.1.3

Fischer, E., & Killmann, D. (2008). *Illustrated field guide to the plants of Nyungwe National Rwanda Rwanda* (1st editio). Koblenz: Koblenz geographical colloquia, Series biogeographical monographs 1.Universität Koblenz-Landau.

Fischer, E., Killmann, D., Ertz, D., & Sérusiaux, E. (2017). Heterodermia pindurae (Physciaceae)—a new foliose lichen from Rwanda. *Phytotaxa*, *311*(3), 277–282. https://doi.org/10.11646/phytotaxa.311.3.8

Forbes, S. (2018). The butterflies (Lepidoptera: Papilionidae) of Semuliki National Park, western Uganda. *Metamorphosis*, *29*, 14–21. Retrieved from http://metamorphosis.org.za/articlesPDF/1459/2018.05.21 Metamorphosis 29_14-21 Forbes.pdf

Forister, M. L., Mccall, A. C., Sanders, N. J., Fordyce, J. A., Thorne, J. H., Brien, J. O., … Shapiro, A. M. (2010). Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *PNAS*, *107*(5), 2088–2092. https://doi.org/10.1073/pnas.0909686107

Fountain, T., Nieminen, M., Sirén, J., Chong, S., Lehtonen, R., & Hanski, I. (2016). Predictable allele frequency changes due to habitat fragmentation in the Glanville fritillary butterfly. *PNAS*, *113*(10), 2678–2683. https://doi.org/10.1073/pnas.1613041113

Gentry, A. H. (1992). Tropical forest biodiversity : distributional patterns and their conservational significance. *Nordic Society Oikos*, *63*(1), 19–28.

Ghazoul, J. (2010). *Tropical rain forest ecology, diversity, and conservation*. Oxford University Press.

Gotelli, N. J., & Colwell, R. K. (2011). Estimating species ricness. In A. E. Magurran & B. J. McGill (Eds.), *Biological diversity: Frontiers in measurement and assessment*. Oxford University Press.

Greenwood, S. R. (1987). The Role Of Food Insects Webs in Tropica. *Ambio*, *16*(5), 267–271. Retrieved from http://www.jstor.org/stable/4313376 .

Gross-Camp, N. D., & Kaplin, B. A. (2011). Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica*, *37*, 578–586. https://doi.org/10.1016/j.actao.2011.04.003

Habel, J. C., Ulrich, W., Eberle, J., & Schmitt, T. (2022). Species community structures of Afrotropical butterflies differ depending on the monitoring method. *Biodiversity and Conservation*, *31*, 245–259. https://doi.org/10.1007/s10531-021-02332-2

Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *PNAS*, *118*(2), e2002543117. https://doi.org/10.1073/PNAS.2002543117

Hansen, M. C., Wang, L., Song, X. P., Tyukavina, A., Turubanova, S., Potapov, P. V., & Stehman, S. V. (2020). The fate of tropical forest fragments. *Science Advances*, *6*, eaax8574. https://doi.org/10.1126/sciadv.aax8574

Hasan, M. A. U., Neha, S. A., Baki, M. A., & Quamruzzaman Babu, M. (2018). An inventory of butterfly species in relation to food sources and climatic factors influencing their diversity and richness in a semi-evergreen forest of Bangladesh. *Arhropods*, *7*(3), 53–68. Retrieved from www.iaees.org

Hill, J. K., Gray, M. A., Khen, C. V., Benedick, S., Tawatao, N., & Hamer, K. C. (2011). Ecological impacts of tropical forest fragmentation: How consistent are patterns in species richness and nestedness? *Philosophical Transactions of the Royal Society B*, *366*, 3265–3276. https://doi.org/10.1098/rstb.2011.0050

Hughes, J. B., Daily, G. C., & Ehrlich, P. R. (1998). Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Revista de Biologia Tropical*, *46*(3), 697–704. https://doi.org/10.15517/rbt.v46i3.20199

Joshi, C., & Arya, M. (2007). Butterfly Communities Along Altitudinal Gradients in a Protected Forest in the Western Himalayas , India. *The Natural History Journal of Chulalongkorn University*, *7*(1), 1–9.

Kaplin, B. A. (2001). Ranging behavior of two species of guenons (Cercopithecus lhoesti and C. mitis doggetti) in the Nyungwe Forest Reserve, Rwanda. *International Journal of Primatology*, *22*(4), 521–548. https://doi.org/10.1023/A:1010716001014

Kielland, J. (1990). *Butterflies of Tanzania*. Hill House publishers , London.

Killmann, D., & Fischer, E. (2007). New records for the lichen flora of Rwanda, East Africa. *Willdenowia*, *35*(1), 193–204. https://doi.org/10.3372/wi.35.35116

Körner, C. (2004). Mountain biodiversity, its causes and function. *Ambio: A Journal of the Human Environment*, *33*(13), 11–17. https://doi.org/10.1007/0044-7447-33.sp13.11

Kremen, C. (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications*, *2*(2), 203–217. Retrieved from http://www.jstor.org/stable/1941776

Larsen, T. B. (1991). *The butterflies of Kenya and their natural history*. New York: Oxford University Press Inc.

Larsen, T. B. (2005a). *Butterflies of West Africa Plate volume*. Stenstrup: Apollo Books.

Larsen, T. B. (2005b). *Butterflies of West Africa Text volume*. Stenstrup: Apollo Books.

Larsen, T. B. (2008). Forest butterflies in West Africa have resisted extinction … so far (Lepidoptera : Papilionoidea and Hesperioidea). *Biodiversity and Conservation*, *17*, 2833–2847. https://doi.org/10.1007/s10531-008-9399-z

Laurance, W. F., Carolina Useche, D., Shoo, L. P., Herzog, S. K., Kessler, M., Escobar, F., … Thomas, C. D. (2011). Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*, *144*, 548–557.

https://doi.org/10.1016/j.biocon.2010.10.010

Leingärtner, A., Krauss, J., & Steffan-Dewenter, I. (2014). Species richness and trait composition of butterfly assemblages change along an altitudinal gradient. *Oecologia*, *175*, 613–623. https://doi.org/10.1007/s00442-014-2917-7

Lewis, S. L., Edwards, D. P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science*, *349*(6250), 827–832.

Liseki, S. D., & Vane-Wright, R. I. (2011). Butterflies (Lepidoptera: Papilionoidea) of mount kilimanjaro: Introduction and family papilionidae. *Journal of Natural History*, *45*(37–38), 2375–2396. https://doi.org/10.1080/00222933.2011.596635

Liseki, S. D., & Vane-Wright, R. I. (2013). Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: family Pieridae, subfamily Coliadinae. *Journal of Natural History*, *47*(19–20), 1309–1323. https://doi.org/10.1080/00222933.2012.752542

Liseki, S. D., & Vane-Wright, R. I. (2014). Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: family Pieridae, subfamily Pierinae. *Journal of Natural History*, *48*(25–26), 1543–1583. https://doi.org/10.1080/00222933.2014.886343

Liseki, S. D., & Vane-Wright, R. I. (2016). Butterflies (Lepidoptera : Papilionoidea) of Mount Kilimanjaro : Nymphalidae subfamilies Libytheinae , Danainae, Satyrinae and Charaxinae. *Journal of Natural History*, *50*(13–14), 865–904. https://doi.org/10.1080/00222933.2015.1091106

Liseki, S. D., & Vane-Wright, R. I. (2018). Butterflies (Lepidoptera: Papilionoidea) of mount kilimanjaro: Nymphalidae subfamily helconiinae. *Journal of Natural History*, *52*(39–40), 2511–2552. https://doi.org/10.1080/00222933.2018.1539780

Lycaenidae, L., Sáfián, S., & Larsen, T. B. (2009). On the ecology and behavior of Cerautola crowleyi and Cerautola miranda (Staudinger , 1889) with descriptionS of early stages, *19*(1), 22–28.

Magurran, A. E. (1988). *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.

Maicher, V., Janeček, Š., Sáfián, S., Murkwe, M., Przybyłowicz, Ł., Fokam, E. B., … Tropek, R. (2018). Flying between raindrops : Strong seasonal turnover of several Lepidoptera groups in lowland rainforests of Mount Cameroon. *Ecology and Evolution*, *8*, 12761–12772. https://doi.org/10.1002/ece3.4704

Maicher, V., Sáfián, S., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., … Tropek, R. (2019). Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *Journal of Biogeography*, *00*, 1–13. https://doi.org/10.1111/jbi.13740

Majewska, A. A., Sims, S., Wenger, S. J., Davis, A. K., & Altizer, S. (2018). Do characteristics of pollinator-friendly gardens predict the diversity, abundance, and reproduction of butterflies? *Insect Conservation and Diversity*. https://doi.org/10.1111/icad.12286

Maleque, A. M., Maeto, K., & Ishii, H. T. (2009). Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. *Applied*

Entomology and Zoology, *44*(1), 1–11. https://doi.org/10.1303/aez.2009.1

Manishimwe, A., Ntirugulirwa, B., Zibera, E., Nyirambangutse, B., Mujawamariya, M., Dusenge, M. E., … Wallin, G. (2022). Warming Responses of Leaf Morphology Are Highly Variable among Tropical Tree Species. *Forests*, *13*, 219. https://doi.org/https://doi.org/ 10.3390/f13020219

Matthews, J. K., Ridley, A., Niyigaba, P., Kaplin, B. A., Grueter, C. C., & Jaya Matthews, C. K. (2019). Chimpanzee feeding ecology and fallback food use in the montane forest of Nyungwe National Park, Rwanda. *American Journal of Primatology*, *81*, e22971. https://doi.org/10.1002/ajp.22971

McAleece, N., Gage, J. D., Lambshead, J., & Patterson, G. L. J. (1997). *Biodiversity Professional*. The Natural History Museum & The Scottish Association for Marine Science, London.

Mccain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, *14*, 1236–1245. https://doi.org/10.1111/j.1461-0248.2011.01695.x

Mertens, J. E. J., Brisson, L., Janeček, Š., Klomberg, Y., Maicher, V., Sáfián, S., … Tropek, R. (2021). Elevational and seasonal patterns of butterflies and hawkmoths in plant-pollinator networks in tropical rainforests of Mount Cameroon. *Scientific Reports*, *11*, 9710. https://doi.org/10.1038/s41598-021-89012-x

Molina-Martinez, A., Leon-Cortes, J. L., & Regan, H. M. (2013). Climatic and geometric constraints as driving factors of butterfly species richness along a Neotropical elevational gradient. *Journal of Insect Conservation*, *17*, 1169–1180.

Molleman, F., Kop, A., Brakefield, P. M., DeVries, P. J., & Zwaan, B. J. (2006). Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodiversity and Conservation*, *15*, 107–121. https://doi.org/10.1007/s10531-004-3955-y

Molleman, F., van Alphen, M. E., Brakefield, P. M., & Zwaan, B. J. (2005). Preferences and Food Quality of Fruit-Feeding Butterflies in Kibale Forest , Uganda. *Biotropica*, *37*(4), 657–663.

Moore, J. F., Mulindahabi, F., Gatorano, G., Masozera, M. K., & Jennifer Moore, C. F. (2018). Shifting through the forest: home range, movement patterns, and diet of the eastern chimpanzee (Pan troglodytes schweinfurthii) in Nyungwe National Park, Rwanda. *American Journal of Primatology*, *80*, e22897. https://doi.org/10.1002/ajp.22897

Mtui, D., Congdon, C., Bampton, I., Kalenga, P., & Leonard, H. (2019). Altitudinal Distribution and Monthly Occurrence of Butterflies in the Kihansi Gorge Forest , Tanzania , with a Checklist of Species. *Tanzania Journal of Science*, *45*(4), 543–558.

Muhirwa, F., Maniragaba, A., & Kaplin, B. A. (2018). Dung beetle distribution , abundance , and diversity along an elevation gradient in Nyungwe National Park , Rwanda : A preliminary survey. *Journal of Entomology and Zoology Studies*, *6*(2), 2637–2640.

Mujawamariya, M., Manishimwe, A., Ntirugulirwa, B., Zibera, E., Ganszky, D., Bahati, E. N., … Uddling, J. (2018). Climate sensitivity of tropical trees along an elevation gradient in rwanda. *Forests*, *9*, 647. https://doi.org/10.3390/f9100647

Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, *10*(2), 58–62. Retrieved from https://doi.org/10.1016/S0169-5347(00)88977-6.

Neate-Clegg, M. H. C., O'Brien, T. G., Mulindahabi, F., & Şekercioğlu, Ç. H. (2020). A disconnect between upslope shifts and climate change in an Afrotropical bird community. *Conservation Science and Practice*, e291. https://doi.org/10.1111/csp2.291

Ngirinshuti, L., Rukera Tabaro, S., & Johanson, K. A. (2019). The trichoptera diversity of Nyungwe National Park, Rwanda, with description of a new species in the family pisuliidae. *European Journal of Taxonomy*, *576*, 1–11. https://doi.org/10.5852/ejt.2019.576

Nsanzurwimo, A. (2021). *Influence of anthropogenic disturbance on the diversity of flora and vegetation of Cyamudongo rainforest , the adjacent forestry plots and the Western Nyungwe main forest block*. PhD. thesis, Univeristy of Koblez-Landau.

Nunez, S., Arets, E., Alkemade, R., Verwer, C., & Leemans, R. (2019). Assessing the impacts of climate change on biodiversity: is below 2 °C enough? *Climatic Change*, *154*, 351–365. https://doi.org/10.1007/s10584-019-02420-x

Nyafwono, M., Valtonen, A., Nyeko, P., & Roininen, H. (2014). Fruit-feeding butterfly communities as indicators of forest restoration in an Afro-tropical rainforest. *Biological Conservation*, *174*, 75–83. https://doi.org/10.1016/j.biocon.2014.03.022

Nyirambangutse, B., Zibera, E., Uwizeye, F. K., Nsabimana, D., Bizuru, E., Pleijel, H., … Wallin, G. (2017). Carbon stocks and dynamics at different successional stages in an Afromontane tropical forest. *Biogeosciences*, *14*(5), 1285–1303. https://doi.org/10.5194/bg-14-1285-2017

Oloya, J., Malinga, G. M., Nyafwono, M., Akite, P., Nakadai, R., Holm, S., & Valtonen, A. (2021). Recovery of fruit-feeding butterfly communities in Budongo Forest Reserve after anthropogenic disturbance. *Forest Ecology and Management*, *491*, 119087. https://doi.org/10.1016/j.foreco.2021.119087

Pires, A. C. V., Barbosa, M., Beiroz, W., Beirão, M. D. V., Marini-Filho, O. J., Duarte, M., … Fernandes, G. W. (2020). Altitudinal variation in butterfly community associated with climate and vegetation. *Anais Da Academia Brasileira de Ciencias*, *92*(Suppl.2), e20190058. https://doi.org/10.1590/0001-3765202020190058

Plumptre, A. J., Davenport, T. R. B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., … Moyer, D. (2007). The biodiversity of the Albertine Rift. *Biological Conservation*, *134*, 178–194. https://doi.org/10.1016/j.biocon.2006.08.021

Plumptre, A. J., Masozera, M., Fashing, P. J., McNeilage, A., Ewango, C., Kaplin, B. A., & Liengola, I. (2002). *Biodiversity surveys of the Nyungwe forest reserve in S.W.Rwanda.WCS working paper no. 19*. Retrieved from http://www.wcs.org/science/

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, *12*, 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Ponce-Reyes, R., Plumptre, A. J., Segan, D., Ayebare, S., Fuller, R. A., Possingham, H. P.,

& Watson, J. E. M. (2017). Forecasting ecosystem responses to climate change across Africa's Albertine Rift. *Biological Conservation*, *209*, 464–472. https://doi.org/10.1016/j.biocon.2017.03.015

Primack, R., & Corlett, R. (2006). *Tropical Rain Forests, An Ecological and Biogeographical Comparison* (2nd ed.). Blackwell Publishing.

Pyrcz, T. W., Wojtusiak, J., & Garlacz, R. (2009). Diversity and distribution patterns of Pronophilina butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in Nort-Western Ecuador. *Neotropical Entomology*, *38*(6), 716–726.

R Core Team, R. (2021). A language and environment for statistical computing. R foundation for statistical Computing. Vienna, Austria.

Raguso, R. a, & Gloster, O. (1993). Preliminary Checklist and Field Observations of the Butterflies of the Maquipucuna Field Station (Pichincha Province, Ecuador). *Journal of Research on the Lepidoptera*, *32*, 135–161.

Rahbek, C., Borregaard, M. K., Antonelli, A., Colwell, R. K., Holt, B. G., Nogues-Bravo, D., … Fjeldså, J. (2019). Building mountain biodiversity: Geological and evolutionary processes. *Science*, *365*, 1114–1119. https://doi.org/10.1126/science.aax0151

Ricotta, C., Acosta, A. T. R., Caccianiga, M., Cerabolini, B. E. L., Godefroid, S., & Carboni, M. (2020). From abundance-based to functional-based indicator species. *Ecological Indicators*, *118*, 106761. https://doi.org/10.1016/j.ecolind.2020.106761

Roche, K. N., Piorkowski, J. M., Sanyaolu, R. A., & Cordeiro, N. J. (2015). Vertical distribution of fruit-feeding butterflies with evidence of sex-specific differences in a

Tanzanian forest. *African Journal of Ecology*, *53*, 480–486.

Rödder, D., Schmitt, T., Gros, P., Ulrich, W., & Habel, J. C. (2021). Climate change drives mountain butterflies towards the summits. *Scientific Reports*, *11*, 14382. https://doi.org/10.1038/s41598-021-93826-0

Rurangwa, M. L., Matthews, T. J., Niyigaba, P., Tobias, J. A., & Whittaker, R. J. (2020). Assessing tropical forest restoration after fire using birds as indicators: An afrotropical case study. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2020.118765

Sáfián, S. (2021). The highly invasive Siam Weed, Chromolaena odorata (L.) King and Robinson (Asteraceae), as a seasonal prime nectar source for butterflies (Lepidoptera: Papilionoidea) and other insects (Insecta: Lepidoptera, Hymenoptera, Coleoptera) in West Africa. *Metamorphosis*, *32*, 49–57.

Sáfián, S., Collins, S. C., & Libert, M. (2015). Descriptions of seven new Pilodeudorix Druce , 1891 from equatorial Africa (Lepidoptera : Lycaenidae : Theclinae). *Metamorphosis*, *26*, 62–78.

Sagwe, R. N., Muya, S. M., & Maranga, R. (2015). Effects of land use patterns on the diversity and conservation status of butterflies in Kisii highlands, Kenya. *Journal of Insect Conservation*, *19*, 1119–1127. https://doi.org/10.1007/s10841-015-9826-x

Saikia, M. K., Kalita, J., & Saikia, P. K. (2010). Seasonality of Nymphalid butterflies in Rani-Garbhanga Reserve Forest, Assam, India. *NeBio*, *1*(4), 10–21.

Sanchez-Rodriguez, J. F., & Baz, A. (1995). The effects of elevation on the butterfly communities of a mediterranean mountain, sierra de javalambre , central spain. *Journal of the Lepidopterists' Society*, *49*(3), 192–207. Retrieved from http://biostor.org/reference/115911

Seimon, A. (2012). *Climatology and Potential Climate Change Impacts in the Nyungwe Forest National Park, Rwanda.* New York, USA. Retrieved from http://www.albertinerift.org/challenges/climatechange/tabid/7525/default.aspx

Senyanzobe, J. M. V., Mulei, J. M., Bizuru, E., & Nsengimuremyi, C. (2020). Impact of Pteridium aquilinum on vegetation in Nyungwe Forest, Rwanda. *Heliyon*, *6*, e04806. https://doi.org/10.1016/J.HELIYON.2020.E04806

Sérusiaux, E., Fischer, E., & Killmann, D. (2006). Nyungwea, a new genus of lichen with goniocyst-producing stipes from Rwanda and Uganda (East Africa). *The Lichenologist*, *38*(2), 115–121. https://doi.org/10.1017/S0024282906005548

Sheldon, K. S., Yang, S., & Tewksbury, J. J. (2011). Climate change and community disassembly : impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, *14*, 1191–1200. https://doi.org/10.1111/j.1461-0248.2011.01689.x

Spehn, E. M., Rudmann-Maurer, K., & Körner, C. (2011). Mountain biodiversity. *Plant Ecology and Diversity*, *4*(4), 301–302. https://doi.org/10.1080/17550874.2012.698660

Stefanescu, C., Soto, D. X., Talavera, G., Vila, R., & Hobson, K. A. (2016). Long-distance autumn migration across the Sahara by painted lady butterflies: Exploiting resource pulses in the tropical savannah. *Biology Letters*, *12*, 20160561.

https://doi.org/10.1098/rsbl.2016.0561

Sun, C., Kaplin, B. A., Kristensen, K. A., Munyaligoga, V., Mvukiyumwami, J., Kajondo, K. ka, & Moermond, T. C. (1996). Tree Phenology in a Tropical Montane Forest in Rwanda. *Biotropica*, *28*(4b), 668–681. Retrieved from http://www.jstor.org/stable/2389053

Syaripuddin, K., Sing, K., & Wilson, J. (2015). Comparison of butterflies , bats and beetles as bioindicators based on four key criteria and DNA barcodes. *Tropical Conservation Science*, *8*(1), 138–149.

Tedrow, R., Nathan, K., Richard, N., & Svenson, G. J. (2014). A new species of Dystacta Saussure , 1871 from Nyungwe National Park , Rwanda (Insecta , Mantodea , Dystactinae). *ZooKeys*, *410*, 1–21. https://doi.org/10.3897/zookeys.410.7053

Uehara-Prado, M., Jr, K. S. B., & Freitas, A. V. L. (2007). Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. *Global Ecology and Biogeography*, *16*, 43–54.

Uwizelimana, J. D. D., Nsabimana, D., & Wagner, T. (2021). A preliminary butterfly checklist (Lepidoptera : Papilionoidea) for Cyamudongo tropical forest fragment, Rwanda. *Metamorphosis*, *32*, 93–103. https://doi.org/https://dx.doi.org/10.4314/met.v32i1.15

Uwizelimana, J. de D., Nsabimana, D., & Wagner, T. (2022). Diversity and distribution of Fruit-feeding butterflies (Lepidoptera: Nymphalidae) in Nyungwe National Park, Rwanda. *African Journal of Ecology*, *00*, 1–12. https://doi.org/10.1111/aje.12997

Valtonen, A., Molleman, F., Chapman, C. A., Carey, J. R., Ayres, M. P., & Roininen, H. (2013). Tropical phenology : bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage. *Ecosphere*, *4*(3), 36.

Van Huis, A. (2019). Cultural significance of Lepidoptera in sub-Saharan Africa. *Journal of Ethnobiology and Ethnomedicine*, *15*(26), 1–13. https://doi.org/10.1186/s13002-019-0306-3

Vande Weghe, G. R. (2010). *Papillons du Gabon*. Wildlife Conservation Society.

Vingerhoedt, E., & Vande Weghe, G. R. (2011). Description d’une nouvelle espèce de Charaxes du Parc national de Nyungwe au Rwanda : Charaxes nyungwensis nova sp. (Lepidoptera : Nymphalidae ; Charaxinae). *Bulletin Des Lépidoptéristes Parisiens*, *20*(48), 2–6.

Whitworth, A., Villacampa, J., Brown, A., Huarcaya, R. P., Downie, R., & MacLeod, R. (2016). Past human disturbance effects upon biodiversity are greatest in the canopy ; A case study on rainforest butterflies. *PLOS ONE*, *11*(3), e0150520. https://doi.org/10.1371/journal.pone.0150520

Williams, M. C. (2015). Classification of the Afrotropical butterflies to generic level. *Metamorphosis*, *26*, 102–108.

Williams, M. C. (2021). Butterflies and Skippers of the Afrotropical Region. Retrieved from https://www.metamorphosis.org.za/?p=articles&s=atb

Wilson, R. J., Davies, Z. G., & Thomas, C. D. (2009). Modelling the effect of habitat fragmentation on range expansion in a butterfly. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 276, pp. 1421–1427). https://doi.org/10.1098/rspb.2008.0724

Wilson, R. J., Gutiérrez, D., Gutiérrez, J., & Monserrat, V. J. (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, *13*, 1873–1887. https://doi.org/10.1111/j.1365-2486.2007.01418.x

Woodhall, S. (2005). *Field guide to butterflies of South Africa*. Struik Nature.

Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., & Wilkes, A. (2009). The melting Himalayas: Cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology*, *23*(3), 520–530. https://doi.org/10.1111/j.1523-1739.2009.01237.x