

Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana

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Abstract. Sacred forest groves in Ghana are centuries old protected areas that were once part of continuous forest cover but now mostly exist as relict forest patches embedded in an agropastoral landscape. We conducted a year-long survey of the fruit-feeding butterfly fauna of four sacred groves and two forest reserves in the moist semi-deciduous forest zone of Ghana to characterize resident species diversity and complementarity among communities. Joint analysis of frugivorous butterfly diversity at these six forest fragments, which ranged in size from 6 to 5000 ha, was used to evaluate the conservation potential of these ancient indigenous reserves. A total of 6836 individuals were trapped across all sites, representing 79 species and five subfamilies. Community diversity was characterized in terms of, (a) number of species accumulated versus sampling effort, (b) rarefied species richness, (c) nonparametric richness estimates, (d) species evenness, (e) Simpson's Index of Diversity, and (f) complementarity of communities. Diversity of the fruit-feeding butterfly communities, quantified in terms of both species evenness and rarefied species richness, was higher at the larger forest reserves than at the small sacred forest groves. Additionally, although all sites had species trapped only at that site, the 5000-ha forest reserve harbored a resident community that was clearly distinctive from and more diverse than the other communities including the other forest reserve. Hence, our findings add to the burgeoning body of data that indicates large reserves are the foundation of successful conservation programs. Nonetheless, we found these small forest patches contribute to biodiversity conservation in at least three ways and these are identified and discussed. We also identify a number of species that appear more or less vulnerable to dynamics of forest fragmentation based on changes in their relative abundance across sites and we interpret these data in the context of potential indicator species and theoretical predictions of at-risk species.

Introduction

The Upper Guinean forests of Ghana are recognized as among the most depleted and fragmented in the world and also among the most biologically unique (Hall and Swain 1981; Hawthorne 1988; Myers 1990; Whitmore 1997, 1998; FAO 1999; Goudie 2000; Myers et al. 2000). Estimates are that 80–90% of original high canopy forest in the country has been eliminated and nearly all

that not set aside as forest reserve is gone (Hawthorne 1988; Hawthorne and Abu-Juam 1995). Pervasive external pressures in the form of residential development, bush fires, illegal logging, mining, and consumption of forest products, threaten remaining forest tracts and some formal reserves are virtually devoid of trees as a result (Hawthorne and Abu-Juam 1995). The Afrotropics have, unfortunately, generally not inspired the same concerted research attention as their Neotropical and Indo-Malayan counterparts (Owen 1971; Andre et al. 1992; Wagner and Cobbinah 1993; Laurance 1997) and empirical data from the fragmented forests of West Africa are exceedingly rare. This hinders development and implementation of the science-based conservation efforts necessary to counter these threats.

Only about 1% of forest cover in Ghana remains outside gazetted reserves and sacred forest groves account for most of this. Sacred groves are areas of land that were set aside by indigenous peoples hundreds of years ago because of their cultural significance and strictly protected via religious sanctions and taboos (Lebbie and Freudenberger 1996; Ntiemoa-Baidu 2001; UNESCO 2003). The potential conservation value of Ghana's indigenous reserves is high. Although originally embedded within continuous forest cover, they were transformed into isolated habitat "islands" as the landscape matrix surrounding them was converted from one of pristine forest to an agropastoral "sea". Their long history of protection coupled with the dramatic and rapid transformation of the surrounding landscape may have allowed for local persistence of rare or patchily distributed forest-endemic species. In some regions of the country, sacred groves also represent the only remaining examples of old-growth forest vegetation. In this context, they count as nuclei to guide reforestation or ecosystem recovery efforts. In a landscape increasingly devoid of forested areas outside the existing protected areas network, Ghana's indigenous reserves likely also serve as vital stepping stones that help link resident communities of discrete forest reserves.

Despite their high potential conservation value, Ghana's sacred forests remain largely undocumented, unexplored, and underappreciated as refugia for forest biodiversity. The present study is a preliminary assessment of the extent to which these indigenous reserves may contribute to the preservation of the country's forest-endemic species. To this end, we conducted a comparative analysis of community structure at four sacred groves and two much larger forest reserves to assess their relative similarities and dissimilarities. Our efforts focused on isolated forest fragments in the moist semi-deciduous forest zone of Ghana, the region of the country where remaining forests are most imminently imperiled.

Forest communities at the six sites were expected to differ as a consequence of the myriad factors that determine which, and how many, individuals and species occupy a habitat fragment (Bierregaard et al. 1992; Turner 1996). Species-area relationships (Connor and McCoy 1979), edge effects (Murcia 1995), nature of the matrix (Turner 1996), relative isolation (MacArthur and Wilson 1967) and environmental stochasticity, are among the more commonly

cited determinants of community composition. Species richness has been the measure of local diversity used most often to compare communities of different habitat patches. Singly, small fragments generally support fewer resident, forest-endemic species (Turner 1996) and are therefore usually viewed as having lower conservation value than larger expanses of forest. But collectively, the number of species supported by multiple small fragments can surpass that found in larger fragments (Fischer and Lindenmeyer 2002; Tschardt et al. 2002). General consequences of fragmentation on other aspects of community diversity, i.e., species abundance–dominance relationships, species identities, intraspecific variation, and trophic interactions, and what these consequences signify in terms of relative conservation value, are much less understood because comparatively few empirical data have been compiled.

We rely on a focal group, the fruit-feeding butterfly species, to quantify three aspects of community diversity, species richness, species evenness, and species composition, at the six forest fragments. Insects are superlative focal species for investigating how fragmentation impacts forest communities due to their abundance, diversity, endemism, ubiquity, and rapid response to environmental change (Brown 1997; Bossart and Carlton 2002). The frugivorous butterflies, in particular, have been beneficially exploited to study numerous aspects of tropical forest ecology in natural (DeVries 1988; DeVries et al. 1999; Hill et al. 2001), managed, (Fermon et al. 2000, 2003; Willott et al. 2000; Hamer et al. 2003, Stork et al. 2003) and degraded ecosystems (Kremen 1992; Daily and Ehrlich 1995; Shahabuddin and Terborgh 1999). This is largely because member species can readily be collected via fruit-baited traps, which facilitates systematic collection of data, they show a diversity of relative sensitivities to environmental change, and they are tightly intertwined with ecological systems as both primary consumers (herbivores) and as food items.

Taxon inventories are the cornerstone of viable *in situ* conservation programs because they identify the current state of the biological systems of interest and provide a guideline from which to operate. To the best of our knowledge, our biodiversity data are the first on insects from Ghana and only the second on this group from the greater western West Africa region. Our sampling scheme also incorporated a significant temporal component, which is an uncommon feature of biodiversity studies, where rapid, “snapshot” surveys are the norm.

Methods

Study sites

Ghana's old-growth forests represent the eastern most range extent of the Upper Guinean forests of western West Africa. These forests comprise four increasingly dry vegetational zones that lie diagonally from northwest to southeast, beginning from the wettest southwest corner of the country and

extending outward as ever drier concentric bands towards the outer margin of the forest block (Figure 1). Virtually all forests remaining in Ghana now exist as isolated habitat islands entirely surrounded by a highly modified landscape matrix. The history of deforestation in Ghana indicates the country's forest islands were created within living memory, and some as recently as approximately 30 years ago (Hawthorne and Abu-Juam 1995 and references therein).

We conducted a joint analysis of the diversity of the fruit-feeding butterfly communities at six forest fragments (hereafter, sites); two large forest reserves and four remnant, sacred forest groves (Table 1; Figure 1), in order to evaluate the relative conservation value of these small forest fragments. Specific sites were identified in consultation with personnel of the Forestry Department of Ghana, Nature Conservation Research Center (NCRC), and Forestry Research Institute of Ghana (FORIG). Individual sacred groves fall under the jurisdiction of local tribal councils, and permission from village elders to enter and collect from each grove was required and secured. All six sites are representatives of moist semi-deciduous forest and all were formerly embedded within the millions of hectares of continuous forest cover that once was the Upper Guinean forests of West Africa. Survey sites were concentrated around Kumasi in the Ashanti administrative region to facilitate ongoing sampling of multiple sites (Figure 1). All sites derive from the same basic habitat type and same general region; hence, β -diversity is assumed to have been low relative to α -diversity prior to deforestation and fragmentation.

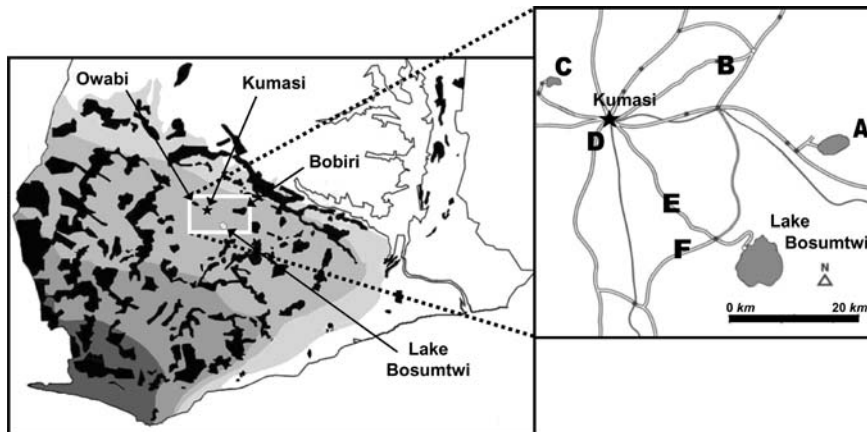


Figure 1. Map of survey sites in relation to Ghana's forest zones and gazetted forest reserves. Forest reserves are in black. Wet evergreen, moist evergreen, moist semi-deciduous, and dry semi-deciduous forest zones are depicted in decreasing intensities of gray, respectively, beginning in the lower southwest corner of the country. The inset shows the location of study sites: (A) Bobiri Forest Reserve, (B) Bonwire Sacred Grove, (C) Owabi Forest Reserve, (D) Kajease Sacred Grove, (E) Gyakye Sacred Grove, and (F) Asantemanso Sacred Grove. Kumasi, Lake Bosumtwi, and Owabi and Bobiri Forest Reserves are shown on both the map and the inset to aid in orientation.

Table 1. Site, trap, and capture specifics.

Site	Size	Global coordinates	Total traps	Trap days ^a	Total captures	Captures/trap day
Bobiri Forest Reserve	5000 ha	6°40' N, 1°19' W	15	330	1581	4.79
Owabi Wildlife Sanctuary	1200 ha	6°44' N, 1°42' W	15	285	1843	6.47
Asantemanso Sacred Grove	259 ha	6°28' N, 1°33' W	10	180	988	5.54
Gyakyee Sacred Grove	11.5 ha	6°33' N, 1°31' W	5	95	315	3.32
Bonwire Sacred Grove	8 ha	6°46' N, 1°28' W	8	144	670	4.65
Kajease Sacred Grove	6 ha	6°38' N, 1°39' W	8	160	1429	8.93

^a Trap days is calculated as the number of traps at a site multiplied by the number of different days the site was sampled.

Trapping methods

Trap sampling was initiated late June 2001 and continued through July 2002. Sampling was more frequent during the rainy season, when the senior author was in the country (approximately late May through early August), and less frequent during the rest of the year. In general, trapping occurred weekly from late June through mid August 2001, monthly between August 2001 and mid May 2002, then biweekly from mid May through late July 2002. Logistical constraints determined sampling schedule. Roads between sites are generally substandard and some are heavily traveled, and substantial time was required to move from site-to-site.

Additionally, significant hiking time was involved at half of the sites. For example, sampling at Bonwire required an approximate 90 min roundtrip hike just to reach the grove. A maximum of two sites could be inventoried per day. Sites in closest proximity were generally sampled on the same day. Additional sites were sampled on sequential days. All six sites were sampled within a 5-day-period during a given sampling bout.

Typical fruit-bait traps were hung in the forest understory, approximately 10 cm above the ground. An initial 4-day experiment indicated that fruit-baited traps hung close to the ground versus those hung at 1 m heights attracted a significantly greater number of captures and species. A total of 61 traps were installed across all sites. Because traps were assembled in the US and subsequently transported to Ghana, this number was set prior to identification of study sites, which constrained our subsequent experimental design. In general, more traps were hung at larger sites, fewer at smaller sites (Table 1). Traps were hung near forest foot paths where possible to facilitate access, but were always installed at least ≥ 3 m off the trail. In most cases, an access trail had to be cut into the forest to place traps because foot paths were nonexistent.

Conscious effort was taken to install all traps in similar micro habitats within areas of closed canopy forest. Five traps were hung in each of three discrete areas at Bobiri and Owabi, and in two at Asanemanso, in order to gain a more representative sample from these larger forests. Four traps were hung in each of two separate areas at Kajease and Bonwire, but the distance between areas was small and restricted by the size and irregular shape of these forests. Five traps total were hung at Gyakye. Individual traps within areas were separated from each other by at least 50 m and by no more than 200 m. Traps were baited with mashed, fermented banana, and butterflies were collected the following day approximately 24 h later. All specimens captured in the traps were collected for subsequent identification.

Species identifications

Butterflies were identified using a variety of taxonomic treatises, including D'Abrera (1981, 1997, 2001), Hecq (1997, 1999, 2000, 2002), Henning (1988) and Larsen (In press). Difficult specimens were identified in consultation with T. B. Larsen, an internationally recognized authority on butterflies of West Africa and elsewhere. Spread specimens were assigned a unique number and then photographed six to a frame with a 300-mm macro lens. Both ventral and dorsal sides were photographed. One set of photographs was then retained by the senior author and a second set was forwarded to Larsen. This system allowed for interactive discussion via the internet on particular specimens when necessary to clarify species identifications.

Community diversity measures

Community diversity was evaluated as: (a) observed richness, which was quantified both as number of species accumulated versus sampling effort and as rarefied species richness; (b) estimated total richness, calculated from a suite of nonparametric richness estimators; (c) species evenness, determined from species rank-abundance distributions; (d) Simpson's Index of Diversity, to capture overall heterogeneity; and (e) complementarity of communities, to quantify dissimilarity among communities with respect to species identities and abundances.

Statistical analyses

Trap data at a given site on a specific date were pooled to generate a single sample for each site-date combination. Pooling of data minimizes variance associated with individual traps (DeVries et al. 1999), e.g., due to differential attractiveness of traps or sporadic destruction of samples by driver ants. An assessment of spatial and temporal variation within sites will be treated elsewhere.

Observed species richness was rarefied to standardize for sample size differences across sites. Rarefaction is a robust statistical technique that calculates

estimates of species richness for sub samples of a specified size drawn at random from the total community (i.e., from the total collection) (Gotelli and Colwell 2001). Richness estimates for sites with larger overall samples are interpolated down to those for sites with smaller overall samples simply by specifying the number of individuals to be randomly drawn. Comparable sized sub samples can then be compared statistically across sites (Heck et al. 1975; Simberloff 1978). Rarefaction curves and 95% confidence intervals were estimated for all sites using EcoSim700 (Gotelli and Entsminger 2003) Rarefied estimates of richness were calculated after 1000 iterations.

Statistical estimates of total richness were calculated using EstimateS, Version 6.0bl (Colwell 2000). EstimateS uses curve fitting models to predict asymptotes of species accumulation curves and computes richness estimates based on a variety of nonparametric estimators and in many cases, their associated standard deviations. Different estimators differ with respect to how they deal with rare species (Chazdon et al. 1996). Input data were formatted as species (rows) by samples (columns) abundance matrices. Individuals within a species were randomly assigned to samples, which removes patchiness due to temporal differences in abundance when the patchiness parameter is set to zero. Sample order was randomized without replacement and mean richness estimates were calculated after 100 iterations of the random sampling algorithm.

Species rank-abundance distributions were graphed to evaluate species evenness among sites. $\text{Log}_{10} p_i$, where p_i is the frequency of the i th species in the total sample, was calculated for each species then plotted against the relative rank for that species. Differences in species evenness among sites are apparent as differences in the comparative shape and steepness of the curves for different sites (Southwood and Henderson 2000; Magurran 2004). PROC GLM (GLM; Type III sum of squares, SAS 1990) was used to quantify heterogeneity-of-slopes across sites, where *Site* was designated as a class variable and *Relative Abundance* and *Rank* were designated as continuous variables, and where the interaction of $\text{Site} \times \text{Rank}$ tests heterogeneity of slopes. The slope of each linear regression curve was used to measure evenness of the community (Tokeshi 1993; Magurran 2004).

Indices of diversity integrate both species richness and evenness into a single measure in an attempt to capture overall heterogeneity at a site. We calculated Simpson's (inverse) Index of Diversity (1/D) using EstimateS, Version 6.01b (Colwell 2000). This index is one of the most robust and most easily interpreted, although no diversity index is considered a perfectly unified measure (Magurran 2004). Values for the Simpson Index range from 1 to the number of species in the sample, with higher values indicating greater overall diversity (Krebs 1999).

Complementarity of community composition among sites was quantified using two quantitative indices of similarity, the *Morisita-Horn Index* (Magurran 2004) and *COMPAH's % Similarity* (Gallagher 1999). Quantitative, as opposed to qualitative, measures of similarity integrate both differences in species uniqueness between sites and differences in relative abundances of shared species. The *Morisita-Horn Index* is generally recognized as the best

overall estimate of similarity because it is less sensitive than others to changes in species richness and sample size (Wolda 1981; Magurran 2004). The *Morisita–Horn Index* is defined as

$$\text{MHS}_{ij} = \sum_{k=1}^S [x_{ik}x_{jk}/(d_i + d_j)N_iN_j],$$

where, S = Number of species, x_{ik} = Abundance of species k in sample i , N_i = Total individuals in sample i , and

$$d_i = \sum_{k=1}^S x_{ik}^2/N_i^2.$$

However, no measure of similarity is free of limitations and the *Morisita–Horn* is sensitive to changes in the abundance of the most common species (Magurran 2004). We calculated a second similarity coefficient, *COMPAH's % Similarity*, for comparison and to corroborate results. The *Bray–Curtis Index* (which has multiple synonyms, e.g., *Pielou's % Similarity*, *Sorenson's Abundance Index*; Gallagher 1999) has also performed well when tested against a variety of similarity measures (Magurran 2004). *COMPAH's % Similarity* is analogous to the *Bray–Curtis Index* except that species abundances are first standardized by sample totals, which is appropriate when sample sizes differ between communities being compared *COMPAH's % Similarity* is defined as

$$\% \text{SIM}_{ij} = \sum_{k=1}^S \min [x_{ik}/N_i, x_{jk}/N_j],$$

where, S = number of species. x_{ik} = Abundance of species k in sample i , and N = total sample size.

Results

Each site was sampled from 18 to 22 times throughout the course of the study (Table 1; trap days divided by total traps), resulting in a total of 6836 individuals captured across all sites combined. Trap productivity, in terms of number of individuals collected per trap day, was highest at Kajease and lowest at Gyakye. Seventy-nine species were collected in total from all sites combined, representing five subfamilies (Appendix 1). This collective total of 79 species accounts for ~33% of the fruit-feeding butterfly guild currently known for the country (Larsen 2001). All but five of the 79 species (*Bicyclus safitza*, *Melanitis leda*, *M. libya*, *Ypthimomorpha itonia*, and *Charaxes varanes*) are forest habitat endemics and of these five, only two specialize on savanna habitat (Appendix 1). Greater than 70% of those collected are considered either moist forest specialists or species found in all forest subtypes, which is as expected given the location of our study sites well within the moist semi-deciduous forest zone.

Considered solely with respect to this sub group of species, our trapping efforts netted approximately 42% of the fruit-feeding butterflies known from these two forest habitat subtypes (Appendix 1).

Observed species richness

The number of butterfly species trapped at each site ranged from a low of 27 at Gyakye to a high of 59 at Bobiri (Table 2; Appendix 1). However, species accumulation curves were still rising at all sites when the study was terminated, indicating that species saturation had not been reached (Figure 2). Only the Owabi sample was clearly approaching an asymptote. This was also the only sample in which the singleton curve was declining (Figure 2), which is as expected when sampling is nearing completion (Magurran 2004). The rate at which new species were being added to the collection at the other sites was still relatively high. In fact, this rate of increase was sufficiently high at Bonwire to suggest the associated accumulation curve might ultimately cross the curve for Owabi. Singleton curves at these other sites were either flat (e.g., Bobiri) or rising (e.g., Bonwire).

Observed species richness was higher at the forest reserves than at the sacred groves (Figure 2; Table 3). Of the two forest reserves, Bobiri was the more species rich. Rarefied values derived from random sub-samples of the total trap data from Bobiri were consistently higher than those derived from comparable sized random sub-samples of the total trap data from Owabi (Table 3, last two columns). Additionally, 17% more species were collected at Bobiri even though

Table 2. Species diversity data for each site.

Site	Total species trapped	Singletons/ Doubletons ^a	Estimates of total richness ^b			Number additional species predicted ^c	Simpson's Index of Diversity ^d
			ACE / ICE	Chao1/ Chao2	Jack1/ Jack2		
Bobiri	59	10/3	66/66	72/69	70/75	6–15	10.07
Owabi	51	5/4	54/54	53/53	56/57	2–6	17.73
Asantemanso	41	10/6	51/51	48/48	50/54	7–13	8.64
Gyakye	27	6/3	32/33	31/33	34/38	4–11	8.03
Bonwire	38	13/1	53/54	79/79	50/61	12–41	13.72
Kajease	41	14/7	61/60	52/52	54/61	11–20	7.25

^a Singletons and doubletons are the number of species represented by one or two individuals, respectively.

^b Nonparametric richness estimators were used to estimate total species richness at a site. ACE and Chao1 are abundance-based richness estimators. All others are incidence-based estimators.

^c The number of additional species estimated to be at each site is the difference between estimated total richness and the number of species actually collected from traps.

^d Simpson's Index was calculated as $1/D$ (the reciprocal), where larger numbers indicate greater diversity.

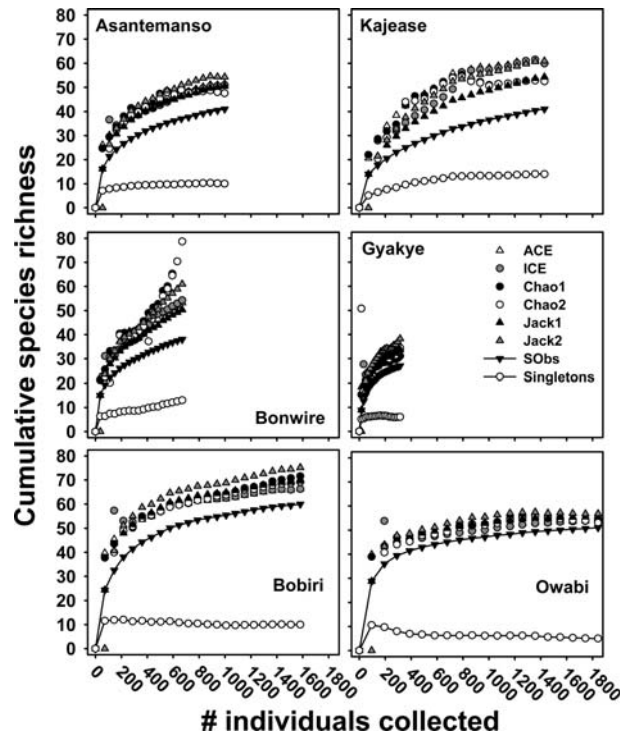


Figure 2. Randomized collectors curves. Number of observed and estimated species, and singletons accumulated at each site as a function of increasing numbers of individuals trapped through time. ACE, ICE, Chao1, Chao2, Jack1, and Jack2 = nonparametric estimates of species richness; SObs = actual species observed in samples; Singletons = # of species represented by a single individual.

the total sample from this site was 15% smaller than that from Owabi. Of the sacred groves, sample species richness was lowest for Kajease. When richness was rarefied to sample sizes that were comparable to those collected from other sites, Kajease samples were always represented by fewer total species. Species richness at the remaining three sacred grove forests was generally similar when compared at the smallest sample size (Table 3). But the total number of 40 species represented by the 672 individuals collected at Bonwire exceeded the rarefied value of species richness at Asantemanso for a sample of similar size.

Estimated species richness

In all cases but one (Bonwire), the Jackknife2 estimator generated the highest estimate of total richness at a site (Table 2; Figure 2). The rank order of all other estimators was inconsistent across sites. Estimates of total species

Table 3. Rarefied species richness.

Comparison site	Actual trap data	Rarefied richness values ^a					
		Bonwire $N = 672$	Asantemanso $N = 988$	Kajease $N = 1429$	Bobiri $N = 1581$	Owabi $N = 1843$	
Gyayke	$S = 27, N = 315$	30.84 (26.84–34.83) [321]	29.90 (25.84–33.96) [323] 36.46 (33.36–39.55) [668]	23.02 (13.43–27.6) [307] 30.91 (26.38–35.44) [681] 35.27 (31.56–38.98) [987]	42.85 (38.03–47.67) [316] 51.32 (47.08–55.56) [663] 55.35 (51.75–59.95) [978]	39.81 (35.76–43.86) [330] 44.55 (41.08–48.01) [658] 47.02 (44.31–49.73) [987]	
Bonwire	$S = 40, N = 672$						
Asantemanso	$S = 41, N = 988$						
Kajease	$S = 41, N = 1429$						
Bobiri	$S = 60, N = 1581$						

Comparisons are presented in order of increasing total sample size collected from different sites.

Numbers in parentheses are 95% confidence intervals; numbers in brackets indicate sub-sample size associated with the rarefied value of species richness given. S = number of species collected at each site. N = total sample size at each site.

^aEach row compares observed species richness at a site that has a smaller overall sample to rarefied species richness at sites with larger overall samples. Rarefied richness values are estimated for comparable sized, sub samples that represent random draws from the larger sample.

richness at Owabi, Asantemanso, and Gyakye were generally in good agreement regardless of the richness estimator used (*standard errors of the mean* of 0.67, 0.919, and 0.992 for Owabi, Asantemanso, and Gyakye, respectively). As few as a single species, and at most three species, separated the different estimates, except with respect to the Jackknife2 estimate, which was 6–12% higher than the others for Asantemanso, and 9–14% higher than the others for Gyakye. Estimates of total richness were more variable at the other three sites (*standard errors off the mean* of 1.43, 5.37, and 4.46 for Bobiri, Bonwire, and Kajease, respectively) and dependent upon the richness estimator used. At Bonwire, for example, the Chao1, Chao2, and Jackknife2 estimates ranged from 12 to 36% higher than the others. Incidence and abundance based estimates of total species richness were very similar (Table 2). ACE (abundance-based) and ICE (incidence-based) coverage estimators were identical or virtually identical in all cases. Similarly, Chao1 (abundance-based) and Chao2 (incidence-based) estimates were identical in all cases except at Bobiri, where the abundance-based estimate was slightly higher.

All estimates of total richness based on the Owabi sample were stable and converging on observed richness as sample size increased (Figure 2). The Chao2 estimates from the Kajease data stabilized at a sample size of approximately 1000, and the ICE estimates from the Asantemanso and Bobiri data, stabilized at a sample size of approximately 1000 and between 1300 and 1400, respectively. Richness estimates in all other cases had not stabilized and continued to increase with increasing sample size. This rate of increase was most extreme at Bonwire.

Estimates of total species richness at Bonwire and Kajease deviated the most from the number of species actually collected in traps (Table 2; Figure 2). At Bonwire, estimates of total richness spanned from 50 to 79, representing a 28–52% increase over the 38 actually collected. At Kajease, estimates of total richness represented a 22–33% increase over the 41 actually collected. Owabi showed the closest correspondence between number of species trapped and estimates of total species richness. Total species richness at Owabi Reserve was estimated to be only 4–6% higher than the number collected in traps.

Bobiri was estimated to have the most species rich community and Gyakye, the least. Among the four remaining sites, relative differences among forests depended upon whether estimates at the low end of the estimated range were compared, or estimates at the high end of the range. At the low end, all sites were estimated to have comparable species richness. At the high end, however, Bonwire and Kajease were predicted to be more speciose than Asantemanso or Owabi, with as many as 32 and 12% more species, respectively.

Species evenness and overall diversity

The percentage of singletons (i.e., species represented by a single individual) trapped at each site ranged from a low of 10% of species at Owabi to a high of

34% of species at both Bonwire and Kajease (Table 2). The rank–abundance or dominance–diversity curve for Kajease declined at the most rapid rate (Figure 3a), indicating the community trapped at this site had the most uneven representation of different species. Indeed, three species, *Euphaedra ceres*, *Gnophodes betsimena*, and *Bicyclus vulgaris*, accounted for 56% of the 1429 individuals trapped at Kajease (Appendix 1). At the other extreme, 14 of the 41 total species collected at this site were represented by a single individual (Table 2).

Species evenness was higher and generally comparable at the other three sacred groves, except with respect to the most common species, where the curve for Bonwire initially declined more slowly. This initial slower drop off indicates this site had more relatively common species than Asantemanso or Gyakye, and their abundances were more equitable than those of commoner species at the other two sites (Figure 3a). For example, the single most common species at Asantemanso and Gyakye accounted for 1/4 of all individuals trapped, whereas the single most common species at Bonwire accounted for only 1/8 of all individuals trapped. In fact, Bonwire's common species were more evenly represented than those at any other site.

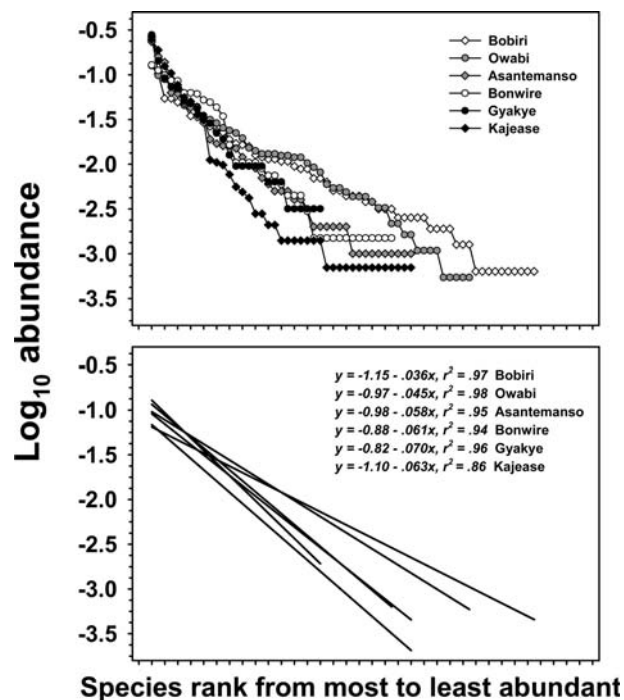


Figure 3. (a) Dominance–diversity curves for the sample communities, where log_{10} abundance is plotted against rank abundance. (b) Linear regressions and model statistics for dominance–diversity curves.

The dominance–diversity curves for the sample communities from the two forest reserves declined at the slowest relative rate, indicating these samples had the highest species evenness (Figure 3). Note the curves overlay each other until the least abundant species factor in, at which point they diverge because collectively more species at Bobiri are represented by each of the rarest abundance classes.

Regression slopes were highly heterogeneous among sites ($F = 41.67$, $p < 0.0001$, $df = 5$) and ranged from a low of -0.036 for the Bobiri sample to a high of -0.070 for the Gyakye sample (Figure 3b). The regression analysis indicated higher evenness at Kajease relative to Gyakye (slopes of -0.063 and -0.070 , respectively). But the Kajease data were less adequately explained by a linear model ($r^2 = 0.86$ versus 0.96 for Kajease and Gyakye, respectively) and the slope of the regression was skewed to the right by the large number of singletons trapped from this site.

The sample collected from Owabi proved to be the most diverse when species richness and evenness were integrated into a single measure of overall heterogeneity (Simpson's Index; Table 2). The sample collected from Bonwire was next, followed by Bobiri, Asantemanso, Gyakye, and Kajease, respectively.

Site complementarity

Eight species, *Euphaedra medon*, *E. ceres*, *E. phaetusa*, *E. themis*, *E. harpalyce*, *Gnophodes betsimena*, *Bicyclus funebris*, and *B. vulgaris*, were generally abundant at all six sites. These eight species accounted for 61–86% of all individuals trapped at the sacred groves (Appendix 1). They accounted for 35 and 53% of all individuals trapped at Bobiri and Owabi, respectively (Appendix 1). In general, a large percentage of species were shared between sites, ranging from the 80% that Gyakye shared on average with the other five sites to the 54% on average that Bobiri shared with other sites.

A number of species were trapped at only one site, and all sites were represented by at least one of these site-specific species (Appendix 1). Bobiri had, by far, the largest number of these at 13, some of which were fairly well represented. Eleven species were exclusive to the sacred groves but nearly all of these were represented by a single individual.

Both indices of similarity produced similar relative results when community pairs were ranked from most to least similar. The main exceptions were the relative rankings of the Bonwire/Gyakye comparison and the Bobiri/Owabi comparison, where the COMPAH index indicated greater community similarity than the Morisita–Horn index. The butterfly community trapped at Bobiri Reserve was the most distinctive overall (Table 4). Both the Morisita–Horn and COMPAH indices were lower in all pairwise comparisons involving Bobiri than when butterfly communities from any other two forests were compared. The communities at Kajease and Gyakye were the most similar (89 and 72% for the Morisita–Horn and COMPAH indices, respectively). On

Table 4. Complementarity of species assemblages among sites.

Sites	Bobiri (60)	Owabi (51)	Asantemanso (41)	Bonwire (39)	Kajease (41)	Gyakye (27)
Bobiri (60)	–	42	33	34	30	23
Owabi (51)	45/58	–	32	35	32	22
Asantemanso (41)	42/51	82/67	–	30	27	22
Bonwire (39)	41/49	74/61	74/60	–	27	21
Kajease (41)	36/31	65/52	86/71	68/58	–	20
Gyakye (27)	34/38	57/53	67/57	65/61	89/72	–

Number of shared species above the diagonal.

Morisita–Horn/COMPAH's quantitative indices of similarity (expressed as percentages) below the diagonal. The total number of species trapped at each site is in parentheses for ease of comparison.

average, communities trapped at the sacred groves were more similar to each other than they were to either forest reserve. There was an average similarity of 75 and 64% (Morisita–Horn and COMPAH indices, respectively) for all pairwise comparisons among the four sacred groves, an average of 70 and 58% between Owabi and the sacred groves, and an average of 38 and 42% between Bobiri and the sacred groves. Of the sacred groves, the community trapped at Asantemanso was the most similar to the communities trapped at the two forest reserves (Table 4). In fact, Asantemanso exhibited, on average, the greatest similarity of any site to all others.

Discussion

Observed species diversity among sites

The fruit-feeding butterfly communities trapped at the sacred groves were generally less speciose than those trapped at the forest reserves, which is consistent with theoretical expectations of species–area relationships, whereby smaller areas tend to support fewer species (Schoener 1976; Rosenzweig 1995; May and Stumpf 2000). The sacred grove communities were also generally less diverse with respect to the relative abundances of member species. In communities, such as Asantemanso, Kajease, and Gyakye, that are dominated by a few very abundant species, the vast majority of individuals in the community will be of these few predominant species. In communities where species are more equitably represented, randomly encountered individuals are more likely to derive from different species, which is a defining characteristic of a diverse community (Purvis and Hector 2000). Interestingly, Simpson's Index of overall diversity proved to be lower for the Bobiri sample than for the Owabi and Bonwire samples. But this diversity measure is heavily weighted by the relative abundance of the most abundant species, which at Bobiri accounted for 1/4 of all individuals trapped, i.e., *B. tentyrus*. Hence, in a broad sense, our findings add to the already substantial body of data that indicate the primary success of biodiversity conservation hinges on protection of large habitat areas.

Trapping at the smallest grove, Kajease, yielded the overall most depauperate sample community. Relatively fewer species were collected at this site given the size of the sample, which was significantly larger than those collected from the other sacred forests, and which nearly rivaled the size of those collected from the two forest reserves. Additionally, over half of the total species collected from this site were represented by a single, or at most two, specimens. Indeed, the eight forest species common at all six sites accounted for nearly 90% of the entire sample collected at Kajease. Not surprisingly, Simpson's Index of Diversity was lower for Kajease than for any other site. This low observed richness and evenness was somewhat surprising, even considering the small size of this forest patch, because the forest retains much of its closed canopy and, judging by the size of the total sample we collected, apparently supports a large number of individuals. However, of the groves we inventoried, the landscape matrix surrounding Kajease is uniquely characterized by intensive residential development directly adjacent to, and in some cases within meters of, the grove. These activities have undoubtedly led to the degradation or disruption of key ecological processes in the grove, e.g., water drainage, and fostered the differential extinction of habitat sensitive species. This highly transformed landscape matrix has likely also served to hinder emigration from and immigration to this isolated forest patch by all but the most robust dispersers.

Bonwire was the most enigmatic and most diverse sacred grove we sampled. Sampling intensity at this site was very similar to that expended at Kajease in terms of patch size and trap days. Yet the number of individuals collected from Bonwire was less than half that collected at Kajease. Indeed, on multiple occasions our sampling efforts yielded only a few specimens and over time we had come to perceive this forest remnant as generally less diverse than the others. The relatively small sample collected from this 8-ha patch, however, ultimately proved to comprise a relatively diverse community. Observed richness at Bonwire exceeded the rarefied richness values at all other sacred grove sites, and member species of this community were more equitably represented than those at the other sacred grove sites. Indeed, when quantified as a single measure of diversity, Bonwire was second only to Owabi in terms of overall heterogeneity. That Bonwire is relatively distant from the village proper and located in a rural area has probably helped preserve the grove's ecological integrity and resident biodiversity. Bonwire, unfortunately, also proved to be the most imminently imperiled grove. Near the end of our study, strong winds associated with a rainy season storm uprooted virtually every old growth, emergent tree in the forest patch. This event stands as a clear testament to the enhanced vulnerability of small isolated forests to further degradation (Laurance et al. 1998).

Owabi was the only site at which most of the resident community of fruit-feeding butterflies attracted to our traps had been collected. The species accumulation curve was approaching an asymptote, the number of singletons in the sample was declining, and estimated and observed richness were converging, all signs that continued trapping would have resulted in the capture of few additional species. Accumulation curves were still climbing at most sites;

however, indicating that our trap data would have yielded additional species had our sampling continued. Bonwire appeared to be the most incompletely sampled site. The species accumulation and singleton curves were sharply increasing and estimated and observed richness showed no sign of convergence.

In any community, new species are initially accumulated quickly as common species are captured, but then are accumulated ever more slowly as rarer, infrequently captured species are added (Gotelli and Colwell 2001). Species missing from our trap collection do indeed include taxa considered to be rare (Larsen 2001; see Appendix 1). But our surveys also failed to trap a significant proportion of species ($>1/3$) thought to be generally to very common occupants of Ghana's moist forests. For example, a number of theoretically common Charaxinae were either entirely absent from our trap data or only rarely represented. Common species generally absent across all sites may have been relatively unattracted to our bait or vertically stratified in the forest, e.g., localized in the canopy (DeVries 1988; DeVries et al. 1997, 1999; Fermon et al. 2003). Such resource or habitat affinities would have set boundaries on the species pool we were likely to sample, i.e., the pool of species attracted to banana and to traps hung near the forest floor. Species rare in samples that are generally abundant members of communities have been termed methodologically rare because their "rarity" is a function of the sampling method used not their actual abundance (Longino et al. 2002). But not all theoretically common species we trapped were equally rare across sites. Our survey of Bobiri, for example, resulted in 422 individuals of *Bebearia tentyrus*, a species generally viewed as common. Indeed, this was by far the most abundant species at this site, accounting for more than 1/4 of all individuals captured (Appendix 1). Yet *B. tentyrus* was hardly represented at the other forests, including the 1500-ha Owabi Wildlife Sanctuary. This wide dichotomy in relative abundance across sites suggests that *B. tentyrus* may be particularly resource sensitive or vulnerable to changes in the landscape matrix. Although intrinsically rare species are generally perceived as more vulnerable to land conversion and fragmentation, numerically abundant species are not impervious to their effects (Vermeij 1993; Skinner 2000; Bossart and Carlton 2002).

Estimated species richness among sites

Observed richness is a strongly biased measure of species diversity at a site because it is highly correlated with sample size and is inevitably an underestimate of true species richness unless sampling is nearly or wholly complete. Nonparametric richness estimators are a powerful and effective alternative for assessing total species richness because they reduce this bias (to varying degrees) and are independent of sample size above some minimum size (Colwell and Coddington 1994; Longino et al. 2002). The ICE and Chao2 estimators have been touted as particularly promising because they perform well at small sample sizes and are relatively insensitive to sample density and species patchiness (Chazdon et al. 1996; Longino et al. 2002; Magurran 2004).

Owabi is the only site where observed richness can be considered a viable measure of the actual number of fruit-feeding butterfly species in the community. At all other sites, observed richness clearly underestimated true species richness, particularly at Kajease and Bonwire where the increasing singleton curves and wide divergence between estimated and observed richness indicates sampling is far from complete. The ICE and Chao2-based estimates were the only ones that tended to level off with increasing sample size, which is consistent with earlier evaluations of estimator performance. Notably, the ICE and/or Chao2 estimates stabilized at approximately 1000 for three of the four samples, i.e., Asantemanso, Kajease, and Owabi, with Bobiri the one exception. This suggests sample sizes of at least 1000 are necessary for estimating true richness of these fragmented communities, and furthermore, may in many cases be the maximum size required.

Richness estimators, in general, are highly influenced by the number of rare species and observed and estimated richness will diverge considerably if the ratio of singletons to doubletons (or uniques to duplicates) is large. Additionally, the ranking of different sites based on relative richness will change unless this ratio remains approximately constant across sites. Of our samples, those from Owabi and Bonwire had the smallest and largest ratio of singletons to doubletons, respectively. Consequently, estimates of total species richness at Owabi showed the least divergence from the number actually collected, whereas estimates of total richness at Bonwire showed the greatest divergence. Because the ratio of singletons to doubletons was inconstant from site-to-site, relative richness of the different sites based on number of species actually collected also differed considerably from that based on estimated total richness. Bobiri and Owabi forest reserves are the most speciose communities and Kajease the least, when viewed in the context of species actually trapped. But when viewed in the context of estimated total richness, the Owabi fruit-feeding butterfly community appears to be no more speciose than that at Asantemanso, and perhaps even less speciose than that at Bonwire or Kajease, and the community at Gyakye sacred grove is clearly the least species rich.

Species composition and site complementarity

Resident communities of small remnant forests and large forest blocks are expected to differ due to, for example, species–area relationships (Schoener 1976; Rosenzweig 1995; May and Stumpf 2000), population size and extinction risk dynamics (Lande 1988), extent of edge habitat and predominance of edge effects (Murcia 1995), and differential tolerance of individual species to relative habitat isolation and fragmentation (Rabinowitz 1981; Gaston 1998; Johnson 1998). Consequently, comparison of species assemblages among forest fragments of markedly different size should reveal clues about ‘winners’ and ‘losers’ with respect to species persistence and extinction in highly fragmented landscapes. Species similarly or more abundant in forest remnants should be those

resistant to dynamics of forest fragmentation, whereas species that show notable decrease in abundance would presumably be those negatively impacted by fragmentation effects.

Eight forest butterfly species were commonly trapped at all six sites despite probable differences in the condition of individual forests and significant differences in forest size. This implies these eight species are relatively tolerant of, or perhaps even benefited by, extreme fragmentation of their resources and the variety of associated changes that small, isolated remnants of forest incur. In theory, effective dispersers that are undeterred from crossing a nonforest landscape matrix, for example, could move between patchily distributed forest fragments and repeatedly re-colonize such habitat islands (Hasting and Harrison 1994; Hanski and Gilpin 1996). Similarly, species characterized by traits that confer resistance to effects of forest deterioration, e.g., generalists versus specialists species (Kunin and Gaston 1997), might be able to maintain viable resident populations in small isolated forest remnants. The eight species abundant in our trap samples are known to be generally common, to have fairly wide ranges, to colonize both intact and disturbed forest, and to fly outside the forest proper (Larsen In press). These are all characteristics thought to facilitate persistence of forest species in highly transformed landscapes.

Species more abundant in the sacred groves versus the forest reserves included the grass-feeding Satyrine species whose increased presence is an apparent sign of forest disturbance (Larsen 1994). Grasses are generally uncommon on the Afrotropical forest floor (Owen 1971) but can colonize and spread in abundance when light penetration into the forest proper increases as a result of, for example, increased edge to interior habitat or degradation of the forest canopy. That some Satyrines might actually benefit from fragmentation and become more abundant in remnant patches is therefore not surprising. This coupled dynamic between grasses and Satyrines also signals the high potential of this group as biodiversity indicators of forest condition, an attribute that could be beneficially exploited to help direct limited conservation resources in economically disadvantaged countries, e.g., to identify priority sites for formal protection or to steer restoration efforts.

Fermon et al. (2000) found that certain Limenitinae were vulnerable to modification of forest habitat as a consequence of logging. Not surprisingly, this vulnerability apparently extends to modification of forest habitat at the broader landscape level as well. We found *Bebearia* and *Euriphene* species, as a group, to be those most sensitive to affects of forest fragmentation (Bossart et al. 2005). The sacred grove collections included 10 or fewer of the 19 total *Bebearia* and *Euriphene* species trapped and these captures were, in many cases, represented by a single individual. Four of the five *Bebearia* collected at Kajease, for example, were singletons (i.e., *B. absolom*, *B. cocalia*, *B. oxione* and *B. zonara*). Perhaps the most telling evidence of the apparent vulnerability of this group of fruit-feeders is that a number of the “absent” species are perceived as generally common residents of moist forests or all forest subtypes, e.g., *B. tentyris* (Appendix 1). Unlike rare species, whose absence could relate

to their lower overall probability and rate of capture, the decreased numbers of these common species are difficult to explain except in the context of sensitivity to dynamics of forest fragmentation.

Conclusions

Species diversity, measured as richness, evenness, and distinctiveness, was generally reduced in the sacred forest groves relative to the larger reserves, despite the long history of protection and restricted use of these indigenous conservation areas. Given these forest 'islands' were embedded within what once was the millions of hectares of continuous Upper Guinean forests of west Africa, our findings imply the geographic ranges of many of Ghana's forest-endemic fruit-feeding butterfly species have contracted as a consequence of the widespread destruction and fragmentation of the country's forest cover. The extrinsic and intrinsic drivers responsible for our observed patterns of community diversity are currently unknown as many factors disproportionately impact smaller versus larger habitat islands, e.g., edge effects, and influence which species occur where. Our studies in the region are ongoing, however, and ultimately we expect to uncover the key predictors, if they exist, that determine diversity of the fruit-feeding butterfly community of Ghana's relict forests.

Our preliminary assessment of frugivorous butterfly diversity in habitat patches adds to the burgeoning evidence that large reserves are the cornerstones of successful conservation strategies because they generally harbor greater forest biodiversity than smaller forest fragments. Nonetheless, small habitat fragments can contribute to the preservation of biodiversity in transformed landscapes (Fischer and Lindenmayer 2002; Tscharntke et al. 2002), and our survey data identify at least three ways that Ghana's indigenous reserves facilitate conservation of forest habitat specialists. First, a number of less common, forest-endemic species were collected from the sacred groves, three of which were collected exclusively from a sacred grove. *Bebearia barce*, which was trapped only at Asantemanso, is the most notable of these. That four individuals of this generally rare species of wet tropical forest were collected exclusively from Asantemanso implies this sacred grove alone supports a resident population. Second, although most aspects of species diversity were lower in the sacred groves versus the forest reserves, estimates of total species richness were comparable between Kajease, Bonwire, Asantemanso, and Owabi despite large differences in fragment size (6–1200 ha). This result was unexpected and at this point we have few insights. For many species local extinctions occur gradually and many of these forest endemic species may ultimately disappear from these fragments given sufficient time. But this explanation doesn't account for the fact that some species were only documented in these small fragments and others actually increased in abundance. Finally, the proportion of total species richness accounted for by Charaxinae species was approximately 2- to 3-fold higher at Asantemanso, Gyakye, and Kajease than at the forest reserves.

Thus, either these small forest fragments are able to support resident populations of these large, robust butterflies, or sacred groves facilitate dispersal of this guild of fruit-feeders among isolated forest patches. Either way, these small relicts of old growth forest are serving to foster persistence of forest species across a landscape matrix that is largely devoid of forest habitat.

The integration of small remnant fragments into mainstream conservation practice is a necessity to mitigate biodiversity loss in degraded landscapes, where large tracts of habitat no longer exist or where the economic cost of their protection is excessive. Sacred natural sites comprise an ancient and global system of small, indigenous reserves that largely remain outside mainstream conservation research and practice (UNESCO). Despite the cultural and biological significance of Ghana's sacred sites, few receive active protection. Many have been completely destroyed and many others are under imminent threat by encroaching farms and residential development, and degradation through consumption of forest products and bush fires, as traditional protective measures have broken down (Ntiamoah-Baidu 2001, GACON). Explicit integration of sacred forest groves into the protected areas network, either through community or governmental based conservation efforts is necessary to ensure these isolated examples of old growth forest continue to persist in a landscape where little unprotected forest habitat remains. Although their protection will never replace or offset the value of or need for formally protected, large contiguous tracts of forest, small islands of old-growth forest have clear and tangible conservation value and their protection is urgently needed to ensure this value is not lost.

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Appendix 1. Butterfly species trapped at each site.

Species	Forest Zone–Abundance Categories	Forest Reserves Sacred Groves					
		Bobiri	Owabi	Asante.	Bonwire	Gyakye	Kajease
Satyriinae							
<i>Bicyclus abnormis</i>	WF–NR	1.27	2.49	0.10	0.15	0.00	0.07
<i>B. dorothea</i>	ALF–VC	0.38	1.25	0.50	0.15	0.00	0.49
<i>B. funebris</i>	DRF–CO	6.27	2.88	4.31	8.51	5.08	3.08
<i>B. madetes</i>	MF–NR	0.32	1.30	0.10	6.27	1.27	0.00
<i>B. martius</i>	MF–CO	0.70	2.22	0.50	11.19	4.76	0.07
<i>B. procora</i>	WF–NR	0.25	0.54	0.00	0.00	0.00	0.00
<i>B. safitza</i>	GUI–NR	0.25	0.22	0.10	0.15	0.00	0.28
<i>B. sandace</i>	ALF–VC	0.19	1.19	1.50	0.00	0.00	0.00
<i>B. sangmelinae</i>	WF–NR	1.14	0.60	0.00	0.00	0.00	1.05
<i>B. taenias</i>	MF–CO	0.13	1.19	0.50	3.43	2.22	0.00
<i>B. vulgaris</i>	ALF–VC	2.91	3.15	6.11	8.66	9.21	12.46
<i>B. xeneas</i>	ALF–NR	0.63	0.33	0.00	0.15	0.00	0.00
<i>B. zinebi</i>	MF–NR	0.51	1.95	0.00	6.12	0.00	0.00
<i>Elymnias bammakoo</i>	MF–CO	0.32	0.33	0.00	0.15	0.95	0.28
<i>Gnophodes betsimena</i>	ALF–CO	5.44	4.45	6.31	6.27	27.94	18.89
<i>G. chelys</i>	MF–CO	1.14	2.55	1.60	1.04	2.86	1.12
<i>Hallelesis halyma</i>	MF–NR	0.06	0.00	0.00	0.00	0.00	0.00
<i>Melanitis leda</i>	UBQ–CO	0.95	1.25	1.90	0.90	1.90	5.60
<i>M. libya</i>	UBQ–NR	0.25	0.22	0.60	0.15	0.00	0.56
<i>Ypthimomorpha itonia</i>	SPE–NR	0.00	0.05	0.00	0.00	0.00	0.00
Limenitinae							
<i>Aterica galene</i>	ALF–CO	4.93	4.40	4.31	1.64	0.95	0.98
<i>Bebearia abesa</i>	MF–NR	0.44	0.00	0.00	0.00	0.00	0.00
<i>Bebearia absolon</i>	ALF–CO	2.28	1.52	0.90	0.00	0.00	0.07
<i>Bebearia cocalia</i>	ALF–CO	1.58	0.92	0.00	0.00	0.00	0.07
<i>Bebearia barce</i>	WF–RA	0.00	0.00	0.40	0.00	0.00	0.00
<i>Bebearia demetra</i>	MF–RA	0.13	0.00	0.00	0.00	0.00	0.00
<i>Bebearia mandinga</i>	ALF–CO	0.89	0.43	0.20	0.15	0.00	0.00
<i>Bebearia mardania</i>	ALF–CO	1.64	1.30	0.20	0.60	0.00	0.00
<i>Bebearia oxione</i>	MF–NR	0.44	0.54	0.00	0.15	0.00	0.07
<i>Bebearia phantasina</i>	ALF–CO	1.20	0.00	0.00	0.00	0.00	0.00
<i>Bebearia sophus</i>	ALF–CO	1.71	6.62	1.20	0.30	0.63	0.77
<i>Bebearia tentyris</i>	MF–CO	26.69	1.30	0.20	0.75	0.63	0.00
<i>Bebearia zonara</i>	MF–CO	5.44	1.03	0.00	0.45	0.00	0.07
<i>Euriphene amicia</i>	WF–NR	0.06	0.00	0.00	0.00	0.00	0.00
<i>Euriphene ampedusa</i>	ALF–NR	0.19	0.81	0.20	1.04	0.32	0.00
<i>Euriphene aridatha</i>	MF–NR	0.51	0.43	0.20	0.75	0.00	0.07
<i>Euriphene barombina</i>	ALF–VC	2.34	2.39	3.31	1.04	0.32	0.00
<i>Euriphene caerulea</i>	MF–CO	0.06	0.00	0.00	0.00	0.00	0.00
<i>Euriphene gambiae</i>	ALF–CO	1.08	0.00	0.00	0.00	0.00	0.00
<i>Euriphene simplex</i>	WF–NR	0.89	0.49	0.70	0.15	0.00	0.00
<i>Euphaedra ceres</i>	ALF–CO	4.62	9.82	23.45	9.85	14.29	24.91
<i>Euphaedra cyparissa</i>	DRF–NR	0.00	0.00	0.00	0.00	0.00	0.07
<i>Euphaedra diffusa</i>	DRF NR	0.00	0.11	0.10	0.15	0.00	0.07
<i>Euphaedra edwardsii</i>	MF–CO	0.00	0.16	1.00	0.45	0.00	0.14
<i>Euphaedra eupalus</i>	WF–RA	0.25	3.15	0.00	0.00	0.00	0.00
<i>Euphaedra gausape</i>	WF–NR	0.06	0.00	0.00	0.00	0.00	0.00

Appendix 1. (Continued).

Species	Forest Zone–Abundance Categories	Forest Reserves Sacred Groves					
		Bobiri	Owabi	Asante.	Bonwire	Gyakye	Kajease
<i>Euphaedra harpalyce</i>	ALF–CO	1.90	4.56	4.81	4.33	7.30	5.04
<i>Euphaedra hebes</i>	WF–NR	0.38	0.00	0.00	0.00	0.00	0.00
<i>Euphaedra inanum</i>	MF–RA	0.44	0.43	0.00	0.00	0.00	0.07
<i>Euphaedra janetta</i>	ALF–CO	1.08	1.41	1.60	1.04	0.95	0.42
<i>Euphaedra medon</i>	ALF–CO	10.31	8.90	16.03	12.84	4.13	10.43
<i>Euphaedra phaetusa</i>	ALF–CO	3.48	12.64	13.83	5.22	6.98	7.70
<i>Euphaedra perseis</i>	WF–NR	0.25	0.00	0.00	0.00	0.00	0.00
<i>Euphaedra themis</i>	DRF–NR	2.66	7.38	1.70	4.93	3.49	3.57
<i>Euphaedra xypete</i>	MF–CO	0.70	0.05	0.30	0.00	0.00	0.00
<i>Eurytela dryope</i>	DRF–NR	0.00	0.00	0.10	0.00	0.32	0.07
<i>Catuna crithea</i>	ALF–CO	0.13	0.11	0.00	0.00	0.00	0.00
<i>Catuna</i> sp. B	?	0.00	0.16	0.00	0.00	0.00	0.00
<i>Cymothoe caenis</i>	ALF–CO	0.00	0.00	0.00	0.15	0.00	0.21
<i>Cymothoe fumana</i>	MF–CO	0.06	0.00	0.00	0.00	0.00	0.00
<i>Harma theobene</i>	MF–CO	0.00	0.11	0.00	0.15	0.00	0.07
<i>Pseudacraea lucretia</i>	ALF–CO	0.06	0.00	0.00	0.00	0.00	0.00
Charaxinae							
<i>Charaxes bipunctatus</i>	WF–NR	0.06	0.00	0.40	0.00	0.63	0.14
<i>Charaxes cynthia</i>	ALF–CO	0.00	0.05	0.00	0.00	0.32	0.00
<i>Charaxes eupale</i>	ALF–CO	0.00	0.00	0.00	0.00	0.32	0.00
<i>Charaxes fulvescens</i>	ALF–CO	0.19	0.00	0.10	0.00	0.00	0.00
<i>Charaxes numenes</i>	ALF–NR	0.06	0.11	0.10	0.00	0.00	0.14
<i>Charaxes pleione</i>	ALF–CO	0.00	0.00	0.10	0.00	0.00	0.00
<i>Charaxes protoctea</i>	ALF–CO	0.32	0.00	0.20	0.45	0.95	0.07
<i>Charaxes tiridates</i>	ALF–CO	0.00	0.05	0.00	0.00	0.00	0.21
<i>Charaxes varanes</i>	GUI–CO	0.06	0.00	0.00	0.00	0.32	0.14
<i>Charaxes zingha</i>	MF–NR	0.00	0.00	0.00	0.00	0.00	0.14
<i>Palla decius</i>	MF–NR	0.00	0.38	0.00	0.00	0.95	0.14
<i>Pala violinitens</i>	MF–NR	0.00	0.00	0.10	0.00	0.00	0.00
Nymphalinae							
<i>Kallima rumia</i>	ALF–CO	0.19	0.00	0.00	0.00	0.00	0.00
<i>Hypolimnas anhedon</i>	ALF–CO	0.00	0.00	0.10	0.00	0.00	0.14
<i>Hypolimnas salmacis</i>	ALF–CO	0.00	0.05	0.00	0.00	0.00	0.00
<i>Junonia terea</i>	ALF–VC	0.00	0.00	0.00	0.00	0.00	0.07
Acraeinae							
<i>Alcrea alciope</i>	ALF–VC	0.00	0.00	0.00	0.15	0.00	0.00
Total collected		1581	1843	998	671	315	1429

Numbers are relative abundances based on the total sample size from that site.

Forest zone and abundance categories are from Emmel and Larsen (1997) and Larsen (2001). Forest zone designations: WF, Wet forest; MF, Moist forest; DRF, Dry forest; ALF, All forest subtypes; GUI, Guinea Savannah; UBQ, Ubiquitous; SPE, Special habitat. Abundance designations: VC, Very common; CO, Common; NR, Not rare; RA, Rare; VR, Very rare.

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