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Forest eternal?
Endemic butterflies of the Bamenda Highlands,
Cameroon, avoid close-canopy forest

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Annotation
I studied habitat preferences of three common endemic butterflies in the Bamenda Highlands, Cameroon. Assuming that the life history traits of taxa with limited geographic distribution reflect past habitat conditions within their ranges, the history and conservation of West African mountain landscape is discussed.

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Abstract

The Gulf of Guinea Highlands, a centre of endemism and tremendous conservation importance, represent the only large mountain system in West and Central Africa. I studied the habitat preferences of three common endemic butterflies in the mosaic landscape of the Bamenda Highlands, Cameroon. All of them avoid close-canopy forests and bracken growths. *Colias electo manengoubensis* prefers grassland, *Bicyclus anisops* and *Mylothris jacksoni knutsoni* prefer scrub formations and forest edges. More detailed analyses accounting for the structure of surrounding habitats indicated that all three butterflies require heterogeneous landscape mosaics. Assuming that the life history traits of taxa with limited geographic distribution reflect past habitat conditions within their ranges, the preferences of the endemic butterflies indicate continuous existence of mosaic of forest and non-forest habitats, including sparse stands and grasslands within the West African mountains. Such a landscape was likely maintained by climatic fluctuation and large herbivores, later supplemented by human impact. This conclusion is consistent with the palaeoenvironmental record and with the requirements of endemics from other groups. Recent conservation activities tend to focus on patches of continuous forests, but the mosaic landscapes are no less threatened by such activities as uniform forest plantations, and should be included to protected areas.

Introduction

The chain of volcanic mountains on the borders of Cameroon and Nigeria known as Gulf of Guinea Highlands, with the highest peak of Mt. Cameroon (4095 m asl), is the only large mountain area in West and Central equatorial Africa. These mountains are isolated from the mountains of East Africa by a band of tropical lowland forests over 1500 kilometres wide (Marzoli *et al.* 2000, Graham *et al.* 2004, Fattorini 2007). Due to its unique mountain climate and history, this region is a hotspot of biodiversity and endemism on a continental scale for a wide variety of taxa (Fishpool & Evans 2001, De Klerk *et al.* 2002, Sedlacek *et al.* 2007). Simultaneously, the region supports some of the highest human population densities in tropical Africa, which renders it one of the most threatened afrotropical areas (Stuart 1986, Fjeldsa *et al.* 2004, Bergl *et al.* 2007).

Although the tremendous biodiversity and conservation importance of the Gulf of Guinea Highlands is universally acknowledged, a majority of both research and conservation efforts focuses almost solely on one particular habitat, mountain forests. The rationale behind this is the widely accepted view that closed-canopy forests comprise the primary land cover in the moist submontane landscape of West Africa (e.g. Stuart 1986, Bergl *et al.* 2007, Burgess *et al.* 2007). This view holds that only two types of non-forest habitats would be "natural" in the region: the mosaic of shrubs, afro-alpine meadows and lava flows at the summit of Mt. Cameroon, kept treeless by high-elevation climate and volcanic activity, and the marshy bottoms of volcanic craters on other peaks (Proctor *et al.* 2007). As a result, the majority of larger protected areas, including proposed ones, consist of large forest remnants (Fjeldsa *et al.* 2004; Bergl *et al.* 2007).

This assumption of pristine deep forest covering, almost eternally the West African mountains, conflicts with the palaeoenvironmental evidence of climatic instability and forests declines during glacial cycles (e.g. Stager & Anfang-Sutter 1999, Maley 2001). Further factors, possibly the opening up of the close-canopy forests, and operating even under climates suitable for forest growth, include rare "catastrophic" disturbance (e.g. hurricanes, wildfires) and "bulldozer" megaherbivores (e.g. forest elephants, buffaloes; Kortlandt 1984), now largely extinct in the area (Maisels *et al.* 2001), but supplemented and substituted by human impact (Cornelissen 2002).

Life traits of organisms (especially habitat requirements) closely reflect the specific histories of their ranges. This applies particularly strongly for taxa with limited geographic

distribution that had presumably evolved to persist in narrow areas of distribution. Therefore, life history traits and habitat requirements of endemic organisms may provide useful instruments for inference about the history of any specific locality. This applies especially to insular biotas, including high mountains, because island endemics cannot escape unfavourable conditions by emigration (Bruhl 1997, MacArthur & Wilson 2001, Kuras *et al.* 2003, Fattorini 2007).

Butterflies (Lepidoptera: Rhopalocera) are among the best known insect groups in tropical West Africa in terms of taxonomy and biogeography (Larsen 2005). As an intensively studied model taxon, they offer the advantage of a relatively good knowledge of life histories and distributions, plus well-developed field methods (Watt & Boggs 2003). Despite this potential, the habitat preferences of no endemic butterfly species have ever been studied in detail in the West African mountains.

This study explores the adult habitat preferences of three common endemic butterflies in the Gulf of Guinea Highlands, comparing them with other endemic groups, and interprets the findings via the historical climatic instability of the area. I argue that these endemic species require mosaics of close-canopy forests and more open conditions, and that conservationists should, besides focusing on Gulf of Guinea mountain forests, also consider more open mountain habitats, such as scrub and grasslands.

Methods

The butterfly nomenclature follows Larsen (2005), plant names follow Cheek *et al.* (2000).
Study area – The study was carried out in the Mendong Buo area (6°5´26´´N, 10°18´9´´E; 2100-2200 m asl), ca 5 km south-east from the Big Babanki (the Kedjom-Keku community), Bamenda Highlands, North-West Province, Cameroon. I worked within an area of about 1 km^2, comprising a mosaic of mountain forest remnants, forest clearings dominated by *Pteridium aquilinum*, submontane grasslands maintained by erratic grazing, species-rich scrub and scrubby vegetation along streams. The forest was represented by two medium-sized patches (ca. 20 ha together) and several small fragments (0.1-1 ha) connected by shrubby corridors. In this area, there is a single wet season from March/April to mid-November, the precipitation varies from 1780 to 2290 mm/year (Cheek *et al.* 2000, Reif *et al.* 2007).

Study species – I studied three endemic submountain butterflies: *Bicyclus anisops* (Karsch, 1892) (Nymphalidae: Satyrinae), *Colias electo manengoubensis* Darge, 1968 (Pieridae: Coliadinae), and *Mylothris jacksoni knutsoni* Aurivillius, 1891 (Pieridae: Pierinae). These three taxa are easily distinguished in the field, share distribution restricted to altitudes above 1200 m (Larsen, 2005), and their global ranges are restricted to the mountains on the Cameroon-Nigeria borders. The closest relatives of *Bicyclus anisops* (*B. dentatus* Sharpe 1898) and other subspecies of *Colias electo* occur in Eastern Africa; another subspecies of *Mylothris jacksoni* occurs in the Kivu area (Monteiro & Pierce 2001, Larsen 2005). Their larval host plants are *Poaceae* (*B. anisops*), *Fabaceae* (*C. e. manengoubensis*) and *Loranthaceae* (*M. j. knutsoni*).

Study design and data sampling – Four habitats were considered: (i) submontane grasslands formed by erratic grazing dominated by *Poaceae* (especially *Sporobolus africanus* and *Pennisetum clandestinum*) and *Crassulariaceae* (herein *grassland*); (ii) *Pteridium aquilinum* dominated plots (herein *bracken*); (iii) montane forests, mainly formed by *Schefflera abysinica*, *S. manii*, *Bersama abyssinica*, *Syzygium staudtii*, *Carapa grandiflora* and *Ixora foliosa* (herein *forest*); (iv) forest edges and stream-side scrub with *Gnidia glauca* and numerous *Labiatae* and *Compositae*, sparse canopy and no large trees (herein *scrub*).

Three plots (0.2 ha each) of each habitat type (i.e. 12 in total) were sampled. Besides geographical coordinates and altitude, each plot was characterised by the following set of environmental variables: (i) *exposition*, expressed on an ordinal 1-4 scale, 4 being the highest intake of sun, i.e., SW + S, 3: SE + W; 2: NW + E; 1: N + NE; no slope – the average values – 2.5; (ii) *slope*, expressed in degrees; (iii) *cover of individual vegetation strata* (E_1: <1m, E_2: 1-5m, E_3: 5-10m, E_4: >10m), expressed as percentage cover of plot area; (iv) *number of the vegetation strata*, (v) *cover of main vegetation components* (grass; *Pteridium*; herbs <0.2m; herbs 0.2-1m; herbs >1m; shrubs <2m; shrubs >2m; trees <10m; trees >10m,), expressed as percentage cover of plot area; (vi) *cover of rocks and exposed soil gaps*, again expressed as percentage cover of plot area; (vii) *bordering habitats*, expressed as percentage of borders with plot area.

The butterflies were counted 6 times from December 2007 to January 2008 (10, 16, 22 and 27 December, 2 and 8 January). I used a time-standardised search, during which I zigzagged entire plots for total of 15 minutes. Compared to linear transect, this time-

standardised counts allowed for thorough searching of hardly accessible vegetation (forest, scrub) and also allowed adjusting the search towards structures with temporarily high concentrations of butterflies, mainly flower patches (cf. Kadlec *et al.* 2008). To minimise repeated counting of the same individuals, butterflies were recorded in a 5 m radius in front of researcher.

The recording was limited to 10:00 h – 15:30 h, when the butterflies' activity was the most intensive, and to suitable weather (at least half a day with no clouds). During each visit, the closest hour, cloudiness, wind strength, actually flowering plant species richness (1, 1-5 genera; 2, 5-10; 3, 10-20; 4, more than 20 genera) and nectar supply (from 1 - less than 5% of the entire plot cover; to 4 - the most plot covered by flowers) were recorded. Sequences of the visits were randomised among day times, habitats, and plots.

Statistical analysis - I used multivariate (ordination) analyses, which allow simultaneous analysing of several response variables. CANOCO for Windows 4.5 was used for computations (ter Braak & Smilauer 2002). I used the redundancy analysis (RDA), a constrained ordination method that assumes linear responses of predictors, and tested for significance of the ordinations using the Monte Carlo permutation tests (999 runs under full model). I used split-plot permutation design for repeated sampling, handling subsequent visits to plots as time series. In all analyses, I used square-root transformed species data and centering by species. Empty rows in the data matrix (zero observations per plot visit) would preclude the use of the split-plot design, therefore I added a small value (0.0001) to each data matrix cell.

We first checked for effects of possible confounding covariables describing geographic position (altitude, longitude and latitude of sites, including polynomials and multiplicative interactions), weather conditions, and predictors describing nectar availability. As none of the covariables exhibited a significant effect on any of the species, I ignored them afterwards.

Next, I tested for separate effects of HABITAT (forest, grassland, bracken and scrub), STRATA (their coverage and number), HAB_STRUCTURE (cover of vegetation components, rocks and soil gaps), SLOPE (slope and exposition) and SUR_HABITATS (percentage of bordering habitats).We then considered all these structural predictors in one model, and used the CANOCO forward selection procedure to select a subset of predictors explaining the highest percentage of variation (*forward selection*, $p < 0.05$).

Results

In total I obtained 171 observations of *B. anisops*, 1493 *C. e. manengoubensis* and 154 *M. j. knutsoni* from the study plot visits. All three study species were by far the most abundant butterflies in the study area during the study period, together with the non-endemic and widespread *Acraea serena* Fabricius, 1775, *Issoria baumanni excelsior* Botler, 1895 (both Nymphalidae), *Mylothris chloris chloris* Fabricius, 1775 (Pieridae), and a few species of Lycaenidae.

The RDA checking for effects of potential covariates (geographic position, weather, nectar availability), revealed that none displayed a significant effect in the distribution of records, nor did slope nor exposition.

model[a]	% of variation[c]			1st axis		all axes	
	1st	2nd	all	F	P[c]	F	P[d]
all three species							
~ HABITAT	80.5	10.4	91.0	279.86	**	227.84	**
~ VEG_STRATA	78.0	10.9	89.3	234.08	**	110.71	**
~ HAB_STRUCTURE	81.6	11.2	93.3	269.68	**	85.17	**
~ SUR_HABITATS	49.5	4.9	54.5	66.58	*	27.17	*
~ SLOPE	10.4	0.2	10.6	7.97	n.s.	4.07	n.s.
~ FW_SELECTED[b]	81.6	11.3	93.5	265.40	**	78.06	**
B. anisops only							
~ HABITAT	71.9	28.1	71.9	174.12	**	58.04	**
C. e. manengoubensis only							
~ HABITAT	95.1	4.9	95.1	1316.81	**	438.97	**
M. j. knutsoni only							
~ HABITAT	68.4	31.6	68.4	147.02	**	49.01	**

Table I. Results of RDA analyses exploring the habitat needs of three the Gulf of Guinea Highlands endemic butterflies.
[a]Model terms following ~ are explanatory variables, those following | are covariables. See "Methods" for description of variables.
[b]Model obtained via a forward selection from all variables representing structural predictors.
[c]Percentage variation in species data accounted for by first, second and all ordination axes, respectively.
[d]P-level assessed via Monte-Carlo permutation tests: n.s. $P > 0.05$; *$P < 0.05$; **$P < 0.001$. Note that 0.001 is the lowest p-level which a 999 permutation test can obtain.
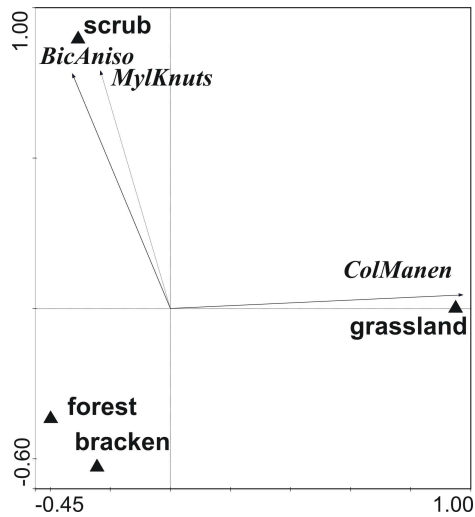
Figure 1. Habitat affinities (RDA diagram) of three endemic butterflies in the Mendong Buo area. See "Methods" for description of habitats. Species abbreviations are created from the first three letters of genus and the first five letters of (sub)species names.

Figure 2. RDA ordination diagrams revealing the affinities of three endemic butterflies to the individual structural predictors: A) relative coverage of vegetation strata and their number; B) coverage of vegetation components, rocks and soil gaps; C) percentage of bordering habitats; D) obtained via a forward selection from all forenamed predictors. See "Methods" for description of habitats. Species abbreviations are created from the first three letters of genus and the first five letters of (sub)species names.

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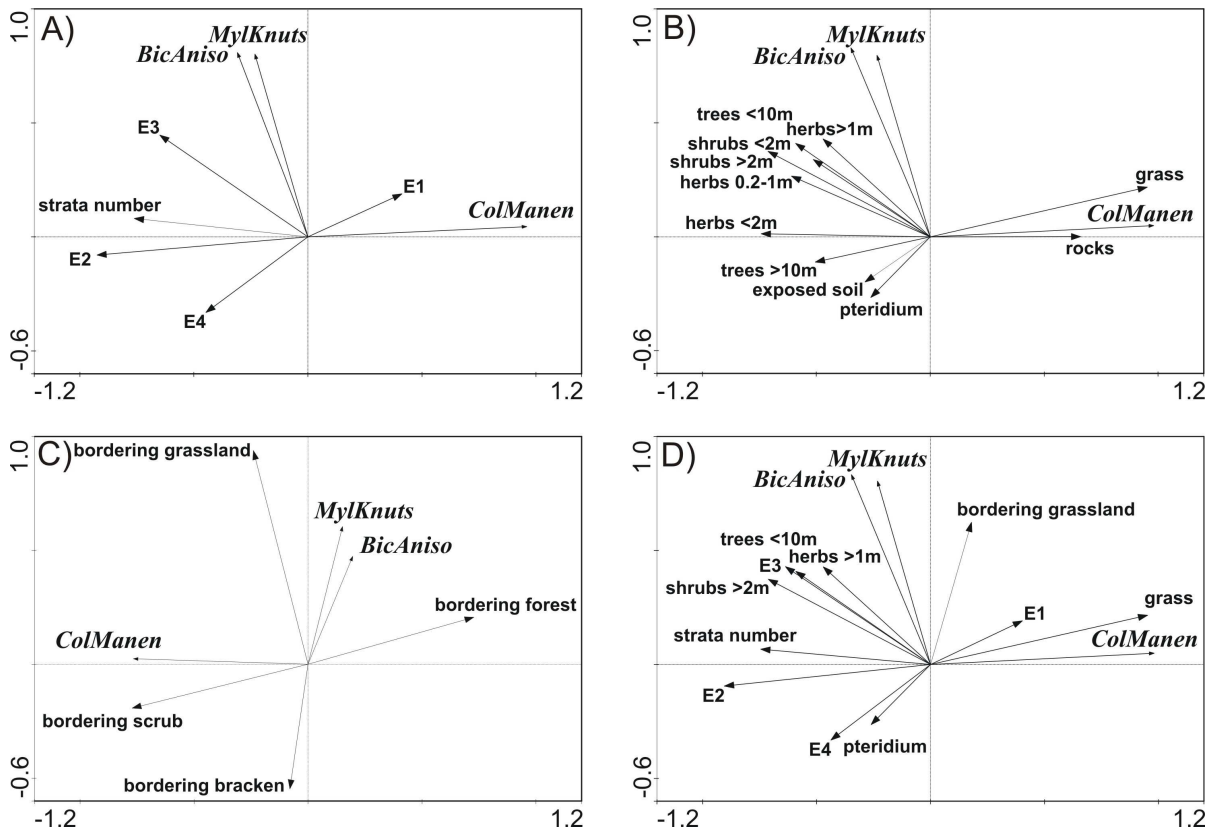Subsequent analyses (Tab. I) revealed that all three studied taxa avoid *forest* and *bracken* habitats. *C. e. manengoubensis* preferred *grassland*, the others were associated with *scrub* (Fig. 1). The general pattern was retained in analyses with the structural predictors (Fig. 2a-b): *C. e. manengoubensis* was associated with a high cover of grass and rocks and with the lowest (E_1) vegetation stratum, whereas *M. j. knutsoni* and *B. anisops* were associated with taller vegetation (0.2 – 10 m). All three species avoided tall trees and bracken. A different pattern emerged for the bordering habitats (Fig. 2c). None of the species preferred a high percentage of its preferred habitat surrounding the plot, such as surrounding grassland for *C. e. manengoubensis*. Instead, *C. e. manengoubensis* preferred a high percentage of bordering scrub, whereas *B. anisops* and *M. j. knutsoni* preferred high percentages of bordering grassland and close-canopy forest.

The forward selection of explanatory variables (Fig. 2d) pointed to the structural predictors appearing as crucial for the butterflies' habitat selection. These were grassland structures for *C. e. manengoubensis*, tall herbs, shrubs and low trees for *B. anisops* and *M. j. knutsoni*, and absence of bracken and the highest vegetation stratum with tall trees for all three species.

Discussion

Three locally abundant endemic butterflies of the West African Gulf of Guinea Highlands avoid close-canopy forests, preferring instead grassland (*Colias electo manengoubensis*) and scrub and forest edges (*Bicyclus anisops* and *Mylothris jacksoni knutsoni*). Because the butterflies are narrowly endemic to the area, it follows that open habitats, akin to present-day grassland and scrub, had to be present in the area in times when these three butterflies have evolved. In addition, all three species preferred varying structures in close vicinity of the rather uniform study plots. The grassland-inhabiting *C. e. manegoubensis* preferred vicinity of scrub, whereas the two species of scrubby formations, *B. anisops* and *M. j. knutsoni*, preferred a vicinity of both grassland and close-canopy forest. This suggests that the landscape where the butterflies have evolved was of a heterogeneous nature, containing all these structures in an interwoven patchwork.

Our results are restricted to just three species and I do not imply that they reflect the preferences of the entire diversity of the Gulf of Guinea Highlands endemics. Although I

observed several other endemic butterflies in the area during the study period (Appendix 1), they were so uncommon that I did not encounter them during the quantitative surveys. Regardless, the existence of even a single species avoiding close-canopy forests requires interpretation, as it contradicts the notion that the highlands would be fully forested in the absence of human influence. Despite being time- and season-limited, the study was balanced, indicated by the lacking effects of potentially confounding geography, time of day and weather covariables.

The preference for mosaics of habitats implies requirements for diverse resources. Species resources may not occur syntopically; for instance, adult and larval resources often differ in butterflies (e.g., Dennis *et al*. 2003, Hardy *et al*. 2007; Vanreusel & Van Dyck 2007). A species' habitat is then located at the intersection of such resources as larval host plant, nectar and shelter, this being responsible for the occurrence of many species in finely-grained biotope mosaics. The few existing information on habitats of West African highlands endemics further corroborates the importance of a mosaic of dense forest and more open habitats. Larsen (2005) enumerates 36 butterflies endemic for the area (Appendix 1), but mentions affiliation with dense forest for only six taxa, whereas forest edges and scrub are mentioned for 10, and non-forest habitats for six taxa. No information is supplied for a further 14 taxa, but even if I tentatively place these species with unknown requirements to dense forests, the ratio of close forest : more open habitats taxa becomes 20 : 16, far from a dominance of close woodlands. Out of eleven species of endemic mammals, five are affiliated with mountain forest, while six species are mountain savannah restricted (Hutterer & Joger 1982). Cheek *et al*. (2000) notes that close-canopy forests are avoided by many endemic plants. Birds represent by far the best-studied group, but a majority of surveys conducted so far has focused on continuous forests (e.g. Stuart & Jensen, 1986, Fotso 2001). The only exception is Reif *et al*. (2007), reporting, from a site identical with the present study, several endemic birds inhabiting the mosaics of non-forest habitats. The authors attributed this to "a high habitat flexibility" of the birds, suggesting that these species would normally occur in dense forests, but have adapted to exploit the relatively recent fragmentation. This pattern, however, can be equally well interpreted as a preference for the open habitat mosaics. In contrast to birds, butterflies (and other insects) are notoriously slow to adapt to environmental change (Thomas *et al*. 2004) and it is highly unlikely that they would change their habitat preference following the relatively recent forest clearance.

At present, the majority of the Gulf of Guinea Highlands is covered by habitat mosaics containing afromontane forest, significantly altered areas (such as plantations) and a variety of habitats between these two extremes (Cheek *et al*. 2001, Larsen 2005, Reif *et al*. 2007). In spite of the widespread notion, palaeoenvironmental results imply that the afromontane landscape would appear rather similar for most of the Holocene. Stager & Anfang-Sutter (1999) studied the Lake Bambili (2264 m asl) sediments and concluded that moist periods alternated with prolonged arid periods for at least 24,000 years, and this was supported by other sediment analyses (e.g. Zogning *et al*. 1997, Maley & Brenac 1998). Maley (2001) linked the arid phases with rapid forest withdrawals and expansions of open habitats. The association of heterogeneous mosaic-like landscapes with alternation of arid and moist periods is also known from East African mountains (Elenga *et al*. 2000).

Besides corroborating the palaeoenvironmental conclusions on the association of rather open habitat with arid periods, our results indicate that the afromontane landscapes had to contain some open-canopy stands, and even grasslands, even during the moist periods. An alternative explanation, stating that the endemic butterflies now depending on open habitats would survive at tiny treeless spots, is highly unlikely. In the moist periods, the timberline reached 3500 m asl (Flenley 1998), covering all summits except Mt. Cameroon. The whole Gulf of Guinea Highlands would be suitable for forest growths, with only very small treeless areas at sites such as rocky outcrops. If covered by dense forests, such landscape would hardly support viable butterfly populations for millennia, especially in the case of butterflies with large area requirements, such as those from genus *Colias* (cf. Watt *et al*. 1977; Ruetschi and Scholl 1985; Konvicka *et al*. 2008).

Our view that the landscape would consist of mosaics of dense forests, sparse stands and gaps is indirectly supported by studies of disturbance impacts on tropical forest diversity. The key role of forest elephants, which open up the canopy by trampling and debarking of trees, has been documented on butterflies (Bonnington *et al*. 2008) and plants (Hawthorne & Parren 2000). The impacts of selective logging, as an activity similar in outcome to elephant disturbance, remains questionable, because the results of studies are inconsistent (c.f. Koh 2007): recent studies demonstrate both enhancement (e.g Hamer *et al*. 1997, Willott *et al*. 2000) and decline (e.g. Hill *et al*. 1995, Ghazoul 2002) of butterfly diversity. Hamer *et al*. (2005) implied a seasonal dependence, Spitzer *et al*. (1993, 1997)

observed adverse effect on narrow-ranged butterflies, whereas Hamer *et al.* (2003) demonstrated that the effects on endemics varied between butterfly families.

Conclusions and implications for conservation

The existence of endemic butterfly taxa inhabiting the Gulf of Guinea Highlands and avoiding close-canopy forest can only be attributed to the continuous existence of mosaic-like landscape with close-canopy forests, sparse stands and grassland habitats, maintained by climatic fluctuations in the long term, and activity of catastrophic disturbance events and large herbivores such as elephants. After the latter went extinct (over 100 years ago for elephants and at least 30 years ago for forest buffalo in the area: Maisels *et al.* 2001), their actions were supplemented and replaced by human impact. Our claim agrees with the palaeoenvironmental evidence and with habitat preferences of multiple endemic species from other groups.

It follows that not only closed-canopy forests have a conservation value in West African highlands. Besides forests (which are priceless for specialised forest interior species), the heterogeneous mosaics of various land uses and succession stages, including small grasslands, deserve the attention of conservationists. It might seem that human activity maintains this heterogeneity via forest fragmentation, but at present there is an increasing tendency for uniform management over large areas. Probably the largest threat are newly established even-aged forest plantations, often of exotic trees, often established under the guise of protecting the environment. Further threats include crop plantations and intensive pastures, both highly vulnerable to alien plant invasions after abandonment (Cheek *et al.* 2000). One possibility to preserve the heterogeneous habitat mosaics could be the establishment of protected areas in managed landscapes. Such areas would not exclude human activity, but would, on the one hand, prevent the establishment of large and uniform pastures and plantation (including plantation forests); and on the other hand, control such destructive activities as logging of remaining forest fragments. This is unthinkable without close cooperation with local communities (for successful projects see e.g. Diaw *et al.* 1997, Thomas *et al.* 2000) and it could, albeit to a limited extent, reconcile conservation with other land uses (Horner-Devine *et al.* 2003, Sekercioglu *et al.* 2007) This of course does not rule out the necessity to conserve selected tracts of undisturbed habitats – but this strategy should be supported by better understanding of habitat needs of focal species.

References

BERGL, R. A., OATES, J. F. & FOTSO R. 2007. Distribution and protected area coverage of endemic taxa in West Africa's Biafran forests and highlands. *Biological Conservation* 134:195-208.

BONNINGTON, C., WEAVER, D. & FANNING, E. 2008. Some preliminary observations on the possible effect of elephant (*Loxodonta africana*) disturbance on butterfly assemblages of Kilombero Valley, Tanzania. *African Journal of Ecology* 46:113-116.

BRUHL, C. A. 1997. Flightless insects: A test case for historical relationships of African mountains. *Journal of Biogeography* 24:233-250.

BURGESS, N. D., LOUCKS, C., STOLTON, S. & DUDLEY, N. 2007. The potential of forest reserves for augmenting the protected area network in Africa. *Oryx* 41:151-159.

CHEEK, M., ONANA, J. M. & POLLARD, J. B. 2000. *The plants of Mount Oku and the Ijim Ridge, Cameroon. A conservation checklist.* Royal Botanic Gardens, Kew. 211 pp.

CORNELISSEN, E. 2002. Human responses to changing environments in Central Africa between 40,000 and 12,000 B.P. *Journal of World Prehistory* 16:197-235.

DE KLERK, H. M., FJELDSA, J., BLYTH, S. & BURGESS, N. D. 2004. Gaps in the protected area network for threatened Afrotropical birds. *Biological Conservation* 117:529-537.

DENNIS, R. L. H., SHREEVE, T. G. & VAN DYCK, H. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos* 102:417-426.

DIAW, M. C., ASSOUMOU, M. H. & DIKONGUE, E. 1997. *Community management of forest resources. conceptual developments and institutional change in the humid forest zone of Cameroon.* A working paper prepared for the launching workshop of EPHTA Humid Forest Margins Benchmark, Cameroun, Yaounde Hilton, May 26-28, 1997. 20 pp.

ELENGA, H., PEYRON, O., BONNEFILLE, R., JOLLY, D., CHEDDADI, R., GUIOT, J., ANDRIEU, V., BOTTEMA, S., BUCHET, G., DE BEAULIEU, J. L., HAMILTON, A. C., MALEY, J., MARCHANT, R., PEREZ-OBIOL, R., REILLE, M., RIOLLET, G., SCOTT, L., STRAKA, H., TAYLOR, D., VAN CAMPO, E., VINCENS, A.,

LAARIF, F. & JONSON, H. 2000. Pollen-based biome reconstruction for southern Europe and Africa 18,000 yr BP. *Journal of Biogeography* 27:621-634.

FATTORINI, S. 2007. Historical relationships of African mountains based on cladistic analysis of distributions and endemism of flightless insects. *African Entomology* 15:340-355.

FISHPOOL, L. D. C. & EVANS, M. I. 2001. *Important Bird Areas in Africa and Associated Islands: Priority Sites for Conservation.* Birdlife International, Cambridge. 1144 pp.

FJELDSA, J., BURGESS, N. D., BLYTH, S. & DE KLERK, H. M. 2004. Where are the major gaps in the reserve network for Africa's mammals? *Oryx* 38:17-25.

FOTSO, R. C. 2001. A contribution to the ornithology of Mount Oku Forest, Cameroon. *Malimbus* 23: 1-12.

FLENLEY, J. R. 1998. Tropical forests under the climates of the last 30,000 years. *Climatic Change* 39: 177-197.

GHAZOUL, J. 2002. Impact of logging on the richness and diversity of forest butterflies in a tropical dry forest in Thailand. *Biodiversity and Conservation* 11:521-541.

GRAHAM, C. H., SMITH, T. B. & LANGUY, M. 2004. Current and historical factors influencing patterns of species richness and turnover of birds in the Gulf of Guinea highlands. *Journal of Biogeography* 32:1371-1384.

HAMER, K. C., HILL, J. K., BENEDICK, S., MUSTAFFA, N., SHERRATT, T. N., MARYATI, M. & CHEY, V. K. 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. *Journal of Applied Ecology* 40:150-162.

HAMER, K. C., HILL, J. K., MUSTAFFA, N., BENEDICK, S., SHERRATT, T. N., CHEY, V. K. & MARYATI, M. 2005. Temporal variation in abundance and diversity of butterflies in Bornean rain forests: opposite impacts of logging recorded in different seasons. *Journal of Tropical Ecology* 21:417-425.

HAMER, K. C., HILL, J. K., LACE, L. A. & LANGAN, A. M. 1997. Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba, Indonesia. *Journal of Biogeography* 24:67-75.

HARDY, P. B., SPARKS, T. H., ISAAC, N. J. B. & DENNIS, R. L. H. 2007. Specialism for larval and adult consumer resources among British butterflies: Implications for conservation. *Biological Conservation* 138:440-452

HAWTHORNE, W. D. & PARREN, M. P. E. 2000. How important are forest elephants to the survival of woody plant species in Upper Guinean forests? *Journal of Tropical Ecology* 16:133-150.

HILL, J. K., HAMER, K. C., LACE, L. A. & BANHAM, W. M. T. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology* 32:754-760.

HORNER-DEVINE, M. C., DAILY, G. C., EHRLICH P. R. & BOGGS, C. L. 2003. Countryside biogeography of tropical butterflies. *Conservation Biology* 17:168-177.

HUTTERER, R. & JOGER, U. 1982. Small mammals of the Adamawa Plateau, Cameroon. *Bonner Zoologische Beitrage* 33:119-132.

KADLEC, T., BENES, J., JAROSIK, V. & KONVICKA, M. 2008. Revisiting urban refuges: changes of butterfly and burnet fauna in Prague reserves over three decades. *Landscape and Urban Planning* 85:1-11.

KOH, L. P. 2007. Impacts of land use change on South-east Asian forest butterflies: a review. *Journal of Applied Ecology* 44:703-713.

KONVICKA, M., BENES, J., CIZEK, O., KOPECEK, F., KONVICKA, O. & VITAZ, L. 2008. How too much care kills species: Grassland reserves, agri-environmental schemes and extinction of *Colias myrmidone* butterfly from its former stronghold *Journal of Insect Conservation* in press.

KORTLANDT, A. 1984. Vegetation research and the 'bulldozer' herbivores of tropical Africa. Pp. 205-226 in Chadwick, A. C. & Sutton, C. L. (eds.). *Tropical Rain-forest: The Leeds Symposium*. Spec. Publ. Leeds Phil. Lit. Society, Leeds. 335 pp.

KURAS, T., BENES, J., FRIC, Z. & KONVICKA, M. 2003. Dispersal patterns of endemic alpine butterflies with contrasting population structures: *Erebia epiphron* and *E. sudetica*. *Population Ecology* 45:115-123.

LARSEN, T. B., 2005. *Butterflies of West Africa*. Apollo Books, Stenstrup. 865 pp.

MACARTHUR, R. H. & WILSON, E. O. 2001. *The Theory of Island Biogeography*. Princeton University Press, Princeton. 203 pp.

MAISELS, F., KEMING, E., KEMEI, M. & TOH, C. 2001. The extirpation of large mammals and implications for montane forest conservation: the case of the Kilum-Ijim Forest, North-west Province, Cameroon. *Oryx* 35:322-331.

MALEY, J. 2001. The impact of arid phases on the African rain forest through geological history. pp. 68-87 in Weber, W., White, L., Vedder, A. & Naughton-Treves, L. (eds.). *African rain forest ecology and conservation. An interdisciplinary perspective.* 588 pp.

MALEY, J. & BRENAC, P. 1998. Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years BP. *Review of Palaeobotany and Palynology* 99: 157-187.

MARZOLI, A., PICCIRILLO, E. M., RENNE, P. R., BELLIENI, G., IACUMIN, M., NYOBE, J. B. & TONGWA, A. T. 2000. The Cameroon volcanic line revisited: petrogenesis of continental basaltic magmas from lithospheric and asthenospheric mantle sources. *Journal of Petrology* 41: 87-109.

MONTEIRO, A. F. & PIERCE, N. E. 2001. Phylogeny of *Bicyclus* (Lepidoptera; Nymphalidae) inferred from COI, COII, and EF-a gene sequences. *Molecular Phylogenetics and Evolution* 18:264-281.

PROCTOR, J., EDWARDS, I. D., PAYTON, R. W. & NAGY, L. 2007. Zonation of forest vegetation and soils of Mount Cameroon, West Africa. *Plant Ecology* 192:251-269.

REIF, J., SEDLACEK, O., HORAK, D., RIEGERT, J., PESATA, M., HRAZSKY, Z. & JANECEK, S. 2007. Habitat preferences of birds in a montane forest mosaic in the Bamenda Highlands, Cameroon. *Ostrich* 78:31-36.

RUETSCHI, J. & SCHOLL, A. 1985. Movement of individually marked *Colias palaeno europome* (Lepidoptera, Pieridae) in a habitat consisting of insularlike subsites. *Revue Suisse de Zoologie* 92:803-810.

SEDLACEK, O., REIF, J., HORAK, D., RIEGERT, J., PESATA, M. & KLVANA, P. 2007. The birds of a montane forest mosaic in Big Babanki area, Bamenda Highlands, Cameroon. *Malimbus* 29:89-100.

SEKERCIOGLU, C. H., LOARIE, S. R., BRENES, F. O., EHRLICH P. R. & DAILY, G. C. 2007. Persistence of forest birds in the Costa Rican agricultural countryside. *Conservation Biology* 21:482-494.

SPITZER, K., JAROS, J., HAVELKA, J. & LEPS, J. 1997. Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation* 80:9-15.

SPITZER, K., NOVOTNY, V., TONNER, M. & LEPS, J. 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *Journal of Biogeography* 20:109-121.

STAGER, J. C. & ANFANG-SUTTER, R. 1999. Preliminary evidence of environmental changes at Lake Bambili (Cameroon, West Africa) since 24,000 BP. *Journal of Paleolimnology* 22:319-330.

STUART, S. N. (ed.) 1986. *Conservation of Cameroon montane forests*. International Council for Bird Preservation, Cambridge. 263 pp.

STUART, S. N. & JENSEN, F. P. 1986. The status and ecology of montane forest bird species in Western Cameroon. Pp. 38-105 in Stuart, S. N. (ed.). *Conservation of Cameroon montane forests*. International Council for Bird Preservation, Cambridge. 263 pp.

TER BRAAK, C. J. F. & SMILAUER P. 2002. *CANOCO reference ranual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5)* Microcomputer Power, Ithaca, NY. 500 pp.

THOMAS, D. H. L., ANDERS, S. & PENN, N. J. 2000. Conservation in the community: the Kilum-Ijim Forest Project, Cameroon. *Ostrich* 71:157-161.

THOMAS, J. A., TELFER, M. G., ROY, D. B., PRESTON, C. D., GREENWOOD, J. J. D., ASHER, J., FOX, R., CLARKE, R. T. & LAWTON, J. H. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303:1879-1881.

VANREUSEL, W. & VAN DYCK, H. 2007. When functional habitat does not match vegetation types: A resource-based approach to map butterfly habitat. *Biological Conservation* 135:202-211

WATT, W. B. & BOGGS, C. V. 2003. Synthesis – Butterflies as model systems in ecology in evolution – Present and future. Pp. 603-613 in Boggs, C. L., Watt, W. B. & Ehrlich, P. R. (eds.). *Butterflies: Ecology and Evolution taking flight*. The University of Chicago press, Chicago. 739 pp.

WATT, W. B., CHEW, F. S., SNYDER, L. R. G., WATT, A. G. & ROTSCHILD, D. E. 1977. Population structure of pierid butterflies 1. Numbers and movements of some montane *Colias* species. *Oecologia* 27:1-22.

WILLOTT, S. J., LIM, D. C., COMPTON, S. G. & SUTTON, S. L. 2000. Effects of selective logging on the butterflies of a Bornean rainforest. *Conservation Biology* 14:1055-1065.

ZOGNING, A., GIRESSE, P., MALEY, J. & GADEL, F. 1997. The Late Holocene palaeoenvironment in the Lake Njupi area, west Cameroon: implications regarding the history of Lake Nyos. *Journal of African Earth Sciences* 24:285-300.

Appendix 1. Habitat preferences of the Gulf of Guinea Highlands endemic butterflies, as stated in Larsen (2005). N.A. – not available, i.e. the preferences not stated by the author. Taxa whose habitat preferences are analysed in this paper are marked by **. Those which were seen within the study area (Mendong Buo area, Bamenda Highlands, Cameroon) in December 2007 – January 2008, but not encountered during the quantitative surveys analysed here, are marked by *.

Papilionidae

Papilio c. charopus Westwood, 1843 — submontane forest

Papilio rex schulteri Auruvilius, 1904 — bare hills in forested areas

Pieridae

***Colias electo manengoubensis* Darge, 1968 — submontane grasslands

***Mylothris jacksoni knutsoni* Aurivilius, 1891 — forest edges

Mylothris yulei bansoana Talbot, 1944 — N.A.

Lycaenidae

Euchrysops banyo Libert, 2001 — N.A.

Euchrysops sagba Libert, 1993 — submontane grassland

Liptena priscilla Larsen, 1995 — submontane forest

**Uranothauma frederikkae* Libert, 1993 — submontane forest

**Uranothauma n. nubifer* Trimen, 1895 — N.A.

Uranothauma antinorii bamendanus Libert, 1993 — submontane forest

Riodinidae

Abisara cameroonensis Callaghan, 2004 — scrub along streams

Abisara neavei latifasciata Riley, 1932 — forest edges

Nymphalidae

Acraea alticola Schultze, 1923 — N.A.

**Acraea karschi* Aurivillius, 1898 — forest and open country

Acraea obliqua obliqua Aurivillius, 1913 — forest edges

Acraea oreas oboti Collins & Larsen, 2000 — N.A.

Acraea wigginsi occidentalis Bethune-Baker, 1926 — submontane grassland

**Amauris echeria occidentalis* Schmidt, 1921 — N.A.

**Antanaria dimorphica mortoni* Howarth, 1966 — forest edges and glades

Aphysoneura scapulifasciata occidentalis Joicey & Talbot, 1924 — N.A.

Bebearia subtentyris Strand, 1912 — N.A.

**Bicyclus anisops Karsch, 1892 — forest edges

Bicyclus saussurei camerunia Strand, 1914 — forest edges

Charaxes obudoensis van Somerer, 1969 — N.A.

Charaxes tectonis Jordan, 1937 — N.A.

Euphaedra imperialis hecqui Darge, 1975 — N.A.

Euriphene bernaudi Hecq, 1994 — submontane forest

Neptis ochracea milbraedi Gaede, 1915 — forest edges

Neptis occidentalis batesii Hall, 1930 — N.A.

Pseudacraea annakae Knoop, 1988 — N.A.

Pseudathyma legeri Larsen & Boorman, 1995 — N.A.

Ypthima albida occidentalis Bartel, 1905 — submontane grassland

Hesperiidae

Ceratrichia lewisi Collins & Larsen, 2000 — open habitats

Chondrolepis nero Evans, 1937 — forest edges

Metisella midas malda Evans, 1937 — submontane grassland