Edge effects at an induced forest-grassland boundary: forest birds in the Ongoye Forest Reserve, KwaZulu-Natal

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Bird species diversity and guild composition between the edge (5–10 m from the margin) of primary forest abutting grassland and the deep interior (> 500 m from the margin) in the Ongoye Forest Reserve were compared. Edge and interior sites were chosen that were homogeneous with respect to habitat physiognomy i.e. influences of habitat structure and complexity were insignificant. There were no statistical differences in bird species diversity between the forest edge and interior. However, there was significantly greater species turnover at the edge. The difference in bird species composition between the forest edge and interior was due to various edge-effects: removal of dead wood for firewood, soil compaction by cattle, and generally greater levels of disturbance. We question the wisdom of the generally applied edge-effect principle in the conservation of forest biodiversity. We suggest that the principle be applied only once there has been critical appraisal of the extent, nature, and effect of an edge and a clear conservation objective with regard to forest birds.

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In avian communities, long-distance migrants, rare species and forest interior species are adversely affected by forest fragmentation (Robbins 1979; Blake & Karr 1984; Newmark 1991; Terborgh 1992). Lovejoy *et al.* (1986) identified edge effects as the most important cause of ecological changes that result from habitat fragmentation (*cf.* Gilbert 1980), with the variety and density of organisms greater at the interface between two habitats than in the interior of a habitat (i.e. edge-effect principle: Kroodsma 1984; Yahner 1988; Longman & Jenik 1992). Although edges can result in higher biodiversity they are not always beneficial (Harris 1988), and fragmentation can result in an increased influence of generalist predators, competitors or brood parasites on forest interior (Kroodsma 1984; Wilcove 1985; Yahner 1987; Andren & Anglestam 1988) and forest edge birds (Laudenslayer 1986; Yahner & Scott 1988).

Although under natural conditions edges may increase biodiversity, human influenced fragmentation rarely results in ecotonal or transitional edges where plant and associated wildlife communities grade into one another. For example, hot fires and a variety of commercial land-use types ensure that most southern African forests are small (less than 1000 ha, Lawes 1992), only rarely have ecotonal edges, and in many cases are so narrow that their ecology is likely to be dominated by processes that characterize the forest margin. We predict that a well defined and abrupt boundary between forest and adjacent grassland will reduce true forest bird species richness through species replacement and turnover at the margin. Thus fragmentation and the maintenance of artificial habitat boundaries results in an edge effect which is detrimental to the conservation of local forest biodiversity.

A higher proportion of the total forest area is influenced by edge effects when habitat fragments are small or of irregular shape since these fragments have a disproportionately large ratio of edge relative to area (Forman & Godron 1986). A corollary of this argument is that the effect of edge processes on biodiversity in a fragment may be confounded by the size of the fragment. Small fragments are dominated by edge effects and interior species are less likely to persist in these small remnants (Temple & Cary 1988; Saunders & Hobbs 1991). Thus, small size and isolation of forest fragments may result in edge effects and other area-dependent effects coinciding to affect avian diversity. To investigate the hypothesis that artificial habitat boundaries create a detrimental edge effect, we recorded avian diversity at the edge and interior of Ongoye forest. We examined the degree to which the edge effect influenced bird community structure and diversity at the forest/grassland interface compared to the forest interior avifauna. In order to be sure that differences in bird community structure between edge and interior were due to the edge effect and not other area-dependent factors we chose a forest that is sufficiently large enough (2800 ha) for there to be potentially separate forest edge and forest interior avifaunal communities.

Materials and Methods

Study area

The Ongoye Forest Reserve (28°50'S; 31°42'E) is situated in northern KwaZulu-Natal province, South Africa, in the Ongoye range of hills (altitude ranging from 305 m to 490 m). The reserve comprises a large contiguous forest patch (approx. 2800 ha, roughly 10 km by 2.8 km) and small (1–30 ha) peripheral forest patches, surrounded by 1072 ha of coastal climax grassland (Oatley 1989). Huntley (1965) and Axelrod & Raven (1978) describe this forest as one of the finest examples of subtropical evergreen forest with structural and floristic affinities to tropical rain forests.

The forest contains substantial populations of four of KwaZulu-Natal's rare forest birds, *Stactolaema olivacea* (green barbet) (Shelley) 1880, *Turdus fischeri* (spotted thrush Hellmayr 1901, *Columba delegorguei* (Delegorgue's pigeon) (Delegorgue) 1847, and *Phyllastrephus flavostriatus* (yellow-streaked bulbul) (Sharpe) 1876. Of these, *S. olivacea* is a southern African regional endemic. Of the 149 subjectively designated forest bird species found in South Africa (Oatley 1989), 73 species have been recorded from this forest (M.J.

Lawes, unpublished data 1985–86) (see Table 3, and McLachlan & Liversidge (1972) for naming authorities of bird species cited throughout). However, this analysis is not restricted to forest birds *per se*, and all birds observed were recorded.

The forest edge is typically an abrupt transition between the forest and surrounding grassland. This forest edge investigated here is mainly caused by burning by local pastoralists to maintain grasslands for grazing, and the activities of cattle along the margin.

Methods

Data on birds, habitat parameters (physiognomy and floral diversity), and food resource availability were collected over 15 days in January 1993 during peak breeding.

Sixteen 25 m × 25 m quadrats, eight at the forest edge (5–10 m in from the edge) and eight in the interior (> 500 m in from the edge) (Figure 1) were sampled. Quadrats were placed a minimum of 200 m apart and as much as 1000 m apart. Quadrats were large enough to obtain a reasonable sample of habitat structure but small enough to census bird species richness and abundance with reasonable precision.

Habitat heterogeneity

It has been suggested that avian α-diversity may be a function of habitat heterogeneity (Lack 1933; MacArthur & MacArthur 1961; Wilson 1974; James & Wamer 1982; Thiollay 1992). To control for the confounding effect of habitat heterogeneity between edge and interior on bird species richness (MacArthur, Recher & Cody 1966; Roth 1976), quadrats were selected for their homogeneity with respect to plant physiognomy, slope and aspect.

Horizontal patchiness, foliage height diversity and percentage vegetation cover were all taken into account in measurements of habitat heterogeneity. Species, abundance and percentage cover of herbs in five randomly chosen 1 m × 1 m quadrats per sample quadrat were recorded. Percentage cover of herbs was ranked on the Walker scale of 0 to 7 (Walker 1976):

Rank:	0	1	2	3	4	5	6	7
% class interval	0	1–10	11–25	26–50	51–75	76–90	91–99	100

In a quadrat, species, abundance, height, and basal area of saplings were recorded in three 25 m × 2 m transects. Sapling height was categorised as either > 1 m or < 1 m. Vines arising within the sapling transect were also counted.

Species, abundance, height, crown diameters (in two directions, at right angles), and circumference at breast height (CBH) of each understorey and canopy tree were recorded for

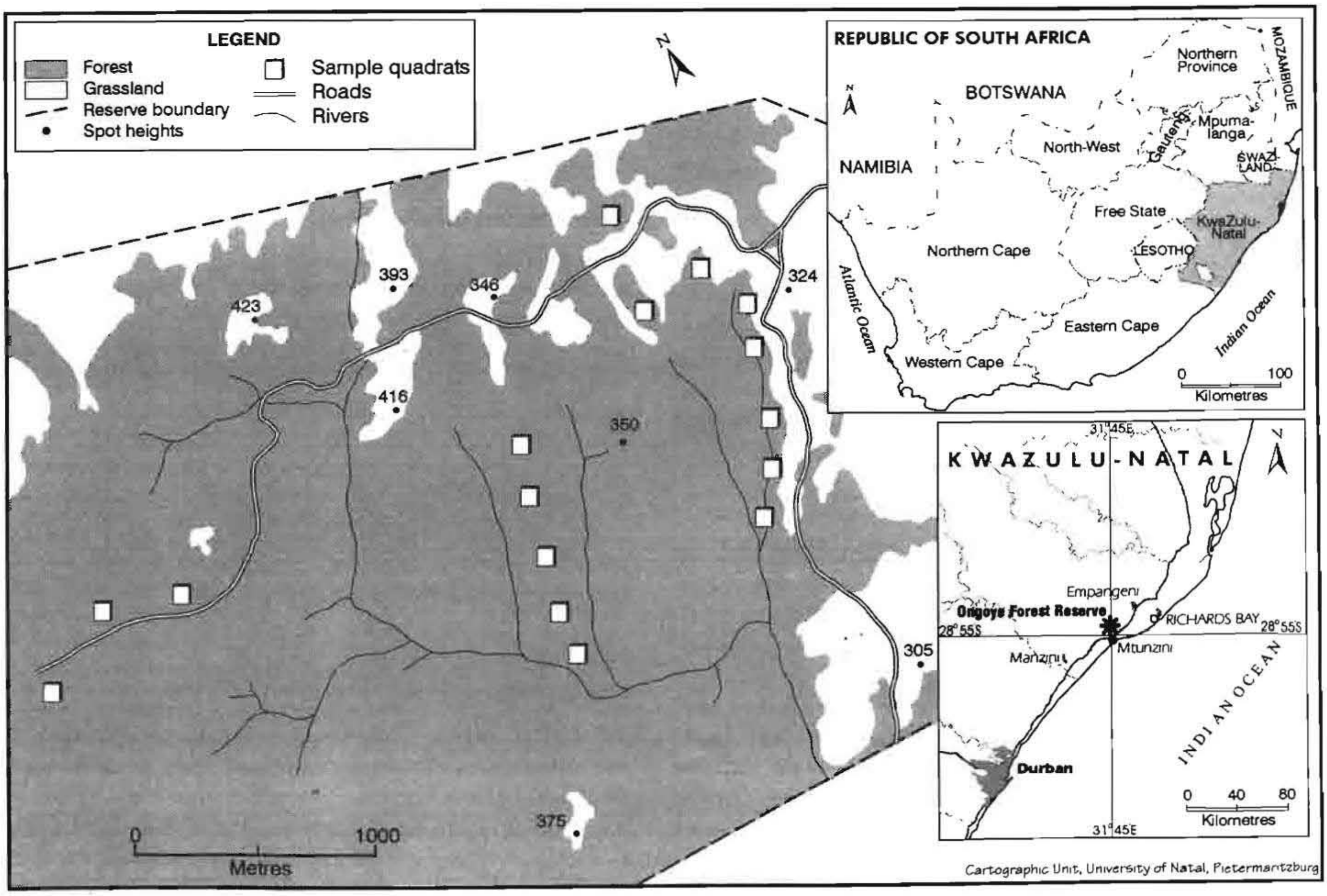

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Figure 1(a) Locality of the Ongoye Forest Reserve in northern KwaZulu-Natal province, South Africa. (b) Map of the north-eastern section of Ongoye Forest showing the relative location of the 16 sample quadrats. Sample quadrats are not drawn to scale and although they are drawn overlapping with rivers, or in close proximity to roads, in reality the influence of either roads or rivers was slight.

each sample quadrat.

To calculate foliage height diversity, foliage density in each of nine height strata (0–0.5 m, 0.5–1 m, 1–3 m, 3–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m and > 25 m) was ranked on the Walker scale of 0–7. Foliage height diversity was scored at eight points in a quadrat and the mean rank value for each height class was calculated from the weighted sum (see Walker 1976):

$$FD = \sum_{i=1}^{8} (n_i c_i)/N, \text{ and } N = \sum_{i=1}^{8} n_i$$

where n_i = the number of sampled points in a quadrat where the height class has rank i; c_i = class midpoint of rank i; N = total number of sample points in a quadrat.

The mean value for each stratum was used to represent the vertical structure of the forest in that quadrat. We used the coefficient of variation (*CV*) of the strata in a quadrat as a summary statistic of the vertical heterogeneity for a quadrat.

The horizontal spatial pattern of the vegetation was estimated using Roth's (1976) heterogeneity index. This index uses the point-centre-quarter (PCQ) method, where distances from a central point to the nearest plant in each quadrant of a circle are measured. These distances give information about dispersion and density of trees in the sample and therefore provide an additional measure of heterogeneity. The coefficient of variation of distances is used to describe the sample distribution (Roth 1976).

The openness of the canopy was measured along three parallel 25-m transects within each quadrat. To do this a rod was held directly above the observer pointing vertically at the canopy every 2 m along the transect. By sighting along the rod the absence of canopy cover was scored if the line of sight intersected an opening in the canopy.

Food resource availability

Food availability and abundance, together with vegetation structure, provide particular combinations of foraging opportunities for birds and may determine what bird species coexist in any habitat (Cody 1983; Robinson & Holmes 1984; Holmes & Recher 1986). Availability of invertebrates and fruit was determined.

Invertebrates

The abundance and wet biomass of surface invertebrates was determined using pitfall traps (Koen 1990). Two transects, 10 m apart, each with four polystyrene cups (diameter = 80 mm; depth = 100 mm) placed 5 m apart were set up in each of the 16 sample quadrats. A detergent was used to retain invertebrates falling into the trap. Pitfall traps were checked three times at four-day intervals. Sampling of surface invertebrates was hampered by *Papio cynocephalus ursinus* (chacma baboon) (Kerr) 1792, *Cercopithecus aethiops pygerythrus* (vervet monkey) (Cuvier) 1821, and *Potamochoerus porcus* (bushpig) (Linnaeus) 1758, removing or damaging the polystyrene cups. Damaged pitfall traps were excluded from the analyses.

Aerial invertebrate abundance and wet biomass was sampled by sticky boards (10 cm × 10 cm plastic plaque coated with Formex^{c} (CIBA-GEIGY)) suspended by wire at 1.5 m (low) and 5–10 m (high) in one tree per plot (*cf.* Koen 1990). Aerial invertebrates were sampled three times at four-day intervals. Because of the difficulty of reaching the canopy, invertebrate resource availability in canopy strata was not sampled.

Fruit

A fruit availability index was calculated for ripe and unripe fruit using the method of Lawes & Piper (1992).

Bird census methods

Birds were censused on clear, windless mornings. We used Koen's (1988) modified stationary spot count method, a modification of Anderson & Shugart's (1974) spot count method (*cf.* Koen 1990). All birds seen or heard within a quadrat during a 10-min period were recorded. This time period was sufficient for the detection of cryptic species and reduced the probability of double counting. Observers moved slowly and randomly about the plot in order to detect cryptic species. Identified birds were located within five vertical strata, either ground (0 m), understorey (3–8 m), or lower/mid/upper canopy (> 8 m). The size and distribution of the sample quadrats allowed a census of all 16 quadrats to be completed by 11 am on each day by two observers (one at the edge and one in the interior). The sequence in which plots were censused, and the observer, were rotated each day in order to eliminate any effect of time of day and observer variation on the census data (Koen & Crowe 1987). Prior to the start of the sample period, observer competence at both visual and aural identification of birds was checked over two days.

We are confident that differences in observer ability were insignificant.

Statistical analysis

Fifteen habitat parameters checked for homoscedasticity and transformed appropriately to achieve statistical normality, were compared between edge and interior plots. To avoid Type I errors induced by testing the same null hypothesis many times, we simultaneously tested for differences between the edge and interior in the dependent habitat variables using MANOVA (SYSTAT 1992). The test statistic Wilks' lambda (likelihood ratio criterion) varies between 0 and 1 and tests the overall significance of the effects of the treatments on the dependent variables. Should this test be significant, the univariate *F*-tests are then consulted to ascertain which of the factors causes the overall significant effects.

Results

Habitat heterogeneity

The habitat variables were divided into two groups (Table 1) and tested separately; those comprising species numbers and numbers of plants for different strata (Wilks'λ = 0.373, $F_{8,7}$ = 1.47, $p > 0.3$) and general physiognomic data (Wilks' λ = 0.543, $F_{7,8}$ = 0.96, $p > 0.5$). The analyses confirmed the overall homogeneity of habitat structure between edge and interior quadrats.

Understorey and canopy tree species composition was compared using detrended correspondence analysis (CANOCO: Ter Braak 1988). Based on species dominance

Table 1 Differences in the 15 habitat parameters between edge and interior for numbers and species of plants (MANOVA: Wilks' $\lambda = 0.373$, $F_{8,7} = 1.47$, $p > 0.3$) and general physiognomic data (MANOVA: Wilks' $\lambda = 0.543$, $F_{7,8} = 0.96$, $p > 0.5$). No parameter differed significantly between edge and interior (see text)

Variable	Edge mean ± *SE*	Interior mean ± *SE*
Plant species richness and stem density (per 25 m × 25 m sample quadrat)		
Number of herb species	17.1 ± 1.0	16.4 ± 1.8
Number of herb layer plants	122.9 ± 27.7	90.1 ± 4.9
Number of sapling species	23.1 ± 1.3	18.8 ± 1.3
Number of saplings	126.8 ± 12.3	126.4 ± 6.2
Number of understorey tree species	12.1 ± 1.1	12.1 + 1.7
Number of understorey trees	42.9 ± 4.2	46.9 ± 1.9
Number of canopy tree species	8.3 ± 1.1	8.625 ± 0.9
Number of canopy trees	16.9 ± 1.7	14.9 ± 1.4
Plant physiognomy		
Sapling cover (m^2)	16.9 ± 2.9	8.5 ± 0.9
Openness of canopy	12.5 ± 0.7	11.0 ± 1.4
Number of vines	23.0 ± 6.6	19.4 ± 4.8
Vertical heterogeneity (% CV)	70.2 ± 3.5	76.9 ± 4.5
Average of the 8 highest trees (m)	15.5 ± 0.7	16. ± 0.2
Av. dist. (PCQ) - canopy trees (m)	6.4 ± 0.3	6.7 ± 0.3

Table 2 Univariate *F*-statistics and summary statistics for food variables between edge and interior (MANOVA, Wilks' $\lambda = 0.195$, $F_{5,6} = 8.26$, $p < 0.01$)

Variable	Edge mean ± *SE*	Interior mean ± *SE*	*F*-value *d.f.* = 1,14
Availability estimate of ripe & unripe fruit	58.5 ± 19.6	27.3 ± 13.7	1.338 n.s.
Number of aerial insects collected from lower (1.5 m) sticky boards	29.1 ± 3.1	51.9 ± 8.34	7.322 $p < 0.02$
Number of aerial insects collected from mid-strata (5–10 m) sticky boards	29.4 ± 5.5	32.1 ± 20.6	0.037 n.s.
Number of surface invertebrates from pitfall traps	344.3 ± 37.4	370.1 ± 49.8	0.161 n.s.
Total wet biomass (g) of surface invertebrates from pitfall traps	10.1 ± 1.1	33.6 ± 6.2	15.74 $p < 0.001$

with 10 rare species down-weighted, there was little difference between edge and interior in understorey species composition (78 species; variance based on eigenvalues — Axis 1 = 17.1%, Axis 2 = 14.7%) or canopy tree species composition (45 species; Axis 1 = 15.2%, Axis 2 = 13.4%).

Food availability

The availability or abundance of five food parameters were compared between edge and interior using MANOVA (Table 2). There was a significant difference between edge and interior in food availability (Wilks' $\lambda = 0.195$, $F_{5,6} = 8.26$, $p < 0.01$). This significant difference is due to the wet biomass of surface invertebrates sampled in pitfall traps ($F_{1,14} = 15.74$, $p < 0.001$) and the numbers of flying insects caught on sticky boards set 1.5 m above the ground ($F_{1,14} = 7.32$, $p < 0.05$) In both instances more invertebrates were recorded in the interior. Although there was a trend toward more fruit at the edge this difference was not significant (Table 2).

Bird species richness

Forty-nine bird species were identified during this study (Table 3). Plots of cumulative species number against the number of counts were inspected for each quadrat. No quadrat differed markedly from another and quadrats were regarded as having equal 'sightability' probabilities. Cumulative species plots of the edge and the interior approached but did not reach the expected asymptote (Figure 2) and we conclude that a subset of the total number of species possible was sampled. We recorded 41 species each from both the edge and interior. Jackknife estimates of bird species richness (Heltshe & Forrester 1983) suggest that we recorded 77% (edge estimate ± 95% c.l. = 53.3 ± 7.5) and 84% (interior estimate ± 95% c.l. = 48.9 ± 3.8) of bird species in edge and interior quadrats respectively. On average 4.56 bird species (1 *S.E.* = 0.17, $n = 240$) were seen during each sample of a plot.

Bird species diversity

We computed the relative abundance of each species at the edge and interior by averaging the numbers of individuals of a species recorded over the 15 sample replicates for each quadrat. These values were then summed for each species across all eight quadrats in the edge and interior. The weighted mean of bird numbers estimated by this method showed a trend toward greater numbers at the edge (mean 1 *S.E.* = 77.8 ± 5.9) than in the interior (mean 1 *S.E.* = 59.8 ± 6.2; $F_{1,4} = 4.38$, $p = 0.055$).

Rank abundance plots of these data show that the edge has more rare species (i.e. species seen on one occasion only) than the interior but there is little difference in the numbers of dominant species (Figure 3). The application of Hill's series of diversity measures and other heterogeneity indices confirms these observations (Table 4). Evenness is greater in the interior and hence the bird fauna is slightly more diverse there (Table 4), although this difference was not significant, using Shannon's diversity index (Magurran 1988, p149) ($H'_{edge} = 3.064$, $s^2_{edge} = 0.001$; $H'_{interior} = 3.118$, $s^2_{interior} = 0.002$; two-tailed *t* test, $t = 0.86$, $d.f. = 821$, $p < 0.5$).

Levels of point diversity across the sample quadrats were surprisingly uniform. The total number of bird species recorded in any quadrat (mean ± 1 *S.E.* = 19.25 ± 0.72) represented approximately 39% (range = 24–49%) of all species recorded. These results suggest that bird species are patchily distributed (i.e. a high turnover between patches). There was no significant difference in the observed species richness between the edge (mean ± 1 *S.E.* = 20.3 ± 0.73) and interior (mean ± 1 *S.E.* = 18.25 ± 1.18) ($F_{1,14} = 2.18$, $p < 0.2$).

Although species richness and diversity were quantitatively similar, the edge and interior each held eight species not shared by the other (Table 3). The change in species between edge and interior (β-diversity) was low (Sorenson's quantitative coefficient $SN = 0.741$; Magurran 1988).

Table 3 Bird species observed in the Ongoye forest. Naming authorities are from McLachlan & Liversidge (1972). An * indicates that the species was observed at the edge and/or the interior

Species		Edge	Interior
Ibis, hadeda	*Bostrychia hagedash* (Latam), 1790		*
Goshawk, African	*Accipiter tachiro* (Daudin), 1800		*
Pigeon,Delegorgue's	*Columba delegorguei* (Delegorgue), 1847	*	
Dove, tambourine	*Turtur tympanistria* (Temminck & Knip), 1810	*	*
Dove, cinnamon	*Aplopelia larvata* (Temminck & Knip), 1810	*	*
Lourie, purplecrested	*Tauraco porphyreolophus* (Vigors), 1831	*	*
Cuckoo, emerald	*Chrysococcyx cupreus* (Shaw), 1792	*	*
Trogon, Narina	*Apaloderma narina* (Stephens), 1815	*	*
Kingfisher, pygmy	*Ispidina picta* (Boddaert), 1783	*	
Woodhoopoe, redbilled	*Phoeniculus purpureus* (Miller), 1794	*	*
Hornbill, trumpeter	*Bycanistes bucinator* (Temminck), 1824	*	*
Barbet, blackcollared	*Lybius torquatus* (Dumont), 1806		*
Barbet, white-eared	*Stactolaema leucotis* (Sundevall), 1850		*
Barbet, green	*Stactolaema woodwardi* (Shelley), 1880	*	*
Barbet, redfronted tinker	*Pogoniulus pusillus* (Dumont), 1806		*
Barbet, goldenrumped tinker	*Pogoniulus bilineatus* (Sundevall), 1850	*	*
Honeyguide, lesser	*Indicator minor* Stephens, 1815	*	
Honeyguide, scalythroated	*Indicator variegatus* Lesson, 1831	*	*
Woodpecker, goldentailed	*Campethera abingoni* (A. Smith), 1836	*	*
Drongo, squaretailed	*Dicrurus ludwigii* (A. Smith), 1834	*	*
Oriole, blackheaded	*Oriolus larvatus* Lichtenstein, 1823	*	*
Bulbul, blackeyed	*Pycnonotus barbatus* (Desfontaines), 1787	*	*
Bulbul, terrestrial	*Phyllastrephus terrestris* Swainson, 1837	*	*
Bulbul, yellow-streaked	*Phyllastrephus flavostriatus* (Sharpe), 1876	*	*
Bulbul, sombre	*Andropadus importunus* (Vieillot), 1818	*	*
Bulbul, yellowbellied	*Chlorocichla flaviventris* (A. Smith), 1834	*	*
Thrush, olive	*Turdus olivaceus* Linnaeus, 1766	*	*
Thrush, spotted	*Turdus fischeri* Hellmayr, 1901	*	*
Robin, chorister	*Cossypha dichroa* (Gmelin), 1789	*	*
Robin, Natal	*Cossypha natalensis* A. Smith, 1840	*	*
Robin, brown	*Erythropygia signata* (Sundevall), 1851		*
Apalis, barthroated	*Apalis thoracica* (Straw & Nodder), 1811	*	*
Warbler, bleating	*Camaroptera brachyura* (Vieillot), 1820	*	*
Flycatcher, dusky	*Muscicapa adusta* (Boie), 1828	*	*
Batis, Cape	*Batis capensis* (Linnaeus), 1766	*	*
Flycatcher, paradise	*Terpsiphone viridis* (Müller), 1776	*	
Boubou, southern	*Laniarius ferrugineus* (Gmelin), 1788	*	*
Puffback	*Dryoscopus cubla* (Shaw), 1809	*	*
Bush shrike, georgeous	*Telophorus quadricolor* (Cassin), 1851	*	*
Bush shrike, greyheaded	*Malaconotus blanchoti* Hartlaub, 1844		*
Starling, blackbellied	*Lamprotornis corruscus* (Nordmann), 1835	*	*
Sunbird, olive	*Nectarinia olivacea* (A. Smith), 1840	*	*
Sunbird, collared	*Anthreptes collaris* (Vieillot), 1819	*	
White-eye, Cape	*Zosterops pallidus* Swainson 1838	*	*
Weaver, forest	*Ploceus bicolor* (Vieillot) 1819	*	*
Waxbill, grey	*Estrilda perreini* (Vieillot), 1817	*	
Mannikin, bronze	*Spermestes cucullatus* (Swainson), 1837	*	
Mannikin, redbacked	*Spermestes bicolor* (Fraser), 1842	*	
Canary, forest	*Serinus scotops* (Sundevall), 1851		*

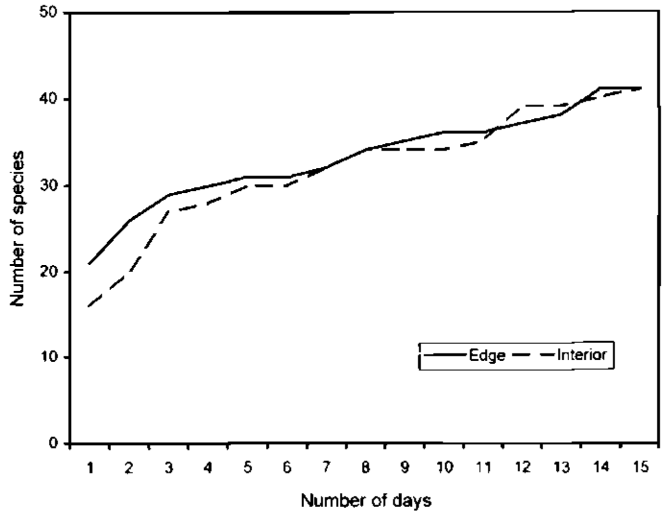

Figure 2 Cumulative numbers of bird species observed over 15 days from (a) edge quadrats, and (b) interior quadrats.

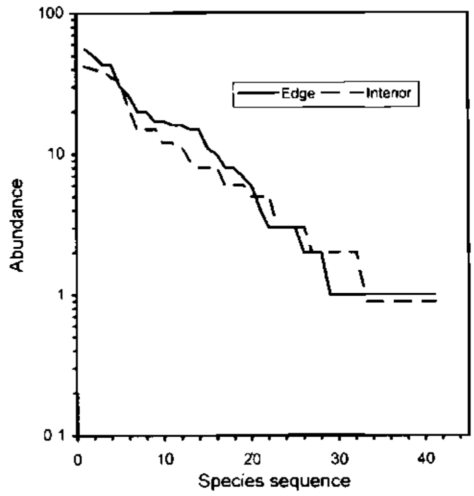

Figure 3 Rank abundance plots of bird species; (a) edge, (b) interior.

Table 4 Avian diversity at the forest edge and interior; (A) diversity indices, (B) fit of species abundance models, and (C) number of birds seen in 0.0625 ha over 10 min

	Edge	Interior
(A) Diversity		
N0 — Species richness (S)	41	41
Number of individuals	469	389
N1 — number of abundant species ($e^{H'}$)	21.43	22.62
N2 — number of very abundant species (1/D)	16.51	17.03
J' (evenness)	0.825	0.839
(B) Fit of models		
Log series	Yes ($p = 0.7$)	Yes ($p = 0.6$)
Log normal	Yes ($p = 0.4$)	Yes ($p = 0.7$)
Broken stick	No	No
(C) Number of birds/0.0625 ha/10 min		
Mean ± 1 *S.E.*	5.17 ± 0.21	3.95 ± 0.20

N0, N1, and N2 = Hill's diversity numbers (Ludwig & Reynolds 1988).

J' = H'/ln(S) (Pielou 1977).

Models fitted using Chi-squared goodness of fit.

Table 5 Univariate *F*-statistics and summary statistics for the amount of dead wood, soil compaction at various depths and soil moisture between the edge and interior (MANOVA, Wilks' $\lambda = 0.527$, $F_{6,9} = 1.35$, $p = 0.33$)

Description	Edge mean ± *SE*	Interior mean ± *SE*	F-value *d.f.* = 1,14
Dead wood (m^3)	1.20 ± 0.41	2.34 ± 0.91	0.02 $p = 0.90$
Soil compaction			
10 cm	3.09 ± 0.16	2.08 ± 0.16	9.56 $p < 0.01$
15 cm	3.69 ± 0.17	3.07 ± 0.18	2.92 $p = 0.11$
20 cm	4.65 ± 0.23	3.99 ± 0.21	1.85 $p = 0.19$
25 cm	5.31 ± 0.21	4.98 ± 0.21	0.61 $p = 0.45$
Soil moisture (% lost)	23.4 ± 0.48	21.8 ± 0.39	0.17 $p = 0.69$

Birds that were most notably absent from the edge are hole nesters *Lybius torquatus* (blackcollared barbet) (Dumont) 1806, *Pogonialis pusillus* (redfronted tinker barbet) (Dumont) 1806, and *Stactolaema leucotis* (white-eared barbet) (Sundevall) 1850.

Firewood is frequently collected from the margin by people from the local tribal lands and it is possible that wood collection is an edge effect which accounts for fewer hole nesters at the edge (Du Plessis 1995). We tested this by quantifying the amount of dead wood and trees suitable for hole nesters in the sample quadrats. Table 5 shows that although there is no significant difference there is a strong trend toward greater volumes of dead wood in the interior compared to the edge. We believe that this trend is biologically important.

Also absent from the edge was a secretive ground dweller, *Erythropygia signata* (brown robin) (Sundevall) 1851. Two notably eurytopic species were recorded only in the interior and are not especially considered forest species (*Bostrychia hagedash* (hadedah ibis) (Latham) 1790, and *Malaconotus blanchoti* (greyheaded bush shrike) Hartlaub 1844. In the case of *B. hagedash* we speculate that their absence from the edge is due to the compaction and lower moisture content of the soil there. Speculation was supported by penetrometer and soil moisture analyses (Table 5). This ibis probes for its food with its long bill and loose soil conditions are more easily met in the interior. A bird of prey, *Accipiter tachiro* (African goshawk) (Daudin) 1800, whose distribution is mostly associated with forest was also observed only in the interior.

Species abundance models

The above species diversity indices make no assumptions about the shape of the underlying species abundance distributions. Three species abundance models were fitted to the data; log series, log normal, and broken stick models (Table 4). Edge data were best described by the log series model ($\chi^2 = 2.19$, 4 *d.f.*, $p = 0.70$) and the interior data by the log normal model ($\chi^2 = 2.13$, 4 *d.f.*, $p = 0.71$) (although a reasonable fit to the log series model is also noted for the interior). This suggests that one or a few factors dominate the ecology of the avian community at the forest edge (Magurran 1988), while the interior community is likely the product of more

more-or-less independent factors (Ludwig & Reynolds 1988). The interior represents a slightly more stable community than the edge, for which species abundance distribution is more typical of environmental disturbance (see Johns 1992, p44). Thus, species abundance models reveal the influence of the proximity to the edge on bird community structure, more specifically the greater numbers of rare species (species observed only once: edge = 13 species, interior = 9 species) caused by species turnover from the adjoining grassland (two *Spermestes* species) and the presence of a typical edge species (*E. perreini).*

Guild structure of the community

Species were classified into a set of trophic-behavioural guilds (Terborgh & Robinson 1986; Terborgh, Robinson, Parker III, Munn & Pierpont 1990). Here we use the relative abundances of the species, as calculated for the estimates of species diversity, to weight the contribution to total biomass of the different guilds. Table 6 illustrates the proportional representation of the different guilds between edge and interior.

In order of decreasing number of species, the insectivorous, omnivorous, and frugivorous guilds contributed most to the species richness of both the edge (99.3%) and interior (98.9%). Granivores and raptors were poorly represented among the guilds. The distribution of species and individuals among the three important guilds at both sites is relatively even, and the most striking difference between edge and interior is the contribution to total biomass of each of the guilds. Fifty-four per cent of biomass in the interior is contributed by the nine frugivorous species, with one species, *Bycanistes bucinator* (trumpeter hornbill) (Temminck) 1824, contributing 55.3% of the frugivore biomass. The larger frugivorous species are more dependent on the distribution and size of discreet food patches and will have large home ranges. The relationship between food distribution and large frugivore abundance would not be represented by our sample procedures. Thus, although there was a trend toward more fruit at the edge, the biomass of frugivores in the interior is greater owing to the differences in bird size and spatial scale of the experiment. In contrast, the total biomass at the edge was distributed relatively evenly (30.7–36.1%) among each of the insectivorous, frugivorous and omnivorous guilds. All guilds were more abundantly represented by arboreal species.

Table 6 Guilds in the bird community of Ongoye Forest. Biomass is weighted according to the relative abundances of the species in each guild (see text)

		Edge			Interior		
Guild	Height	No. species	% indiv.	% biomass	No. species	% indiv.	% biomass
Insectivore		20	50.7	36.1	18	48.8	26.3
	Arboreal	15	35.8	23.8	12	36.5	18.4
	Terrestrial	5	14.9	12.2	6	12.3	14.0
Frugivore		7	11.5	30.7	9	19.8	54.0
	Arboreal	6	9.4	27.0	8	18.5	52.2
	Terrestrial	1	2.1	3.7	1	1.3	1.7
Omnivore		11	37.1	33.1	10	30.3	17.2
	Arboreal	9	31.1	21.8	8	26.0	13.5
	Terrestrial	2	6.0	11.3	2	4.4	3.7
Granivore		3	0.6	0.1	1	0.3	0.1
	Arboreal	0	0.0	0.0	1	0.3	0.1
	Terrestrial	3	0.6	0.1	0	0.0	0.0
Carnivore		0	0.0	0.0	2	0.8	2.4
	Arboreal	0	0.0	0.0	2	0.8	2.4
	Terrestrial	0	0.0	0.0	0	0.0	0.0
Total		41	$n = 469$	19211g	41	$n = 389$	20500g

Discussion

Many different processes have been cited as ultimately responsible for differences in bird species richness and diversity between the edge and interior of forest. These include forest fragmentation (Blake & Karr 1984; Newmark 1991), selective logging (Thiollay 1992), increased incidence of nest parasitism and predation at the edge (Wilcove 1985; Andren & Angelstam 1988; Yahner, Morrell & Rachael 1989; Gates & Giffen 1991), and various disturbances by human or domestic animals at the forest edge (e.g. trampling and compaction of soil at margins by cattle, fire invasion, wood collection; Taylor 1986; Lovejoy *et al.* 1986; Du Plessis 1995). The proximate cause of the difference in species richness is mainly the invasion of the interior by species common at the edge (Gates & Giffen 1991; Newmark 1991; Thiollay 1992). Relatively rare, forest interior, and understorey bird species are most affected by fragmentation, the result being reduction in size, and the increase in extent of the edge in these forests (Yahner 1988; Newmark 1991).

Preliminary evidence from this study suggests that a wide variety of edge effects, unrelated to those of inherent habitat heterogeneity, affect bird species richness in the Ongoye Forest. (1) Three species of barbet, which are hole nesters, appear to be absent from the edge because of the removal of nesting material for fire wood (see Table 5 and results). (2) An ibis species that typically probes for food in soft ground is unable to cope with the trampled and compacted soil at the edge. (3) *Indicator minor* (lesser honeyguide), a brood parasite commonly found in woodland savannah is found at the edge. (4) At least one locally common, but secretive, interior understorey species, *E. signata*, is absent from the edge. (5) There could be higher predation pressure at the edge, because more of the pitfall traps were disturbed by baboons and vervet monkeys there.

Two of the species seen at the edge, *C. delegorguei* (Delegorgue's pigeon) and *Terpsiphone viridis* (paradise flycatcher) (Müller) 1776, were also seen in the interior during casual observation but were not recorded in the interior quadrats. *C delegorguei* is a secretive bird with a limited geographical distribution. It is common only in the Ongoye and Dhlinza forests (Maclean 1993), the latter being only 170 ha in extent (Cooper 1985). While *C. delegorguei* is confined to forest in southern Africa, and sometimes very small forests, we do not consider it a typical edge species. At least two species, *Spermestes cucullatus* (bronze mannikin) (Swainson) 1837 and *Spermestes bicolor* (redbacked mannikin) (Fraser) 1842, found exclusively at the edge were invasives from the surrounding grassland. *Estrilda perreini* (grey waxbill) (Vieillot) 1819, was also found only at the edge, and although regarded as a forest species (Oatley 1989), is a typical forest edge inhabitant (Maclean 1993).

The principle that edges are zones of high diversity, is almost a basic tenet of conservation ecology (Leopold 1933; Wiens 1976; Gates & Gysel 1978; Kroodsma 1984; Harris 1988). Normally the edge is described as the junction of two landscape elements (Forman & Godron 1986) forming a boundary or transition zone (ecotone) where plant and animal wildlife communities grade into one another (Yoakum & Dasmann 1971; Yahner 1988). As a wildlife conservation measure, management to increase forest/wildlife diversity through creation of secondary (non-climax) vegetation communities should be encouraged. These latter 'edges' are a long-term feature of the landscape. However, one should not lose sight of the fact that the edge-effect principle was intended for application to a particular type of edge, and unfortunately, conservationists are seldom faced by such secondary 'edges'. Edges in a fragmented landscape typically owe their origin and maintenance to short-term disturbance phenomena such as fire, and management practices such as grazing, and are thus primarily artificial edges (Lovejoy *et al.* 1986). Our findings show that induced edges in a southern African forest may be associated with high rates of avifaunal turnover, but not with higher point diversity *per se*. Indeed, this study shows that true forest bird species richness decreases at an induced edge. Similar findings have been reported from inherent edges in rainforest. Terborgh *et al.* (1990) found no evidence from a variety of inherent forest edges (open water, swamp, early successional stages) in Amazonian Peru to support the edge-effect principle.

By choosing a large forest and thus controlling for effects of forest size on diversity, and by removing the confounding effect of habitat heterogeneity at the edge (since there was no ecotone we argue that this is necessary), we can conclude that forest bird species richness and diversity at an artificial forest-field boundary is lower than in the forest interior. In this case forest bird species richness decreased by 19.5% (eight of 41 forest species were replaced at the edge by species uncommon in forest). Those edge effects noted at Ongoye are mostly anthropogenic and can be ameliorated relatively easily by focusing management practises on limiting both the intrusion of large numbers of cattle and wood-collectors along the margins.

There are at least two further points worthy of consideration in interpreting the findings of this study. Firstly, Cody (1983) suggested that the number of bird species in a habitat is related to the structural diversity of the habitat which in turn is related to the resource diversity or resource partitioning. We explicitly controlled for the influence of vegetation structure on bird species richness by choosing edge and interior sample quadrats carefully. However, Koen & Crowe (1987) found in their study of the Knysna forest bird communities, some 800 km south-west of Ongoye, that vegetation structure and composition did not influence the composition of the community. Secondly, in controlling for the effect of vegetation structure this field test was performed in one forest physiognomic type at the edge and the interior, and the bird species assemblage associated with this type does not cover all of the 73 potential forest bird species to be found at Ongoye. These data do not, therefore, describe all potential edge effects on the whole forest bird community at Ongoye.

From a conservation point of view, a prograding successional forest edge (ecotone) may cause a notable increase in avian diversity at the edge. However, this increase will come from an invasion of species from the habitats surrounding forest and this is unlikely to increase overall forest-dependent bird species richness. By arguing that the aim of conservation is to maintain and preserve regional biodiversity, we feel that the primary motivation for encouraging the development of forest ecotones should not be to increase local faunal diversity, but to provide an effective buffer to the impact of disturbance agents on forest such as fire. Critical appraisal must be given to the extent, quality, types of edges, and adjacent land-use practices, and there must be a clear conservation objective in order to sensibly conserve forest biodiversity (Ranney, Bruner & Levenson 1981; Harris 1988; Yahner 1988; Laurance 1991; Geldenhuys 1993). The effects of fire, grazing, pole-cutting and other forms of exploitation and disturbance on southern African forests have been poorly documented. The complacent view that forest can be protected by passive management strategies (i.e. nothing beyond proclamation of forest reserves and boundary delineation) must be challenged. This short-term study has highlighted some edge effects on a highly vagile taxon. Research into the impact of edge effects on more sedentary taxa (e.g. earthworms, rodents, anurans; see Laurance 1990) is overdue. We also agree with Oatley (1989) that dependence on forest habitat for breeding requirements is a sufficient criterion for categorizing species as being forest dependent and would like to encourage its use in conservation applications in the region.

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