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Towards Developing Sustainable, Biodiversity-Rich Agricultural Systems in Uganda

Authors

Chamberlain, D.E.[1], Katebaka, R.[2], Senfuma, I.[3], Pomeroy, D.[2], Nalwanga-Wabire, D.[2], Byaruhanga, A.[4], Atkinson, P.W.[1] & Vickery, J.A.[1*]

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1 British Trust for Ornithology, The Nunnery, Thetford, Norfolk, IP24 2PU, UK.
2 Makerere University Institute of Environment and Natural Resources, P O Box 7298 Kampala, Uganda
3 Mabira Forest Centre, National Forest Authority, Kampala, Uganda
4 NatureUganda, P O Box 27034 Kampala, Uganda

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU

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Chamberlain, D.E.[1], Katebaka, R.[2], Senfuma, I.[3], Pomeroy, D.[2], Nalwanga-Wabire, D.[2], Byaruhanga, A.[4], Atkinson, P.W.[1] & Vickery, J.A.[1*]

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1. SUMMARY

1. In the developing world, rapidly increasing human populations are requiring ever increasing food production. Agriculture impacts on biodiversity in two ways; first, through the clearance of natural habitats for new planting and second, through the intensification of existing systems to increase yields per unit area. Green *et al*. (2005) developed a theoretical model, the density-yield function, to determine whether intensifying existing farmland whilst protecting pristine habitats (‘land sparing’), or expanding into pristine habitats with wildlife-friendly farming (‘land sharing), is the best strategy to minimise impacts on biodiversity through increasing yields.

2. Data were collected on bird abundance across a yield gradient from relatively intact forest (yield ≈ 0), through a gradient of increasingly intensive farmland within the banana-coffee arc around Lake Victoria in Uganda. The aim was to construct density-yield functions for bird species and hence determine which strategy, land sparing or land sharing, would be the best to strategy to adopt for the region.

3. Point counts were undertaken at 42 sites (19 forest, 23 farmland). Farmland sites were surveyed as part of a larger separate project – the data used were collected January-April 2007. Forest sites were selected using the Biomass Map of Uganda, followed up by visits undertaken to determine site suitability (sites where there was too much degradation were not included) and access. Forest bird surveys were undertaken in February-April 2008. Bird survey methods were identical in both forest and farmland.

4. Variables derived were: density (derived from Distance sampling) of individual species and species groups; abundance within 25m radius of the sampling point of individual species and species groups; species richness (standardised to 50 individuals using rarefaction) of all species, and of species groups classified according to their major habitat types; and, Simpson’s diversity index of all species and species classified by habitat.

5. A total of 248 species were recorded across the whole survey, 165 in the forest surveys and 141 in farmland. There was relatively little overlap between habitats, with 109 species unique to forest, 85 unique to farmland and 54 species occurring in both habitats. There were more species of conservation concern in the forest habitat.

6. Yield data, estimated as price of the total crops produced per ha, was analysed in relation to species abundance, richness and diversity. Species that showed significant associations with yield tended to be generalists with a broad distribution across habitats. For most of these species, there was a significant increase in abundance with an increase in yield, or in fewer cases, a peak in abundance at intermediate values of yield indicating declines with higher intensity farmland. A smaller number of species/groups, more closely linked to forested landscapes, showed a significant decline in abundance with increasing yield. Patterns in species richness with respect to the yield gradient also showed a significant linear decline with yield. There were many species where it was not possible to model density in relation to yield as they were very scarce or absent on farmland.

7. Forest bird abundance, richness and diversity were analysed in relation to total forest area and fragmentation (measured as total forest perimeter) in the surrounding landscape (within 5km radius) for forest sites only. There was a broad variation in abundance, and variable responses to forest cover and fragmentation. The richness and diversity of forest interior (FF) species increased significantly with forest area as expected, but there were several individual FF species that showed no significant association or where the association was not in the direction expected.

8. The study has highlighted a number of key research areas that need to be explored in order to more fully understand the impacts of intensifying the agricultural landscape on biodiversity, and the precise factors that are responsible for fine-scale variations in the biodiversity value of farmland and forest sites. These include: continued monitoring of the point count locations (most of which can be precisely re-located by GPS reference), ideally on a five-yearly basis; fine-scale habitat data collection on farmland (farm management and non-crop habitat) and forest (forest structure, degradation and disturbance) sites; analysis of density-yield functions at the landscape rather than the site level; and, consideration of the social and economic implications of a land sparing strategy.

9. The results of this study show that land sharing is only likely to be a viable option for relatively common habitat generalist species. Farmland and forest sites had relatively little overlap in bird species, suggesting that the majority of forest species are intolerant of any form of farmland. There were more species of conservation concern in forest than farmland. **Therefore, land sparing (protecting intact habitat and intensifying existing farmland) is the best strategy for increasing yield whilst minimising impacts on biodiversity.**

10. The fact that small patches of forest held relatively rich forest bird communities suggests that even highly fragmented forests within intensified landscapes are worthy of protection. Nevertheless, the occurrence of several forest species, whether forest specialists or (more commonly) those inhabiting a range of forest types (including forest edge and secondary forest), in some farmland sites suggests that some types of farmland may hold relatively high biodiversity and also be worthy of protection. Maintenance of some traditionally managed farmland as part of a land sparing strategy, through creation of buffer zones surrounding forests or through creation of forest corridors across the farmland matrix, has potential to increase the resilience of forest fragments.

2. INTRODUCTION

Agricultural land occupies approximately 38% of the planet's (non-marine) surface (FAO 2007) and the spread and intensification of agriculture are recognised as two of the most important global threats to wildlife (e.g. Matson *et al*. 1997, BirdLife International 2004, Niesten *et al*. 2004, Scharlemann *et al*. 2005). In the developing world in particular, rapidly increasing human populations are requiring ever increasing food production. Agriculture impacts on biodiversity in two ways; first, through the clearance of pristine habitats for new planting and second, through the intensification of existing systems, resulting in increased yields per unit area. Direct comparisons of the relative impacts on wildlife of agricultural expansion and intensification are difficult, but the effects of the loss of pristine habitats might be disproportional to its area as there is a tendency for higher rates of agricultural spread in regions with high biodiversity (Scharlemann *et al*. 2004).

Several lines of evidence suggest that farming is changing faster in the developing than the developed world, both in terms of increases in the areas of cropped land and in annual growth in yield, and similar differences are apparent with respect to the effect of agricultural change on biodiversity (Green *et al*. 2005). Two possible solutions to minimise impacts on biodiversity have been suggested: wildlife-friendly farming and land sparing. The former usually comprises low intensity or extensive agriculture, which often supports higher levels of biodiversity compared to intensive farming methods, but usually with lower yields. Land sparing considers a situation where farmland is managed intensively thus reducing the threat of further conversion of key natural habitats to agriculture. If wildlife friendly farming reduces yield, then a larger area may need to be farmed to meet demand, and even benign farming typically has lower biodiversity than the natural habitat that it replaces (Green *et al*. 2005). In such cases the best way to meet food production and conservation goals may be to increase yields on already converted land and so reduce the need to convert remaining natural habitats. The choice is therefore between having a greater area of low yielding wildlife friendly farmland and less natural habitat, or having a smaller area of high yielding though less wildlife friendly farmland and a greater area available for wild nature.

Green *et al*. (2005) present a theoretical model that resolves which of these options, wildlife-friendly farming or land sparing, is preferable under different levels of yield and biodiversity. Crucial to the model is knowledge of how the density of key species varies according to the agricultural yield per unit area in a landscape, the density-yield function, and in particular whether this relationship is concave or convex (Fig. 1). Very little data exist to test this potentially extremely important model. There is a need to measure components of biodiversity and agricultural yield and estimate the target agricultural production required for human consumption at a range of land-use intensities, from continuous natural habitats where yield ≈ 0 (note that there may be some yield from these areas, for example from very small scale cultivation within forests), through increasingly fragmented low-intensity farmland landscapes to areas of highly intensive agriculture.

The theoretical model offers a quantitative comparison of the benefits to biodiversity of wildlife-friendly farming and land sparing, but it can only be adopted in decision making with knowledge of the density-yield function. Data to construct these models exist for some parts of this gradient (e.g. low versus high intensity agriculture), but data are needed from the full spectrum of land use within a region in order to make full use of the model and thus to inform land use policy. Fig. 1 demonstrates the importance of gaining information from sites where yield = 0, as the initial rate of change can be crucial in determining which land use solution is optimal.

3. AIMS

The aim was to determine patterns of bird density across a yield gradient from forest (yield ≈ 0) to highly intensive agriculture in Uganda, within the framework of the density-yield function. Bird survey data already exist from a range of farming systems from traditional, low intensity mixed cropping to more intensive single crop systems within the banana-coffee agro-ecological farming system of central Uganda, collected during the project 'Conserving Biodiversity in Modernising Farmed Landscapes of Uganda' funded by the Darwin Initiative (project reference number 162-14-032, hereafter referred to as the Darwin Project). To fully parameterise the density-yield model, data need to be collected for landscapes dominated by natural forest (i.e. where yield ≈ 0) from which these agricultural systems derived. This project collected bird data from natural forest habitats and then combined these data with those collected under the Darwin Project. In conjunction with existing yield data, the combined dataset enabled construction of density-yield curves (Fig. 1) for this region of Uganda. The shape of the density-yield function enables a determination of which land use strategy (land sparing or wildlife-friendly farming) would minimise impacts on bird communities at a landscape scale.

4. METHODS

4.1 Site selection

Study sites were selected from native forest patches within the banana-coffee arc around Lake Victoria, corresponding to study areas used in the Darwin Project, where 23 farmland sites, each approximately 1km^2 in area, were surveyed in January –April 2007. Thirty forest patches of at least 1km^2 in area were identified from the Biomass Map of Uganda (Anon 1999). Each of these sites was subject to a 'recce' visit in November 2007 in order to determine (i) whether the forest patch still existed (ii) the extent of degradation and (iii) whether there were any access problems. Degradation was recorded by noting the presence of charcoal burning and/or cultivation within a patch, and taking simple measures of the tree canopy above 8 metres high (into three categories: <50% cover, 50-80% cover, >80% cover) and woody understorey (dense = very difficult to walk and usually needed a machete to clear vegetation; moderate = some vegetation, but not too difficult to walk through; open = very little vegetation, easy to walk through). Sites that had large clear-felled areas for cultivation or charcoal burning, and that therefore had open canopies (all sites <50% canopy cover), were not included. There were 20 sites selected for the bird surveys after the recce visits.

Further preliminary survey visits were made to these sites in February 2008 in order to identify transect routes and trial bird survey methods (see below). There was one site where significant deforestation had occurred since the recce visit and this was dropped from the short list, leaving a total of 19 sites (Fig. 2). Surveys were based on point counts, where for each site a series of surveys at points along a transect was carried out. Each point was 200m apart on the transects and there were up to 10 points per site (although some sites were too small to fit in more than a few points). The distance between points was determined either through GPS readings or (when no reading could be obtained, usually due to dense canopy cover), by pacing out the route (with knowledge of fieldworkers' average pace length). Transect routes began at least 100m, but not more than 200m, from the forest edge. Where possible, the GPS co-ordinates for the entry point to each forest patch was recorded, and also for each point (although in several cases, readings were not possible inside the forest, as before). Notes were taken on particular habitat features at each point, so subsequent surveys could be carried out from the same location.

4.2 Bird surveys

Survey methods were identical to farmland surveys in the Darwin Project. For each point, observers (one bird guide and one data recorder) undertook a ten-minute count, recording all birds seen or heard into one of three distance bands (<25m, 25-50m and >50m from the point); birds in flight were recorded as a separate category. Double-counting of individual birds was minimised by dividing the point count area into quadrants, and not recording birds of the same species twice from the same quadrant (unless the observer had good evidence to suggest that different individuals were involved). For the preliminary visit, counts were carried out at the first point (or sometimes the first few points) without a 'settling' period. However, observations suggested that activity increased over time at the point (Appendix 1), so for the main survey, counts were started after a settling period of 2 minutes at the point. Each point was subject to two main survey visits.

4.3 Habitat surveys

For each farmland site, land use has been mapped at six monthly intervals to coincide with the two annual cropping seasons. Coinciding with these surveys, ten farmers in each square were interviewed about their cropping practices and yield data were collected, allowing part of the density-yield curve to be described. This involved estimating for all crops grown, the yield in terms of biomass and the area that the crop covered on each holding, for up to ten landowners. The value in terms of dollars per hectare was then calculated, using fixed market values. The average per crop per site was then calculated by multiplying the average price per crop per hectare by the area of that crop at the 1 ha scale. The yield as defined in this study was then the summed price across all the crops, expressed as dollars per ha (but note although we expressed yield in dollars, this is an estimate of the total value of the crops whether sold for profit or used for food). Yield data was available only for 21 of the 23 farmland sites, so analyses involving yield differ accordingly in sample size. Yield for each forest site was set at 0.

The Biomass Map of Uganda (Anon 1999) was used to determine the area of forest and the degree of forest fragmentation within the wider landscape for each forest site. The Biomass Map provides a detailed map of various habitat types for the whole of Uganda in a GIS database. Two types of forest were classified, fully stocked and degraded, based on ground-truthing surveys. The Biomass Map was compiled some 14 years previous to the bird survey, so there was the potential for deforestation to render the forest area estimates obsolete. We used these classifications to determine the total area of both forest types and the total length of forest perimeter within a 5-km radius of each site. To check this, outlines of forest patches (both types) within each 5-km radius area were super-imposed on recent satellite photographs of the study areas available in Google Earth™. There were no cases where substantial deforestation had occurred (all <5% as estimated by visual inspection), therefore the Biomass Map can be used as a reliable measure of forest area. However, there were three sites surveyed that were recorded as non-forest habitat categories in the Biomass Map, Kasonke (classed as scrub), Runga and Ziika (classed as woodland), although they had many mature trees, closed canopies, and were structurally similar to many of the other sites that were classed as forest (suggesting some possible errors in the Biomass Map). Furthermore, although change in forest area could be confidently assessed, it was not possible to determine the extent of forest degradation that may have occurred over the period since the Biomass Map was compiled. For these reasons, the area and perimeter of fully-stocked and degraded forest combined was considered in the analysis. Forest perimeter:area was also determined for each site, but was found to be highly negatively correlated with forest area ($r^2 = -0.82$), so this was not used in subsequent analyses (correlation between forest area and total perimeter was $r^2 = -0.13$). Aerial photos of the study site locations, including the 5km radius from which forest data were derived, are shown in Fig. 3. The area of forest and length of forest perimeter within 5-km radius of the site is given in Table 1.

4.4 Analysis

4.4.1 Species density

Density estimates were derived from the programme Distance 5.0 (Thomas *et al*. 2006). Point count data were analysed from the first two distance bands only (<25m and 25-50m), the outer unbounded distance band being discarded. Models were fitted with a half-normal detection function and a hermite polynomial model expansion. Density was extracted per study site using the detection function derived across all sites. Detection probability is likely to vary across different habitat types, in this case forest and farmland. Therefore, these two main habitats were defined as covariates in the model, to allow for differences in detection probability. Point count data from the farmland surveys were extracted from visits that were carried out at a similar time of year to those in the forest survey (March to May). There was only a single visit to each farmland site within this period, compared to two visits to each forest site during this period. This was accounted for by defining 'effort' in the Distance program. Model reliability increases with an increasing number of individual registrations, which should not be less than 40. Only species with at least 40 individuals recorded across the two habitats (a minimum of 20 in each habitat) were considered for Distance analysis. In addition, density for groups of similar species was estimated. These groups were defined partly on taxonomy, but also on the likely detectability assessed according to the expert opinion of the project participants (especially those involved with the fieldwork), so birds within the same group were assumed to be equally detectable (either by sight or sound). The defined groups are shown in Appendix 2.

4.4.2 Species count

Densities can only be calculated using Distance for species that are generally relatively abundant. For other species, count data rather than density estimates were analysed, but using data only from the first distance band (within 25m of the point count location) for the combined analysis of forest and farmland sites. Although there may still be differences in detectability between different habitats, using only the closest distance band should minimise these differences. Nevertheless, interpretation of these results needs to be made with some caution. For forest sites only, further analysis was undertaken considering species count within 50m radius of each sampling point. Such measures may provide a less accurate measure of actual densities than using Distance, but if it is assumed that detectability does not vary significantly across sites (which is likely to be reasonable given that all sites were closed-canopy forest), it should provide a good index of relative abundance across sites. Furthermore, there are advantages to using count rather than density estimates. First, there is less of a restriction on minimum sample sizes, so more species can be analysed (species were analysed that had a minimum total count of 20 individuals across all sites). Second, use of the count data enables greater flexibility in model fitting (so fewer species are discarded due to poor model fit).

4.4.3 Species richness and diversity

The sampling effort (i.e. the number of point counts) varied between sites (Table 1) due to site size, as some sites were only able to accommodate a small number of points that fulfilled the criteria (at least 100m from forest edge and 200m distance between points). Measures of species richness and diversity are typically closely related to sampling effort (Magurran 2004), so estimates of species diversity that were robust to variations in sampling effort were used: Rarefaction and Simpson's Index. Rarefaction estimated species richness per site based on a standard fifty individuals, although this number was constrained by the actual number of individuals detected (i.e. it is not possible to estimate this if fewer than fifty individuals were counted at any given site). In addition, species richness was determined for separate groups according to the habitat classification of Bennun *et al*. (1996); FF (forest interior species), F (species inhabiting a range of forest types including forest edge and secondary forest), f (species that visit the forest for food, although they are generally found in other habitats). Other species were classed as G (generalist species not usually associated with forest). There were few 'G' species recorded, so these were pooled with the 'f' species category.

4.4.4 Generalised Linear Modelling

Species density was analysed with respect to yield using a general linear model with normal errors. Density was log(x+1) transformed prior to analysis. There were some species/species groups where transformation did not result in a better fit of the data to a normal distribution, usually due to a high number of zero counts. Visual inspection of the rarefaction estimates revealed normally distributed data, so a normal errors model was used. For Simpson's index, use of the index in the form –ln (D) (Magurran 2004) was found to approximate to a normal distribution (other forms of D led to highly over-dispersed models).

For combined farmland and forest analysis, species count within 25m radius of the point count was analysed in relation to yield and yield^2 using a generalised linear model. Total count per site was the analysis variable, with log(number of points surveyed) included as an offset to account for differences in sampling effort between sites. In order to ensure standardisation of effort between forest and farmland surveys, only one count, randomly selected from the two visits, was used for the forest surveys to match up with data from the single visit farmland surveys.

For analysis of forest sites, bird counts were summed across points per site on each visit and the log of the number of points surveyed per site was included as an offset in the model (as above). Site was fitted as a random factor to account for the repeated sampling of points across the two survey visits. Species count was analysed in relation to forest area and forest perimeter length, including both linear and quadratic terms. The closest correlate(s) of bird count were identified by sequential deletion of non-significant terms.

For both analyses, count was initially analysed using a Poisson errors model. In all cases where model fit, as measured by deviance/df, was poor (>2.0 or <0.5), a model with negative binomial errors was fitted, which improved the model fit.

5. RESULTS

A total of 248 species was recorded across the whole survey, 165 in the forest surveys and 141 in farmland. A full list of species and their occurrence rates across the forest and farmland survey sites is given in Appendix 2. There was relatively little overlap between habitats, with 109 species unique to forest, 85 unique to farmland and 54 species occurring in both habitats. There were more species of conservation concern in the forest habitat (Fig. 4), based on classifications in Carswell *et al.* (2005). In particular, there were seven species restricted to forest in the highest regionally vulnerable category, but no species in the farmland survey were recorded in this category.

5.1 Species density

There were only 12 species that were sufficiently numerous in both forest and farmland habitats for density estimates to be derived. The mean density in the two main habitat types for these species is shown in Table 2a. Also presented are the significance levels for the effects of yield and yield^2 on bird density (log-transformed). Due to a large number of zero values, it was not possible to model the data distribution for many species. There were ten species that showed significant effects of yield. Eastern-grey Plantain-eater, Common Bulbul, Grey-backed Camaroptera and Yellow White-eye showed an increase in density with increasing yield; Vieillot's Black Weaver showed a non-linear relationship, with densities peaking at medium yield sites; Tambourine Dove, Great Blue Turaco, Yellow-rumped Tinkerbird, Little Greenbul and Splendid Starling showed a decline in density with yield (Fig. 5). For most species, there was considerable scatter in the data ($r^2 < 0.50$), although Common Greenbul ($r^2 = 0.69$) and Little Greenbul ($r^2 = 0.79$) showed better fits.

Results for species groups are shown in Table 2b. Of the ten groups that showed a significant association with yield, three (barbets, hornbills and starlings) showed a decrease with increasing yield, two (kingfishers and tinkerbirds) showed a non-linear association, with the suggestion of an intermediate peak in density at farmland sites with lower yield, and five (bulbuls, finches, parrots/turacos, pigeons, sunbirds) showed an increase with increasing yield (Fig. 6). Common Bulbul was by far the most widespread, and usually numerous, species across the whole sample, which may have had a large influence on the bulbul species group results. When Common Bulbul was omitted, there was no longer a significant effect of yield for bulbuls. For most species, r^2 was less than 0.5, the exception being for finches ($r^2 = 0.83$). However, the latter result is somewhat misleading as this arose due to forest densities being low and having relatively little variation. Several finch species occur in Ugandan forests (e.g. Stevenson & Fanshaw 2002, Carswell *et al.* 2005), but detectability is likely to be amongst the lowest of all species groups. The result should therefore be treated with some caution.

5.2 Species count

A total of 39 species were sufficiently numerous to be analysed (a list of these species and model results for those showing significant effects are given in Appendix 3). Species showing a significant correlation between count within 25m of the point and yield were usually those species that only occurred on farmland. In general these species showed an increase with increasing yield (Speckled Mousebird, African Thrush, Tawny-flanked Prinia, Black-headed Weaver, Bronze Mannikin and Yellow-fronted Canary) or a peak (Wattled Plover, Red-faced Cisticola, Variable Sunbird, Grey-headed Sparrow and Red-billed Firefinch) in density in sites with intermediate yield (Fig. 7). The exception, showing a decline along the yield gradient, was Speckled Tinkerbird.

5.3 Species richness and diversity

Species richness standardised to 50 individuals (using rarefaction) was significantly higher in the forest sites (mean ± sd = 27.32 ± 3.06, n = 19) than in the farmland sites (21.90 ± 4.63, n = 23; t_{40} = 4.37, $P < 0.001$). There was a significant linear decline in species richness with an increase in yield (Fig. 8), although there was less apparent difference between species richness of forest sites and those of the lowest intensity farmland (species richness for farmland sites where yield < \$200/ha = 25.53 ± 2.31, n = 10; t_{27} = 1.72, P < 0.10). There was no significant difference in Simpson's diversity index between farmland (2.74 ± 0.48, n = 23) and forest sites (2.97 ± 0.54, n = 19; t_{40} = 1.51, P < 0.09) and there was no significant association between diversity index and yield ($F_{1,30}$ = 3.07, P < 0.09).

5.4 Forest extent

There was often considerable variation in density, abundance and diversity within the forest sites (Table 1 and Figs. 5-8). When analysing bird data in relation to yield, there were no sites with a yield of <\$138/ha, because even for small traditional farms, there is still a dominance of cultivation. For the forest sites, the assumption that yield = 0 may only hold at relatively small scales (i.e. at the scale of the point count transects). If considered at larger scales (e.g. 5-km radius), yield for smaller fragmented forest patches is likely to be above 0 and within the range of yield < \$138/ha. Use of yield may therefore be better at slightly larger scales and may improve the fit of some of the models presented in Figs 5-7. Yield data were not available from the forest sites. However, for these sites only, the extent of forest and the degree of forest fragmentation at a larger scale may act as a proxy for yield. Therefore, for forest sites, we analysed species density, richness and diversity in relation to total forest area and forest perimeter length (both linear and quadratic terms) within a 5-km radius of each study site.

There was no significant correlation between species diversity and either forest area or forest perimeter. There was a significant linear correlation with diversity of forest specialist (FF) species and forest area (Fig. 9). Results were similar for species richness, with a linear correlation between the richness of forest specialists and forest area (Fig. 10), but no other significant results.

Out of 67 species analysed, 20 showed significant associations with either forest area or forest perimeter (a list of these species and model results for those showing significant effects are given in Appendix 4). There were 11 species that showed a significant association between species count within 50m radius of the point and forest area (Fig. 11). There was a wide variation in the direction of the relationship: 2 species showed a general increase in abundance with forest cover (Forest Robin, Velvet-mantled Drongo), 7 species showed a decrease (Crowned Hornbill, Yellow-rumped Tinkerbird, Little Greenbul, White-throated Greenbul, Green Crombec, Little Green Sunbird and Splendid Glossy Starling) and 2 species showed a non-linear response (Great Blue Turaco and Red-tailed Bristlebill).

There were nine species that showed a significant association with forest perimeter length (Fig. 12). Five species showed a decrease with increasing perimeter (Little Grey Greenbul, Yellow-whiskered Greenbul, Yellow-browed Camaroptera, Green-headed Sunbird and Yellow White-eye), two species showed and increase (Black and White Casqued Hornbill and Red-tailed Greenbul) and two species showed a non-linear response (Green-tailed Bristlebill and Grosbeak Weaver). There was a single species, Pale-breasted Illadopsis, where both forest area and forest perimeter were significant in the final model. The effects of both of these variables were positive, although these relationships were apparently driven by one or two outliers (Fig. 13).

Species showing a significant association with forest area or forest perimeter (Figs 11 and 12) were grouped according to their habitat requirements (i.e. FF, F or f) and, based on Figs 11 and 12, were also classed in relation to their likely response to deforestation, where a decrease in forest area or an increase in forest perimeter was considered to represent deforestation. As many FF species showed a negative response to deforestation as showed a positive response (Fig. 14), and there were five species where non-linear or positive effects were noted: Red-tailed and Green-tailed Bristlebills, Red-tailed Greenbul, White-throated Greenbul and Little Green Sunbird. For F species, there was a mixture of positive and negative effects and for forest visitors (f), there were no negative effects.

Total abundance of all species within each of the three habitat classifications were analysed in relation to forest cover and perimeter using the same analytical approach as for individual species count.

There was no significant effect of either variable on abundance of F or f species. There was a significant non-linear relationship between the abundance of FF species and forest area, where abundance decreased with forest area up to intermediate values, but there was the suggestion of a subsequent increase in abundance at the highest levels of forest cover (Fig. 15).

6. DISCUSSION

Forest and farmland bird communities were fairly distinct, with little overlap in species. There were 109 species that were confined to forest, 85 that were confined to farmland and 54 species common to both habitats. There were more species of conservation concern in forests, including seven classified as 'Regionally Vulnerable' (Ayers' Hawk Eagle, Crowned Eagle, Forest Wood-hoopoe, Cassin's Honeybird, Purple-throated Cuckoo-shrike, Toro Olive Greenbul and Weyn's Weaver), but no farmland species were in this category. For species confined to forest, it was not possible to statistically fit a relationship with yield, but these species could be viewed as having extreme concave density-yield curves, and therefore land sparing (i.e. leaving forest intact and intensifying existing farmland) is clearly the only conservation strategy for many of these species if yields are to be increased with minimum biodiversity impact. This was also the case for a few species that occurred on farmland, but at lower density than in forest (Tambourine Dove, Speckled Tinkerbird, Little Greenbul and the barbet species group).

Whilst a large number of species were recorded from the forest surveys, it is likely that species richness was underestimated, as the point count method was biased towards highly visible, and especially highly vocal, species. For example, Davenport *et al*. (1996) list 16 FF species occurring in Mabira that were not recorded in the survey (including Nahan's Francolin *Francolinus nahani*, Buff-spotted Flufftail *Sarothrura elegans*, Lemon Dove *Aplopelia lavata*, African Broadbill *Smithornis capensis*, Green-breasted Pitta *Pitta reichenowi* and Grey-winged Robin-chat *Cossypha poliopterus*). Attempts to compile full species lists require intensive efforts using a number of different methods, including mist-netting and play-back techniques. However, the point count methods used in this project are easily applied and, crucially, are highly repeatable, hence they provide the opportunity for standardised measures of change in the surveyed species in the future (see below). Such biases also occur in the farmland habitat, but it seems likely that the closed structure and consequent poor visibility in the forest habitat would lead to species richness being under-estimated to a greater degree. The differences observed between forest and farmland in terms of species richness and diversity can therefore be considered conservative.

Species that showed significant associations with yield tended to be generalists with a broad distribution across habitats. For most of these species, there was a significant increase in abundance (i.e. either density or count) with an increase in yield, or in fewer cases, a peak in abundance at intermediate values of yield (Figs 5 - 7), indicating declines with higher intensity farmland. A smaller number of species/groups showed a significant decline in abundance with increasing yield. These, not surprisingly, were those more closely linked to forested landscapes (Figs 5-7). Patterns in species richness with respect to the yield gradient also showed a significant linear decline with yield (Fig. 8). Such a pattern, where the number of species declines, but the number of individuals of a smaller group of species increases, is relatively common across gradients of human disturbance in a landscape, i.e. from natural through to highly modified habitats (e.g. urban habitats; Chace & Walsh 2006). These results therefore suggest that for several widespread habitat generalists, land sharing (i.e. encroaching on pristine habitats with low intensity farmland) is likely to be a feasible option to increase yield and minimise impacts on biodiversity, but for birds requiring some forested elements, the opposite is true. However, it should be noted that the impact of intensification may have been underestimated as no yield data were collected from two of the most intensively managed sites, one tea plantation and one sugarcane plantation. These had notably lower diversity than the other farmland sites (they had the lowest overall species richness and diversity index estimates) and also had very low abundances of a number of species that showed a positive association with yield (e.g. pigeons, Speckled Mousebird, Common Bulbul, African Thrush, Yellow White-eye, sunbirds). Including these sites may have altered the response of some farmland species to the yield gradient (i.e. made the relationship non-linear), although it should be noted that it cannot necessarily be assumed that these sites would have a higher yield per unit area than other, more traditionally managed, farm sites.

The lowest yield recorded on a farmland site was \$138/ha, and there was therefore a 'gap' in the distribution which meant that precise relationships between density and yield may have been poorly estimated (e.g. Figs. 5j, 6c and 6e, where the model fits a peak in abundances at low values of yield where no observed data currently exist). When measured at the level of the survey site, yield is not likely to be much lower than the observed minimum because at lower yields, it may not be economically viable to cultivate land for even the lowest intensity 'traditional' farmland. However, an assessment of yield at larger scales (e.g. 2-km or 5-km radius) would have produced a more even distribution because many of the forest sites were highly fragmented patches within an agricultural matrix (Fig. 3) and therefore at larger scales would not have yield = 0.

For most pre-dominantly farmland species, there was usually a wide variation in abundance across farmland sites, including the many species that occurred primarily on farmland but did not show any significant variation with respect to yield. This suggests that many other factors that are independent of yield influence biodiversity value. For farmland of a given intensity, the biodiversity could be maximised without compromising yield if these factors were identified. Both habitat structure and distance to forest have been shown to influence the bird communities on Kenyan farmland (Laube *et al*. 2008). The presence of mature fruiting trees is also likely to be a key factor, especially for forest species recorded in farmland. Although this research suggests that a land sparing approach may ultimately be the best way to increase yield while minimising impacts on overall biodiversity, it should be acknowledged that some farmland sites were also relatively species rich. Intensification of traditional low intensity farmland may not have the impact that would ensue with encroachment onto forest habitats, but nevertheless there may still be some significant costs in terms of lost biodiversity. The danger of ignoring biodiversity issues on farmland has become evident in Europe (e.g. Wilson *et al*. 2009), and such large biodiversity losses should be avoided in the developing world if at all possible. Further research into fine-scale habitat associations with respect to land management of existing farmland in Uganda, and other parts of the developing world, is therefore required.

Previous studies on the influence of measures of forest fragmentation on African birds have had diverse results. For example, Manu *et al*. (2007) found in general that patch area had little influence on species richness in Nigerian forests, although isolation and distance to forest edge were often important predictors, whereas Wethered & Lawes (2005) found forest area to be an important predictor of bird communities in South Africa. Several studies have, however, found distance of survey location to forest edge to be important determinants of bird abundance and community composition (Watson *et al*. 2004, Wethered & Lawes 2005, Manu *et al*. 2007). In this study, we effectively control for edge effects as all sites were relatively close to the forest perimeter (Fig. 3). Furthermore, our measure of forest area was at the landscape, rather than the patch scale and as such incorporates both isolation and patch area. In common with Manu *et al*. (2007), we found a broad variation in density and variable responses to forest cover and fragmentation (as measured by total forest perimeter) at an individual species level, and there were several FF species that showed no significant association or where the association was not in the direction expected. (For certain species, in particular Red-tailed and Green-tailed Bristlebills, Red-tailed Greenbul, White-throated Greenbul and Little Green Sunbird, the habitat classification should possibly be reviewed in the light of these results). However, although the response of individual FF species was not as expected (Fig. 14), there were a number of forest specialists that were too scarce for analysis, but which occurred solely, or at their highest densities, in the sites from the Mabira forest complex (e.g. Grey Longbill, Brown Illadopsis, Sooty Boubou, Red-headed Malimbe), which could be indicative of fragmentation processes that we were unable to detect in our sample, which was made up mostly of small forest fragments. Richness and diversity of FF species did increase with forest area, suggesting that there was an overall effect when forest specialists were considered as a group. There were two clear outliers, both within the Mabira forest complex, which had much higher forest cover (Figs. 9 – 13) which may have unduly influenced the model results. A more robust analysis would have been achieved with more sites surveyed from such highly forested landscapes.

In common with results from the farmland sites, results from the forest sites may also suggest that simple landscape-level measures are not adequate and that finer-scale habitat data (e.g. on forest structure and levels of disturbance) are needed to more fully understand determinants of forest bird density. For example, human disturbance has been shown to affect forest bird communities in

Northern Kenyan forests (Borghesio 2008). A key point, however, is that even in the smallest sites within an intensive farmland matrix (e.g. Kyengeza, Runga, Ziika; Table 1, Fig. 3), there were still relatively species-rich communities containing several FF species, suggesting some resilience to fragmentation. Therefore, even small forest patches retain biodiversity value, although their size and sometimes isolation from other patches is likely to enhance the vulnerability of forest species in these patches to local extinction. The occurrence of several forest species, whether forest specialists or (more commonly) those inhabiting a range of forest types (including forest edge and secondary forest), suggest that there is potential to increase the resilience of forest fragments through creation of forest corridors across the farmland matrix.

6.1 Further research

The results of this study have been informative in formulating biodiversity-friendly farming strategies within the banana-coffee arc of southern Uganda. However, the study has also highlighted a number of key research areas that need to be undertaken in order to more fully understand the impacts of intensifying the agricultural landscape on biodiversity and the precise factors that are responsible for fine-scale variations in the biodiversity value of farmland and forest sites.

6.1.1 Continued monitoring

These surveys provide an invaluable baseline to monitor future changes in bird abundance and distribution. All sites are GPS-referenced (to within at least 1-km) and in the majority of cases, point count locations have been recorded to a few metres accuracy (although this was not possible in all forest sites due to poor signal reception). Future survey locations can therefore be very closely, and in many cases precisely, matched. Analysis of changes in bird communities over time with respect to changing land use (measured, for example, using remotely-sensed data) would be a key output of any such work. Given the rapid changes in human population, land use and climate that the area is currently experiencing, we suggest that such a survey should be undertaken at five-yearly intervals.

6.1.2 Fine-scale habitat associations

It is clear that, whilst some species were reasonably well predicted by fairly course habitat variables (e.g. yield, forest area), there were many species that showed no significant relationships. Furthermore, even when significant associations were found there was sometimes much scatter within either farmland or forest sites. It is likely that fine-scale habitat differences have a significant influence on the density of many species. Collection of point count level habitat data in farmland (e.g. precise cropping patterns, number of mature trees or remnant forest patches, presence of water courses) and forest sites (e.g. tree density, foliage height diversity, measures of disturbance) may therefore provide a better measure of habitat quality.

6.1.3 Scale effects on the density-yield function

The scale at which a study is undertaken, and in particular over which yield is calculated, may strongly influence the density-yield function. Yield data (or an appropriate surrogate) collected over a larger area could be easily combined with the current data to produce density-yield functions that may be more appropriate, given that the theoretical model of Green *et al*. (2005) was designed for the 'province' rather than the site level.

6.1.4 Socio-economics of land sparing

If land sparing was to be adopted as a serious land management strategy to minimise impacts of agriculture on biodiversity, there are many wider social and economic implications. For example, how would inhabitants perceive a potential intensification of agricultural land at the expense of local biodiversity (and potentially loss of associated benefits such as ecosystem services)? The answer to such questions is outside the scope of this study, but research into socio-economic aspects of implementing such land sparing strategies is necessary before they can be taken forward as serious resolutions to the conflict between increasing demand for resources and biodiversity conservation.

7. CONCLUSIONS

The results of this study show that land sharing, whereby intact natural habitats are developed for low-intensity agriculture whilst also maintaining relatively low intensity in existing agriculture, is only likely to be a viable option for relatively common habitat generalist species. Farmland and forest sites had relatively little overlap in bird species, suggesting that the majority of forest species are intolerant of any form of farmland, a result also found by Laube *et al*. (2008) in Kenya. All species classed as 'Regionally Vulnerable' (the highest level of conservation concern of the species surveyed) occurred in forest sites only. Therefore, land sparing (protecting intact habitat and intensifying existing farmland) is the best strategy for increasing yield whilst minimising impacts on biodiversity. The fact that even small patches of forest held relatively rich forest bird communities suggests that highly fragmented forests within intensified landscapes are worthy of protection. If a land sparing strategy were to be implemented, then it could only work if existing high biodiversity sites were protected and not subject to further degradation, something that has proved difficult in most areas of the world. Such encroachment could be exacerbated if high intensity agricultural land and biodiversity rich areas were immediately adjacent. Strategies to increase the resilience of forest fragments, such as the creation of buffer zones, through maintaining low intensity farmland surrounding protected sites, and creation of forest corridors across the farmland matrix, should be considered in tandem with land sparing as a means to protect biodiversity in the face of increasing demand for resources.

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Site	Forest area (ha)	Forest perimeter (km)	No. points	S_obs	S_rare50	D_log
Bbale	5.27	40.21	8	111	31.16	3.27
Butugiro	10.22	89.85	10	102	25.37	2.44
Buwola	70.78	26.96	10	103	31.01	3.57
Dimo	17.19	93.23	10	98	28.30	3.07
Gangu/Nabuzi	19.77	97.32	7	81	26.27	2.98
Gulwe	21.74	71.01	3	65	20.22	1.45
Kabasanda	24.62	128.15	10	108	32.37	3.64
Kasonke	1.91	13.32	6	84	26.72	2.93
Koko	14.70	114.10	6	81	23.72	2.38
Kyengeza	27.05	129.73	4	70	27.35	3.24
Kyizzi-Kyeru	10.27	82.01	8	94	25.12	2.30
Mpanga	17.69	104.99	10	97	28.44	3.31
Mulubanga	27.26	90.39	4	79	26.20	2.98
Nagoje	35.83	75.07	10	108	32.17	3.72
Namugobo/Ssanya	11.60	78.79	10	98	26.31	2.91
Namunsa	67.77	55.53	10	108	29.15	3.30
Rain Forest Lodge	36.78	77.27	10	103	28.53	3.15
Runga	5.71	28.01	3	62	25.65	3.01
Ziika	9.99	111.70	4	62	24.98	2.88

Table 1 Forest site descriptions and diversity/richness measures. Forest area is the total area of forest within a 5-km radius of the site, forest perimeter is the total length of forest perimeter within 5-km radius of the site, No. points is the number of point counts per visit undertaken at each site, S_obs is the total number of species recorded per site, S_rare50 is the total number of species recorded, standardised to 50 individuals (by rarefaction), D_log is Simpson's diversity index.

(a) Individual species

Species	Forest mean	SE	Farm mean	SE	yield	$yield^2$	r^2
Green Pigeon	0.64	0.16	0.85	0.24	ns		
Tambourine Dove	3.69	0.41	2.89	0.46	0.001		0.36
Great Blue Turaco	2.82	0.43	2.08	0.43	0.001		0.27
Eastern-grey Plantain-eater	2.97	0.57	4.69	0.55	0.001		0.24
White-throated Bee-eater	1.70	0.70	1.46	0.63	ns		
Yellow-rumped Tinkerbird	2.89	0.38	2.14	0.44	0.012		0.16
Common Bulbul	7.42	1.85	15.57	1.80	<0.001		0.69
Little Greenbul	11.04	1.80	4.03	1.01	<0.001		0.79
Grey-backed Camaroptera	4.31	0.75	7.16	0.88	0.001		0.27
Yellow White-eye	2.07	0.60	3.48	0.64	<0.001		0.33
Splendid Starling	2.00	0.56	1.76	0.42	0.015		0.15
Vieillots Black Weaver	0.47	0.13	1.14	0.31	0.008	0.008	0.18

(b) Species groups

Species	Forest mean	SE	Farm mean	SE	yield	$yield^2$	r^2
PIGEON	3.52	0.28	5.03	0.55	0.007		0.18
PARROT/TURACO	4.04	0.47	5.73	0.47	0.004		0.19
CUCKOO	3.16	0.28	4.41	0.56	ns		
KINGFISHER	1.83	0.24	2.49	0.74	0.010	0.003	0.25
HORNBILL	3.25	0.47	2.35	0.40	<0.001		0.32
TINKERBIRD	3.32	0.33	3.75	0.42	0.042	0.011	0.25
BARBET	3.11	0.36	2.42	0.38	<0.001		0.46
BULBUL	14.27	1.03	17.29	1.20	0.001		0.39
FLYCATCHER	2.79	0.29	2.74	0.50	ns		
SUNBIRD	3.84	0.39	6.34	0.66	<0.001		0.31
STARLING	3.03	0.49	2.52	0.41		<0.001	0.40
WEAVER	17.21	4.45	7.87	1.01	ns		
FINCH	8.00	2.22	15.81	2.64	<0.001		0.83

Table 2 Density of (a) individual species and (b) species groups, calculated from the program Distance, and the association between density and yield. Only the species/groups presented occurred in sufficient numbers in both habitats for density estimates to be made. Sample sizes for forest and farmland sites respectively were 19 and 23 for means and 19 and 21 for the analysis of yield. r^2 values and P values are given for linear and (if applicable) quadratic effects of yield if significant.

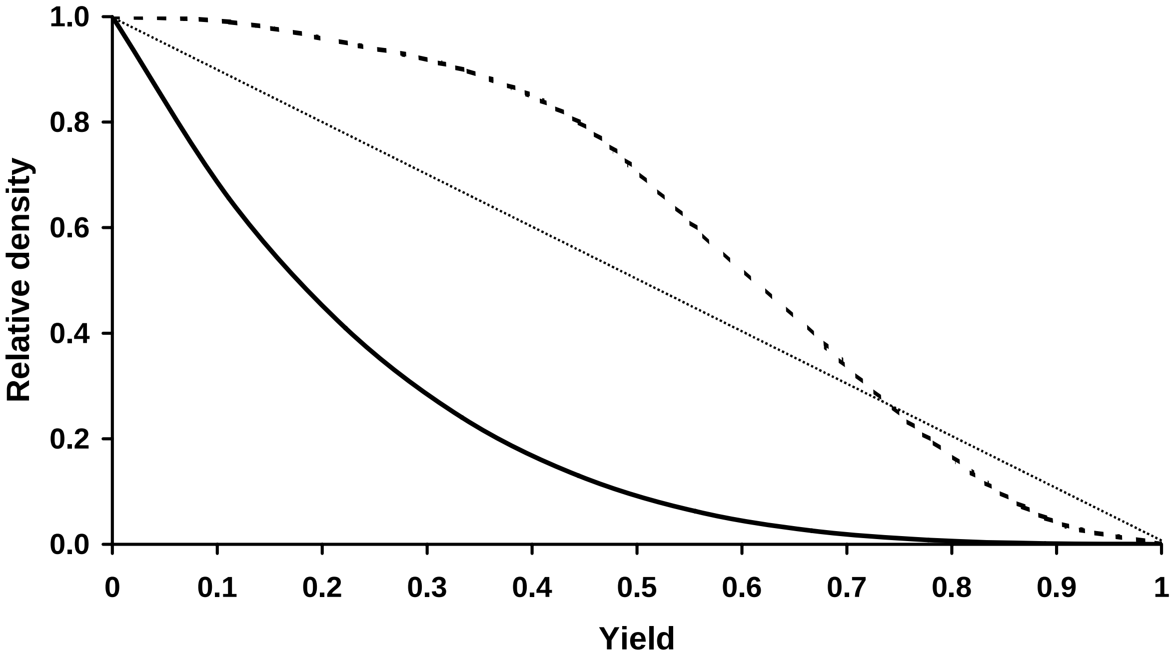


Figure 1 An example of two different density-yield functions. The diagonal dotted line is the density achievable under maximum yield farming (land sparing) and is termed the critical chord. If the density on farmed land drops off rapidly with increasing yield (lower curve) and is therefore lower than the critical chord, then maximum density may be attained by having areas of high yield farming and retaining patches of pristine habitats. If the density drops off slowly with yield and is greater than the maximum chord (upper curve), then density may be maximised by low intensity agriculture throughout the area. Note however that land sparing would maximize relative density under both curves at higher yields (>0.75).

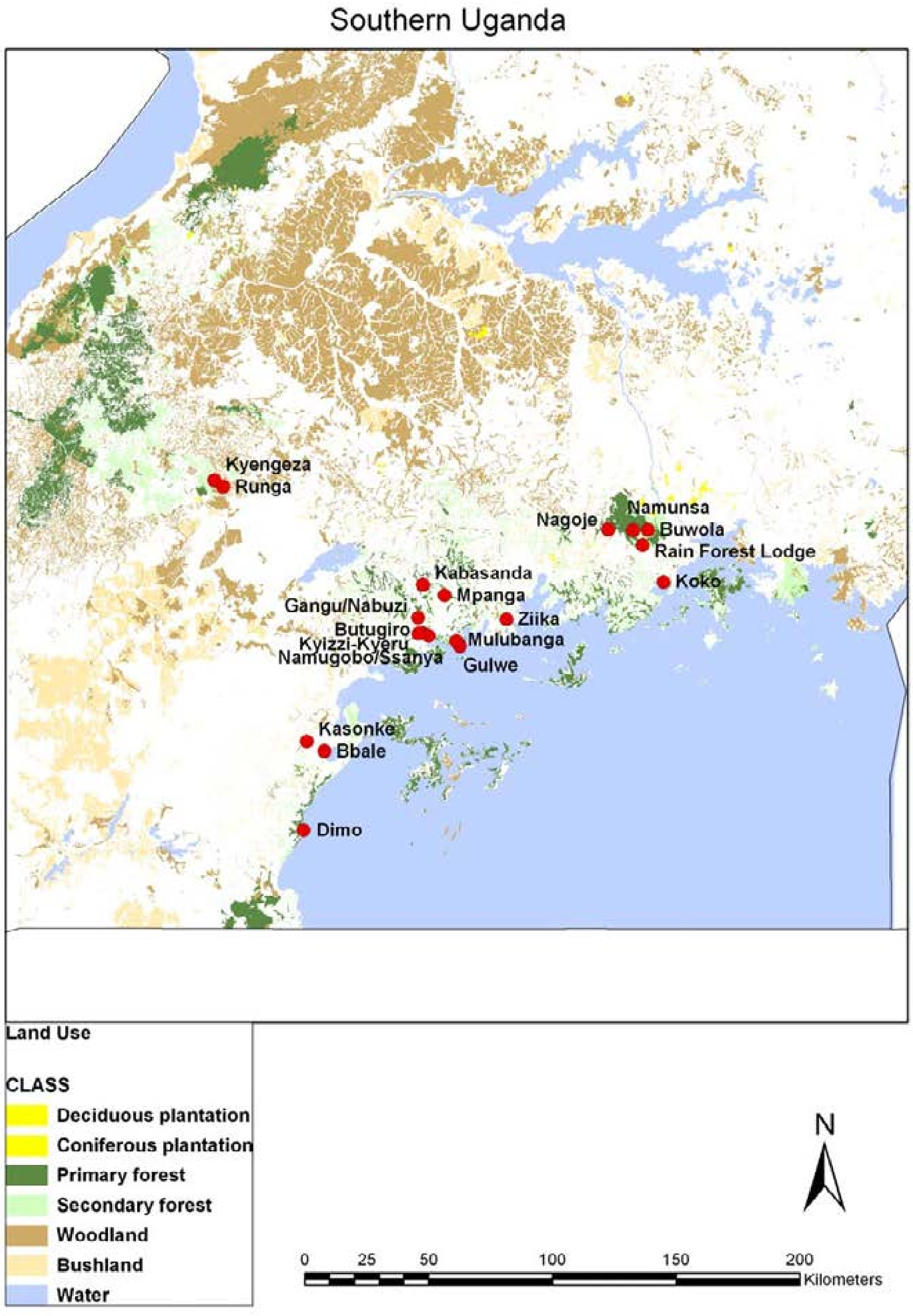
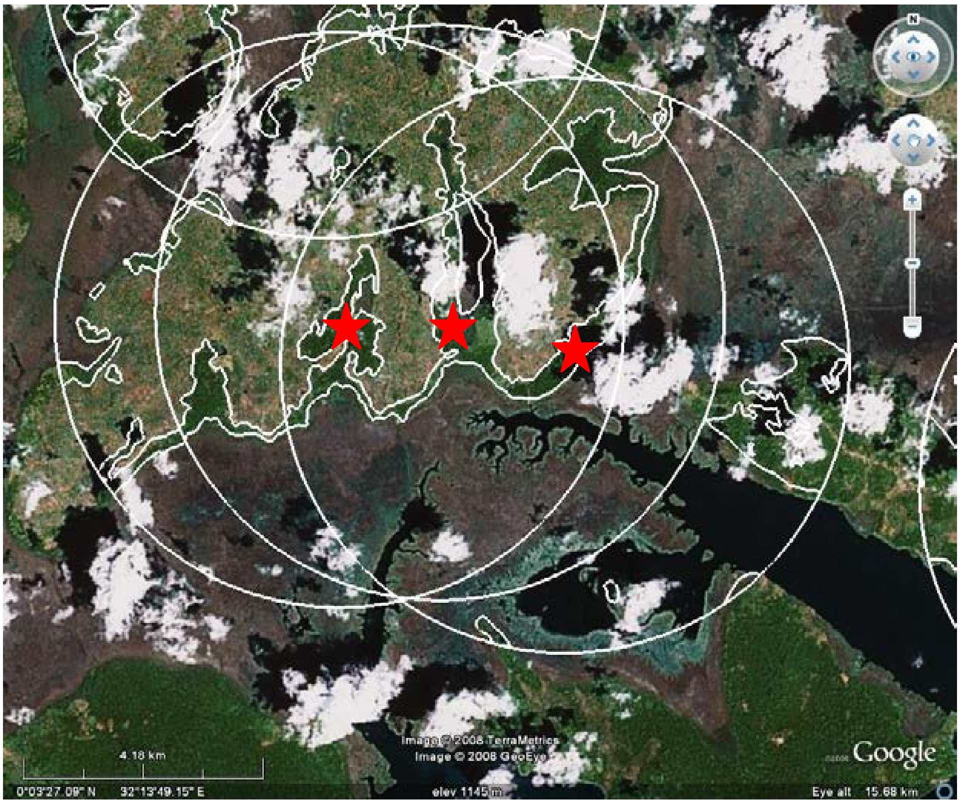


Figure 2 Map of the study area, showing major land use types, and the location of the forest survey sites (red dots).

(a) Bbale

Figure 3 Maps of individual study areas. Survey site locations are shown as red stars. The extent of fully stock and degraded forest from the 1995 biomass map is shown outlined in white, super-imposed on recent images from GoogleEarth™. The circle is the 5-km radius from which forest area and total forest perimeter were calculated. Note that other forest survey sites in close proximity may also be shown on a map.

(b) Butugiro; Kyizzi-Kyeru; Namugobo/Ssanya



(c) Buwola

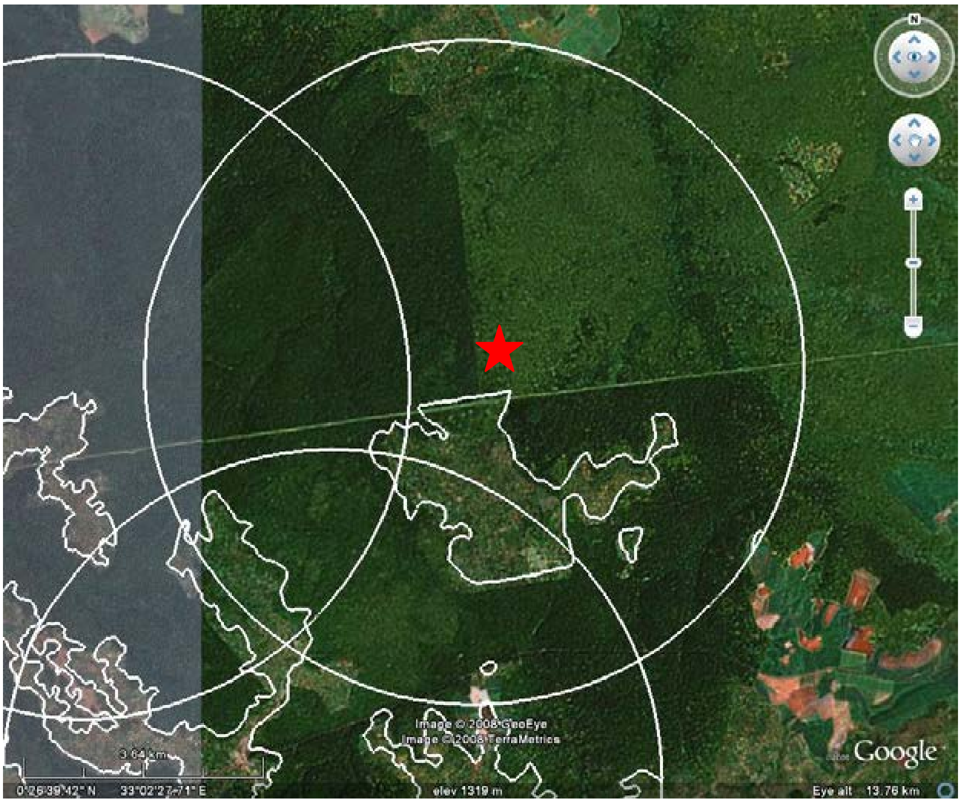
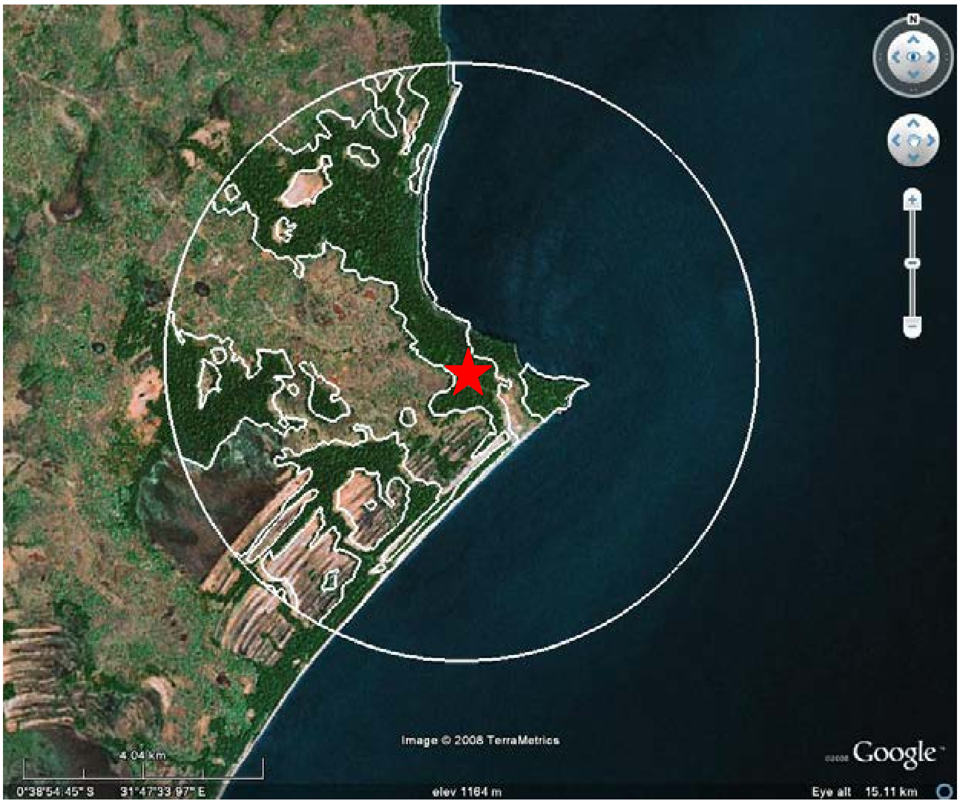


Figure 3 (continued)

(d) Dimo



(e) Gangu/Nabuzi

Figure 3 (continued)

(f) Mulubanga; Gulwe

(g) Kabasanda

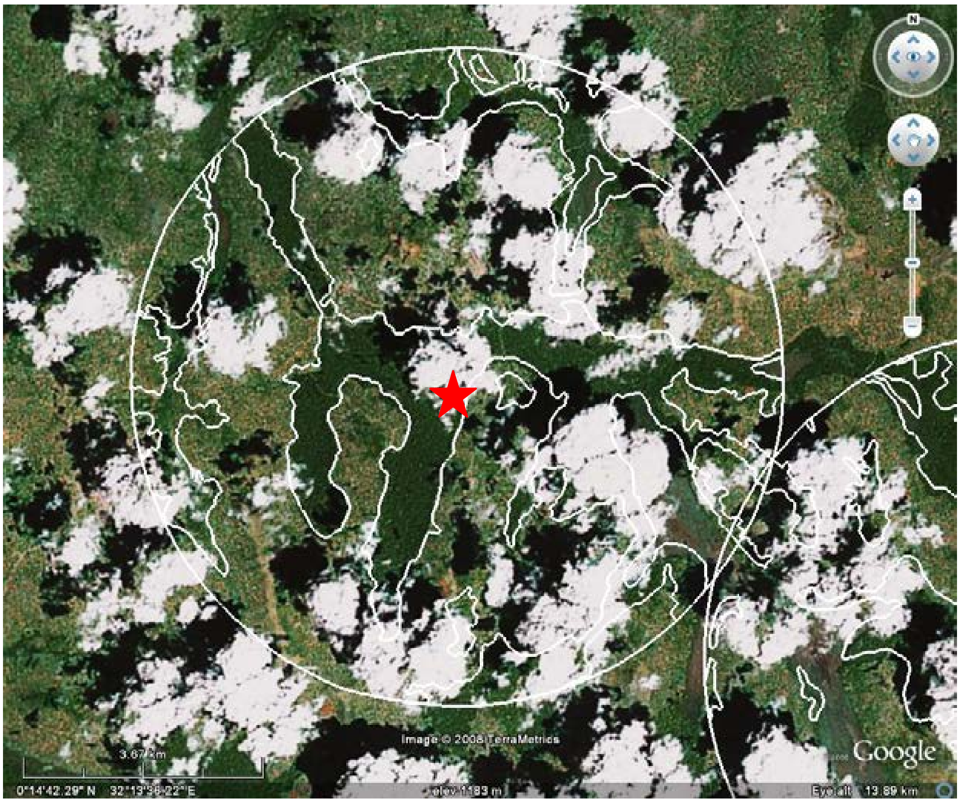
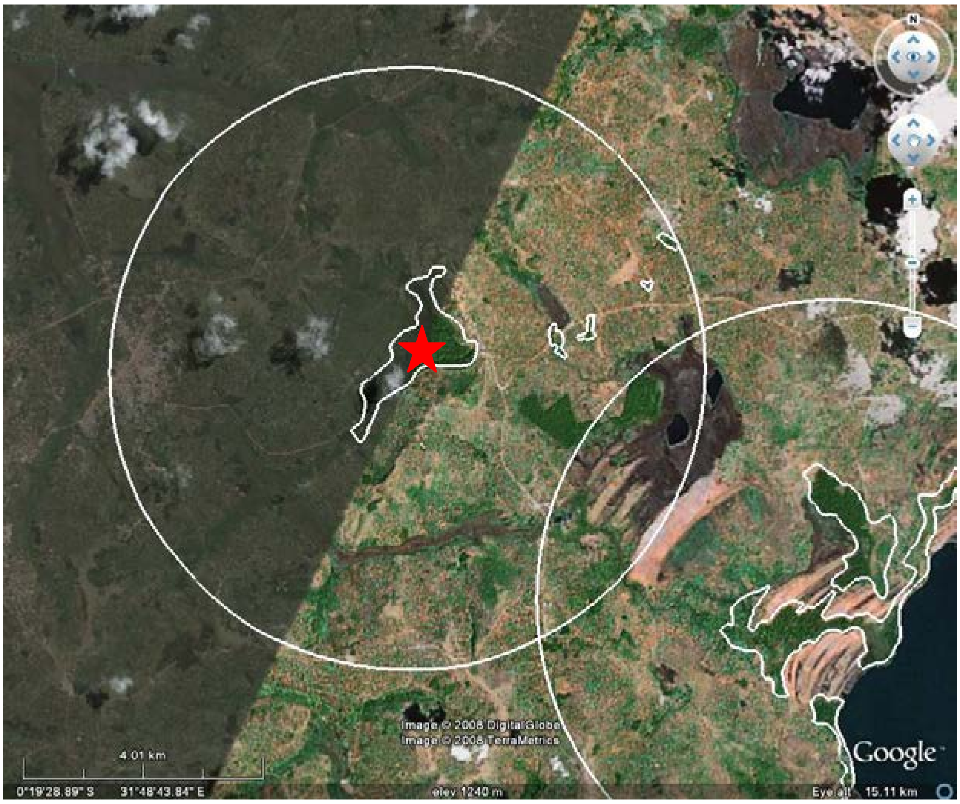


Figure 3 (continued)

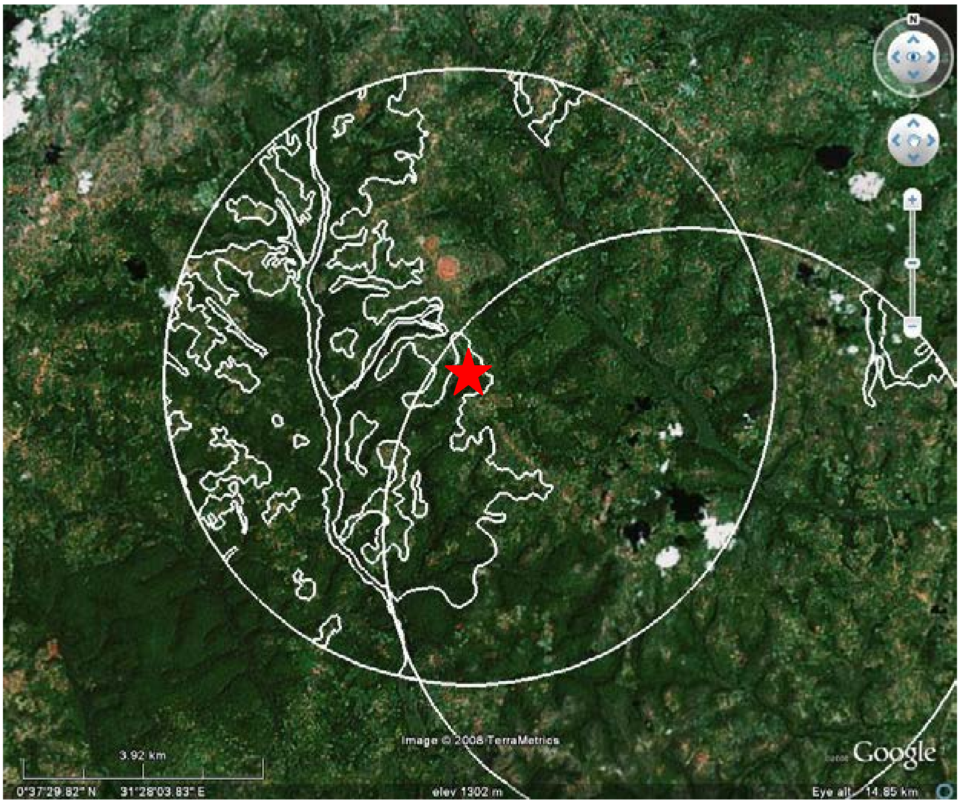
(h) Kasonke



(i) Koko

Figure 3 (continued)

(j) Kyengeza



(k) Mpanga

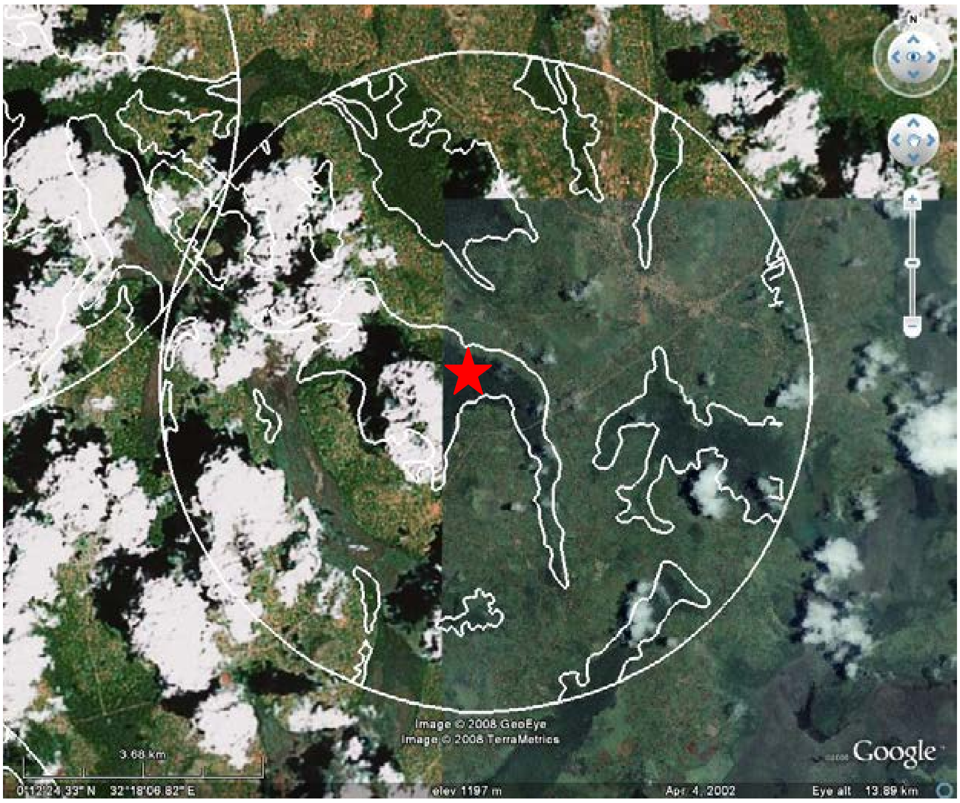
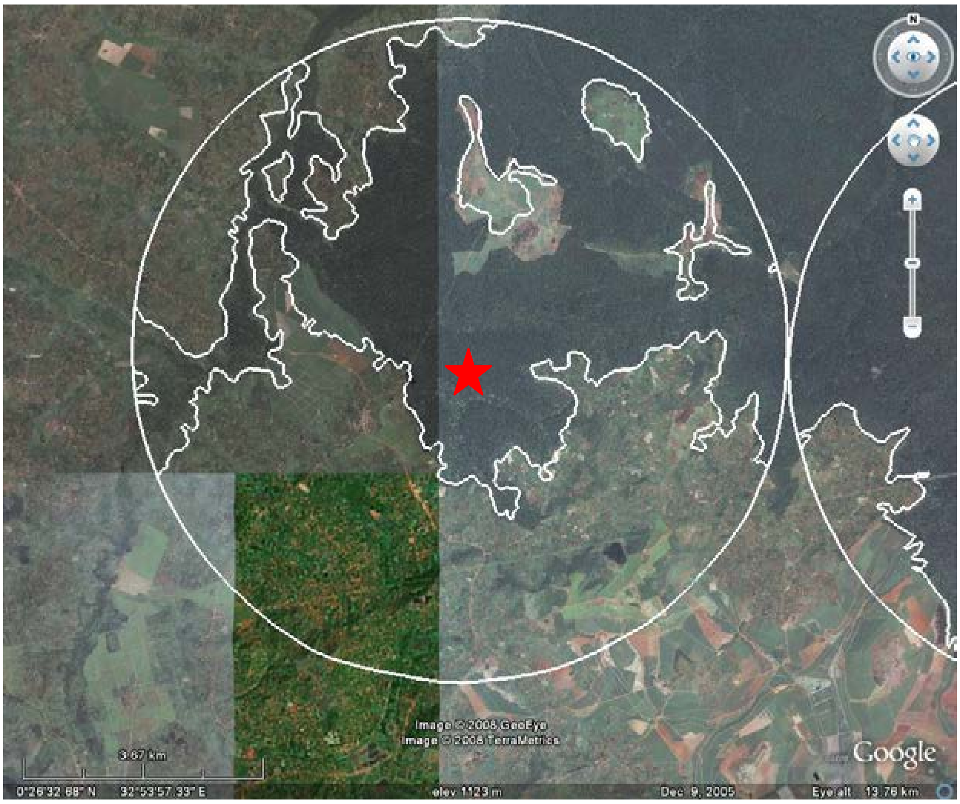


Figure 3 (continued)

(l) Najoge



(m) Namunsa

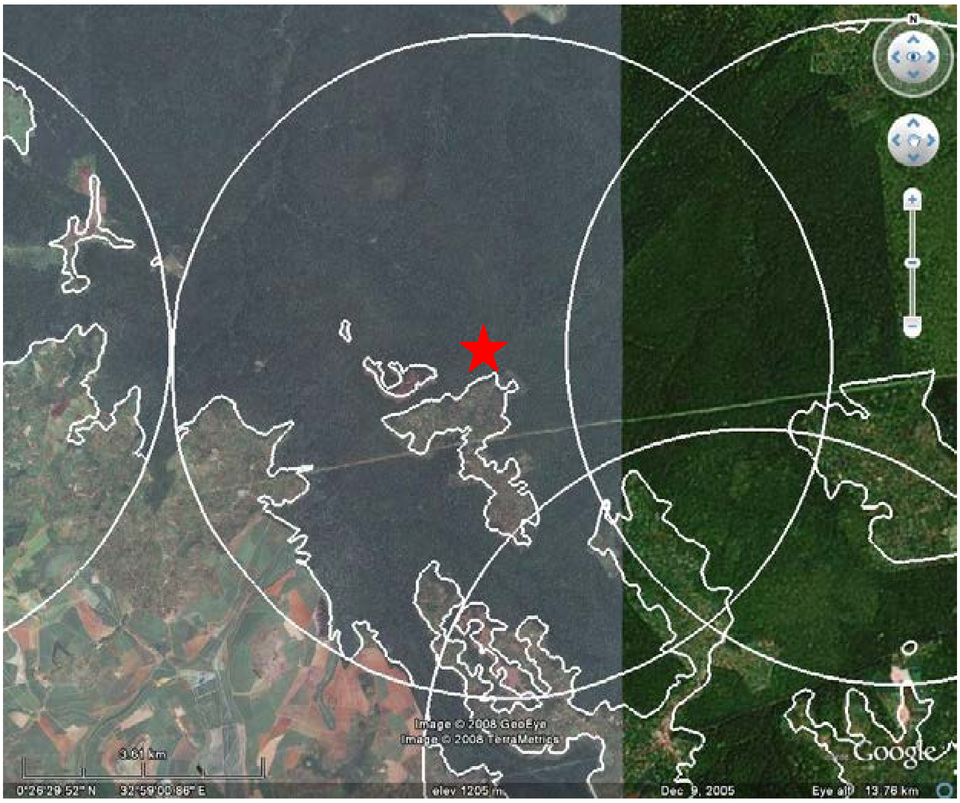
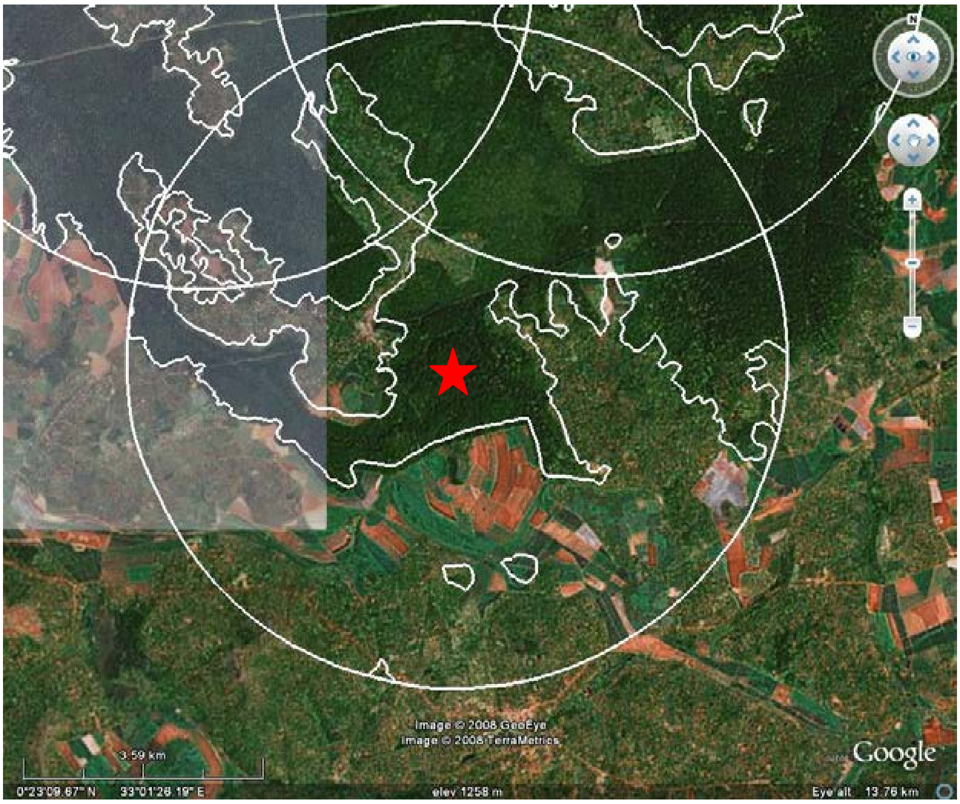


Figure 3 (continued)

(n) Rain Forest Lodge



(o) Runga

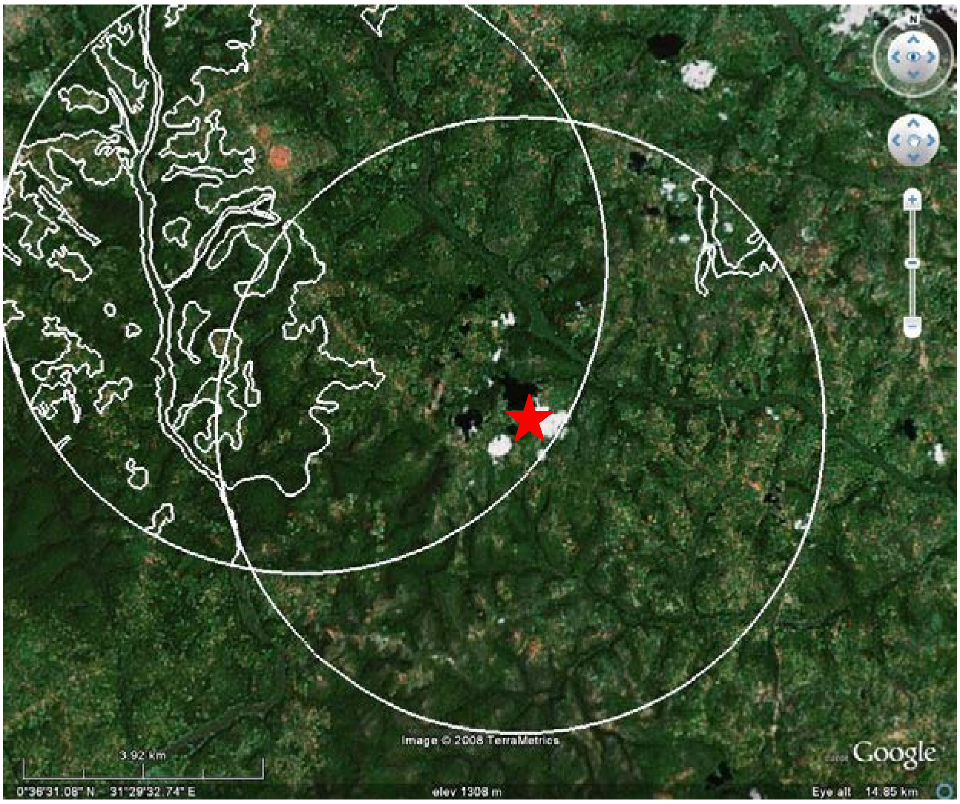


Figure 3 (continued)

(p) Ziika

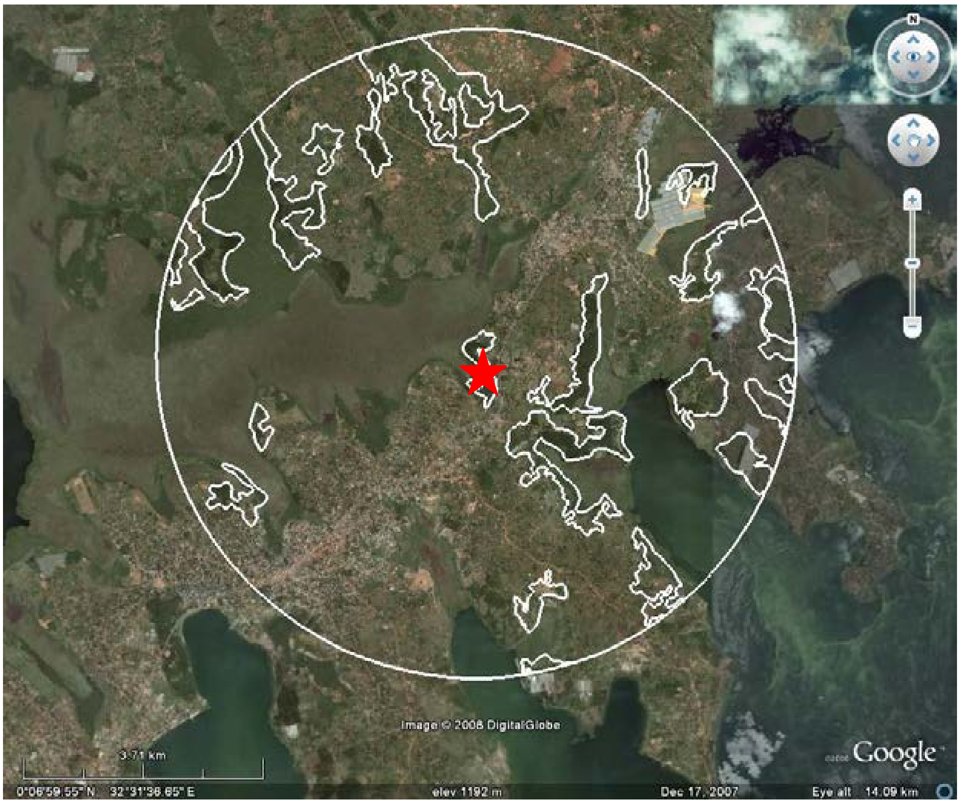


Figure 3 (continued)

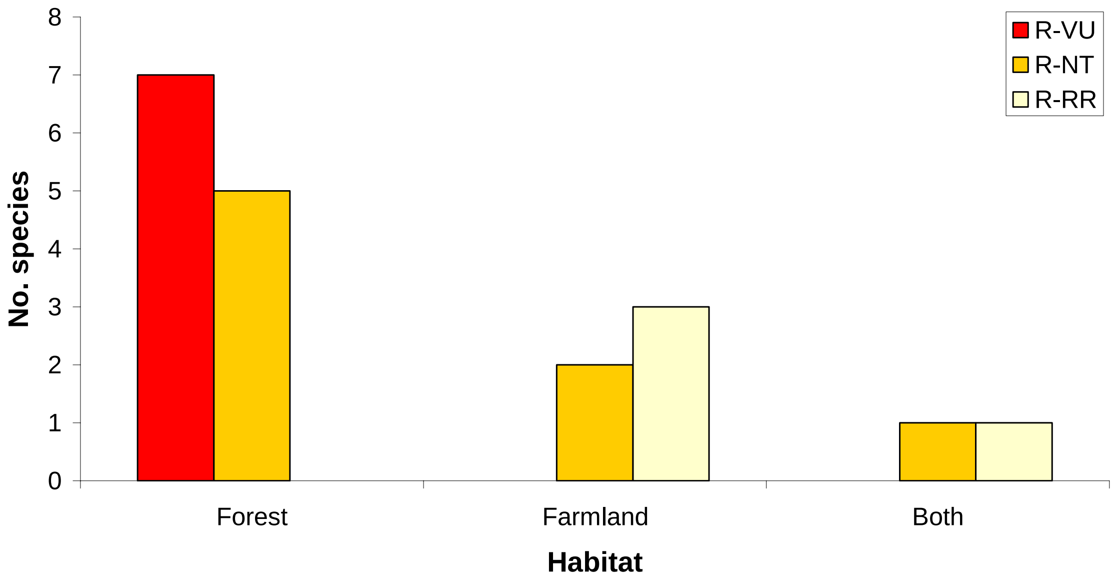


Figure 4 Number of species recorded in forest-only, farmland-only and in both habitats according to conservation threat status as defined in Carswell *et al*. (2005). The categories are (in order of decreasing conservation concern): regionally vulnerable (R-VU), regionally near-threatened (R-NT) and species of regional responsibility (R-RR).

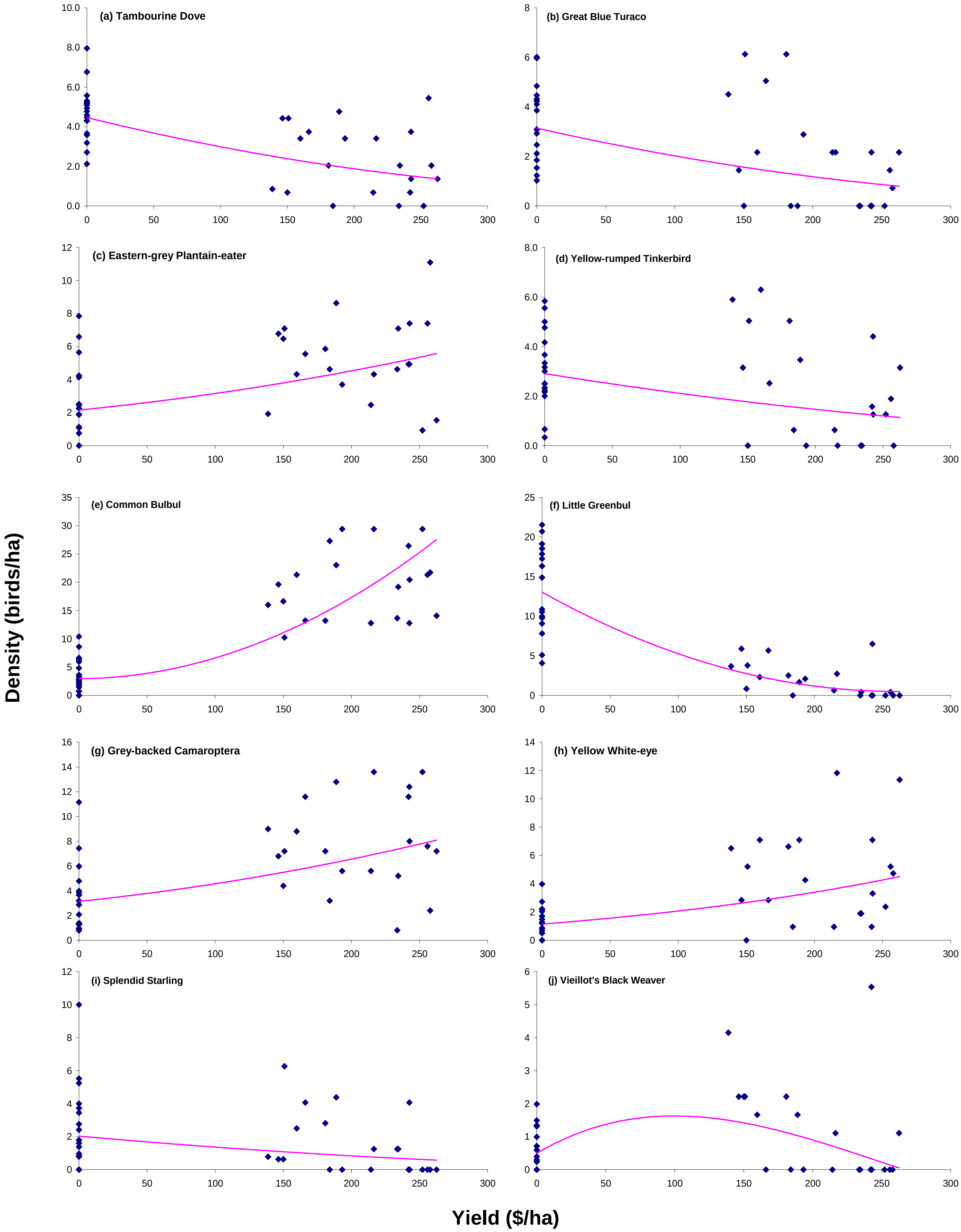


Figure 5 Relationship between species density and yield. Fitted values (pink line) are back-transformed from a regression of log(density + 1) against yield. All relationships were significant at $P < 0.05$.

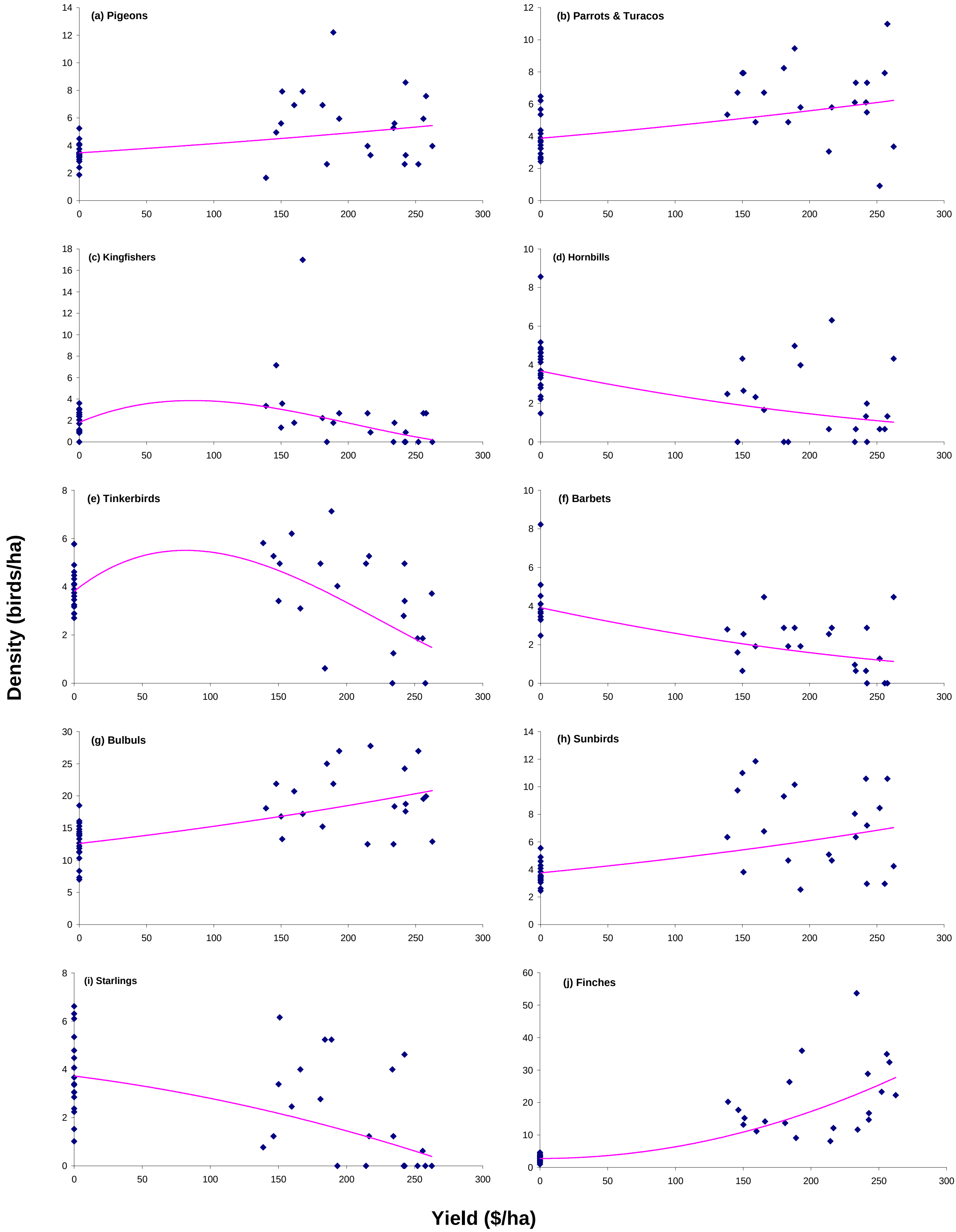


Figure 6 Relationship between species group density and yield. Details as per Figure 5.

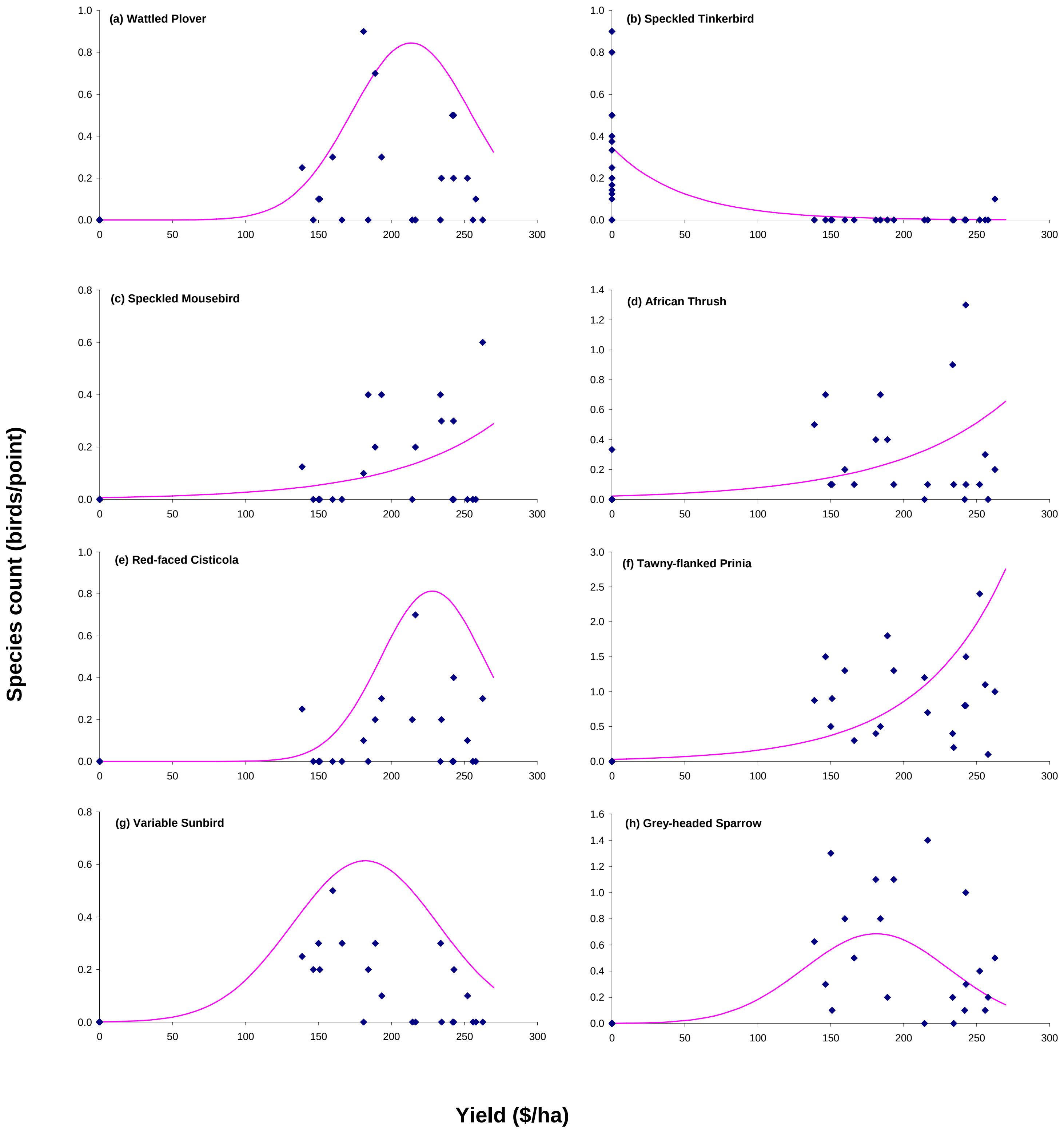


Figure 7 Relationship between species count per visit (within 25m of the point count location) and yield. Fitted values (pink line) are back-transformed from negative binomial (African Thrush, Tawny-flanked Prinia, Black-headed Weaver, Bronze Mannikin, Yellow-fronted Canary) or Poisson (all other species) model parameter estimates.

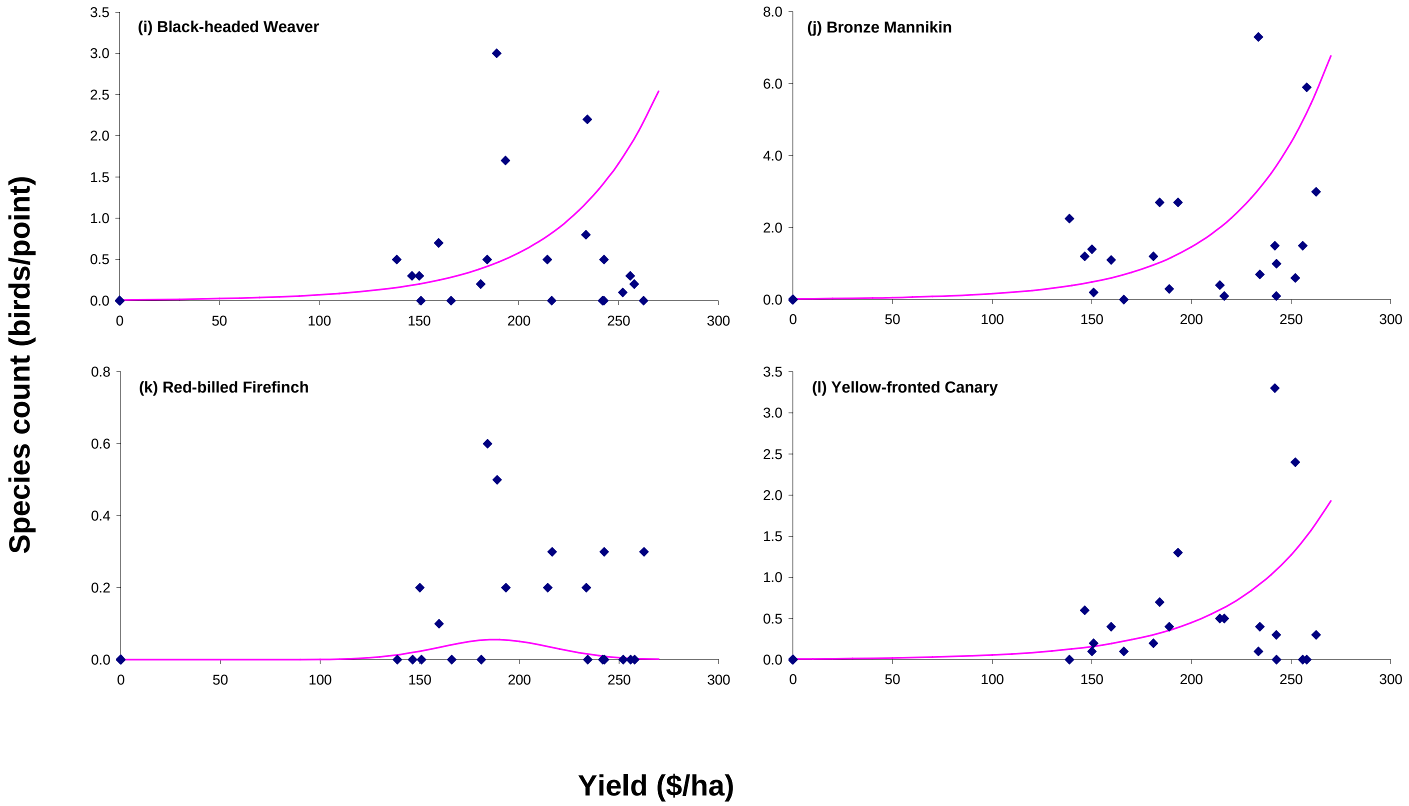


Figure 7 (continued)

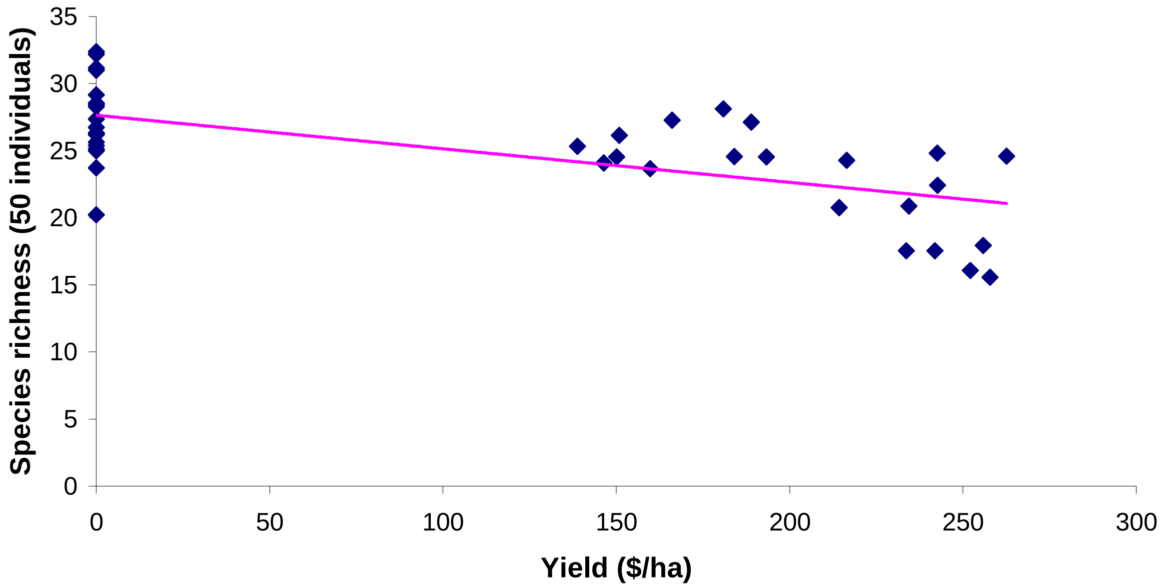


Figure 8 Relationship between species richness, standardised to 50 individuals using rarefaction, and yield. Model: species richness = -0.025yield + 27.64. The model was highly significant ($F_{1, 38} = 29.46$, $P < 0.001$, $r^2 = 0.44$).

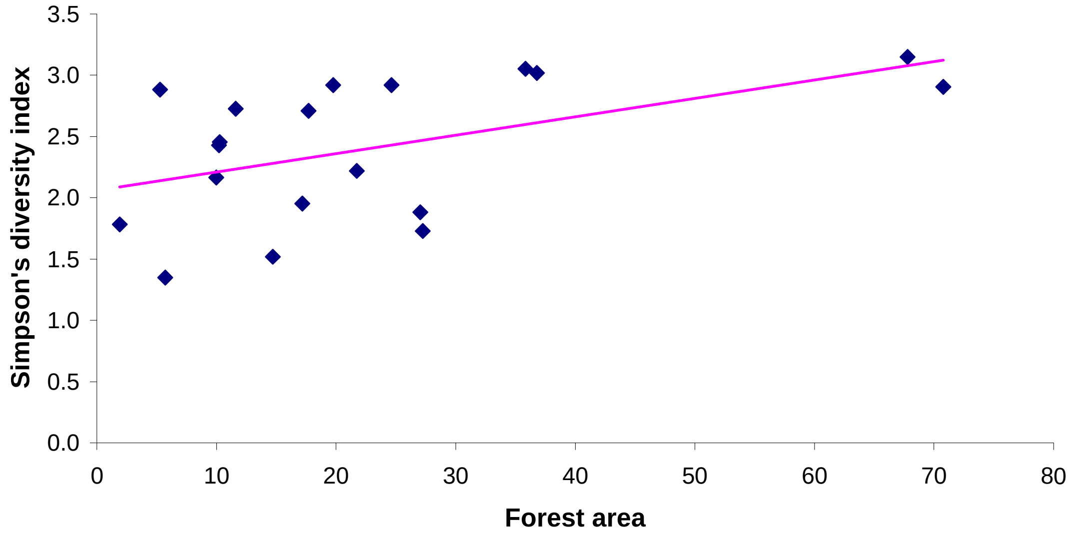


Figure 9 Relationship between Simpson's diversity index and forest area for forest specialist (FF) species. Model: diversity = 0.015AREA + 2.06. The model was significant ($F_{1, 17}$ = 9.05, P < 0.029, r^2 = 0.25).

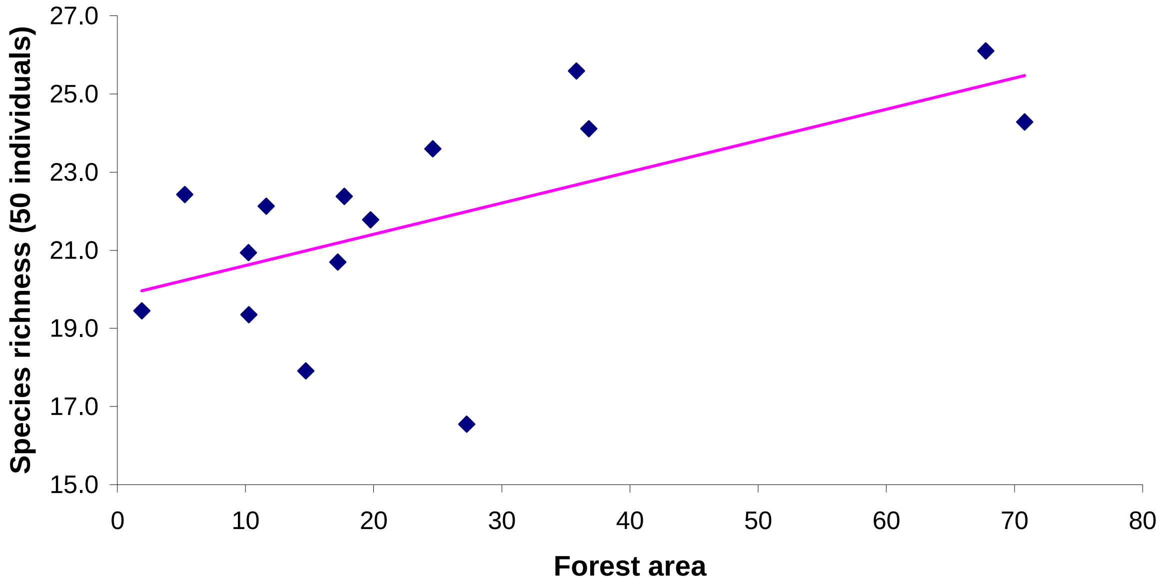


Figure 10 Relationship between species richness, standardised to 50 individuals using rarefaction and forest area for forest specialist (FF) species. Model: diversity = 0.08AREA + 19.81. The model was significant ($F_{1, 13}$ = 7.38, P < 0.016, r^2 = 0.38). Note that there were 5 sites where overall abundance was not high enough to estimate species richness based on 50 individuals.

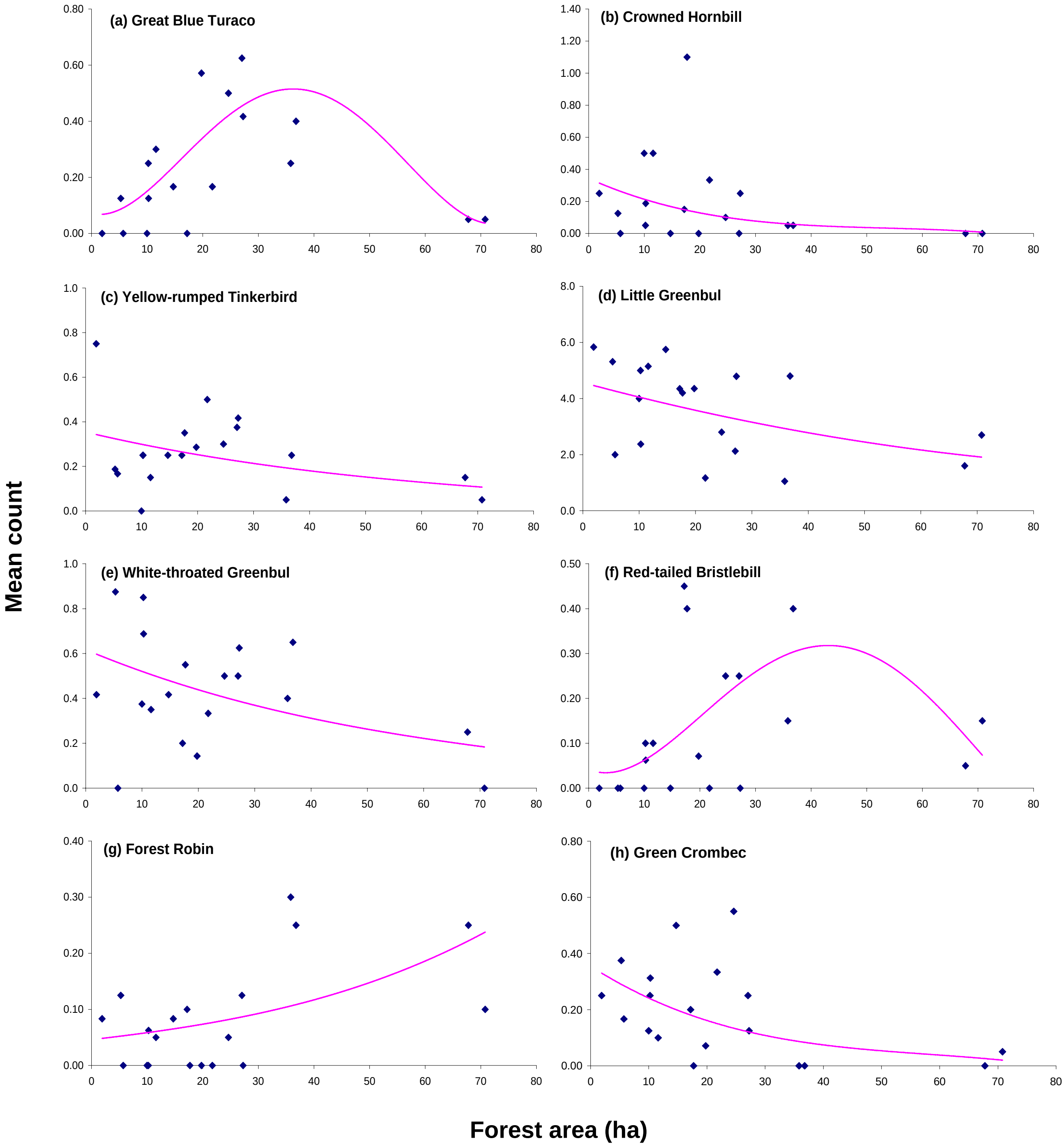


Figure 11 Relationship between bird abundance within 50m radius sampling area and the extent of forest (ha) within a 5-km radius of the study site. Points represent mean counts per point per visit. Lines represent significant relationships derived from generalised linear models with negative binomial (Little Greenbul and Splendid Glossy Starling) or Poisson errors (all other species), back-transformed to estimated count from model fitted with a log-link function. Site was fitted as a random factor to account for repeated observations at the same site over two survey visits.

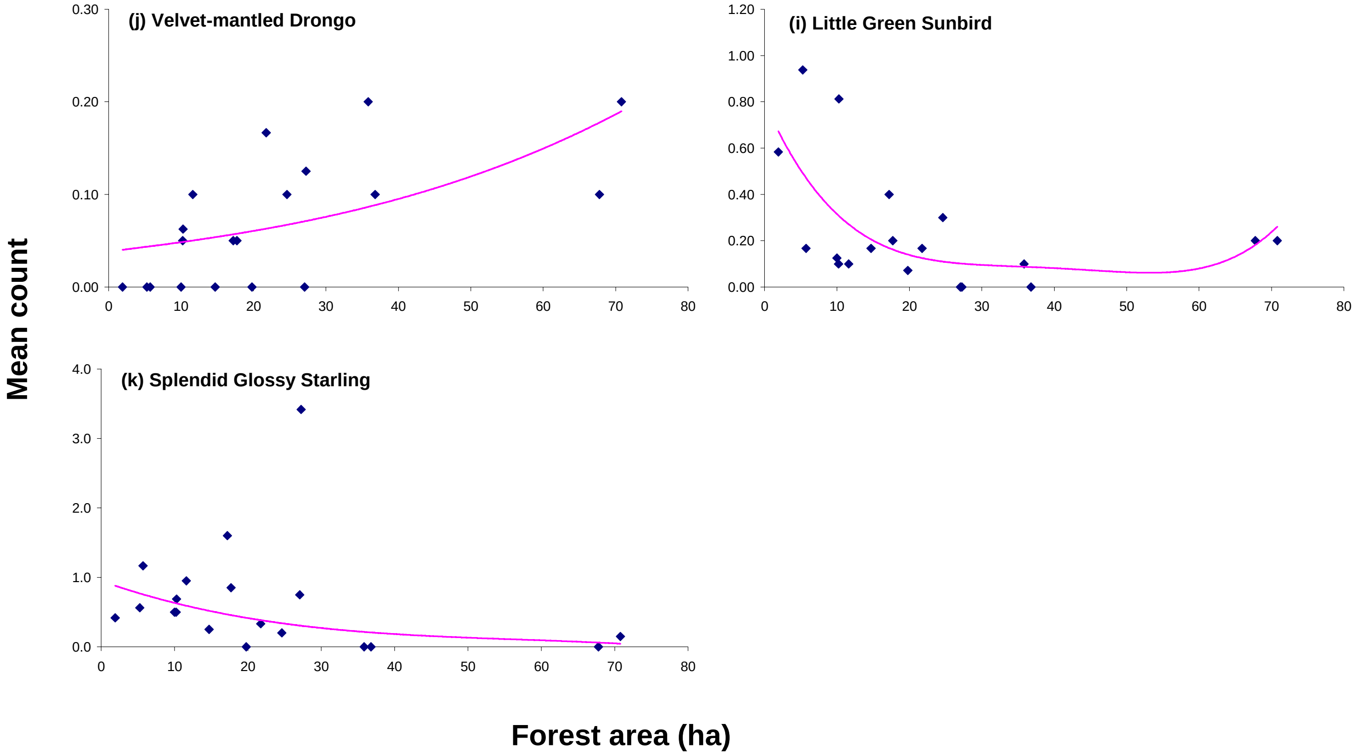


Figure 11 (continued)

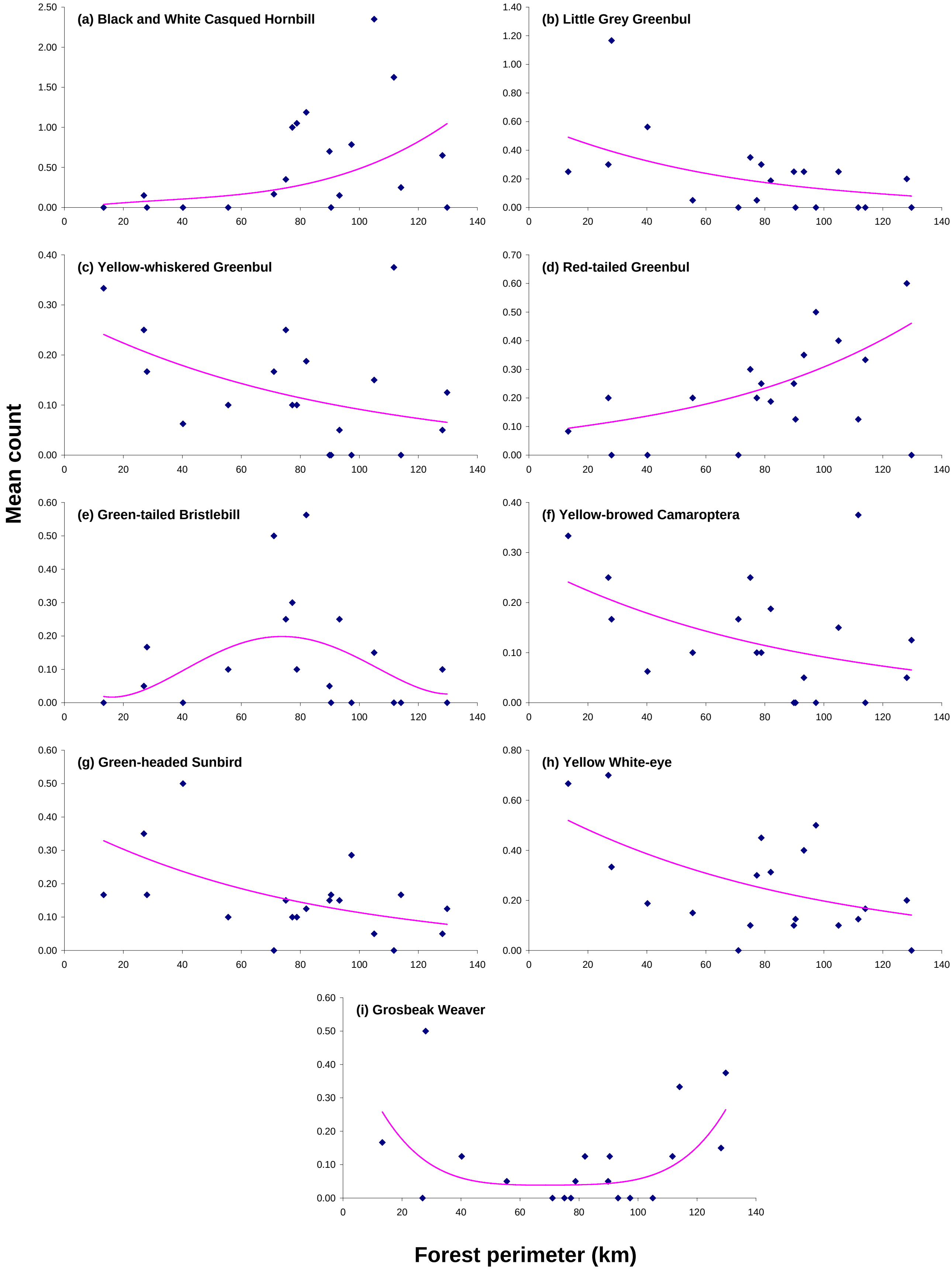


Figure 12 Relationship between bird abundance within 50m radius sampling area and the total perimeter of forest (km) within a 5-km radius of the study site. Other details are as per Figure 11.

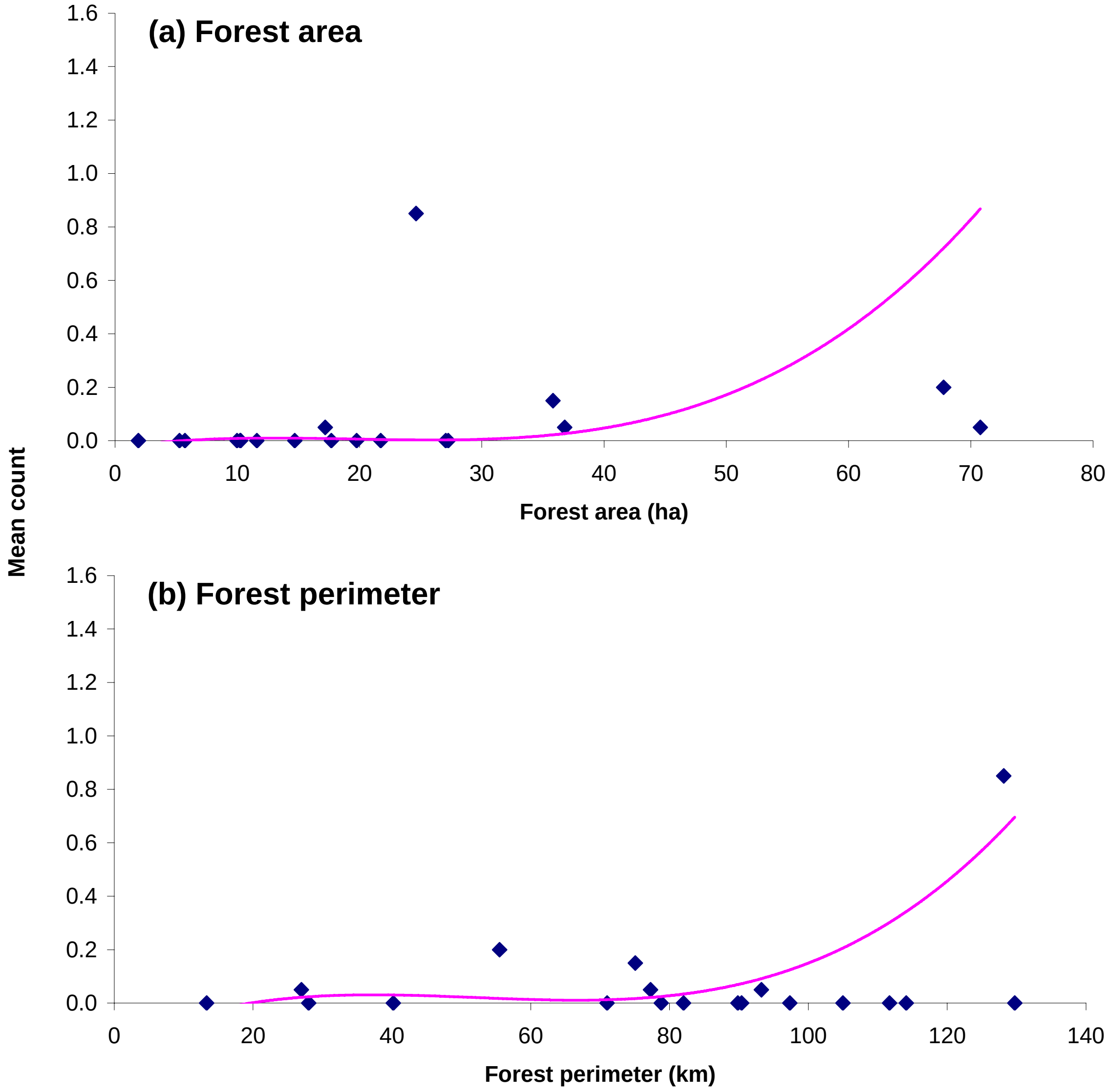


Figure 13 Relationship between the abundance of Pale-breasted Illadopsis within 50m radius of the point and (a) forest area (b) forest perimeter. Both variables were significant ($P < 0.05$). Curves were fitted by using a constant median value of forest perimeter (a) and forest area (b) to assess the effects of varying only a single parameter at a time. Other details are as per Figure 11.

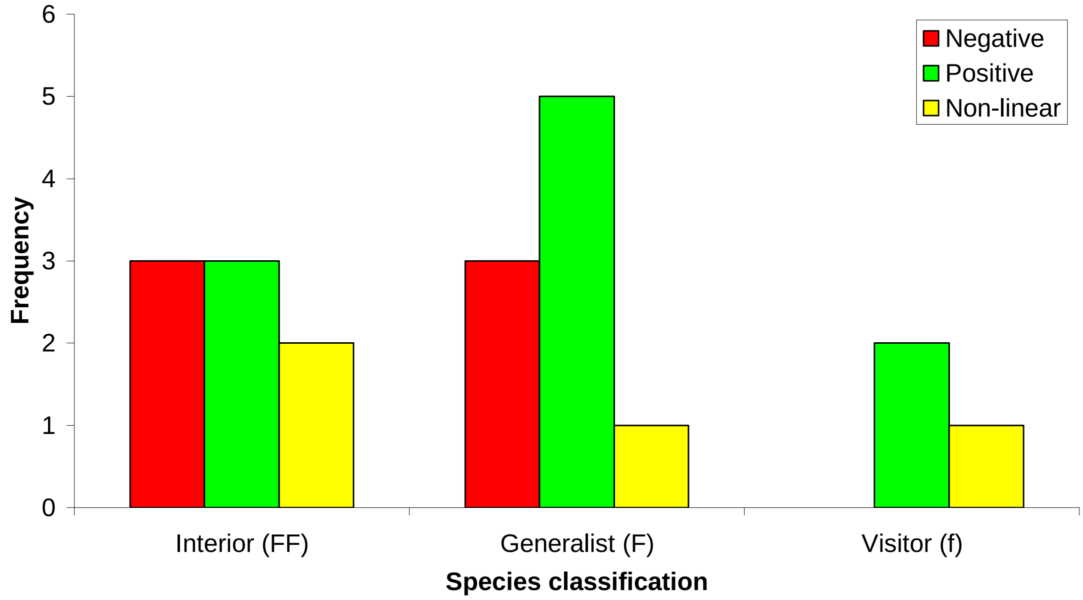


Figure 14 The number of species showing negative, positive or non-linear responses to deforestation according to habitat classifications (based on Bennun *et al*. 1996). Response to deforestation is defined according to relationships with forest area and forest perimeter (Figures 11-13), where a significant positive relationship with forest area or a significant negative relationship with forest perimeter is considered to represent a negative effect of deforestation.

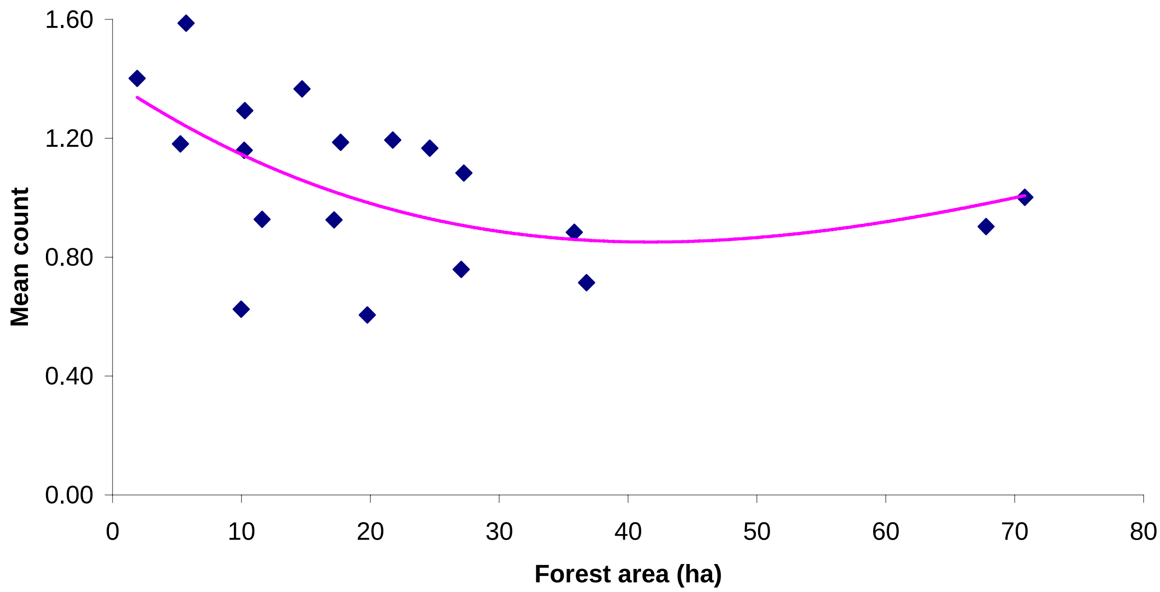


Figure 15 Relationship between total count of all FF species within 50m radius sampling area and the extent of forest (ha) within a 5-km radius of the study site. Both FOR ($F_{1,18} = 6.60$, $P < 0.019$) and FOR^2 ($F_{1,18} = 4.82$, $P < 0.042$) had significant effects. Model estimates: count = -0.023FOR + 0.0003FOR2 + 0.3381. Other details as per Figure 11.

Appendix 1 The Effects of a 'Settling Period' on Forest Bird Surveys.

The total number of registrations per point and the total number of species recorded per point were determined for preliminary surveys (without the two-minute 'settling period') and the same points in the main survey (including the two minute settling period). Differences (preliminary – main survey) were tested for significance using paired t-tests where a given species was recorded on a minimum of five sites (the site was the basic analytical unit – where more than one point was surveyed for the preliminary survey, data were summed and compared with the same points from the main surveys).

Mean difference for species richness, and for species showing significant differences, are shown in Table A1.1. There were few individual species where significant differences were found, although there was some tendency for forest species (classed as FF or F) to have fewer registrations in the preliminary survey (Dusky Long-tailed Cuckoo, Western Nicator, Buff-throated Apalis, Green Crombec, Purple Headed Starling), although Little Grey Greenbul was a forest species that showed the opposite trend. Importantly, species richness was significantly higher (by over four species on average) in the first main visit compared to the preliminary survey. The decision to adopt a two-minute settling period therefore appears justified.

(a) Main survey visit 1

Species	Mean difference	se	n	T	P
Eastern-grey Plantain-eater	1.167	0.458	12	2.548	0.027
Dusky Long-tailed Cuckoo	-0.444	0.176	9	-2.530	0.035
Black & White Casqued Hornbill	1.000	0.458	15	2.185	0.046
Western Nicator	-0.583	0.149	12	-3.924	0.002
Little Grey Greenbul	0.714	0.286	7	2.500	0.047
Green Crombec	-0.833	0.307	6	-2.712	0.042
Buff-throated Apalis	-3.429	1.417	14	-2.420	0.031
Purple-headed Starling	-2.700	1.146	10	-2.357	0.043
Species richness	-4.333	1.457	18	-2.899	0.010

(b) Main survey visit 2

Species	Mean difference	se	n	T	P
Blue-spotted Wood Dove	-0.800	0.327	10	-2.449	0.037
Dusky Long-tailed Cuckoo	-0.667	0.167	9	-4.000	0.004
Western Nicator	-0.833	0.345	12	-2.419	0.034
African Thrush	-0.800	0.200	5	-4.000	0.016
Species richness	-1.444	0.908	18	-1.590	0.130

Table A1.1 Mean difference in total bird registrations and species richness between preliminary and main survey visits. N = number of site pairs (sites where a species was absent on both visits are not included).

Appendix 2 Species recorded during the survey.

Species are listed in taxonomic order. Species in bold were restricted to forest sites. The proportion of sites where the species occurred is given where 'ALL' is calculated across all sites (n = 42), 'FOREST' is calculated across forest sites (n = 19) and 'FARMLAND' is calculated across farmland sites (n = 23). 'SPP GROUP' refers to the groupings used in Figure 6 (if blank, the species was not included in the analysis). 'HABITAT' identifies the main habitat of each species with particular reference to forest using the classification of Bennun *et al*. (1996); FF (forest interior species), F (species inhabiting a range of forest types including forest edge and secondary forest), f (species that visit the forest for food, although they are generally found in other habitats) – blank indicates habitat generalists, species associated with water or unclassified species (all of which were classed as generalists for the analysis).

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Cattle Egret *Bubulcus ibis*	0.17	0.00	0.30		
Black-headed Heron *Ardea melanocephala*	0.14	0.00	0.26		
Hamerkop *Scopus umbretta*	0.02	0.00	0.04		
Marabou Stork *Leptoptilos crumeniferus*	0.10	0.00	0.17		
Hadada Ibis *Bostrychia hagedash*	0.29	0.00	0.52		
Sacred Ibis *Threskiornis aethiopica*	0.02	0.00	0.04		
Lizard Buzzard *Kaupifalco monogrammaticus*	0.69	0.53	0.83		F
Gabar Goshawk *Micronisus gabar*	0.02	0.00	0.04		
African Goshawk *Accipiter tachiro*	0.05	0.11	0.00		F
Little Sparrowhawk *A. minullus*	0.05	0.11	0.00		f
Great Sparrowhawk *A. melanoleucus*	0.21	0.47	0.00		F
Bat Hawk *Macheiramphus alcinus*	0.02	0.05	0.00		F
Black Kite *Milvus milvus*	0.19	0.00	0.35		
Fish Eagle *Haliaeetus vocifer*	0.05	0.00	0.09		
Hooded Vulture *Necrosyrtes monachus*	0.02	0.00	0.04		f
Brown Snake-Eagle *Circaetus cinereus*	0.05	0.00	0.09		
African Harrier-hawk *Polyboroides typus*	0.33	0.58	0.13		f
African Hawk-eagle *Hieraaetus spilogaster*	0.05	0.11	0.00		
Ayres Hawk-eagle *H. ayresii*	0.02	0.05	0.00		f
Cassins Hawk-eagle *Spizaetus africanus*	0.05	0.11	0.00		FF
Long-crested Eagle *Lophaetus occipitalis*	0.17	0.05	0.26		F
Crowned Eagle *Stephanoaetus coronatus*	0.10	0.21	0.00		FF
Common Kestrel *Falco tinnunculus*	0.02	0.00	0.04		
Helmeted Guineafowl *Numida meleagris*	0.19	0.11	0.26		
Crested Guineafowl *Guttera pucherani*	0.21	0.47	0.00		F
Scaly Francolin *Francolinus squamatus*	0.17	0.26	0.09		F

Table A2.1 Species recorded during the survey.

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Red-necked Spurfowl *F. afer*	0.05	0.00	0.09		
White-spotted Flufftail *Sarothrura pulchra*	0.45	1.00	0.00		F
Grey-crowned Crane *Balearica regulorum*	0.02	0.00	0.04		
Wattled Plover *Vanellus senegallus*	0.45	0.00	0.83		
Green Pigeon *Treron calva*	0.52	0.68	0.39	PIGEON	F
Afep Pigeon *Colomba unicinta*	0.36	0.79	0.00	PIGEON	FF
Feral Pigeon *C. livia*	0.05	0.00	0.09	PIGEON	
Blue-spotted Wood Dove *Turtur afer*	0.79	0.74	0.83	PIGEON	F
Tambourine Dove *T. tympanistria*	0.88	1.00	0.78	PIGEON	F
Red-eyed Dove *Streptopelia semitorquata*	0.83	0.74	0.91	PIGEON	f
Grey Parrot *Psittacus erithacus*	0.36	0.74	0.04	PARROT/TURACO	FF
Brown Parrot *Poicephalus meyeri*	0.14	0.00	0.26	PARROT/TURACO	
Red-headed Lovebird *Agapornis pullarisu*	0.10	0.11	0.09	PARROT/TURACO	F
Great Blue Turaco *Corythaeola cristata*	0.76	1.00	0.57	PARROT/TURACO	F
Ross's Turaco *Musophaga rossae*	0.71	0.89	0.57	PARROT/TURACO	F
Black-billed Turaco *Tauraco schuetti*	0.29	0.63	0.00	PARROT/TURACO	FF
Eastern-grey Plantain-eater *Crinifer zonorus*	0.93	0.89	0.96	PARROT/TURACO	
Levaillant's Cuckoo *Oxylophus levaillantii*	0.05	0.05	0.04	CUCKOO	f
Red-chested Cuckoo *Cuculus solitarius*	0.74	1.00	0.52	CUCKOO	
Black Cuckoo *C. clamosus*	0.21	0.47	0.00	CUCKOO	FF
Dusky Long-tailed Cuckoo *Cercococcyx mechowi*	0.43	0.95	0.00	CUCKOO	FF
Diederik Cuckoo *Chrysococcyx caprius*	0.43	0.26	0.57	CUCKOO	
Klaas Cuckoo *C. klaas*	0.64	1.00	0.35	CUCKOO	f
Emerald Cuckoo *C. cupreus*	0.60	0.95	0.30	CUCKOO	F
Yellowbill *Ceuthmochares aereus*	0.45	1.00	0.00	CUCKOO	F
White-browed Coucal *Centropus superciliosus*	0.40	0.00	0.74	CUCKOO	
African Wood Owl *Strix woodfordii*	0.05	0.11	0.00		F
Cassins Spinetail *Neafrapus cassini*	0.02	0.05	0.00		FF
Palm Swift *Cypsiurus parvus*	0.05	0.05	0.04		
White-rumped Swift *Apus caffer*	0.02	0.00	0.04		
Little Swift *A. affinis*	0.07	0.00	0.13		
Speckled Mousebird *Colius striatus*	0.31	0.00	0.57		
Narina Trogon *Apaloderma narina*	0.33	0.74	0.00		F

Table A2.1 (continued)

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Blue-breasted Kingfisher *Halcyon malimbica*	0.40	0.89	0.00	KINGFISHER	F
Woodland Kingfisher *H. senegalensis*	0.21	0.00	0.39	KINGFISHER	
Striped Kingfisher *H. chelicuti*	0.12	0.00	0.22	KINGFISHER	
Pygmy Kingfisher *Ispidina picta*	0.43	0.53	0.35	KINGFISHER	f
Dwarf Kingfisher *I. lecontei*	0.12	0.26	0.00	KINGFISHER	FF
White-bellied Kingfisher *Alcedo leucogaster*	0.02	0.05	0.00	KINGFISHER	FF
Malachite Kingfisher *A. cristata*	0.02	0.00	0.04	KINGFISHER	
Little Bee-eater *Merops pusillus*	0.05	0.00	0.09		
White-throated Bee-eater *M. albicollis*	0.57	0.74	0.43		f
Lilac-breasted Roller *Coracias caudata*	0.05	0.00	0.09		
Broad-billed Roller *Eurystomas glaucurus*	0.26	0.11	0.39		
Blue-throated Roller *E. gularis*	0.07	0.16	0.00		FF
Forest Wood-hoopoe *Phoeniculus castaneiceps*	0.10	0.21	0.00		FF
Crowned Hornbill *Tockus alboterminatus*	0.71	0.95	0.52	HORNBILL	f
Grey Hornbill *T. nasutus*	0.02	0.00	0.04	HORNBILL	
Pied Hornbill *T. fasciatus*	0.50	0.95	0.13	HORNBILL	F
Black & White Casqued Hornbill *Bycanistes subcylindricus*	0.67	1.00	0.39	HORNBILL	F
Yellow-rumped Tinkerbird *Pogoniulus bilineatus*	0.81	1.00	0.65	TINKERBIRD	F
Yellow-throated Tinkerbird *P. subsulphureus*	0.43	0.95	0.00	TINKERBIRD	FF
Speckled Tinkerbird *P. scolopaceus*	0.79	1.00	0.61	TINKERBIRD	F
Yellow-fronted Tinkerbird *P. pusillus*	0.33	0.11	0.52	TINKERBIRD	f
Grey-throated Barbet *Gymnobucco bonapartei*	0.36	0.79	0.00	BARBET	F
Hairy-breasted Barbet *Tricholeama hirsute*	0.48	0.95	0.09	BARBET	F
Spot-flanked Barbet *T. lachrymose*	0.36	0.00	0.65	BARBET	
White-headed Barbet *Lybius leucocephalus*	0.05	0.00	0.09	BARBET	
Double-toothed Barbet *L. bidentatus*	0.29	0.16	0.39	BARBET	
Yellow-spotted Barbet *Buccanodon duchaillui*	0.45	1.00	0.00	BARBET	FF
Yellow-billed Barbet *Trachylaemus purpuratus*	0.40	0.89	0.00	BARBET	FF
Greater Honeyguide *Indicator indicator*	0.12	0.26	0.00		f
Lesser Honeyguide *I. minor*	0.19	0.37	0.04		f
Least Honeyguide *I. exilis*	0.10	0.21	0.00		FF
Cassins Honeybird *Prodotiscus insignis*	0.02	0.05	0.00		FF
Nubian Woodpecker *Campethera nubica*	0.05	0.00	0.09		

Table A2.1 (continued)

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Buff-spotted Woodpecker *C. nivosa*	0.24	0.53	0.00		FF
Brown-eared Woodpecker *C. caroli*	0.26	0.58	0.00		FF
Cardinal Woodpecker *Dendropicos fuscescens*	0.05	0.11	0.00		
Yellow-crested Woodpecker *D. xantholophus*	0.36	0.79	0.00		FF
White-headed Saw-wing *Psalidoprocne albiceps*	0.24	0.11	0.35		f
Sand Martin *Riparia riparia*	0.07	0.00	0.13		
Lesser Striped Swallow *Hirundo abyssinica*	0.26	0.11	0.39		
Barn Swallow *H. rustica*	0.05	0.00	0.09		
Angola Swallow *H. angolensis*	0.19	0.00	0.35		
House Martin *Delichon urbica*	0.10	0.00	0.17		
Yellow Wagtail *Motacilla flava*	0.07	0.00	0.13		
African Pied Wagtail *M. aguimp*	0.12	0.00	0.22		
Yellow-throated Long-claw *Macronyx croceus*	0.10	0.00	0.17		
Red-shouldered Cuckoo-shrike *Campephaga phoenicea*	0.02	0.00	0.04		
Black Cuckoo-shrike *C. flava*	0.14	0.32	0.00		f
Purple-throated Cuckoo-shrike *C. quiscalina*	0.10	0.21	0.00		FF
Western Nicator *Nicator chloris*	0.45	1.00	0.00		F
Common Bulbul *Pycnonotus barbatus*	0.95	0.89	1.00	GREENBUL	f
Yellow-whiskered Greenbul *Andropadus latirostris*	0.45	1.00	0.00	GREENBUL	F
Little Greenbul *A. virens*	0.79	1.00	0.61	GREENBUL	F
Slender-billed Greenbul *A. gracilorostris*	0.40	0.89	0.00	GREENBUL	FF
Little Grey Greenbul *A. gracilis*	0.36	0.79	0.00	GREENBUL	FF
Cameroon Sombre Greenbul *A. curvirostris*	0.36	0.79	0.00	GREENBUL	FF
Toro Olive Greenbul *Phyllastrephus hypochloris*	0.17	0.37	0.00	GREENBUL	FF
White-throated Greenbul *P. albigularis*	0.40	0.89	0.00	GREENBUL	FF
Red-tailed Bristlebill *Bleda syndactyla*	0.43	0.95	0.00	GREENBUL	FF
Green-tailed Bristlebill *B. eximia*	0.36	0.79	0.00	GREENBUL	FF
Red-tailed Greenbul *Criniger calarus*	0.36	0.79	0.00	GREENBUL	FF
Joyful Greenbul *Chlorocichla laetissima*	0.02	0.05	0.00	GREENBUL	FF
Yellow-throated Greenbul *C. flavicollis*	0.14	0.26	0.04	GREENBUL	f
Honeyguide Greenbul *Baeopogon indicator*	0.17	0.37	0.00	GREENBUL	FF
Forest Robin *Stiphrornis erythrothorax*	0.29	0.63	0.00		FF
Brown-chested Alethe *Alethe poliocephala*	0.19	0.42	0.00		FF

Table A2.1 (continued)

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Fire-crested Alethe *A. diademata*	0.40	0.89	0.00		FF
Blue-shouldered Robin-chat *Cossypha cyanocampter*	0.31	0.68	0.00		F
White-browed Robin-Chat *C. heuglini*	0.24	0.00	0.43		f
Snowy-headed Robin-chat *C. niveicapilla*	0.29	0.53	0.09		F
Red-capped Robin-chat *C. natalensis*	0.24	0.53	0.00		F
African Thrush *Turdus pelios*	0.74	0.53	0.91		f
Rufous Flycatcher-thrush *Stizorhina fraseri*	0.45	1.00	0.00		FF
Brown-backed Scrub-Robin *Cercotrichas hartlaubi*	0.17	0.00	0.30		f
White-browed Scrub-Robin *C. leucophrys*	0.07	0.00	0.13		
Whinchat *Saxicola rubetra*	0.12	0.00	0.22		
Sooty Chat *Myrmecocichla nigra*	0.07	0.00	0.13		
Icterine Warbler *Hippolais icterina*	0.05	0.00	0.09		
Red-faced Cisticola *Cisticola erythrops*	0.38	0.00	0.70		
Winding Cisticola *C. galactotes*	0.05	0.00	0.09		
Willow Warbler *Phylloscopus trochilus*	0.10	0.11	0.09		f
Wood Warbler *P. sibilatrix*	0.07	0.16	0.00		
Green Hylia *Hylia prasina*	0.45	1.00	0.00		
Green Crombec *Sylvietta virens*	0.36	0.79	0.00		F
Northern Crombec *S. brachyuran*	0.02	0.05	0.00		
Red-faced Crombec *S. whytii*	0.05	0.00	0.09		F
Yellow Longbill *Macrosphenus flavicans*	0.19	0.42	0.00		FF
Grey Longbill *M. concolor*	0.21	0.47	0.00		FF
Black-faced Rufous Warbler *Bathmocercus rufus*	0.05	0.11	0.00		FF
Tawny-flanked Prinia *Prinia subflava*	0.55	0.00	1.00		
White-chinned Prinia *P. leucopogon*	0.17	0.37	0.00		F
Grey-backed Camaroptera *Camaroptera brachyuran*	0.98	1.00	0.96		f
Olive-green Camaroptera *C. chloronata*	0.36	0.79	0.00		FF
Yellow-browed Camaroptera *C. supercilliaris*	0.38	0.84	0.00		FF
Buff-throated Apalis *Apalis rufogularis*	0.43	0.95	0.00		FF
Black-throated Apalis *A. jacksoni*	0.10	0.21	0.00		FF

Table A2.1 (continued)

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Northern Black Flycatcher *Melaenornis edolioides*	0.33	0.16	0.48	FLYCATCHER	
Ashy Flycatcher *Muscicapa caerulescens*	0.29	0.58	0.04	FLYCATCHER	F
African Dusky Flycatcher *M. adusta*	0.14	0.05	0.22	FLYCATCHER	F
Lead-coloured Flycatcher *Myioparus plumbeus*	0.17	0.37	0.00	FLYCATCHER	F
Grey-throated Flycatcher *M. griseigularis*	0.36	0.79	0.00	FLYCATCHER	FF
Dusky-blue Flycatcher *M. comitata*	0.05	0.11	0.00	FLYCATCHER	F
African Shrike-flycatcher *Megabias flammulatus*	0.33	0.74	0.00	FLYCATCHER	FF
Black & White Shrike-flycatcher *Bias musicus*	0.48	0.53	0.43	FLYCATCHER	f
Brown-throated Wattle-eye *Platysteira canea*	0.38	0.84	0.00		f
Chestnut Wattle-eye *Dyaphorophyia castanea*	0.40	0.89	0.00		FF
Jamesons Wattle-eye *D. jamesoni*	0.17	0.37	0.00		FF
African Paradise-Flycatcher *Terpsiphone viridis*	0.40	0.00	0.74	FLYCATCHER	f
Red-bellied Paradise Flycatcher *T. rufiventer*	0.43	0.95	0.00	FLYCATCHER	F
Blue-headed Crested-flycatcher *Trochocercus nitens*	0.05	0.11	0.00	FLYCATCHER	FF
Dusky Crested-flycatcher *T. nigromitratus*	0.21	0.47	0.00	FLYCATCHER	F
African Blue Flycatcher *Elminia longicauda*	0.43	0.42	0.43	FLYCATCHER	f
Scaly-breasted Illadopsis *Illadopsis albispectus*	0.40	0.89	0.00		FF
Brown Illadopsis *I. fulvescens*	0.24	0.53	0.00		FF
Pale-breasted Illadopsis *I. rufipennis*	0.19	0.42	0.00		FF
Brown Babbler *Turdoides plebejus*	0.02	0.00	0.04		
Black-lored Babbler *T. sharpei*	0.05	0.00	0.09		
Dusky Tit *Parus funereus*	0.14	0.32	0.00		FF
White-shouldered Tit *P. guineensis*	0.10	0.21	0.00		
Black Tit *P. leucomelas*	0.02	0.00	0.04		f
Tit-hylia *Pholidornis rushiae*	0.02	0.05	0.00		FF
African Penduline-Tit *Anthoscopus caroli*	0.05	0.11	0.00		f
Yellow White-eye *Zosterops senegalensis*	0.88	0.89	0.87		f
Green-headed Sunbird *Cyanomitra verticalis*	0.55	0.89	0.26	SUNBIRD	F
Blue-throated Brown Sunbird *C. cyanolaema*	0.36	0.79	0.00	SUNBIRD	FF
Olive Sunbird *C. ulivacea*	0.43	0.95	0.00	SUNBIRD	FF
Olive-bellied Sunbird *Cinnyris chloropygia*	0.33	0.16	0.48	SUNBIRD	F
Marico Sunbird *C. mariquensis*	0.12	0.00	0.22	SUNBIRD	
Red-chested Sunbird *C.s erythrocerca*	0.17	0.00	0.30	SUNBIRD	

Table A2.1 (continued)

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Variable Sunbird *C. venusta*	0.36	0.00	0.65	SUNBIRD	f
Superb Sunbird *C. superba*	0.21	0.47	0.00	SUNBIRD	F
Copper Sunbird *C. cuprea*	0.14	0.00	0.26	SUNBIRD	f
Green-throated Sunbird *Chalcomitra rubescens*	0.29	0.63	0.00	SUNBIRD	F
Scarlet-chested Sunbird *C. senegalensis*	0.71	0.47	0.91	SUNBIRD	f
Green Sunbird *Anthreptes rectirostris*	0.29	0.63	0.00	SUNBIRD	FF
Little Green Sunbird *A. seimundi*	0.40	0.89	0.00	SUNBIRD	FF
Grey-headed Sunbird *Deleornis axillaries*	0.21	0.47	0.00	SUNBIRD	FF
Collared Sunbird *Hedydipna collaris*	0.45	1.00	0.00	SUNBIRD	F
Common Fiscal *Lanius collaris*	0.02	0.00	0.04		
Grey-backed Fiscal *L. excubitoroides*	0.02	0.00	0.04		f
Brown-crowned Tchagra *Tchagra australis*	0.10	0.00	0.17		
Black-crowned Tchagra *T. senegala*	0.10	0.00	0.17		
Northern Puffback *Dryoscopus gambensis*	0.29	0.16	0.39		F
Pink-footed Puffback *D. angolensis*	0.02	0.05	0.00		FF
Bocages Bush-shrike *Malaconotus bocagei*	0.19	0.42	0.00		F
Sooty Boubou *Laniarius leucorhynchus*	0.21	0.47	0.00		FF
Tropical Boubou *L. aethiopicus*	0.19	0.00	0.35		f
Black-headed Gonolek *L. erythrogaster*	0.05	0.00	0.09		f
African Drongo *Dicrurus adsimilis*	0.12	0.00	0.22		f
Velvet-mantled Drongo *D. modestus*	0.36	0.79	0.00		F
Western Black-headed Oriole *Oriolus brachyrhynchus*	0.43	0.95	0.00		F
Black-headed Oriole *O. larvatus*	0.14	0.00	0.26		f
Pied Crow *Corvus albus*	0.05	0.00	0.09		
Chestnut-winged Starling *Onychognathus fulgidis*	0.07	0.16	0.00	STARLING	FF
Purple-headed Starling *Lamprotornis purpureiceps*	0.40	0.89	0.00	STARLING	F
Ruppells Long-tailed Starling *L. purpuropterus*	0.26	0.00	0.48	STARLING	
Splendid Glossy Starling *L. splendidus*	0.67	0.84	0.52	STARLING	F
Violet-backed Starling *Cinnyricinclus leucogaster*	0.24	0.53	0.00	STARLING	f
Grey-headed Sparrow *Passer griseus*	0.50	0.00	0.91	WEAVER	
Spectacled Weaver *Ploceus ocularis*	0.12	0.21	0.04	WEAVER	f

Table A2.1 (continued)

Appendix 2 (continued)

Species	ALL	FOREST	FARMLAND	SPP GROUP	HABITAT
Black-necked Weaver *P. nigricollis*	0.52	1.00	0.13	WEAVER	f
Baglafecht Weaver *P. baglafecht*	0.02	0.00	0.04	WEAVER	f
Weyns Weaver *P. weynsi*	0.38	0.84	0.00	WEAVER	F
Yellow-mantled Weaver *P. tricolour*	0.26	0.58	0.00	WEAVER	FF
Vieillots Black Weaver *P. nigerrimus*	0.52	0.63	0.43	WEAVER	f
Black-headed Weaver *P. cucullatus*	0.50	0.00	0.91	WEAVER	
Fan-tailed Widowbird *Euplectes axillaris*	0.17	0.00	0.30	WEAVER	
Grosbeak Weaver *Amblyospiza albifrons*	0.38	0.84	0.00	WEAVER	f
Red-headed Malimbe *Malimbus rubricollis*	0.17	0.37	0.00	FINCH	FF
Grey-headed Negrofinch *Nigrita canicapilla*	0.52	1.00	0.13	FINCH	F
White-breasted Negrofinch *N. fusconota*	0.43	0.95	0.00	FINCH	F
Green-backed Twinspot *Mandigoa nitidula*	0.17	0.37	0.00	FINCH	FF
Red-headed Bluebill *Spermophaga ruficapilla*	0.38	0.84	0.00	FINCH	F
Black-bellied Seedcracker *Pyrenestes ostrinus*	0.19	0.42	0.00	FINCH	F
African Firefinch *L. rubricata*	0.02	0.00	0.04	FINCH	
Crimson-rumped Waxbill *Estrilda rhodopyga*	0.02	0.00	0.04	FINCH	
Black-crowned Waxbill *E. nonnula*	0.24	0.00	0.43	FINCH	f
Common Waxbill *E. astrild*	0.02	0.00	0.04	FINCH	
Red-cheeked Cordon-bleu *Uraeginthus bengalus*	0.14	0.00	0.26	FINCH	
Bronze Mannikin *Lonchura cucullata*	0.55	0.00	1.00	FINCH	
Black & White Mannikin *L. bicolor*	0.17	0.00	0.30	FINCH	f
Magpie Mannikin *L. fringilloides*	0.02	0.05	0.00	FINCH	f
Village Indigobird *Vidua chalybeata*	0.12	0.00	0.22	FINCH	
Pin-tailed Whydah *V. macroura*	0.17	0.00	0.30	FINCH	
African Citril *Serinus citrinelloides*	0.05	0.00	0.09	FINCH	f
Yellow-rumped Seedeater *S. atrogularis*	0.02	0.00	0.04	FINCH	
Yellow-fronted Canary *S. mozambicus*	0.48	0.00	0.87	FINCH	
Golden-breasted Bunting *Emberiza flaviventris*	0.02	0.00	0.04	FINCH	

Table A2.1 (continued)

Appendix 3 Species where count within 25m radius of the point count was analysed in relation to yield, and model details for those species where significant effects were detected.

Cattle Egret	Grey-backed Camaroptera
Lizard Buzzard	Buff-throated Apalis
Wattled Plover	Blue Flycatcher
Red-eyed Dove	Yellow White-eye
Great Blue Turaco	Olive Sunbird
Eastern-grey Plantain-eater	Olive-bellied Sunbird
White-browed Coucal	Variable Sunbird
Speckled Mousebird	Scarlet-chested Sunbird
Woodland Kingfisher	Little Green Sunbird
White-throated Bee-eater	Purple-headed Starling
Black & White Casqued Hornbill	Splendid Glossy Starling
Speckled Tinkerbird	Grey-headed Sparrow
White-headed Saw-wing	Weyns Weaver
Lesser Striped Swallow	Vieillots Black Weaver
Common Bulbul	Black-headed Weaver
Yellow-whiskered Greenbul	Red-billed Firefinch
Little Greenbul	Black-crowned Waxbill
African Thrush	Bronze Mannikin
Red-faced Cisticola	Yellow-fronted Canary
Tawny-flanked Prinia	

Table A3.1 A list of species considered in the analysis (minimum 20 individuals recorded across the whole sample).

Species	Error	D	Variable	Estimate	SE	P
Wattled Plover	P	1.501	yield	0.128	0.068	<.0001
			$yield^2$	-0.0003	0.0002	0.0004
Speckled Tinkerbird	P	0.979	yield	-0.020	0.005	<.0001
Speckled Mousebird	P	1.366	yield	0.014	0.004	<.0001
African Thrush	NB	0.817	yield	0.013	0.003	0.0209
Red-faced Cisticola	P	1.142	yield	0.182	0.088	0.0008
			$yield^2$	-0.0004	0.0002	0.0069
Tawny-flanked Prinia	NB	0.811	yield	0.0167	0.003	0.0022
Variable Sunbird	P	0.682	yield	0.073	0.024	<.0001
			$yield^2$	-0.0002	0.0001	<.0001
Grey-headed Sparrow	P	1.886	yield	0.073	0.029	<.0001
			$yield^2$	-0.0002	0.0001	<.0001
Black-headed Weaver	NB	0.667	yield	0.021	0.005	0.009
Bronze Mannikin	NB	0.768	yield	0.022	0.003	0.0034
Red-billed Firefinch	P	1.048	yield	0.226	0.079	<.0001
			$yield^2$	-0.001	0.0002	<.0001
Yellow-fronted Canary	NB	0.664	yield	0.021	0.004	0.0014

Table A3.2 Model details where significant effects of yield on species count were found. Error indicates whether Poisson (P) or negative binomial errors (NB) were specified, D is model fit (deviance/df). Parameter estimates and their standard errors (SE), intercepts (Int) and significance levels for type 3 tests (P) are also presented.

Appendix 4 Species in forest sites where count within 50m radius of the point count was analysed in relation to forest area and perimeter at the landscape-scale (within 5-km radius of the site), and model details for those species where significant effects were detected.

White-spotted Flufftail	Forest Robin
Green Pigeon	Fire-crested Alethe
Afep Pigeon	Blue-shouldered Robin-chat
Tambourine Dove	Rufous Flycatcher-thrush
Great Blue Turaco	Green Hylia
Eastern-grey Plantain-eater	Green Crombec
Red-chested Cuckoo	Grey-backed Camaroptera
Dusky Long-tailed Cuckoo	Olive-green Camaroptera
Yellowbill	Yellow-browed Camaroptera
Narina Trogon	Buff-throated Apalis
Blue-breasted Kingfisher	Ashy Flycatcher
White-throated Bee-eater	Grey-throated Flycatcher
Crowned Hornbill	Chestnut Wattle-eye
Pied Hornbill	Pale-breasted Illadopsis
Black & White Casqued Hornbill	Yellow White-eye
Yellow-rumped Tinkerbird	Green-headed Sunbird
Yellow-throated Tinkerbird	Blue-throated Brown Sunbird
Speckled Tinkerbird	Olive Sunbird
Grey-throated Barbet	Little Green Sunbird
Hairy-breasted Barbet	Collared Sunbird
Yellow-spotted Barbet	Velvet-mantled Drongo
Yellow-billed Barbet	Western Black-headed Oriole
Yellow-crested Woodpecker	Purple-headed Starling
Western Nicator	Splendid Glossy Starling
Common Bulbul	Violet-backed Starling
Yellow-whiskered Greenbul	Black-necked Weaver
Little Greenbul	Weyns Weaver
Slender-billed Greenbul	Yellow-mantled Weaver
Little Grey Greenbul	Vieillots Black Weaver
Cameroon Sombre Greenbul	Grosbeak Weaver
White-throated Greenbul	Grey-headed Negrofinch
Red-tailed Bristlebill	White-breasted Negrofinch
Green-tailed Bristlebill	Red-headed Bluebill
Red-tailed Greenbul	

Table A4.1 A list of species considered in the analysis (minimum 20 individuals recorded across the sample of forest sites).

	Error	D	Variable	Estimate	SE	P
Great Blue Turaco	P	1.430	FOR	0.139	0.045	0.006
			FOR^2	-0.002	0.001	0.004
Crowned Hornbill	P	0.960	FOR	-0.050	0.023	0.041
Black & White Casqued Hornbill	P	1.920	PERM	0.026	0.011	0.024
Yellow-rumped Tinkerbird	P	1.290	FOR	-0.017	0.008	0.043
Yellow-whiskered Greenbul	P	0.770	PERM	-0.010	0.004	0.020
Little Greenbul	NB	1.020	FOR	-0.012	0.005	0.031
Little Grey Greenbul	P	1.480	PERM	-0.015	0.006	0.023
White-throated Greenbul	P	1.580	FOR	-0.017	0.008	0.036
Red-tailed Bristlebill	P	1.160	FOR	0.132	0.053	0.022
			FOR^2	-0.002	0.001	0.027
Green-tailed Bristlebill	P	1.520	PERM	0.101	0.042	0.027
			$PERM^2$	-0.001	0.000	0.023
Red-tailed Greenbul	P	1.240	PERM	0.014	0.004	0.005
Forest Robin	P	0.810	FOR	0.023	0.010	0.039
Green Crombec	P	0.860	FOR	-0.040	0.016	0.023
Yellow-browed Camaroptera	P	1.710	PERM	-0.011	0.005	0.045
Pale-breasted Illadopsis	P	0.70	FOR	0.101	0.039	0.019
			PERM	0.056	0.025	0.036
Yellow White-eye	P	1.940	PERM	-0.011	0.005	0.024
Little Green Sunbird	P	0.990	FOR	-0.117	0.040	0.009
			FOR^2	0.001	0.001	0.018
Green-headed Sunbird	P	1.250	PERM	-0.012	0.005	0.015
Velvet-mantled Drongo	P	0.760	FOR	0.022	0.009	0.018
Splendid Glossy Starling	NB	0.980	FOR	-0.042	0.017	0.022
Grosbeak Weaver	P	1.160	PERM	-0.083	0.033	0.023
			$PERM^2$	0.001	0.000	0.017

Table A4.2 Effects of forest area (FOR) or forest perimeter length (PERM) on species count, where significant. Error indicates whether Poisson (P) or negative binomial errors (NB) were specified, D is model fit (deviance/df). Parameter estimates and their standard errors (SE), intercepts (Int) and significance levels for type 3 tests (P) are also presented.