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The successional pathway of the tree community and how it shapes the fruit-feeding butterfly community in an Afrotropical forest

Anu Valtonen[1,2,*], Geoffrey M. Malinga[1,3], Margaret Nyafwono[1,4], Philip Nyeko[5], Arthur Owiny[1] and Heikki Roininen[1]

[1] Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland
[2] Center for Ecological Research, Kyoto University, Hirano 2, Otsu, Shiga 520–2113, Japan
[3] Department of Biology, Gulu University, P.O. Box 166, Gulu, Uganda
[4] Department of Environment and Natural Resources Management, Gulu University, P.O. Box 166, Gulu, Uganda
[5] Department of Forestry, Biodiversity and Tourism, Makerere University, P.O. Box 7062, Kampala, Uganda

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Abstract: The relative importance of different bottom-up-mediated effects in shaping insect communities in tropical secondary forests are poorly understood. Here, we explore the roles of vegetation structure, forest age, local topography (valley vs. hill top) and soil variables in predicting fruit-feeding butterfly and tree community composition, and tree community composition in predicting fruit-feeding butterfly community composition, in different-aged naturally regenerating and primary forests of Kibale National Park, Uganda. We also examine which variables are best predictors of fruit-feeding butterfly species richness or diversity. Butterflies (88 species) were sampled with a banana-baited trap and trees (98 taxa) with a 40 × 20-m sampling plot at 80 sampling sites. The environmental variables explained 31% of the variation in the tree community composition, the best predictors being local topography, forest age and cover of *Acanthus pubescens* (a shrub possibly arresting succession). The fruit-feeding butterfly community composition was better predicted by tree community composition (explaining 10% of the variation) rather than vegetation structure, local topography or soil factors. Environmental variables and tree species richness (or diversity) were poor predictors of butterfly species richness (or diversity). Our results emphasize the importance of tree community to recovery of herbivorous insect communities in tropical secondary forests.

Key Words: community composition, diversity, forest regeneration, insects, Lepidoptera, primary forest, secondary forest, species richness, Uganda, vegetation structure

INTRODUCTION

The relative importance of different bottom-up-mediated effects in shaping insect communities in tropical secondary forests recovering from anthropogenic disturbances are poorly understood. The severity of a disturbance, vegetation surviving after the disturbance, landscape matrix (proximity of seed sources), soil fertility and texture, altitude, local topography, climate and microclimate play important roles in the recovery processes of plant communities (reviewed by Chazdon 2003, 2008; Guariguata & Ostertag 2001). Changes taking place in vegetation structure, plant community composition and microclimate are expected to lead to changes in animal communities, because species vary in their requirements for resources and habitats (Pinotti *et al.* 2012). Increases in accumulated biomass and tree height should lead to increases in the variety of feeding, resting, oviposition sites, shelter and hiding places from enemies (Lawton 1983). Changes taking place in plant community composition, or differences in plant communities emerging on different soil types and local topography, can impact the emerging herbivore communities because the majority of tropical herbivorous insects seem to be host-specialized to at least some degree, typically at the plant genus level (Dyer *et al.* 2007, Forister *et al.* 2015, Novotny & Basset 2005).

Here, we explore the successional pathway of a tree community and how it shapes the fruit-feeding butterfly community in different-aged naturally regenerating and primary forests of Kibale National Park, Uganda. We

* Corresponding author. Email: anu.valtonen@uef.fi

hypothesized that the tree community composition can be predicted not only by forest age but also by soil characteristics and local topography (because they could produce divergence in community composition during succession; Chazdon 2008), or cover by plant species potentially arresting succession and preventing the establishment of seedlings (Chapman & Chapman 1999, Chapman *et al.* 1999) (Hypothesis 1). Fruit-feeding butterflies are heterotrophs dependent on plants as larvae and rotting fruits on the forest floor as adults (Molleman *et al.* 2005). Larval hosts of some of these species are known (Molleman 2012). If most fruit-feeding butterflies are relatively specialized on their larval hosts (and are relatively local in their movements), or specialized in their adult feeding requirements, or both, then tree community composition will be a better predictor of butterfly communities than vegetation structure and other physical conditions of the forest (Hypothesis 2). The opposite would be true if the species are specialized more strongly to certain physical conditions of the forest (e.g. canopy closure). If the fruit-feeding butterflies are strongly host-specialized, an increasing species richness and diversity of trees will be associated with an increasing species richness (Lewinsohn *et al.* 2005; Hypothesis 3) or diversity (Hypothesis 4) of fruit-feeding butterflies, respectively.

METHODS

Study area

Our study was conducted in Kibale National Park (0°13′–0°41′N, 30°19′–30°32′E), which is a moist, evergreen medium-altitude (approximately 1500 m asl) tropical forest in western Uganda, East Africa. The mean daily minimum temperature is 14.9°C, the mean daily maximum temperature is 20.2°C and the mean annual rainfall is 1749 mm (Chapman *et al.* 2005). The soils are lixic ferralsols (Majaliwa *et al.* 2010). The vegetation in Kibale represents mainly moist evergreen forests, but includes also regenerating forests, grasslands, swamps and woodland thickets (Chapman & Lambert 2000, Struhsaker 1997). Within forest gaps created by logging, shrubs (mainly *Acanthus pubescens* Engl.) can form a dense cover, reducing the light and nutrient availability to potential colonizers (Duclos *et al.* 2013), potentially arresting the forest succession.

Fruit-feeding butterfly dataset

We used the fruit-feeding butterfly dataset collected in naturally regenerating and primary forests of Kibale National Park, published in Nyafwono *et al.* (2014a). The dataset was collected with 80 banana-baited butterfly traps, each located in one sampling site (see map and details in Nyafwono *et al.* 2014a). The traps were hung 40–50 cm above the ground (i.e. understorey traps), and were sampled monthly for 1 y from May 2011 to April 2012. The 80 sampling sites were randomly located (but always > 100 m apart; Nyafwono *et al.* 2014a) within: (1) four regenerating clear-cut forests (9, 11, 14 and 19 y old; previously conifer plantations; RAC9–19 of Nyafwono *et al.* 2014a; coded here as R); (2) two 43-y-old selectively logged forest compartments (K13 and K15 of Nyafwono *et al.* 2014a; coded here as K); and (3) two forest compartments in continuous primary forests (K30 and K31 of Nyafwono *et al.* 2014a, coded here as P). The dataset included 16,728 individuals representing 88 fruit-feeding butterfly species. For the analyses, the number of butterflies within each species and each sampling site were summed (over the year).

Tree community, vegetation structure, local topography and soil datasets

At the same sampling sites where traps were located, data on tree community composition, vegetation structure, local topography and soil variables were collected from April to October 2011 (Owiny *et al.* 2016). The tree community dataset included 98 tree taxa (92 identified at species level, four at genus level and two unidentified), and 8200 counted stems, collected within a 40 × 20-m plot located at each sampling site (see details in Owiny *et al.* 2016). For each species in each plot, the density of stems (number ha^{-1}), and basal area (m^2 ha^{-1}) (of trees with diameter at breast height ≥ 5 cm) was estimated (the community composition datasets).

Five vegetation structure variables were recorded at each sampling plot: (1) total estimated stem density and (2) total estimated basal area which were calculated as sums across species from the community composition datasets described above; (3) tree canopy closure (the proportion of the sky covered by vegetation when viewed from a single point; Jennings *et al.* 1999); (4) gap cover (area not covered by trees and shrubs); and (5) cover of *A. pubescens*. The cover values were estimated visually within the 40 × 20-m plots on a scale: 0 (0%), 0.5 (<10%), 1 (10%), 2 (20%), 3 (30%), . . . , 10 (100%).

Local topography and 11 soil variables were measured at each sampling site. Local topography was measured as height (m) above the lowest recorded elevation (range 1433–1604 m asl), i.e. the lowest sampling site on a valley bottom received a value of 0. In each plot, five soil samples (~450 g) were excavated; four soil samples were taken from the border points of the 40 × 20-m plot, and one from the middle. Samples were collected from depths of 0–15 cm and 15–30 cm using a 2-cm-diameter soil

auger. Samples were separately stored in polythene bags, air dried to halt biological transformation, and sieved through a 2-mm screen to remove stone particles and roots. Samples from each plot and depth were then bulked and ~5 g were analysed for: (1) pH; (2) soil organic matter (Walkley-Black Method); (3) N (total nitrogen, Kjeldahl method); (4) available phosphorus (P; Bray and Kurtz No. 1 method); (5) K; (6) Na; (7) Ca (flame photometer); (8) Mg (AAS); and soil texture (hydrometer method), as percentages of (9) sand, (10) clay and (11) silt. The soil analyses were conducted at the soil science laboratory of the Makerere University. For all soil variables the average of the values from the two depths was calculated for each plot.

Data analysis

To determine whether the variables describing vegetation structure, forest age, local topography and soil factors predicted tree and butterfly community compositions, we used predictive canonical correspondence analysis (CCA; ter Braak 1986). CCA is a multivariate analysis technique that relates community composition to environmental variables. The age of the forest was added to CCA models as a factor with six levels: 9, 11, 14, 19, 43 y, and primary forest. To avoid collinearity, we included only continuous variables that did not correlate strongly with each other (Pearson $\rho \leq 0.5$). The tree community composition was predicted with forest age, gap cover, *A. pubescens* cover, local topography (which correlated with soil organic matter, $\rho = 0.53$) and the soil variables including pH, N, P, Na, K (which correlated with Ca, $\rho = 0.51$), Mg (which correlated with Ca, $\rho = 0.63$), clay (which correlated with sand, $\rho = -0.88$) and silt (which correlated with sand, $\rho = -0.51$). The tree community composition at each study site was first described as the stem density of each tree species, emphasizing the smaller trees, and then as the estimated basal area of each tree species, emphasizing the larger trees. The fruit-feeding butterfly community composition (the number of individuals of each butterfly species at each study site) was predicted using forest age, canopy closure (which correlated with stem density, $\rho = 0.54$; basal area, $\rho = 0.59$; soil organic matter, $\rho = -0.57$; and soil N, $\rho = -0.52$), gap cover, *A. pubescens* cover, local topography (which correlated with soil organic matter) and soil variables including pH, P, Na, K (which correlated with Ca), Mg (which correlated with Ca), clay (which correlated with sand) and silt (which correlated with sand). Prior to the analyses, the response datasets, i.e. stem densities of trees, and counts of fruit-feeding butterflies were $\log_e(x+1)$ transformed, and tree basal areas $\log_e(100x+1)$ transformed to decrease the influence of the most abundant species. The tree canopy closure, gap cover and *A. pubescens* cover were first transformed to proportions and then logit transformed (Warton & Hui 2011), the total basal area of trees square-root transformed, and P, K, Ca and Mg $\log_e$-transformed to reduce the skewness in their distributions. Four sampling sites were excluded from CCA analyses due to missing values in soil variables. To perform CCAs, first, we selected all predictor variables and tested how many constrained CCA axes were significant in explaining the community composition (499 permutations). This was done to determine how many axes to keep in the final model. Second, to determine whether the tree or butterfly community composition was associated with the predictors of the final model, a permutation test was conducted (499 permutations). To adjust for probable spatial autocorrelation in community composition, we conducted the conditional variation partitioning analyses of Canoco (ter Braak & Šmilauer 2012) (Appendix 1).

To answer the question whether tree community composition predicts the butterfly community composition, we used predictive co-correspondence analysis (CoCA; Schaffers *et al.* 2008, ter Braak & Schaffers 2004). CoCA is an ordination method which relates two types of community, and attempts to identify the patterns which are common to both communities (ter Braak & Schaffers 2004). The influence of the most abundant species was decreased by performing $\log_e(x+1)$ transformations on the butterfly community and tree stem density datasets prior to the analyses. We assessed the accuracy of the CoCA model using the cross-validatory fit percentage, with values above zero indicating that the model prediction is better than expected by chance alone (ter Braak & Schaffers 2004). The cross-validatory fit describes the percentage of explained variation but it is not comparable with the percentages of explained variation in CCA (Schaffers *et al.* 2008). The number of CoCA ordination axes for the final model was selected based on both cross-validatory fit (the local maximum was selected to keep the model as simple as possible; ter Braak & Schaffers 2004) and by testing the significance of each ordination axis with a permutation test (499 permutations; ter Braak & Schaffers 2004); if the two methods disagreed, the smaller of the two values was selected.

To test whether tree community composition is a better predictor of butterfly communities than vegetation structure and physical conditions of the forest, we first re-fitted the CCA model excluding the factor forest age. We then ran a simple randomization test to judge whether differences among the model fits that predicted fruit-feeding butterfly communities (CCA vs. CoCA) were statistically significant (van der Voet 1994). From each model, the predicted $\log_e(x+1)$ transformed count of individual fruit-feeding butterflies of each species at each site was extracted. The difference in mean-squared prediction errors was calculated and used as a test statistic, and the mean-squared prediction errors of the sites were

re-arranged 999 times. We tested a two-sided alternative hypothesis, i.e. mean-squared prediction error of CCA model ≠ mean-squared prediction error of CoCA model (van der Voet 1994).

To determine how well tree species richness or diversity and environmental variables predicted fruit-feeding butterfly species richness or diversity, linear regression models were fitted. For each sampling site, fruit-feeding butterfly and tree species richness were estimated using Colwell's combined rarefaction-extrapolation method (species richness estimated for 120 butterfly individuals or 1428 tree stems, i.e. extrapolated to maximum three times the smallest observed number). Diversity was measured as Simpson's $D = 1-\Sigma((N_i(N_i-1))/(N(N-1))$, where N_i = number of individuals in species i, and N = total number of individuals, a measure of the probability that two individuals drawn at random belong to different species (Maurer & McGill 2011). Tree species richness and diversity were calculated from the estimated stem densities dataset, rounded to integers. For linear regression models, we included only variables that did not correlate strongly with each other (Pearson $\rho \leq 0.5$). Butterfly species richness was explained by tree species richness (which correlated with stem density, $\rho = 0.66$; basal area, $\rho = 0.73$; canopy closure, $\rho = 0.57$ and local topography, $\rho = -0.59$), *A. pubescens* cover and gap cover. Butterfly diversity was explained by tree diversity, total basal area of trees (which correlated with stem density, $\rho = 0.69$ and canopy closure, $\rho = 0.59$), *A. pubescens* cover, gap cover and local topography. The fits of all possible combinations of these explanatory variables were compared using an Information Theoretic approach (AICc) (Anderson 2008). The linear regression models assume independence of the samples (here sampling sites) but we assumed this was not violated because no evidence of spatial autocorrelation among the sampling sites in terms of species richness values was found (Mantel test; Nyafwono *et al.* 2014a).

CCA and variation partitioning analyses were conducted with Canoco, version 5 (ter Braak & Šmilauer 2012), CoCA analyses with the package cocorresp (http://cran.at.r-project.org/web/packages/cocorresp/cocorresp.pdf) in R (http://www.r-project.org/), species richness values were estimated with EstimateS (http://viceroy.eeb.uconn.edu/estimates/), Simpson's D was calculated with Primer-E, version 6 (Clarke & Gorley 2006) and all other analyses were conducted with R version 2.14.1.

RESULTS

Predictors of tree community composition (Hypothesis 1)

The environmental variables (forest age, gap cover, *A. pubescens* cover, local topography and soil pH, N, P, Na, K, Mg, clay and silt) explained 31.0% of the variation in the tree community composition (stem densities of trees as the response dataset; final CCA model with two axes: permutation test for all axes, *pseudo-F* = 1.7; P = 0.002). The CCA ordination presents the patterns in community composition explained by the environmental variables (arrows in Figure 1) and forest age (triangles in Figure 1), the length of each arrow showing the proportional importance. The first CCA axis is the local topography gradient (intra-set correlation = 0.74) but also separates the tree communities of young recovering forests from older forests (intra-set correlation with forest age group primary forest = −0.64). The forest age group 43-y-old forests (0.54) and cover of *A. pubescens* (0.53) correlated most strongly with the second CCA axis. For example, the tree species *Craterispermum schweinfurthii* and *Leptonychia mildbraedii* were relatively most abundant in valley-bottom primary-forest sites; *Albizia grandibracteata* and *Bridelia micrantha* in young hill-top sites; *Carapa procera* and *Hallea rubrostipulata* in sites with high coverage by *A. pubescens*; *Craterispermum schweinfurthii* and *Pancovia turbinata* in sites with low coverage by *A. pubescens* (Figure 1; Appendix 2). This analysis (stem densities of trees used as the response dataset) emphasizes small trees but the CCA ordination was very similar if basal areas of trees were included as the response dataset, emphasizing large trees (final CCA model with three axes explaining

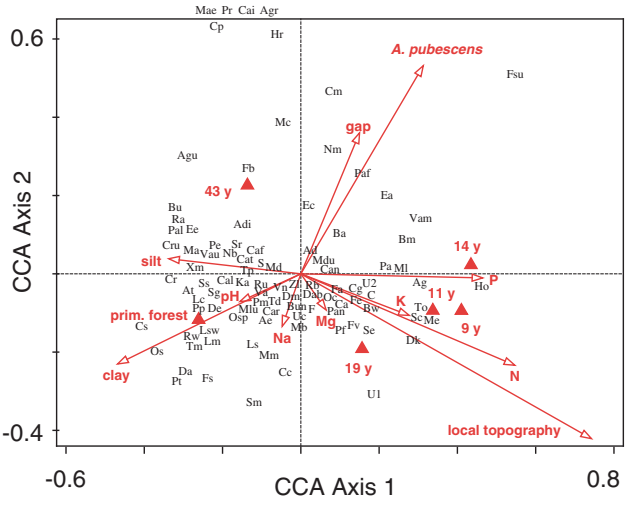

Figure 1. Tree community predictors: Canonical correspondence analysis (CCA) ordination diagram showing how community composition of trees changed along gradients of environmental variables in secondary and primary forests of Kibale National Park, Uganda. Community composition at the 76 sampling sites (40 × 20-m plots) was measured as stem densities of trees. Tree species names are abbreviated (see full names in Appendix 2), continuous predictors are shown as arrows, and the factor levels of forest age with triangles. Symbols of certain species are moved slightly to improve readability and the few outliers are located outside the graph edge. The first CCA axis explained 9% and the second, 5% of the variation.

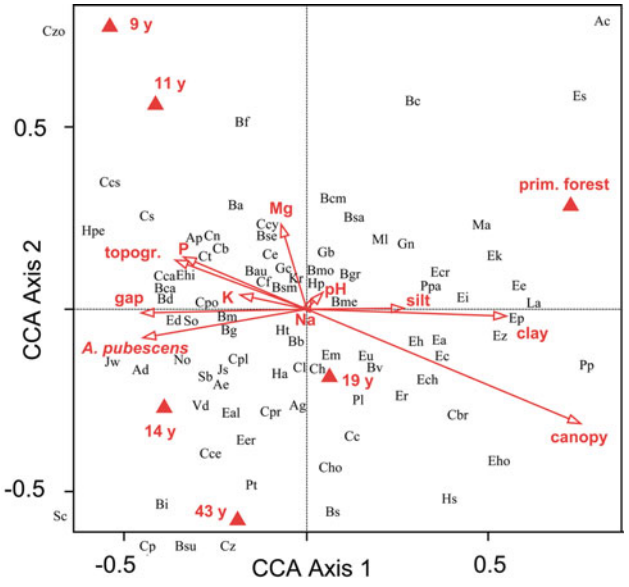

Figure 2. Butterfly community predictors: Canonical correspondence analysis (CCA) ordination diagram showing how community composition of fruit-feeding butterflies changed along gradients of environmental variables in secondary and primary forests of Kibale National Park, Uganda. Community composition at the 76 sampling sites was collected with one banana-baited butterfly trap. Butterfly species names are abbreviated (see full names in Appendix 2), continuous predictors are shown as arrows, and the factor levels of forest age with triangles. Symbols of certain species are moved slightly to improve readability and the few outliers are located outside the graph edge. The first CCA axis explained 10% and the second axis, 4% of the variation.

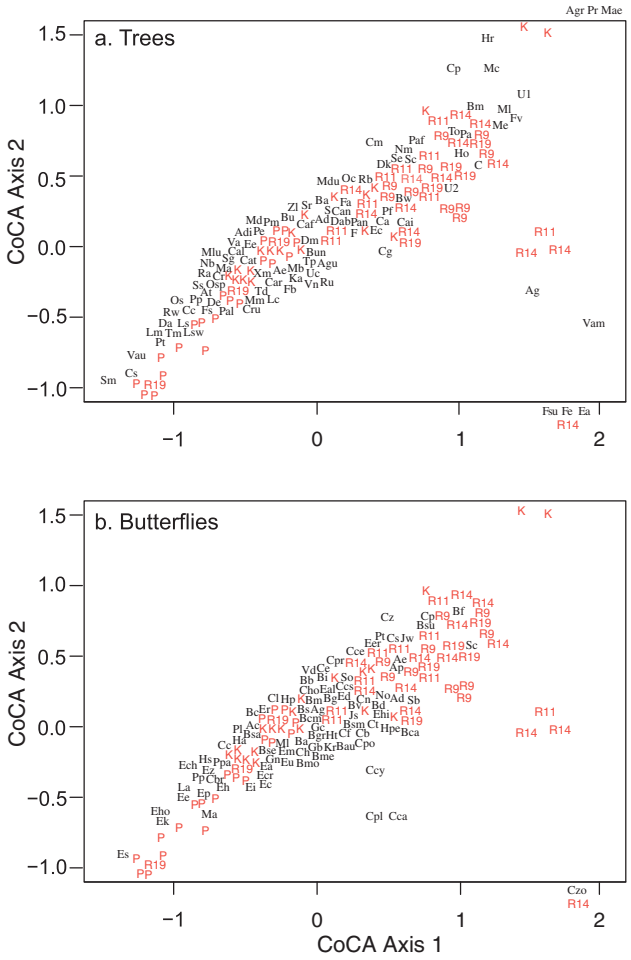

Figure 3. Predictive co-correspondence analysis (CoCA) bi-plots showing the common gradient in tree (a), and butterfly community composition (b), in naturally regenerating and primary forests of Kibale National Park, Uganda. Species names are abbreviated (see full names in Appendix 2); tree species predict the butterfly species which are located in the same part of the plots. Sampling sites (red) are indicated with symbols: P = primary forests; K = 43-y-old forests; R9–19 = young forests. Some symbols are moved slightly to improve readability and the few outliers are located outside the graph edge.

30.6% of variation: permutation test for all axes, *pseudo-F* = 1.6; P = 0.002).

Predictors of butterfly community composition (Hypothesis 2)

The environmental variables (forest age, canopy closure, gap cover, *A. pubescens* cover, local topography and soil pH, P, Na, K, Mg, clay and silt) explained 31.8% of the variation in the fruit-feeding butterfly community composition (final CCA model with two axes: *pseudo-F* = 1.7; P = 0.002). The first CCA axis is the canopy-closure gradient which separates primary-forest communities from the secondary-forest communities; forest age primary forest (intra-set correlation = 0.82) and tree canopy closure (0.75) were the most important variables correlating with CCA axis 1 (Figure 2). The forest age group 43-y-old forests (−0.57) correlated most strongly with the second CCA axis. For example, species of *Bicyclus* and *Charaxes* were relatively most abundant in young or intermediate-aged secondary forests and low canopy closure, and of *Euphaedra* in primary forests with high canopy closure (Figure 2; Appendix 2).

The tree community composition (measured as stem densities of trees) significantly explained the fruit-feeding butterfly community composition (cross-validatory fit of the CoCA model > 0). The final model (including four significant axes) explained 10.2% of the variation in butterfly community composition, but note that the percentage represents the cross-validatory fit and is not comparable with the percentages of explained variation in CCA. The CoCA biplots identify the pattern which is common to both tree and butterfly communities (Figure 3). In these plots, tree species predict the butterfly species which are located in the same part of the plots. The pattern revealed follows the disturbance gradient where the primary forest sites (P) receive mostly low

values, 43-y-old forests (K) intermediate values, and the youngest forests (R) high values for CoCA axis 1 (although 9–19-y-old forests do not show a clear age-gradient among themselves). Only a few butterfly species were found at the young end of the gradient (all being singletons or doubletons), predicted by several tree species such as *Bridelia micrantha*, *Macaranga capensis*, *Maesa lanceolata* and *Trema orientalis*. Species of *Euphaedra* were most common at the old end of the gradient, predicted, for example, by tree species *Trilepisium madagascariensis*, *Craterispermum schweinfurthii*, *Leptonychia mildbraedii* and *Pancovia turbinata*.

According to the randomization test, the tree community composition was a significantly better predictor (P = 0.001) of butterfly community composition (CoCA; mean of squared prediction errors = 0.18) than vegetation structure, local topography and soil variables (CCA; mean of squared prediction errors = 0.60).

What explains species richness and diversity of butterflies (Hypotheses 3 and 4)?

We found no significant associations between butterfly species richness (or diversity) and the tree species richness (or diversity) or the environmental variables. The highest-ranked models (i.e. the models with the lowest AICc) explaining butterfly species richness (P = 0.24; R^2 adj. = 0.005) or diversity (P = 0.10; R^2 adj. = 0.03) were not significant.

DISCUSSION

Our results illustrate a possible pathway shaping tree and insect communities in tropical secondary forests: the tree community composition showed stratification along the local topographic gradient and was also explained by succession (forest age) and factors potentially arresting the succession (*A. pubescens*), confirming Hypothesis 1. The fruit-feeding butterfly community composition was strongly associated with the tree community composition, confirming Hypothesis 2. It was no surprise perhaps that the tree communities showed stratification according to the local topography which is associated with variation in edaphic conditions and soil, i.e. hilltops are considered to be more prone to drought, while soils on slopes and valley bottoms are likely to be moister (Ghazoul & Sheil 2010). Our results also suggest that *A. pubescens*, a shrub that arrives in forest gaps created by logging and potentially arrests the succession (Chapman *et al.* 1999), can shape the tree community composition, independent of forest age. The mechanism could be twofold. It is known that elephants can suppress tree regeneration in Kibale, and they may be attracted to gaps by *A. pubescens* (Lawes & Chapman 2006). On the other hand, dense cover by *A. pubescens* can change light and nutrient availability and may be an important factor explaining seedling growth in Kibale (Duclos *et al.* 2013).

The strong relationship between tree and butterfly community composition suggests that most fruit-feeding butterflies could be relatively specialized in their larval hosts or trees used for adult feeding, or both. The abundance of lepidopteran species is known to correlate with the biomass of their host plants (Yamamoto *et al.* 2007), but among Central European moths this is true only for monophagous species (Lepš *et al.* 1998) and the association between macromoths and plant community composition was stronger for specialists than for generalists (Müller *et al.* 2011). An alternative explanation could be that the tree community composition captures the complex habitat conditions better than the measured vegetation structure, local topography and soil variables (Schaffers *et al.* 2008). Plant community composition has been found to be an important predictor of the community composition of various groups of herbivorous, carnivorous and omnivorous arthropods (Gioria *et al.* 2011, Schaffers *et al.* 2008, ter Braak & Schaffers 2004), and fruit-feeding butterflies in young restored and primary forests in Kibale National Park, where it was an equally good predictor as vegetation structure (Nyafwono *et al.* 2014b, 2015). Across various arthropod groups, plant community composition has been found to explain 2–18% of the variation (cross-validatory fit; Schaffers *et al.* 2008), hence the explained variation in our study (10%) is substantial.

The locations of tree and butterfly species on the corresponding gradient (Figure 3) suggest that the gradient could be, at least partly, explained by specialization in larval host use. For example, some butterfly species, especially species of *Euphaedra* whose larval host-plants are known (Molleman 2012), had their highest densities near their host trees, such as *Lepisanthes senegalensis*, *Blighia unijugata*, *Pancovia turbinata*, *Parinari excelsa* and *Uvariopsis congensis*. Some of the studied fruit-feeding butterflies also use non-tree larval hosts (Molleman 2012), in which case the tree-butterfly associations could be either explained by specialization in adult resources or indirectly by light or moisture conditions preferred both by trees and the non-tree host plants of the butterflies. However, if the gradient was mainly explained by specialization in larval host use, this would require that the adults are relatively local in their movements. Little is known about the spatial structure and dispersal capabilities of tropical adult butterflies, but the few studies indicate that they can vary from highly local to those that can disperse or migrate long distances (Bonebrake *et al.* 2010). The corresponding gradient of butterflies and trees might also be explained by the strong associations between

fruit-feeding butterflies and their adult food resources (fruit-bearing trees). For example, fruits of *Ficus* spp., *Mimusops bagshawei*, *Uvariopsis congensis*, *Diospyros abyssinica* and *Strychnos mitis* are used by the adults of the studied butterfly species (Molleman *et al.* 2005), some of which are also their larval host plants (Molleman 2012). Finally, it is also theoretically possible that since our sampling covered understorey only, canopy specialists would only be found where canopy cover is low and understorey specialists only where canopy cover is high, but in our case no such division was found (see species categorizations to different forest strata in Molleman *et al.* 2006), although the relatively few canopy specialists more typically were found in the younger rather than in the older ends of the CCA and CoCA gradients.

Our results demonstrate how recovery in species richness or diversity (no clear gradients) and in community composition (strongly associated with environmental gradients) are independent processes; contrary to our hypotheses (3 and 4), there were no positive associations between tree and butterfly species richness or diversity. While species richness or diversity of trees and animals may recover relatively rapidly during tropical forest succession, the recovery of community composition may require centuries (Chazdon 2008, Dunn 2004, Finegan 1996). In our study system the lack of youngest forests possibly explains the lack of clear patterns in diversity measures, while the changes in community composition were continuing at the time scale studied. Our results also demonstrate how the recovery of tree and butterfly species richness do not necessarily go hand-in-hand. In secondary and mature forests of Mt Kilimanjaro, the diversity of Geometridae and the species number of Dicotyledoneae correlated negatively (Axmacher *et al.* 2004).

Understanding the patterns and mechanisms of succession in animal communities is needed when assessing the potential of regenerating forests to prevent or slow down the mass extinction of tropical forest fauna (Gibson *et al.* 2011, Wright & Muller-Landau 2006). Based on our results, if tree communities are altered due to human disturbance, this ultimately will also lead to altered fruit-feeding butterfly communities. Due to the strong link between the tree and fruit-feeding butterfly communities, our results emphasize the role of tree community to recovery of herbivorous insect communities in tropical forests recovering from human disturbance.

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Appendix 1. Variation partitioning analyses

To adjust for probable spatial autocorrelation in community composition in CCA analyses, we conducted the conditional variation partitioning analyses of Canoco (ter Braak & Šmilauer 2012). With variation partitioning it is possible to test if the effects of vegetation structure, forest age, local topography and soil are significant after spatial arrangement (latitude and longitude) of the sampling sites is taken into account, and vice versa.

Vegetation structure, forest age, local topography and soil explained variation in tree communities independent of spatial arrangement (latitude and longitude) of the sampling sites ($P = 0.002$; 81% of the explained variation). Also latitude and longitude explained variation independent of vegetation structure, forest age, local topography and soil ($P = 0.002$; 18% of the explained variation), indicating spatial autocorrelation.

Vegetation structure, forest age, local topography and soil explained variation in butterfly communities independent of spatial arrangement (latitude and longitude) of the sampling sites ($P = 0.002$; 82% of the explained variation). Also the latitude and longitude of the sampling sites explained variation independent of vegetation structure, forest age, local topography and soil ($P = 0.002$; 27.0% of the explained variation), indicating spatial autocorrelation.

Appendix 2. Tree and butterfly species recorded in the studied secondary and primary forest sites in Kibale National Park, Uganda. Abbreviations indicate codes in Figures 1–3.

Abbreviation	Tree species
Ae	*Aeglopsis eggelingii* M. Taylor
Ag	*Albizia grandibracteata* Taub.
Agu	*Albizia gummifera* (J. F. Gmel.) C. A. Sm.
Ad	*Allophylus dummeri* Baker f.
Agr	*Anthocleista grandiflora* Gilg
At	*Antiaris toxicaria* Lesch.
Adi	*Apodytes dimidiata* Arn.
Bw	*Balanites wilsoniana* Dawe & Sprague
Bu	*Beilschmiedia ugandensis* Rendle
Ba	*Bersama abyssinica* Fresen.
Bun	*Blighia unijugata* Baker
Bm	*Bridelia micrantha* (Hochst.) Baill.
Cp	*Carapa procera* DC.
Cr	*Casearia runssorica* Gilg
Cru	*Cassipourea ruwensorensis* (Engl) Alston
Ca	*Celtis africana* Burm. f.
Cg	*Celtis gomphophylla* Baker
Car	*Chaetacme aristata* Planch.
Caf	*Chionanthus africanus* (Knobl.) Stearn
Cal	*Chrysophyllum albidum* G. Don
Cat	*Citropsis articulata* (Spreng.) Swingle & Kellerm.
Can	*Clausena anisata* (Willd.) Benth.
Cc	*Coffea canephora* A. Froehner
Cai	*Cordia africana* Lam.
Cs	*Craterispermum schweinfurthii* Hiern
Cm	*Croton macrostachyus* Delile
C	*Cupressus* spp.
De	*Dasylepis eggelingii* J. B. Gillett
Da	*Dictyandra arborescens* Hook. f.
Dab	*Diospyros abyssinica* (Hiern) F. White
Dk	*Dombeya kirkii* Mast.
Dm	*Dovyalis macrocalyx* (Oliv.) Warb.
Ec	*Ehretia cymosa* Thonn.
Ea	*Erythrina abyssinica* DC.
Ee	*Euadenia eminens* Hook. f.
Fa	*Fagaropsis angolensis* (Engl.) Dale
Fb	*Ficus barteri* Sprague
Fe	*Ficus exasperata* Vahl
Fs	*Ficus sansibarica* Warb.
Fsu	*Ficus sur* Forssk.
Fv	*Ficus vallis-choudae* Delile
F	*Funtumia* spp.
Hr	*Hallea rubrostipulata* (K. Schum.) J.-F. Leroy
Ho	*Hoslundia opposita* Vahl
Ka	*Kigelia africana* (Lam.) Benth.
Ls	*Lepisanthes senegalensis* (Poir.) Leenh.
Lm	*Leptonychia mildbraedii* Engl.
Lsw	*Lovoa swynnertonii* Baker f.
Lc	*Lychnodiscus cerospermus* Radlk.
Mc	*Macaranga capensis* (Baill.) Sim
Ml	*Maesa lanceolata* Forssk.
Me	*Maesopsis eminii* Engl.
Md	*Margaritaria discoidea* (Baill.) G. L. Webster
Mlu	*Markhamia lutea* (Benth.) K. Schum.
Mdu	*Millettia dura* Dunn
Mb	*Mimusops bagshawei* S. Moore
Mm	*Monodora myristica* (Gaertn.) Dunal
Ma	*Myrianthus arboreus* P. Beauv.
Mae	*Mystroxylon aethiopicum* (Thunb.) Loes.
Nm	*Neoboutonia macrocalyx* Pax
Nb	*Newtonia buchananii* (Baker) G. C. C. Gilbert & Boutique
Oc	*Olea capensis* L.
Os	*Oncoba spinosa* Forssk.
Osp	*Oxyanthus speciosus* DC.
Pt	*Pancovia turbinata* Radlk.
Pe	*Parinari excelsa* Sabine
Pa	*Persea americana* Mill.
Pr	*Phoenix reclinata* Jacq.
Pp	*Pleiocarpa pycnantha* (K. Schum.) Stapf
Pf	*Polyscias fulva* (Hiern) Harms
Pal	*Pouteria altissima* (A. Chev.) Baehni
Pan	*Premna angolensis* Gürke
Paf	*Prunus africana* (Hook. f.) Kalkman
Pm	*Pseudospondias microcarpa* (A. Rich.) Engl.
Ra	*Ritchiea albersii* Gilg
Ru	*Rothmannia urcelliformis* (Hiern) Robyns
Rw	*Rothmannia whitfieldii* (Lindl.) Dandy
Rb	*Rytigynia beniensis* (De Wild.) Robyns
S	*Sapium* spp.
Sr	*Scolopia rhamniphylla* Gilg
Se	*Senna* spp.
Sc	*Spathodea campanulata* P. Beauv.
Ss	*Strombosia scheffleri* Engl.
Sm	*Strychnos mitis* S. Moore
Sg	*Symphonia globulifera* L. f.
Tp	*Tabernaemontana pachysiphon* Stapf

Appendix 2. Continued.

Abbreviation	Tree species
To	*Trema orientalis* (L.) Blume
Td	*Trichilia dregeana* Sond.
Tm	*Trilepisium madagascariensis* DC.
U1	Unidentified 1
U2	Unidentified 2
Uc	*Uvariopsis congensis* Robyns & Ghesq.
Va	*Vangueria apiculata* K. Schum.
Vn	*Vepris nobilis* (Delile) Mziray
Vam	*Vernonia amygdalina* Delile
Vau	*Vernonia auriculifera* Hiern
Xm	*Xymalos monospora* (Harv.) Warb.
Zl	*Zanthoxylum leprieurii* Guill. & Perr.
	Butterfly species
Ad	*Antanartia delius* (Drury, 1782)
Ac	*Apaturopsis cleochares* (Hewitson, 1873)
Ae	*Ariadne enotrea* (Cramer, 1779)
Ap	*Ariadne pagenstecheri* (Suffert, 1904)
Ag	*Aterica galene* (Brown, 1776)
Ba	*Bebearia absolon* (Fabricius, 1793)
Bc	*Bebearia cocalia* (Fabricius, 1793)
Bs	*Bebearia sophus* (Fabricius, 1793)
Bau	*Bicyclus auricruda* (Butler, 1868)
Bb	*Bicyclus buea* (Strand, 1912)
Bca	*Bicyclus campina* (Aurivillius, 1901)
Bcm	*Bicyclus campus* (Karsch, 1893)
Bd	*Bicyclus dentata* (Sharpe, 1898)
Bf	*Bicyclus funebris* (Guérin-Méneville, 1844)
Bg	*Bicyclus golo* (Aurivillius, 1893)
Bgr	*Bicyclus graueri* (Rebel, 1914)
Bi	*Bicyclus istaris* (Plötz, 1880)
Bm	*Bicyclus mandanes* Hewitson, 1873
Bme	*Bicyclus mesogena* (Karsch, 1894)
Bmo	*Bicyclus mollitia* (Karsch, 1895)
Bsa	*Bicyclus sambulos* (Hewitson, 1877)
Bsu	*Bicyclus saussurei* (Dewitz, 1879)
Bse	*Bicyclus sebetus* (Hewitson, 1877)
Bsm	*Bicyclus smithi* (Aurivillius, 1928)
Bv	*Bicyclus vulgaris* (Butler, 1868)
Cc	*Catuna crithea* (Drury, 1773)
Cb	*Charaxes bipunctatus* Rothschild, 1894
Cbr	*Charaxes brutus* (Cramer, 1779)
Cca	*Charaxes candiope* (Godart, 1824)
Ccs	*Charaxes castor* (Cramer, 1775)
Ccy	*Charaxes cynthia* Butler, 1866
Ce	*Charaxes etheocles* (Cramer, 1777)
Cf	*Charaxes fulvescens* (Aurivillius, 1891)
Cn	*Charaxes numenes* (Hewitson, 1859)
Cp	*Charaxes paphianus* Ward, 1871
Cpl	*Charaxes pleione* (Godart, 1824)
Cpo	*Charaxes pollux* (Cramer, 1775)
Cpr	*Charaxes protoclea* Feisthamel, 1850
Cs	*Charaxes smaragdalis* Butler, 1866
Ct	*Charaxes tiridates* (Cramer, 1777)

Appendix 2. Continued.

Abbreviation	Butterfly species
Cz	*Charaxes zelica* Butler, 1869
Czo	*Charaxes zoolina* (Westwood, [1850])
Cce	*Cymothoe caenis* (Drury, 1773)
Ch	*Cymothoe herminia* (Grose-Smith, 1887)
Cho	*Cymothoe hobarti* Butler, 1900
Cl	*Cymothoe lurida* (Butler, 1871)
Ea	*Euphaedra alacris* Hecq, 1978
Ec	*Euphaedra christyi* Sharpe, 1904
Ee	*Euphaedra edwardsi* (van der Hoeven, 1845)
Eh	*Euphaedra harpalyce* (Cramer, 1777)
Eho	*Euphaedra hollandi* Hecq, 1974
Ei	*Euphaedra imitans* Holland, 1893*
Ek	*Euphaedra kakamegae* van Someren, 1934
Em	*Euphaedra medon* (Linnaeus, 1763)
Ep	*Euphaedra preussi* Staudinger, 1891
Eu	*Euphaedra uganda* Aurivillius, 1895
Ez	*Euphaedra zaddachi* Dewitz, 1879
Er	*Euriphene ribensis* (Ward, 1871)
Es	*Euriphene saphirina* (Karsch, 1894)
Eal	*Euryphura albimargo* Joicey & Talbot, 1921
Ech	*Euryphura chalcis* (Felder & Felder, 1860)
Ed	*Eurytela dryope* (Cramer, 1775)
Ehi	*Eurytela hiarbas* (Drury, 1770)
Ecr	*Euxanthe crossleyi* (Ward, 1871)
Eer	*Euxanthe eurinome* (Cramer, [1775])
Gb	*Gnophodes betsimena* (Boisduval, 1833)
Gc	*Gnophodes chelys* (Fabricius, 1793)
Gn	*Gnophodes* new**
Ht	*Harma theobene* Doubleday, 1848
Hp	*Heteropsis peitho* (Plötz, 1880)***
Hpe	*Heteropsis perspicua* (Trimen, 1873)***
Ha	*Hypolimnas anthedon* (Doubleday, 1845)
Hs	*Hypolimnas salmacis* (Drury, 1773)
Js	*Junonia stygia* (Aurivillius, 1894)
Jw	*Junonia westermanni* Westwood, 1870
Kr	*Kallimoides rumia* (Doubleday, 1849)
La	*Lachnoptera anticlia* (Hübner, 1819)
Ma	*Melanitis ansorgei* Rothschild, 1904
Ml	*Melanitis leda* (Linnaeus, 1758)
No	*Neptidopsis ophione* (Cramer, 1777)
Pp	*Phalanta phalantha* (Drury, 1773)
Ppa	*Protogoniomorpha parhassus* (Drury, 1782)
Pt	*Protogoniomorpha temora* (Felder & Felder, 1867)
Pl	*Pseudacraea lucretia* (Cramer, [1775])
Sa	*Salamis cacta* (Fabricius, 1793)
Sb	*Sevenia boisduvali* (Wallengren, 1857)
So	*Sevenia occidentalium* (Mabille, 1876)
Vd	*Vanessa dimorphica* Howarth, 1966

**Euphaedra eusemoides imitans* (Molleman 2012).
**Molleman (2012).
***now *Brakefieldia* (Aduse-Poku *et al.* 2016).