ORIGINAL PAPER



Tree community composition and vegetation structure predict butterfly community recovery in a restored Afrotropical rain forest

Margaret Nyafwono · Anu Valtonen · Philip Nyeko · Arthur Arnold Owiny · Heikki Roininen

Received: 2 June 2014/Revised: 16 January 2015/Accepted: 28 January 2015/ Published online: 5 February 2015 © Springer Science+Business Media Dordrecht 2015

Abstract Anthropogenic disturbances have led to a dramatic loss of biodiversity in the tropics. Habitat restoration can mitigate biodiversity loss but studies describing insect community recovery during tropical forest restoration are limited in Africa. Our aim was to compare the predictive power of tree community composition versus vegetation structure for butterfly community composition during tropical rain forest restoration. A fruit-feeding butterfly dataset from two primary and six restored forest areas of Kibale National Park (Uganda) was used. At the same sites, the tree community composition and six variables describing the vegetation structure, namely; (1) total stem density per hectare; (2) tree canopy cover; (3) elephant grass cover; (4) "other grass" cover; (5) shrub cover; and (6) herb cover, were sampled. Co-correspondence analysis and canonical correspondence analysis were used to predict butterfly community composition from tree community composition or vegetation structure, respectively. Both tree community composition and vegetation structure predicted butterfly community equally well. We also found a corresponding successional gradient of butterfly and tree communities, associated with the age of the forest since restoration started. Most butterfly species had their peak abundance (optima) in the late successional or primary forests, while most tree species had their optima in primary forests. Elephant grass cover and tree canopy cover were the most important predictors of the butterfly community composition. Our results demonstrate how tropical forest restoration can ignite successional changes in tree communities and

Communicated by Peter J. T. White.

M. Nyafwono (\boxtimes) · A. Valtonen · A. A. Owiny · H. Roininen Department of Biology, University of Eastern Finland, P.O. Box 111, 80101 Joensuu, Finland e-mail: margarny@student.uef.fi; nyaffs@yahoo.co.uk

P. Nyeko

Department of Forestry, Biodiversity and Tourism, Makerere University, P.O. Box 7062, Kampala, Uganda

vegetation structure, which in turn restructure the animal communities, according to resource availability and species-specific habitat requirements.

Keywords Biodiversity · Forest clearing · Insect · Kibale · Lepidoptera · Reforestation

Introduction

Human alteration of ecosystems, e.g. through agricultural expansion, wood extraction and extension of infrastructure has led to a dramatic loss of natural habitats in the tropics (Geist and Lambin 2002; FAO 2010). As a result, there is a growing need to actively restore tropical forests (Lamb et al. 2005). Habitat restoration can mitigate biodiversity loss in degraded tropical ecosystems (Elliot et al. 2013). During forest restoration, the successful establishment of tree and other plant communities is crucial for the reintroduction of a diverse community of insect herbivores and other fauna (Elliot et al. 2013). With time, successional changes in plant species community, diversity, and vegetation structure are expected to restructure animal communities according to resource availability and species-specific habitat requirements (Pinotti et al. 2012; DeWalt et al. 2003).

Insects are the most abundant tropical macroinvertebrates and play important roles in ecosystem service provision (Wilson 1987; Maleque et al. 2006). Like other tropical species, insects are threatened by clearing, degradation, and fragmentation of tropical forests (Bobo et al. 2006; Koh 2007; Leidner et al. 2010) and could benefit from restoration efforts. However, it is not known how well plant community composition or vegetation structure can predict the recovery of insect communities during tropical restoration. Plant community composition has been shown to be a good predictor of arthropod community composition in grasslands of temperate regions (Ter Braak and Schaffers 2004; Schaffers et al. 2008; Müller et al. 2011). One important reason could be due to the many specialist herbivores, which accept only one or a few species as host for larvae (Novotny and Basset 2005). Also, generalist insect species may be associated with certain plant communities where their resources are abundant (Müller et al. 2011).

Vegetation structure also has a significant influence on animal community composition and distribution (Morris 2000; Hogsden and Hutchinson 2004; Kitahara 2004). Overall, an increase in biomass accumulation (Omeja et al. 2011; Pinotti et al. 2012) and a decrease in light availability (Pinotti et al. 2012) are expected during restoration. Taller and more complex vegetation provides a greater variety of resources for insects, birds and mammals (e.g. feeding, resting, oviposition sites, shelter, and hiding places) than less heterogeneous vegetation (Lawton 1983; Tscharntke and Greiler 1995; DeWalt et al. 2003).

In this study, fruit-feeding butterfly communities in a tropical rainforest restoration area in Kibale, Uganda, were used to compare the predictive power of tree community composition versus vegetation structure for butterfly community composition. Fruit-feeding butterflies were chosen because they are readily sampled in the field, are taxonomically tractable and frequently used as indicators of change for many other terrestrial insect groups (Ghazoul 2002; Thomas 2005). In addition, they are forest-dependent, making them potentially good indicators of restoration success (Ghazoul and Hellier 2000).

Methods

Study area

Kibale National Park covers an area of 795 km² (Struhsaker 1997) and is located in western Uganda ($0^{\circ}13'-0^{\circ}41'N$ and $30^{\circ}19'-30^{\circ}32'E$). It is a medium-altitude tropical rainforest with an elevation range of 1,000 – 1,500 m above sea level. The mean annual rainfall distributed between two distinct wet and dry seasons is 1,749 mm; mean daily minimum and maximum temperatures are 14.9 and 20.2 °C, respectively (1990–2001; Chapman et al. 2005). The park is composed of a mosaic of vegetation types. About 57.9 % is mature evergreen forest, 14.6 % is grassland, and the remaining percentage is shared among other habitat types (Struhsaker 1997; Chapman et al. 2005).

The study was conducted within the 10,000 ha of the Uganda Wildlife Authority-Forests Absorbing Carbon Dioxide Emissions (UWA-FACE) project area, south of Kibale National Park. It is an area undergoing recovery from past agricultural encroachment that lasted more than 20 years (Chapman and Lambert 2000; UWA-FACE 2006). Since 1994, the FACE Foundation and UWA have been replanting native trees in the encroached areas to enhance carbon sequestration and recovery of biodiversity (UWA-FACE 2006). The restoration sites are of different sizes (310–1,410 ha) and ages ranging from 3–16 years (Nyafwono et al. 2014a).

The main vegetation types prior to restoration included degraded forest, abandoned farms, and grasslands (Chapman and Lambert 2000). The eastern side of restoration sites were adjacent to the relatively intact *Cynometra* forest. Two main shrubs, *Lantana camara* and *Acanthus pubescens*, and one dominant grass, *Pennisetum purpureum*, colonised the abandoned sites soon after the eviction of the agricultural encroachers (UWA-FACE 2006). Based on our previous works, fruit-feeding butterfly abundance and diversity show an increasing pattern from the youngest restored forests to primary forests in the area (Nyafwono et al. 2014a). In addition, the butterfly community composition between differently aged forests is distinct, but there is a gradual increase in butterfly community similarity with the primary forest communities, explained by the time since restoration began (Nyafwono et al. 2014a).

Butterfly dataset

We used the fruit-feeding butterfly dataset described by Nyafwono et al. (2014a). It is composed of 10,092 individuals representing 79 species, obtained from 40 traps laid across eight forest areas of different ages that were sampled monthly for 1 year (May 2011–April 2012). Six of the forest areas were replanted, which were 3, 5, 8, 11, 14, and 16 years old, and two were primary forests adjacent to the restoration sites. The data was collected with white cylindrical butterfly traps (height 125 cm, diameter 35 cm) hung at 40–50 cm height above the ground (Molleman et al. 2005). The minimum distance between the trap locations was 100 m, and the distances depended on the size of restoration forest area or primary forest patch (details in Nyafwono et al. 2014a). For analyses, we summed the number of butterflies of each species at each sampling site.

Vegetation dataset

From each butterfly sampling site, information regarding tree community composition and vegetation structure was collected. The nested quadrat method, modified after Tabuti

(2007) was used to obtain the tree community composition data (Owiny et al., unpublished). At each site, large trees (>20 cm diameter at breast height; dbh) were enumerated in a 40 m × 20 m plot. Small trees and poles (10–20 cm dbh) were enumerated in a 20 m × 20 m plot, saplings (5–10 cm dbh) in a 20 m × 10 m plot and seedlings (<5 cm dbh) in a 10 m × 10 m plot; all plots being nested and sharing one corner. The dataset was composed of 79 tree species and 3,191 counted stems. For analysing the tree community composition at each sampling site for each tree, the estimated number of stems per hectare was calculated.

The vegetation structure variables included: (1) total stem density per hectare (summed across all tree species); (2) tree canopy cover; (3) elephant grass cover; (4) "other grass" cover (i.e., any grass other than elephant grass); (5) shrub cover; and (6) herb cover. The cover measures were estimated visually, within 40 m \times 20 m plots, on a scale of 0–10 [i.e. 0, 0.5 (<10 %), 1 (10 %), 2 (20 %), 3 (30 %), 4 (40 %), 5 (50 %), 6 (60 %), 7 (70 %), 8 (80 %), 9 (90 %), and 10 (100 %)]. Although visual estimation of the cover measures always includes a risk of subjective error (e.g. Korhonen et al. 2006) the method is widely used, and in our case the same person conducted the estimation task within one season (which reduces the error).

Data analysis

To predict butterfly community composition from tree community composition, we used Co-Correspondence Analysis (CoCA; Ter Braak and Schaffers 2004; Schaffers et al. 2008). Two separate CoCA analyses were conducted using two different levels of measurement of tree community composition: (a) presence/absence and (b) stem density of tree species. Butterfly counts and tree stem densities were loge(x+1) transformed prior to analyses in order to slightly decrease the influence of the most abundant species. For each CoCA model, the cross-validatory fit (%), a measure of the accuracy of the prediction (Ter Braak and Schaffers 2004), was calculated. A cross-validatory fit greater than zero indicates that the model prediction is better than expected due to chance. The cross-validatory fit was also used to select the number of CoCA ordination axes for the final model; the local maximum (instead of global maximum) was selected to keep the model as simple as possible, in accordance with Ter Braak and Schaffers (2004). Additionally, we tested the significance of each ordination axis with a permutation test (99 permutations; Ter Braak and Schaffers 2004). Biplots based on predictive CoCA (Ter Braak and Schaffers 2004), of the tree community dataset with the higher cross-validatory fit were presented. Analyses were performed with the software package "cocorresp" (Simpson 2013) in R (R Development Core Team 2008) version 2.14.1.

To predict butterfly community composition from vegetation structure variables, we used predictive Canonical correspondence analysis (CCA; Ter Braak 1986). Prior to analyses, the butterfly counts were $\log_e (x+1)$ transformed (to slightly decrease the influence of the most abundant species), and the vegetation structure variables were square-root transformed (to lessen the skewness of their distributions). We first tested how many constrained axes were significant in explaining the butterfly community (permutation test with 499 permutations) in order to decide how many axes to keep in the final model. Secondly, we ran a permutation test to determine if butterfly community composition was associated with vegetation structure variables (all axes of the final model; 499 permutations). Third, we inspected the intra-set correlations to investigate which vegetation structure variables the selected CCA axes represented. Fourth, we asked which vegetation structure variables were the most important in predicting the butterfly community

composition by inspecting the conditional effects (partial effects of each vegetation structure variable; permutation tests with 499 permutations). All CCA analyses were conducted using Canoco version 5 (Ter Braak and Smilauer 2012).

We ran simple randomisation tests (van der Voet 1994) to judge whether differences among the model fits (among the two tree community models from predictive CoCA and between the best predictive tree community model and the vegetation structure model from predictive CCA) were statistically significant. For this, we extracted the predicted values (log_e(x+1) transformed butterfly counts) from the CoCA and CCA models. The differences in mean squared prediction errors for the two compared models were used as the test statistics and mean squared prediction errors of traps were re-arranged 999 times. A twosided alternative hypothesis (mean squared prediction errors of model A \neq mean squared prediction errors of model B) was tested (van der Voet 1994).

Results

Tree community composition of restored and primary forests significantly predicted the community composition of fruit-feeding butterflies (Fig. 1). Stem densities of tree species explained 11.5 % (final model included three significant axes), and presence/absence of tree species 10.7 % (one axis) of the variation in butterfly community composition (percentages represent cross-validatory fits from the two CoCA models). However, according to the randomisation test, there was no significant difference in prediction accuracy between the two models (P = 0.081).

The CoCA biplots of the best-fitting tree community model (stem densities of trees) show gradients that are common to both tree and butterfly communities (Fig. 1). The first gradient (x-axis) represents the age of the sites from the youngest restoration forests (left) to primary forests (right). The CoCA biplots show graphically which tree species predicts



Fig. 1 Predictive co-correspondence analysis (CoCA) biplots showing butterfly community (**a**) against tree community (stem densities/ha) (**b**), in Kibale National Park, Uganda. Circled numbers represent the optima of the butterfly and tree species sampled (species codes in Appendix Table 2). Optima (location of the peak abundance along the gradients) of some species are moved slightly to improve readability. Traps are indicated with (non-circled) symbols [P = primary forest; R = restored forest with median age of recovery 3–16 years, see details in Nyafwono et al. (2014a)]

which butterfly species (species with optima at the same part of the gradient). Optimum here refers to the point along an environmental gradient where a species thrives best and so has its maximum abundance there (Ter Braak 1996). For example, the abundances of the butterfly genera *Euphaedra*, *Lachnoptera*, *Euriphene*, and *Cymothoe* peaked mostly in primary forests where the trees *Cynometra alexandri*, *Chrysophyllum albidum*, *Uvariopsis congensis*, *Pterygota mildbraedii*, *Aphania senegalensis*, *Blighia unijugata*, and *Mimusops bagshawei* also had their optima (Fig. 1, Table 2 in Appendix . *Sevenia* and *Charaxes* butterfly genera had their optima most often in middle parts of the restoration gradient, the most suitable locations also for tree species *Sapium ellipticum*, *Albizia grandibracteata*, *Celtis durandii*, and *Rauvolfia vomitoria*. The youngest restoration forests were the most suitable habitats for butterfly species *Bicyclus safitza*, *B. funebris*, *B. sandace*, *B. campus*, and *Junonia westermanni* and tree species *Ficus capensis*, *F. vallis*, *Croton* spp., *Bridelia micrantha*, and *Maesa lanceolata*. For most tree species, the optimum is in the primary forest and for most butterfly species either at the primary forest end or in the middle parts of the gradient.

Vegetation structure also significantly predicted the fruit-feeding butterfly community composition (Fig. 2; final CCA model with two axes: permutation test for all axes, pseudo-F = 2.1, P = 0.002; first axis P = 0.002, second axis P = 0.046). The vegetation structure variables accounted for 27.2 % of the variation in butterfly data. The eigenvalues (importance measures of ordination axes) and explained cumulative variance



Fig. 2 Canonical correspondence analysis (CCA) ordination diagram showing the butterfly species (optima indicated with circled numbers; see species codes in Appendix Table 2) and vegetation structure variables (*arrows*) in Kibale National Park, Uganda. Optima of some species are moved slightly to improve readability

Variable	Variance (%)	Pseudo-F	Р	Intra-set correlations	
				Axis 1	Axis 2
Elephant grass cover	10.9	4.7	0.002	0.833	0.539
Canopy cover	6.5	2.9	0.002	-0.816	0.433
Shrub cover	3.3	1.5	0.010	0.420	-0.727
Tree density	2.9	1.3	0.110	-0.705	0.604
Herb cover	1.8	0.8	0.776	-0.512	0.053
Other grass cover	1.7	0.8	0.788	0.574	0.042

 Table 1
 Conditional effects table from canonical correspondence analysis (CCA) ordination showing the partial effect of each predictor, representing the variation (and its significance) on butterfly community composition, and their intra-set correlations with CCA axes. The predictors are listed in the order of their decreasing explained variation

for the selected CCA axes 1 and 2 were 0.19 and 13.8 %, and 0.06 and 18.4 %, respectively.

Elephant grass cover correlated positively, and canopy cover and total stem density correlated negatively with CCA axis 1. Elephant grass cover, total stem density, and canopy cover correlated positively but shrub cover negatively with CCA axis 2 (see intraset correlations in Table 1). Elephant grass cover and tree canopy cover were the most important variables predicting the butterfly community composition (see results of conditional effects in Table 1). Elephant grass cover explained 11 % and tree canopy cover 7 % of the variation in butterfly community composition.

Based on the CCA ordination diagram, the majority of butterfly species had their optima in habitats with moderate or closed canopies (Fig. 2). Several species from the genus *Euphaedra*, as well as *Melanites ansorgei*, *Cymothoe herminia*, *C. hobarti*, *C. lurida*, and *Bicyclus sambulos* were most often found in sites with medium or closed canopies. Sites with less than average canopy cover but higher than average cover of shrubs and grasses were most suitable for *Sevenia occidentalium*, *Gnophodes betsimena*, *Bicyclus smithi*, and *Euphaedra medon*. Sites with high cover of elephant grass were preferred, e.g. by five species from the genus *Bicyclus*.

Based on the randomisation test, the prediction accuracy of the best-fitting tree community composition model (measured as tree stem densities per hectare) and the vegetation structure model did not differ significantly from each other (P = 0.074). The mean squared prediction error of the tree stem density model was 0.16 and of the vegetation structure model 0.21.

Discussion

Our results demonstrate how the tropical forest restoration can ignite successional changes in tree communities and vegetation structure, which in turn restructure the animal communities, following resource availability and species-specific habitat requirements. Previously, evidence of rain forest restoration enabling animal communities to become more similar with the communities in nearby primary forests have been obtained from butterflies in Brazil (Sant'Anna et al. 2014), beetles in Australia (Grimbacher and Catterall 2007), and birds in Costa Rica (Reid et al. 2014). This is crucial, because the possibilities of species returning to restored tropical forests are strongly influenced by the recovery of other species, and ultimately, the success of restoration depends on how well the critical ecosystem services (seed dispersal, pollination and pest control) recover (e.g. Montoya et al. 2012).

Tree community composition is a good predictor of the fruit-feeding butterflies among differently aged restored and primary forest plots in Kibale National Park, Uganda. A general pattern appears to be that for the relatively host-specialised insects like butterflies and moths (Novotny et al. 2002; Müller et al. 2011), and other animals e.g. fish communities (Cvetkovic et al. 2010) that depend directly on plants for adult and larval food, plant composition is important in predicting their community composition. This is also true for predatory insects (Ter Braak and Schaffers 2004; Schaffers et al. 2008; Gioria et al. 2011). Our prediction of 11.5 % explained variation by crossvalidatory fit for fruit-feeding butterfly communities in Kibale was lower than for the temperate arthropod groups, e.g. 18.3 % for hoppers (Schaffers et al. 2008), 19 % for carabid beetles (Ter Braak and Schaffers 2004), 19.6 % for moths (Müller et al. 2011), and 28 % for water beetles (Gioria et al. 2011). One reason could be that, in this study, only trees were studied. Yet, trees generally support more insect species compared with other plants (Lawton 1983). The differences in results could be also attributed to the spatial and temporal scales of the studies, strength of the association between the taxonomic groups studied, and insects' response to local environmental conditions (Gioria et al. 2011).

Butterflies and trees expressed a clear successional gradient following the restoration age of the plots (see also results in Nyafwono et al. 2014a). Most butterfly species were most abundant in middle-aged restoration or primary forests; most tree species had their optima in primary forests. Early successional plots were dominated by pioneer woody species (e.g. Bridelia micrantha, Ficus spp., Maesa lanceolata, and Croton spp.). It appears that for some butterfly species, the tree species with which they closely associate are either adult food sources, larval host plants, or both. For instance, the trees A. senegalensis, B. unijugata, and Parinari excelsa, which had their optima in primary forests, are larval host plants for the genus Euphaedra (Molleman 2012), primary forest specialists (Larsen 1996; Nyafwono et al. 2014b). Also generalist butterflies may prefer sites for oviposition close to adult food resources, even when eggs are not necessarily laid on the adult food plants themselves (Janz 2005), which could also be the case for some of the Kibale butterflies. The four most abundant butterfly genera, Bicyclus, Euphaedra, Charaxes, and Cymothoe, are attracted to fruits of Ficus spp., Minusops bagshawei, U. congensis, Diospyros abyssinica, and Strychnos mitis (Molleman et al. 2005). Some of the preferred adult food plants are also their larval host plants, e.g. Mimusops bagshawei and U. congensis are larval host plants for Cymothoe hobarti and Euphaedra eusemoides, respectively (Molleman 2012).

Furthermore, vegetation structure explains butterfly communities among sites of different ages. The cover of elephant grass and tree canopy cover were the most important predictors. According to our results, some butterfly species prefer open sites, others prefer closed canopy sites, and most species prefer intermediate sites. This is probably due to their different requirements of resources and may be related to preference for enemy-free space (Lawton 1983; Hunter and Price 1992; Tscharntke and Greiler 1995). Vegetation structure also has been found to explain significant variation in butterfly (Hogsden and Hutchinson 2004; Kitahara 2004), spider, true bug, carabid, other arthropod (Ter Braak 1986; Downie et al. 1995; Schwab et al. 2002; Brose 2003), and bird (Zhang et al. 2013) communities in the temperate region, as well as lizard and bird communities in the Neotropics (Pearman 2002; Garda et al. 2013).

Elephant grass covered areas were shunned by most fruit-feeding butterflies, with the exception of five species from the genus *Bicyclus*. These areas are relatively open, exposing the majority of butterflies to predation. For butterflies to persist in open habitats, Larsen (1996) argued that they must be fast fliers, unpalatable to predators, or have cryptic designs on their bodies to escape predation. *Bicyclus* butterflies are not fast fliers but do have prominent eye-spots on their wings probably to confuse predators. Also, while at rest, they resemble dead/dry leaves (M.N., pers. obs.), an important camouflage. Some of them use grass (Molleman 2012), for example, elephant grass (Larsen 2005), as their larval host plants. However, areas covered with elephant grass had few or no fruiting trees to attract butterflies (M.N., pers. obs.).

It seems evident that both tree community composition and vegetation structure mirror the successional pattern of the restoration gradient. The best-fitting tree community composition and the vegetation structure models did not differ significantly between each other. During rainforest succession, parallel changes take place in both tree community composition and vegetation structure (DeWalt et al. 2003). This involves an increase in the number of plant species and increased complexity in the structure of the vegetation (Denslow and Guzman 2000; Guariguata and Ostertag 2001; Elliot et al. 2013). Such is the case in Kibale where Valtonen et al. (unpublished) found that the fruit-feeding butterfly species richness increased along with increasing tree species richness, but levelled off at high tree species richness values, whereas butterfly diversity increased monotonically along with tree diversity. Such changes may cause parallel increases in the number of habitat generalists and specialists (Pardini et al. 2009) as well as the number of species per feeding guild (Novotny et al. 2010).

To conclude, tree community composition significantly predicted fruit-feeding butterfly community composition in restored and primary forests of Kibale National Park. Vegetation structure also significantly explained the variation in the butterfly community composition. The most important vegetation structure variables in predicting the butterfly community composition were elephant grass cover and tree canopy cover. The majority of butterfly species were associated with intermediate stages of the restoration and primary forests. Our results indicate that both tree community composition and vegetation structure can be used as predictors of insect community composition in restored tropical rainforests. Our work illustrates how the tropical forest restoration can ignite successional changes in tree communities and vegetation structure, which in turn restructure the animal communities, according to resource availability and speciesspecific habitat requirements.

Acknowledgments Special thanks to I. Mwesige, E. Agaba, J. Mwesige, B. Balyeganira, F. Katuramu, J. Koojo and R. Sabiiti for assisting with the fieldwork, F. Molleman for butterfly identification, and V. Lehtovaara for map production. The authors thank also Makerere University Biological Field Station, Kibale National Park for support. Funding was provided by the Finnish Academy (Grant No. 138899 to H.R.). Permission to conduct this research was given by the Office of the President, Uganda, the National Council for Science and Technology, Uganda and the Uganda Wildlife Authority.

Appendix

See Table 2.

Code number	Butterfly species	Code number	Tree species	
1	Antanartia delius	1	Acacia hockii	
2	Apaturopsis cleochares	2	Albizia grandibracteata	
3	Ariadne enotrea	3	Albizia gummifera	
4	Ariadne pagenstecheri	4	Alchornea laxiflora	
5	Aterica galene	5	Aningeria altissima	
6	Bebearia absolon	6	Antiaris toxicaria	
7	Bebearia cocalia	7	Aphania senegalensis	
8	Bebearia sophus	8	Balanites wilsoniana	
9	Bicyclus auricruda	9	Bequaertiodendron blanceolatum	
10	Bicyclus buea	10	Bersama abyssinica	
11	Bicyclus campinus	11	Blighia unijugata	
12	Bicyclus campus	12	Bosquea phoberos	
13	Bicyclus dentatus	13	Bridelia micrantha	
14	Bicyclus funebris	14	Cassipourea ruwensorensis	
15	Bicyclus golo	15	Celtis africana	
16	Bicyclus graueri	16	Celtis durandii	
17	Bicyclus mandanes	17	Chaetacme aristata	
18	Bicyclus mesogena	18	Chrysophyllum albidum	
19	Bicyclus mollitia	19	Citropsis articulata	
20	Bicyclus safitza	20	Clausena anisata	
21	Bicyclus sambulos	21	Coffea spp.	
22	Bicyclus sandace	22	Combretum molle	
23	Bicyclus sebetus	23	Cordia millenii	
24	Bicyclus smithi	24	Croton spp.	
25	Bicyclus vulgaris	25	Cynometra alexandri	
26	Catuna crithea	26	Dasylepis eggelingii	
27	Charaxes ameliae	27	Dictyandra arborescens	
28	Charaxes bipunctatus	28	Diospyros abyssinica	
29	Charaxes candiope	29	Dombeya mukole	
30	Charaxes castor	30	Dovyalis macrocalyx	
31	Charaxes cynthia	31	Ehretia cymosa	
32	Charaxes etheocles	32	Erythrina abyssinica	
33	Charaxes eupale	33	Euadenia eminens	
34	Charaxes fulvescens	34	Fagaropsis angolensis	
35	Charaxes numenes	35	Ficus capensis	
36	Charaxes pleione	36	Ficus dawei	
37	Charaxes pollux	37	Ficus urceolaris	
38	Charaxes protoclea	38	Ficus vallis	
39	Charaxes smaragdalis	39	Funtumia spp.	

 Table 2
 Butterfly and tree species codes as used in the co-correspondence analysis (CoCA) biplots (Fig. 1) and canonical correspondence analysis (CCA) ordination plot (Fig. 2)

Table 2 continued

Code number	Butterfly species	Code number	Tree species	
40	Charaxes tiridates	40	Hoslundia opposita	
41	Charaxes zingha	41	Kigelia moosa	
42	Cymothoe herminia	42	Leptonychia mildbraedii	
43	Cymothoe hobarti	43	Linociera johnsonii	
44	Cymothoe lurida	44	Lovoa swynnertonni	
45	Euphaedra alacris	45	Lychnodiscus cerospermus	
46	Euphaedra christyi	46	Maesa lanceolata	
47	Euphaedra edwardsi	47	Maesopsis eminii	
48	Euphaedra eusemoides	48	Margaritaria discoidea	
49	Euphaedra harpalyce	49	Markhamia platycalyx	
50	Euphaedra hollandi	50	Maytenus undata	
51	Euphaedra kakamegae	51	Millettia dura	
52	Euphaedra medon	52	Mimusops bagshawei	
53	Euphaedra preussi	53	Monodora myristica	
54	Euphaedra uganda	54	Myrianthus arboreus	
55	Euphaedra zaddachi	55	Newtonia buchananii	
56	Euriphene ribensis	56	Olea welwitschii	
57	Euryphura albimargo	57	Oxyanthus stenocarpus	
58	Eurytela hiarbas	58	Pancovia turbinata	
59	Euxanthe crossleyi	59	Parinari excelsa	
60	Gnophodes betsimena	60	Perseaa mericana	
61	Gnophodes chelys	61	Pleiocarpa pycnantha	
62	Gnophodes new	62	Premna angolensis	
63	Harma theobene	63	Prunus africana	
64	Heteropsis peitho	64	Pseudospondias microcarpa	
65	Hypolimnas salmacis	65	Psidium guajava	
66	Junonia stygia	66	Pterygota mildbraedii	
67	Junonia westermanni	67	Randia malleifera	
68	Kallimoides rumia	68	Rauvolfia vomitoria	
69	Lachnoptera anticlea	69	Rothmannia urcelliformis	
70	Melanitis ansorgei	70	Sapium ellipticum	
71	Melanitis leda	71	Spathodea campanulata	
72	Melanitis libya	72	Strombosia scheffleri	
73	Neptidopsis ophione	73	Strychnos mitis	
74	Protogoniomorpha cacta	74	Tabernaemontana ventricosa	
75	Protogoniomorpha parhassus	75	Teclea nobilis	
76	Pseudacraea lucretia	76	Trichilia splendida	
77	Sevenia boisduvali	77	Uvariopsis congensis	
78	Sevenia occidentalium	78	Vangueria apiculata	
79	Sevenia umbrina	79	Warburgia ugandensis	

References

- Bobo KS, Waltert M, Fermon H et al (2006) From forest to farmland: butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. J Insect Conserv 10:29–42
- Brose U (2003) Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? Oecologia 135:407–413
- Chapman CA, Lambert JE (2000) Habitat alteration and the conservation of African primates: case study of Kibale National Park, Uganda. Am J Primatol 50:169–185
- Chapman CA, Chapman LJ, Struhsaker TT et al (2005) A long-term evaluation of fruiting phenology: importance of climate change. J Trop Ecol 21:31–45
- Cvetkovic M, Wei A, Chow-Fraser P (2010) Relative importance of macrophyte community versus water quality variables for predicting fish assemblages in coastal wetlands of the Laurentian Great Lakes. J Great Lakes Res 36:64–73
- Denslow JS, Guzman S (2000) Variation in stand structure, light and seedling abundance across a tropical moist forest chronosequence, Panama. J Veg Sci 11:201–212
- DeWalt SJ, Maliakal SK, Denslow JS (2003) Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. For Ecol Manag 182:139–151
- Downie IS, Butterfield JEL, Coulson JC (1995) Habitat preferences of sub-montane spiders in northern England. Ecography 18:51–61
- Elliot SD, Blakesley D, Hardwick K (2013) Restoring tropical forests: a practical guide. Royal Botanic Gardens, Kew
- FAO (2010) Global forest resources assessment 2010, main report, FAO forestry paper 163. FAO, Rome
- Garda AA, Wiederhecker HC, Gainsbury AM et al (2013) Microhabitat variation explains local-scale distribution of terrestrial Amazonian lizards in Rondonia, western Brazil. Biotropica 45:245–252
- Geist HJ, Lambin EF (2002) Proximate causes and underlying driving forces of tropical deforestation. Bioscience 52:143–150
- Ghazoul J (2002) Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. Biodivers Conserv 11:521–541
- Ghazoul J, Hellier A (2000) Setting critical limits to ecological indicators of sustainable tropical foresty. Int For Rev 4:243–253
- Gioria M, Bacaro G, Feehan J (2011) Evaluating and interpreting cross-taxon congruence: potential pitfalls and solutions. Acta Oecol 37:187–194
- Grimbacher PS, Catterall CP (2007) How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? Biol Conserv 135:107–118
- Guariguata MR, Ostertag R (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. For Ecol Manag 148:185–206
- Hogsden KL, Hutchinson TC (2004) Butterfly assemblages along a human disturbance gradient in Ontario, Canada. Can J Zool 82:739–748
- Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732
- Janz N (2005) The relationship between habitat selection and preference for adult and larval food resources in the polyphagous butterfly Vanessa cardui (Lepidoptera: Nymphalidae). J Insect Behav 18:767–780
- Kitahara M (2004) Butterfly community composition and conservation in and around a primary woodland of Mount Fuji, central Japan. Biodivers Conserv 13:917–942
- Koh LP (2007) Impacts of land use change on South-east Asian forest butterflies: a review. J Appl Ecol 44:703–713
- Korhonen L, Korhonen KT, Rautiainen M, Stenberg P (2006) Estimation of forest canopy cover: a comparison of field measurement techniques. Silva Fenn 40:577–588
- Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. Science 310:1628–1632
- Larsen TB (1996) The butterflies of Kenya and their natural history. Oxford University Press, New York Larsen TB (2005) Butterflies of West Africa. Apollo Books, Stenstrup
- Lawton JH (1983) Plant architecture and the diversity of phytophagous insects. Annu Rev Entomol 28:23–39
- Leidner AK, Haddad NM, Lovejoy TE (2010) Does tropical forest fragmentation increase long-term variability of butterfly communities? PLoS One 5:e9534
- Maleque MA, Hiroaki TI, Kaoru M (2006) The use of arthropods as indicators of ecosystem integrity in forest management. J For 104:113–117
- Molleman F (2012) Butterflies of Uganda: Kibale forest. Tour guide publications, Kampala
- Molleman F, Van Alphen ME, Brakefield PM, Zwaan BJ (2005) Preferences and food quality of fruitfeeding butterflies in Kibale forest, Uganda. Biotropica 37:657–663

- Montoya D, Rogers L, Memmott J (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. Trends Ecol Evol 27:666–672
- Morris MG (2000) The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biol Conserv 95:129–142
- Müller J, Stadler J, Jarzabek-Müller A et al (2011) The predictability of phytophagous insect communities: host specialists as habitat specialists. PLoS One 6:e25986
- Novotny V, Basset Y (2005) Host specificity of insect herbivores in tropical forests. Proc R Soc B 272:1083–1090
- Novotny V, Basset Y, Miller SE et al (2002) Host specialization of leaf-chewing insects in a New Guinea rainforest. J Anim Ecol 71:400–412
- Novotny V, Miller SE, Baje L et al (2010) Guild-specific patterns of species richness and host specialization in plant—herbivore food webs from a tropical forest. J Anim Ecol 79:1193–1203
- Nyafwono M, Valtonen A, Nyeko P, Roininen H (2014a) Fruit-feeding butterfly communities as indicators of forest restoration in an Afro-tropical rainforest. Biol Conserv 174:75–83
- Nyafwono M, Valtonen A, Nyeko P, Roininen H (2014b) Butterfly community composition across a successional gradient in a human-disturbed Afro-tropical rain forest. Biotropica 46:210–218
- Omeja PA, Chapman CA, Obua J et al (2011) Intensive tree planting facilitates tropical forest biodiversity and biomass accumulation in Kibale National Park, Uganda. For Ecol Manag 261:703–709
- Pardini R, Faria D, Accacio GM et al (2009) The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. Biol Conserv 142:1178–1190
- Pearman PB (2002) The scale of community structure: habitat variation and avian guilds in tropical forest understory. Ecol Monogr 72:19–39
- Pinotti BT, Pagotto PC, Pardini R (2012) Habitat structure and food resources for wildlife across successional stages in a tropical forest. For Ecol Manag 283:119–127
- R Development Core Team (2008) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. http://www.R-project.org. Accessed 22.11.2013
- Reid JL, Mendenhall CD, Rosales JA, Zahawi RA, Holl KD (2014) Landscape context mediates avian habitat choice in tropical forest restoration. PLoS One 9:1–8
- Sant'Anna CLB, Ribeiro DB, Garcia LC, Freitas AVL (2014) Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. Restor Ecol. doi:10.1111/rec.12091
- Schaffers AP, Raemakers IP, Sykora KV, Ter Braak CJF (2008) Arthropod assemblages are best predicted by plant species composition. Ecology 89:782–794
- Schwab A, Dubois D, Fried PM, Edwards PJ (2002) Estimating the biodiversity of hay meadows in northeastern Switzerland on the basis of vegetation structure. Agric Ecosyst Environ 93:197–209
- Simpson GL (2013) Package "cocorresp." http://cran.r-project.org/web/packages/.../cocorresp.pdf. Accessed 14.12.2013
- Struhsaker TT (1997) Ecology of an African rain forest. Logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville
- Tabuti JRS (2007) The uses, local perceptions and ecological status of 16 woody species of Gadumire Subcounty, Uganda. Biodivers Conserv 16:1901–1915
- Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179
- Ter Braak CJF (1996) Unimodal models to relate species to environment. Agricultural Mathematics Group, Wagenigen
- Ter Braak CJF, Schaffers AP (2004) Co-correspondence analysis: a new ordination method to relate two community compositions. Ecology 85:834–846
- Ter Braak CJF, Smilauer P (2012) Canoco reference manual and user's guide: software for ordination (version 5.0). Microcomputer power, Ithaca, NY
- Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philos Trans R Soc Lond B Biol Sci 360:339–357
- Tscharntke T, Greiler HJ (1995) Insect communities, grasses, and grasslands. Annu Rev Entomol 40:535–538 UWA-FACE (2006) Project plan of operation report-January-December 2006. Kampala, Uganda
- Van der Voet H (1994) Comparing the predictive accuracy of models using a simple randomisation test. Chemometr Intell Lab Syst 25:313–323
- Wilson EO (1987) The little things that run the world (the importance and conservation of invertebrates). Conserv Biol 1:344–346
- Zhang Q, Han R, Huang Z, Zou F (2013) Linking vegetation structure and bird organization: response of mixed-species bird flocks to forest succession in subtropical China. Biodivers Conserv 22:1965–1989