



# Individual-level size distribution patterns in fruit-feeding butterfly communities along a forest restoration gradient in the Afrotropics

Ryosuke Nakadai<sup>a,b,\*</sup>, Perpetra Akite<sup>c,2</sup>, Silje Holm<sup>d,3</sup>, Richard Kigenyi<sup>e</sup>,  
Eveliina Korkiatupa<sup>f,4</sup>, Lotta Leinonen<sup>g,5</sup>, Geoffrey M. Malinga<sup>h,6</sup>,  
Margaret Nyafwono<sup>i,7</sup>, Wouter van Goor<sup>j</sup>, Anu Valtonen<sup>f,k,\*\*,8</sup>

<sup>a</sup> Faculty of Environment and Information Sciences, Yokohama National University, Tokiwadai 79-7, Hodogaya-ku, Yokohama, Kanagawa 240-8501, Japan

<sup>b</sup> Research Institute for Humanity and Nature, 457-4 Motoyama, Kamigamo, Kita-ku, Kyoto 603-8047, Japan

<sup>c</sup> Department of Zoology, Entomology and Fisheries Sciences, Makerere University, P. O. Box 7062, Kampala, Uganda

<sup>d</sup> Swedish University of Agricultural Sciences (SLU), Department of Ecology, Ulls väg 18B, Uppsala 75651, Sweden

<sup>e</sup> Uganda Wildlife Authority, Kibale National Park, Uganda

<sup>f</sup> Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 111, Joensuu 80101, Finland

<sup>g</sup> Finnish Museum of Natural History, University of Helsinki, P.O. Box 17, Helsinki 00014, Finland

<sup>h</sup> Department of Biology, Gulu University, P. O. Box 166, Gulu, Uganda

<sup>i</sup> Department of Environment and Natural Resources Management, Gulu University, P.O. Box 166, Gulu, Uganda

<sup>j</sup> Face the Future, Hollandseweg 7H, Wageningen 6706KN, the Netherlands

<sup>k</sup> Department of Ecology and Environmental Science, Umeå University, Umeå SE-901 87, Sweden

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## ABSTRACT

The loss and degradation of tropical rainforests pose significant challenges to global conservation, yet the impact of forest restoration on the functional diversity of animal communities, particularly at the intraspecific level, remains poorly understood. This study investigates the size distribution of fruit-feeding butterflies along a gradient of tropical forest restoration ages in Kibale National Park, Uganda. Study sites were categorised into three forest age groups: younger restored (10–16 years), older restored (21–26 years), and primary forests. Butterflies were sampled across 48 sites, and individual forewing lengths were measured to analyse changes in mean forewing length, diversity, skewness, and kurtosis. The mean forewing length and diversity increased, while skewness and kurtosis decreased, towards primary forest age group. Significant

\* Corresponding author at: Faculty of Environment and Information Sciences, Yokohama National University, Tokiwadai 79-7, Hodogaya-ku, Yokohama, Kanagawa 240-8501, Japan.

\*\* Corresponding author at: Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 111, Joensuu 80101, Finland.

E-mail addresses: [nakadai-ryosuke-pt@ynu.ac.jp](mailto:nakadai-ryosuke-pt@ynu.ac.jp), [r.nakadai66@gmail.com](mailto:r.nakadai66@gmail.com) (R. Nakadai), [anu.valtonen@umu.se](mailto:anu.valtonen@umu.se) (A. Valtonen).

<sup>1</sup> 0000-0002-9512-8511

<sup>2</sup> 0000-0002-0302-1822

<sup>3</sup> 0000-0002-2000-4899

<sup>4</sup> 0000-0001-7279-7424

<sup>5</sup> 0009-0006-8739-2597

<sup>6</sup> 0000-0002-6551-2897

<sup>7</sup> 0000-0003-0946-6029

<sup>8</sup> 0000-0003-1532-1563

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differences in size metrics were observed among forest age groups, with younger restored forests showing lower diversity compared to older restored and primary forests. Intraspecific differences in forewing length were detected in six of the 12 species studied, highlighting the nuanced insights provided by individual-level data compared to species-level analyses. Kernel density plots demonstrated a gradual shift towards more uniform size distributions along the restoration gradient, suggesting that morphological diversity increases as forests mature. These findings underscore the value of considering intraspecific variation in understanding community responses to forest restoration. The study highlights the prolonged but steady progress towards primary forest, offering important implications for tropical forest conservation and applied ecology.

## 1. Introduction

In recent years, the rapid loss and degradation of humid tropical forests have raised growing concerns (Vancutsem et al., 2021), posing a significant challenge to global conservation efforts. In response to the urgent need to mitigate the impacts of climate change and the ongoing loss of tropical forest cover, active forest restoration has emerged as a crucial strategy for conservation and carbon sequestration (Chazdon, 2019; Griscom et al., 2017; Koch and Kaplan, 2022). However, rainforests do not regenerate to resemble old-growth forests in the short term even with active restoration efforts (Valtonen et al., 2021). Forest structure and tree species composition undergo significant changes during the extended process of tropical forest succession, which can span more than 200 years (Chazdon, 2008).

The changes in forest structure and tree species composition that occur during tropical forest restoration can significantly impact various types of animal communities, which are responsive to changes in forest architecture, microclimatic conditions, and available resources, including host plants. For example, communities of birds (Catterall et al., 2012; Latja et al., 2016), beetles (Audino et al., 2014; Derhé et al., 2016; Grimbacher and Catterall, 2007), galling insects (Fernandes et al., 2010), butterflies (Nyafwono et al., 2014; Oloya et al., 2021; Sant'Anna et al., 2014), and soil macrofauna (Amazonas et al., 2018) in restored forests have become increasingly similar to that of primary forest.

In recent years, many studies have highlighted the need to understand the role and recovery of functional diversity, which is based on species traits, along the trajectory of tropical forest restoration and succession (e.g., Audino et al., 2014; Spaniol et al., 2019). Species traits are often associated with the use of niche spaces (Case et al., 1983; Kearney et al., 2010; Violle and Jiang, 2009). A well-known example of the relationship between morphological traits and ecological niches is that of Darwin's finches, whose beak and body sizes are closely associated with the types of resources they exploit (Grant and Grant, 2002a, b). Historically, studies of trait distribution within species have focused on detecting niche differentiation and natural selection during evolution (Grant and Grant, 2002b; Lande and Arnold, 1983). However, relatively few studies in conservation ecology (e.g., Spaniol et al., 2019) have used species-level trait data to assess community-level patterns. Therefore, our understanding of the impacts of forest restoration on community-level functional diversity, as indicated by the available niche space for animals, remains limited. Furthermore, to fully comprehend changes in available niche space along the forest restoration gradient, intraspecific trait data, not just species-level data, are essential. Such evaluation is crucial for assessing the recovery of tropical forests as habitats for targeted animal communities.

In the present study, we investigated changes in the size distribution (Begon and Townsend, 2021) of fruit-feeding butterflies, a widely used indicator taxonomic group (Bonebrake et al., 2010), along a tropical forest restoration age gradient, while considering intraspecific variation. Size is frequently referred to as a “master trait” because body size often interacts with the surrounding physical and biotic environment and thus is directly related to the fitness and performance of each individual (Andersen et al., 2016; Brown et al., 2004; Miller et al., 1988). We used adult forewing length as a proxy for the body size of each individual butterfly because it is the one often used as a standard measure in Lepidoptera (e.g., Beck and Kitching, 2007; Hawkins and Lawton, 1995; Nakadai et al., 2018, 2021). Data was collected between 2020 and 2021 from Kibale National Park, Uganda (for details, also see Korkiatupa et al., 2023). Previous studies from the same location reported a change in the species composition of fruit-feeding butterfly communities as the forests recovered (Korkiatupa et al., 2023; Nyafwono et al., 2014). However, the change in size distribution in this system, or in other fruit-feeding butterfly communities of restored tropical forests, has not been studied.

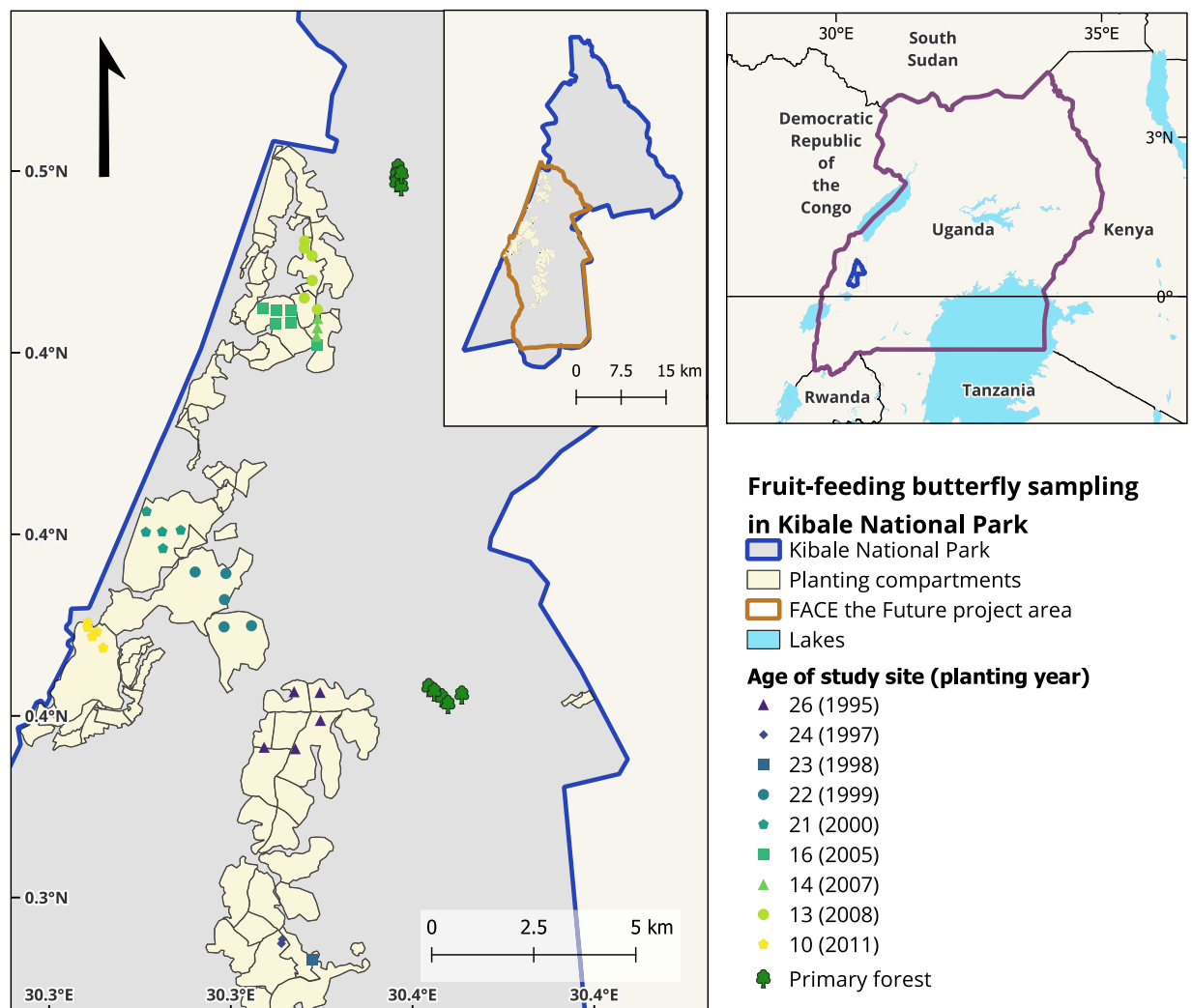
Based on ecological theory, we predicted that as forest restoration progresses, the butterfly community would shift towards larger body sizes due to increased structural complexity, resource availability, and microhabitat stability typical of older forests (Chown and Gaston, 2010; Ribeiro and Freitas, 2011). This is because larger species often require more stable and resource-rich environments, while smaller species tend to dominate disturbed or early successional habitats. Consequently, we hypothesised that mean forewing length and morphological diversity would increase along the restoration gradient. We further speculated that the size distribution would become more symmetrical and less peaked (i.e., reduced skewness and kurtosis), reflecting a broader and more even occupation of the niche space in mature forests (Wieczynski et al., 2019; Violle and Jiang, 2009; Fontana et al., 2016). These predictions are rooted in trait-based ecology and the concept of niche expansion during succession and are consistent with the idea that niche differentiation during community assembly can reduce kurtosis and skewness in trait distributions, thereby promoting broader trait space occupation (Gross et al., 2021).

## 2. Materials and methods

### 2.1. Study area

Kibale National Park is located in Western Uganda and comprises a medium-altitude tropical moist forest (Hartter et al., 2011; Struhsaker, 1997; Fig. 1). The park covers an area of 795 km<sup>2</sup> with an elevation spanning 900–1590 m above sea level. The average annual precipitation based on the long-term dataset (1970–2020) is 1646 mm, and the monthly average minimum and maximum temperatures are 16 and 28 °C respectively (Chapman et al., 2021). The rainy season occurs twice a year, with the heaviest rains in April and October, whereas the driest periods are between January and February and June and July (Chapman et al., 2021). Kibale is a part of the biodiversity-rich Albertine Rift Valley. For example, over 100 fruit-feeding butterfly species (Molleman, 2012; Valtonen et al., 2013), 13 primate species, over 350 tree and shrub species, and 325 bird species (Howard et al., 1996) have been recorded in the primary forests of Kibale National Park.

Kibale National Park includes pristine forest areas but also has a long history of human disturbance (Struhsaker, 1997). In the 1970s, approximately 10,000 ha of forests in the southwestern part of the park were cut down by agricultural encroachers, leaving the area nearly devoid of trees except for some remaining patches of primary forest (van Orsdol, 1986). However, in 1994, the Uganda Wildlife Authority (UWA) and the FACE (Forest Absorbing Carbon Emissions) Foundation, currently known as Face the Future, started a rainforest restoration project in the area (Riemer, 2020; UWA-FACE, 2015; Wheeler et al., 2016). Approximately 2500 ha of deforested land started to regenerate naturally, but elsewhere forest succession was arrested (i.e., the area remained as shrubland or



**Fig. 1.** The study area in Kibale National Park, Uganda, included 48 study sites in the Uganda Wildlife Authority and Forests Absorbing Carbon dioxide Emissions (UWA-FACE) restoration area and primary forest. Data sources: Lakes: Africa – Water bodies dataset (The World Bank, 2018, CC-BY 4.0); country borders: Africa Boundaries (Ruth, 2021, CC0). The map was created using QGIS Desktop 3.20.3 (QGIS.org, 2021).

grassland) (Chapman and Chapman, 1999; Riemer, 2020; UWA-FACE, 2015; Wheeler et al., 2016). Active (tree planting) and passive (exclusion of grazing, fire protection, and invasive species removal) restoration have taken place since 1995 (UWA-FACE, 2015). The data used in this study were collected from areas where forest recovery occurred only through active tree planting, as well as from primary forest sites (Omeja et al., 2011; UWA-FACE, 2015; Wheeler et al., 2016). In these areas, the UWA-FACE project has planted over 4400 ha of land with indigenous tree species (400 seedlings ha<sup>-1</sup>) (van den Tweel, 2023). In addition, we used reference sites in the primary forest surrounding the project area to the east (Fig. 1).

## 2.2. Sampling of fruit-feeding butterflies

Fruit-feeding butterflies were sampled from a total of 48 study sites (Fig. 1), 38 of which represented actively restored compartments planted between 1995 and 2011, and 10 were in the primary forest. More detailed information on the study sites can be found in the studies by Nyafwono et al. (2014) and Korkiatupa et al. (2023). We used a combination of data from Korkiatupa et al. (2023) study and from three additional sites (planted in 1997–1998).

Fruit-feeding butterflies were sampled in 2020–2021. The sampling covered months of March, July, and October 2020 then January, May, and September 2021. As an exception, at three study sites (planted during 1997–1998), data for the first sampling month (March 2020) are not available because sampling was not conducted at that time. For statistical analyses, data across the study months were pooled for each site, and we classified the study sites into three forest age groups: (1) younger restored forests (aged 10–16 years), 20 study sites; (2) older restored forests (aged 21–26 years), 18 study sites; (3) primary forests, 10 study sites.

Fruit-feeding butterflies were caught using a white cylindrical butterfly trap (one trap per study site) hanging 40–50 cm above the ground (Molleman et al., 2006; Nyafwono et al., 2014). The bait was two spoonful (~ 100 g) of three-day-old fermented bananas. After the traps were set at the sites, they were sampled on three consecutive days (between 08:00 and 16:00) of each sampling month.

Butterflies were identified using field guide books by Molleman (2012) and Williams (2021); see Korkiatupa et al. (2023) for further details. In addition, trained field assistants identified the specimens based on wing patterns, measured forewing lengths, and determined sex (if possible). Finally, we excluded the five unidentifiable nymphalid individuals and all facultative fruit-feeding species (*Pseudoneptis bugandensis* and *Vanessula milca*, and tribes Neptini and Acraeini) from the data analyses.

## 2.3. Measurement of individual forewing length

A total of 10,627 individuals, representing 97 butterfly species and one group of closely related species that are difficult to separate in detail (*Gnophodes grogani* group) (details in Korkiatupa et al., 2023) were trapped. The forewing length of 10,530 individuals were successfully measured (i.e., information on forewing length for approximately 1 % of the individuals was lost because they escaped during handling). The data for younger restored, older restored, and primary forests included 3403, 4023, and 3104 individuals, respectively. Additionally, the sex of each individual was determined whenever possible based on wing patterns and the presence or absence of hair pencils (6978 individuals, 65.7 % of total).

## 2.4. Data analyses on community-wide size distributions

First, we calculated the mean forewing length of each species to compare the community-wide size distribution of fruit-feeding butterflies between individual- and species-level data. We used kernel density plots to visualise the differences between forest groups for both individual- and species-level data.

To compare the differences between forest age groups, we evaluated four site-level measures of trait distribution, including mean forewing length, diversity, skewness, and kurtosis. The mean forewing length was calculated at each site. Forewing length diversity was calculated as the mean absolute difference for all possible individual pairs at each site. Skewness and kurtosis, which are commonly used measures to evaluate the properties of trait distributions (Gross et al., 2021; Kraft et al., 2008; Wiczyński et al., 2019), indicate the asymmetry and sharpness of the data distribution, respectively. Skewness quantifies whether the distribution is skewed to the left or right, with positive values indicating a longer tail to the right, and negative values indicating a longer tail to the left. On the other hand, kurtosis measures whether the distribution is more or less peaked compared to a normal distribution. A positive kurtosis indicates a more peaked distribution, whereas a negative kurtosis indicates a flatter distribution. The mean forewing length derived from the species-level mean is equivalent to the community-weighted mean value. To statistically test the differences between the forest age groups, first we conducted a Kruskal–Wallis test to assess overall differences among the three groups. When significant, we then applied the Wilcoxon rank-sum test for pairwise comparisons on both individual- and species-level data, using Holm's method to adjust for multiple comparisons across the four measures. Additionally, to account for the contribution of possible sex ratio differences between sites, we used linear modelling with forest age groups (i.e., younger restored, older restored, and primary forests) and sex ratio (i.e., defined here as the percentage of males) as explanatory variables for each measure.

## 2.5. Data analyses on intraspecific forewing length difference among forest age groups

When differences were found in the community-level comparisons above, we also tested for differences in within-species variation in forewing length among the three forest age groups. All species with more than 10 individuals distributed across all three forest age groups were chosen as targets for testing intraspecific variation among forest age groups. Accordingly, we selected 12 species, including *Bicyclus auricruda*, *Bicyclus buea*, *Bicyclus golo*, *Bicyclus mesogena*, *Bicyclus mollitia*, *Bicyclus smithi*, *Brakefieldia peitho*, *Charaxes*

*fulvescens*, *Euphaedra medon*, *Melanitis ansorgei*, *Melanitis leda*, and *Sevenia boisduvali*. To statistically test the intraspecific differences between forest age groups, first we performed a Kruskal–Wallis test for each species to detect overall differences among the groups. When significant, we then conducted Wilcoxon rank-sum tests for pairwise comparisons of forewing length, applying Holm’s method for multiple comparisons.

All analyses were performed using the statistical program R (ver. 4.3.1; R Core Team, 2023). The *density* function was used to compute kernel density estimates with default settings, the *kruskal.test* function was used to test whether samples originate from the same distribution by the Kruskal–Wallis test, and the *pairwise.wilcox.test* function was used to compare differences between habitats.

### 3. Results

The size (measured as forewing length) of individual butterflies ranged from 12.0 mm to 58.0 mm, with an overall average of 28.7 mm. The average sizes within the younger restored, older restored, and primary forests were 25.7 mm (min-max: 13.0–58.0 mm), 28.9 mm (13.0–58.0 mm), and 31.7 mm (14.0–57.0 mm), respectively.

#### 3.1. Comparison of size distributions based on individual-level and species-level data

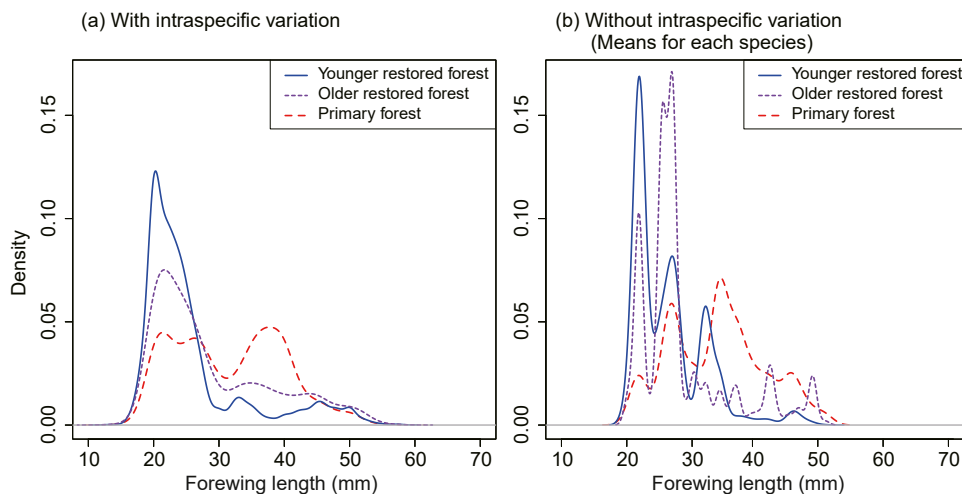
The community-wide size distributions of fruit-feeding butterflies from younger restored- to primary forests (Fig. 2) showed a general increase in both the mean and diversity of forewing length and a decrease in skewness and kurtosis towards primary forest communities (Fig. 3). Mean forewing length increased from younger restored to older restored and primary forests, with all three forest age groups being significantly different from each other in both individual- and species-level analyses (Fig. 3a, b, Table S1).

The forewing length diversity of younger restored forests was significantly poorer than both older restored and primary forests, whereas no significant difference between older restored and primary forests was observed (Fig. 3c, d, Table S1). The analyses of skewness and kurtosis, which generally exhibit a decrease towards the primary forest, yielded differing results between individual- and species-level data (Fig. 3e–h). Specifically, when using individual-level data, significant differences in skewness and kurtosis were observed among the three forest age groups. However, with species-level data, significant differences were observed only between the primary and restored forest groups, with no significant difference between the younger and older restored forests (Fig. 3e–h).

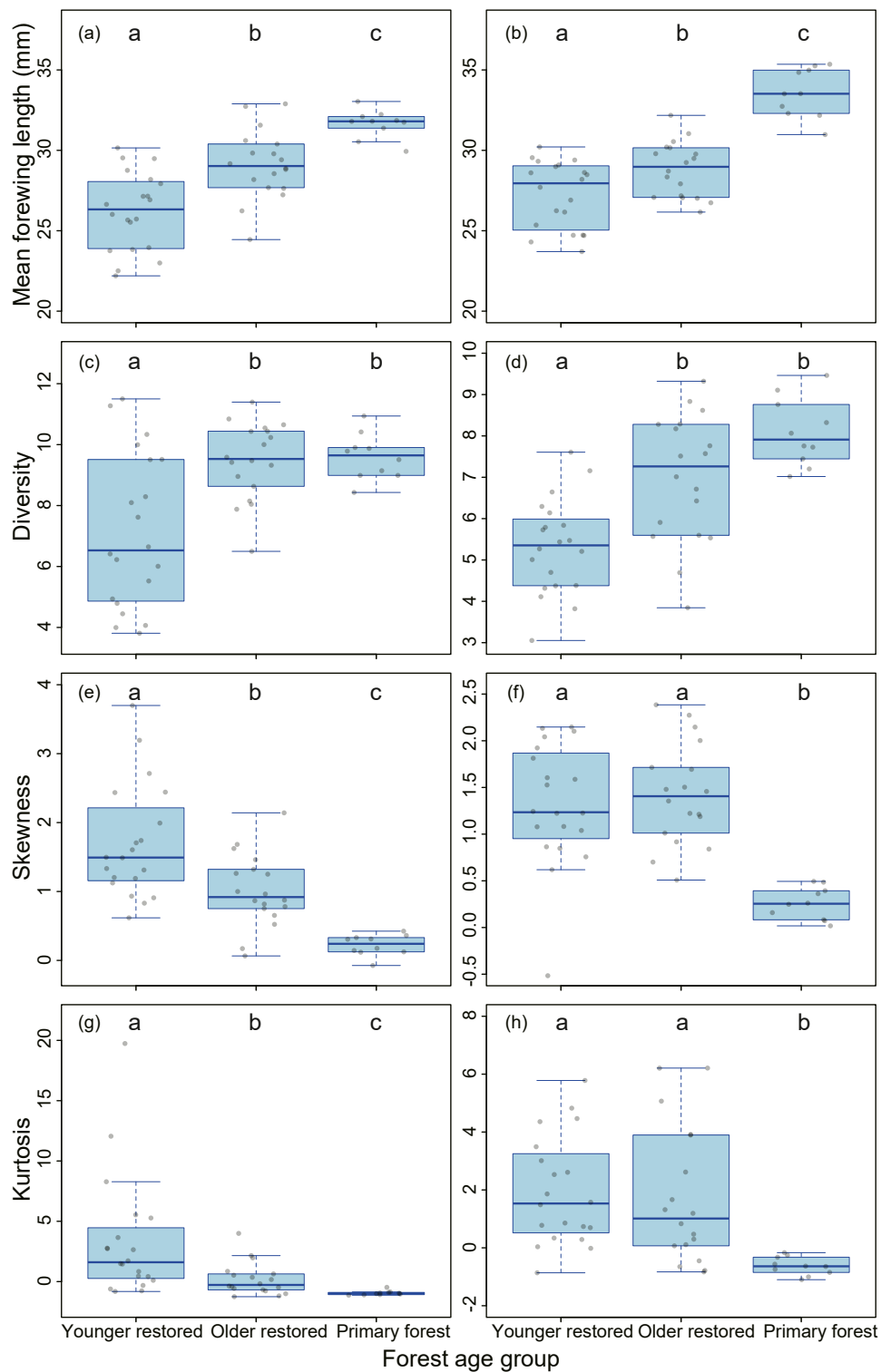
The box plot of sex ratio, measured as the percentage of males, across forest age groups appears to show a slightly decreasing trend along the forest age gradient (Figure S1); however, there were no statistically significant differences among groups based on the Kruskal–Wallis test. In addition, the linear model conducted to assess the contribution of sex ratio (i.e., percentage of males) identified a significant effect of sex ratio based solely on kurtosis calculated from individual-level information (Table S2).

#### 3.2. Intraspecific forewing length of the 12 abundant species

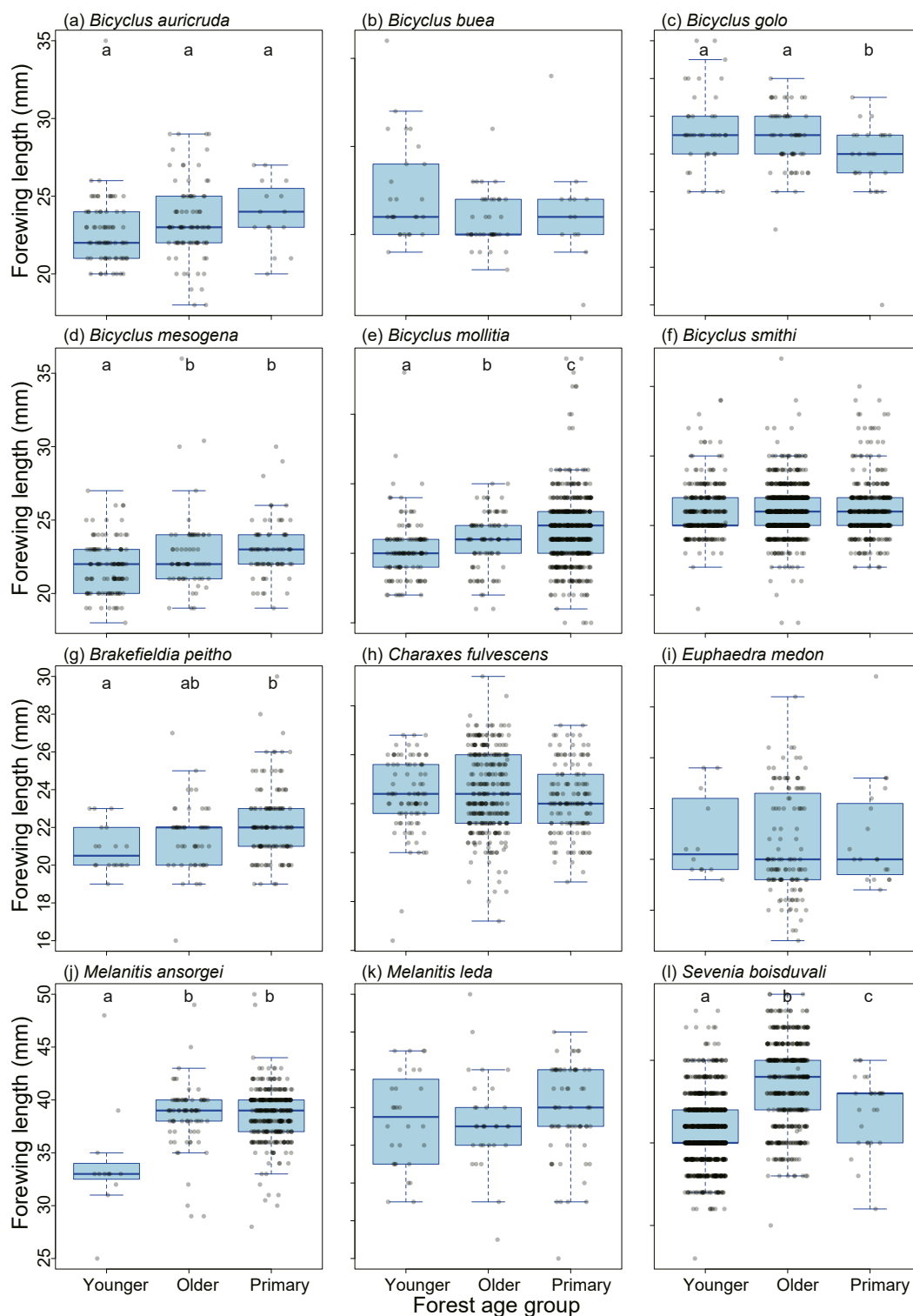
Based on the analysis of the 12 most abundant species, we found significant intraspecific differences in forewing length among the three forest age classes for six of the 12 species (Fig. 4, Table S3). Specifically, four out of six species showed significant differences between younger restored and older restored forests, two out of six species showed significant differences between older restored and primary forests, and six out of six species showed significant differences between younger restored and primary forests (for directions of changes, see Fig. 4). Furthermore, 10 out of the 12 species showed significantly smaller sizes in males compared to females within the species based on the pairwise Wilcoxon rank sum test (Figure S2, Table S4).



**Fig. 2.** Kernel density plots for both individual-level (a) and species-level (b) forewing length data. Blue, purple, and red lines correspond to younger restored, older restored, and primary forests, respectively.



**Fig. 3.** Comparison of the four types of site-level measures, i.e., mean forewing length (a and b), diversity (c and d), skewness (e and f), and kurtosis (g and h), among forest age groups (i.e., younger restored, older restored, and primary forests). Left and right panels are based on individual- and species-level data, respectively. Each point represents a site-level observation. Forest age groups labelled with the same letter did not differ significantly in this measure based on the Wilcoxon rank sum test with the Holm's method for multiple comparisons. The Wilcoxon rank sum tests were conducted only when Kruskal–Wallis tests indicated significant overall differences ( $p < 0.05$ ). Detailed information on the results of the Wilcoxon rank sum test can be found in [Table S1](#).



**Fig. 4.** Comparison of forewing length between forest age groups (i.e., younger restored, older restored, and primary forests) for 12 butterfly species. Each point represents an individual butterfly. Forest age groups labelled with the same letter were not significantly different for that species based on the Wilcoxon rank sum test with the Holm's method for multiple comparisons. The Wilcoxon rank sum tests were conducted only when Kruskal–Wallis tests indicated significant overall differences. In case of no significant differences were detected by the Kruskal–Wallis tests ( $p > 0.05$ ), the letters are not shown. Detailed information on the results of the Wilcoxon rank sum test can be found in [Table S3](#).



#### 4. Discussion

Our results are broadly consistent with our hypotheses. As predicted, both the mean and diversity of forewing length increased with forest age, and the shape of the distribution became less skewed and peaked, particularly in older restored and primary forests. These patterns support the idea that forest maturation expands the range of available niches and allows for the persistence of both smaller and larger species, contributing to more evenly distributed trait values (Wieczynski et al., 2019; Violle and Jiang, 2009; Fontana et al., 2016). The observed reduction in skewness and kurtosis along the restoration gradient aligns with theoretical expectations from trait-based community ecology, which suggest that older ecosystems tend to support more functionally diverse and stable communities. It is worth noting, however, that some study sites within the same recovery category were located in close geographic proximity, potentially introducing spatial autocorrelation (Korkiatupa et al., 2023). Although our analyses did not explicitly model this spatial structure, such proximity could potentially affect the assumption of independence among sites. This limitation should be taken into account when interpreting group-level comparisons.

Our analysis revealed that with an increase in the age of the restored forest, the morphological diversity of fruit-feeding butterflies increases, marked by a gradual increase in variation and evenness in forewing lengths across individuals. Specifically, the kernel density plots illustrating forewing length exhibited a shift from highly skewed distributions, peaking at smaller sizes, towards progressively more uniform patterns as forest restoration advanced (Fig. 2). Without individually measured forewing lengths (i.e., using means for each species, which is the typical case in community studies [Bolnick et al., 2011; Violle et al., 2012]), it is difficult to capture these patterns visually (Fig. 2). These observed trends were statistically robust: skewness and kurtosis analyses based on individual-level data starkly contrasted those based on species-level data (Fig. 3). This discrepancy underscores the potential inadequacy of species-level data in capturing the nuanced changes in the niche space for butterflies along the forest age gradient. In fact, both within-species comparisons of forewing lengths (Fig. 4) and individual-level comparisons of skewness and kurtosis (Fig. 3) revealed differences between younger and older restored forests, whereas the species-level analysis failed to detect such differences (Fig. 3). In the skewness and kurtosis analyses, relying solely on species-level data would incur the risk of overlooking the transitional process from younger to older restored forests towards primary forest conditions. Consequently, species-level findings may inaccurately suggest that certain morphological characteristics, including skewness and kurtosis, remain stagnant as restored forests age. Therefore, this study emphasises the critical importance of incorporating individual-level morphological trait data for accurate monitoring and assessment of changes in animal communities along a forest restoration gradient.

The discrepancy in sensitivity between mean forewing length and diversity, as opposed to skewness and kurtosis, regarding individual- and species-level data, may stem from their respective calculation methods. Skewness and kurtosis are directly derived from numerical values within trait distributions, whereas mean forewing length and diversity represent summary statistics calculated based on the overall mean or mean of differences. When focusing solely on approximate statistical summary measures, variations in data resolution may not significantly affect the results; however, in cases where finer distinctions are crucial, such differences can lead to biased conclusions. This observation holds particular relevance in applied ecology, where understanding changes in community structure and ecosystem functioning relies more on the trait distribution of the entire community rather than summary statistics alone (Begon and Townsend, 2021).

Numerous butterfly species exhibit sexual dimorphism in size, typically with males being smaller than females (Singer, 1982). Consistent with this, our results showed that 10 out of the 12 dominant species exhibited significantly smaller sizes in males compared to females within the species (Figure S2, Table S4). Although behavioural differences between sexes (Reim et al., 2019) could theoretically explain potential differences in sex ratios across forests of varying ages, our site-level analysis, utilising individual-level data, did not reveal significant contributions of sex ratio to variations in forewing length between sites, with the exception of kurtosis (Table S2). Visual examination of sex ratio, measured as the percentage of males, across different forest age groups exhibited a slight declining trend along the forest age gradient, indicating a decrease in the proportion of males as forests aged (Figure S1). However, these trends were not statistically significant. Factors such as forest structure, natural enemies, and food resources could influence this pattern. For instance, higher survival rates or increased longevity among females (Sielesniew et al., 2020) might lead to their higher proportion in older forests. In this study, elucidating the precise influence of forest restoration on sex ratios presents challenges, necessitating further studies into this aspect.

Previous research in the Neotropics has shown that early successional forests tend to have smaller butterfly species compared to primary forests (Spaniol et al., 2019). Conversely, in other insect taxa, a contrasting trend prevails, with insect body sizes decreasing as succession progresses (Chown and Gaston, 2010; Moir et al., 2005). Larger fruit-feeding butterfly species are presumed to be more sensitive to environmental variations and resource availability (Ribeiro and Freitas, 2011), thus serving as indicators of the relatively stable environmental or resource conditions found in older restored and primary forests (Valtonen et al., 2017). These interpretations are consistent with the results of our study. In addition, our results show that forest restoration not only impacts the mean values at the community level but also influences more nuanced size distributions, including diversity, skewness, and kurtosis (Fig. 3). Furthermore, these patterns vary depending on whether species- or individual-level mean trait values are considered (Fig. 3).

It is essential to note the potential risk of misinterpreting community patterns along a forest restoration gradient. Sole reliance on species-level information may underestimate the effect of forest restoration on fruit-feeding butterfly communities, as evidenced in our study (Fig. 3f, h vs. Fig. 3e, g). In addition, intraspecific variations in fruit-feeding butterfly sizes can contribute to differences among forest age groups. The detected intraspecific variation in size along the restoration gradient in six of the 12 most common species studied by us could be attributed to sex differences or phenotypic plasticity, that is, variations resulting from distinct environmental conditions encountered during the early developmental stages (Brakefield, 1987; Kemp and Jones, 2001). Both intraspecific size variations and sex ratios are features of the community that cannot be accurately captured solely through conventional species-level



analysis.

## 5. Conclusion

The exploration of variations in traits and interactions within species has emerged as a rapidly evolving topic in ecology in recent years (Fontana et al., 2016, The Herbivory Variability Network et al., 2023). While this debate is currently prevalent in basic ecological discourse, we anticipate that it will increasingly gain importance in the applied fields. Our findings indicate that older restored tropical forests possess greater potential to harbour morphological diversity among fruit-feeding butterflies. Although the time frame for the size distribution to revert to a state resembling the primary forest stage is protracted, the older restored forests examined in this study (aged 21–26 years) are steadily progressing towards the primary forest conditions. Nonetheless, a comprehensive understanding of the effect of niche space restoration on fruit-feeding butterflies necessitates individual-level measurements of morphological traits.

## CRedit authorship contribution statement

**Ryosuke Nakadai:** Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Formal analysis, Conceptualization. **Perpetra Akite:** Writing – review & editing. **Sille Holm:** Writing – review & editing. **Richard Kigenyi:** Writing – review & editing, Investigation, Conceptualization. **Eveliina Korkiatupa:** Writing – review & editing, Writing – original draft, Visualization. **Lotta Leinonen:** Writing – review & editing. **Geoffrey M. Malinga:** Writing – review & editing, Investigation, Conceptualization. **Margaret Nyafwono:** Writing – review & editing. **Wouter van Goor:** Writing – review & editing, Investigation, Conceptualization. **Anu Valtonen:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Conceptualization.

## Ethics statement

Our research involved using animals but not killing specimens. Fruit-feeding butterflies were captured in the field using banana-baited butterfly traps which were checked each day. Captured individuals were identified and their forewing lengths measured, after which they were released to nature. Hence, the field work did not involve killing specimens. Our research permits include permit from Uganda National Council for Science and Technology (Ref NS 678) and Uganda Wildlife Authority (COD/96/05).

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Wouter van Goor reports a relationship with the Face the Future which includes employment. Richard Kigenyi reports a relationship with the Uganda Wildlife Authority, which includes employment. All other 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. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03679](https://doi.org/10.1016/j.gecco.2025.e03679).

## Data availability

Data on community- and individual-level forewing lengths are available on Figshare (DOI: [10.6084/m9.figshare.29323304](https://doi.org/10.6084/m9.figshare.29323304)).

## References

- Amazonas, N.T., Viani, R.A.G., Rego, M.G.A., Camargo, F.F., Fujihara, R.T., Valsechi, O.A., 2018. Soil macrofauna density and diversity across a chronosequence of tropical forest restoration in southeastern Brazil. *Braz. J. Biol.* 78, 449–456. <https://doi.org/10.1590/1519-6984.169014>.
- Andersen, K.H., Berge, T., Gonçalves, R.J., Hartvig, M., Heuschele, J., Hylander, S., Jacobsen, N.S., Lindemann, C., Martens, E.A., Neuheimer, A.B., Olsson, K., Palacz, A., Prowe, A.E.F., Sainmont, J., Traving, S.J., Visser, A.W., Wadhwa, N., Kjørboe, T., 2016. Characteristic sizes of life in the oceans, from bacteria to whales. *Annu. Rev. Mar. Sci.* 8, 217–241. <https://doi.org/10.1146/annurev-marine-122414-034144>.

- Audino, L.D., Louzada, J., Comita, L., 2014. Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? *Biol. Conserv.* 169, 248–257. <https://doi.org/10.1016/j.biocon.2013.11.023>.
- Beck, J., Kitching, J.J., 2007. Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo-Australian tropics. *Glob. Ecol. Biogeogr.* 16 (3), 341–349. <https://doi.org/10.1111/j.1466-8238.2007.00289.x>.
- Begon, M., & Townsend, C.R. 2021. *Ecology. From individuals to ecosystems*. Wiley Blackwell. ISBN: 978-1119279358.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H., Schreiber, S.J., Urban, M.C., Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26 (4), 183–192. <https://doi.org/10.1016/j.tree.2011.01.009>.
- 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. *Biol. Conserv.* 143 (8), 1831–1841. <https://doi.org/10.1016/j.biocon.2010.04.044>.
- Brakefield, P.M., 1987. Tropical dry and wet season polyphenism in the butterfly *melanitis leda* (Satyriinae): phenotypic plasticity and climatic correlates. *Biol. J. Linn. Soc.* 31 (2), 175–191. <https://doi.org/10.1111/j.1095-8312.1987.tb01988.x>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85 (7), 1771–1789. <https://doi.org/10.1890/03-9000>.
- Case, T.J., Faaborg, J., Sidell, R., 1983. The role of body size in the assembly of west Indian bird communities. *Evolution* 37 (5), 1062–1074. <https://doi.org/10.2307/2408419>.
- Catterall, C.P., Freeman, A.N., Kanowski, J., Freebody, K., 2012. Can active restoration of tropical rainforest rescue biodiversity? A case with bird community indicators. *Biol. Conserv.* 146 (1), 53–61. <https://doi.org/10.1016/j.biocon.2011.10.033>.
- Chapman, C.A., Chapman, L.J., 1999. Forest restoration in abandoned agricultural land: a case study from east Africa. *Conserv. Biol.* 13 (6), 1301–1311. <https://doi.org/10.1046/j.1523-1739.1999.98229.x>.
- Chapman, C.A., Galán-Acedo, C., Gogarten, J.F., Hou, R., Lawes, M.J., Omeja, P.A., Sarkar, D., Sugiyama, A., Kalbitzer, U., 2021. A 40-year evaluation of drivers of African rainforest change. *For. Ecosyst.* 8, 66. <https://doi.org/10.1186/s40663-021-00343-7>.
- Chazdon, R.L., 2008. Chance and determinism in tropical forest succession. In: Carson, W.P., Schnitzer, S.A. (Eds.), *Tropical Forest Community Ecology*. Chichester: Wiley-Blackwell, pp. 384–408. ISBN: 978-1405189521.
- Chazdon, R.L., 2019. Towards more effective integration of tropical forest restoration and conservation. *Biotropica* 51 (4), 463–472. <https://doi.org/10.1111/btp.12678>.
- Chown, S.L., Gaston, K.J., 2010. Body size variation in insects: a macroecological perspective. *Biol. Rev.* 85 (1), 139–169. <https://doi.org/10.1111/j.1469-185X.2009.00097.x>.
- Derhé, M.A., Murphy, H., Monteith, G., Menéndez, R., 2016. Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. *J. Appl. Ecol.* 53 (6), 1714–1724. <https://doi.org/10.1111/1365-2664.12728>.
- Fernandes, G.W., Almada, E.D., Carneiro, M.A.A., 2010. Gall-inducing insect species richness as indicators of forest age and health. *Environ. Entomol.* 39 (4), 1134–1140. <https://doi.org/10.1603/EN09199>.
- Fontana, S., Petchey, O.L., Pomati, F., 2016. Individual-level trait diversity concepts and indices to comprehensively describe community change in multidimensional trait space. *Funct. Ecol.* 30 (5), 808–818. <https://doi.org/10.1111/1365-2435.12551>.
- Grant, P.R., Grant, B.R., 2002a. Adaptive radiation of Darwin's finches: recent data help explain how this famous group of galapagos birds evolved, although gaps in our understanding remain. *Am. Sci.* 90 (2), 130–139. <https://www.jstor.org/stable/27857627>.
- Grant, P.R., Grant, B.R., 2002b. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296 (5568), 707–711. <https://doi.org/10.1126/science.1070315>.
- Grimbacher, P.S., Catterall, C.P., 2007. How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? *Biol. Conserv.* 135 (1), 107–118. <https://doi.org/10.1016/j.biocon.2006.10.002>.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Siikamäki, J.V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Fargione, J., 2017. Natural climate solutions. *Proc. Natl. Acad. Sci.* 114 (44), 11645–11650. <https://doi.org/10.1073/pnas.1710465114>.
- Gross, N., Le Bagousse-Pinguet, Y., Liancourt, P., Saiz, H., Violle, C., Munoz, F., 2021. Unveiling ecological assembly rules from commonalities in trait distributions. *Ecol. Lett.* 24 (8), 1668–1680. <https://doi.org/10.1111/ele.13789>.
- Hartter, J., Ryan, S.J., Southworth, J., Chapman, C.A., 2011. Landscapes as continuous entities: forest disturbance and recovery in the albertine rift landscape. *Landsc. Ecol.* 26, 877–890. <https://doi.org/10.1007/s10980-011-9616-0>.
- Hawkins, B.A., Lawton, J.H., 1995. Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia* 102, 31–36. <https://doi.org/10.1007/BF00333307>.
- Howard, P., Davenport, T., Baltzer, M., 1996. *Biodiversity report. Kibale National Park. Forest Department, Kampala*, p. 115.
- Kearney, M., Simpson, S.J., Raubenheimer, D., Helmuth, B., 2010. Modelling the ecological niche from functional traits. *Philos. Trans. R. Soc. B Biol. Sci.* 365 (1557), 3469–3483. <https://doi.org/10.1098/rstb.2010.0034>.
- Kemp, D.J., Jones, R.E., 2001. Phenotypic plasticity in field populations of the tropical butterfly *hypolimnas bolina* (L.) (Nymphalidae). *Biol. J. Linn. Soc.* 72 (1), 33–45. <https://doi.org/10.1111/j.1095-8312.2001.tb01299.x>.
- Koch, A., Kaplan, J.O., 2022. Tropical forest restoration under future climate change. *Nat. Clim. Change* 12 (3), 279–283. <https://doi.org/10.1038/s41558-022-01289-6>.
- Korkiatupa, E., Malinga, G.M., Nakadai, R., Nyafwono, M., Akite, P., Holm, S., van Goor, W., Kigenyi, R., Valtanen, A., 2023. Recovery patterns in community composition of fruit-feeding butterflies following 26 years of active forest restoration. *Ecosphere* 14 (5), e4514. <https://doi.org/10.1002/ecs2.4514>.
- Kraft, N.J.B., Valencia, R., Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an amazonian forest. *Science* 322 (5901), 580–582. <https://doi.org/10.1126/science.1160662>.
- Lande, R., Arnold, S.J., 1983. The measurement of selection on correlated characters. *Evolution* 37 (6), 1210–1226. <https://doi.org/10.2307/2408842>.
- Latja, P., Valtanen, A., Malinga, G.M., Roininen, H., 2016. Active restoration facilitates bird community recovery in an afro-tropical rainforest. *Biol. Conserv.* 200, 70–79. <https://doi.org/10.1016/j.biocon.2016.05.035>.
- Miller, T.J., Crowder, L.B., Rice, J.A., Marshall, E.A., 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. Aquat. Sci.* 45 (9), 1657–1670. <https://doi.org/10.1139/f88-197>.
- Moir, M.L., Brennan, K.E.C., Koch, J.M., Majer, J.D., Fletcher, M.J., 2005. Restoration of a forest ecosystem: the effects of vegetation and dispersal capabilities on the reassembly of plant-dwelling arthropods. *For. Ecol. Manag.* 217 (2–3), 294–306. <https://doi.org/10.1016/j.foreco.2005.06.012>.
- Molleman, F., 2012. *Butterflies of Uganda Kibale Forest*. Kampala: Tourguide Publications. ISBN: 978-9970-637-22-5.
- Molleman, F., Kop, A., Brakefield, P.M., De Vries, P.J., Zwaan, B.J., 2006. Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. *Biodivers. Conserv.* 15, 107–121. <https://doi.org/10.1007/s10531-004-3955-y>.
- Nakadai, R., Hashimoto, K., Iwasaki, T., Sato, Y., 2018. Geographical co-occurrence of butterfly species: the importance of niche filtering by host plant species. *Oecologia* 186 (4), 995–1005. <https://doi.org/10.1007/s00442-018-4062-1>.
- Nakadai, R., Nyman, T., Hashimoto, K., Iwasaki, T., Valtanen, A., 2021. Fundamental resource specialization of herbivorous butterflies decreases towards lower latitudes. *J. Biogeogr.* 48 (10), 2524–2537. <https://doi.org/10.1111/jbi.14218>.
- Nyafwono, M., Valtanen, A., Nyeko, P., Roininen, H., 2014. Fruit-feeding butterfly communities as indicators of forest restoration in an Afro-tropical rainforest. *Biol. Conserv.* 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., Valtanen, A., 2021. Recovery of fruit-feeding butterfly communities in budongo forest reserve after anthropogenic disturbance. *For. Ecol. Manag.* 491, 119087. <https://doi.org/10.1016/j.foreco.2021.119087>.
- Omeja, P.A., Chapman, C.A., Obua, J., Lwanga, J.S., Jacob, A.L., Wanyama, F., Mugenyi, R., 2011. Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in kibale national park, Uganda. *For. Ecol. Manag.* 261 (3), 703–709. <https://doi.org/10.1016/j.foreco.2010.11.029>.

- QGIS.org, 2021. QGIS Geographic Information System. QGIS Association, Switzerland. (<https://www.qgis.org>).
- R Core Team, 2023. R: a language and environment for statistical computing. Vienna. R. Found. Stat. Comput. (<https://www.r-project.org/>).
- Reim, E., Kahl, S., Metschke, K., Fischer, K., 2019. Sexual differences rather than flight performance underlie movement and exploration in a tropical butterfly. *Ecol. Entomol.* 44 (5), 648–658. <https://doi.org/10.1111/een.12738>.
- Ribeiro, D.B., Freitas, A.V., 2011. Large-sized insects show stronger seasonality than small-sized ones: a case study of fruit-feeding butterflies. *Biol. J. Linn. Soc.* 104 (4), 820–827. <https://doi.org/10.1111/j.1095-8312.2011.01771.x>.
- Riemer, K. 2020. Verified Carbon Standard. Monitoring Report 2017–2020. Natural High Forest Rehabilitation Project on degraded land of Kibale National Park. Uganda Wildlife Authority & Face the Future. October 6, 2020. (<https://registry.verra.org/app/projectDetail/CCB/673>).
- Ruth, M. 2021. Africa Boundaries. Available at: (<https://hub.arcgis.com/datasets/07610d73964e4d39ab62c4245d548625/explore>) (Accessed on 24 November 2023).
- Sant'Anna, C.L., Ribeiro, D.B., Garcia, L.C., Freitas, A.V., 2014. Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. *Restor. Ecol.* 22 (4), 480–485. <https://doi.org/10.1111/rec.12091>.
- Sielezniew, M., Kostro-Ambroziak, A., Körösi, Á., 2020. Sexual differences in age-dependent survival and life span of adults in a natural butterfly population. *Sci. Rep.* 10 (1), 10394. <https://doi.org/10.1038/s41598-020-66922-w>.
- Singer, M.C., 1982. Sexual selection for small size in male butterflies. *Am. Nat.* 119 (3), 440–443. <https://doi.org/10.1086/283924>.
- Spaniol, R.L., Duarte, L.D.S., Mendonça Jr, M.D.S., Iserhard, C.A., 2019. Combining functional traits and phylogeny to disentangling amazonian butterfly assemblages on anthropogenic gradients. *Ecosphere* 10 (8), e02837. <https://doi.org/10.1002/ecs2.2837>.
- Struhsaker, T.T., 1997. Ecology of an African rain forest: Logging in Kibale and the Conflict between Conservation and Exploitation. Gainesville: University Press of Florida. EBSCOhost. ISBN: 978-0813014906.
- The Herbivory Variability Network, Robinson, M.L., Hahn, P.G., Inouye, B.D., Underwood, N., Whitehead, S.R., Abbott, K.C., Bruna, E.M., Cacho, N.I., Dyer, L.A., Abdala-Roberts, L., Allen, W.J., Andrade, J.F., Angulo, D.F., Anjos, D., Anstett, D.N., Bagchi, R., Bagchi, S., Barbosa, M., Barrett, S., Baskett, C.A., Wetzel, W.C., 2023. Plant size, latitude, and phylogeny explain within-population variability in herbivory. In: *Science*, 382, pp. 679–683. <https://doi.org/10.1126/science.adh8>.
- The World Bank, 2018, Data Catalog – Africa Water Bodies. The World Bank. (<https://datacatalog.worldbank.org/search/dataset/0040797/Africa—Water-Bodies>). (Accessed on 1 August 2023).
- UWA-FACE, 2015, Natural high forest rehabilitation project on degraded land of Kibale National Park, Uganda: CCB Project Design Document. Uganda Wildlife Authority & Face the Future, ([https://registry.verra.org/mymodule/ProjectDoc/Project\\_ViewFile.asp?FileID=44111&IDKEY=kq934lkmsad39asjdkfj90qlkalsdkngaf98ulkandDfdvDdfh360829069](https://registry.verra.org/mymodule/ProjectDoc/Project_ViewFile.asp?FileID=44111&IDKEY=kq934lkmsad39asjdkfj90qlkalsdkngaf98ulkandDfdvDdfh360829069)).
- Valtonen, A., Korkiatupa, E., Holm, S., Malinga, G.M., Nakadai, R., 2021. Remotely sensed vegetation greening along a restoration gradient of a tropical forest, Kibale National Park, Uganda. *Land Degrad. Dev.* 32 (18), 5166–5177. <https://doi.org/10.1002/ldr.4096>.
- Valtonen, A., Malinga, G.M., Nyafwono, M., Nyeko, P., Owiny, A., Roininen, H., 2017. The successional pathway of the tree community and how it shapes the fruit-feeding butterfly community in an afrotropical forest. *J. Trop. Ecol.* 33 (1), 12–21. <https://doi.org/10.1017/S0266467416000560>.
- 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), 1–28. <https://doi.org/10.1890/ES12-00338.1>.
- van den Tweel, B., 2023. CCB Monitoring report 2020–2023. Uganda Wildlife Authority & Face the Future. June 6, 2023. (<https://registry.verra.org/app/projectDetail/CCB/673>).
- van Orsdol, K.G., 1986. Agricultural encroachment in Uganda's Kibale forest. *Oryx* 20, 115–117.
- Vancutsem, C., Achard, F., Pekel, J.F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Araga, L.E.O.C., Nasi, R., 2021. Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Sci. Adv.* 7 (10), eabe1603.
- Vielle, C., Enquist, B.J., McGill, B.J., Jiang, L.I.N., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27 (4), 244–252. <https://doi.org/10.1016/j.tree.2011.11.014>.
- Vielle, C., Jiang, L., 2009. Towards a trait-based quantification of species niche. *J. Plant Ecol.* 2 (2), 87–93. <https://doi.org/10.1093/jpe/rtp007>.
- Wheeler, C.E., Omeja, P.A., Chapman, C.A., Glipin, M., Tumwesigye, C., Lewis, S.L., 2016. Carbon sequestration and biodiversity following 18 years of active tropical forest restoration. *For. Ecol. Manag.* 373, 44–55. <https://doi.org/10.1016/j.foreco.2016.04.025>.
- Wieczynski, D.J., Boyle, B., Buzzard, V., Duran, S.M., Henderson, A.N., Hulshof, C.M., Kerkhoff, A.J., McCarthy, M.C., Michaletz, S.T., Swenson, N.G., Asner, G.P., Bentley, L.O., Enquist, B.J., Savage, V.M., 2019. Climate shapes and shifts functional biodiversity in forests worldwide. *Proc. Natl. Acad. Sci.* 116 (2), 587–592. <https://doi.org/10.1073/pnas.1813723116>.
- Williams, M.C., 2021. Afrotropical Butterflies and Skippers. A Digital Encyclopaedia. Metamorphosis. (<http://metamorphosis.org.za/?p=articles&s=atb>).