Distance from Edge Determines Fruit-Feeding Butterfly Community Diversity in Afrotropical Forest Fragments

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ABSTRACT We studied the impact of forest edges on the fruit-feeding butterfly communities of three forest remnants in Ghana, West Africa. Community diversity was assessed using traps baited with fermenting banana. Two 200-m, edge-to-interior transects of five traps each were established in each forest. Sampling spanned 1 yr for a total of 180–210 trap days per site and resulted in 2,634 specimens and 56 species. We found significant support for an effect of forest edge on butterfly diversity. The impact of distance from edge on point estimates of diversity, i.e., total trap captures, weighted species richness, and Simpson's diversity, was unique to each forest. Multivariate analyses, which integrated species composition along with relative abundance and richness, uncovered two broad community types, interior communities (those 100, 150, and 200 m distant from the edge) and exterior communities (edge communities and those 50 m distant), indicating that edge habitat generally extends at least 50 m into the forest. However, effects of edges on community diversity were still detected as far as 100 m into the forest. Three species relatively tolerant of forest degradation emerged as indicators of edge habitat. No species were indicative of core habitat.

KEY WORDS edge effects, fragmentation, nonmetric multidimensional scaling, sacred groves, West Africa

Human transformation of landscapes has converted former expanses of intact habitat into remnant, and often degraded, habitat patches embedded in a derived landscape matrix. Although habitat fragmentation is pervasive at all landscape scales and affects virtually all habitat types, fragmentation of forested areas generally has the most significant implications for biodiversity because the ensuing contrast between transformed versus untransformed landscape is so severe. This creation of an open, structurally simplified surrounding matrix amplifies the impacts of external influences on the forest patch and impedes metapopulation dynamics (Laurance and Bierregaard 1997).

A fundamental consequence of fragmentation is an increase in the extent of boundary or edge habitat relative to unaffected interior or core habitat. Forest edges catalyze myriad physical and ecological changes to the forest patch environment because of this shared boundary with a sharply contrasting surrounding landscape (Saunders et al. 1991, Matlock 1993, 1994, Murcia 1995, Donovan et al. 1997). The severity and extent of these modifications, or edge effects, depend on the size of the forest patch and degree to which specific external influences are able to penetrate the patch interior (Murcia 1995, Didham et al. 1998, Ries and

Sisk 2004, Ewers et al. 2007). Edge effects can be so pervasive in small forest fragments that in essence these patches cease to function as forest habitat or to support forest-specific species.

Forest fragmentation is a primary determinant of global biodiversity decline (Czech and Krausman 1997, Laurance and Bierregaard 1997). Undoubtedly, at least part of this decline is caused by the cascading ramifications of decreased patch quality that stems from increased edge exposure. Most of what we know about the impact of edges on fragmented forest communities derives largely from study of vertebrate species, especially birds and their nest predators (e.g., see references in Ries et al. 2004). Much less is known about the impact of edges on arthropod communities even though arthropods are superlative ecological indicators because of their enormous numbers; functional, life history, and taxonomic diversity; high rates of endemism and speciation; global and ecological ubiquity; and rapid response to environmental change. The large majority of edge effects studies have, additionally, generally targeted a single species or a very small group of species; investigations of their impact on community diversity per se are uncommon.

Few regions in the world have experienced as extensive fragmentation as the Upper Guinean forests of Ghana, West Africa (Hall and Swain 1981, Hawthorne 1989, Whitmore 1997, Goudie 2000, Myers et al. 2000). Historically, most of the southwestern one third of the country was covered by forest, interspersed by dense

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Table 1. Site-specific data

Forest fragment	Size (ha)	Global coordinates	Total trap days	Total captures	Observed species richness	Menhinick's richness	Simpson's diversity
Bobiri Forest Reserve	5,000	6°40′N1°19′W	210	708	44	1.65	6.15
Owabi Wildlife Sanctuary	1,200	6°44′N1°42′W	190	1030	47	1.47	17.87
Asantemanso Sacred Grove	100	6°28′N1°33′W	180	896	31	1.04	7.74

Total trap days is the no. of sampling trips to a site multiplied by the total no. of traps.

Guinea Savanna. However, much of this former forested landscape has been converted to highly derived manmade savanna or agropastoral lands. Remaining forested areas are thought to comprise only 10–15% of their original extent, and these are highly isolated (Hawthorne and Abu-Juam 1995). Nearly no closed canopy forests exist outside reserve boundaries. Of the ≈1% that does, most is in the form of small remnants that persist solely because of their cultural significance as sacred forest groves and their long history of protection through traditional belief systems (Lebbie and Freudenburger 1996, Ntiamoa-Baidu 2001). Although broad scale fragmentation of the country's forests has almost certainly detrimentally affected Ghana's forest dependent species, empirical data from study of these communities are just beginning to accumulate (Decher 1997, Beier et al. 2002, Brashares 2003, Davis and Phillips 2005, Bossart et al. 2005, 2006). Such data are increasingly needed given the external pressures that continue to undermine sustained protection of forest reserves in the country (McCullough et al. 2007).

Nearly all arthropod-focused, forest edge-to-interior studies conducted to date have targeted beetles, particularly the carabids (Didham et al. 1998, Davies and Margules 1998, Heliölä et al. 2001, Magura et al. 2001, Koivula et al. 2004, Spector and Ayzama 2003, Phillips et al. 2006, Baker et al. 2007, Ewers et al. 2007, although see Bolger et al. 2001, Martin and Major 2001, Vandergast and Gillespie 2004). Here we quantify community structure of fruit-feeding butterflies along forest edge-to-interior transects in three forest fragments in the moist semideciduous forest zone of Ghana, West Africa. Butterflies are excellent model systems for evaluating community dynamics in transformed landscapes (Kremen 1992; DeVries et al. 1997; Brown and Freitas 2000; Fermon et al. 2000, Hamer et al. 2003, Stork et al. 2003). They show a diversity of relative sensitivities to environmental change, span the array of inherent abundances, from exceedingly rare to very common, are tightly intertwined with ecological systems as both primary consumers (herbivores) and food items (prey), and are easily and systematically collected.

This study is one of a series from our on going investigations of the impact of fragmentation on forest butterfly communities. Our primary goals here were to assess how overall forest community structure changed with increasing distance from the edge, to identify the distance to which edge effects penetrate the forest and impact community structure, and to determine whether particular species would emerge as indicators of core versus edge habitat. To the best of our knowledge, this study represents the first on edge effects from the fragmented forests of West Africa.

Materials and Methods

Study Area and Sites. The forests of Ghana comprise four increasingly dry vegetational zones. These are arranged as concentric bands, beginning with the wet evergreen forests in the southwest corner of the country, extending outward through the moist evergreen, moist semideciduous, and dry semideciduous forest zones (Hawthorne and Abu-Juam 1995). Our study was conducted in three isolated forest fragments located in the moist semideciduous forest zone of Ghana (Table 1). The study fragments ranged in size from ≈100 to 5,000 ha. All three are located in the Ashanti Region and situated within an ≈35-km radius of Kumasi (shown in Bossart et al. 2006), which facilitated recurring sampling of multiple sites. Two of the three forest sites are gazetted reserves (Bobiri Forest Reserve and Owabi Wildlife Sanctuary). The third is a long-protected, sacred grove (Asantemanso Sacred Forest). Each forest is completely surrounded by an anthropogenically derived farm bush savanna matrix, except for Owabi, which on one side abuts the reservoir that supplies drinking water to the city of Kumasi. The edge perimeter of each forest constitutes a severe and abrupt boundary between forest vegetation and the surrounding, matrix.

Sampling Design. The fruit-feeding butterfly communities at each site were surveyed using typical fruit-baited traps. Two forest edge-to-interior transects of five traps each were established in each forest for a total of 30 traps across all sites (10 traps at each of three sites). Transects within a site were separated by >300 m. Each transect was established by walking perpendicular from the forest edge into the forest interior using a compass to set direction and a meter tape to determine distance. A machete was used where necessary to gain passage through the understory. Traps were hung ≈10–15 cm above the ground at 50-m intervals along the 200-m transect. The first and last trap on a transect were hung at the forest edge and the 200-m point, respectively. Conscious effort was taken to establish transects in areas of closed canopy forest and to place all traps in similar micro habitats within the forest.

Sampling occurred from late June 2001 through July 2002. Sampling was more frequent during the rainy season when the senior author was in the country

(roughly, mid-May through early August) and less frequent during the remainder of the year. In general, sampling occurred weekly from June through mid-August 2001, monthly between September 2001 and May 2002, and biweekly thereafter. Sampling at a given site consisted of baiting the traps with mashed, fermenting banana and retrieving trap collections the following day $\approx$24 h later. Different sites were sampled on sequential days within a 5-d period during a given sampling bout.

Identifications. Species were identified by the senior author using taxonomic treatises by D'Abrera (2001), Hecq (1997, 1999, 2000, 2002), Henning (1988), and Larsen (2005). The vast majority of Ghana's butterflies are easily identified based on wing color patterns and wing morphology. The few difficult specimens were identified in consultation with Dr. Torben Larsen, an internationally renowned expert on butterflies of West Africa, and Dr. John Rawlins, Associate Curator, Section of Invertebrate Zoology, Carnegie Museum of Natural History (CMNH). Voucher specimens of species collected during the study have been deposited at the CMNH, Section of Invertebrate Zoology.

Statistical Analyses. Community diversity of trap collections was quantified in two ways: first using the point statistics, total trap captures, species richness, and Simpson's index of diversity, and second, using the multivariate ordination procedure, nonmetric multidimensional scaling (NMDS; CAP 3.11, Pisces Conservation 2004).

Point Statistics. Species richness and total sample size are strongly positively correlated unless the total number of species at a site has been completely sampled (Gotelli and Colwell 2001, Magurran 2004). In our study, new species were still being accumulated when sampling ended (Bossart et al. 2006). To compensate for richness-sample size correlations, we used the intuitively meaningful and easily calculated, Menhinick's Index of species richness (Magurran 2004). This index is given by $D_{MN} = S/\sqrt{N}$, where S is observed total richness in a sample and N is the total number of specimens collected in that sample.

Simpson's index is an overall measure of community heterogeneity that combines both species richness and evenness into a single number and is given by $D_{SM} = \sum [n_i(n_i - 1)] / [N_i(N_i - 1)]$ for a finite community, where n_i is the abundance of the ith species and N_i is total sample size. Increasing values of D_{SM} indicate decreasing evenness, and hence, lower community diversity. We calculated the inverse form ($1/D_{SM}$), such that larger numbers would correspond with greater diversity, using EstimateS, Version 6.01b (Colwell 2000). Although single measures of overall diversity can be problematic (Magurran 2004), they continue to be widely requested and reported. Simpson's index is considered the most robust and biologically meaningful of those available (Magurran 2004).

We used the general linear method (GLM; SAS 2004) to quantify the relative contribution of forest site (forest effect), transects nested within forests [transect(forest) effect], trap distance from forest edge (trap effect), and forest by trap interaction (forest $\times$ trap effect) to variance in each measure of diversity (i.e., Menhinick's and Simpson's diversity) and to the number of specimens collected in traps. To further explore the specific form of the relationship between each dependent variable and trap distance from edge (our primary interest), least square means for each forest–trap combination generated from the GLM analysis were subsequently regressed on distance from edge.

Multivariate Statistics. Our community data comprise an N sample units (traps) $\times$ M species matrix, where each element of the matrix is the abundance of a given species in a given trap sample. Snapshot measures of community diversity, such as species richness and Simpson's diversity, are unable to capture the full information available in complex multivariate data sets. NMDS uncovers patterns of covariation in species distributions among trap samples by reducing the dimensionality of an $N \times M$ species abundance matrix into a few ordination axes. This ordination procedure is considered the overall most effective and the best choice for analysis of community data (McCune and Grace 2002). NMDS first converts N lists of species and their abundances into a matrix of single numbers by calculating the distance between pairwise comparisons of all N samples (i.e., it calculates a dissimilarity matrix). It then uses an iterative process to position these distance values in multidimensional space such that "stress" is minimized. Stress is minimized when the most similar community samples are grouped as close together as possible in space, while at the same time the most dissimilar samples are kept as distant as possible.

Raw data were square root transformed before analysis to give less weight to species that dominated the community data (Jongman et al. 1995). The initial distance matrix was calculated using the Bray-Curtis abundance based index (also known as the Sørensen quantitative index), which is considered the generally most effective measure of community similarity (Legendre and Gallagher 2001, McArdle and Anderson 2001, Magurran 2004). In CAP, initial starting coordinates for the NMDS can be assigned using either a random numbers generator or a principal coordinates analysis (PCA). We ran the program multiple times using the random numbers generator and compared results with those obtained from the PCA to ensure that our analysis had converged on a global, rather than local, stress minimum. In all cases, the algorithm was run for 200 iterations.

Axis-1 and axis-2 ordinate values generated from the NMDS were subsequently subjected to joint analysis using multivariate analysis of variance (MANOVA statement in GLM, SAS 2004) to statistically test whether trap samples clustered in two-dimensional space because of the effects of forest site, transects within forest, trap distance from edge, and forest by trap interaction (Gotelli and Ellison 2004). Ordinal values were also analyzed for each axis independently to assess how effects included in the model contributed to separation of samples along a single axis. In

Table 2. GLM analysis of point estimates of diversity

Source of variation	df	Total captures		Menhinick's richness		Simpson's diversity	
		MS	F ratio	MS	F ratio	MS	F ratio
Forest[a]	2	2457.23	1.90	1.4520	62.74[b]	298.087	88.09[b]
Transect(forest)	3	1294.97	5.05[c]	0.0696	0.25	3.366	0.57
Trap	4	2935.78	11.44[b]	0.3693	0.96	2.436	0.41
Forest × trap	8	1274.86	4.97[d]	0.7023	0.93	18.472	3.11[c]
Error	12	256.63		0.0942		5.943	

[a] F test denominator for forest was $MS_{Transect(Forest)}$.
[b] $P \leq 0.006$.
[c] $P \leq 0.05$.
[d] $P \leq 0.01$.

both the MANOVA and independent analysis of variances (ANOVAs), we used linear contrasts (CONTRAST statement in GLM; SAS 2004) to test specific hypotheses about how traps clustered with respect to their relative order on the edge-to-interior transect. Four hypotheses were tested (1) edge traps differ from all others, (2) the exterior most traps (edge and 50-m traps) differ from the interior most traps (150- and 200-m traps), (3) traps differ along a linear gradient, and (4) traps at 100 m differ from all others. These tests involved both planned (i.e., numbers 1–3) and unplanned (i.e., number 4) comparisons. To ensure an experiment-wise error rate of $\alpha \leq 0.05$, we used a corrected critical value of $P = 0.013$ to assess significance of each of the four comparisons following the method of Dunn-Šidák. The corrected critical value, α', is given as $1 - (1 - \alpha)^{1/k}$, where k is the number of individual comparisons to be made (Sokal and Rohlf 1995). Least square means generated from the MANOVA for each trap distance were plotted for axis-1 and axis-2 to further explore the relationship among trap collections.

We used the method of Dufrêne and Legendre (1997) to quantify species' indicator values (McCune and Mefford 1999; PC-ORD, version 4.25). This analysis integrates both species fidelity (the degree to which a species is found only in a particular group) with its relative abundance. Indicator values range from 0 (no indication) to 100 (perfect indication). Perfect indication occurs if all individuals of a particular species are found only in a single group and if that species is present in all sites of that group. Statistical significance is assessed using Monte Carlo randomization. In our case, group is defined as trap distance from edge. Thus, a perfect indicator species for a particular trap distance would be found only at that distance and in all traps at that distance.

Results

Point Statistics. Each site was sampled from 18 to 21 times throughout the course of the study, resulting in a total of 56 species collected from the 30 traps. Although the largest number of species was collected from the 10 traps at Owabi, more specimens were also collected from this site than from the other sites (Table 1). Menhinick's richness was highest at Bobiri, exceeding that at Owabi and Asantemanso by 13 and 60%, respectively (Table 1). Simpson's index of overall diversity differed markedly between Owabi and the other two sites. At Owabi, this value was more than double that at Bobiri or Asantemanso, indicating the relative abundances of species in Owabi trap collections were much more equitably represented than the abundances of species in Bobiri or Asantemanso collections.

Forest site explained a significant portion of the variation in least square mean captures, Menhinick's richness, and Simpson's diversity (Table 2, forest effect). In contrast, trap distance from edge, our primary factor of interest, only accounted for variation associated with total trap captures (Table 2, trap effect), and this effect was forest dependent (Table 2, forest × trap effect). At Owabi and Asantemanso, significantly more butterflies were caught in traps closer to the edge versus interior traps (Fig. 1a). This difference was especially pronounced at Owabi, where edge trap collections were nearly twice as large as those from any other trap. At Bobiri, however, total captures in edge traps was no different than the number collected from other traps along the transect (Fig. 1a). The absence of an overall effect of trap distance from edge on Menhinick's and Simpson's index is partially explained by the divergent patterns of response in the different forests (Fig. 1b,c; Table 2, forest × trap effect). In Owabi, both richness and overall diversity increased with increased distance from the edge ($r^2 = 0.60$, $P = 0.009$ and $r^2 = 0.51$, $P = 0.012$ for Menhinick's richness and Simpson's undex, respectively). However, in Bobiri, overall diversity decreased with increased distance from the edge ($r^2 = 0.57$, $P = 0.007$) and richness remained relatively constant ($r^2 = 0.06$, $P = 0.492$). In Asantemanso, neither diversity measure was significantly linked with distance from edge ($r^2 = 0.21$, $P = 0.178$ and $r^2 = -0.03$, $P = 0.423$).

Multivariate Statistics. The NMDS algorithm produced nearly identical solutions regardless of whether a PCA or a random numbers generator was used to set initial starting conditions. We report results obtained using PCA to determine the initial configuration, the default condition in CAP. Three-dimensional NMDS solutions generated stress values that were slightly less (0.121 ± 0.0030 SD) than those obtained from two-dimensional solutions (0.163 ± 0.0045 SD). However, all relevant separations of trap samples were readily
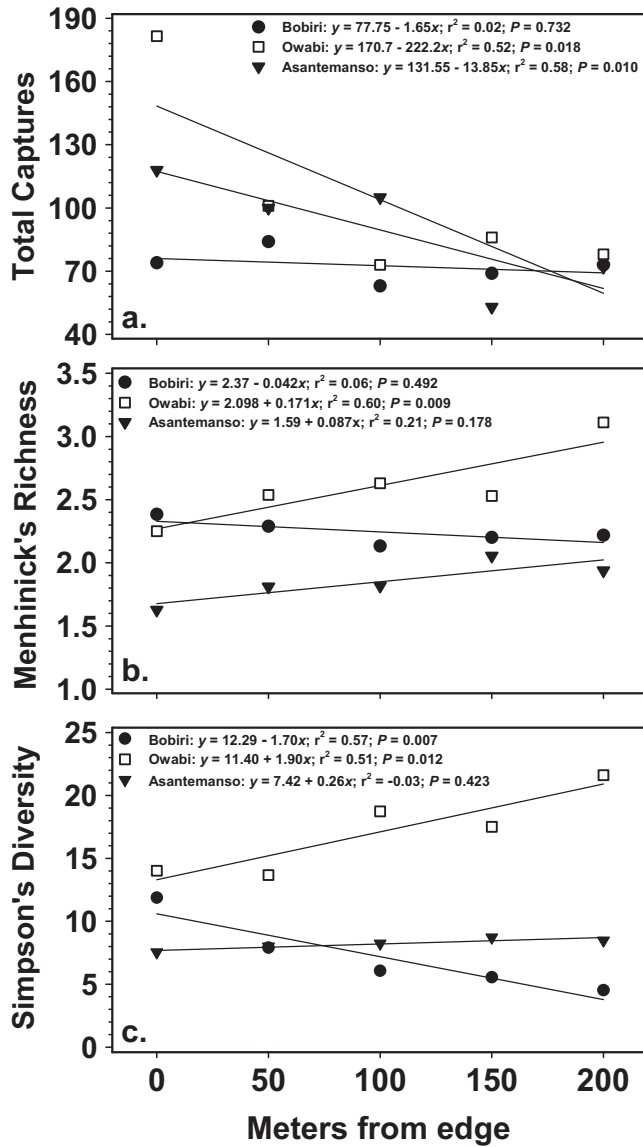
Fig. 1. Regressions of point estimates of diversity on trap distance from forest edge for each of three forest sites. (a) Total trap captures. (b) Menhinick's species richness. (c) Simpson's index of community diversity.

apparent in only two dimensions (Fig. 2), so only these are reported here for ease of visual interpretation.

With a full model fitted to the data, the relative effect of trap distance from edge did not differ across forests (forest × trap effect, $P = 0.648$, $P = 0.562$, and $P = 0.490$ from a MANOVA, axis-1 ANOVA, and axis-2 ANOVA, respectively). Thus the reduced model, with forest, trap, and transect(forests) as the independent variables, more accurately accounts for expressed variation and is the more powerful test of the effect of each factor on the ordering of trap samples in two-dimensional space.

Trap samples separated foremost with respect to forest site (Fig. 2; Table 3, forest effect), indicating that trap collections from each forest were more sim-

ilar to each other than to those from other forests. Clustering of forest samples was largely a consequence of separation along axis one (Table 4a versus 4b, forest effect), where Bobiri, Owabi, and Asantemanso samples were ordered from left to right along the axis, respectively (Fig. 2). Although Owabi samples seemed to also separate away from Bobiri and Asantemanso samples along axis-2 (Fig. 2), this difference was not significant (Table 4b, forest effect). Transects within forests also determined the composition of butterfly communities collected in traps [Table 3, transect(forest) effect]. These differences among transects were entirely a consequence of separation of transect one and two collections along axis-2 [Table 4a versus 4b, transect(Forest) effect], largely because
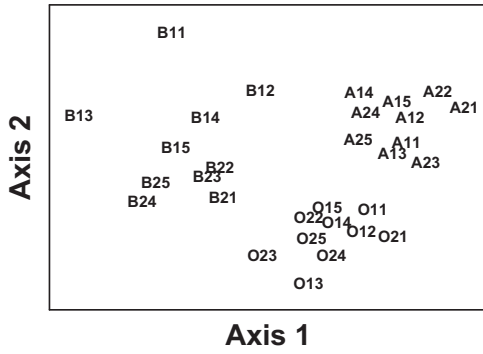
Fig. 2. Nonmetric multidimensional scaling ordination of trap collections of fruit-feeding butterflies. Points indicate trap locations coded by forest (first position: A, Asantemanso; B, Bobiri; O, Owabi), transect (second position: 1 or 2), and distance from edge (third position: 1, edge; 2, 50 m; 3, 100 m; 4, 150 m; 5, 200 m). Trap collections that are closer together are more similar to each other and vice versa.

of differences between the two transects at Bobiri (Fig. 2).

We found significant support for our primary hypothesis that distance from edge determines the structure of butterfly communities collected in traps (Table 3, trap effect). The most obvious clustering was of traps 150 and 200 m distant from the edge (Fig. 2). Within each forest, these interior-most traps were positioned in close proximity regardless of which transect they were located on. Although not as definitive, edge traps and those 50 m distant from the edge also tended to cluster together within forests. Both axes contributed to the significant separation of traps in two-dimensional space, but this ordering was most pronounced along axis-1 (Table 4a versus 4b, trap effect), where traps 150 and 200 m into the forest interior typically positioned to the left of traps at the edge and 50 m in.

Three of the four comparisons that tested the relative order of traps along the transect were significant (Table 3, planned contrasts). In general, change in community structure with increasing distance from

Table 3.   MANOVA of NMDS ordinal data

Effect	F ratio	N df	D df	P
Forest[a]	11.35	4	6	0.0058
Transect(forest)	3.26	6	40	0.0105
Trap	2.47	8	40	0.0282
Contrasts among traps[b]				
1 versus all others	4.19	2	19	0.0311
1 and 2 versus 4 and 5	7.76	2	19	0.0034
Linear	6.95	2	19	0.0054
3 versus all others	6.78	2	19	0.0060

Probability values reported are for Pillai's trace. Contrasts among traps: 1, edge traps; 2, 50-m traps; 3, 100-m traps; 4, 150-m traps; 5, 200-m traps.

[a] F test denominator for forest was $MS_{Transect(Forest)}$.

[b] A Dunn-Šidák corrected critical value of $P = 0.013$ was used to determine significance of individual contrasts to ensure an experiment-wise error rate of $\alpha = 0.05$.

Table 4.   ANOVA of axis-1 (a) and axis-2 (b) ordinal data

Source	df	Mean square	F ratio	P
(a) Axis-1				
Forest[a]	2	7.4948	177.77	<0.0018
Transect(forest)	3	0.0422	0.53	0.6700
Trap	4	0.2822	3.51	0.0250
Contrasts among traps[b]				
1 versus all others	1	0.4909	6.11	0.0225
1 and 2 versus 4 and 5	1	0.8000	9.96	0.0050
Linear	1	0.7599	9.46	0.0060
3 versus all others	1	0.3223	4.01	0.0588
(b) Axis-2				
Forest[a]	2	3.6030	5.15	0.1070
Transect(forest)	3	0.6990	9.24	0.0005
Trap	4	0.2177	2.88	0.0494
Contrasts among traps[b]				
1 versus all others	1	0.0948	1.25	0.2762
1 and 2 versus 4 and 5	1	0.2577	3.41	0.0797
Linear	1	0.1978	2.61	0.1215
3 versus all others	1	0.5678	7.51	0.0126

Contrasts among traps: 1, edge traps; 2, 50-m traps; 3, 100-m traps; 4, 150-m traps; 5, 200-m traps.

[a] F test denominator for Forest was $MS_{Transect(Forest)}$.

[b] A Dunn-Šidák corrected critical value of $P = 0.013$ was used to determine significance of individual contrasts to ensure an experiment-wise error rate of $\alpha = 0.05$.
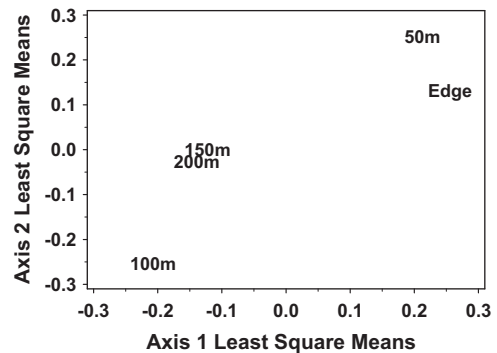
edge was broadly linear (Fig. 3; Table 3, planned contrast: linear), as is expected if community dissimilarity increases from the forest edge to the interior. However, this linearity was nearly entirely a consequence of separation of the exterior most versus interior most trap collections. Edge and 50-m collections were most similar to each other and statistically distinctive from the 150- and 200-m collections, which were likewise most similar to each other (Fig. 3; Table 3, planned contrast: 1 and 2 versus 4 and 5). Notably, collections from traps at the midpoint on the transects, i.e., 100 m, were a conspicuous exception to this overall pattern of linear change (Fig. 3). These midpoint collections were expected to comprise a mixture of the exterior and interior collections and hence to position in between, and in line with, the other values. But instead the intermediate trap communities

Fig. 3. Plot of least square means for each trap distance from forest edge. Trap distance is used as the point symbol. Least square means are from a MANOVA of the NMDS ordinal values.

shared less similarity with the edge and 50-m collections than did those from even further into the forest (Fig. 3) and had a structure uniquely distinctive from all the rest (Table 3, unplanned contrast: 3 versus all others).

Only 3 of the 56 species collected (*Euphaedra ceres*, *Bicyclus vulgaris*, and *Melanitis leda*) emerged as indicator species and these were far from a perfect indication of 100 (indicator values ranged from 37 to 45%; $P \leq 0.05$). Although all three were predominately associated with traps on or near the edge, they were found at more interior traps as well (Appendix 1). No species was characteristic of interior/core habitat.

Discussion

When measured as point estimates of diversity (total captures, weighted species richness, and Simpson's diversity), effects of forest edge on butterfly community structure differed across our three study sites. The only apparent impact on the Asantemanso community was a decrease in the numbers of butterflies collected from the interior-most traps relative to traps nearer the edge. At Bobiri, Simpson's index was correlated with distance but not Menhinick's richness or total captures. This suggests that changes along the edge-interior gradient were caused by differences in relative species abundances rather than total species richness. Additionally, because overall diversity decreased with increasing distance from edge, relatively more species benefited by edge-associated environmental changes. At Owabi, both the number of species and overall diversity were significantly correlated with distance and in a direction opposite that observed at Bobiri. This positive distance-diversity association indicates that relatively more species were detrimentally affected by edge habitat in this community, with some apparently avoiding edges.

Inherent differences in butterfly community structure among forest fragments are likely both a basis for and consequence of the differential impact of edges on each. Responses to edges are species specific and altered by a complex interplay of fragment- and matrix-associated characteristics, e.g., fragment size and condition, age and orientation of the edge, and features of the surrounding landscape (Ries and Sisk 2004, Ewers and Didham 2006, Ewers et al. 2007, Laurance et al. 2007). In our case, all transects were established where forest habitat formed an abrupt edge with adjoining farm bush savanna and the vegetational structure of the surrounding landscape was broadly similar. Fragment size, however, is very different among forests and was undoubtedly a key mitigating factor both in terms of size of resident communities (i.e., species-area relationship issues) and relative extent and penetrance of edge effects (i.e., higher in smaller fragments). Edge and area have been shown to interact synergistically in forest beetle communities, changing both the strength and slope of the response (Ewers et al. 2007).

Ghana's forest butterflies also differ substantially in terms of their relative rarity and tolerance to forest degradation (Larsen 2005), and species found in smaller fragments comprise only a subset of those found in larger fragments (Bossart et al. 2005, 2006). Many of those lost from smaller forest patches are forest-floor specialists and restricted to high quality forests with complete canopy (Bossart et al. 2005, Larsen 2005). This differential loss of sensitive species could explain the apparent lack of a distance-diversity relationship at Asantemanso, where most species that comprise this smaller community are generally tolerant of forest degradation (Bossart et al. 2005). However, results for Bobiri and Owabi are opposite to what we would have predicted. Bobiri is the largest forest with the largest species pool, and many member species are particularly vulnerable to habitat degradation (Bossart et al. 2005). Owabi is a significantly smaller forest with a significantly less speciose forest butterfly community, and a greater percentage of the community that is generally tolerant of forest degradation (because vulnerable species have already been lost). Consequently, relatively more forest species should have been adversely affected by edges at Bobiri rather than at Owabi, but in fact, the opposite was observed.

Although measurable changes in point estimates of total diversity are evidence that edge effects are at work, the reverse is not necessarily the case. Species richness, for example, is routinely used to quantify impacts of edges on community diversity (Davies and Margules 1998, Spector and Ayzama 2003, Ries et al. 2004, Vandergast and Gillespie 2004), and edge effects are concluded to be absent when observed richness is similar across habitats. Total richness, however, does not show changes in community composition, and two communities could have equal numbers of species with zero species overlap. Ordination analyses permit a more holistic evaluation of heterogeneity of species assemblages along environmental gradients. Our study is a case in point. Total richness at Asantemanso and Bobiri was not correlated with distance from edge. Yet the ordination analysis revealed a significant influence of edge perimeter on both these forest communities, most obviously as clustering among the interior-most trap collections (Fig. 2).

Our most intriguing and also most puzzling result concerns trap collections at the midpoint along transects. These collections separated from the others, particularly along axis-2, and did not follow our a priori expectation that assemblages would vary monotonically with distance from edge (Table 3, contrasts among traps: 3 versus all others; Fig. 3). This result does not seem to be an artifact given that at least four traps from two different transects within each of two different forests (Asantemanso and Owabi) showed the same response (Fig. 2). What is driving this idiosyncratic response? Multiple edge effects can have additive, opposing, or synergistic influences, and response intensity and

slope can be modified by proximity of other edges and extent of habitat contrast with the adjacent matrix (Ries et al. 2004, Ewers et al. 2007). For variables that exhibit continuous change (e.g., species richness or leaf water content) response peaks and depressions (i.e., waves) at intermediate distances along edge-interior gradients are not uncommon (Kroodsma 1982, Kapos 1989, Hester and Hobbs 1992, Dignan and Bren 2003), and these are thought to be a consequence of cascading interactions among abiotic and biotic effects (Murcia 1995). Our ordination analyses, however, quantified overall similarity/dissimilarity among pairs of trap communities rather than change in a single response variable. How multiple edge induced changes could integrate to produce communities that share more features with distant communities (e.g., 50- and 200-m collections) than with proximal communities (e.g., 50-m and midpoint collections) is not immediately obvious to us. Studies designed to explicitly reveal the nature of this response and factors at work will be necessary to resolve this issue.

The pattern of separation of trap communities suggests a general conclusion regarding the distance to which edge effects penetrate the forest interior. First, only two broad community groupings separated along axis-1 (Fig. 3): habitat edge communities (i.e., edge and 50-m traps) and habitat core communities (i.e., all the rest). Second, communities trapped at 150 and 200 m were tightly clustered, both within forests (Fig. 2) and averaged across forests (Fig. 3). Finally, the idiosyncratic response of the intermediate collections indicates at least some edge effects penetrate at least 100 m into the forest interior. Considered together, this suggests that edge habitat generally extends at least 50 m into the forest interior, resulting in close similarity between the two exterior-most trap communities. Most edge induced changes no longer impact community structure by 100 m, although those that do persist impact communities in unobvious ways. Communities apparently cease to be modified by edge effects at some distance past 100 m but before 150 m, resulting in tight resemblance between the 150- and 200-m collections.

Our previous research established that Ghana's forest butterflies exhibit differential sensitivities to fragmentation, with smaller communities having a much smaller fraction of vulnerable species relative to larger communities (Bossart et al. 2005, 2006). Based on these earlier findings, we predicted that certain species would emerge as valuable indicators of intact forest by virtue of their association with deep forest. However, no species was a clear edge avoider and trapped only in the forest interior. In general, the presence of particular species along the transect could not be unambiguously linked to distance from edge, even at a very basic level (Appendix 1). All three of the edge indicator species were also trapped well within the forest interior. Similarly, a number of species originally predicted to be definite edge avoiders because of their fidelity to

high quality forest and sensitivity to fragmentation were trapped at the edge. Considered in combination, these results suggest that increased edge exposure may not be a major factor underlying the differential loss of sensitive species from the smaller forest fragments we are studying, at least not directly.

References Cited

Baker, S.C.B., L. A. Barmuta, P. B. McQuillan, and A.M.M. Richardson. 2007. Estimating edge effects on ground-dwelling beetles at clearfelled non-riparian stand edges in Tasmanian wet eucalypt forest. Forest Ecol. Manag. 239: 92–101.

Beier, P., M. van Drielen, and B. O. Kankam. 2002. Avifaunal collapse in West African forest fragments. Conserv. Biol. 164: 1097–1111.

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2001. Arthropods in urban habitat fragments in southern California: area, age, and edge effects. Ecol. Appl. 10: 1230–1248.

Bossart, J. L., E. Opuni-Frimpong, S. Kuudaar, and E. Nkrumah. 2005. Fruit-feeding butterfly communities of forest 'islands' in Ghana: survey completeness and spatial correlates of diversity, pp. 151–158. *In:* B. A. Huber, B. J. Sinclair, and K.-H. Lampe (eds.), African biodiversity: molecules, organisms, ecosystems. Proceedings of the 5th International Symposium on Tropical Biology. Springer, New York, New York.

Bossart, J. L., E. Opuni-Frimpong, S. Kuudaar, and E. Nkrumah. 2006. Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. Biodiv. Conserv. 15: 333–359.

Brashares, J. S. 2003. Ecological, behavioral, and life-history correlates of mammal extinctions in West Africa. Conserv. Biol. 17: 733–743.

Brown, K. S., Jr., and A.V.L. Freitas. 2000. Atlantic Forest butterflies: indicators for landscape conservation. Biotropica 32: 934–956.

Colwell, R. K. 2000. EstimateS: statistical estimation of species richness and shared species from samples. Version 6.0b1. User's guide and application. (http://viceroy.eeb.uconn.edu/EstimateS).

Czech, B., and P. R. Krausman. 1997. Distribution and causation of species endangerment in the United States. Science 277: 1116–1117.

D'Abrera, B. 2001. The concise atlas of butterflies of the world. Hill House Publishers, Melbourne, Australia.

Davies, K. F., and C. R. Margules. 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. J. Anim. Ecol. 67: 460–471.

Davis, A.L.V., and T. K. Phillips. 2005. Effect of deforestation on a Southwest Ghana dung beetle assemblage (Coleoptera: Scarabaeidae) at the periphery of Ankasa Conservation Area. Environ. Entomol. 31: 319–330.

Decher, J. 1997. Conservation, small mammals, and the future of sacred groves in West Africa. Biodiv. Conserv. 6: 1007–1026.

DeVries, P., D. Murray, and R. Lande. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. Biol. J. Linn. Soc. 62: 343–364.

Didham, R. K., P. M. Hammond, J. H. Lawton, P. Eggleton, and N. E. Stork. 1998. Beetle species responses to tropical forest fragmentation. Ecol. Monogr. 68: 295–323.

Dignan, P., and L. Bren. 2003. Modeling light penetration edge effects for stream buffer design in mountain ash forest in southeastern Australia. Forest Ecol. Manag. 179: 95–106.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology 78: 2064–2075.

Dufrêne, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67: 345–366.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. 81: 117–142.

Ewers, R. M., S. Thorpe, and R. K. Didham. 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. Ecology 88: 96–106.

Fermon, H., M. Walter, T. B. Larsen, U. Dall'Asta, and M. Muhlenberg. 2000. Effects of forest management on diversity and abundance of fruit-feeding Nymphalid butterflies in south-eastern Cote d'Ivoire. J. Insect Conserv. 4: 173–189.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4: 379–391.

Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer, Sunderland, MA.

Goudie, A. 2000. The human impact on the natural environment, 5th ed. MIT Press, Cambridge, MA.

Hall, J. B., and M. D. Swain. 1981. Distribution and ecology of vascular plants in a tropical rain forest: forest vegetation of Ghana. W. Junk Publishers, The Hague.

Hamer, K. C., J. K. Hill, B. N. Mustaffa, T. N. Sherratt, M. Maryati, and V. K. Chey. 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. J. Appl. Ecol. 40: 150–162.

Hawthorne, W. D. 1989. The flora and vegetation of Ghana's forests, pp. 8–13. In J.L.G. Wong (ed.), Ghana forest inventory proceedings. Overseas Development Agency/ Ghana Forestry Department, Accra, Ghana.

Hawthorne, W. D., and M. Abu-Juam. 1995. Forest protection in Ghana. IUCN/ODA. IUCN Publishers, Cambridge, United Kingdom.

Hecq, J. 1997. Euphaedra. Lambillionea, Tervuren, Belgium.

Hecq, J. 1999. Euphaedra. In E. Bauer and T. Frankenbach (eds.), Butterflies of the world, part 4, Nymphalidae III. Goeke and Evers, Keltern, Germany.

Hecq, J. 2000. Bebearia. In E. Bauer and T. Frankenbach (eds.), Butterflies of the world, part 9, Nymphalidae IV. Goeke and Evers, Keltern, Germany.

Hecq, J. 2002. Euriphene. In E. Bauer and T. Frankenbach (eds.), Butterflies of the world, part 15, Nymphalidae VI. Goeke and Evers, Keltern, Germany.

Heliölä, J., M. Koivula, and J. Niemelä. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conserv. Biol. 15: 370–377.

Henning, S. F. 1988. The Charaxinae butterflies of Africa. Aloe Books, Capetown, South Africa.

Hester, A. J., and R. J. Hobbs. 1992. Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. J. Veg. Sci. 3: 101–108.

Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. Van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, New York.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. J. Trop. Ecol. 5: 173–185.

Koivula, M., V. Hyyryläinen, and E. Soininen. 2004. Carabid beetles (Coleoptera: Carabidae) at forest-farmland edges in southern Finland. J. Insect Conserv. 8: 297–309.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. Ecol. Appl. 2: 203–217.

Kroodsma, R. L. 1982. Edge effect on breeding forest birds along a power-line corridor. J. Appl. Ecol. 19: 361–370.

Larsen, T. B. 2005. Butterflies of West Africa. Appolo Books, Svenborg, Denmark.

Laurance, W. F., and R. O. Bierregaard, Jr. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL.

Laurance, W. F., H.E.M. Nascimento, S. G. Laurance, A. Andrade, R. M. Ewers, K. E. Harms, R.C.C. Luizao, and J. E. Ribeiro. 2007. Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. PLOS One 2: e107.

Lebbie, A. R., and M. S. Freudenberger. 1996. Sacred groves in Africa: forest patches in transition, pp. 300–324. In J. Schelhas and R. Greenberg (eds.), Forest patches in tropical landscapes. Island Press, Washington, DC.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia (Berl.) 129: 271–280.

Magura, T., B. Tóthmérész, and T. Molnár. 2001. Forest edge and diversity: carabids along forest-grassland transects. Biodiv. Conserv. 10: 287–300.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Malden, MA.

Martin, T. J., and R. E. Major. 2001. Changes in wolf spider (Araneae) assemblages across woodland-pasture boundaries in the central wheat-belt of New South Wales, Australia. Austral. Ecol. 26: 264–274.

Matlock, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biol. Conserv. 66: 185–194.

Matlock, G. R. 1994. Vegetation dynamics of the forest edge—trends in space and successional time. J. Ecol. 82: 113–123.

McArdle, B. H., and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82: 290–297.

McCullough, J., L. E. Alonso, P. Naskrecki, H. E. Wright, and Y. Osei-Owusu. 2007. A rapid biological assessment of the Atewa Range Forest Reserve, Eastern Ghana. RAP Bulletin of Biological Assessment 47. Center for Applied Biodiversity Science, Conservation International, Arlington, VA.

McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data, PC-ORD, version 4.25, MjM Software, Gleneden Beach, OR.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software Design, Gleneden Beach, OR.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10: 58–62.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Ntiamoa-Baidu, T. 2001. Indigenous versus introduced biodiversity conservation strategies: the case of protected area systems in Ghana, pp. 385–394. In: W. Weber, L.J.T. White, A. Vedder, and L. Naughton-Treves (eds.), African rain forest ecology & conservation. Yale University Press, New Haven, CT.

Pisces Conservation. 2005. CAP 3.1. Pisces Conservation, New Milton, United Kingdom.

Phillips, I. D., T. P. Cobb, J. R. Spence, and R. M Brigham. 2006. Salvage logging, edge effects, and carabid beetles: connections to conservation and sustainable forest management. Environ. Entomol. 35: 950–957.

Ries, L., and T. D. Sisk. 2004. A predictive model of edge effects. Ecology 85: 2917–2926.

Ries, L., R. J. Fletcher, Jr., J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu. Rev. Ecol. Syst. 35: 491–522.

SAS Institute. 2004. SAS/STAT user's guide, 9th ed. SAS Institute, Cary, NC.

Saunders, D. A., R. J. Hobbs, and C. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. 5: 1–15.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman and Co., New York.

Spector, S., and S. Ayzama. 2003. Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian Neotropical forest-savanna ecotones. Biotropica 35: 394–404.

Stork, N. E., D. S. Srivastava, A. D. Watt, and T. B. Larsen. 2003. Butterfly diversity and silvicultural practice in lowland rainforests of Cameroon. Biodiv. Conserv. 12: 387–410.

Vandergast, A. G., and R. G. Gillespie. 2004. Effects of natural forest fragmentation on a Hawaiian spider community. Environ. Entomol. 33: 1296–1305.

Whitmore, T. C. 1997. Tropical forest disturbance, disappearance, and species loss, pp. 3–12. In W. F. Laurance and R. O. Bierregaard, Jr. (eds.), Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, IL.

Appendix 1. Relative abundances of species trapped along forest edge-to-interior transects with individuals pooled across forests and transects for each trap distance

Species	Trap distance from edge				
	Edge	50 m	100 m	150 m	200 m
Aterica galene	4.26	3.82	5.07	5.73	4.34
Bebearia absolon	0.82	1.04	1.69	1.67	1.60
B. barce	0.14	0.35	0.00	0.00	0.00
B. cocalia	0.55	0.35	0.00	0.00	0.00
B. demetra	0.00	0.17	0.21	0.00	0.00
B. mandinga	0.41	0.52	0.21	1.67	0.00
B. mardania	0.69	0.35	0.42	0.24	0.46
B. oxione	0.27	0.35	0.21	0.48	0.46
B. phantasina	0.41	0.35	0.21	0.00	0.00
B. tentyris	5.77	11.46	9.94	13.37	16.21
B. zonara	1.92	1.04	2.11	2.63	3.20
Bicyclus abnormis	0.69	1.04	1.48	1.19	1.83
B. dorothea	1.51	0.52	0.00	0.24	0.68
B. funebris	4.67	3.47	2.75	5.49	4.34
B. madetes	0.55	0.69	0.63	0.95	0.23
B. martius	1.24	1.39	0.42	1.19	1.83
B. procora	0.00	0.00	1.27	0.48	0.23
B. safitza	0.27	0.00	0.00	0.00	0.23
B. sandace	2.75	0.87	0.63	0.95	0.23
B. sangmelinae	0.27	0.69	0.42	0.24	0.00
B. sophus	5.49	3.65	3.59	3.10	2.74
B. taenias	0.82	0.87	1.27	0.48	0.91
B. vulgaris	7.83	3.82	3.17	2.86	4.11
B. xeneas	0.55	0.17	0.21	0.00	0.23
B. zinebi	0.27	0.69	0.42	1.91	1.14
Catuna crithea	0.00	0.17	0.21	0.00	0.00
Charaxes cynthia	0.14	0.00	0.00	0.00	0.00
C. numenes	0.00	0.00	0.00	0.00	0.46
C. protoclea	0.00	0.17	0.21	0.24	0.00
C. tiridates	0.00	0.00	0.00	0.00	0.23
Elymniopsis bammakoo	0.41	0.00	0.21	0.00	0.68
Euphaedra ceres	17.86	11.81	14.80	8.35	10.27
E. diffusa	0.14	0.00	0.21	0.00	0.00
E. edwardsii	0.55	0.35	0.63	0.48	0.23
E. eupalus	0.96	1.74	1.48	1.67	1.14
E. gausape	0.14	0.00	0.00	0.00	0.00
E. harpalyce	2.61	4.69	4.02	6.21	2.28
E. inanum	0.27	0.35	0.63	0.48	0.00
E. janetta	0.82	0.87	0.21	1.19	1.14
E. medon	12.09	12.50	13.11	12.41	11.87
E. phaethusa	8.10	11.46	10.36	7.40	7.76
E. themis	3.71	3.30	4.23	3.34	2.97
E. xypete	0.27	0.17	0.21	0.00	0.00
Euriphene ampedusa	0.27	0.00	0.21	0.72	0.68
E. aridatha	0.00	0.00	0.00	0.48	0.23
E. barombina	0.55	1.74	3.17	2.63	2.97
E. gambiae	0.00	0.69	0.21	0.48	0.00
E. simplex	0.00	0.69	0.21	0.48	0.00
Gnophodes betsimena	5.63	7.99	5.71	5.97	5.48
Gnophodes chelys	1.24	0.87	1.90	1.67	4.11
Hallelesis halyma	0.00	0.00	0.21	0.00	0.00
Hypolimnas salmacis	0.00	0.00	0.00	0.00	0.23
Melanitis leda	1.37	2.60	1.06	0.72	1.14
M. libya	0.27	0.17	0.42	0.00	0.91
Palla decius	0.41	0.00	0.00	0.00	0.23
P. violinitens	0.00	0.00	0.00	0.24	0.00