

The conservation importance of luxuriant tree plantations for lower storey forest birds in south-west Ghana

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Summary

The exceptionally rapid degradation and fragmentation of the Upper Guinea Forest, caused by slash-and-burn farming and selective logging, oblige bird conservationists to examine critically the conservation value of unprotected areas, which may provide buffer zones or connecting corridors to protected forests. This paper assesses the utilisation of various tree-crop plantations by mainly lower storey forest birds in south-west Ghana, through avifaunal comparisons of shaded cash crops (rustic cocoa; neglected coconut) and exotic tree plantations (*Cedrela*, *Gmelina*) with nearby closed forest. Plantations adjacent to, or within, large ($>200 \text{ km}^2$), biodiverse forests are superior bird habitats compared to similar plantations within small ($<50 \text{ km}^2$) and species-poor forests. A relatively high forest tree density in cash crop ($15\text{--}20 \text{ ha}^{-1}$) and exotic ($15\text{--}35 \text{ ha}^{-1}$) tree plantations, combined with a luxuriant woody undergrowth (not slashed for $>5\text{--}10$ years), may additionally explain the presence of many forest specialists, including regionally 'Vulnerable' and locally 'Endangered' species. Overall, 50% of species of conservation importance found in forests were represented in plantations. These findings highlight the importance of shaded plantations with long periods between understorey weeding, as appropriate land-use systems that enhance the area under effective conservation and improve the connectivity of protected forest fragments. Results are compared to similar studies in the Old and New World tropics, and implications for off-reserve land-use management are compared and discussed in regional and global contexts.

Introduction

Since the early era of commercial logging, annual rates of deforestation in West Africa have been up to 70% above the global average (Martin 1991), and Ghana is no exception. The former 82,000 km^2 stretch of continuous forest in Ghana, which makes up the eastern part of the Upper Guinea forest, is now reduced to c. 15,000 km^2 (Hawthorne and Abu Juam 1993). Current satellite images (e.g. Google Earth) clearly show that the >200 state-protected high forest areas have become almost completely isolated islands in a mosaic of converted habitats and degraded forest remnants. The present ecological integrity of the Ghanaian forest biome is highly limited, with the largest contiguous area of inter-linked protected forests covering just 1,500 km^2 .

Current reforestation policies in Ghana focus on development of large-scale plantations, particularly Oil Palm *Elaeis guineensis* (national goal of 200 km^2 per year), Cocoa *Theobroma cacao* and Rubber *Hevea brasiliensis*, and no protected area $>5 \text{ km}^2$ has been established in the high forest zone since the mid-1970s (Hawthorne and Abu Juam 1993). This, combined with the past decades of accelerating subsistence farming throughout the forest zone of Ghana, makes

establishment of new, nationally protected areas very unlikely. Furthermore, the fact that selective logging reaches even the most remote corners of any forest reserve highlights the importance of unreserved forest areas as extension zones that increase effective forest cover and improve linking networks between forest fragments. In effect, to maintain long-term forest ecosystem integrity in Ghana it is imperative to assess the conservation value of various land-use practices, and identify factors that facilitate the viability of forest bird populations and secure their genetic variability through local migration.

Unreserved tropical forest areas in Ghana and the rest of the world fall into six basic categories of land-use: 1) forest remnants; 2) various stages of farm/plantation abandonment and secondary successions, both subject to variable 'non-timber forest-products' (NTFP) harvesting; 3) annual crops; 4) perennial cash-crop plantations, either for subsistence or regularly harvested commercially; 5) perennial native or exotic tree plantations for long-term harvesting of timber or pulp, and 6) residential areas, including parks and gardens. Whereas land-uses 2 and 3 are usually products of the pan-tropical traditional shifting cultivation, various management practices characterise the production systems of perennial plantations, and reflect variations in their complexity and the diversity of the vertical vegetation structure. Hence, a principal task for combined bird conservation and sustained crop production is to identify regionally and locally adapted systems that address both interests (Gordon *et al.* 2007). Since the 1960s, conservationists have steadily evaluated the ornithological importance of these land-uses (Elgood and Sibley 1964, Terborgh and Weske 1969), though with a different emphasis in each part of the tropics. In a brief review of studies from the past two decades on impacts on the forest avifauna of land-uses (1–6) mentioned above, it is evident that isolated small forest remnants, maturing secondary forest (>5–10 years old), and abandoned plantations are superior forest bird habitats compared to early secondary successions (<5 years), non-arboreal or annual crops, and residential areas, that are only visited by few forest generalists (e.g. Blankespoor 1991, Kofron and Chapman 1995, Raman 2001, Marsden *et al.* 2001, Hughes *et al.* 2002, Jones *et al.* 2003, Waltert *et al.* 2005a, Bolwig *et al.* 2006, Marsden *et al.* 2006, Posa and Sodhi 2006, Soh *et al.* 2006, Borges 2007).

Several studies have unambiguously emphasised that industrially managed 'sun' plantations of cash crops such as e.g. Coffee *Coffea* spp., Cocoa, Oil Palm, and Rubber (Wilson and Johns 1982, Danielsen and Heegaard 1995, Aratrakorn *et al.* 2006, Soh *et al.* 2006), or timber monocultures such as Teak *Tectona grandis* or conifers (Carlson 1986, Beehler *et al.* 1987, Komar 2002, Sekercioglu 2002, Wijesinghe and Brooke 2005) do not benefit forest obligates. In contrast, recent data from both the New (Moguel and Toledo 1999, Faria *et al.* 2006, Komar 2006) and Old World (Raman and Sukumar 2002, Raman 2004, Waltert *et al.* 2004, 2005a,b) highlight the importance for forest bird conservation of traditionally managed 'rustic' cash-crops shaded by a planted, mono-dominant or variably-native intact canopy. Similarly, traditionally managed and floristically diverse agroforests (or 'forest gardens') of Rubber, native or exotic timber trees are also important for forest bird conservation in Indo-Malayan anthropogenic forest landscapes (Mitra and Sheldon 1993, Beukema *et al.* 2007, Thiollay 1995, Marsden *et al.* 2006), just as extensively managed, native mixed-timber plantations in Côte d'Ivoire (Waltert 2000) and Kenya (Farwig *et al.* 2008) support many resident forest birds. As outlined in the previous sections, very few avifaunal studies on West African plantations exist, although plantation development is rapidly expanding here.

In this paper I assess the importance of shaded cash-crop (Cocoa and Coconut *Cocos nucifera*) and exotic timber (*Gmelina arborea*, *Cedrela odorata*) plantations for bird conservation, with particular reference to Guineo-Congolian understorey forest specialists in evergreen forests of south-west Ghana. Comparisons with similar studies from both the Old and New World tropics are made. Implications for off-reserve conservation management are discussed from global and regional perspectives. The present study was parallel to a study of the impact of selective logging and forest fragmentation on Ghanaian forest avifauna (Holbech 2005).

Study area and sites

The study was conducted from September 1993 to August 1995. Five plantation habitats were selected, adjacent to or within a protected area of south-west Ghana (Figure 1), covering wet evergreen (WE) and moist evergreen (ME) forest zones (Hall and Swaine 1976). WE-zone receives >2,000 mm of rain annually and the closed canopy reaches an average height of 35–40 m. Annual rainfall in ME-zone is 1,750–2,000 mm per year and the height of the discontinuous canopy ranges between 35 and 45 m. Both faunal and floral diversity is highest in the WE-zone, although the majority of large vertebrates occur in both zones. All selected sites lie in a lowland area with altitudes between 25 and 300 m a.s.l.

Two partially shaded cash crop plantations, ‘Boin Cocoa’ and ‘Ankasa Coconut’, as well as three exotic timber plantations, ‘Subri Gmelina’, ‘Neung Cedrela’ and ‘Tano Cedrela’, were included in this survey. Common to all five plantations was a well-developed secondary plant community made up of pioneer species (e.g. *Musanga cecropioides*, *Cecropia peltata*) or large forest trees. Undergrowth slashing had been abolished for several years giving these plantations a luxuriant appearance. The two Cedrela plantations formed the basis of a collapsed re-afforestation and agroforestry programme following illegal logging and farming. The Gmelina plantation was industrially managed but had some ‘biodiversity zones’ or ‘riparian strips’ conserved in marginal areas (steep slopes, narrow ridges and swamps), in which undergrowth slashing was limited.

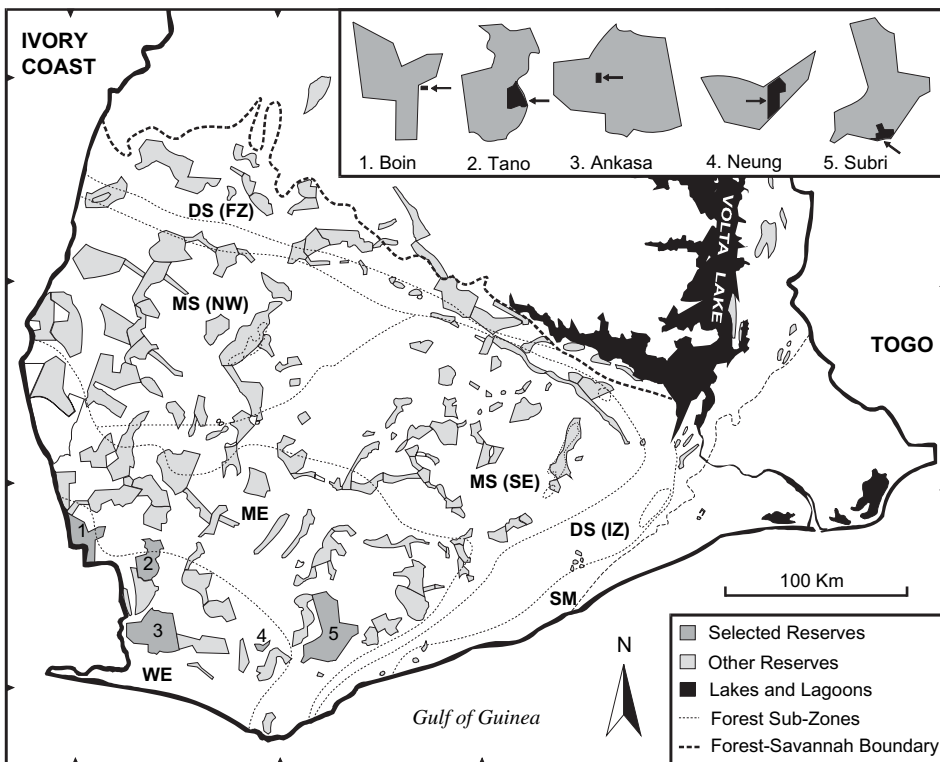


Figure 1. Map of the fragmented high forest zone in southern Ghana showing remaining reserves, forest type sub-zones and the selected study areas. Each study area is singly enlarged, indicating approximate size and location of plantations (black areas and arrows). Note that the scale of enlargements is not compatible between sites.

Table 1 outlines a general description of the 10 study sites. Detailed information on logging intensity for the five forest sites is found in Holbech (2005).

Methods

Assessment of vegetation parameters in plantations

Three simple forest-bird habitat-quality parameters were assessed; 1) the density of native forest trees (planted or wild) $>c. 0.5$ m dbh; 2) density of planted exotics of any size, and 3) the extent of closed canopy. Living trees were counted systematically within 5 m of all transects. Hence, the number of counted trees per km transect, roughly equals tree density ha^{-1} ($10\text{ m} \times 1,000\text{ m} = 1\text{ ha}$). The extent of closed canopy areas in each plantation was estimated by sectioning all transects for every 25 m and assessing whether each section passed through this habitat type. The percentage of closed canopy areas was then calculated as the cumulated closed-canopy sections divided by the total transect length for each plantation surveyed. Sections that passed through areas devoid of canopy were originally clear-cut for farming purposes but presently overgrown by dense vine tangles, ferns and in particular the invasive, perennial, exotic shrub Siam Weed *Chromolaena odorata*.

Mist-netting of birds

Mist netting at ground level (0–3 m) is repeatable and has no biases related to observer-skills and seasonal fluctuations in, for example vocalisation frequency, and is the best method for detecting cryptic, shy and silent species otherwise easily missed by audio-visual counts (Karr 1981, Derlindati and Caziani 2005). A limitation however, is that bird sampling is strongly biased towards lower storey birds and cannot be used to census whole forest bird communities (Poulsen 1994, Remsen and Good 1996). Our mist-nets were set 0–10 m from the centre-line of each transect, on both sides. Nets were 6, 9 or 12 m long, 4-shelved, with 15 mm mesh and 2.7 or 3.2 m high. The bottom of the lowest shelf was normally set 5–10 cm above the forest floor. Ten to 12 nets (90–126 m) were operated simultaneously. Nets were spaced at intervals of 100–150 m along

Table 1. Description of the 10 study sites in the south-west Ghana.

Area	Forest zone ^a	Size (km ²)	Isolation ^b (km)	Logging periods (up to 1995)	Age (years)	Max. tree height (m) ^c	GHI ^d
Ankasa RR	WE	348.7	0	1960–74	–	35–40	301
Ankasa Coconut	WE	<0.1	<0.5	1960–74	20–25	10–15 (>35)	?
Boin FR	WE-ME	277.7	0	1964–73	–	35–45	93
Boin Cocoa	WE-ME	~0.1	0.5–1.0	1964–73	15–20	4–10 (>35)	?
Subri FR	ME	587.9	0	1966–95	–	35–45	140
Subri Gmelina	ME	12.0	1.0–3.0	1966–95	21–23	15–25	?
Tano FR	WE-ME	205.9	0	1957–92	–	35–45	122
Tano Cedrela	WE-ME	9.8	0.5–1.5	1957–92	20–25	15–30 (>30)	?
Neung FR	WE	45.0	4	1973–87	–	35–40	269
Neung Cedrela	WE	6.4	0.5–1.0	1973–87	20–25	15–20 (>30)	?

^aFrom Hall and Swaine (1976): WE, wet evergreen ($>2,000$ mm); ME = moist evergreen (1,750–2,000 mm).

^bBiogeographical isolation: The distance of transects to nearest other protected forest (0 km = joined with another forest).

^cFor plantations, the numbers refer to the crop height range, whereas those in brackets refer to maximum height of shading trees making up a discontinuous canopy.

^dFrom Hawthorne and Abu Juam (1993): Genetic Heat Index (GHI) based on the rarity of tree species in Ghana.

each transect and kept open (closed during rains) from 06h00–06h30 to 17h00–18h30 and inspected regularly by a three-person team. To reduce problems associated with recaptures and net shyness, nets were moved every 2–4 days, according to the bird activity encountered. Birds were not banded but marked with a permanent ink colour pen on contour and down feathers, for recapture detection purposes.

Avifaunal classification-feeding guilds, forest habitat preferences and local status

All species were grouped according to food preference and foraging height (Brosset and Erard 1986, Gatter 1998), and foraging behaviour (from the literature, including 'The Birds of Africa', Vols. 1–7). A total of 11 major feeding guilds were identified (see Appendix in supplementary materials). Each species was also classified to the three forest-habitat preference categories defined in Bennun *et al.* (1996), i.e. forest specialists (FF), forest generalists (F) and forest visitors (f). Additionally, the differentiation between primary (P), secondary (S) and riverine (R) forest birds based on Thiollay (1985) was also used. Largely, species-specific forest habitat categorisation follows Bennun *et al.* (1996), with only seven exceptions. Birds of the same species may actually have slightly different habitat preferences within their range, particularly for birds with large ranges (Bennun *et al.* 1996); Dranzoa (1998) categorised some 10 species differently to Bennun *et al.* (1996) for Kenya/Uganda.

Three extensive bird surveys covering both evergreen and deciduous forest types in Ghana were used to determine the local status of birds (Beier *et al.* 2002, Dowsett-Lemaire and Dowsett 2005a–j, Holbech 2005, including the present survey). Presence/absence data for each of the three surveys were assessed, and the percentage occurrence for each species was determined accordingly. Percentage occurrences in Beier *et al.* (2002) were based on $n = 121$ sampled transects, in Dowsett-Lemaire and Dowsett (2005a–j) on $n = 10$ reserves surveyed, and in Holbech (2005) on $n = 20$ forest-zone habitats including the five plantations of the present study. The mean of the calculated three %-occurrences represents the general local status of a species in Ghanaian forests. Five local status categories were distinguished between; 'rare' with a mean occurrence $\leq 10.0\%$, 'uncommon' (10.1–25.0%), 'fairly common' (25.1–50.0%), 'common' (50.1–75.0%), and 'widespread' ($\geq 75.1\%$). Rare and uncommon species were classified as of conservation importance, as these are area sensitive and restricted to the interior of the Ghanaian high forest.

Data analyses

As sampling efforts for each site were stratified according to its size and accessibility, the observed species richness could not be directly compared as species number and sampling efforts are highly correlated. Instead, three species richness estimators and one commonly used ecological diversity index were calculated using the computer software EstimateS version 8.0.0. (Colwell 2006). The estimators used follow recommendations by Colwell and Coddington (1994) on robustness towards sampling size, i.e. Chao 2 and Jack-knife 2, together with the Abundance-based Coverage Estimator (ACE). Additionally, the Shannon-Wiener index (H') of diversity provides information on the evenness component of species diversity (Magurran 1988).

The richness-weighted α (log series) index of diversity was applied to assess bird guild diversity as this index has low sensitivity to sample size and a good ability to discriminate between sites (Magurran 1988). To assess species similarity between the ten sites, the quantitative Morisita-Horn index (C_{MH}) was applied. This index is little biased by differences in sample size and species richness, and it is the most appropriate measure for large species assemblages with relatively few dominant and many rarely recorded species (Magurran 1988). A low similarity between two sites is equivalent to a high complementarity between these. As bird guild data on relative abundance and ecological diversity did not follow a normal distribution (skewness and

kurtosis tests performed), these were compared using non-parametric Mann-Whitney *U*-tests (z distribution only for $n > 20$).

Results

Tree density and percentage of closed canopy

Whereas the closed canopy percentages in the two cash-crop plantations were fairly similar, the density of large trees in Boin Cocoa was almost twice that of Ankasa Coconut (Table 2 and Figure 2). The Tano Cedrela plantation had 50–100% more large forest trees than the two other plantations, whereas the density of exotics was lowest here. In contrast, the Subri Gmelina had the highest exotic-tree density, but also the lowest density of large forest trees. Hence, among the three exotic plantations, the density of exotics seems to be inversely proportional to large forest-tree density. The fact that Tano Cedrela had the highest density of large forest trees, yet a relatively low percentage of closed canopy areas, indicates that, as with cash-crop plantations, large forest trees were unevenly distributed here. In terms of overall large tree density (exotics and native), Neung Cedrela ranked as the exotic plantation offering lowest bird habitat quality, whereas Ankasa Coconut overall served as the poorest habitat for forest dependent birds. However, when considering the percentage of large forest trees Subri Gmelina represented the lowest forest bird habitat quality with only 29% forest trees and Tano Cedrela the richest (75%). Contrastingly, in terms of closed canopy percentage, Tano Cedrela was the most degraded exotic plantation, and Boin Cocoa the overall most degraded habitat. When combining the three determinants of habitat quality, Ankasa Coconut was the most degraded habitat, whereas Tano Cedrela was only slightly superior to the other two and fairly similar exotic plantations. Overall, Boin cocoa rated as an ‘intermediary’ bird habitat quality with fairly high forest tree density but also a relatively low proportion with closed canopy (<50%).

Overall relative bird abundance

Relative bird abundance is in this study defined as captures per net-metre-hours (NMH). Overall capture rates (Table 3) were significantly higher ($U = 24.0$, $P < 0.05$) in plantations (0.052 ± 0.016) compared to forest controls (0.0310 ± 0.004). Capture rates for the two cash crop plantations were 86–151% times that of their respective forest references, partly due to the Yellow-whiskered Greenbul *Andropodus latirostris* accounting for 34–67% of overall abundance. When excluding *A. latirostris*, only Ankasa Coconut remained 53% higher than Ankasa RR. Hence, understorey bird abundance was generally higher in Ankasa Coconut, whereas only one species dominated the captures in Boin Cocoa. Capture rates for Tano Cedrela and Subri Gmelina were *c.* 65% (39–56% exclusive of *A. latirostris*) higher than respective forest references, whereas Neung habitats did not differ significantly, indicating that understorey-bird abundance was relatively high in exotic plantations adjacent to large natural forests. In summary, overall bird abundance appeared highest in cash-crop plantations, second highest in

Table 2. Tree density (ha^{-1}) and percentage of closed canopy areas in cash-crop and exotic tree plantations of south-west Ghana. Figures in brackets are percentage of all large trees (exotics and forest trees = 100%).

Habitat	Planted trees		Forest trees (dbh > 0.5 m)	All trees (dbh > 0.5 m)	Closed canopy areas (%)
	(any size)	(dbh > 0.5 m)			
Ankasa Coconut	–	–	12.7 (100)	12.7 (100)	51.7
Boin Cocoa	–	–	23.1 (100)	23.1 (100)	45.5
Subri Gmelina	697	36.0 (71)	14.8 (29)	50.8 (100)	92.2
Neung Cedrela	95.3	18.7 (49)	19.5 (51)	38.2 (100)	95.6
Tano Cedrela	65.6	11.4 (25)	33.8 (75)	45.2 (100)	80.4

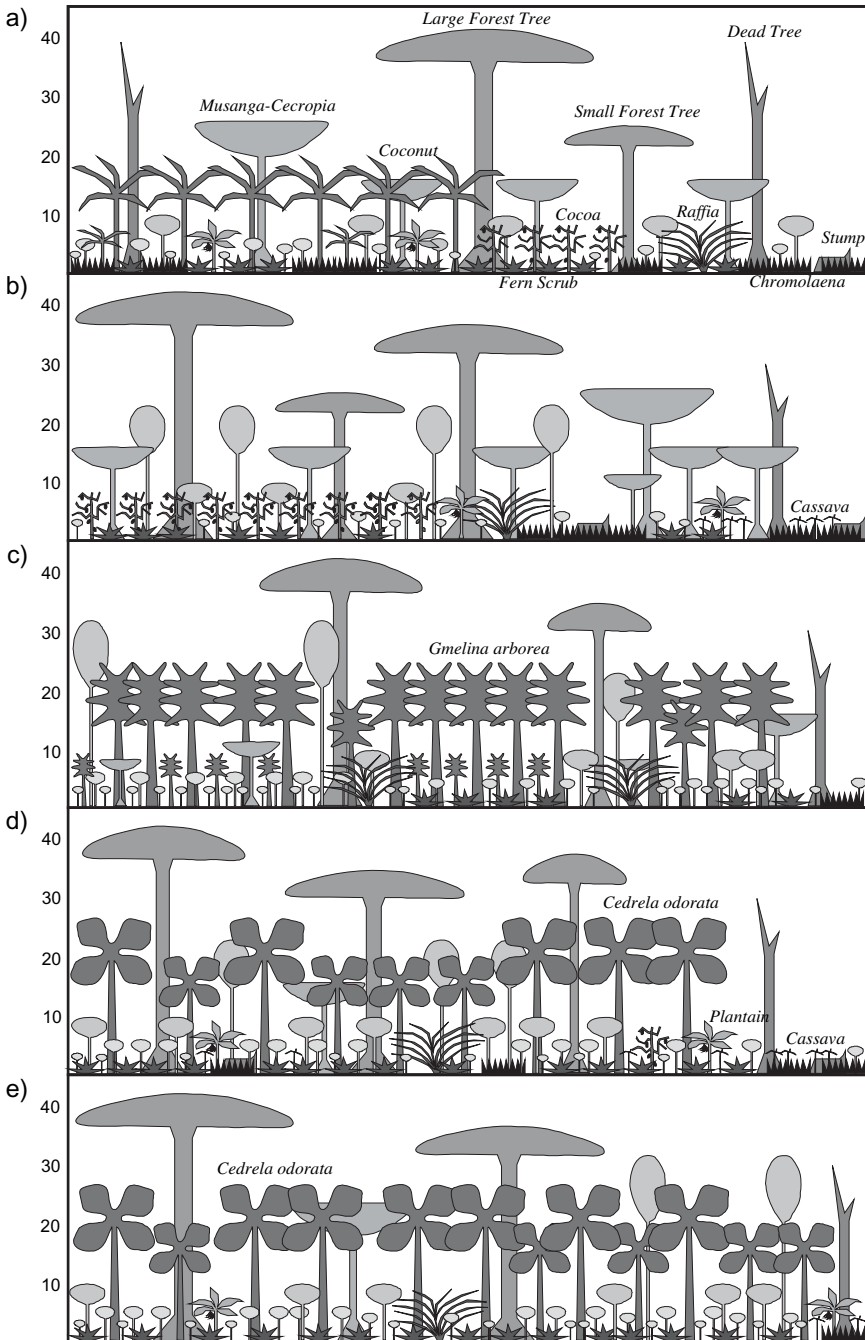


Figure 2. Schematic diagram of the structural vegetation profile of a) Ankasa Coconut, b) Boin Cocoa, c) Subri Gmelina, d) Tano Cedrela and e) Neung Cedrela. For simplicity, climbers and epiphytes are not shown. Strata height indicated in metres.

exotic plantations and lowest in reserves, though dominated by a few species in plantations, particularly *A. latirostris*, Green Hylia *Hylia prasina*, Olive Sunbird *Cyanomitra olivaceus* and Red-bellied Paradise Flycatcher *Terpsiphone rufiventer*.

Species richness and ecological diversity

Among the four diversity descriptors, only Jack 2 was significantly higher ($U = 25.0, P < 0.05$) in forests compared to respective plantations, whereas ACE and Shannon showed a 'probably significant' ($U = 23.0, P = 0.05$) difference between forests and plantations (Table 3). When combining the four diversity descriptors, all reserves were superior to their respective plantation. Among the five plantations, Tano Cedrela ranked highest for a combined score of all four descriptors, making up 96% of its forest reference, followed by Ankasa RR with 61% of its associated forest. In contrast, Neung Cedrela displayed by far lowest diversity scores, making up <25% of that of the Neung FR, whereas Boin Cocoa and Subri Gmelina were almost equally diverse. Hence, plantations situated outside reserves (Boin Cocoa) or adjacent to small impoverished reserves (Neung Cedrela) represented the poorest forest avifaunas.

Species similarity and complementarity

Species similarity was highest between Neung FR and Subri Gmelina ($C_{MH} = 0.981$), and lowest between Boin Cocoa and Tano FR ($C_{MH} = 0.457$) (Table 4). Overall, similarity was highest among forests (0.902 ± 0.052), and lowest on average between forests and plantations (0.791 ± 0.143), yet the average similarity between forests and respective plantations was relatively high (0.811 ± 0.155), suggesting that plantations were colonised by surrounding forests (Table 5). The average similarity among exotic plantations (0.890 ± 0.051) was high, indicating that such habitats supported similar bird fauna irrespective of the nearby forest. Exotic plantations and their respective forest associations were also similar (0.902 ± 0.054), whereas cash-crop plantations were more complementary to nearby forest habitats (0.675 ± 0.170). When comparing mean similarity figures in Table 5, only one comparison was significantly different

Table 3. Diversity statistics (using EstimateS with 100 randomisations without replacement; Colwell 2006) for the five plantation habitats and their respective forest references in south-west Ghana. In an overall assessment of habitat ranking, a score index has been calculated for each of the four diversity measures (points of 1–10), and the cumulated score expresses the overall ecological diversity of each habitat. Figures in brackets indicate the relative (%) overall diversity score of each plantation compared to forest associate.

Study site	RA ¹	ACE ²	Chao II ³	Jack II ⁴	Shannon ⁵	Score
Boin FR	0.0296	71.80	72.17	84.35	2.67	37
Subri FR	0.0280	50.72	51.00	58.12	2.78	33
Ankasa RR	0.0335	50.08	48.68	54.04	2.83	31
Tano FR	0.0254	45.36	43.32	48.83	2.82	23
Neung FR	0.0364	46.96	48.27	54.53	2.39	23
Tano Cedrela	0.0419	47.37	41.50	48.85	2.51	22 (96)
Ankasa Coconut	0.0622	43.00	51.50	46.25	2.20	19 (61)
Boin Cocoa	0.0743	40.91	55.00	44.33	1.47	16 (43)
Subri Gmelina	0.0465	35.00	35.28	41.30	2.45	11 (33)
Neung Cedrela	0.0340	30.35	28.50	32.90	1.95	5 (22)

¹Relative abundance = birds netted per net-meter-hours.

²Abundance-based Coverage Estimator of species richness.

³Chao 2 estimator of species richness.

⁴Jack-knife 2 estimator of species richness.

⁵Shannon-Wiener index of species diversity (H').

Table 4. Species similarity between five plantation habitats and their respective forest associates in south-west Ghana, as shown by the quantitative Morisita-Horn index (C_{MH}).

Area	An RR	An Co	Bo FR	Bo Co	Su FR	Su Gm	Ta FR	Ta Ce	Ne FR	Ne Ce
An RR	–	0.796	0.901	0.546	0.936	0.877	0.901	0.743	0.832	0.733
An Co	–	–	0.908	0.772	0.809	0.924	0.816	0.837	0.953	0.918
Bo FR	–	–	–	0.555	0.947	0.911	0.970	0.877	0.899	0.798
Bo Co	–	–	–	–	0.507	0.751	0.457	0.542	0.777	0.871
Su FR	–	–	–	–	–	0.893	0.956	0.816	0.844	0.749
Su Gm	–	–	–	–	–	–	0.864	0.881	0.981	0.944
Ta FR	–	–	–	–	–	–	–	0.853	0.832	0.710
Ta Ce	–	–	–	–	–	–	–	–	0.894	0.844
Ne FR	–	–	–	–	–	–	–	–	–	0.960
Ne Ce	–	–	–	–	–	–	–	–	–	–

$$C_{MH} = 2\sum (a_i \cdot b_i) / (da + db) \cdot aN \cdot bN, \text{ where } da = \sum a_i^2 / aN^2 \text{ and } db = \sum b_i^2 / bN^2$$

($z = 2.48, P = 0.01, n = 35$), namely between all forests and all forests versus plantations. These data suggest that complementarity among plantations was higher than among forests in general, just as cash crops were more complementary to respective forests than were exotics.

Distribution of feeding guilds

In terms of relative abundance (captures NMH^{-1}) only lower strata (<10 m) foliage-gleaners were significantly more abundant in plantations ($U = 24.0, P < 0.05$) (Table 6). Lower strata birds were generally also significantly more abundant in plantations ($U = 24.0, P < 0.05$), due to the high dominance of *A. latirostris*, an understorey (0–3 m) foliage-gleaning omnivore. However, when this species is removed from the data, the difference between plantations and forests was insignificant. With respect to within-guild diversity (α -log series index) only mid-level (10–30 m) foliage-gleaners were probably more diverse in plantations ($U = 23.0, P = 0.05$). These results indicate that trophic organisation of the understorey bird community in forests and plantations were similar, and emphasise the potential of these plantations for some feeding guilds that are vulnerable to forest disturbance, e.g. salliers, bark- and litter-gleaners.

Distribution of birds and forest habitat preferences

Of 78 species netted, 47 (60%) were forest specialists (FF), 30 (39%) forest generalists (F) and only one (1%) a forest visitor (f). Relative abundance (captures NMH^{-1}) of FF-birds was not significantly different between forests and plantations, whereas F-birds were significantly

Table 5. Mean and standard deviation (SD) of similarity values between different habitat categories: forests, exotic (Gmelina or Cedrela) and cash crop (Cocoa or Coconut) plantations, based on values obtained in Table 4.

Habitat category	Mean \pm SD
All forests ($n = 10$)	0.902 \pm 0.052
All plantations ($n = 10$)	0.828 \pm 0.119
All forests and plantations ($n = 25$)	0.791 \pm 0.143
Respective forest and plantation ($n = 5$)	0.811 \pm 0.155
Exotic plantations only ($n = 3$)	0.890 \pm 0.051
Cash crop plantations only ($n = 1$)	0.772
Exotic plantations and forest associates ($n = 3$)	0.902 \pm 0.054
Cash crop plantations and forest associates ($n = 2$)	0.675 \pm 0.170

Table 6. Mean (\pm SD) relative abundance (captures per 1,000 NMH) and species diversity (α log-series) for 23 bird guilds found in five forest and five plantation habitats of south-west Ghana. Significant differences between forests and respective plantations were determined by Mann-Whitney *U*-tests (2-tailed, $n = 5$). Significant results in bold. ID = insufficient data; ns = not significant ($P > 0.05$).

Bird guilds	Relative abundance			Species diversity (α -log series)		
	Forests	Plantations	Statistical test	Forests	Plantations	Statistical test
Raptors	0.07 \pm 0.07	0.18 \pm 0.16	<i>U</i> = 18.5, ns	1.13 \pm 1.37	ID	ID
Foliage-gleaning granivores (Fru/Gra/Ins)	0.22 \pm 0.19	0.40 \pm 0.44	<i>U</i> = 14.0, ns	0.30 \pm 0.17	0.76 \pm 1.09	<i>U</i> = 14.0, ns
Nectarivores (Fru/Ins/Nec)	6.24 \pm 1.62	9.89 \pm 4.52	<i>U</i> = 21.0, ns	0.34 \pm 0.19	0.28 \pm 0.13	<i>U</i> = 13.0, ns
Litter-gleaners (Gra/Ins/Omn)	8.33 \pm 3.01	6.87 \pm 3.23	<i>U</i> = 17.0, ns	2.72 \pm 0.37	2.72 \pm 1.84	<i>U</i> = 16.0, ns
Bark-gleaning insectivores (GU-UM)	0.26 \pm 0.10	0.28 \pm 0.24	<i>U</i> = 12.5, ns	2.09 \pm 0.99	0.68 \pm 0.63	ID
GU/GU-LM Foliage-gleaners (Fru/Ins/Omn)	7.95 \pm 4.27	24.8 \pm 14.9	<i>U</i> = 24.0, <i>P</i> < 0.05	1.00 \pm 0.30	0.62 \pm 0.18	<i>U</i> = 21.0, ns
LM/LM-UM/ Foliage-gleaners (Fru/Ins/Omn)	4.12 \pm 0.41	3.32 \pm 1.71	<i>U</i> = 17.0, ns	2.04 \pm 0.57	3.20 \pm 0.90	<i>U</i> = 23.0, <i>P</i> = 0.05
UM-C/C Foliage-gleaners (Fru/Ins)	1.12 \pm 0.49	2.32 \pm 1.51	<i>U</i> = 19.0, ns	1.89 \pm 0.58	1.63 \pm 0.78	<i>U</i> = 15.0, ns
GU/GU-LM Salliers (Ins/Pis)	0.81 \pm 0.37	1.06 \pm 0.26	<i>U</i> = 19.0, ns	1.47 \pm 0.98	1.15 \pm 0.25	<i>U</i> = 13.0, ns
LM/LM-UM/GU-UM Salliers (Car/Ins)	1.31 \pm 0.33	2.57 \pm 1.45	<i>U</i> = 17.0, ns	1.07 \pm 0.53	1.20 \pm 0.76	<i>U</i> = 14.0, ns
UM/UM-C Salliers (Car/Ins)	0.13 \pm 0.11	0.04 \pm 0.08	<i>U</i> = 19.0, ns	1.65 \pm 1.14	0.01 \pm 0.03	<i>U</i> = 17.0, ns
Others (<i>I. exilis</i> only)	0.03 \pm 0.04	0.00 \pm 0.00	ID	ID	ID	ID
Lower strata birds (GU, GU-LM, LM)	27.4 \pm 4.26	46.2 \pm 14.5	<i>U</i> = 24.0, <i>P</i> < 0.05	6.10 \pm 0.34	5.05 \pm 1.07	<i>U</i> = 22.0, ns
Upper strata birds (LM-UM, UM, UM-C, C)	2.07 \pm 0.65	3.35 \pm 1.75	<i>U</i> = 17.0, ns	6.23 \pm 1.67	5.71 \pm 4.92	<i>U</i> = 18.0, ns
Strata generalists	1.07 \pm 0.43	2.27 \pm 1.19	<i>U</i> = 19.0, ns	0.39 \pm 0.08	0.69 \pm 0.25	<i>U</i> = 20.0, ns
All insectivores	11.71 \pm 2.59	12.2 \pm 2.92	<i>U</i> = 16.0, ns	7.62 \pm 0.62	7.17 \pm 1.66	<i>U</i> = 15.0, ns
All insectivore-frugivores	2.01 \pm 1.28	4.04 \pm 1.86	<i>U</i> = 22.0, ns	1.98 \pm 0.79	2.11 \pm 2.02	<i>U</i> = 18.5, ns
Ant-followers (AF)	9.37 \pm 2.86	7.71 \pm 2.83	<i>U</i> = 17.0, ns	2.90 \pm 0.65	3.70 \pm 1.70	<i>U</i> = 18.0, ns
Forest specialists (FF)	12.5 \pm 3.31	9.76 \pm 4.75	<i>U</i> = 18.0, ns	8.60 \pm 0.97	8.68 \pm 3.20	<i>U</i> = 13.0, ns
Forest generalists (F)	18.10 \pm 5.12	42.0 \pm 16.2	<i>U</i> = 25.0, <i>P</i> < 0.05	2.79 \pm 0.32	<i>U</i> = 17.0, ns	
Forest visitors (f)	0.01 \pm 0.03	0.00 \pm 0.00	ID	ID	ID	ID
Red-list endemic species	0.98 \pm 0.46	0.17 \pm 0.18	<i>U</i> = 25.0, <i>P</i> < 0.05	1.27 \pm 1.08	0.00 \pm 0.00	ID
Conservation important birds	1.80 \pm 1.08	0.51 \pm 0.31	<i>U</i> = 23.0, <i>P</i> = 0.05	3.05 \pm 0.68	ID	ID

Car = Carnivore, Fru = Frugivore, Ins = Insectivore, Nec = Nectarivore, Gra = Granivore, Pis = Piscivore, Omn = Omnivore, GU = Ground-understorey (0–3 m), LM = Lower mid-storey (3–10 m), UM = Upper mid-storey (10–30 m), C = Canopy (>30 m).

($U = 25.0$, $P < 0.05$) more abundant in plantations (Table 6). In terms of diversity, no differences between forests and plantations were established. Only one f-species was netted, Grey-backed Camaroptera *Camaroptera brachyura* (Subri FR), and no non-forest species were netted anywhere. Hence, plantations supported rather diverse assemblages of FF-species, although F-species in terms of relative abundance dominated here. The F-dominance was particularly attributed to *A. latirostris* but also Little Greenbul *Andropadus virens* and Olive Sunbirds.

Distribution of ant-followers

Birds following army ants are often sensitive to forest disturbance (Roberts *et al.* 2000, Barlow *et al.* 2006). Among 16 ant-following species netted, all plantations had fewer of these birds compared to forest associates (mean 69%), ranging from 36% (Neung Cedrela) to 91% (Subri Gmelina), although the comparative tests on relative abundance and diversity were both insignificant (Table 6). These data indicate that army ants occur in plantations at relatively high densities with the exception of the small and heavily disturbed Neung Cedrela plantation.

Distribution of red list endemics and other species of conservation importance

Three species categorised by IUCN (2001) as threatened Upper Guinea Forest endemics were netted in the present study: Yellow-bearded Greenbul *Criniger olivaceus*, Green-tailed Bristlebill *Bleda eximius* and Rufous-winged Illadopsis *Illadopsis rufescens*, all specialised understory insectivores (ant-follower or bark-gleaner). The mean abundance of these birds was significantly higher for all forest sites compared to plantation associates ($U = 25.0$, $P < 0.05$) (Table 6). Only four individuals were netted in three plantations. Hence, plantations are only marginal habitats for these birds, and it is most likely that their presence here relied on the proximity of surrounding high forest.

Of the 78 species netted, four species were classified as 'rare' and 15 as 'uncommon'. Cassin's Flycatcher *Muscicapa cassini* was also determined as 'uncommon', but is a riverine species and hence excluded from the analysis of species of conservation importance. Two red list endemics were determined as 'fairly common', but were also included as important for conservation in Ghana due to their critical conservation status. Hence, the total number of species of conservation importance was 20, and high numbers of these birds are indicative of a diverse and complex forest bird community. The majority of these 20 species are FF-species (80%) and Guineo-Congolian or Upper Guinea endemics (75%).

The mean abundance of species of conservation importance was probably significantly higher ($U = 23.0$, $P = 0.05$) in forests than plantations (Table 6). Sixteen species of conservation importance were netted in forests (12 exclusively here), and eight in plantations, i.e. 50% of the number found in forests. The mean percentage of these species found in plantations compared to forest associates was 26% (range 17–43%). Despite relatively low densities, the presence of these birds in plantations is indicative of a fairly complex bird community. The African Piculet *Sasia africana* and Lemon-bellied Crombec *Sylvietta denti* (both FF/P-species) were netted in only three plantations, but not in 15 Ghanaian forest reserves (Holbech 2005).

Discussion

Factors influencing the conservation importance of plantations for forest birds

According to general theories of biogeography and species diversity (e.g. MacArthur 1972, Diamond 1973), four prime factors may determine resident forest bird diversity in plantations; 1) distance to the nearest source of forest birds; 2) the bird community at that source; 3) habitat quality of corridors (Sieving *et al.* 2000, Jansen 2005, and 4) habitat quality of the plantation, which is often highly linked to size of the area. Factors 1–3 are all determinants of bird dispersal

magnitude into plantations, whereas factor 4 reflects the capability of plantations *per se* to sustain viable forest bird populations. Where plantations are close to and/or well connected to little-disturbed natural forests, it is difficult to determine whether birds only make temporary and spatially facultative use of the plantations, or are actually persisting there. Resolving that issue would require monitoring individual movements or identifying breeding territories and feeding home ranges. Hence detection of the presence of birds does not necessarily indicate bird persistence or functional habitat use (Peh *et al.* 2005), particularly in the case of highly mobile species with large home ranges, e.g. raptors (Thiollay 1993), pigeons, hornbills and parrots (Kofron and Chapman 1995, Marsden and Pilgrim 2003). However, when plantations have been isolated for decades, in areas with no significant nearby forest, the presence of forest birds likely reflects their adaptability to the plantation habitat (Greenberg *et al.* 1997a,b, 2000). This is particularly true for species with low mobility and high territoriality in small areas, e.g. for many edge-shy, terrestrial or understorey insectivores.

All but one of the five plantations were situated within moderately logged natural forest, and as these were relatively more diverse and similar compared to the more isolated Boin Cocoa, it suggests use rather than forest bird persistence in these plantations. Several recent studies around the world have indicated that distance to nearby forest is the major contributing factor to forest bird diversity in plantations (Naidoo 2004, Sodhi *et al.* 2005a, Tejada-Cruz and Sutherland 2004, Waltert *et al.* 2005a, Soh *et al.* 2006, Bolwig *et al.* 2006). This apparent distance-effect depends on the extensiveness or patchiness of nearby forests, as indicated by plantation studies adjacent to small patches of remnants (Reitsma *et al.* 2001, Waltert *et al.* 2005b, Lindenmayer *et al.* 2005). In line with this, sensitivity to distance isolation in matrix ecotones depends on the mobility and territoriality of each species as mentioned above, whereby aggregates of bird community species diversity may not always be simply correlated with forest coverage alone (Lindenmayer *et al.* 2005). Finally, distances to nearest natural forest play minor roles in industrial monoculture plantations (no canopy shade and heavy undergrowth weeding) situated in heavily degraded areas with very poor forest habitat connectivity (Aratrakorn *et al.* 2006).

In the present study, measures of similarity strongly indicate that exotic plantation avifaunas were closely related to their adjacent forest compared to other distant forests and plantations. In particular the depauperate avifauna of Neung Cedrela clearly reflected the already highly impoverished degraded bird habitat of adjacent Neung FR. Peh *et al.* (2005) also found higher species diversity in anthropogenic matrix landscapes close to 800 km² large forest compared to 300 km² forest, just as Faria *et al.* (2006) found higher forest bird diversity in plantations situated in an extensively forested zone compared to similar plantations in areas with only 4.8% remnants of 1–300 ha. At the microscale level, the size of forest patch remnants has also been shown to affect overall bird diversity in plantations relatively more than the mere distance from remnants (Tubelis *et al.* 2004).

Although the relative species richness of the Boin Cocoa ranked lowest among the five plantations, a number of FF-species were present up to >500 m from the forest edge, e.g. White-crested Hornbill *Tropicranus albocristatus*, Red-headed Dwarf-kingfisher *Ceyx lecontei*, Red-tailed Greenbul *Criniger calurus*, Western Bearded Greenbul *Criniger barbatus*, White-tailed Ant-thrush *Neocossyphus poensis*, Brown-chested Alethe *Alethe poliocephala*, and Blue-headed Crested-flycatcher *Trochocercus nitens*. Many of these birds were associated with army-ant swarms. The presence of these species suggests some level of habitat connectivity between the very diverse Boin FR and the shaded cocoa plantation by virtue of the complex matrix of forest remnants, secondary forest and farmland. Habitat connectivity has been shown to play a vital role for dispersal of forest specialists between forest remnants and various types of plantation agro-ecosystems in otherwise heavily disturbed matrix landscapes (Estrada *et al.* 1997, Graham 2001, Raman 2004, Castelletta *et al.* 2005, Faria *et al.* 2006), and may in some cases moderate the pronounced decline of forest birds related to distance isolation of small and otherwise ecologically disintegrated habitat units (Reitsma *et al.* 2001). Due to their close proximity and excellent connectivity, it is likely that the Boin Cocoa and surrounding land-use matrix may

increase the functional habitat for FF-species deriving from the nearby Boin FR, but long-term capture-mark-recapture is necessary to evaluate persistence of these species in the plantation.

Tree plantations and forest bird conservation – a pan-tropical comparative evaluation

It has recently been shown that the structural and floristic diversity of plantations (factor 4) is positively correlated with forest bird species diversity (Raman and Sukumar 2002, Carlo *et al.* 2004, Waltert *et al.* 2005a, Cruz-Angón and Greenberg 2005). A number of inter-related factors may contribute to the vertical and horizontal vegetation complexity of plantations, including choice and density of crop species, plantation age, and most importantly, the intensity of management and control of the secondary plant community. Basically two major structural types of plantations can be identified in the tropics; 1) where the primary crop makes up the understorey level (<c. 5 m) of the vegetation, and is either non-shaded or shaded by a canopy of native or planted trees (e.g. Coffee, Cocoa); or 2) where the primary crop variably makes up the canopy level (>c. 10 m), and in which native plants may variably dominate the understorey together with seedlings and saplings of the crop (e.g. Rubber, Coconut, Oil Palm, Teak, Gmelina). Hence, cash-crop plantations may conform to both ‘understorey-tree’ plantations (e.g. Coffee) and ‘canopy-tree’ plantations (e.g. Oil Palm). On the other hand Rubber or timber plantations are always the latter. I have found no published bird studies in combined timber and cash-crop plantations, perhaps because the two are incompatible in terms of problems with nutrient competition or damage to cash crops during timber harvest.

According to the above division I have compiled data on biogeography, vegetation structure and forest bird conservation importance from 23 understorey-tree and 23 canopy-tree plantations throughout the tropics, including the five Ghanaian plantations (Tables 7 and 8). Though this is

Table 7. Comparison of 23 understorey tree-plantations in the Old and New World tropics, including the rustic cocoa plantation of this study in Ghana (*). The plantations are ranked in order of relative forest bird conservation importance: H = high (>75% or >50% of respectively all species (AS) or (priority) forest species (FS) present in variably disturbed native forest, similarity index (S) > 0.50, diversity index (H') > 2.50); M = moderate (AS = 50–75%, FS = 25–50%, S = 0.25–0.50); L = low (AS < 50%, F < 25%). Understorey and canopy codex: D = Diverse, multi-storied, large climbers, epiphytes; MD = moderate diverse, semi-storied, shrubs, vines; P = poor, single storey dominated by plantings, herbs and/or grasses.

Habitat	Country	Isolation (km)	Crop (m)	Understorey (height in m)	Canopy height (m)	Conservation importance % of AS/(FS), S = similarity
Rustic cardamom ²	Guatemala	Matrix	<2	MD, woody	D, c. 14	H, 132 (100)
Rustic cardamom ³	India	Adjacent	<2	P, <1, herbs	D, c. 28	H, 52 (89), S = 0.78
Rustic coffee ⁴	India	Adjacent	Mature	P, herbs	MD, 15–17	H, 89 (87), H' = 2.69
Semi-rustic coffee ³	India	Adjacent	<2	P, <1, shrubs	MD, c. 15	H, 82 (78)
Rustic cocoa Una ⁵	Brazil	0–1	c. 5	P, herbs	D, 15–20 ¹	H, 135, H' = 4.33, S = 0.76
Rustic cocoa Illhéus ⁵	Brazil	0–1	c. 5	P, herbs	D, 15–20 ¹	H, 95, H' = 3.73, S = 0.57
Rustic cocoa (Boin)*	Ghana	0.5–1	4–6	D, 5–10	D, 20–25 ¹	H, 74 (57), S = 0.56, H' = 3.38

Table 7. Continued.

Habitat	Country	Isolation (km)	Crop (m)	Understorey (height in m)	Canopy height (m)	Conservation importance % of AS/(FS), S = similarity
Abandoned cardamom ⁶	India	Adjacent	Very old	MD, 1–5	D, 20–25	H, 57–68 (43), S = 0.70–0.87
Rustic cocoa/coffee ⁷	Cameroon	5–7	Mature	MD, woody	D, 20–25 ¹	M, 88 (75), S = 0.46
Rustic coffee ⁸	Mexico	Degraded	3–5	MD, woody	MD, 12–14	M, 84 (78), S = 0.33
Mono-shade cocoa ⁹	Indonesia	Adjacent	3–4	P, herbs	P, 9–15	M, S = 0.32
Mono-shade coffee ⁸	Mexico	Degraded	2–3	P, herbs	P, 12–14	M, 79 (64), S = 0.21
Mono-shade coffee ¹⁰	Mexico	<0.3	2–3	P, herbs	D, c. 11	M, 90 (35)
Rustic coffee ¹⁰	Mexico	<0.1	3–5	P, herbs	D, c. 16	M, 88 (35)
Rustic coffee/cocoa ¹¹	Mexico	0.2–6	12–15 yrs	MD, woody	MD, >15	M, 55–69
Shaded cocoa ¹²	Costa Rica	Matrix	<20 yrs	P, weeding	MD, 18	L, 101 (16) ¹⁵
Abandoned cocoa ¹²	Costa Rica	Matrix	>20 yrs	P, shrubby	MD, 21	L, 111 (16) ¹⁵
Semi-rustic cocoa ¹³	Mexico	No forest	4–5	P, herbs	MD, c. 15	L, 64 (6) ¹⁵
Mono-shade coffee ²	Guatemala	Matrix	2–3	MD, shrubby	MD, 6–8	L, 70 (0) ¹⁵
Sun coffee ²	Guatemala	Matrix	2–3	P, weeding	P, 5–6	L, 68 (0) ¹⁵
Horticulture ¹⁴	Uganda	Matrix, 5	<2	P, < 1, shrubs	MD, <2	L, 18 (0)
Mono tea ¹⁴	Uganda	Matrix, 10	<2	P, < 1, herbs	P, <2	L, 11 (0)
Sun coffee ¹⁰	Mexico	Matrix	2–3	P, weeding	P, c. 5	L, <10 (0)

¹Some forest tree emergents up to 40–50 m (>100 years old); good habitat connectivity to nearby forest.

²Greenberg *et al.* (1997a): Mono-shaded coffee (40–50%) by mainly *Inga* or *Gliricidia* spp., and respectively 45 and 29 other tree species. Sun coffee negligible canopy cover. Rustic cardamom shaded (69%) by native secondary forest; all systems in a matrix of forest remnants and secondary shrubbery (matorral).

³Raman (2004): Cardamom with native canopy (88% cover) and coffee under mixed exotic/native canopy (69% cover), both within a matrix of forest remnants and plantations, and adjacent to 20–26 km² large forest blocks and/or small remnants (0.3–650 ha).

⁴Beehler *et al.* (1987): Incomplete canopy of remnant forest trees and an exotic tree in a disturbed forest area.

⁵Faria *et al.* (2006): Rustic 'cabruacas' situated in an area with 4.8% small (1–300 ha) forest remnants (Illneus) or in an area with >50% large (up to 110 km²) remnants (Una).

⁶Raman and Sukumar (2002): Shaded old plantation abandoned for 5–15 yrs; canopy cover 72–91% of forest trees and exotics.

⁷Walter *et al.* (2005a): Shaded coffee or cocoa plantations with forest tree density of c. 25 h⁻¹ (dbh > 0.50m).

⁸Greenberg *et al.* (1997b): Rustic coffee under native almost intact canopy. Mono-shaded coffee dominated by *Inga* spp.; very few nearby closed forest remnants along ridges.

⁹Walter *et al.* (2004): Mono-shaded cocoa by mainly *Gliricidia* spp., adjacent to closed forest.

¹⁰Tejeda-Cruz and Sutherland (2004): Mono-shaded (41%) coffee dominated by *Inga* spp. Rustic coffee shaded (60%) by an almost original canopy cover. Sun coffee no shade at all. All plantations situated in a buffer zone with 60% dense forest.

¹¹Estrada *et al.* (1997): Native shaded plantations in a matrix area with isolated forest remnants (1–2,000 ha) and good habitat connectivity through live fences.

¹²Reitsma *et al.* (2001): Mono- or multi-species shaded; matrix of forest patches (1–200 ha), farms and pastures.

¹³Greenberg *et al.* (2000): Plantations with 60 species of planted shade trees (no single dominant species); no nearby closed forest, not even remnants.

¹⁴Bolwig *et al.* (2006): Commercial large-scale plantations in a matrix landscape, with forest remnants > 1 km².

¹⁵Relatively high diversity of woodland and migrant forest species, but few or no resident forest specialists.

a rather problematic task, the plantations are ranked according to their relative importance in providing suitable habitats for forest birds, irrespective of the degree of forest bird persistence (use of plantations indicated by their presence). The ranking has particularly emphasised the extent (%) to which true forest birds and/or species of conservation importance are found in plantations compared to native primary or variably disturbed forest. Other complementary

Table 8. Comparison of 23 canopy tree-plantation systems in Southeast Asia and Africa, including the four plantations of the present study in Ghana (*). The plantations are ranked in order of relative forest bird conservation importance: H = high (>75% or >50% of respectively all species [AS] or [priority] forest species [FS] present in variably disturbed native forest, similarity index [S] > 0.50, diversity index [H'] > 3.50); M = moderate (AS = 50–75%, FS = 25–50%, S = 0.25–0.50, H' = 2.50–3.50); L = low (AS < 50%, FS < 25%, H' < 2.50). Understorey and canopy codex: D = Diverse, multi-storied, large climbers, epiphytes; MD = moderate diverse, semi-storied, shrubs, vines; P = poor, single storey dominated by plantings, herbs and/or grass.

Habitat	Country	Isolation (km)	Age (years)	Understorey (height in m)	Canopy height (m)	Conservation importance % of AS/(FS), S = similarity
Mono terminalia ²	Ivory Coast	0	5	P, weeding, <2	P, 15–25	H, 104 (86), H' = 4.10, S = 0.76
Subri gmelina*	Ghana	0	20–23	MD, woody, 3–5	D, 20–25 ¹	H, 86 (75), S = 0.85, H' = 3.85
Ankasa coconut*	Ghana	0	c. 25	MD, woody, 3–5	MD, 20–25 ¹	H, 103 (75), S = 0.76, H' = 3.83
Traditional rubber ³	Indonesia	c. 3	>25 (40)	D, woody, 1–10	D, 20–40	H, 96 (68), H' = 3.34
Mono albizia ⁴	Malaysia	1–2	7	D, woody, 5	P, 28	H, 75 (60), H' = 3.87, S = 0.95
Tano cedrela*	Ghana	0	24	D, woody, 5–10	D, 20–25 ¹	H, 96 (57), S = 0.83, H' = 3.82
Neung cedrela*	Ghana	0	c. 20	D, woody, 4–6	D, 20–25 ¹	H, 85 (85), S = 0.87, H' = 3.70
Rubber agroforest ⁵	Indonesia	c. 10	20–30	D, woody, 1–10	D, 20–30	M, 57 (38), H' = 3.99, S = 0.43
Mono teak ⁶	India	Adjacent	Mature	P, shrubby, 1–2	P, 16–18	M, 51 (56), H' = 2.68
Damar agroforest ⁵	Indonesia	0	<70	D, woody	D, 35–45	M, 48 (30), H' = 3.57
Mono cypress ⁷	El Salvador	Adjacent	>25	P-MD, <2, shrubs	MD, 15–35	M, 55 (41)
Young mono pine ⁸	Kenya	Adjacent	Young	P, brackens, bare	P, 12–16	M, 44 (32) ¹⁴
Durian agroforest ⁵	Indonesia	>100	<70	MD, woody	D, 30–45	M, 39 (19), H' = 3.29
Mono rubber ⁹	Malaysia	Adjacent	>15	MD, shrubs	P, 10–15	L, 44 (24)
Mature mono pine ¹⁰	Indonesia	Adjacent	c. 50	P, shrubby	P, >20	L, 21 (23)
Mature mono pine ⁸	Kenya	Adjacent	Mature	P, shrubby, 2–3	P, 20–27	L, 44 (14) ¹⁴
Mono oil palm ⁹	Malaysia	Adjacent	>15	MD, shrubs	P, <10	L, 28 (20)

Table 8. Continued.

Habitat	Country	Isolation (km)	Age (years)	Understorey (height in m)	Canopy height (m)	Conservation importance % of AS/(FS), S = similarity
Mono rubber ¹¹	Indonesia	5	8–9	P, weeding	P, c. 15	L, 40 (10), H' = 1.59
Mono rubber ¹²	Thailand	0–6	20	Virtually none	P, 10–15	L, 38
Mono oil palm ¹²	Thailand	0–6	20	P, weeding	P, c. 10	L, 38
Old mono teak ¹³	PNG	Adjacent	20	P, legumes, 0–4	P, 16–24	L, 36
Young mono teak ¹³	PNG	Adjacent	11	P, bamboo, 0–6	P, 12–15	L, 28
Mono oil palm ¹¹	Indonesia	6	Mature	P, weeding	P, c. 11	L, 25 (5), H' = 2.17

¹Some forest tree emergents up to 40–50m (>100 years old).

²Waltert (2000): *Terminalia/Triplochiton* spp. (native timber trees) in abandoned cocoa and deforested areas within a forest reserve.

³Beukema *et al.* (2007): Traditionally rubber-enriched secondary fallow, 25 years after slash-and-burn agriculture; 36% of canopy rubber trees (dbh > 0.1m), of which 66% were still being tapped.

⁴Mitra and Sheldon (1993): Thin canopy of only *Albizia falcataria* (exotic), a with rich, woody and tangled undergrowth, situated 1–2 km from circumscribed stands of primary forest.

⁵Thiollay (1995): Traditionally managed multi-species 'garden forests' that originated 150 years ago. Rubber (exotic): 30–80% *Hevea*; Durian (exotic): <70% canopy cover of mainly *Durio zibethinus*; Damar (native): Continuous canopy of 56–80% *Shorea javanica* (Dipterocarp). Plantations host at most 20–40 tree species ha⁻¹.

⁶Beehler *et al.* (1987): Sub-mature plantation with uniform canopy and thin mid-storey in a disturbed forest area.

⁷Komar (2002): 3 km² Mexican cypress situated in between montane cloud forest (25 km²) and sub-montane pine-oak forest (150 km²).

⁸Carlson (1986): *Pinus radiata* (exotic) monocultures in a matrix of cultivated fields and primary forest remnants.

⁹Peh *et al.* (2006): Large-scale mono-culture plantations on 30–35 years old forest clear-cut land, but adjacent to extensive contiguous forest areas, and interspersed with subsistence farming (open areas).

¹⁰Sodhi *et al.* (2005b): 120 ha *Pinus merkusii* native plantation in heavily degraded Java (2.3% forest left), close to 255 km² large remnant.

¹¹Danielsen and Heegaard (1995): Forest completely converted to industrial plantations with sparse undergrowth due to regular weeding.

¹²Aratrakorn *et al.* (2006): Forests completely converted to industrial plantation with sparse undergrowth.

¹³Bell (1979): Thin continuous canopy of only teak (exotic) with few epiphytes, lichens and vines. Understorey of planted *Laucaena* legume.

¹⁴Relatively high diversity of Palaearctic migrant forest species, but few or no resident forest specialists.

conservation importance indicators are species similarity (S = various kinds) and diversity (H'). The main bias in this comparison comes from whether plantations are compared to large tracts of primary forest or heavily disturbed forest fragments, in the latter case explaining why plantations can attain very high percentages of important forest species compared to already depleted 'control' sites. However, even though some of the compared parameters vary between studies, this analysis provides a useful general outline of patterns, and is at least able to discriminate between plantations with very high versus very low importance.

Since forest bird diversity is low in any non-shaded (sun) understorey-tree plantation, the crop *per se* plays a minor role for forest bird conservation (Table 7). However, in shaded understorey-tree plantations, it may be that Cardamom *Elettaria cardamomum* and Coffee are more compatible with forest bird conservation than Cocoa. If true, the superiority of Cardamom and Coffee may be related to a higher degree of co-existence of these crops with a more diverse

sub-canopy plant community, as these crops are, on the average, lower and less shady than Cocoa trees. In the rustic Ghanaian Cocoa plantation, understorey-weeding had been abolished for several years allowing dense under- and mid-storey regrowth in open canopy patches (~55%). In otherwise intensively managed rustic plantations elsewhere in Ghana, the 5–10 m high Cocoa trees inhibit most plant growth, creating sparse undergrowth dominated by ferns and herbs. The understorey avifauna of such plantations is depauperate and dominated by a few abundant forest generalists.

Table 7 compares three basic shade types for understorey-tree plantations; 1) mono-type shading by a single shade tree (e.g. *Inga* or *Gliricidia*); 2) shade provided by a semi-rustic canopy consisting of up to 60 planted tree species, and 3) rustic canopy cover of almost intact native forest. When comparing plantations across these categories, taking account of biogeographical factors, data indicate that rustic plantations are superior bird habitats compared to the two other agro-forestry systems that are similar in terms of forest bird conservation value. Hence, planting one dominant or several shade species in a mixture appears to play a minor role compared to leaving the natural canopy as shade.

Among industrial canopy-tree plantations, Oil Palm seems to provide a less suitable forest bird habitat than Rubber (Table 8), probably due to a thin-tall Rubber tree canopy that transmits enough sunlight for diverse sub-canopy plant growth. Industrial Oil Palm and Cocoa plantations form a very dense evergreen canopy that restrains a dark and poorly developed shrub layer (Peh *et al.* 2006). Although Aratrakorn *et al.* (2006) describe Oil Palm and Rubber as having similar bird communities, sallying and litter-gleaning insectivores were more abundant in Rubber. Similarly, Peh *et al.* (2006) observed bark-gleaners in Rubber but never in Oil Palm. In Ghana, Coconuts did not form a closed canopy, and as Coconut crowns transmit more light than Oil Palm, a luxuriant understorey flourished below the tall palms. Coconut palms easily attained heights of 15–20 m and co-existed with a diverse undergrowth of >10 m including several forest interior birds, e.g. Forest Robin *Stiphornis erythrothorax*, Finsch's Flycatcher-thrush *Stizorhina finschi*, *Bleda eximius* and Blue-headed Dove *Turtur brehmeri*. Marsden and Pilgrim (2003) found diverse hornbill and parrot assemblages in similar coconut agro-forests of PNG, in which four parrot species fed on the coconut flowers.

Comparing similarly managed coniferous and deciduous wood plantations suggests that mature conifers represent inferior forest bird habitats (Table 8), reflecting the depauperate understorey beneath the dense evergreen canopy (Carlson 1986, Komar 2002, Sodhi *et al.* 2005b). It appears that the choice of deciduous species is less important than the age, and hence height, of the trees (Bell 1979, Mitra and Sheldon 1993). The choice of a native versus exotic species in mono- and poly-cultures (<5 spp.) seems also to be of limited importance for forest birds, so far as plantings co-exist with a structurally and floristically diverse secondary plant community, particularly at the sub-canopy levels. In commercial oil palm and rubber plantations of Thailand, the presence of even sparse undergrowth has a significant positive impact on the forest avifauna (Aratrakorn *et al.* 2006).

Land-use management implications and future research focus

Substantial evidence from the tropics, including Ghana, emphasises that although complex plantations may serve as important avifaunal supplements or complements, they can never be a substitute for natural forest. In effect, this implies that buffer zones or corridors of appropriately managed agro-silvicultural ecosystems, identified earlier in this paper, may significantly increase the functional habitats and hence effective conservation area for many restricted range forest specialists, otherwise confined to small or heavily disturbed forests.

In the case of Ghana, I believe that such diverse agro-ecosystems may increase impoverished populations of forest specialists above the minimum viable threshold, and actually link up nearby (<5 km apart) otherwise isolated reserves currently surrounded by intensive sun Cocoa

plantations and indiscriminate slash-and-burn shifting cultivation. Future research should therefore focus on finding the optimum state of agro-silvicultural management in relation to avifaunal conservation, through cost-benefit analyses that integrate costs of weeding, pesticides and fertilizers (Fitzherbert *et al.* 2008). In particular, more information is needed on how much a secondary plant community affects crop yields and whether the optimum level of plant control can be maximized in terms of crop varieties, crop mixtures, bio-fertilizers and biological pest control. In terms of fertilizers, many rainforest trees and legumes are able to enrich leached tropical soils through mycorrhizal-mutualistic symbiosis, emphasising the need for more trees on the farm for other reasons than bird conservation.

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