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Recovery of fruit-feeding butterfly communities in Budongo Forest Reserve after anthropogenic disturbance

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ABSTRACT

Understanding of how biodiversity can recover after anthropogenic disturbances, such as selective logging, is important for planning conservation strategies for tropical forests and for more sustainable timber harvest regimes. However, the knowledge of insect community compositions in regenerating logged forests is still limited, especially in the Afrotropics. Here, we evaluated the recovery patterns of fruit-feeding butterfly communities in four different-aged secondary forest compartments and one primary forest compartment in the Budongo Central Forest Reserve, Uganda. In each compartment, butterflies were sampled monthly for five consecutive months in 2017 using traps baited with fermented bananas. A total of 3,778 individuals, representing 82 species (78 identified at the species level and four morphogroups) were recorded. The fruit-feeding butterfly community composition differed among forest compartments and study months. Fruit-feeding butterfly communities of the oldest 72-year-old secondary forest compartment were similar to the primary forest compartment. In the younger secondary forest compartments the seasonal variation was large; especially the communities of the “core” rainy season months were distinct from the communities in primary and oldest secondary forest. The majority of individuals captured from both primary and secondary forests represented forest-dependent species. Primary forests are irreplaceable for preserving the diversity of tropical forests in the long-term. Nevertheless, our study demonstrates that selective logging can allow fruit-feeding butterfly community composition to recover if enough time (>70 years) is allowed for recovery.

1. Introduction

Tropical forests are diminishing rapidly due to the widespread cutting of trees majorly for timber production, fuelwood, agriculture, and human settlements (Hansen et al., 2013; FAO, 2016; IPCC, 2019). The Global Forest Resources Assessment 2015 reported a global decline in the forest area of 129 million ha between 1990 and 2015 (FAO, 2016). In Uganda, the forest coverage shrunk from 4.9 to 2.3 million ha during the same period (MWE, 2016). In addition to deforestation, tropical forests are also facing other human-induced disturbances such as selective logging. For example, at the global scale, partial canopy cover loss was detected in 9% of tropical forest area (FAO, 2016). In the recent past, nearly 20% of the forest area in Africa was estimated to be under selective logging (Asner et al., 2009). Selective logging can modify ecosystem functioning and generate biodiversity losses (Gibson et al., 2011; Edwards et al., 2014; Franca et al., 2017). The degree and timescales at which biodiversity can recover in the resulting secondary forests need to be profoundly understood.

Budongo Central Forest Reserve is the largest forest reserve in Uganda, and it used to be the main source of hardwood timber (Babweteera et al., 2018). The forest has been managed for timber production with selective logging since the 1930 s (Plumptre, 1996). In addition, the application of arboricide chemicals was done in the 1950 s and 1960 s to selectively eliminate non-commercial tree species

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(Plumptre, 1996). At present, Budongo Central Forest Reserve is a mosaic of large areas (compartments) of several-hundred-hectares which were logged and treated with arboricide at different times, as well as unlogged compartments (Lukwago et al., 2020). Biodiversity and emerging communities in these naturally regenerating areas have been studied for a wide range of taxa including trees (Plumptre, 1996; Bahati, 1998; Sheil, 2001; Mwavu et al., 2008; Kirika et al., 2010), climbers (Babweteera et al., 2000), primates (Plumptre and Reynolds, 1994), birds (Owiunji and Plumptre, 1998; Dale et al., 2000; Owiunji, 2000, 2001; Uwimbabazi et al., 2013), amphibians (Lukwago et al., 2020), a wide range of canopy arthropods (Wagner, 2001), including canopy beetles (Wagner, 2000) and canopy ants (Schultz and Wagner, 2002). However, published data on fruit-feeding butterflies is currently lacking. Such information is highly needed given their high diversity and important roles in the tropical forest food-webs (Bonebrake et al., 2010).

Fruit-feeding butterflies (of family Nymphalidae) have long been used as indicator species for monitoring habitat changes and the effects of disturbance in tropical forests (e.g., Aduse-Poku et al., 2012; Barlow et al., 2007a,b; Bonebrake et al., 2010; Nyafwono et al., 2014). Many of the species in this guild are specific to closed-canopy forest (Wood and Gillman, 1998). They play important roles in tropical forest food-webs as herbivores, pollinators, prey (e.g., for birds), and hosts for parasitoids and parasites (Bonebrake et al., 2010). They are also relatively easy to sample and their taxonomy and ecology are fairly well known in many tropical regions (e.g., Williams, 2019).

Previous studies in the tropics have shown that diversity of fruit-feeding butterflies can become altered in secondary forests, although the results have yielded mixed patterns. Some studies have reported either lower (Barlow et al., 2007b; Schulze et al., 2004) or higher (Bobo et al., 2006; Montejo-Kovacevich et al., 2018) species richness in secondary compared to primary forests, whereas others have found no differences (Lewis, 2001; Ribeiro and Freitas, 2012). The higher species richness in old secondary forests, compared to young secondary forests or primary forests follows the Intermediate Disturbance Hypothesis (IDH; Connell, 1978). Connell (1978) used tree communities of Budongo to explain IDH, predicting that tree diversity peaks at intermediate-aged forests. This is because diversity is low immediately after disturbance, when only tree species that were not removed by logging and those that are located within the dispersal range, and have had time to arrive, are present. The diversity increases as more species arrive during succession but declines again in the final stage of succession ("climax" state) which is dominated by a few strong competitors. Lately, further support for the IDH pattern has been found in tree communities of Budongo (Sheil, 2001) and in the dry tropical forests of Ghana (Bongers et al., 2009). Because plants are the key providers of biomass and physical structure in terrestrial communities, successional gradients in tree communities are expected to trigger successional changes in consumer communities (Begon et al., 2006; p. 486). Thus, it is important to understand if the diversity patterns of fruit-feeding butterflies, many of which are specialized to specific tree species or genera as their larval hosts (Molleman, 2012; Williams, 2019), follow the patterns found in tree communities.

Along with diversity, community composition of fruit-feeding butterflies can become significantly altered in secondary forests compared to primary forests (Barlow et al., 2007a; Ribeiro and Freitas, 2012; Nyafwono et al., 2014). However, in Ghana, a previous study by Sáfián et al. (2011) showed that fruit-feeding butterfly communities can recover in 50–60 years. Attention should also be paid to seasonal variation in community compositions, which could differ in primary and secondary forests (Wagner, 2001; Hamer et al., 2005; Barlow et al., 2007a). Primary and secondary forest communities could also differ in the ecological characteristics of the species, e.g., due to differences in species' tolerances, or dispersal abilities (Spaniol et al., 2019). A more comprehensive understanding of recovery times and patterns of tropical forest communities after logging is important for planning future conservation strategies and allows forest management to plan for more sustainable timber harvest regimes.

The present study assessed the recovery patterns of fruit-feeding butterfly diversity and communities after forest disturbance in the Budongo Central Forest Reserve, Uganda. Butterflies were sampled for five consecutive months in four compartments which were logged and treated with arboricide at different times, and in one primary forest compartment. Our specific study questions were: 1) is there significant spatial (or temporal) variability in butterfly species richness (or density), abundance, diversity or community composition among the secondary and primary forest compartments (or study months), and 2) does community composition differ among compartments with respect to species' ecological characteristics (adult size or habitat preference)?

2. Materials and methods

2.1. *Study area*

This study was conducted in Budongo Central Forest Reserve, a medium-altitude (1100 m a.s.l.) moist semi-deciduous forest located on the escarpment above Lake Albert in the western rift valley, Uganda (1.617–2.000°N, 31.367–31.767°E) (Plumptre, 1996). It represents one of the few large remaining forest blocks in this region (Twongyirwe et al., 2015). For management purposes, the reserve has been divided into numerous compartments (average size 650 ha; Plumptre, 1996; Owiunji and Plumptre, 1998). Most compartments have been subjected to various intensities of logging and other disturbances in the past decades, leaving only a few compartments unlogged, i.e., in the state of primary forest (Plumptre, 1996). The two rainy seasons are typically timed from March to May and September to November, with annual rainfall between 1200 mm and 1800 mm (Sheil, 2001). Satellite-derived estimates of precipitation and vegetation greenness in the study area during our study months are shown in Appendix A, Fig. S1 (data derived from IRI/LDEO Climate Data Library, 2021a, 2021b, 2021c).

Butterflies were sampled in five compartments: four compartments which were logged and treated with arboricide at different times (72-year old N1, 68-year old N3, 64-year old N4, 51-year old W22), and one unlogged compartment N15, which is a primary forest managed as a strict nature reserve (Fig. 1; Table 1). The 72-year-old compartment N1 has dense undergrowth of shrubs, saplings and poles in the understorey due to large gaps in the canopy (J.O., pers. obs.). The upper-storey is formed by a few large trees with extensive foliage. The 68-year-old compartment N3 has dense undergrowth of shrubs, saplings and poles in the understorey but not throughout the compartment. Its canopy has plenty of gaps. The 64-year-old compartment N4 has much lower fairly spaced canopy and large gaps with thick undergrowth of shrubs, saplings and poles in the understorey. The 51-year-old compartment W22 has thick undergrowth, and upper-storey canopy trees are scarce. Compartment N15 (primary forest) is a strict nature reserve and has probably not experienced any form of illegal logging (Plumptre and Reynolds, 1994; Lukwago et al., 2020).

2.2. *Sampling of butterflies*

Butterflies were sampled along two linear transects (measuring 400 m), located approximately 100–200 m from each other, in each of the five forest compartments, over five months from February to June 2017. Traps were alternately placed 10 m away from the transect line at 100 m intervals. A total of ten traps were located in each compartment, summing up to a total of 50 traps in the study (Fig. 1). The distances among compartments (centre coordinates of traps in each compartment) ranged between 721 and 3950 m.

Fruit-feeding butterflies in the family Nymphalidae were sampled using white cylindrical butterfly traps baited with fermented banana (DeVries et al., 1997; Molleman et al., 2006). The traps (65 cm high and 25 cm in diameter) were baited with yellow ripe bananas that were smashed, uniformly mixed and allowed to ferment in a 20 l plastic

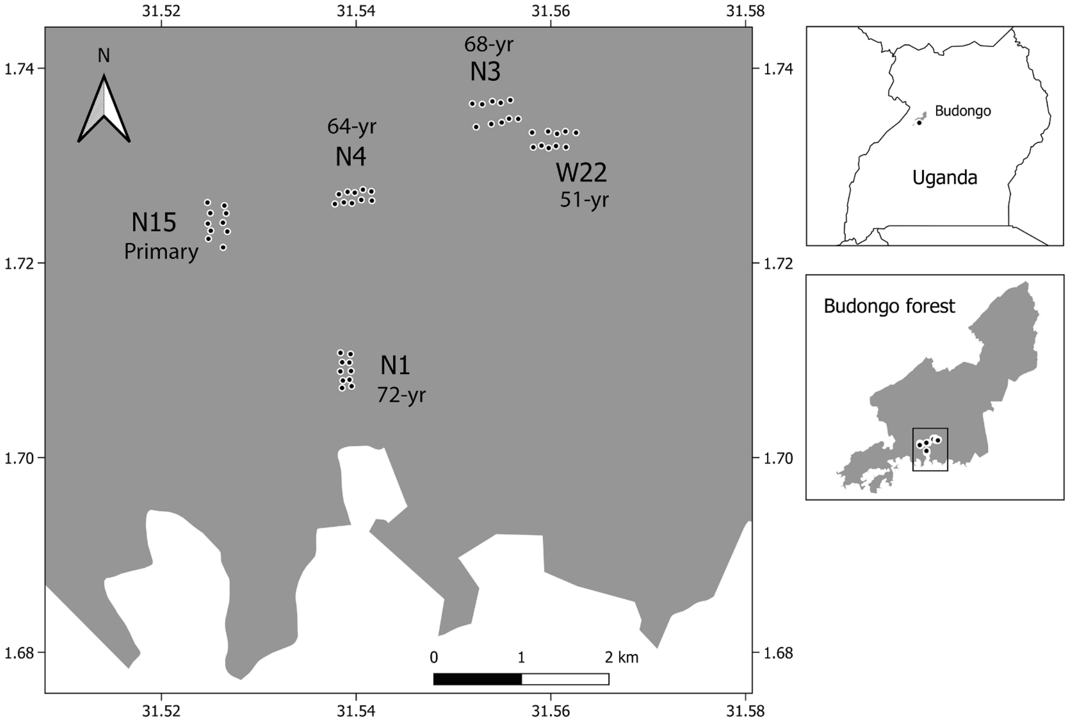

Fig. 1. Locations of study sites (trap points) in the five forest compartments (the gray area in all panels indicating Budongo Central Forest Reserve, Uganda). Year-code indicates the average number of years since logging.

Table 1
Description of the studied forest compartments in the Budongo Central Forest Reserve, Uganda (Plumptre, 1996). Code indicates the average number of years since logging.

Code	Compartment name	Area (ha)	Years logged	Timber[a] volume removed (m^3 ha^{-1})	Years treated with arboricide	Average elevation (m a.s.l.)
72-yr	N1	412	1945[b]	58.7	1962–63	1072
68-yr	N3	620	1947–52	80.0	1959–61	1077
64-yr	N4	341	1952–54	94.0	1960–62	1082
51-yr	W22	1036	1965-67[c]	35.9	1966	1096
Primary	N15	777				1063

[a] Timber volume removed only shows timber removed by sawmills and does not include timber removed by pit sawyers (Plumptre, 1996).
[b] Also, illegal logging by pit-sawyers between 1990 and 2000 (Babweteera et al., 2000; Lukwago et al., 2020).
[c] Also, logged 1996–97 (Kirika et al., 2010).

bucket for four days. Two spoonfuls of bait were placed in a small plastic plate fitted on a plywood base. The baited traps were hanged at 40–50 cm height above the ground (Molleman et al., 2006). Each month, the traps were baited on the first day of setting and checked once daily for five consequent days between 07:00–17:00 h. Individuals were identified using standard identification field guides (Williams, 1969; Molleman, 2012) and numbers of each species were recorded. We followed the nomenclature of Williams (2019), except *Gnophodes minchini* (*Gnophodes* "new" in Molleman, 2012; F. Molleman, pers. com.). Reference specimens of all species captured have been preserved and stored at the Sonso field station. The rest were released (without marking) at approximately 1–1.5 km away from the trap location to minimize the possibility for recapture (majority of the species have poor dispersal abilities; Vlasanek et al., 2013; Marchant et al., 2015). Fresh bait was added to each trap every second and fourth day of sampling to maintain the freshness and a fairly uniform odour production across the sites.

2.3. Data analyses

To assess sample completeness and to compare patterns of species richness among the five compartments and the five studied months, we generated individual-based species accumulation curves (and their 95% confidence intervals) using EstimateS version 9.1.0 (100 runs of randomizations; Colwell, 2013). Patterns of relative species abundance were illustrated using rank abundance plot.

We described patterns in fruit-feeding butterfly diversity and abundance with three univariates: 1) the total number of species (species density sensu Gotelli and Colwell, 2011), 2) the total number of individuals and 3) Shannon's diversity index $H' = -\Sigma(P_i \log_e(P_i))$, where P_i = the proportion of the total sample belonging to the i^{th} species. The values were calculated for each combination of study month and compartment. Analysis of Variance (ANOVA) was used to find out if compartment or month (as fixed variables) explain the variation in each of the three univariates. Analyses were run in R version 3.5.3 (R Core Team, 2014).

We visualized patterns in fruit-feeding butterfly community composition using non-metric multidimensional scaling (NMDS) (with 50 restarts) and fitted Permutational multivariate analysis of variance (PERMANOVA; type III sum of squares and 9999 permutations; Anderson, 2001) to find out if compartment or month (fixed variables) explain the variation in community composition. Prior to NMDS and PERMANOVA: 1) for each combination of study month and compartment, we summed the counts of butterflies, 2) square root transformed the data to reduce the effect of the most abundant species (Clarke and Gorley, 2006), and 3) calculated the Bray-Curtis similarity matrix among samples. To investigate if the communities are more variable (if there is more seasonal variation in community composition) in some compartments than in others, we used permutational test for homogeneity of multivariate dispersions (PERMDISP) (using distances among compartment centroids; 9999 permutations; Anderson, 2006).

We also calculated the overall similarity of community compositions among the five compartments. For this, we first pooled all data in each compartment, square root transformed the counts of individuals and then calculated the Bray-Curtis similarity matrix among compartments. To test if the overall similarity of community composition correlates with the physical distance among the compartments (centre coordinates of traps in each compartment), we calculated Spearman rank correlation coefficient using the PRIMER-E routine “Relate” (9999 permutations). All multivariate analyses were performed using PRIMER-E (version 6.1.15; Clarke and Gorley, 2006; Anderson et al., 2008).

Finally, to analyse whether the ecological characteristics of species in communities differ among the five compartments, we compiled information on species’: 1) adult size and 2) habitat preference (Appendix A, Table S1). Wingspan (the distance between the tips of the forewings) was used as a proxy for adult body size and dispersal ability (Sekar, 2012) and consequently, the adult size was classified as S = small (male wingspan < 50 mm), M = medium (male wingspan 50 – 60 mm) and L = large (male wingspan > 60 mm). As a primary source, we collated wingspan data from Williams (2019). However, in cases where information was not available, we used data either from Martins and Collins (2016) or Williams (1969), or our observations. Butterfly species were allotted into four habitat preference categories (Davenport, 1996): F = Forest dependent (classes F, FH, FL of Davenport, 1996), f = forest edges/woodland, O = open habitat and W = widespread. Species for which habitat preference category was not available were classified as “information Not Available” (“NA”). Differences among the five compartments in frequencies of individuals representing the different ecological classes were tested with Pearson’s Chi-square (contingency table) test (or Fisher’s exact test, if data was not sufficient; class “NA” was omitted from all contingency table tests). Our data included four morphogroups, i.e., species groups which were difficult to separate from each other. For *Bicyclus smithi/B. golo/B. istaris* group we used ecological class of *B. smithi*, which was most likely the most common species among the three. For morphogroups *Bicyclus funebris/B. campinus*, *Bicyclus vulgaris/B. jefferyi*, and *Euphaedra alacris/E. rattrayi*, we assigned the class only if it was shared by both species.

3. Results

3.1. Butterfly species richness, abundance and diversity

We captured a total of 3,778 individuals from the Nymphalidae family, representing 78 species and four morphogroups (Appendix A, Table S1). The most abundant species across all the compartments was *B. smithi/B. golo/B. istaris* group (24% of all individuals caught), followed by *Bicyclus mesogena* (13%), *Gnophodes minchini* (9%) and *Gnophodes chelys* (7%). Singletons (14 species) accounted for 0.4% of the total individuals and 17% of total number of species.

The individual-based species accumulation curves did not reach asymptotes, implying that new species would have been most likely encountered had the sampling continued for a longer time (Fig. 2). Based on the rarefied species richness (estimates for the highest shared number of individuals), the 72-year-old secondary forest compartment

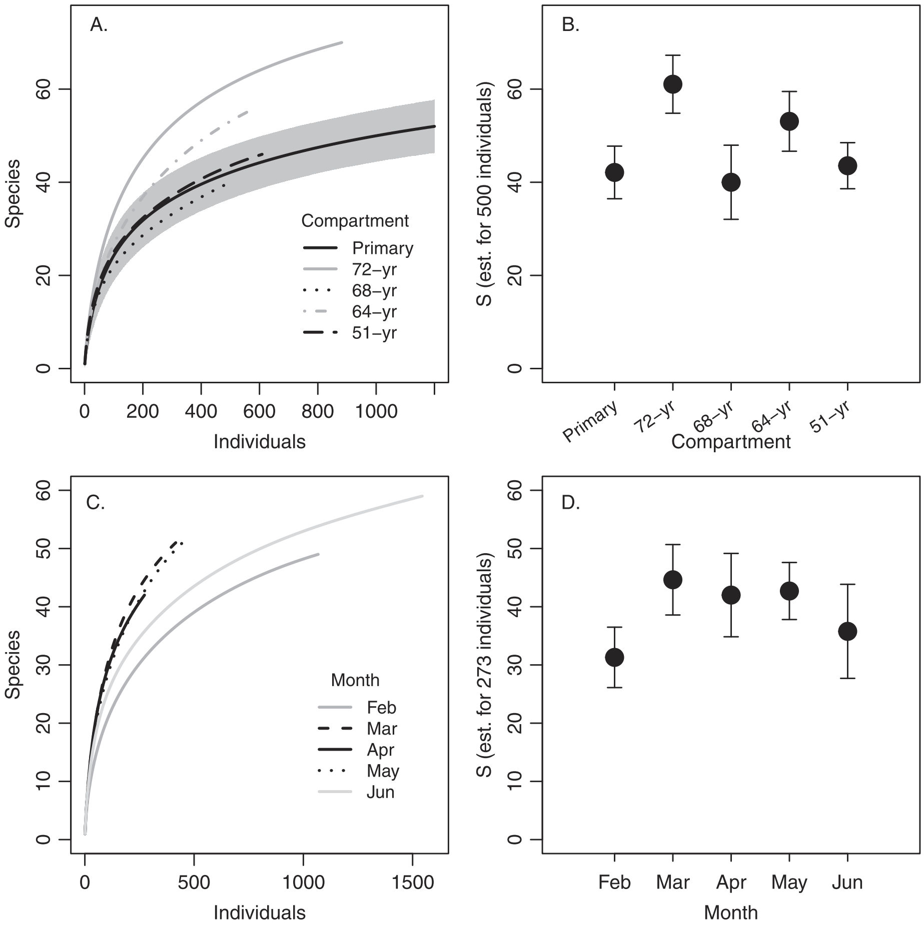

Fig. 2. (A.) Individual-based species accumulation plot and (B.) the estimated species richness for the five compartments (estimate for the highest shared number of individuals), shown with the 95% confidence interval, in Budongo Central Forest Reserve, Uganda. In the species accumulation plot (A.), the grey shading indicates 95% confidence interval for primary forest. (C.) Individual-based species accumulation plot and (D.) the estimated species richness for the five studied months (estimate for the highest shared number of individuals), shown with the 95% confidence interval.

had higher species richness than the primary forest compartment (the 95% confidence intervals did not overlap; Fig. 2B). Furthermore, March and May had higher species richness than February (Fig. 2D).

The rank abundance curve was steepest for primary forest, which showed the highest percentual dominance of the most abundant species and the lowest proportion of the rarest species (Appendix A, Fig. S2). The most dominant species covered 35% of all individuals in primary forest, 23% in 72-year-old, 25% in 68-year-old, 17% in 64-year-old, and 19% in 51-year-old compartment. *B. smithi/B. golo/B. istaris* group was the most dominant species in all other compartments except W22, where the most dominant species was *Gnophodes minchini.*

Based on results of ANOVA, the total number of species (species density) was explained both by compartment ($F_{4,16} = 8.6$; $p < 0.001$) and month ($F_{4,16} = 5.7$; $p = 0.005$). The 72-year-old compartment and the primary forest compartment had higher species densities than the younger secondary forest compartments (Fig. 3A). The species density was generally lowest from March to May (Fig. 3A), opposite to the pattern in rarefied species richness (Fig. 2D). These months represent the "core" of the rainy season, i.e., the typical timing of rainy season in our study region (Appendix A, Fig. S1). Both compartment ($F_{4,16} = 6.5$; $p = 0.003$) and month ($F_{4,16} = 22.8$; $p < 0.001$) also explained the variation in the number of individuals captured. The fruit-feeding butterfly abundances tended to be lowest in the "core" of rainy season (Fig. 3B). With respect to Shannon's H', the variation was explained by compartment ($F_{4,16} = 4.7$; $p = 0.011$) but not month ($F_{4,16} = 1.6$; $p = 0.220$) (Fig. 3C).

3.2. Butterfly community compositions

As visualized by NMDS ordination, the community compositions encountered in the studied compartments were partly overlapping; some of the secondary forest community compositions were similar to primary forest communities while others were clearly distinct (Fig. 4A). There was a clear temporal pattern in community composition: February and June were more similar than the "core" months of the rain season, March–May (Fig. 4B). Notably, during the "core" of the rainy season, the communities of the young (<70-year old) secondary forest compartments were clearly distinct from the primary forest compartment. Based on PERMANOVA, the largest source of variation in the butterfly community composition was explained by month, followed by compartment (Table 2).

The community compositions of the compartments were not equally

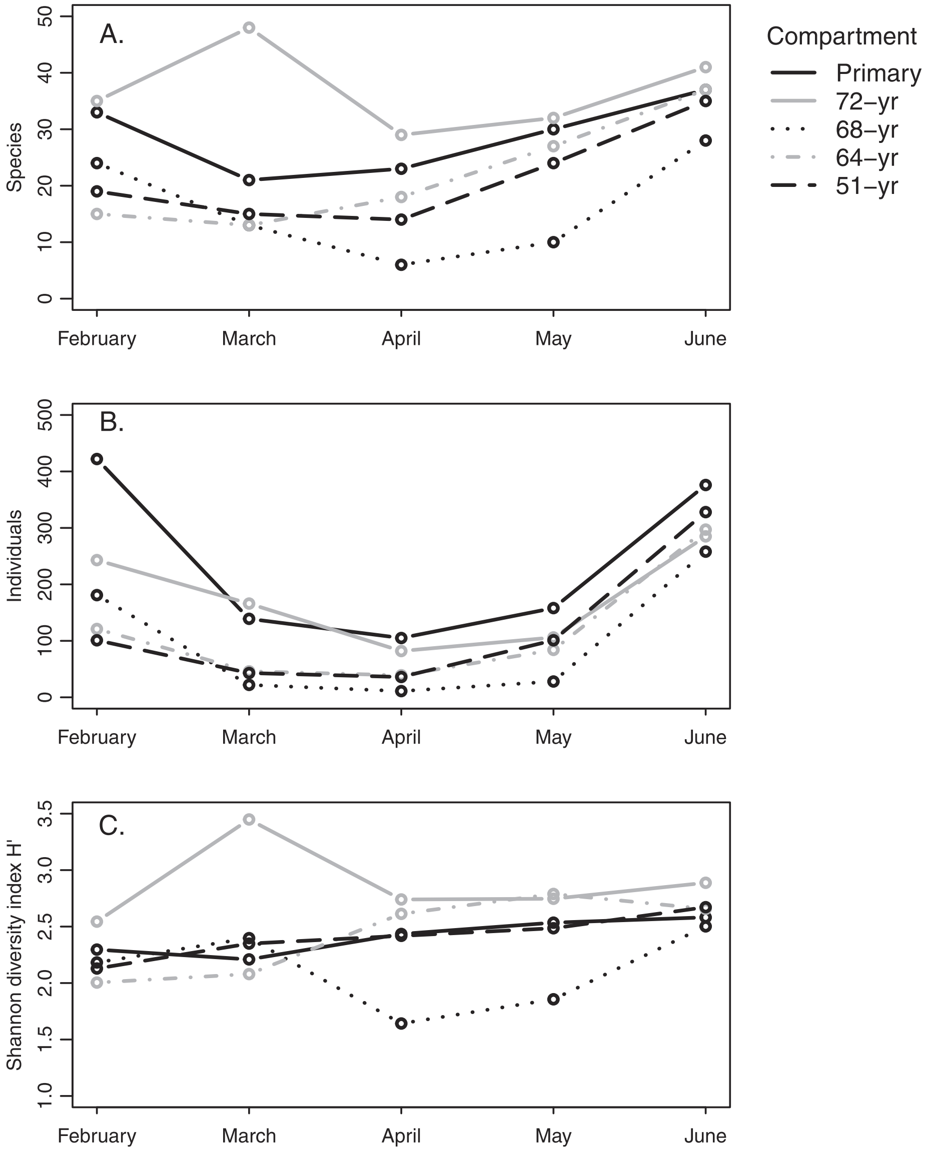

Fig. 3. (A.) Total number of butterfly species, (B.) total number of individuals, and (C.) Shannon diversity index H' shown separately for the five compartments and the five study months in the Budongo Central Forest Reserve, Uganda.

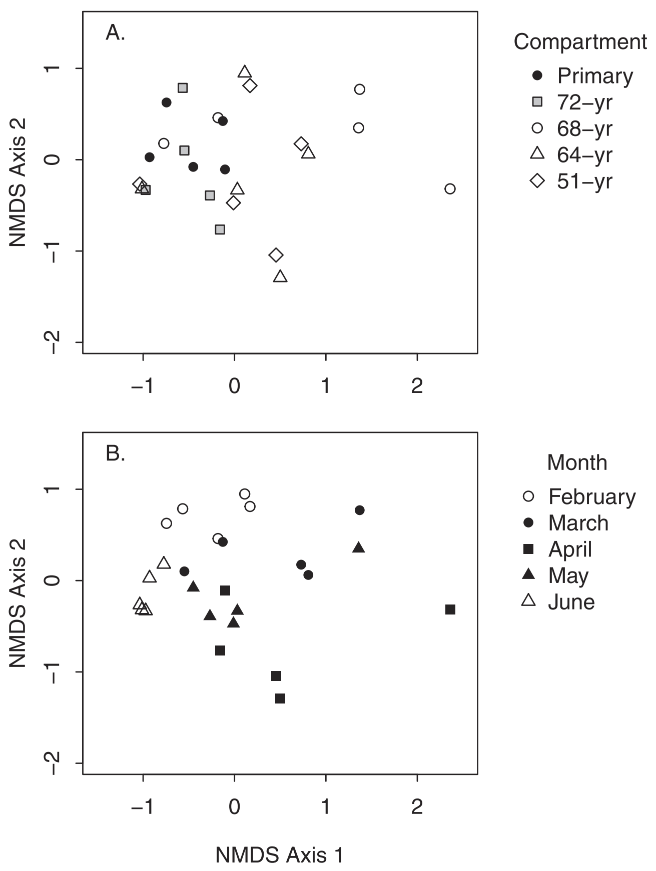

Fig. 4. Non-metric multidimensional scaling (NMDS) ordination of fruit-feeding butterfly communities in Budongo, Uganda (Bray-Curtis similarity; stress 0.12). (A.) Forest compartments and (B.) months shown separately. Symbols represent butterfly communities in each studied compartment and month; the closer the symbols, the more similar the community composition was.

Table 2
Results of Permutational multivariate analysis of variance (PERMANOVA), showing how month and compartment explain fruit-feeding butterfly community composition (Bray-Curtis similarity) in Budongo Central Forest Reserve, Uganda. Sq. var = square root of the estimates of components of variation.

Source	df	SS	MS	Pseudo-F	P	Sq. var
Month	4	15,771	3942.8	4.302	<0.001	24.6 (35.3%)
Compartment	4	7999.9	2000	2.1822	0.002	14.7 (21.2%)
Residual	16	14,664	916.5			30.3 (43.5%)
Total	24	38,435				

variable across months, i.e., in some compartments, the seasonal variation was larger than in others (PERMDISP; $p = 0.001$). Mean deviation from centroid was highest in 68-year old (41.1 ± standard error (SE) 2.2), 64-year old (38.2 ± 2.0) and 51-year old compartment (35.5 ± 2.8) and lowest in 72-year old (30.3 ± 2.3) and primary forest compartment (25.9 ± 0.9).

Overall, the community composition of the 51-year old compartment was most dissimilar to primary forest compartment, followed by the 64-year old compartment, the 68-year old compartment, and the 72-year old compartment, which was most similar to the primary forest (Table 3). This pattern was not confounded by the spatial arrangement of the compartments; the similarity of community compositions did not correlate with the physical distances among the compartments (RELATE; Spearman's Rho = 0.21; $p = 0.31$).

Table 3
The Bray-Curtis similarities (%) of the fruit-feeding butterfly community compositions among the five compartments in Budongo Central Forest Reserve, Uganda.

Compartment	72-yr	68-yr	64-yr	51-yr
72-yr				
68-yr	66.5			
64-yr	74.3	70.7		
51-yr	72.0	69.6	79.7	
Primary	75.5	68.7	68.6	66.3

We found differences in frequencies of individuals representing different size classes (Pearson's Chi-square test, $p < 0.001$), and habitat preference classes (Fisher's exact test, $p < 0.001$) among the compartments (Fig. 5; class "information Not Available" omitted from statistical tests). However, the majority of individuals captured both in primary and secondary forest compartments represented forest-dependent species (Fig. 5B). Smaller species tended to be proportionally slightly more common in primary forest compartment and in the 68-year old compartment, while larger and widespread species tended to be proportionally more common in the youngest 51-year old compartment (Fig. 5). The difference in size categories was largely explained by the dominant *Bicyclus smithi/B. golo/B. istaris* group and *Bicyclus mesogena* (size "small") being more frequent in the primary forest than in the youngest secondary forests, while *Gnophodes minchini* (size "large") expressed the opposite pattern.

4. Discussion

Our results suggest that after selective logging, fruit-feeding butterfly communities in Budongo Forest Reserve became altered for many decades; similar patterns have been previously reported elsewhere in tropical secondary forests (Barlow et al., 2007a; Cleary et al., 2009; Ribeiro and Freitas, 2012; Nyafwono et al., 2014). However, the communities show capacity to recover. The communities of the 72-year old compartment already closely resemble those found in primary forest. In a previous study in Ghana, fruit-feeding butterfly communities were estimated to recover in 50–60 years (Sáfián et al., 2011). The findings demonstrate that the recovery times of butterflies in tropical forests after

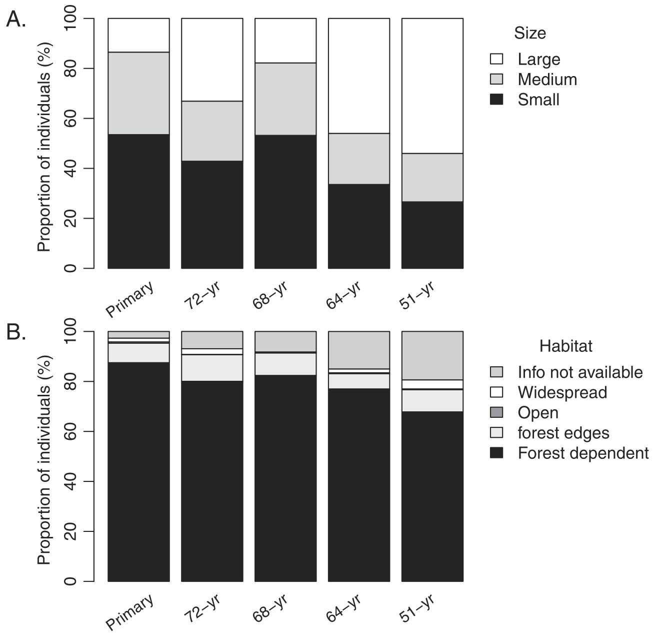

Fig. 5. The proportion of fruit-feeding butterfly individuals classified based on the species' (A.) adult size, and (B.) habitat preference in the five studied forest compartments in Budongo Central Forest Reserve, Uganda.

disturbance can be highly variable and may depend on various factors, e.g., the intensity of disturbance altering the forest structure (Ribeiro and Freitas, 2012). The time for forest structure to recover varies across studies. For example, in Budongo, the forest structure is estimated to take $>$ 50 years to recover to pre-logging state (Plumptre, 1996) but in Kibale National Park, Uganda, a much longer recovery time has been recorded (Bonnell et al., 2011).

Although the community similarities were not confounded by geographic distances among the compartments, the recovery times of tropical forest communities after logging are likely to depend on landscape context, i.e., the degree of isolation from remaining primary forest (Dent and Wright, 2009). The presence of primary forest compartments in Budongo may have aided forest-dependent species to colonize naturally regenerating logged compartments as they aged. However, it is also possible that the communities in the remaining unlogged forest compartments of Budongo have become impoverished after decades of isolation. The responses of fruit-feeding butterfly communities and diversity to forest fragmentation and isolation can be highly variable (Daily and Ehrlich, 1995; Shahabuddin and Terborgh, 1999; Bossart and Antwi, 2016). Some studies have recorded that even small and isolated forest patches can maintain high conservation value and diversity of butterflies (Shahabuddin and Terborgh, 1999; Bossart and Antwi, 2016).

Our results also show that the seasonal pattern of tropical insect communities can express marked differences in primary and secondary forests, a pattern found also in some previous studies (e.g., Wagner, 2001; Hamer et al., 2005; Barlow et al., 2007a). Differences in fruit-feeding butterfly community composition between primary vs. the youngest secondary forests were most pronounced during the “core” rain season months when the abundance of fruit-feeding butterflies were at their lowest. In tropical forests, seasonal variation is typically related to precipitation (Davis, 1945; Dobzhansky and Pavan, 1950; Wolda, 1980, 1988; Valtonen et al., 2013). It has been suggested that the leaf flush of host plants during and after rainy seasons could control the phenology of fruit-feeding butterfly communities via enhanced survival of the larvae (Barlow et al., 2007a). Secondary and primary forests could differ in the seasonal pattern of host plant dynamics or seasonal pattern in quality of microhabitats (Hamer et al., 2003), which could lead to differences in larval mortality (e.g., D’Amico and Elkinton, 1995). In our case, primary and oldest secondary forest habitats with more closed canopies may provide more stable conditions (e.g., more stable microclimate) throughout the seasons, unlike in logged forests where the structural variation is generally high (Wagner, 2001; but see Hamer et al., 2003). The differences could also be explained by species’ morphology or phenology. Interestingly, Ribeiro and Freitas (2011) reported stronger seasonal variation among larger-sized than smaller-sized fruit feeding butterflies. In our data, larger-sized species were proportionally more abundant in the younger successional forests than in the primary forest, although the opposite pattern has been found in the Amazonian butterfly assemblages (Spaniol et al., 2019). The effect on adult resources (fruits) is more unlikely (Barlow et al., 2007a) although not well studied in the Afrotropics. For example, Hamer et al. (2005) witnessed seasonal variation in fruit-feeding butterfly diversity of Bornean rainforests, although the fruit availability did not vary during the same study period.

There is now ample evidence that selective logging allows biodiversity to recover more effectively than many other types of anthropogenic disturbances in tropical forests (Schulze et al., 2004; Dent and Wright, 2009; Gibson et al., 2011; Edwards et al., 2014) and anthropogenic disturbances could even enhance diversity (Connell, 1978; Sheil, 2001). In Budongo, species richness of fruit-feeding butterflies of the 72-year-old forest compartment was significantly higher than in the primary forest. The higher species richness in these oldest secondary forests could be explained by their higher tree species richness (Plumptre, 1996; Sheil, 2001), providing a wider range of host plant species for Lepidopteran larvae, many of which are specialized to specific host plants. Therefore, larval specialism to host plants (e.g., Silva-Brandao et al., 2008), or niche adaptations to specific habitats or vertical strata (Molleman et al., 2006) could explain the observed pattern. The selectively logged forests in Budongo are also suggested to offer more heterogeneous forest structures than the primary forest (Wagner, 2001). Nevertheless, it should be noted that the majority of the individuals both in primary and secondary forests represented forest-dependent species. However, our results should be interpreted with caution since we were able to sample only one primary forest compartment, and only understory, which complicates the generalization of our results.

Our findings are an important contribution to enhancing understanding of how the secondary forest ecosystems have recovered in Budongo, arguably one of the best-studied forests in the Afrotropics. In Budongo, also bird diversity has been shown to peak in the logged forests (Owiunji, 2000). Logged forests in Budongo maintained higher abundances of frugivores, bark-gleaning insectivores, nectarivores and omnivores but lower abundances of sallying insectivores and leaf-gleaning insectivores compared to primary forests (Owiunji and Plumptre, 1998). On the other hand, the diversity of amphibians (Lukwago et al., 2020), canopy beetles (Wagner, 2000) and canopy ants (Schultz and Wagner, 2002) has been found to be higher in primary forests compared to secondary forests, while primates have shown variable response patterns (Plumptre and Reynolds, 1994) in Budongo. Although Connell’s Intermediate Disturbance Hypothesis (Connell, 1978) has been suggested to explain the peak of tree species richness in old secondary forests of Budongo, its effect on higher trophic levels appears to be taxon dependent. Mobile animal taxa are more likely to colonize the secondary forests than more sessile trees and lianas, but differences among species groups can be large (Barlow et al., 2007b). As the case studies addressing various taxonomic groups are becoming accumulated, future studies should aim to better understand biological interactions (e.g., food webs and mutualistic webs) which would help for planning more effective conservation strategy targeting the whole ecosystem and its functioning.

5. Conclusions

This study demonstrates that the fruit-feeding butterfly communities of the younger ($<$70-year-old) logged compartments of Budongo Central Forest Reserve have not yet fully recovered to resemble communities found in primary forest. However, in the 72-year-old compartment, the fruit-feeding butterfly community composition is already similar to that found in the primary forest. In the younger secondary forest compartments, the seasonal variation was large, and especially the communities of the “core” rainy season months were clearly distinct from the primary forest communities. Furthermore, the species richness in the 72-year-old compartment exceeded that observed in the primary forest compartment. These results suggest that human-induced disturbances in the tropical forests can have long term impacts on butterfly communities – highlighting the eminent need to conserve primary forests as a long-term conservation strategy for butterfly species and fauna in general. Nevertheless, our results also show that recovery is possible, at least if primary forests are nearby, and enough time is allowed for recovery.

CRediT authorship contribution statement

Oloya Joseph: Conceptualization, Investigation, Writing - original draft. **Geoffrey M. Malinga:** Writing - review & editing, Supervision, Project administration. **Nyafwono Margaret:** Writing - review & editing. **Akite Perpetra:** Writing - review & editing. **Nakadai Ryosuke:** Formal analysis, Writing - review & editing. **Holm Sille:** Writing - review & editing. **Valtonen Anu:** Formal analysis, Visualization, Writing - review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119087.

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