Tropical phenology: bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage

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Abstract. Temporal variation and phenology of tropical insect communities and the role of environmental factors controlling this variation is poorly understood. A better understanding is needed, for example, to predict the effects of climate change on tropical insect communities and to assess the long-term persistence of tropical communities. We studied seasonal and inter-annual variation in tropical fruit-feeding butterflies by exploiting a unique 137-month abundance time series of >100 species, sampled at 22 locations in the medium altitude montane rain forest of Kibale National Park, western Uganda. Precipitation peaked twice per year, about 20 d after each equinox. Vegetation greenness peaked approximately 33 d later. Species richness and abundance of butterflies peaked about 2 and 3 months, respectively, after the greenness peak. Furthermore, temporal shifts in peaks of butterfly abundances of each 6-month cycle positively correlated with temporal shifts in peaks of vegetation greenness approximately three months before. The butterfly assemblages of ENSO warm phase years differed significantly from assemblages of the other years. To our knowledge this is the first elucidation of bi-annual rhythms in butterfly assemblages. Host plant availability could explain the seasonal cycles in butterfly abundance and species richness, because the 3-month lag observed matches with the egg-to-adult development time in the studied species.

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INTRODUCTION

Knowledge of phenology and inter-annual variation of tropical communities is essential to predict and measure effects of climate change, impacting e.g., biodiversity, forestry, agriculture, human health and ecosystem level processes (including carbon cycling). In tropical forests, where seasonal changes in temperature are small, seasonality can be much weaker than in high and mid-latitude communities; these forests can be always green and animal populations can reproduce continuously. However, the existence of seasonal rhythms also in tropical communities,

typically related to the seasonal variation in precipitation, has been well established for a long time (Davis 1945, Dobzhansky and Pavan 1950, Wolda 1980, 1988, 1989). Since then, phenology, the study of seasonal timing of periodic life cycle events (Rathcke and Lacey 1985), has become an important field of study in tropical systems, addressing both species level phenomena, e.g., leaf phenology (Reich et al. 2004) or timing of reproduction in insects (Frederickson 2006) as well as community level events, e.g., changes in vegetation greenness (Pau et al. 2010), or insect assemblage structure (Ahrens et al. 2009).

With short generation times, high abundance, and species richness, insect model systems are well suited to address the temporal dynamics and phenology of tropical communities. Tropical insects show remarkable variation in their seasonal patterns (Wolda 1988). While the abundance of many species increases in the rainy season and decreases in the dry season (Wolda 1980, Wolda and Fisk 1981, Novotny and Basset 1998), an opposite pattern has been found in areas with very mild dry seasons (Janzen 1973, Hamer et al. 2005). Populations of some other species fluctuate aseasonally (Grimbacher and Stork 2009, Kishimoto-Yamada et al. 2010). Additionally, there are some long-lived tropical insect species that seem to keep remarkably stable (adult) population sizes over multiple generations (Owen and Chanter 1972).

Seasonal weather fluctuations may control population fluctuations or phenology of tropical insect populations either directly or via the amount of available resources or enemies (Azerefegne et al. 2001). Seasonal variation in abundances can also rise from phenological adaptations to seasonal environmental fluctuations, i.e., species could respond to environmental cues such as changes in photoperiod, temperature, or moisture, which help them to time the life-cycle optimally (Tauber et al. 1986, Wolda 1989). Such seasonality may be mediated by diapause (Tauber et al. 1986, Molleman et al. 2005a). For certain species, the seasonal variation in abundance can also be explained by their ability to track resources spatially and migrate over long distances, often over several generations (Brower 1996, Larsen 2005).

The role of different environmental factors controlling the phenology of tropical insect communities has remained poorly understood because time series that encompass multiple generations and years along with long-term data on environmental variation have been hard to collect. To our knowledge, only two long-term studies have addressed the influence of precipitation on seasonal variation in tropical insect communities. A 13-year study of Panamanian cicadas showed strong seasonality in their activity, which did not correlate with the inter-annual variation in timing of rainy seasons (Wolda 1989). In a 10-year study of Ecuadorian fruit-feeding butterflies, the species diversity and similarity followed the seasonal rhythm of dry and wet seasons (Grøtan et al. 2012), but the effect of inter-annual variation in timing of rainy seasons was not addressed. To our knowledge, none of the long-term studies have studied correlations between plant phenology and temporal dynamics of tropical insect communities. Among the short-term studies, no correlation was found between leaf beetle population fluctuations and leaf-flushing phenology in Borneo (Kishimoto-Yamada et al. 2010), while the abundance of geometroid moths in Malaysia correlated positively with amount of flowering and leaf-flushing in the previous month (Intachat et al. 2001).

In addition to seasonal changes, natural populations of short lived organisms also experience annual fluctuations in their abundance, and therefore, tropical insect communities can be expected to change at inter-annual time scales as well. Such changes could be caused e.g., by inter-annual variation in precipitation due to large-scale climate processes such as El Niño Southern Oscillation (ENSO; e.g., Kishimoto-Yamada et al. 2009). The degree of inter- vs. intra-annual variation in tropical insect communities has rarely been assessed. A short-term study of beetle populations in Borneo found inter-annual variation to greatly exceed intra-annual variation, which supported the characterization of this rainforest as generally aseasonal with a strong ENSO effect (Kishimoto-Yamada et al. 2009).

In addition, there could be long-term directional community changes caused by changes in the environment, e.g., elephant disturbance (Bonnington et al. 2007), fires (Cleary and Genner 2006), deforestation and forest fragmentation (Cleary and Genner 2006, Savilaakso et al.

2009), changes in tree composition due to decimation of seed dispersers (Chapman and Onderdonk 1998), or climate change (Chen et al. 2009). Even in protected tropical forests, much uncertainty remains in how the communities will persist in the presence of habitat disruption, hunting and forest product exploitation and environmental changes immediately outside the reserves (Laurance et al. 2012).

Our long-term study was designed to elucidate assemblage patterns of fruit-feeding butterflies in a protected African rain forest. This is a guild of butterflies attracted by rotten fruits on the forest floor (Molleman et al. 2005b), utilizing a wide range of larval host plants including grasses, vines and trees (Molleman 2012). With almost 12 years of records, this is one of the longest running fruit-feeding butterfly studies in the world on record and one of the few long-term butterfly trapping studies outside the Neotropics. In this study, we first evaluate time-series to see if there are regular seasonal patterns in temperature, precipitation, greenness of vegetation, butterfly abundance, species richness, or diversity. We then ask how the inter-annual variation in the seasonal patterns of butterfly assemblages is associated with inter-annual variation in seasonal patterns of precipitation and/or vegetation greenness. We assess the proportion of variation in butterfly assemblage structure explained by inter- and intra-annual components, and ask, does the assemblage structure differ between ENSO years vs. other years and is there an inter-annual directional change in the assemblage structure. Flexibility in phenology that is associated with interannual variability in environmental seasonality can buffer populations from some deleterious effects of climate change (Cleland et al. 2012). Conversely, if seasonality is constrained to be invariant among years, (e.g., if there are strong photoperiodic controls on the timing of insect life history events; Wolda 1989), we might expect climate change disrupt the temporal fit of butterfly populations with their environment.

METHODS

Study area and data collection

The study area was located next to Makerere University Biological Field Station (MUBFS; 0°35′ N and 30°20′ E; approximately 1500 m a.s.l.) in Kibale National Park (795 km^2), Western Uganda. The park encompasses medium altitude moist evergreen forests as well as swamps, grasslands, woodland thickets and colonizing shrubs (Struhsaker 1997, Chapman and Lambert 2000) and is surrounded by agricultural land, including tea plantations and small farms. The mean annual rainfall is 1696 mm with two distinct rainy seasons (1990–2011; C. A. Chapman, *unpublished data*; Chapman and Lambert 2000, Stampone et al. 2011). In this paper, we will use the term "dry season" for months December, January, February, June, and July and "rainy season" for months March, April, May, August, September, October, and November (Struhsaker 1997). In Kibale, the seasonality in tree flowering and fruiting is known to be weak although several different seasonal patterns of leaf production have been distinguished among tree species (Struhsaker 1997).

Altogether 22 butterfly traps were placed in the forest understory at locations >100 m apart in closed canopy forest (map of trap locations and details of the trapping method can be found in Molleman et al. 2006). Butterfly captures were recorded over 11.5 years between May 2000 and December 2011. Every four weeks baits of fermented banana were placed in traps (Monday), and the trap was emptied on the four subsequent days, comprising a study period (total of 144 study periods), each assigned to represent one month (total of 137 study months). Butterflies were identified in the field and released or collected in glassine envelopes for later identification. Further details on the butterfly data are given in Appendix A.

We obtained daily minimum and maximum temperature and precipitation data (2000–2011) from the weather station at Kanyawara (collected by C. A. C.) and calculated the monthly averages for temperature measures and daily precipitation (further details in Appendix A). To characterize seasonal variation in the greenness of the vegetation we used the product MOD13C2 of the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra, downloaded from the NASA Earth Observing System data gateway Reverb (http://reverb.echo.nasa.gov/reverb/). This product contains the satellite-derived monthly values of the Enhanced Vegetation Index (EVI) starting from February 2000 at a

spatial resolution of 0.05° latitude × 0.05° longitude (Solano et al. 2010). The EVI is calculated based on spectral reflectances in the blue, red and near-infrared channels (Huete et al. 2002) and it describes the structural variations in canopy such as leaf area index and canopy structure (Gao et al. 2000). The values of the 496 squares (15,278 km^2) covering the Kibale National Park and agricultural landscape surrounding it (delimited by latitudes 0.10 and 0.85 and longitudes 30.25 and 31.75) were selected for analyses (further details in Appendix A).

Statistical analysis

To estimate if our data is likely to include the majority of the butterfly species of the studied assemblage, the Chao2 extrapolator, which estimates the true number of species in the studied assemblage (Colwell and Coddington 1994) was calculated with program Primer-E, v6 (Clarke and Gorley 2006; calculated with 999 permutations).

Seasonal patterns.—We evaluated time series of the monthly values for: (1) average daily maximum temperature, (2) average daily minimum temperature, (3) average daily precipitation, (4) EVI, (5) butterfly abundance (individuals/day/trap), (6) rarefied species richness and (7) Simpson diversity index values. The butterfly abundance was the average monthly number of individuals across samples representing combinations of each period, trap and day. Species richness and Simpson's D were calculated from the total sum of individuals each study month, but due to differences in sampling intensity per month, only the first period recorded each month was considered for calculations (if there was a seasonal turnover of species, months sampled twice could have more species than months sampled only once). The number of species was estimated with rarefaction (with program Primer-E, v6; Clarke and Gorley 2006), by calculating the species estimate for the sample size of 115 individuals (the minimum number of individuals observed across all samples representing study months). Simpson's D was calculated as $1 - \Sigma((N_i \times (N_i - 1))/(N \times (N - 1)))$, where N_i = number of individuals in species i and N = total number of individuals.

To find out if there are regular seasonal cycles, the time series of the monthly values were modeled with Fourier series, i.e., as sums of sinusoidal curves with different periods (e.g., Laguardia 2011). Harmonic periods of 12, 6 and 3 months were fitted with program R 2.12.0 (R Development Core Team 2008). We used the information theoretic approach (Burnham and Anderson 2002) to rank all the possible subsets of harmonic periods and the null model (model including only intercept) based on corrected Akaike Information Criterion (AICc).

To investigate in more detail the bi-annual cycles revealed, we developed a non-linear model which was fitted to the monthly precipitation and EVI values. One parameter of this model describes the timing and another describes the peak value of each half-year cycle. The model has two identical parts (but allows for different parameter estimates for both) and sums their predicted values when either is > 0. The values of the first part are positive coarsely across the first half-year cycle and the values of the second across the second half-year cycle. The non-linear model is:

$$y_x = S_{1x} + S_{2x} \quad (1)$$

where:

$$S_{1x} = \begin{cases} W_{1x}, & \text{if } W_{1x} > 0 \\ 0, & \text{if } W_{1x} \leq 0 \end{cases} \quad (2)$$

$$S_{2x} = \begin{cases} W_{2x}, & \text{if } W_{2x} > 0 \\ 0 & \text{if } W_{2x} \leq 0 \end{cases} \quad (3)$$

$$W_{Sx} = z_S \left(\frac{-\cos[\frac{2\pi}{365}(t_S + 365 - x)] + \cos(l_S\pi)}{\cos(l_S\pi) - 1} \right) \quad (4)$$

and S = season (half-year cycle; 1 = January to June or 2 = July to December) of year, x = days from previous winter solstice, z = zenith, i.e., peak value reached (e.g., mm/day), t = time when peak value is reached (days from previous winter solstice), and l = length of the cycle, i.e., proportion of the 365-day period when the predicted values > 0.

To model the average bi-annual cycles and the inter-annual variation in these cycles, we estimated the best-fit parameter values for z_1, t_1, l_1, z_2, t_2, and l_2 for all years combined and for each year separately (JMP, SAS Institute, Cary, NC, 1989–2007). For abundance, species-richness and

diversity data on whole, and for years 2001, 2006, and 2010 of precipitation, and 2003 and 2007 of EVI data, the non-linear model optimization algorithm did not converge and parameter values could not be estimated. In these cases, the Fourier model predicted peak month (mid-day of the month) and its predicted value was designated as t_i and z_i (estimates for values across years), or the highest value reached each half-year cycle and its timing was designated as z_i and t_i (estimates for each year). For precipitation, EVI, abundance and diversity, the highest values were searched between January and June (1st half-year cycle) and between July and December (2nd half-year cycle). To better cover the observed cycles in species richness, its highest values were searched between December and May (1st half-year cycle) and between June and November (2nd half-year cycle). Before analyses, the EVI values were scaled to range from 0 to 1.

Inter-annual variation in seasonal patterns.—To determine if shifts in the seasonal peaks of butterfly abundance, species richness or diversity are associated with parallel shifts in seasonal peaks of precipitation or greenness of the vegetation, we calculated for each half-year cycle and for each variable (precipitation, EVI, butterfly abundance, species richness and diversity) the shift in timing (=time of peak for a given half-year cycle − average time of peak for full time series) and deviation in peak value (=peak value at a given half-year cycle − average peak value for full time series). To account for the possibility that the start of the rainy season is more important in determining vegetation phenology than the peak of the rainy season, we also calculated shift in start of rainy season (=time when 30% of the precipitation of each half-year cycle was achieved − average time when 30% of the precipitation was achieved for all years). We then evaluated possible multiple regression models to explain the timing and peaks in butterflies (abundance and species richness) with the timing and peaks in precipitation and/or EVI. Shifts and deviations in precipitation and EVI of the same half-year cycle and the previous half-year cycle were considered. The information theoretic approach (Burnham and Anderson 2002) was used to rank the models with all possible subsets of the eight variables.

Temporal shifts in assemblage composition.—For

the multivariate analyses, the butterfly assemblage matrix (individuals/day in each trap-period combination) was square root transformed to moderately downweigh the contribution of dominant species. For non-metric multi-dimensional scaling, Permanova and distance-based linear model, zero adjusted Bray-Curtis similarity matrix between samples was then calculated, after adding a dummy variable 1. This adjusts the Bray-Curtis similarity values in near-blank samples (Clarke and Gorley 2006). Non-metric multi-dimensional scaling (MDS; conducted with program Primer-E; number of restarts = 50) was used to graphically explore seasonal patterns and variation among years. MDS ordination attempts to represent the samples as points in two-dimensional space so that their relative distances are in the same rank order as the relative dissimilarities measured by Bray-Curtis similarity index. Due to the very large number of data points (3092) a full MDS graph turned out to be overcrowded. Therefore, MDS graphs representing the distances among centroids of months and distances among centroids of years were generated. This method uses PCO axes (with which distances to centroids can be calculated; Anderson et al. 2008).

To illustrate any average seasonal pattern in butterfly assemblage structure or any trend over the years, a Bray-Curtis similarity matrix (after adding a dummy variable 1) was calculated for each pair of study months (after averaging data over traps and periods) and the average similarity between combinations of two months was plotted for each possible time lag (1 month up to 11.5 years; Grøtan et al. 2012).

The Permanova+ routine of Primer-E (Anderson et al. 2008) was used to test if, and to what degree, year (fixed factor), month (fixed), trap (random) or their 2-way interactions explain the variation in butterfly assemblages, on the basis of the Bray-Curtis similarity matrix. Permanova partitions the total sum of squares and obtains the p-values for each term using permutation procedures (Anderson 2001). We conducted 999 random permutations using method 'permutations of residuals under a reduced model' and type III sums of squares.

It is known that Kibale can experience large monthly and inter-annual variation in precipitation due to large-scale climate processes, mainly

ENSO, the warm phase of which is predicted to increase the rainfall in East Africa (Trenberth 1997). The warm phases coinciding with our study were October 2002–September 2003, October 2006–September 2007 and October 2009–September 2010 (COAPS 2012). Therefore, we conducted a separate Permanova analysis to test whether the butterfly assemblages of years with presumably largest impact of ENSO (2003, 2007 and 2010) differed from the rest of the study years.

To test for a directional change in the butterfly assemblages, a distance-based linear model (DISTLM, conducted with program Primer-E), was fitted, where the Bray-Curtis similarity matrix is modeled with year as a continuous predictor variable. The DISTLM routine resembles Permanova, but partitions the total sum of squares according to a regression model (Anderson et al. 2008). The partially studied year 2000 was excluded from this analysis.

RESULTS

Altogether 113,562 individuals representing 102 species of fruit-feeding butterflies were recorded during the study (list of species, species accumulation curve and the monthly abundances of the 10 most common species are given in Appendix B). The value of Chao2 estimator (108) provides strong evidence that the 11.5 years of sampling has found almost all of the possible species in the studied butterfly assemblage.

Seasonal patterns in environment

Annual or bi-annual seasonal patterns were revealed in monthly time-series of average daily maximum and minimum temperature, precipitation and EVI (Fig. 1). For all variables, a superior model (delta AICc $\geq$ 2) was found (details of model comparison results in Appendix C). According to the most parsimonious Fourier model (model with harmonic periods of 12 and 6 months, adj. $R^2 = 0.33$), the daily maximum temperatures followed an annual cycle with highest values predicted in February (>28°C) and lowest in June (<25.5°C). The daily minimum temperatures followed a bi-annual cycle with the first predicted peak in April (>15.6°C) and the second, smaller, peak in October (>15°C; model with harmonic periods of 12 and 6

months, adj. $R^2 = 0.15$). Also the daily precipitation followed a bi-annual cycle. There was a distinct "small" rainy season, which tended to peak in April (>5 mm/day) and a "large" rainy season that tended to peak in October (>8 mm/day; model with harmonic periods of 12 and 6 months, adj. $R^2 = 0.51$). The differences in annual precipitation were large: e.g., year 2001 averaged >5.2 mm/day vs. only 3.6 mm/day in 2004 (Appendix A: Fig. A1). The four wettest years were 2001, 2006, 2010 and 2003 (>4.7 mm/day) and the four driest 2004, 2011 and 2007 and 2005 (<4.3 mm/day). According to the most parsimonious Fourier model (harmonic periods of 12, 6 and 3 months, adj. $R^2 = 0.65$), the EVI expressed two approximately equal annual peaks; the first tended to occur in May (>0.53) and the second in November (>0.55). The inter-annual variation in height of EVI peaks was small (Fig. 1).

While Fourier models identified seasonal patterns in precipitation and EVI, the non-linear model fits allowed more detailed estimates of the timing and magnitude of the two annual peaks (Appendix D). The first peak in precipitation occurred approximately on 8th of April (SE = ±5 days) with 5.1 mm (±0.34 mm) of precipitation/day and the second peak on 10th of October (±3 days) with 7.7 mm (±0.34 mm) of precipitation/day ($R^2 = 0.52$). Thus, the precipitation peaks occurred approx. 20 days after spring and fall equinoxes (respectively), when the sun reaches zenith at the equator. EVI reached its first peak on 13th of May (±2.2 days) and the second peak on 13th of November (±2.2 days; $R^2 = 0.65$). That is, the first annual peak in greenness followed the first annual peak in precipitation with approximately 34 days lag and the second annual peak of greenness followed the second annual peak in precipitation by approximately 33 days.

Seasonal patterns in butterfly abundance, species richness and diversity

Both butterfly abundance and species richness also followed bi-annual seasonal patterns, although there was higher residual variation around the model predictions than for the environmental data, and no superior Fourier model was found for either variable (Fig. 1; Appendix C). The two Fourier models with similar support from the data (delta AICc < 2) both described the first peak in abundances to
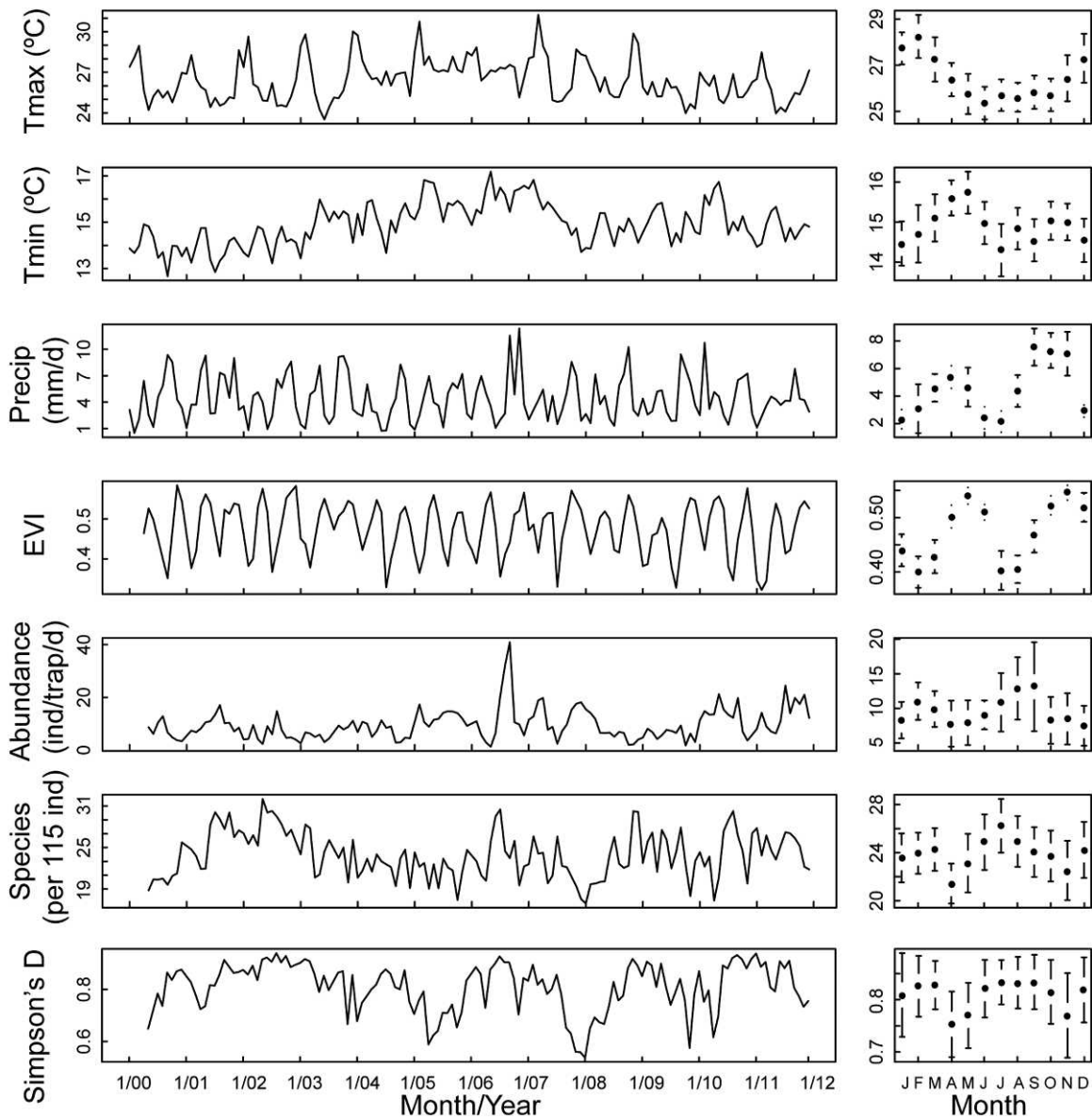
Fig. 1. Full time series (left column) and average monthly values with 95% confidence intervals (right column) of average daily maximum temperature, average daily minimum temperature, daily precipitation, Enhanced Vegetation Index (EVI), butterfly abundance (individuals/day/trap), species richness estimate for 115 individuals and Simpson's D, in Kibale NP, Uganda. For the three missing months (1/01, 8/03, 1/06) in butterfly variables, averages of previous and following month were taken.

take place in February (>11.7 individuals/day/trap) and the second in August (>11.7 individuals/day/trap; predictions from model with 6 month harmonics, adj. $R^2 = 0.05$). With respect to species richness, the top two Fourier models both described the first peak to be in January (>25

species per 115 individuals) and second in July (>25 species; predictions from model with 6 month harmonics, adj. $R^2 = 0.05$). According to the most parsimonious Fourier model (harmonic periods of 6 months, adj. $R^2 = 0.03$), Simpson's D expressed two annual peaks, first in February

(predicted probability that two random individuals came from different species >0.83) and second in August (>0.83). Thus, based on Fourier model predictions, the two annual peaks in abundance and diversity followed the two annual peaks in species richness by approximately one month. Furthermore, both annual (Fourier model predicted) peaks in butterfly abundance and diversity occurred three months later than the peaks in EVI (or four months after the peaks in precipitation) and both Fourier model predicted peaks in species richness occurred two months later than the peaks in EVI (or three months after the peaks in precipitation; Appendix D: Fig. D3).

Inter-annual variation in seasonal patterns

The non-linear model fits also provided insight into the inter-annual variation in timing and magnitude of precipitation and EVI peaks. The shift in timing of the precipitation peaks at each half-year cycle did not correlate with the shift in timing of the EVI peaks (Pearson's correlation $\rho = 0.15$, p = 0.49), i.e., later/earlier than average precipitation peak was not detectably related to later/earlier than average EVI peak. Neither did the shift in timing of the start of rainy season correlate with the shift in timing of the EVI peaks ($\rho = 0.26$, p = 0.24). There was no correlation between the deviation in peak values of the precipitation at each half-year cycle and the deviation in peak values of the EVI peak ($\rho = 0.27$, p = 0.21), i.e., heavier/lighter than average precipitation did not correlate with higher/lower than average EVI peak (full correlation matrix in Appendix E).

The inter-annual variation in timing and height of precipitation and EVI peaks provided insights into the potential controls of butterfly assemblage phenology. The timing of butterfly abundance peaks positively correlated with shifts in EVI peaks at previous half-year cycle ($EVIt_{i-1}$), i.e., the earlier/later than average EVI peak approx. three months earlier correlated positively with earlier/later than average abundance peak of butterflies. There was no superior model relating shifts in timing of butterfly peaks to shifts and deviations in precipitation and greenness, but all four models with substantial empirical evidence from the data included the positive effect of $EVIt_{i-1}$ (the most parsimonious model: $y = 22.2 +$ $1.5 \times EVIt_{i-1}$, adj. $R^2 = 0.31$; details in Appendix E).

There was a superior model relating timing of Simpson's D peaks to timing of precipitation peaks at the same half-year cycle ($Precipt_i$) and height of precipitation peaks at previous half year cycle ($Precipz_{i-1}$), i.e., the diversity peaked later than average when the timing of precipitation peak was earlier than average at the same half-year cycle and the precipitation peak was higher than average in the previous half-year cycle ($y = 37.1 - 2.3 \times Precipt_i + 13.3 \times Precipz_{i-1}$, adj. $R^2 = 0.46$). There was no superior model, or set of models distinct from the null model, relating height of butterfly abundance peaks (z in Eq. 4), or timing (t in Eq. 4) or height (z in Eq. 4) of species richness peaks, or height (z in Eq. 4) of Simpson's D peaks to shifts and deviations in precipitation and greenness (Appendix E).

Temporal shifts in assemblage composition

Butterfly assemblage structure showed a bi-annual seasonal pattern as illustrated by a dampening bi-annual cyclic pattern in similarity values between pairs of study months (Fig. 2). In other words, the assemblages generally became more dissimilar with increasing temporal difference, but were repeatedly more similar at lags of 6 and 12 months (see also MDS graphs in Appendix F). The seasonal and inter-annual patterns in assemblage structure were statistically significant. Based on Permanova analysis, the largest source of variation in the butterfly assemblages was explained by interaction between year and month (19%) and year (14%), confirming that the temporal change in assemblage between months differed across the studied years (Table 1). Month explained 9%, trap 11%, interaction between year and trap 8% and interaction between month and trap 4% of the variation in butterfly assemblages. A separate Permanova analysis comparing the ENSO years (2003, 2007 and 2010) with the rest of the years also revealed a significant difference in butterfly assemblages (p = 0.001; ENSO explaining 13% of the variation in butterfly assemblages). There was a statistically significant directional change in the butterfly assemblage, as year explained a significant, but minor, proportion of the variation in the similarity matrix (DISTLM model; p = 0.001; $R^2 = 0.01$).
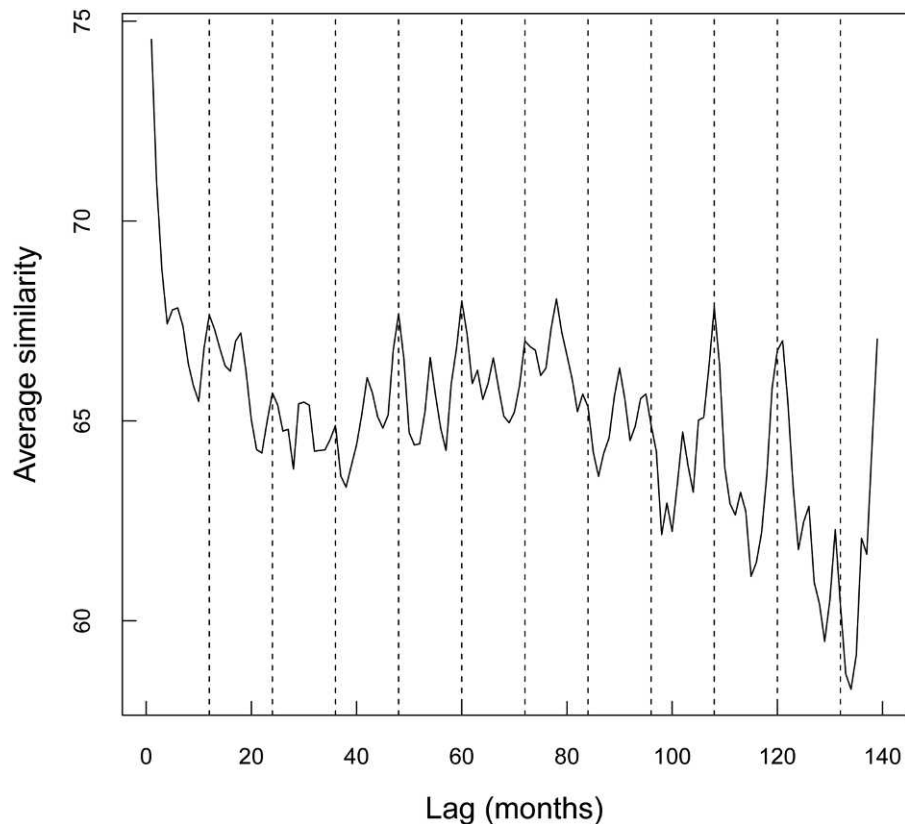
Fig. 2. The average Bray-Curtis similarity between samples representing study months plotted against the time-lag between the samples, in Kibale NP, Uganda. 12-month intervals are indicated with dashed vertical lines.

DISCUSSION

The fruit-feeding butterfly assemblage in Uganda follows the seasonal rhythms of rainy and dry seasons, a pattern found also in the two previous long-term studies on tropical insect communities in seasonal environments (Wolda 1989, Grøtan et al. 2012). The bi-annual seasonal rhythms were revealed both in univariate (abundance, species richness, diversity) and multivariate measures (assemblage similarity), emphasizing the importance of addressing both aspects of communities together, because each can give different insights on the processes involved in seasonality (e.g., strong seasonality in assemblage composition suggests seasonal turnover in species relative abundances or composition, while strong seasonality in abundances only, would suggest that the seasonal variation in weather or host plant availability could be driving the changes in population sizes more equally across species).

The bi-annual seasonal pattern may be general in our study area: e.g., the abundances of sweep netted arthropods also correlated with rainfall with a lag of approximately three months (Nummelin 1989). However, at a global scale, bi-annual cycles in tropical insect communities could be uncommon, since areas where precipitation typically peaks twice a year mainly occur at two bands a few degrees away from the equator (van Schaik et al. 1993).

Finding a seasonal pattern in tropical insect communities is not self-evident. The other available (mostly short-term) studies, suggest that the degree of seasonality in tropical insect communities is highly variable. Seasonal population patterns were not found in leaf beetles in an aseasonal Bornean rainforest (Kishimoto-Yamada et al. 2010) and can be absent in tropical areas with distinct seasonal variation in precipitation. For example, the Ecuadorian butterflies express annual seasonal pattern in their assem-

Table 1. Results of the Permanova analysis, based on the Bray-Curtis similarity values of butterfly assemblages (individuals/day in each trap and period), showing the partitioning of multivariate variation and test for the factors and their two-way interactions; UP = unique permutations, Sq. var = square root of the component of variation.

Source	df	MS	Pseudo-F	p	UP	Sq. var (%)
Year (Y)	11	39958	23.22	0.001	996	12.4 (13.5%)
Month (M)	11	16569	13.79	0.001	995	7.9 (8.6%)
Trap (T)	21	14086	13.27	0.001	996	9.7 (10.6%)
Y × M†	114	8143	7.67	0.001	990	17.8 (19.5%)
Y × T†	225	1733	1.63	0.001	988	7.5 (8.2%)
M × T	231	1205	1.14	0.001	988	3.5 (3.9%)
Residual	2478	1062				32.6 (35.7%)
Total	3091					

† The term had one or more empty cells.

blage similarity and diversity, but not in total abundances (Grøtan et al. 2012). A four-year study of beetle abundances in distinctively seasonal Australian rainforest revealed weak seasonality (Grimbacher and Stork 2009). Furthermore, there can be large differences among species in degree of seasonality, as shown by two butterfly studies in seasonal West-Africa (Larsen et al. 1979, Libert 1994). Most of the studies addressing seasonality in insect communities have been relatively short-term, covering only a few years. As demonstrated by the wide inter-annual variation in our study, one or two years of study could be too short to capture the nature of possibly subtle seasonal patterns in tropical insect communities, which long-term sampling can reveal, such as previously found in tree flowering and fruiting phenology (Chapman et al. 1999) and monkey birthrates (M. E. Arlet et al., *unpublished data*).

The butterfly species richness and abundance followed the vegetation greenness with lags of two and three months, respectively, i.e., the January and February peaks in species richness and abundance followed the greenness peak in November, while July and August peaks followed the greenness peak in May. Although these regular cycles explained a relatively small proportion of variation in both univariate time series and in multivariate data, the high proportion of variance explained by interaction between year and month helps to understand this pattern; the assemblage follows a seasonal pattern, which is different each year, possibly due to inter-annual variation in timing of precipitation or greenness cycles. The Panamanian cicadas fol-

lowed seasonal patterns in their activity, not correlated with intra-annual variation in meteorological seasons, which led Wolda (1989) to suggest that photoperiod, via physiology of host plants, could work as the seasonal cue in this group of tropical insects. In our study, the low proportion of variation in the assemblage structure explained by month argues against strong photoperiodic controls in this fruit-feeding butterfly assemblage.

Temporal shifts in vegetation greenness in the previous half-year cycle were positively correlated with temporal shifts in peaks of butterfly abundances, meaning that if the greenness peaked earlier/later than average, also the abundance peaked earlier/later than average approximately three months later. This suggests that the host plant availability could play a role in controlling the phenology of this fruit-feeding butterfly assemblage. A manipulative experiment on a tropical leaf-mining moth on an understorey host plant (Hopkins and Memmott 2003) and a two-year study of herbivores associated with an Australian rainforest canopy tree (Basset 1991), both suggest that the phenology of host trees can drive changes in herbivore abundance, in which case abundance peaks occur at the same time or shortly after leaf flush. Larvae of many tropical herbivores seem to prefer young leaves, based on the fact that young leaves experience higher rates of herbivory compared to mature leafs (Coley 1983). Young leaves tend to be less tough, less fibrous and more nutritious than mature leaves (Coley 1983, Chapman and Chapman 2002). If the young leaves provide better quality food for larvae, the seasonality in butterfly abundances

could be a result of higher survival of larvae when fresh leaves are abundant, migration to areas where this resource is abundant or be mediated by diapause or non-diapause mechanisms (Tauber et al. 1986) which help to synchronize larval feeding with the time when fresh leaves are abundant. The egg-to-adult time in Neotropical butterfly species varies from a few weeks up to three months (DeVries 1987), an interval which matches well with pattern observed here. Even if not all species use new leaves and feed on mature leaves instead, which seems to be the case with many fruit-feeding butterflies in Kibale (Molleman 2012), this needs not to be in conflict with the observed pattern, because also the availability of mature leaves must be seasonal in the area, based on the EVI data.

It is more difficult to explain, why the timing of diversity peaks were negatively correlated with timing of precipitation peaks at the same half-year cycle. The environmental conditions at the same half-year cycle could influence the adult butterflies via mortality or changes in their catchability. Although we can not exclude the possibility that there is weather induced variation in butterfly catchability in the data, it is unlikely that our results are confounded with it because the presumably better catchability of butterflies in the driest or the hottest months does not coincide with the two butterfly peak abundance months observed in this study.

The greenness of the vegetation followed the precipitation predictably with a one-month lag, when modeled across years. The overall close relationship between rainfall and greenness of the vegetation is not surprising, given that the production of new leaves is often limited by water availability in tropical forests experiencing dry seasons (Würth et al. 2005). The small rainy season was wet enough to induce as high a peak in greenness as the large rainy season (Fig. 1) and the deviations in peak values of precipitation did not lead to parallel deviations in peak values of EVI at each half-year cycle. This suggests that the amount of rainfall during the rainy season is not limiting vegetation greenness. To our surprise, the temporal shifts in peak precipitation or in the start of the rainy season, at each half-year cycle, also did not correlate with shifts in timing of EVI peaks. Previous studies on tropical trees in areas with annual dry seasons suggest that the timing of leaf-out and leaf-drop are strongly related to the seasonal changes in tree water status and, therefore, indirectly with water availability in the soil (Reich and Borchert 1984). Alternatively, the phenology of the vegetation could also be sensitive to photoperiodic cues (e.g., Wareing 1956).

The inter-annual variation in similarity of butterfly assemblages was high (Table 1), one potential cause being ENSO, the positive phase of which is known to both increase the rainfall and the intermonthly variation in rainfall in Kibale (Struhsaker 1997). During the studied years, the highest annual precipitation occurred in 2001 (not coinciding), followed by 2006, 2003, and 2010 (all coinciding with the positive El Niño phases). Previously, the effects of an ENSO event (severe droughts and consequent synchronous flowering and leaf-production in Southeast Asian rainforests) on insect communities have been reported in several short-term studies (Harrison 2000, Intachat et al. 2001, Kishimoto-Yamada et al. 2009). In Central-America, the ENSO has been associated with increases in the migrating adults of a butterfly species via increased soil moisture and leaf flushing of the host plants (Srygley et al. 2010).

We also found evidence of significant, but marginal (based on explained variance), long-term directional change in the butterfly assemblage similarity. The directional change is weak considering that during the past decades Kibale has experienced meaningful forest regeneration after years of logging (Struhsaker 1997, Bonnell et al. 2011). On the other hand, many forest species in Kibale remain threatened by boundary encroachment for wood extraction, livestock grazing and poaching (Mackenzie et al. 2012), great reduction of forest outside the park boundaries (Hartter et al. 2011), and increased numbers of elephants and baboons at the study site that, for example, have markedly reduced the abundance of the main larval host-plants (large *Setaria* grasses) of the butterfly *Gnophodes chelys* (F. Molleman, *personal observation*). Additionally, over the past decades, the monthly average maximum temperatures have increased by 3.5°C and this has been accompanied by varied changes in fruiting phenology of many tree species (Chapman et al. 2005).

Conclusions

Analyses of a 12-year time-series of fruit-feeding butterflies, in a medium altitude rain forest with two annual rainy seasons, revealed bi-annual seasonal cycles in butterfly assemblages. Our results also showed that one or two years of study could be too short to capture the nature of seasonal patterns in tropical insect communities, which can be more subtle than in systems that go from green to brown annually, and can be obscured by extensive inter-annual variation. The bi-annual seasonal cycles in butterfly abundance correlated with temporal variation in vegetation greenness, which, to our knowledge, has never been shown before. As far as we know, this is the first study connecting long-term tropical insect assemblage data with long-term environmental datasets on precipitation and satellite-derived greenness of vegetation, and therefore our results cast new light on the environmental controls of phenology in tropical insect communities.

In higher latitudes, the ecological effects of climate change have frequently involved changes in insect phenology, such as earlier spring flight (Forister and Shapiro 2003, Parmesan and Yohe 2003) or increased voltinism (Pöyry et al. 2011) due to increased temperatures. In the tropics, climate change is predicted to affect rainfall patterns, including our study site (IPCC 2007). To understand the potential ecological consequences of climate change on phenology of tropical insects, we should understand how well they can phenologically track the environmental changes generated by climate change (Cleland et al. 2012). If the proportion of species controlled by photoperiod, or other mechanisms not influenced by climate change is high, as suggested for Panamanian cicadas (Wolda 1989), the risk that species become mismatched from their resources in a changed environment is higher, with possible consequences on species diversity and ecosystem functioning. The assemblage of fruit-feeding butterflies, studied here, was showing flexibility in phenology that was associated with interannual variability in environmental seasonality, which could help species in this assemblage to track the environmental changes in the long run.

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SUPPLEMENTAL MATERIAL

APPENDIX A

DETAILS ON DATA COLLECTION

Butterfly data

The butterfly data was collected every four weeks, on four subsequent days, comprising a total of 144 study periods. Due to adverse weather or some accident, in 76% out of the possible 576 study days data from all traps was acquired and data from eight study periods were totally lost. Each study period was assigned to represent only one month so that the month which most of the study days represented was selected but if the two months received even number of days, then the first month was selected.

The analyses excluded the facultatively fruit-feeding *Neptis* and others such as *Pseudoneptis*, *Vanessula*, Acraeinae, Danainae, Lycaenidae, Hesperidae, Riodinidae and Papilionidae. The females of *Bicyclus smithi*, *B. golo* and *B. istaris* (difficult to distinguish from each other) were assigned to these species in proportion to those found in males. If there were no males caught during the sampling day, then the proportion during the same trap and period was used, and if there were no males in that trap and period, then the proportion during the same period was used instead.

Some names changed since the Molleman et al. (2006) publication due to insight from molecular studies and natural history. *Henotesia* became *Heteropsis*, *Kamilla ansorgei* became *Junonia ansorgei*, and *Antanartia dimorphica* became *Vanessa dimorphica*. Two *Gnophodes* identifications were corrected. The smaller one with the costal streak on the hindwing upperside is *betsimena* (previously erroneously called *grogani*), and what had been called *betsimena* may be an undescribed species, here listed as new (Molleman 2012).

Selected and representative specimens have been donated to the Zoologisch Museum Amsterdam (The Netherlands), the African Butterfly Research Institute (ABRI) in Nairobi, and to Niklas Wahlberg for molecular phylogenetic work (e.g., Kodandaramaiah and Wahlberg 2007, Aduse-Poku et al. 2009).

Temperature and precipitation data

The average daily minimum and maximum temperatures for each month were calculated from the temperature measures after excluding the occasional missing daily values (0.5%). Due to equipment failure, daily maximum temperature data from entire December 2006 was missing and it was replaced by the average of the
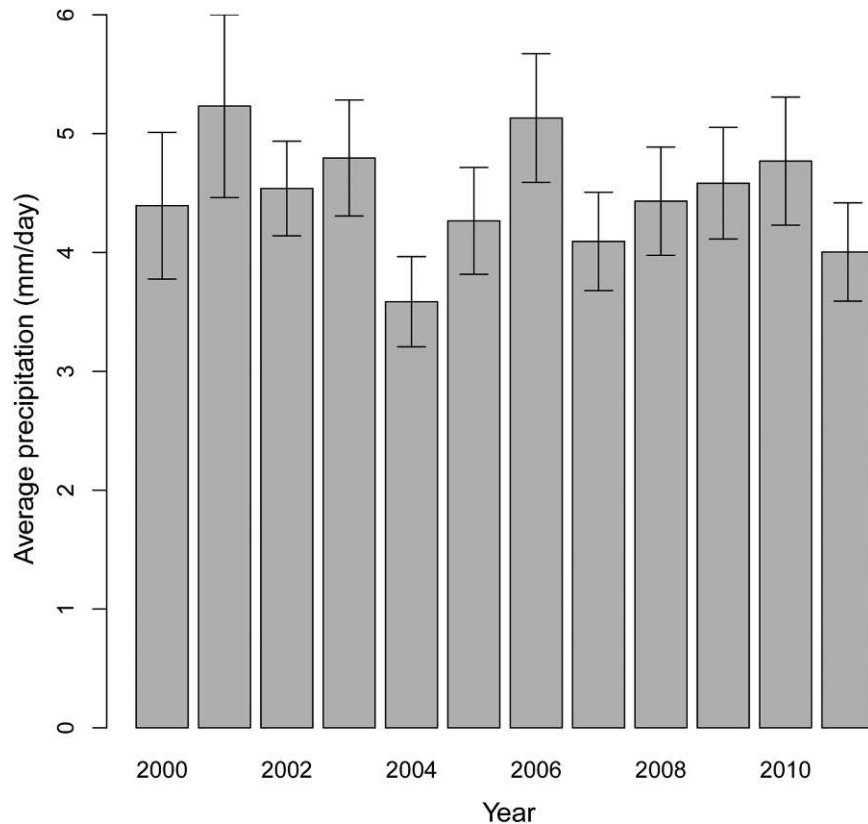
Fig. A1. The average daily precipitation in each studied year ± SE.

previous and following month.

The average daily precipitation for each month was calculated by summing the monthly precipitation after replacing the missing daily values (8.7%) with zero and dividing the sum with number of days of each month. This was done, because the precipitation of the missing day remained in the gauge and was thus recorded the next day when the precipitation was measured. The average daily precipitation in each studied year is given in Fig. A1. In order to estimate the start of the rainy season (=time when 30% of the precipitation of each half-year cycle was achieved) the cumulative precipitation of each day was also calculated after replacing the missing daily values with zero.

Enhanced Vegetation Index (EVI) data

The EVI data (Product MOD13C2; http://reverb.echo.nasa.gov/reverb/) have been produced by the MODIS Vegetation Index (VI) algorithm, which gathers information on 250 or 500 m pixel-basis over 16-day cycles and then filters the data based on its quality (Solano et al. 2010). Only higher quality, cloud-free, filtered data have been accepted for compositing. The monthly values at 0.05° resolution have been achieved by temporal and spatial averaging.

In this product, the two quality layers give further information on the pixel reliability. The summary quality layer has six categories: (1) no data, (2) good data, use with confidence, (3) marginal data, usefull but look at other QA information, (4) snow/ice, (5) cloudy, (6) estimated from MODIS historical time series. The 'VI Quality Assessment Science Data Sets' layer gives further detailed information on the pixel reliability in eight categories including, e.g., aerosol quantity, adjacent clouds and mixed clouds.

Monthly EVI values of 496 squares covering the Kibale National Park and agricultural landscape surrounding it were selected. This area excludes Rwenzori mountains and large lakes.
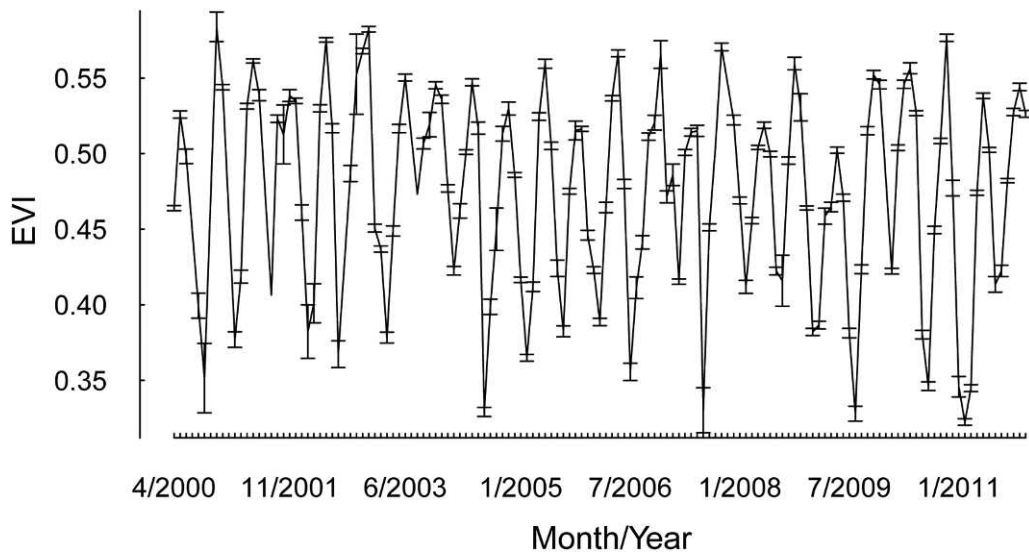
Fig. A2. The monthly averages of the filtered EVI values ± SE. SE values are not given for the eight datapoints for which zero pixels remained after filtering (and values represent averages of the previous and following month) and for the three datapoints where only one pixel remained after filtering.

Prior to final usage, the EVI data has to be filtered so that clouds, shadows and aerosol contaminated data are omitted (Samanta et al. 2010). Samanta et al. (2010) used 'The VI Quality Assessment Science Data Sets' layer of the 1-km 16-day resolution data to filter the data based on the binary quality flags "adjacent cloud detected", "mixed clouds" and "possible shadow". Because the MOD13C2 product does not provide a quality flag for possible shadow, we decided to filter the data based on the summary quality layer by selecting only pixels receiving flag 'good
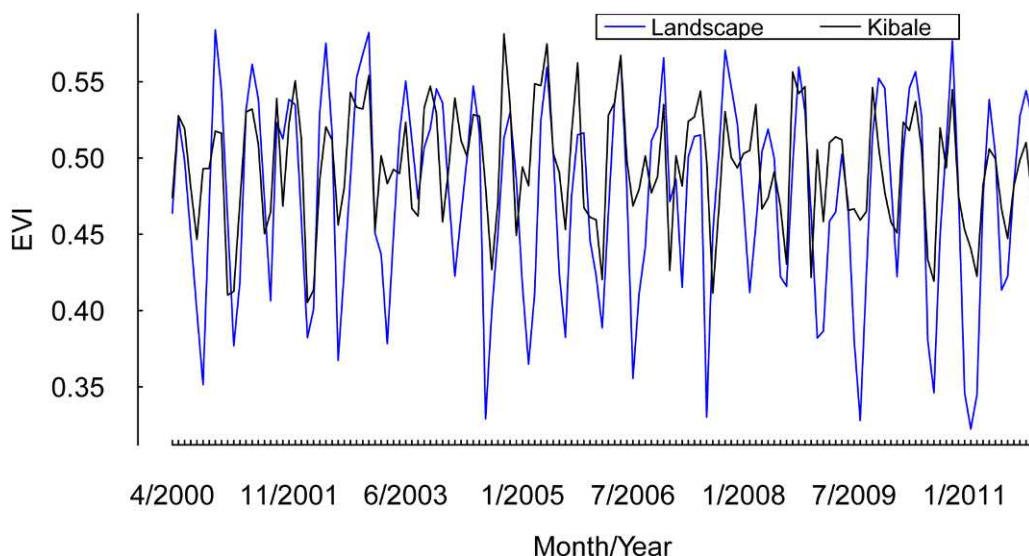

Fig. A3. The monthly averages of the unfiltered values of the eight pixels located inside Kibale National Park (Kibale) shown together with the monthly average values of the filtered data across the landscape surrounding Kibale (Landscpe), the latter which were used in the final analyses.

data, use with confidence'. Thus, all other pixel values were omitted (filtered out) from the data and the average EVI value of the remaining pixels was used as the monthly estimate of the vegetation greenness. The variation in the remaining pixel values within each month was generally small (Fig. A2).The months for which none of the pixel values remained after filtering were either excluded from the time-series (2/2000 and 3/2000) or replaced by the average value calculated based on the previous and following month (7/2000, 1/2001, 7/2001, 8/2002, 7/2003, 11/2007, 1/2010).

We could not use data of only those pixels located inside Kibale National Park in our analyses, due to a very small proportion of the pixel values remaining after filtering. However, the timing of EVI cycles of the larger area selected for final analyses (Landscape) followed closely the timing of the EVI cycles of the unfiltered data covering pixels located inside Kibale forest (Kibale; Fig. A3). The average values in the large selected area do, however, reach lower values during the least green months, presumably because grasses prevailing in agricultural areas lose much more of their greenness during dry seasons than the partly deciduous rain forest.

Appendix B

Details of the Butterfly Data
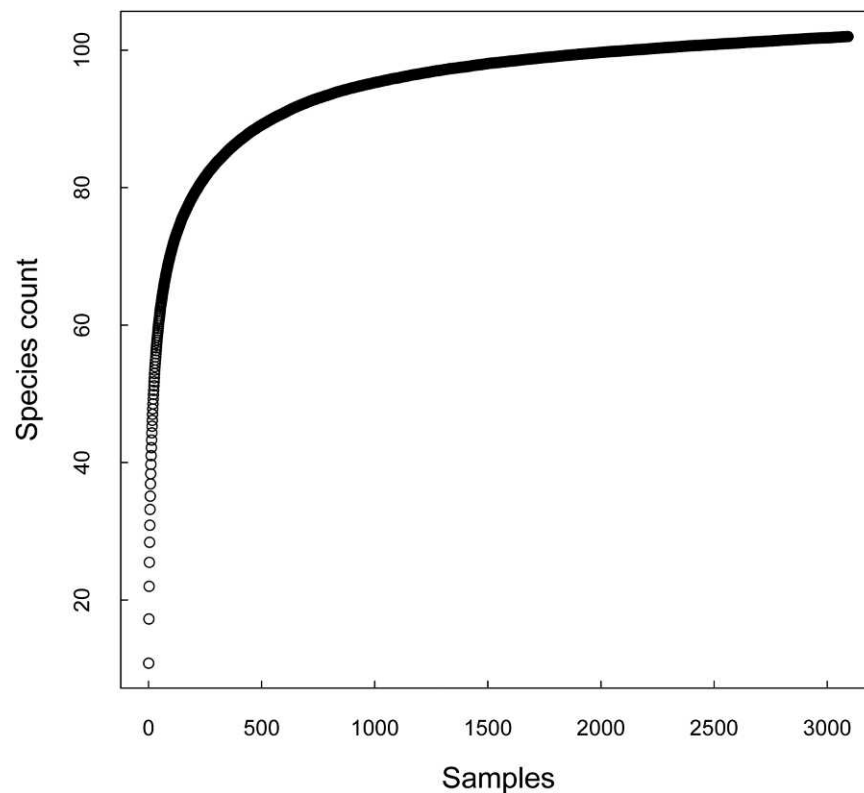
Fig. B1. Species-accumulation curve for fruit-feeding butterflies, generated with program Primer-E, v6 (Clarke and Gorley 2006). In this graph, the increasing total number of species is plotted as samples (species count in each period of each trap) are successively pooled, the order of samples permuted 999 times.

Fig. B2. Monthly abundances of the ten most common butterfly species. For the three missing months (1/01, 8/03, 1/06) averages of previous and following month were taken.

Table B1. List of species.

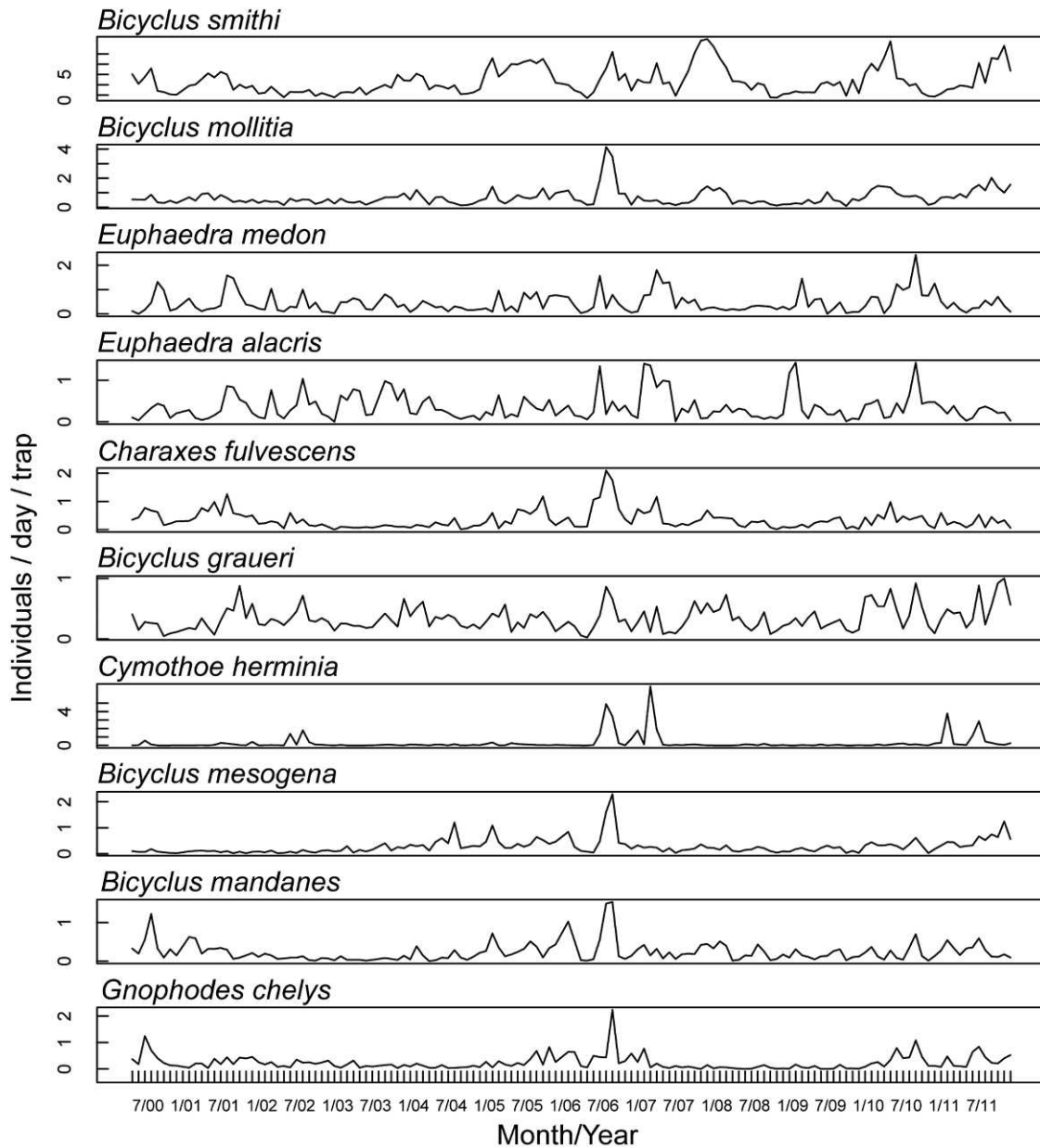| Species	Total count
Bicyclus smithi	44347
Bicyclus mollitia	7628
Euphaedra medon	5547
Euphaedra alacris	4255
Charaxes fulvescens	4251
Bicyclus graueri	4036
Cymothoe herminia	3283
Bicyclus mesogena	3135
Bicyclus mandanes	2875
Gnophodes chelys	2844
Bicyclus auricruda	2815
Kallimoides rumia	2653
Harma theobene	2336
Bicyclus golo	2039
Cymothoe lurida	1857
Euphaedra harpalyce	1525
Euphaedra christyi	1249
Euphaedra preussi	1176
Aterica galene	1139
Heteropsis peitho	1056
Euphaedra uganda	1032
Eurytela hiarbas	985
Euphaedra eusemoides	953
Bicyclus buea	785
Catuna crithea	778
Sevenia boisduvali	647
Bebearia sophus	569
Sevenia occidentalium	539
Melanitis leda	456
Euphaedra edwardsi	452
Euphaedra zaddachi	417
Gnophodes new	396
Bicyclus dentatus	380
Cymothoe hobarti	370
Lachnoptera anticlia	368
Junonia gregorii	302
Gnophodes betsimena	295
Bicyclus sebetus	286
Neptidopsis ophione	269
Bicyclus sambulos	215
Bicyclus istaris	201
Charaxes bipunctatus	200
Ariadne enotrea	193
Pseudacraea lucretia	190
Euphaedra kakamegae	184
Charaxes cynthia	155
Charaxes pollux	146
Euriphene ribensis	140
Bebearia absolon	133
Melanitis ansorgei	129
Charaxes numenes	128
Euryphura chalcis	89
Apaturopsis cleocharis	73
Euphaedra hollandi	69
Salamis cacta	69
Antanartia delius	67
Charaxes protoclea	64
Phalanta eurytis	64
Bicyclus funebris	63
Charaxes pleione	63
Charaxes candiope	59
Bicyclus campinus	45
Charaxes etheocles	45
Cymothoe caenis	41
Charaxes tiridates	38
Phalanta phalantha	32
Junonia ansorgei	31

Table B1. Continued.

Species	Total count
Ariadne pagenstecheri	28
Hypolimnas salmacis	24
Junonia westermanni	22
Bicyclus vulgaris	19
Euxanthe crossleyi	16
Sevenia umbrina	16
Bicyclus safitza	14
Euriphene saphirina	14
Hypolimnas anthedon	13
Protogoniomorpha parhassus	13
Bebearia cocalia	12
Mesoxantha ethosea	12
Bicyclus sandace	11
Charaxes paphianus	10
Bicyclus campus	9
Protogoniomorpha temora	8
Pseudacraea eurytus	8
Vanessa dimorphica	8
Charaxes varanes	7
Eurytela dryope	7
Bicyclus jefferyi	5
Charaxes etesipe	5
Hypolimnas dinarcha	5
Charaxes anticlea	4
Bicyclus anynana	3
Charaxes eupale	3
Charaxes smaragdalis	3
Euxanthe eurinome	3
Charaxes brutus	2
Charaxes zelica	2
Bicyclus ignobilis	1
Charaxes kahldeni	1
Charaxes porthos	1
Melanitis libya	1
Pseudacraea clarki	1

APPENDIX C

DETAILS OF FOURIER MODEL RESULTS

The seasonal cycle of butterfly abundances is strongly influenced by the most abundant species *B. smithi*, the average abundances which peak four times a year (February, May, September and November). If *B. smithi* is excluded from the data, the abundance of the rest of the species also follows a bi-annual cycle, with predicted peaks in February (6.6 individuals / day / trap) and in August (9.0; the superior Fourier model with harmonic periods of 12 and 6 months; adj. $R^2 = 0.13$).

Table C1. The eight models compared. Numbers 12, 6 and 3 in model name indicate the harmonic periods included in the model.

Model	Terms
m0	$y = a$ (null model)
m12	$y = a + b \times \sin(t \times 2 \times \pi) + c \times \cos(t \times 2 \times \pi)$
m6	$y = a + b \times \sin(2 \times t \times 2 \times \pi) + c \times \cos(2 \times t \times 2 \times \pi)$
m3	$y = a + b \times \sin(3 \times t \times 2 \times \pi) + c \times \cos(3 \times t \times 2 \times \pi)$
m12–6	$y = a + b \times \sin(t \times 2 \times \pi) + c \times \cos(t \times 2 \times \pi) + d \times \sin(2 \times t \times 2 \times \pi) + e \times \cos(2 \times t \times 2 \times \pi)$
m6–3	$y = a + b \times \sin(2 \times t \times 2 \times \pi) + c \times \cos(2 \times t \times 2 \times \pi) + d \times \sin(3 \times t \times 2 \times \pi) + e \times \cos(3 \times t \times 2 \times \pi)$
m12–3	$y = a + b \times \sin(t \times 2 \times \pi) + c \times \cos(t \times 2 \times \pi) + d \times \sin(3 \times t \times 2 \times \pi) + e \times \cos(3 \times t \times 2 \times \pi)$
m12–6-3	$y = a + b \times \sin(t \times 2 \times \pi) + c \times \cos(t \times 2 \times \pi) + d \times \sin(2 \times t \times 2 \times \pi) + e \times \cos(2 \times t \times 2 \times \pi) + f \times \sin(3 \times t \times 2 \times \pi) + g \times \cos(3 \times t \times 2 \times \pi)$

Note: t = order of observation in time series/12.

Table C2. The highest ranked Fourier models according to information theoretic approach (Burnham and Anderson 2002), describing the seasonal cycles in maximum and minimum daily temperature, precipitation, Enhanced Vegetation Index, butterfly abundance, species richness (estimated for 115 individuals) and Simpson's diversity index. Models were ranked based on their corrected Akaike Information Criterion (AICc) value and only models with substantial empirical evidence (ΔAICc < 2) are shown.

Variable	Model	n	K	AICc	ΔAICc	L	w_i	adj R^2
Tmax	m12–6	144	6	483.7	0.0	1.0	0.82	0.33
Tmin	m12–6	144	6	371.5	0.0	1.0	0.82	0.15
Precip	m12–6	144	6	588.5	0.0	1.0	0.89	0.51
EVI	m12–6-3	141	8	−509.0	0.0	1.0	0.56	0.65
Abundance	m6	140	4	888.1	0.0	1.0	0.48	0.05
	m12–6	140	6	888.6	0.5	0.8	0.37	0.07
Species	m6	140	4	737.8	0.0	1.0	0.41	0.05
	m12–6	140	6	738.3	0.5	0.8	0.32	0.06
Simpson	m6	140	4	−265.3	0.0	1.0	0.55	0.03

Note: n = number of observations, K = number of estimated parameters, ΔAICc = difference in AICc between this model and the best model in the set, L = likelihood of the model, given the data, and w_i = model probability, i.e., "Akaike weight".

APPENDIX D

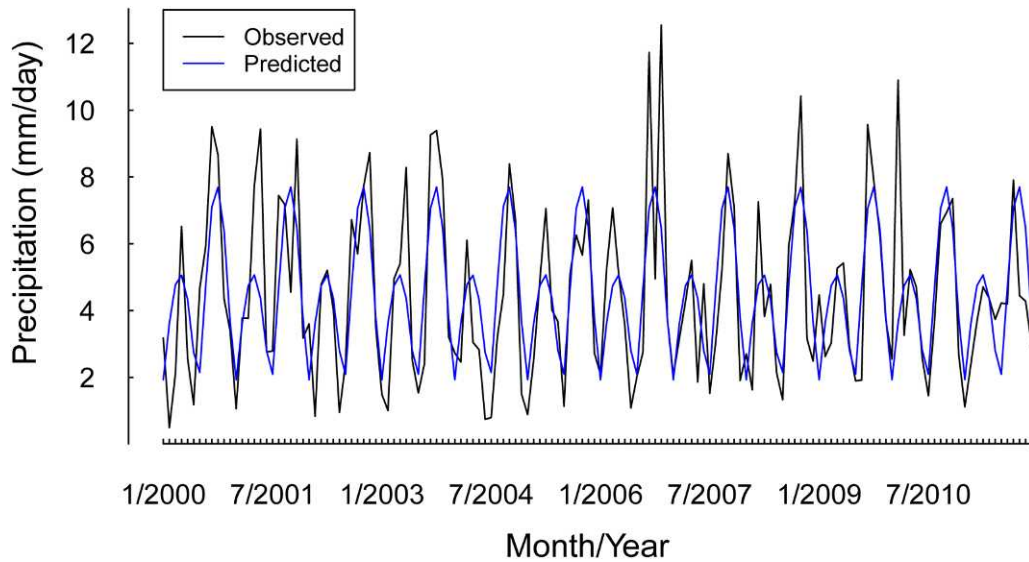DETAILS OF NON-LINEAR MODEL RESULTS

Fig. D1. Observed and non-linear model predicted daily precipitation (model fitted for all years combined).
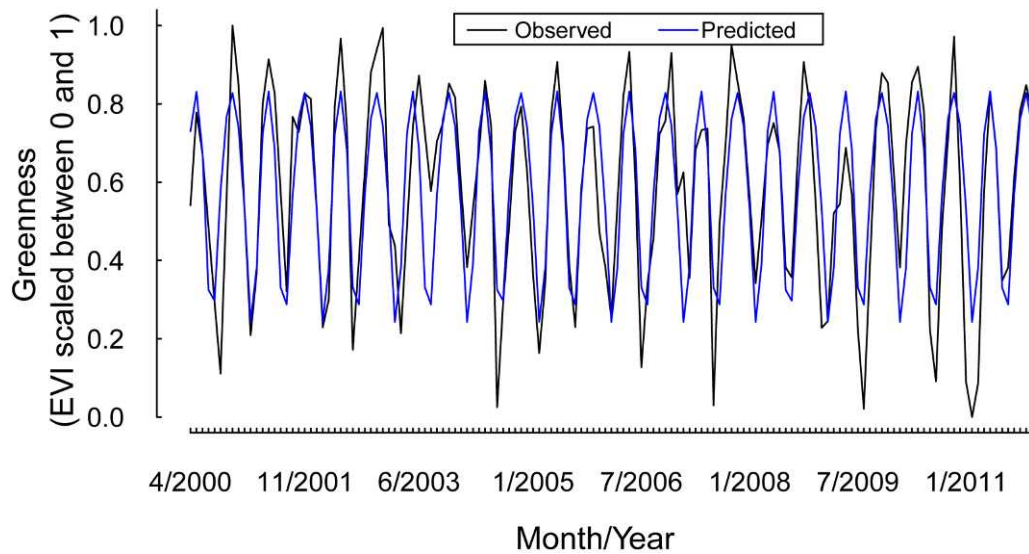

Fig. D2. Observed and non-linear model predicted monthly greenness (model fitted for all years combined).
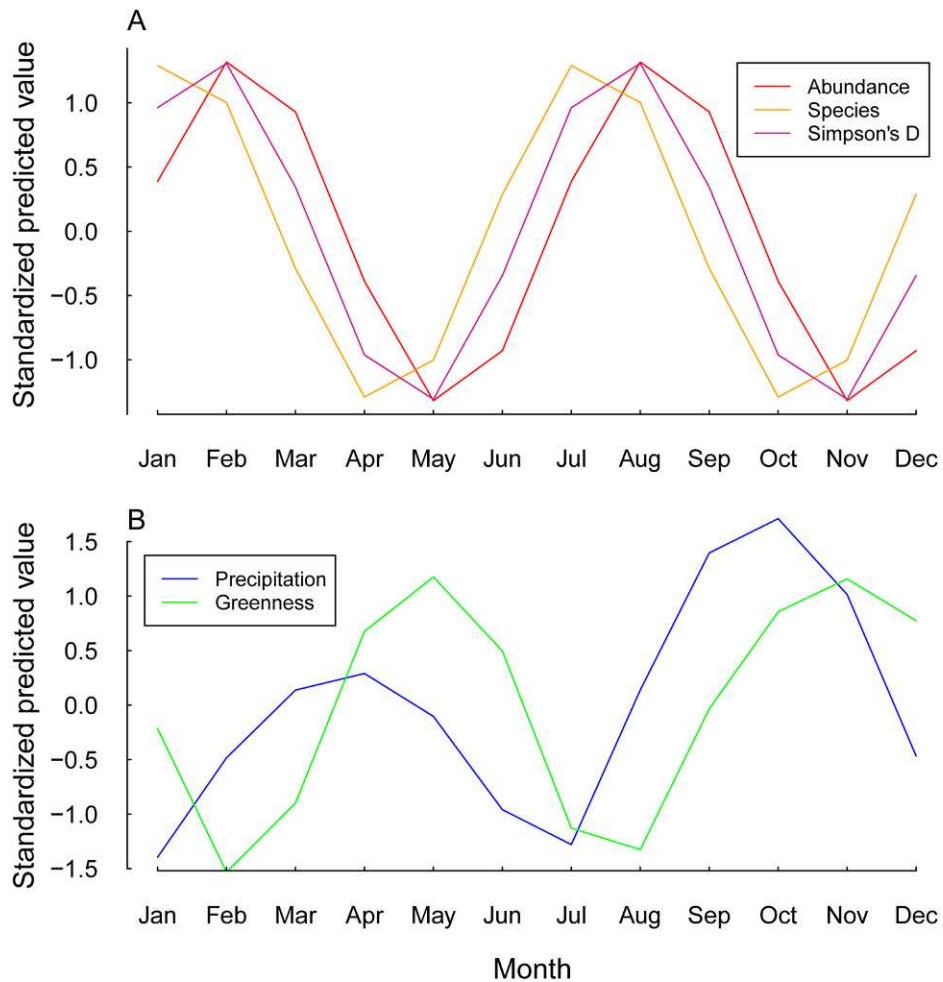
Fig. D3. Relative timing of the seasonal cycles; (A) standardized Fourier model predicted monthly values for abundance, species richness and Simpson's D, and (B) standardized non-linear model predicted monthly values of precipitation and greenness.

Table D1. Summary of parameter values of precipitation and EVI, estimated by nonlinear models for each year. For years 2001, 2006, and 2010 of precipitation, and 2003 and 2007 of EVI data, the non-linear model optimization algorithm did not converge and parameter values could not be estimated.

Variable	Precipitation			EVI		
	$\bar{x}$	SE	n	$\bar{x}$	SE	n
z_1	5.362	0.347	9	0.843	0.034	10
t_1	112.4	4.1	9	147.7	5.0	10
l_1	0.534	0.067	9	0.461	0.023	10
z_2	7.789	0.308	9	0.866	0.027	10
t_2	292.5	2.9	9	331.2	6.4	10
l_2	0.542	0.043	9	0.66	0.051	10

Note: z = zenith, i.e., peak value reached (e.g., mm/day), t = time when peak value is reached (days from previous winter solstice), and l = length of the cycle, i.e., proportion of the 365-day period when the predicted values are >0. Subscript index = season 1 or 2 of the year.

DETAILS OF THE SHIFTS IN TIMING AND
DEVIATIONS IN PEAK VALUES OF THE
SEASONAL CYCLES

If the individuals of the most abundant species
B. smithi, are excluded from the data, none of the
shifts or deviations in environmental variables
correlate significantly with deviations in peak
values of abundance peaks (Abuz_i), and the only
environmental variable correlating significantly
with shifts in timing of abundance peaks (Abut_i)
is the shift in timing of EVI peaks in the previous
half-year cycle (EVI t_{i-1}; Pearson's correlation $\rho =$
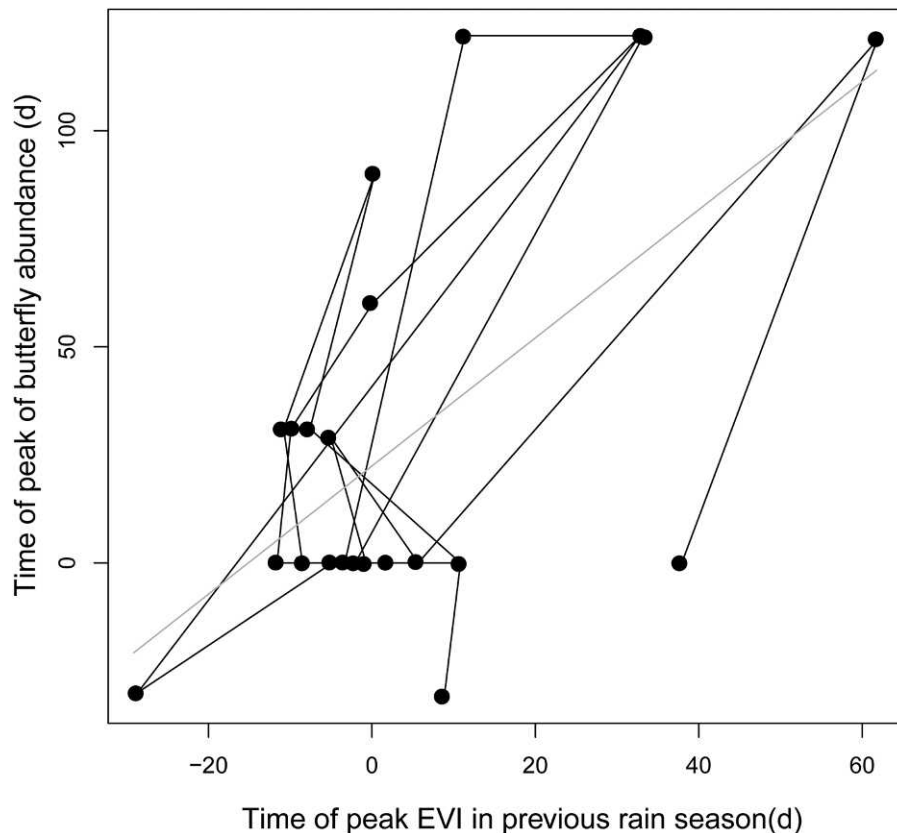0.49, p = 0.019).

Fig. E1. The shifts in timing of butterfly peak abundance (of each half-year cycle) plotted against the shifts in timing of the EVI peak (at previous half-year cycle). The trajectory connects the successive data points over time (indicating no serial auto-correlation) and the grey line shows the predicted values of the most parsimonious model (y = 22.4 + 1.5 × EVIt_{i-1}).

Table E1. Pearson correlation coefficients between deviations in height (zenith; z) and shifts in timing (t) of abundance (A), species richness (Sp), Simpson's D (Si), precipitation (P), EVI (E), and start of rainy season (RS) at same half year cycle (i) and the previous half-year cycle ($i-1$). N = 23.

Variable	Az_i	At_i	Spz_i	Spt_i	Siz_i	Sit_i	Pz_i	Pz_{i-1}	Pt_i	Pt_{i-1}	Ez_i	Ez_{i-1}	Et_i	Et_{i-1}
At_i	0.0													
Spz_i	0.1	−0.0												
Spt_i	−0.3	−0.4*	−0.2											
Siz_i	−0.1	0.1	−0.8**	0.1										
Sit_i	−0.3	−0.0	−0.4	0.4*	0.3									
Pz_i	0.3	0.4	0.0	−0.1	−0.1	−0.0								
Pz_{i-1}	0.3	0.1	0.3	−0.2	−0.2	0.0	−0.1							
Pt_i	0.2	−0.0	0.4*	−0.3	−0.2	−0.6**	0.0	0.4*						
Pt_{i-1}	−0.2	0.0	−0.0	−0.1	0.0	0.2	−0.2	−0.0	−0.2					
Ez_i	−0.0	0.3	−0.1	0.1	−0.1	0.3	0.3	−0.2	−0.3	0.2				
Ez_{i-1}	0.1	0.1	0.2	−0.3	−0.1	−0.2	0.3	0.3	0.3	−0.3	−0.3			
Et_i	−0.1	−0.1	−0.2	0.3	−0.1	0.0	−0.0	0.3	0.2	0.0	0.1	−0.1		
Et_{i-1}	−0.1	0.6**	−0.2	−0.4	0.0	−0.2	0.2	−0.1	0.2	0.1	0.5*	−0.1	0.2	
RS_i	−0.1	0.1	−0.0	0.0	0.2	−0.6**	0.1	−0.1	0.6**	−0.2	−0.2	0.2	0.3	0.2

Notes: A single asterisk indicates that the correlation is significant at the 0.05 level (two-tailed); two asterisks indicate that the correlation is significant at the 0.01 level (two-tailed). Correlation matrix was calculated with SPSS (IBM SPSS Statistics, Version 19).

Table E2. The highest ranked linear regression models according to information theoretic approach (Burnham and Anderson 2002) describing the deviations in height (z) and shifts in timing (t) of abundance (Abu), species richness (Spe) and Simpson's D (Sim). Models are ranked based on their corrected Akaike Information Criterion (AICc) value and only models with substantial empirical evidence (ΔAICc < 2) are shown. In all cases N = 23.

Variable	Model	K	AICc	ΔAICc	L	w_i	adj R^2
Abu$z$	$y = 3.3$	2	161.0	0.0	1.0	0.07	
	$y = 2.3 + 1.2 \times Precipz_i$	3	161.4	0.3	0.8	0.06	0.05
	$y = 2.1 + 1.2 \times Precipz_{i-1}$	3	161.6	0.6	0.7	0.05	0.04
	$y = 0.9 + 1.3 \times Precipz_i + 1.3 \times Precipz_{i-1}$	4	161.6	0.6	0.7	0.05	0.12
	$y = 3.1 + 0.1 \times Precipt_i$	3	162.9	1.9	0.4	0.03	0.00
Abu$t$	$y = 22.4 + 1.5 \times EVIt_{i-1}$	3	242.0	0.0	1.0	0.11	0.31
	$y = 17.3 + 6.7 \times Precipz_i + 1.4 \times EVIt_{i-1}$	4	242.6	0.6	0.7	0.08	0.35
	$y = 23.5 − 0.6 \times EVIt_i + 1.6 \times EVIt_{i-1}$	4	243.3	1.3	0.5	0.06	0.33
	$y = 17.6 + 4.7 \times Precipz_{i-1} + 1.5 \times EVIt_{i-1}$	4	243.9	1.9	0.4	0.04	0.31
Spe$z$	$y = 1.7 + 0.1 \times Precipt_i$	3	119.6	0.0	1.0	0.09	0.14
	$y = 1.8 + 0.1 \times Precipt_i − 0.05 \times EVIt_i$	4	120.0	0.4	0.8	0.07	0.19
	$y = 1.9 + 0.1 \times Precipt_i − 0.04 \times EVIt_{i-1}$	4	120.3	0.7	0.7	0.06	0.18
	$y = 1.9$	2	121.4	1.8	0.4	0.04	
Spe$t$	$y = 33.0 + 228.3 \times EVIz_i + 1.1 \times EVIt_i − 1.7 \times EVIt_{i-1}$	5	253.1	0.0	1.0	0.05	0.27
	$y = 42.3 + 1.0 \times EVIt_i − 178.2 \times EVIz_{i-1} − 1.3 \times EVIt_{i-1}$	5	253.4	0.2	0.9	0.05	0.26
	$y = 48.1 + 1.4 \times EVIt_i − 10.5 \times Precipz_{i-1} − 1.4 \times EVIt_{i-1}$	5	253.5	0.4	0.8	0.04	0.26
	$y = 44.6 − 195.6 \times EVIz_{i-1} − 1.1 \times EVIt_{i-1}$	4	253.5	0.4	0.8	0.04	0.18
	$y = 37.9 + 1.1 \times EVIt_i − 1.3 \times EVIt_{i-1}$	4	253.5	0.4	0.8	0.04	0.18
	$y = 35.0 + 228.1 \times EVIz_i − 1.5 \times EVIt_{i-1}$	4	254.0	0.9	0.6	0.03	0.17
	$y = 39.9 − 1.0 \times EVIt_{i-1}$	3	254.2	1.0	0.6	0.03	0.09
	$y = 42.1 + 192.9 \times EVIz_i + 1.4 \times EVIt_i − 8.7 \times Precipz_{i-1} − 1.8 \times EVIt_{i-1}$	6	254.3	1.2	0.6	0.03	0.31
	$y = 37.4 + 183.3 \times EVIz_i + 1.0 \times EVIt_i − 139.9 \times EVIz_{i-1} − 1.7 \times EVIt_{i-1}$	6	254.6	1.4	0.5	0.03	0.30
	$y = 34.4$	2	254.7	1.6	0.4	0.02	
	$y = 38.3 − 181.4 \times EVIz_{i-1}$	3	254.7	1.6	0.4	0.02	0.07
	$y = 39.9 + 176.9 \times EVIz_i − 159.0 \times EVIz_{i-1} − 1.5 \times EVIt_{i-1}$	5	254.8	1.7	0.4	0.02	0.21
	$y = 39.4 − 0.6 \times Precipt_i + 1.2 \times EVIt_i − 1.2 \times EVIt_{i-1}$	5	255.0	1.9	0.4	0.02	0.21
	$y = 49.1 + 1.3 \times EVIt_i − 8.1 \times Precipz_{i-1} − 138.6 \times EVIz_{i-1} − 1.4 \times EVIt_{i-1}$	6	255.1	1.9	0.4	0.02	0.29
Sim$z$	$y = 0.05$	2	−69.4	0.0	1.0	0.14	
	$y = 0.04 + 0.01 \times Precipz_{i-1}$	3	−68.1	1.3	0.5	0.07	0.01
Sim$t$	$y = 37.1 − 2.3 \times Precipt_i + 13.3 \times Precipz_{i-1}$	4	247.6	0.0	1.0	0.24	0.46

Note: K = number of estimated parameters, ΔAICc = difference in AICc between this model and the best model in the set, L = likelihood of the model, given the data, and w_i = model probability, i.e., "Akaike weight".

Table E3. Relative importance (w_+; Burnham and Anderson 2002) of each environmental variable in explaining the shifts in timing (t) and deviations in height (z) of abundance (Abu), species richness (Spe) and Simpson's D (Sim). The relative importance is calculated by summing the Akaike weights across all models in the set where the variable occurs. Larger values indicate that the variable is more important, relative to the other variables.

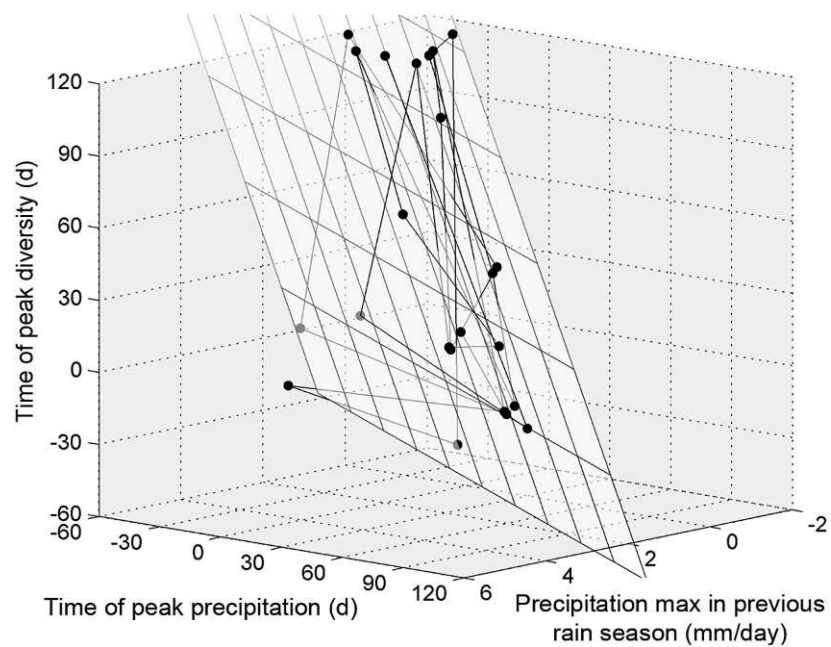| Variable	Abu$z$	Abu$t$	Spe$z$	Spe$t$	Sim$z$	Sim$t$
Precipz_i	0.43	0.38	0.16	0.16	0.18	0.15
Precipz_{i-1}	0.41	0.34	0.25	0.26	0.28	0.70
Precipt_i	0.21	0.24	0.69	0.21	0.21	0.99
Precipt_{i-1}	0.19	0.15	0.16	0.16	0.17	0.15
EVIz_i	0.17	0.15	0.20	0.34	0.19	0.20
EVIz_{i-1}	0.18	0.17	0.17	0.39	0.19	0.15
EVIt_i	0.24	0.35	0.38	0.54	0.19	0.16
EVIt_{i-1}	0.19	0.97	0.32	0.74	0.18	0.18

Fig. E2. The shifts in timing of butterfly peak diversity (of each half-year cycle) plotted against the shifts in timing of the precipitation peak (at the same half-year cycle) and deviations in height of the precipitation peaks (at the previous half-year cycle). The trajectory connects the successive data points over time (indicating no serial auto-correlation) and the surface shows the predicted values of the most parsimonious model ($y = 37.1 - 2.3 \times$ Precip$t_i + 13.3 \times$ Precipz_{i-1}). Figure generated with MATLAB (R2011b, The MathWorks Inc. Natick, MA).
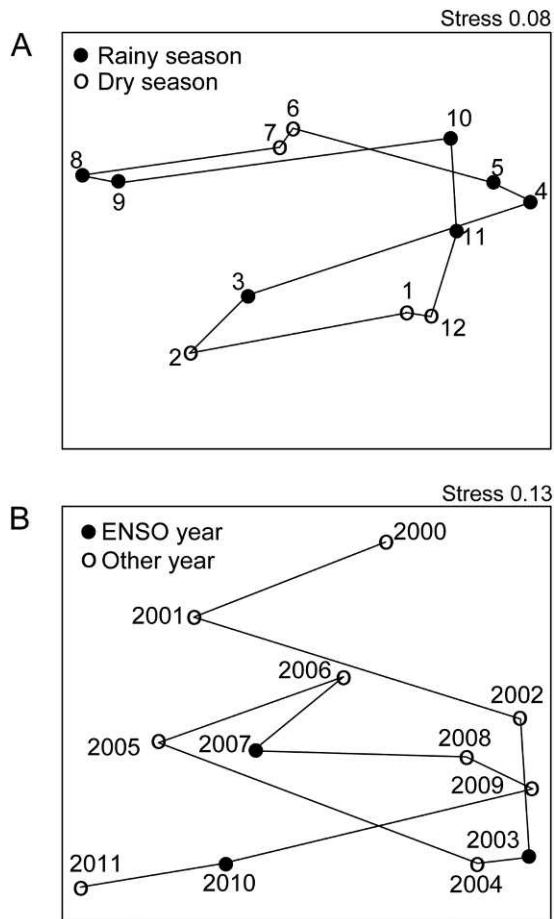
Appendix F

Non-metric Dimensional Scaling Graphs of Assemblage Change

Fig. F1. Differences in fruit-feeding butterfly assemblages among (A) months and (B) years. The plots represent the non-metric dimensional scaling (MDS) ordinations using Bray-Curtis similarity matrix of samples representing centroids of years or months, respectively. The trajectory connects the successive data points. The low stress values indicate that the ordinations are nearly perfect representations of the centroids of high-dimensional assemblage structures.
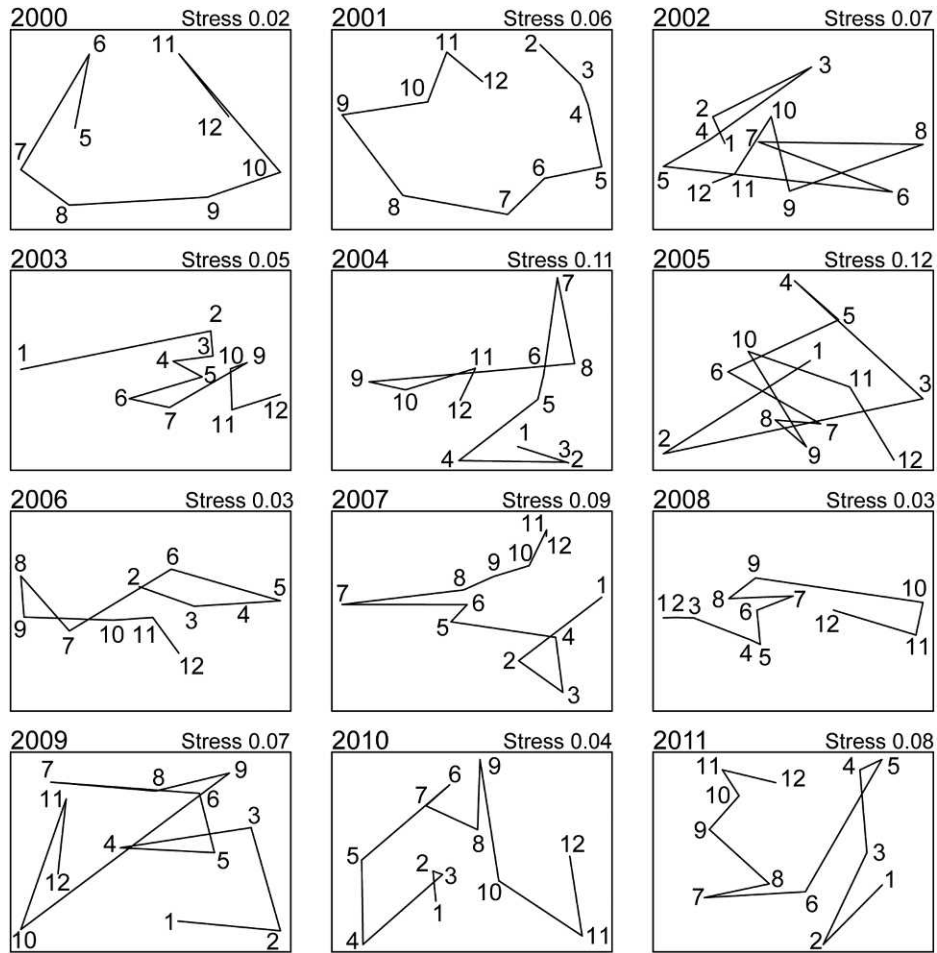
Fig. F2. Differences in fruit-feeding butterfly assemblages among the studied months within each studied year (2000-2011). The plots represent the non-metric dimensional scaling (MDS) ordination using Bray-Curtis similarity matrix of samples representing centroids of months. The trajectories connect the successive data points. The low stress values indicate that the ordinations are nearly perfect representations of the centroids of high-dimensional assemblage structures.