An investigation into the effect on abundance and diversity of terrestrial invertebrates of a changing environmental gradient: looking at the edge effect of primary, tropical submontane forest to monoculture tea plantation habitats

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Abstract

Natural and artificial fragmentation on a variety of scales present to organisms sharp boundaries between contrasting habitat types. Altered microclimates and microhabitats occurring along such an edge ultimately impact on biota, and in environments where high endemicity is continually threatened by increasing fragmentation through other land use, it is crucial to understand the extent of edge effects on organism dispersal and mobility at both the individual and species level. The study, conducted in Amani Nature Reserve, East Usambara Mountains, considered the effect of prominent forest/tea boundaries on abundance, species diversity and species similarity of terrestrial vertebrates along the habitat gradient across the edge. Abundance and diversity were found to differ significantly across the edge (ANOVA, $F_{4,45} = 3,6$; $p = 0.01$ & $F_{4,60} = 6.47$, $p < 0.001$ respectively), with similarly high values when crossing from forest to edge. Clear decreases in mean abundance and diversity by 40% and 50% respectively were observed when moving from the edge to the tea habitat. Changes in similarity in species composition showed a greater rate of decline when moving from the forest habitat to tea than in the opposite direction. It is evident from our preliminary study that even over such short distances edge effects on biotic diversity and abundance do exist. In an already heavily fragmented habitat where patches are continually being created, it is important to consider to what extent increasing fragmentation impacts on endemic flora and fauna.

Introduction

The tropical submontane forest of the Eastern Arc mountains (north-east Tanzania) represent an area of high ecological diversity facilitated through isolation over geological time and fragmentation. Over 2000 plant species (of which 25% are endemic) have been documented here (Rodgers & Homewood, 1982), such that it has been considered one of the 24 globally important forest biodiversity 'hotspots' by Conservation International. Indeed several initiatives since the 1980's have been set up for its protection.

One such protected area includes the East Usambaras, which represents just one fragment of the Eastern Arc mountain chain. This is an area of enhanced endemism promoted by a moist climate (just 40km from the Indian Ocean), whilst its catchments area (the Sigi river watershed, 1100km^2) provides an economically important water source to surrounding towns. However the proportion of forest cover has declined since the 1900's from 80% to 50% cover today (Moreau, 1935), with areas cleared for subsistence and cash crop agriculture, commercial timber and tea estates.

Such agriculture has provided a major source of income to the local population. Large-scale coffee plantations established during German colonialism were converted to tea plantations following British rule in the 1950's (Rodgers & Homewood, 1982), and these still remain as dominant monoculture patches over other cash crops grown (such as spices and cassava) in and amongst the primary forest landscape.

Although major commercial logging was halted in the late 1980's, the extent of tea plantations remain as patches in a landscape of declining forest cover. To reduce such dominance, plantations within the Amani Nature Reserve ((ANR)an area of 8380 ha.) have undergone some restrictions in regards to the extent of plantation area, whilst other smaller agricultural uses have been limited to specific zones under the ANR management plan (personal communication, C.T. Sawe). Encouragement of local co-operative out-growers has also promoted tea production on a smaller, less land-intensive scale, reducing the risk of erosion and further possible increases in forest fragmentation and patch isolation throughout threatened forested areas (Rodgers & Homewood, 1982). These widespread forest-tea boundary existence within the Amani Nature Reserve presents an opportunity for so-called 'edge effects' to be imposed upon existing flora and fauna present. Such effects are set up within a landscape where native remnant vegetation lies adjacent to patches of managed land, resulting in a discontinuity in environmental gradient.

At these ‘edges’, changes in physical parameters such as temperature, moisture, wind and soil characteristics (Newmark 2001), and biological factors such as increased predation (Carlson & Hartman, 2001) and a change in niche availability (Donovan et al. 1997), will affect the mobility and consequent ‘permeability’ of an organism through edges of varying boundary types (Morrision et al. 1992; Saunders et al. 1991). The degree of this permeability of such an edge to a species will ultimately be specific to the organism in question (Didham et al. 1998). Different parameters at the edge will therefore influence the direction and magnitude of movement of an organism. This edge will affect the ecology of the flora and fauna present to varying degrees.It must be considered when studying the impact of habitat fragmentation and patch isolation on species mobility and extinction (Turner, 1996, Didham et al., 1998; Kapos et al. 199?). Indeed it has been found in some studies that there is an increase in faunal density towards the forest edge (Turner, 1996; Didham et al., 1998).

Such understanding is crucial in ecologically important fragmented habitats such as the Usambaras. Fragmentation within this ecosystem exists on a variety of scales, and can have significant effects on abundance, species richness, composition and distribution of the existing biodiversity. Such sharp changes therefore, in both physical and biological parameters at the edge (that may or may not act in either of the contrasting habitat types), must be understood in order to appreciate fully the apparency of this edge and the potential barrier it may present to faunal or floral species.

Our aim was to investigate the effect on abundance and diversity of terrestrial invertebrates of a changing environmental gradient from primary tropical sub montane forest to monoculture tea plantation habitats. We hypothesise that the number of individuals and of species will significantly differ between the two habitats, and expect the edge to exhibit enhanced abundance and diversity due to the existence of species from both habitats converging at the habitat boundary.

An understanding of the change in mobility of faunal species with increasing distance from their habitat of origin will also be approached, whilst measurements of physical parameters (temperature, light intensity and humidity) will be considered briefly. Other confounding variables such as floral diversity and litter cover were not considered in this preliminary study of edge effects.

Methodology

The study environment

This study was carried out over two weeks in September 2003 during the dry season, in Amani Nature Reserve (Elevation: 836m; S 05^{o} 06' 05.0"; E 038^{o} 37' 44.4"), Tanzania. The sites selected lie within the continuous forested fragment of the East Usambara Mountains, adjacent to Derema Forest and its recently established Derema Corridor. Our study area involved the assessment of two heavily contrasting habitats: primary, tropical montane forest of the Eastern Usambaras, and tea monoculture plantation. The former represents an existing fragment of the once-continuous Eastern Arc Mountains. The latter habitat was established approximately 40-50 years ago, receiving regular pesticide (bimonthly) and clipping (every 2-3 years) management. The individual site locations are shown in table 1 below.

Table 1. Site location and general characteristics

Site	Dist'ce from ANR (km)	Boundary length (m)	Boundary direction	Elevation (m)	Longitude (South)	Latitude (East)
1	1.8	110	NE-SW	861	05^{o}05'02.6"	038^{o}38'10.4"
2	2.7	185	NW-SE	860	05^{o}05'02.7"	038^{o}38'10.5"
3	2.4	115	NW-SE	821	05^{o}05'06.5"	038^{o}38'18.3"
4	1.9	115	NW-SE	854	05^{o}05'18.2"	038^{o}38'24.3"

Experimental design

We selected four adjacent yet independent sites as our study area. Each site had a clear boundary between continuous forest and tea plantation. Each boundary chosen were of similar length (a minimum of 100m), avoiding other available and accessible sites where understorey bushes (such as *Clidemia* or *Lantana*) reduced the clarity of this boundary 'edge' between the two habitat types. For each of the boundaries assessed, sampling was carried out at four transects extending 40m into both the forest and tea habitat from the boundary edge. These transects were set approximately 20m apart along the length of the boundary. At 5 distances (10m and 40m into each habitat type, and at the edge between the two habitat types along each of these transects) two pitfall traps containing a dilute soap solution were set (table 2).

Table 2. Sampling design: location of pitfall traps per transect at each site boundary

Transect	(Forest)		Edge	(Tea)	
1	-40m	-10m	0m	10m	40m
2	-40m	-10m	0m	10m	40m
3	-40m	-10m	0m	10m	40m
4	-40m	-10m	0m	10m	40m

Physical parameters

For each of the four transects, light intensity (using Extech™ Light Meters, cross-calibrated (Lux)), temperature (degrees Celcius) and Relative Humidity (Hygrometer (%)) readings were taken at at 10m intervals from the edge (-40, -30, -20, -10, -0 (forest edge), +0 (tea edge), +10, +20, +30, +40m). Readings for Sites 1 & 2 and 3 & 4 were conducted on the 19th and 20th of September 2003 respectively, between 1 and 3pm. The weather conditions were consistent during the timeframe that readings were taken as well as between the two days (overcast and cloudy).

Biota

Forty traps per site were left planted for four consecutive nights prior to collection. Traps at sites 1 and 2 were planted on the afternoon of the 16thof September 2003 and collected on afternoon of the 19th. Traps at Sites 3 and 4 were planted on the afternoon of the 17th, and collected on the afternoon of the 20th. Samples were sieved and bottled in-situ prior to cleaning, sorting, preservation and identification in the laboratory.

Results

Physical Parameters

Temperature

Mean temperature ranged from 21.5 ± 0.2 ºC (standard error) moving from within the primary forest habitat, increasing to 22.4 ± 0.3 ºC at the edge, and further increasing to 24.3 ± 0.5 ºC within the tea plantation. Mean temperature readings per site within either habitat type were constant, as illustrated in Figure 1. An increase in temperature by 1-2 degrees is obvious at the edge (0m), this trend being consistent throughout the sites sampled.

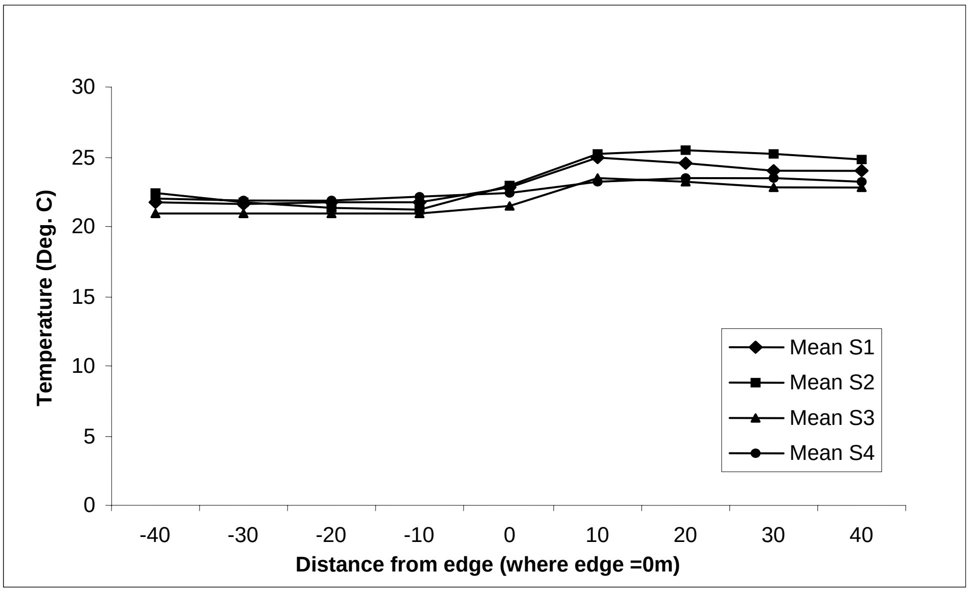

Figure 1. Mean temperature from forest (-m) to tea (+m) per site sampled.

Light Intensity

Low light intensity within the forest habitat was consistent between the four sites measured, with the overall mean intensity changing from 11.2 ± 2 Lux at 40m into the forest, to 93.8 ± 21.5 Lux at the edge, and 295.4 ± 73.3 Lux at 40m within the tea plantation. Light intensity within the tea plantation was up to 60 times higher than the forest readings, and varied between the four sites to a greater extent than that measured within the forest, as illustrated in Figure 2.

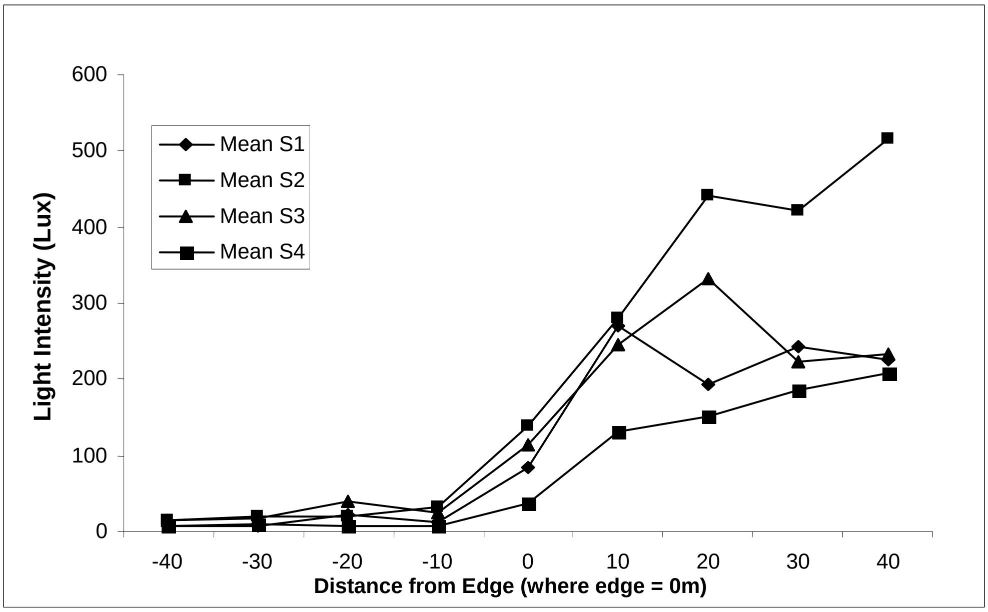

Figure 2. Mean light intensity measured at points along transects (n=4) from forest (-m) to Tea (+m) per site sampled (Lux)

Relative Humidity

Mean humidity measurements per site showed greater variation within the forest (ranging from 62 to 72.5%) than within the tea habitat (ranging from 64.8 – 69.8%), as seen in Figure 3. The overall mean humidity for all four sites at both habitats were similar, with perhaps a slight elevation at the edge (humidity ranged from 68.4 ± 1.8% at 40m into the forest, to 69 ± 1.3% at the edge and 68.6 ± 0.4% at 40m into the tea plantation).

Biota

Abundance

3827 individuals were sampled and identified over this study, and involved 80 pitfall traps left for 4 consecutive nights prior to collection (whereby two traps represented one sample). The number of individuals found at each of the five sampling distances per transect per site were tested using two-way ANOVA. Lack of significant difference in the number of individuals between these transects within each of the sites allowed the data from these pseudo-replicates to be pooled (Two-way ANOVA; $F_{3,64} = 1.84$; p =

0.15). Figure 4 & 5 illustrates the change in abundance in relation to distance from the edge to the two contrasting habitats.

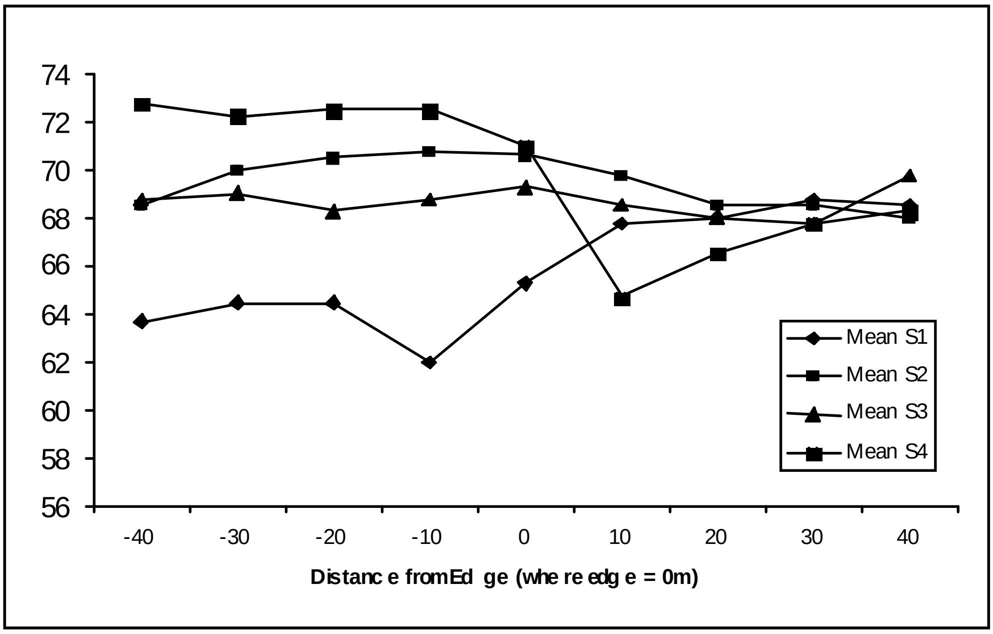

Figure 3. Mean relative humidity measured at points along transects (n=4) from forest (-m) to tea (+m) per site sampled (%)

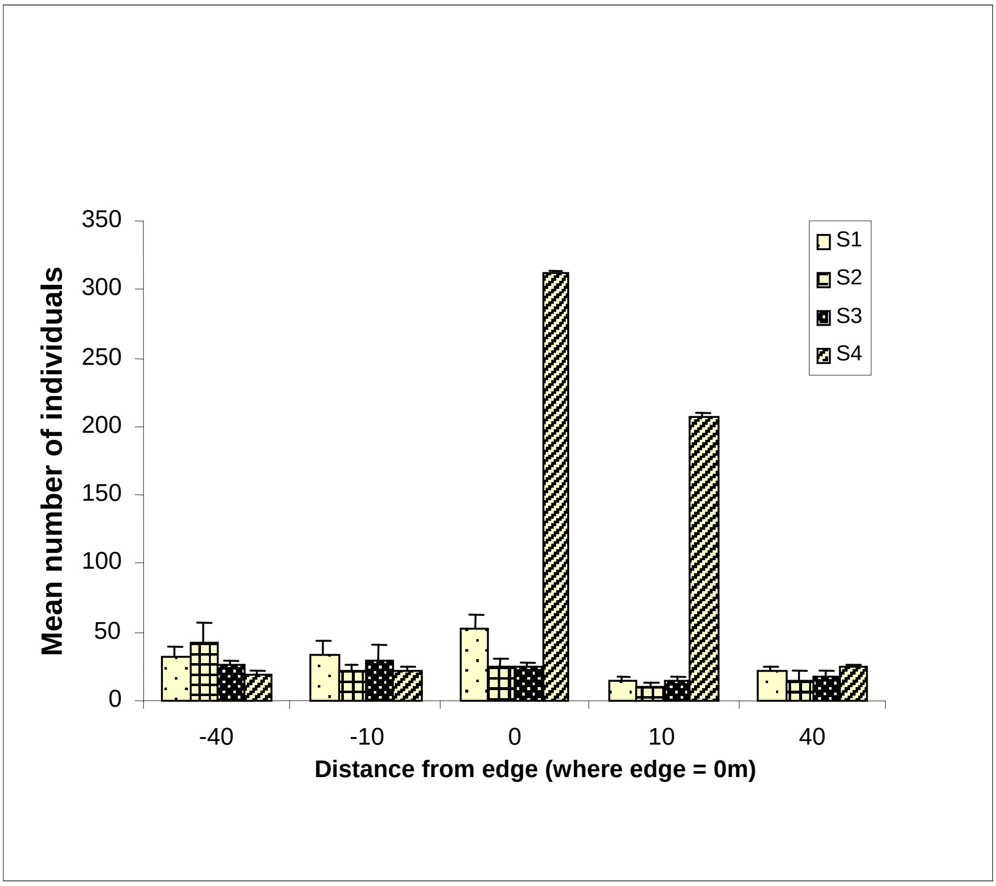

Figure 4. Mean number of individuals per transect point (per pair of pitfall traps) for each of the four sites (S) crossing from forest (-40m) to tea (+40m)

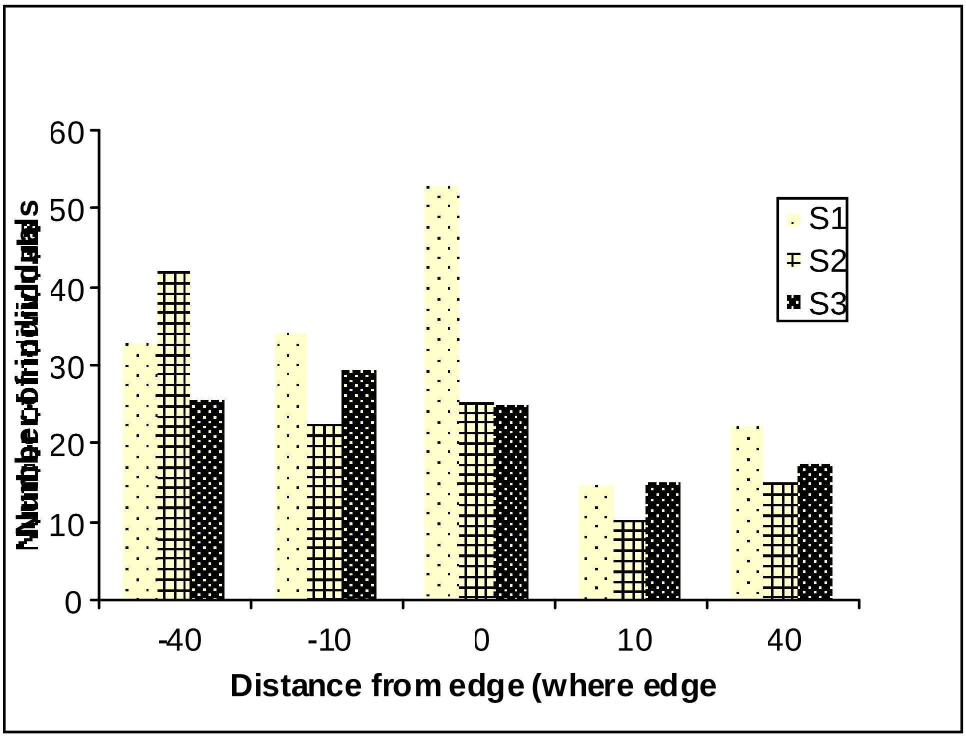

Figure 5. Mean number of individuals per transect point (per pair of pitfall traps) for three sites (S1, 2, 3) crossing from forest (-40m) to tea (+40m)

Replicate sites 1-3 were found not to differ with each other in terms of abundance found at each of the five sampling distances (Two-way ANOVA; $F_{2,45} = 0.93$; $p = 0.4$), and this justified the further pooling of data for these three sites. Sampling at site 4 however, resulted in anomalously high numbers of Formicidae present in some of the samples. Transformation of the data was not adequate to reduce the extent of this anomaly, and so data from this site was not pooled for further analysis. Considering data from sites 1-3 only, it was found that the changes in the abundance of individuals with distance from the edge of the boundary were significant (Two-way ANOVA; $F_{4,45} = 3.6$; $p = 0.01$). This change is illustrated in Figure 6 and 7.

It is evident here that greater abundance is apparent within the forest and the edge than within the tea plantation, when looking at either pooled transect data per site (Figure 6), or when looking at pooled site data (Figure 7). We see an almost 50% decrease in individual abundance between samples collected at 40m into the forest and 40m into the tea (33.4 ± 8.59 at –40m in comparison to 18.2 ± 4.5 at +40m per transect sample point (Figure 6), & 134 ± 16 at –40m in comparison to 72 ± 7.6 individuals per site sample point (Figure 7) respectively).

The greatest decline in abundance was found to occur between the edge and tea (+10m), whereby abundance was seen to drop to a value 2.5 times lower than at the edge (the drop in abundance from -10m forest to the edge was relatively absent). Thereafter lower abundance in the tea plantation was consistently recorded. This trend was also evident on pooling of replicate data (Figure 6 & 7).

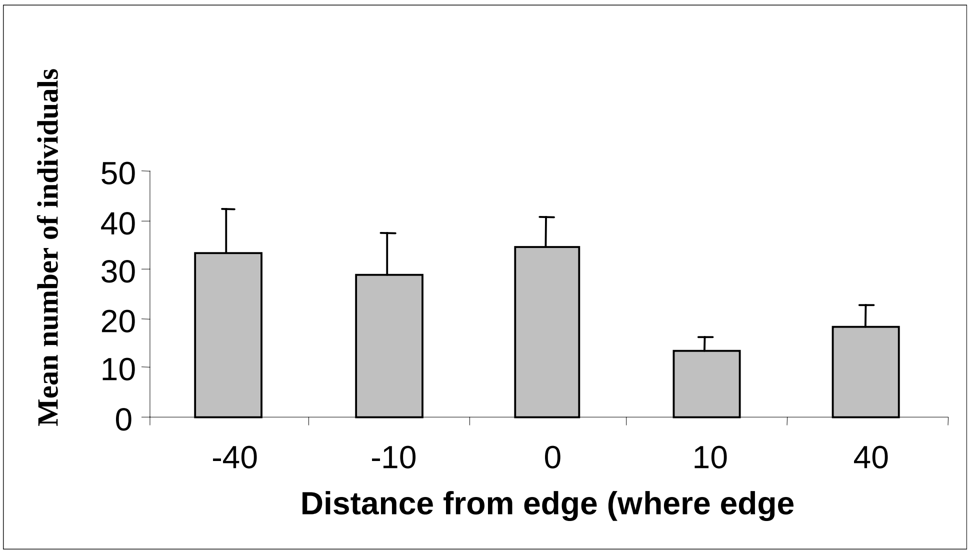

Figure 6. Mean number of individuals per transect point (per pair of pitfall traps) found when crossing from forest (-40m) to tea (+40). Pooled data for sites 1-3; n=12; p=0.01.

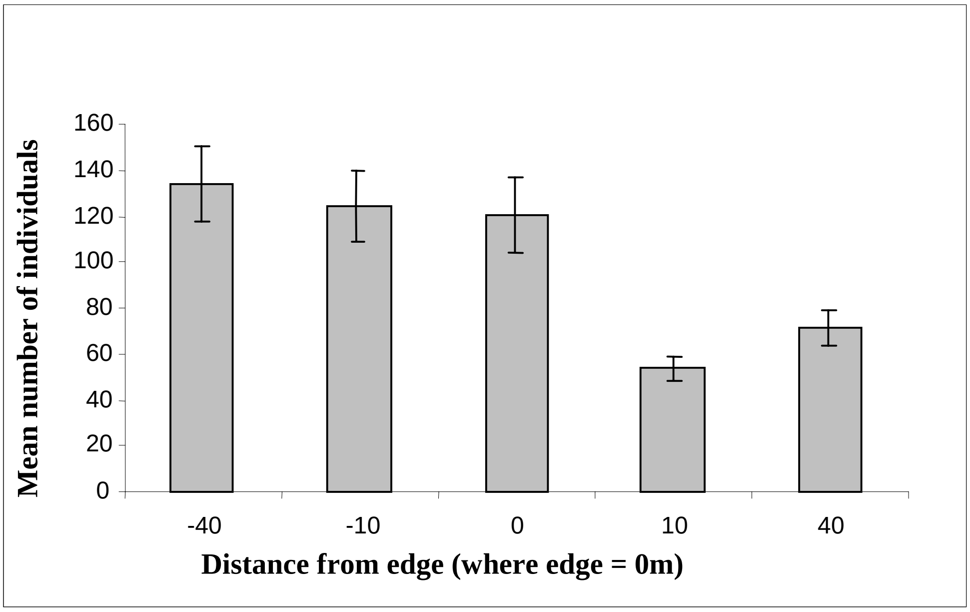

Figure 7. Mean number of individuals sampled when crossing habitats of forest (-40m) to tea (+40) per site (n=12; (24 traps; data for site 4 excluded))

Species diversity

A total of 175 taxa were sampled and identified in total, with 165 assigned to morphospecies level. All four site replicates and all four transect pseudo-replicates within each site were found to not differ significantly with each other (Two-way ANOVA; Factor: transect, $F_{3,64} = 0.16$, $p = 0.925$; Factor: site; $F_{3,64} = 1.55$, $p = 0.210$), enabling data to be pooled for further analysis.

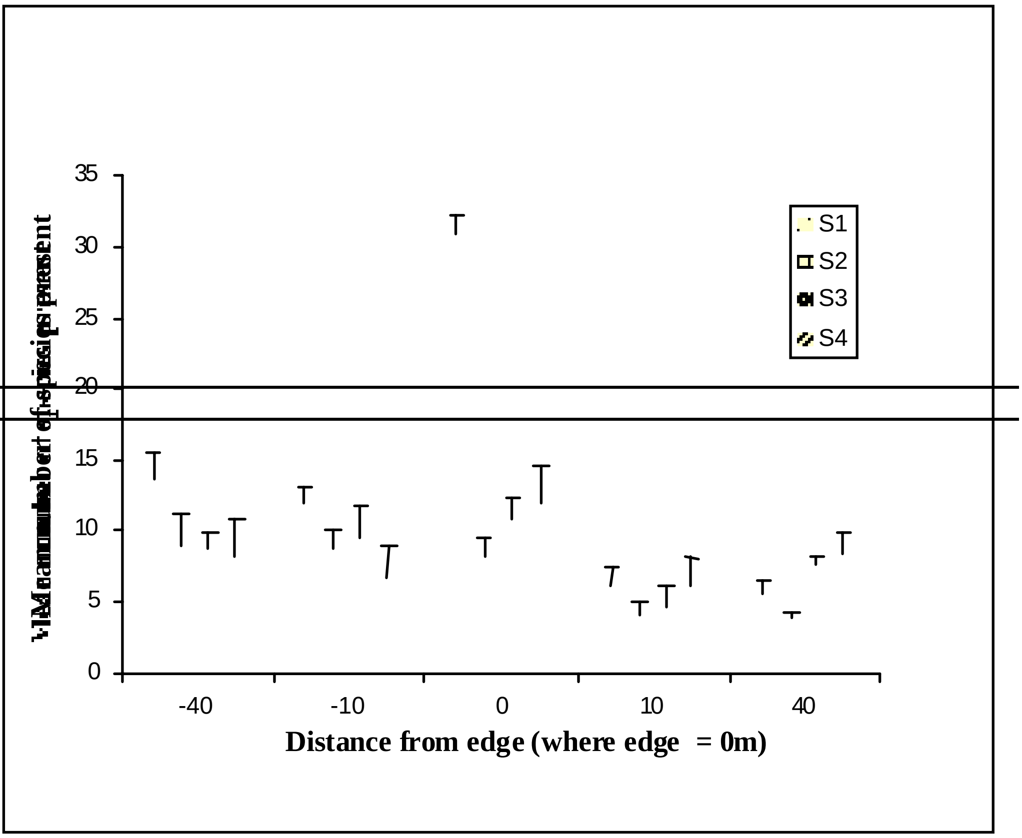

Figure 8. Mean number of species per transect point (per pair of pitfall traps) for each of the four sites (S) crossing from forest (-40m) to tea (+40m); n=4 per site.

Figure 8 above illustrates the change in the number of species sampled per site, when crossing 40m into the two habitat types from the edge. The mean number of species occurring at different distances from the edge differed significantly from each other (two-way ANOVA, $F_{4,60} = 6.47$, $p < 0.001$). It is evident that the greatest mean number of species sampled occurred at the edge (32 ± 2.6 species sampled per site), with changes in species numbers from edge to forest (30 ± 3.4 at –10m & 28 ± 1.1 –40m), less obvious than from edge to tea (18 ± 2.3 at +10m & 16 ± 2.3 at 40m), where the number of species almost halves. The change in the mean number of species sampled when crossing habitats is illustrated both for transect (Figure 9) and site (Figure 10).

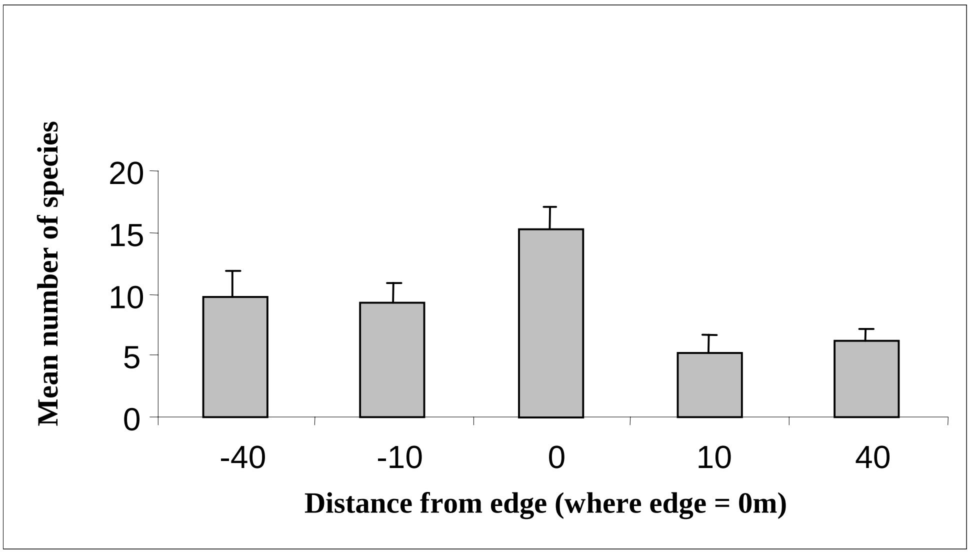

Figure 9. Mean number of species per transect point (per pair of pitfall traps) found when crossing from forest (-40m) to tea (+40); (pooled data for all four sites (n=16); p=<0.01)

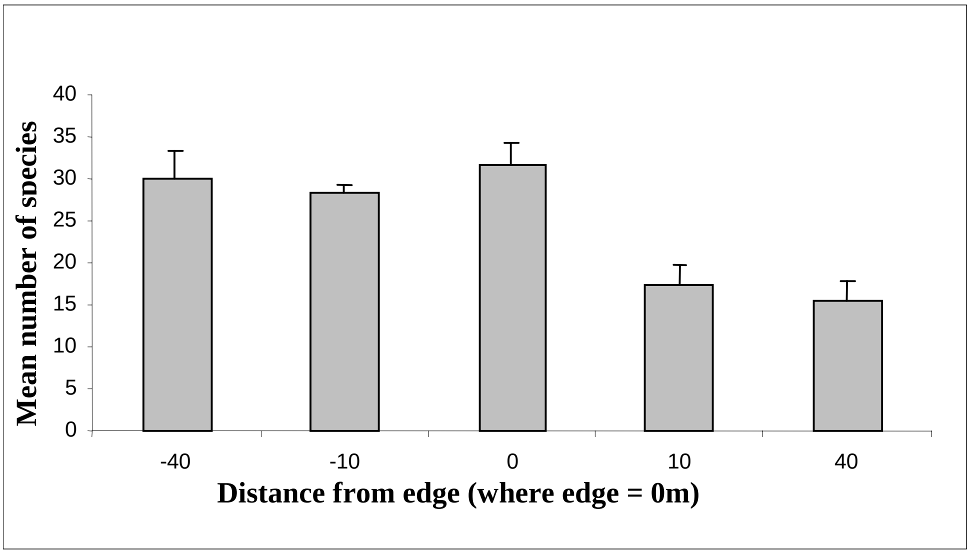

Figure 10. Mean number of species sampled when crossing habitats of forest (-40) top tea (+40m) per site (n=16 (32traps)

Table 3 summarises the change in physical and biological factors sampled over the four sites.

Faunal overlap

We used Sorenson's Similarity Index to generate a measure of similarity in species sampled between any two sampled points in the forest, at the edge, or within the tea per site. The general trend is evident in Table 3 below, with species similarity declining with distance from the initial sampling site measured.

Slopes were generated to describe the rate of this decline in similarity of species identified, comparing similarity in samples collected at 40m into the forest with that found at -10, 0, +10 & +40m into the tear(Figure 11). The slope of $y = -0.2x + 35.4$ was identified, with distance being responsible for 23% of this decline in the similarity of species sampled ($R^2 = 0.23$) (Regression analysis; $F_{1,14} = 6.22$, $p = 0.026$).

Table 3. Summary of physical factors with abundance and diversity

Factors	**Forest (-40m)**	**Edge (0m)**	**Tea (+40m)**	**Test statistics**
Mean Temp ºC	21.5±0.2	22.5±0.3	24.3±0.5	N/a
Mean Light Intensity (LUX)	11.2±2	93.8±21.5	294±73.3	N/a
Mean Rel. humidity (%)	68.4±1.8	69±1.3	68.6±0.4	N/a
Mean Abundance (Sites 1,2,&3)	134±16	121±17	72±7.6	ANOVA $F_{4,45}$ =3.6, p = 0.01
Diversity (sites 1-4)	28±1.1	32±2.6	16±2.3	ANOVA $F_{4,6}$=6.47; p=0.001

Table 4. Sorenson's similarity index (2C/(A+B)

Site 1	F40	F10	E	T10
F10	0.39			
E	0.22	0.42		
T10	0.18	0.24	0.15	
T40	0.19	0.25	0.22	0.27

Site 3	F40	F10	E	T10
F10	0.40			
E	0.29	0.32		
T10	0.40	0.37	0.23	
T40	0.33	0.20	0.24	0.29

Site 2	F40	F10	E	T10
F10	0.37			
E	0.45	0.45		
T10	0.24	0.17	0.19	
T40	0.19	0.37	0.34	0.41

Site 4	F40	F10	E	T10
F10	0.43			
E	0.35	0.44		
T10	0.37	0.24	0.33	
T40	0.30	0.22	0.32	0.32

This was similarly done for the tea habitat, comparing similarity when moving across the boundary edge into the forest habitat. The slope of y = 0.1x + 28.1 was identified, with distance being responsible for only 5.8% of this decline (R^2 = 0.058) (Regression analysis; $F_{1.14}$ = 1.92, p = 0.188).

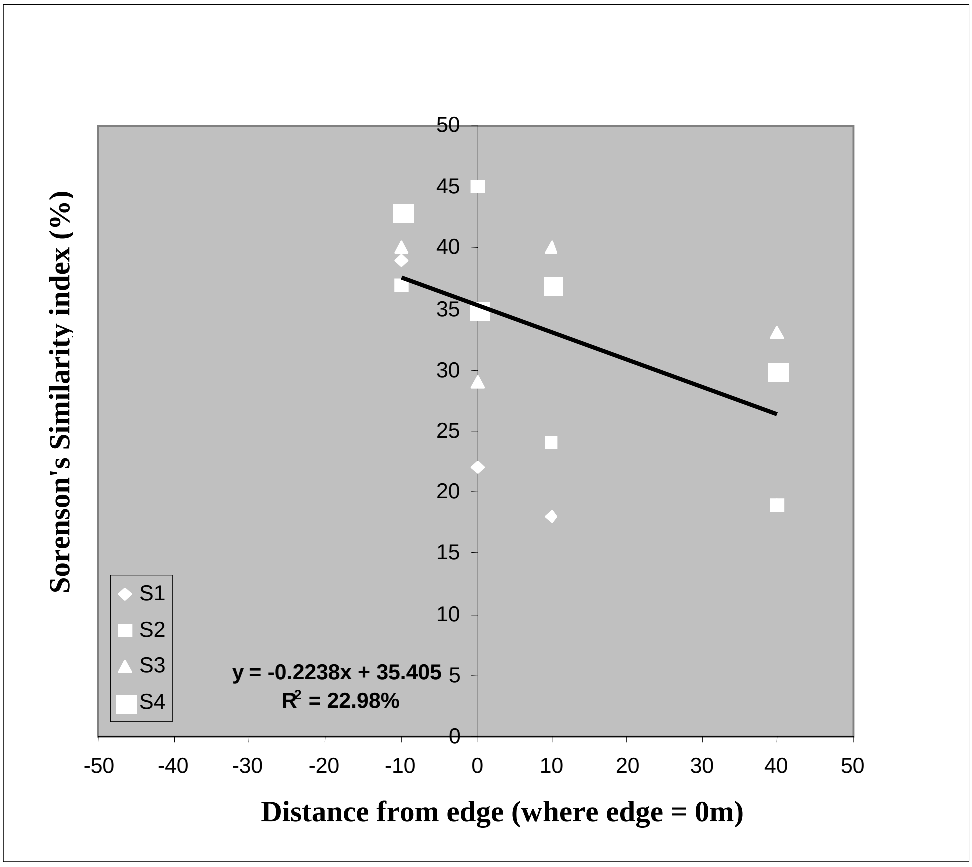

Figure 11. Decline in faunal overlap: looking at the similarity of species found at –40m into the forest to that found at –10m (forest), 0m (edge), 10 and 40m (tea).

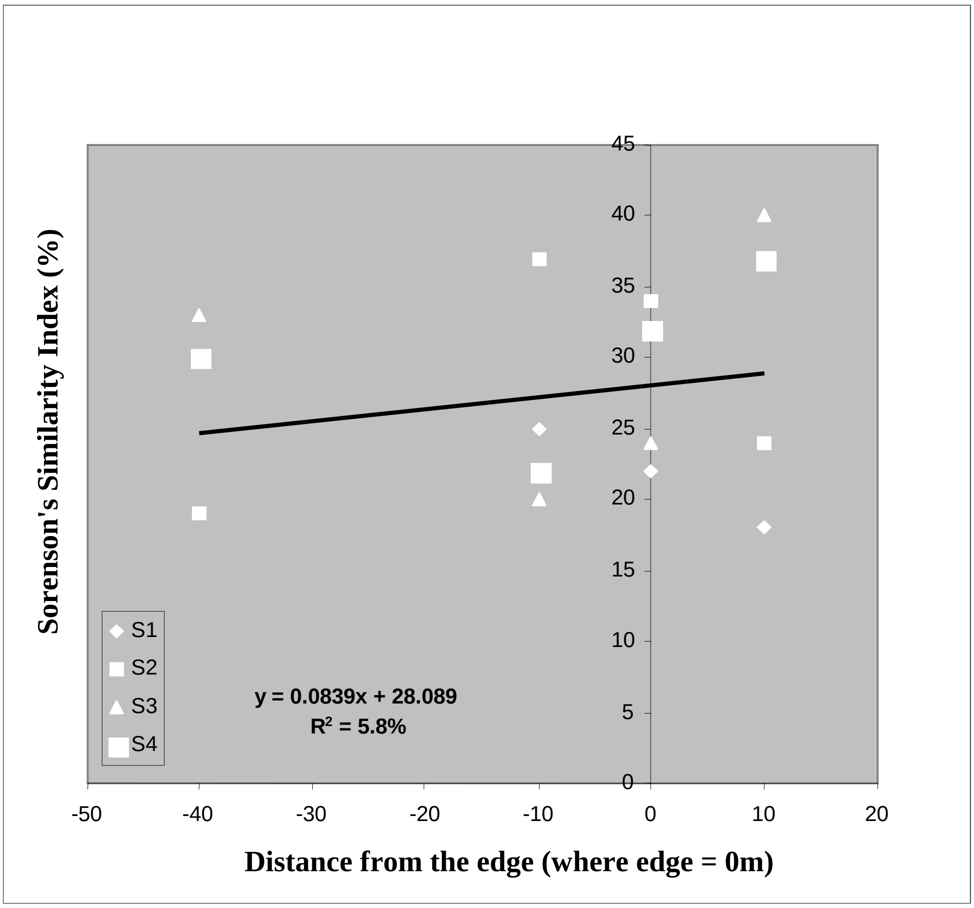

Figure 12. Decline in faunal overlap: looking at the similarity of species found at 40m into tea to that found at 10, 0, -10, and –40m into the forest.

Discussion

Increasing conversion of primary forest for agricultural and other land uses has led to an overall patchy distribution of the remaining forest. The formation of sharp interfaces between natural forest and disturbed or managed areas result in isolation of habitat patches and fragments and introduce or change a range of ecological factors (Lovejoy et al. 1986). Several previous investigations have revealed a number of edge effects, varying in their operative extent depending on boundary type and species ecology. Kapos et al. (1989) confirmed clear gradients in microenvironmental conditions between newly created tropical forest edges adjacent to undisturbed forest, with the edge exhibiting hotter and drier microclimates. Natural processes such as wind, temperature, light intensity and humidity were amongst the parameters that varied at the edge.

Physical parameters

Lower temperatures and consistent low light intensity within the forest showed immediate change at the boundary edge, where a sharp increase in temperature and a tenfold increase in light intensity occurred. Humidity was found not to vary greatly across the two habitats, although this may be due to the overcast conditions experienced on the days of sampling, where cloud cover may have repressed temperature extremes during midday. However the tea habitat indicated greater consistency in relative humidity than in the forest, most probably due to higher uniformity in vegetation structure of the monoculture habitat, with reduced heterogeneity in vegetative transpiration rates.

Terrestrial invertebrate abundance

Abundance changed significantly with distance, declining in value from forest to tea, with the number of individuals found at 40m into tea being effectively 50% of that found at 40m into the forest habitat. Abundance in the forest towards the edge showed no real decline, yet that at the edge was almost three times greater than that encountered just 10m into the tea plantation.

The forest represents greater niche and microclimate heterogeneity due to higher floral diversity and complexity in forest structure. A greater availability of resources can therefore exist (food, nesting sites, more favourable habitat types), whilst lower temperature extremes and higher moisture content may facilitate and promote mobility of terrestrial invertebrates that are otherwise highly susceptible to desiccation. Such promotion of mobility may in turn accommodate an increase in foraging effort for example, and could further enhance habitat flexibility, whereby an organism is not restricted to one habitat type. As such, the threshold of abundance within such a heterogeneous ecosystem can be enhanced.

Greater similarity in abiotic conditions between the forest and edge most likely support the maintenance of high abundance. The edge inherently shares some of the heterogeneity of the forest, and also receives shade from the canopy overhead. Physical parameters such as wind, light intensity, humidity and temperature are therefore less likely to undergo fluctuations as extreme as in the tea habitat. The contrasting homogeneity and simplicity in structure of the tea plantation is likely to provide a reduced diversity in hospitable niches, restricting the threshold of individuals supported within this habitat.

A higher number of individuals was found at 40m than 10m within the tea plantation, and it may be that the greater density and reduced patchiness in plant stand closer to the centre of the plantation may reduce light intensity and other abiotic extremes for organisms living below the tea cover. Greater constancy in shading may reduce temperature extremes and promote the retention of moisture at ground level, providing a more constant environment within the plantation than that nearer the edge, where greater surface area exposure most likely experiences harsher abiotic fluctuations.

Terrestrial invertebrate diversity

Highest diversity in terms of number of species sampled occurred at the edge. Diversity within the forest did not differ to that at the edge, again following a similar trend as with abundance. Consequently, diversity is supported more greatly within the heterogeneous forest matrix. In addition, the edge represents an area where both species from either habitat can co-exist, as it offers alternative potential niches. For example, forest species that may not necessarily be well adapted to the high moisture of the forest may exist more successfully at the drier edge. Similarly, species that inhabit the tea environment may exist more optimally at the edge, where greater moisture or shading occurs.

Alternatively, this edge may represent a boundary that species adapted to either habitat type cannot cross. Their dispersal ability and ecology will therefore ultimately define how fine or coarse the edge will appear specifically to them, and may explain why the number of species found in the forest and at the edge drops to over half that sampled when crossing over to the tea habitat. It may be that only the more generalist species or those species that can regulate or tolerate aspects such as water loss, reduced niche heterogeneity and food resource, can cross the boundary into the tea habitat. Alternatively, species composition within the tea habitat may comprise of a very different species community specialised or adapted to the environment offered by the monoculture plantation. Unfortunately, composition and distribution were not measured in this study.

Terrestrial invertebrate similarity

The general trend of declining species similarity as one moves away from a point of origin is obvious from our data. Higher abundance and diversity within the forest habitat, along with more favourable abiotic conditions promoting and facilitating mobility to the edge can explain why the similarity in 'forest-habitat species' to those species sampled at the edge is higher than looking at the similarity of 'tea-habitat species' to those found at the edge (indicated by the higher intercept of the slope).

The decline in similarity of 'forest-habitat species' sampled when moving from the forest to tea is significantly greater in magnitude than the decline in similarity of 'tea-habitat species' to those sampled within the forest. From this we can assume that the sharp change in diversity described earlier between the edge and tea habitat may be more likely due to the presence of a completely different species composition rather than a reduced one. However the relationship between similarity and distance is not strong, with only 23% of this rate of decline accounted for by distance, and hence the latter explanation cannot be dismissed (it is most likely that both circumstances are occurring).

Conclusions

It is clear that the boundary between primary, tropical submontane forest and tea monoculture offers a stark contrast in habitat types and related abundance, diversity and similarity in species composition. The apparency of this edge is evident through both physical and biological parameters studied here, whilst the degree to which this edge acts as a barrier will ultimately and crucially depend on the ecology of the species in question. Consideration of terrestrial, non-vestigial invertebrates in this study enabled us to consider shorter distances over which to measure and identify edge effects. More crucially it is apparent from this preliminary study that even over such short distances edge effects on biota diversity and abundance do exist. In an already heavily fragmented habitat where patches are continually being created either naturally or artificially, the widening of the fragmented extent is inevitable in the future. It is therefore important to consider to what extent such fragmentation will have on the high endemicity of flora and fauna of the East Usambaras and other similar ecologically important areas.

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