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Identification of birds as biological markers along a neotropical urban–rural gradient (Cayenne, French Guiana), using co-inertia analysis

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This article examines the utility of particular bird species and guilds as bioindicators in a complex habitat mosaic, namely that of the tropical city of Cayenne (French Guyana). For this purpose, an urbanization gradient was divided up into nine classes based on 576 standard bird counts (using the point-count method) conducted in and around Cayenne between 1992 and 1995. Each point-count location was characterized by 10 habitat variables. A multiple correspondence analysis of this data set, followed by a cluster analysis, was used to establish a classification of eight habitats, according to level of anthropogenic disturbance and diversity of vegetation. 13 667 birds, belonging to 136 species, were recorded. A co-inertia analysis linking the point-counts and the 72 most common bird species and the urban–rural gradient classes showed that the bird populations were distributed along an anthropogenic gradient extending from second-growth forest to the old city center. The bird species fell into 11 trophic guilds. Six of these guilds, which had a high relative density or were homogenous in distribution, were not used in the characterization of the habitats. The large differences in relative density among the five other guilds allowed them to serve as habitat indicators. The eight dominant species were wide-ranging, and could not be used as biological markers. The co-inertia analysis brought out associations with some habitats of 64 other species. Each omnivorous marker was specific of an anthropogenic step in the gradient, while each insectivorous marker was associated with an increased diversity in vegetation structure. With an investment of just 10 sampling points, it was possible to characterize these habitats using a combination of observations on a maximum of 11 species. The Cayenne case shows a methodology to understand the relationships between environmental changes and avifaunal responses. The conclusions will be useful for the management of open spaces in growing towns along the tropical belt.

Keywords: biological markers, co-inertia analysis, neotropical avifauna, trophic guild, urban–rural gradient.

Introduction

With the growth of metropolitan areas, it is becoming increasingly important to study the ways in which urbanization influences ecosystems (McDonnell and Pickett, 1990). Birds have been found to be useful biological indicators in this respect, because they are ecologically versatile, respond to secondary changes resulting from primary causes, and can be monitored relatively inexpensively (Koskimies, 1989). Also, because of their high mobility, birds react very rapidly to changes in their habitat (Hilden, 1965; Morrison, 1986; Fuller *et al*., 1995; Louette *et al*., 1995). It is at the edges of urban areas, where the vegetation structure is highly developed and diversified (Curry, 1991; Smith and Schaefer, 1992), that relations between human and bird communities are easiest to study (Cody, 1985). In Europe and North America, both of which have a long history of urban settlement, bird colonization of urban areas took place well before ornithologists were able to record its progress. Some studies on changes in bird populations due to urbanization have, however, been carried out in the USA (Emlen,

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1974; Diamond, 1986; Dowd, 1992), Canada (Erskine, 1992; Sodhi, 1992; Edgar and Kershaw, 1994), northern Europe (Hohtola, 1978; Kalivodova and Darolova, 1995). The tropics are less well documented (Mason, 1985; Lenz, 1990).

In the tropical belt, over the last 20 years, dramatic increases in human urban populations have brought about changes in the biological balance between human and avian communities. Natural areas have become fragmented, large amounts of vegetation cleared, ponds polluted or drained, and cultivated areas replaced by slums or waste disposal sites. The maintenance or restoration of the biological integrity of urban and suburban areas must begin with a comprehensive study of the links between biota and land use, and in this context bird communities are often used in investigations of habitat changes (Koskimies, 1989). There are two main difficulties. First, that of characterizing anthropogenic gradients in urban and suburban zones where mosaics of human-made features and successional stands of vegetation are highly interlinked. Second, the characterization of bird species or guilds as biological markers: birds ability to fly makes it much easier for them than for most other taxonomic groups to exploit human-made habitats (Rolstad, 1991). With their rapid expansion, neotropical towns offer many opportunities for research, especially for birds. A key area of interest is the comparison with communities typical of closed forests (Terborgh *et al.*, 1990; Thiollay, 1986, 1990, 1994; Erard, 1992; Jullien and Thiollay, 1998).

The small town of Cayenne, in French Guyana, has a similar urban structure like many other former colonial towns around the world: it was first situated on a peninsula then it increased on the nearby primary forest. An increasing human population has resulted in a pattern of habitat and environmental modifications across a wide range of conditions (Clergeau *et al.*, 1998). Cayenne covers an area of less than 2000 ha, and is considered in this study like an experimental station where relationships between avifauna and environmental conditions could be followed accurately with only one observer using suitable methodology and analysis.

The first object of the present study was to standardize the classification of bird observation stations in an urban–rural gradient, with regard to both anthropogenic and biotic variables by the way of a co-inertia analysis. The second was to establish the conditions in which bird species and guilds were associated with particular classes of habitat, and their potential utility as biological markers. Bird data reflect habitat changes, the analysis identifies the most important factors that can cause changes in bird population and bird species or guilds which are more suitable to represent these changes.

We used co-inertia analysis in this study (Dolédec and Chessel, 1994; Chessel and Mercier, 1993). This is a multivariate analysis method which, like Canonical Correspondence Analysis (Ter Braak, 1986), can be used to study relationships between species distributions and environmental variables. Co-inertia analysis is used to combine the two types of analysis, and to determine the relationships between species distributions and environmental parameters. It extends the analysis of ecological profiles, which deals with species presence-absence tables, to species distribution tables. It has already been used in various other domains, including chemometry (Devillers and Chessel, 1995), phytopathology (Lamouroux *et al.*, 1995), hydrobiology (Dolédec and Chessel, 1994; Castella and Speight, 1996), limnology (Verneaux *et al.*, 1995), phyto-ecology (Bornette *et al.*, 1994), nematology (Cadet *et al.*, 1994), and molecular biology (Thioulouse and Lobry, 1995).

Study area and methods

Study site

Cayenne (4°56′ N, 52°20′ W) has the Atlantic ocean to the north, two large rivers, the Cayenne and the Mahury, to the east and west, and marshes to the south (Figure 1). Precipitation is approximately 3000 mm a year. The study covered an area of 1924 ha. The human population was 37 647 in 1982, and 40 993 in 1990. The annual increase in human population is only about 1%, but it varies from place to place (showing either increases, decreases or stability) within the city itself and its surroundings. Habitats vary from highly urbanized areas in the old city center to patches of old secondary

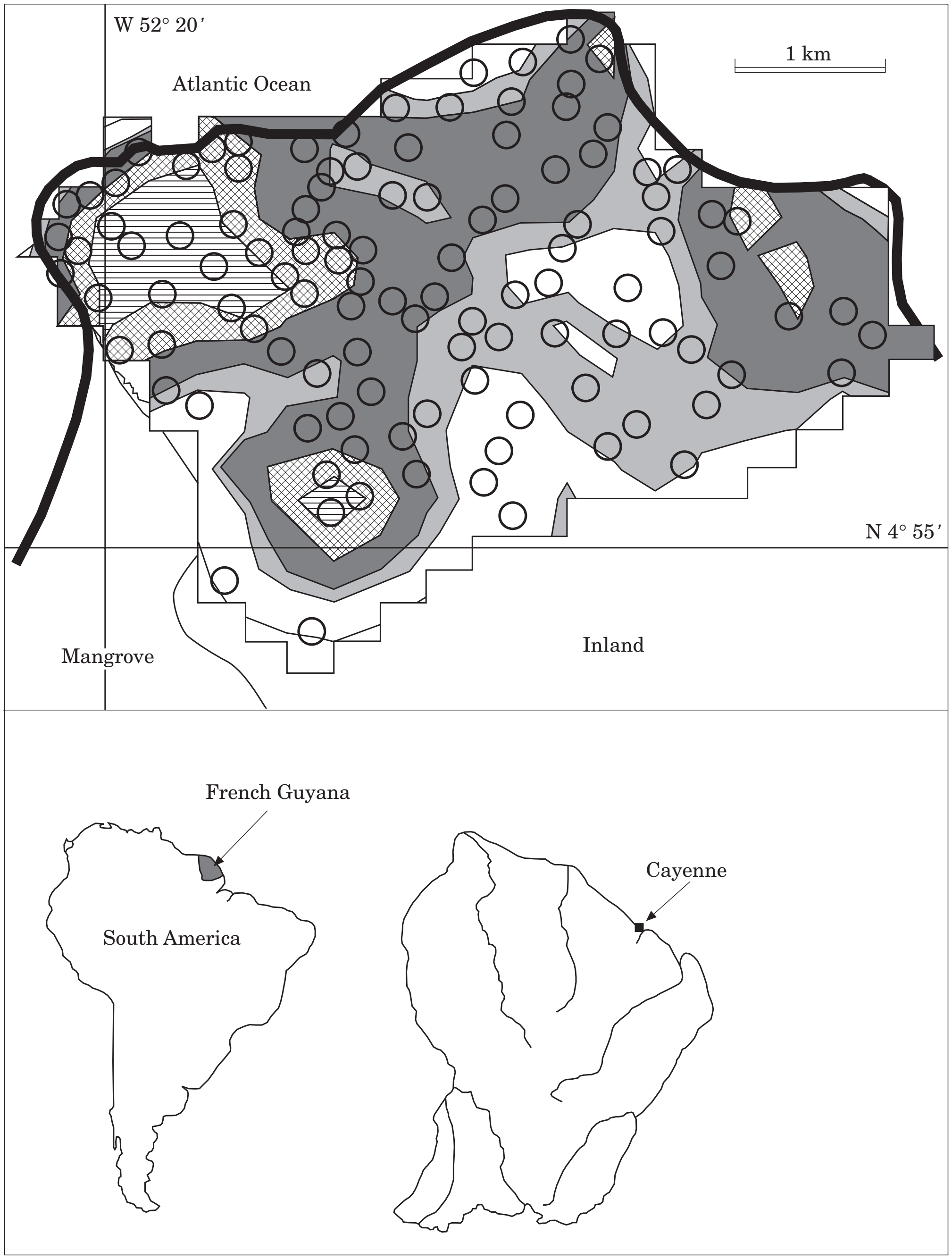

Figure 1. Map of the study area. Circles indicate survey stations. Land-use patterns are shown by the five classes of building coverage pictures, with contour lines (Thioulouse *et al*., 1995). Percentage of building coverage: 0–10, □; 10–25, ░; 25–35, ▓; 35–50; ■; +50, □.

forest, typical of a continuous increase of urbanization at the expense of primary forest.

Landscape gradient

Cayenne was built around a small fortress on the coast. A concentric ring of small cottages was surrounded by farms dotted along the freshwater channels in areas which had once contained primary and riparian forests. Since 1970, this structure has been altered by rapid increases in human population (Reynaud, 1995), and the need for more living space (Figure 1). Most of the farms have now disappeared and been replaced by residential or commercial buildings, or have gone fallow and been covered by impenetrable vines, though there are many cases where traditional cottages and farms still exist side-by-side. Within the town, residential areas compete with patches of secondary forest, mainly on rocky hills and in seasonally waterlogged hollows. Ruined houses are numerous in the downtown district. This mix of old and new development has resulted in a mosaic of habitats (Wiens, 1994). Soil cover is differentiated, as has been shown by aerial pictures and Landsat satellite imagery (Loïal, 1993).

The survey stations were initially chosen according to a single parameter, namely the annual increase in the human population between 1982 and 1990 (IP). This parameter was easy to calculate using data collected in the 1982 and 1990 population censuses (Reynaud, 1995). The 115 stations were distributed symmetrically on either side of the zero annual increase line. A decline in the human population (as much as −10% a year) had occurred in slums and in some old ex-colonial areas, but had been compensated for by a marked increase (as much as 12% a year) in that of the countryside, and also that of some areas on the outskirts of the town where there were apartment blocks. Between these two extremes there was a suburban zone which had already reached a relative degree of stability, due mainly, though only over the latter 5 years, to human population equilibrium and a fast-growing residential zone.

Environmental data set

Each survey station was characterized by a combination of 10 qualitative variables, each with five categories concerning the main differences in vegetation (de Granville, 1992), the level of anthropogeny, and their distance from fresh water and the ocean. These data were used to carry out a multiple correspondence analysis (MCA) as a way of categorizing the urban–rural gradient which was used to determine bird distributions.

These 10 descriptive variables of landscape structure are: AN, structural features of increasing urbanization: from old secondary forest (1) to high concentrations of office buildings downtown (5); HU, human activities: population density and noise, from quiet footpaths (1) to busy shopping streets (5); UD, understory density: from an absence of understory (1) to impenetrable vines (5); IP, level of annual variation in human population between 1982 and 1990: −10% to −3% (1) up to 7% or more (5); CS, size of trees: the top of the canopy is at a height of between 5 m (1) and more than 20 m (5); TC, percentage of tree coverage: the canopy covers between less than 10% (1) and 50% or more (5); GC, percentage of grass coverage: between less than 20% (1) and 60% or more (5); BC, percentage of building coverage: between less than 10% (1) and 50% or more (5); FW, distance from fresh water: between less than 5 m (1) and more than 1000 m (5); SW, distance from sea water: between less than 200 m (1) and more than 2100 m (5).

Because of rapid population growth, each survey station was reclassified for each new observation.

Census technique

To carry out a census of the birds in Cayenne meant finding places that were of adequate size, and also quiet enough not to disturb the birds: most of the species in question are secretive, live in dense vegetation or the high canopy, and have short singing periods. To cover a large number of habitats, and to limit bias resulting from varying detectabilities, a fixed-radius point-count method was used (Blondel, 1975; Blondel *et al.*, 1970). We used a car to go to each station, it was regard as the central point.

We used 10 × 42 binoculars to identify species up to 25 m away to the right and left at the central point; the average area of observation was 0·10 ha. Birds singing or hunting at heights of up to 25 m, nesting, or crossing the observation volume, were counted. 576 point-counts of 20 min each were carried out for 115 survey stations, in fine weather, between 6:30 am and 10:00 am, between February 1992 and May 1995.

Statistical analysis

The Shannon-Weaver diversity index H′ gives a measure of the richness and relative density of a species (Frontier and Pichod-Viale, 1991). The index of similarity between habitats is given by $IE = (2A - B - C) \times 50/A$, where A is the number of species in a given habitat, B the number of species in a second habitat, and C the number of species in common between the two habitats (Camargo, 1992). Values of IE go from 0 to 100. A low value of IE means that there is a high degree of similarity between populations occupying two different habitats, and *vice versa* (Ferry, 1976).

The theory behind the co-inertia analysis is based on Tucker's inter-battery analysis (1958), which determines the relationship between two quantitative matrices (i.e. between two principal component analyses). It has been extended to two other kinds of data, i.e. contingency tables and qualitative variable tables, by Dolédec and Chessel (1994), and Chessel and Mercier (1993). Here, we applied it to the analysis of species abundances and qualitative environment variables. A correspondence analysis was performed on the first table, and an MCA on the second. A cluster analysis of the first two factors in the MCA was used to classify sampling sites in the urban–rural gradient. In the co-inertia analysis, each class in the gradient was positioned at the mean of the point-counts that constituted the class.

Computations and graphical displays were carried out using the ADE-4 statistical software package, available free at: http://pbil.univ-lyon1.fr/ADE-4/ (Thioulouse *et al*., 1995, 1997).

Results

Habitat classification

The 576 point-counts were analyzed by MCA for the 10 descriptive variables of landscape structure (Figure 2(a)). Changes in the level of anthropization (AN) and of human activity (HU), correlated positively with axis 1, while the annual rate of increase of the human population (IP), the density of understory (UD) and the tree coverage (TC) correlated negatively with this axis. Axis 2 mainly expresses either two (AN, UD, BC, IP) or three (HU, FW, SW) classes of variables, and illustrates the complexity of the landscape description (CS, GC). The eigenvalues diagram (Figure 2(b)) shows that these first two axes covered 63% of the data structure. Eight point-count classes were defined by a Cluster Analysis (UPGMA method) on the first two MCA factor scores (Figure 2(b)). These classes are as follows:

- 'secondary forest' (SEC): old secondary forest with a predominance of *Protium heptaphyllum*, Rubiaceae and Marantaceae, some residual primary-forest trees (*Carapa guianensis*), and more or less open understory;
- 'cottage clearing' (MOS): mosaics of cottages with ornamental gardens surrounded by secondary forest bordered by waterlogged clearings covered with Malpighiaceae and *Attalea* sp., close to freshwater ponds or riparian strip corridors, 10 m to 50 m wide, with Clusiaceae, *Philodendron acutanum* and Rhizophora mangle;
- 'dense bush' (OFA): old re-growth stage after total deforestation, surrounded by patches of secondary forest (*Cecropia* sp.). The dominant vegetation here is *Casearia rusbyana, Vismia latifolia, Miconia fragilis*, and *Sapium paucinervium*; and there is dense bush 2–4 m high, entangled with vines: a combination of Convolvulacea, Passifloracea and Vitacea;
- 'mimosa clearing' (CLE): clear-cuts covered with Mimosaceae (*Mimosa pigra, Mimosa pudica*), and some remaining large trees;
- 'small farms' (FAR): traditional farming, fruit trees: banana trees, *Mangifera indica, Averrhoa carambola, Spondias monbin, Carica papaya, Chrysobalanus icaco*, quickset hedges with fruit vine (*Pasiflora* sp.), and old anthropic vegetation, running wild;
- 'parks and gardens' (GAR): parks, stadia and cemeteries around the city: introduced trees (*Casuarina* sp. *Eucalyptus* sp.), lawn (*Panicum* sp.), and quickset hedges;
- 'center-city old houses' (DTH): downtown ruined houses with small enclosed courtyards containing creepers and old fruit trees (e.g. *M. indica, Anacardia* sp., *Terminalia catapa*);
- 'downtown gardens' (DTG): lawn and palm trees (*Mauritia flexuosa*) surrounded by office buildings.

Axis 1 expresses the anthropization process: from undisturbed areas (negative values of SEC, OFA) to highly anthropized, built-up areas (DTG, DTH, GAR). Axis 2 expresses the diversity of the vegetation: the higher mosaic of habitats, hence that of food sources and

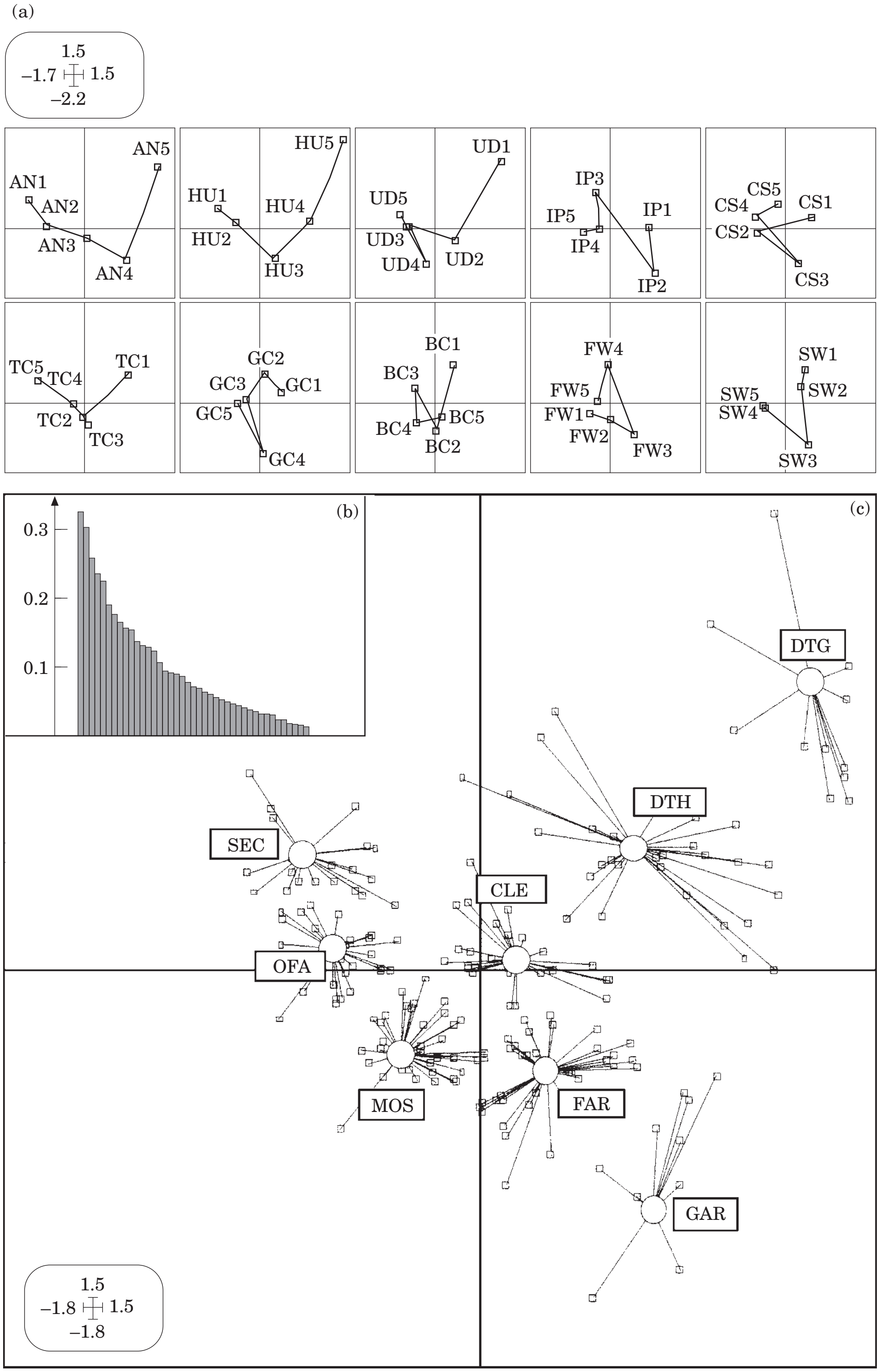

Figure 2. (a) Multiple Correspondence Analysis on the 10 qualitative variables that describe the landscape; (b) eigenvalues; AN, urbanization; HU, human activities; UD, understory density; IP, annual variation in human population; CS, size of trees; TC, % tree coverage; GC, % grass coverage; BC, % building coverage; FW, distance from fresh water; SW, distance from sea water. (c) groups formed by the Cluster Analysis on the first two factor scores: secondary forest (SEC); cottage clearing (MOS); dense bush (OFA); mimosa clearing (CLE); small farms (FAR); parks and gardens (GAR); center-city old houses (DTH); downtown gardens (DTG). Axis 1 represent the urbanization gradient, axis 2 the vegetation gradient.

nesting supplies (negative values of MOS, FAR, GAR), and the zones with the lowest diversity (positive values of DTG, SEC, DTH, CLE).

Avifauna data analysis

The 576 point-counts gave 13 667 birds of 136 species and 30 families. Table 1 summarizes the comparative structures of the avifauna in each of the urban–rural gradient classes.

To find out if the number of point-counts was large enough for the urban–rural gradient class, in each case, and if interspecies comparisons could be carried out for the different classes, we considered the slope of the curves of the cumulative number of birds, for each species. These slopes mean the lack to reach the total richness. This was calculated for the difference between the last point (e.g. for DTG: $S_{\mathrm{n}}=x=44, y=31$) and the last but one, $S_{\mathrm{n}-1}$, so that $S_{\mathrm{n}-1}-S_{\mathrm{n}}=a/N$, where a is the number of species of frequency 1, N the number of point-counts, and a/N the probability of recording a new species in an additional sample plot. An a:N ratio of 1:10 means that ten more point-counts will be needed to find a new species (Ferry, 1976). As a/N increases, the number of point-counts needed to find a new species decreases. The expected species richness was assessed by a Jackknife estimate, so that $SA=\Sigma O(\mathrm{i})+\{N-1/N\}K$, where K is the total number of species recorded in just one point-count (Baltanas, 1992).

The number of observations for a given gradient class showed no particular relationship with either the Jackknife estimate of richness or the a/N values. The lowest class (downtown gardens, with 44 observations) reached a high level of observed richness compared to the maximum level (81%). The higher class (cottage clearing, with 100 observations) reached a level of 89%, but more observations in downtown gardens were required to find a new species, although just three more observations were enough to find a new species in cottage clearing areas. The relationship between the number of observations and the degree of richness was less important than the specificity of the habitat.

The avifauna diversity index was highest in cottage clearing areas, being 1·5–11% higher than in the other classes, except for the downtown gardens areas (31%). With regard to both richness and equitability, downtown gardens areas had a low level of habitat resources. The 10 most abundant species included 79% of the birds recorded, compared with 53–57% in the other habitats. The equitability index was higher in open habitats (parks and gardens, mimosa clearing) than in high-richness classes (small farms, dense bush), but this difference (2–3·5%) was too small to be significant.

The class of the urban–rural gradient whose avifauna composition (Table 2) was most similar to that of the other classes was traditional farming (FAR), a habitat that is highly attractive to many bird species because of the diversity of food sources, and of perching and nesting sites. The avifauna composition of the center-city old houses (DTH) was very close (IE = 15) to that of clear-cuts after total deforestation (mimosa clearing), which meant that most of the former bird species had disappeared and

Table 1. Bird-community structure for the different classes of urban–rural gradient

Gradient classes	DTG	DTH	GAR	FAR	CLE	OFA	MOS	SEC
N	44	80	46	88	59	87	100	72
$O_{(i)}$	31	64	46	78	63	78	91	80
Mean richness/point-count	16·8	23	28·5	22	24	25·7	23	26
Jacknife estimate of Richness	38	75	59	90	75	90	103	94
a	5	16	9	25	22	22	28	22
a/N	0·11	0·20	0·20	0·28	0·37	0·25	0·28	0·31
Species diversity index: H’	3·530	4·643	4·543	4·979	4·874	4·998	5·067	4·939
Species equitability index: E	0·712	0·771	0·818	0·790	0·812	0·795	0·777	0·779
Ten most abundant species (%)	79	63	61	55	56	53	56	57

(Left to right) in Cayenne: DTG, downtown gardens; DTH, old house gardens; GAR, parks and stadia; FAR, traditional farming; CLE, mimosa clearing; OFA, old fallows; MOS, mosaics of cottages and riparian corridors; SEC, secondary forest. N, number of observations; $O_{(i)}$, number of species; *a*, number of species of frequency = 1.

Table 2. Similarity of the avifauna structure along the urban–rural gradient (left to right) in Cayenne

	DTH	GAR	FAR	CLE	OFA	MOS	SEC
DTG	55	41	63	54	63	68	65
DTH		35	28	15	26	35	31
GAR			45	34	45	52	45
FAR				26	13	20	17
CLE					27	36	32
OFA						21	20
MOS							23

been replaced by more ubiquitous species. Downtown gardens (DTG) and anthropized features (parks and gardens) were the classes which were least similar to the others.

As the main purpose of this study was to identify the bird species that could serve as markers for the urban–rural gradient classes, the bird species were divided up into four categories, according to relative frequency and density (see the Appendix): dominant species (nine species: frequency above 45%, relative density above 3·5%); accessory species (23 species: frequency between 45 and 5%, relative density between 3·5 and 1%); incidental species (40 species: frequency between 5 and 1%, relative density between 1 and 0·07%); and 64 other species which were considered as vagrants. Further analysis was performed on the first three categories (72 species).

Co-inertia analysis

The results of the co-inertia analysis for the descriptive variables of landscape structure (Figure 3(a)) show the effect of anthropization on axis 1 (AN, HU, UD), and the distance from the ocean (SW). Axis 2 shows a decrease in grass coverage (GC), and an increase in tree coverage (TC), i.e. the contrast between open and closed habitats. The distribution of high trees (CS), which dominate the landscape here and there, and the distance from fresh water (FW), are not easy to explain.

The urban–rural gradient classes (Figure 3(b)) shows the importance of axis 1: there is an opposition between, on the one hand, classes DTG, DTH, GAR and CLE, which describe highly anthropized areas, and, on the other hand, classes FAR, MOS, OFA and SEC, which correspond to a lesser degree of anthropization. Axis 2 distinguishes areas characterized mainly by SEC (i.e. secondary forest with a dense canopy) from GAR and CLE (i.e. open lawn with sparse introduced trees), which are representative of totally-anthropized vegetation.

The results of the co-inertia analysis (Figure 4(a)) shows, on axis 1, the opposition between species living in quiet, wild habitats, and species adapted to the city and to vegetation close to the seaside. On axis 2, the opposition is between species living in open country close to fresh water and understory species. The map of the classes with respect to the distribution of species clearly shows the urban–rural gradient (Figure 4(b)).

The maps in Figure 5 illustrate the distribution of the species given in Figure 4(a), in terms of their membership of trophic guilds. It can be seen that the species are clustered into 11 trophic guilds, according to food type (Terborgh *et al*., 1990; Thiollay, 1986; Blake and Loiselle, 1991; Table 3). Species belonging to a given guild are not often associated with just one particular habitat, though it is true that the water birds (WA) are dependent on the vicinity of fresh water, and the bark-dwelling insectivores (IB) on the high canopy (CS4-5). The distribution of species follows axis 1 (the urban–rural gradient) for granivores (GR), aerial insectivores (IE), nectarivores (NI), and raptors (RP). Frugivores (FR), sallying insectivores (IA) and terrestrial insectivores (IT) are related to the understory-open country gradient. Omnivores are ubiquitous in their distribution.

Steps of birds selection as biological markers

An initial trial using the eight dominant species (52% of the total number of birds) gave disappointing results (Table 4). All the

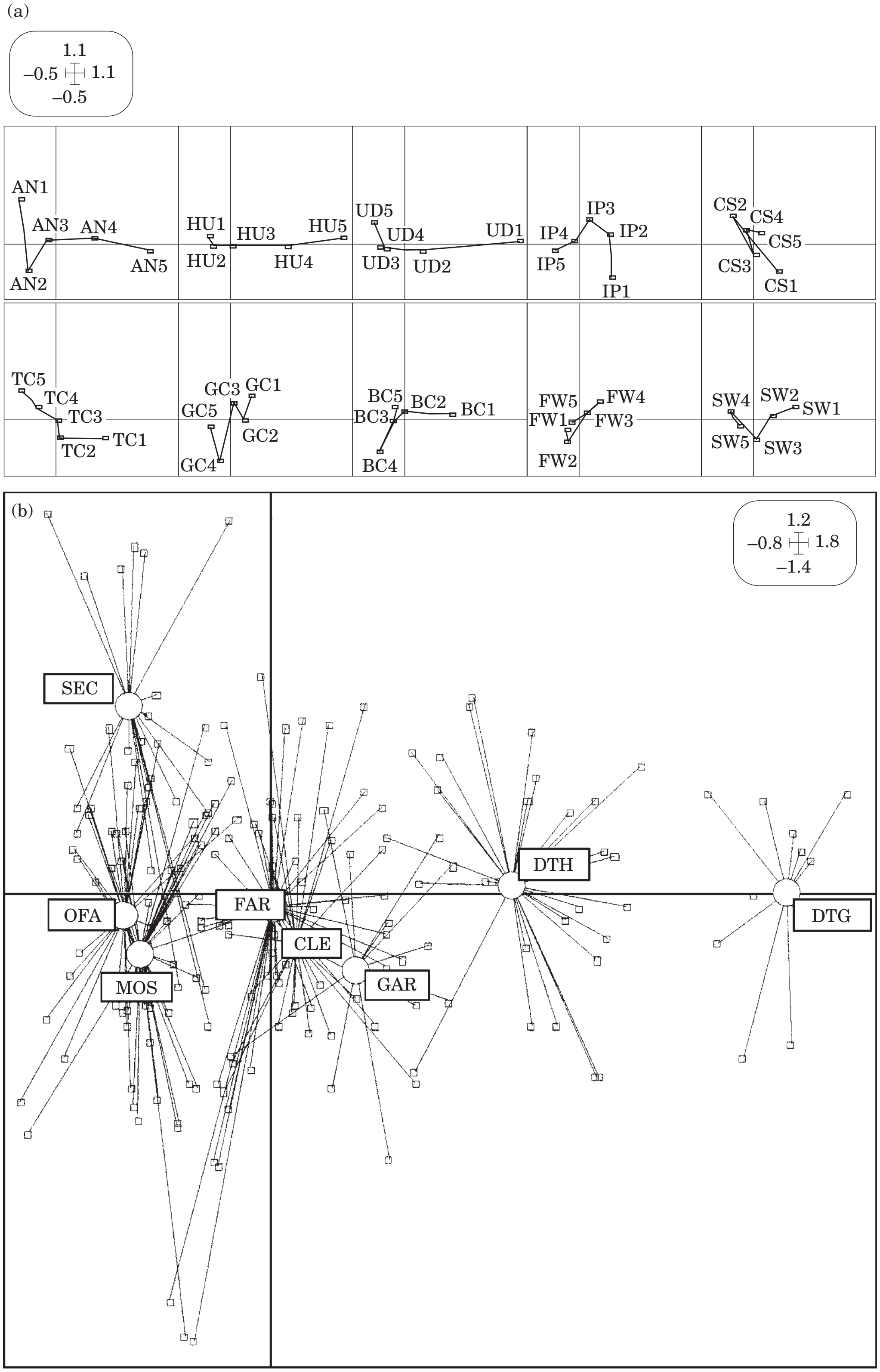

Figure 3. First factor map of the co-inertia analysis for the landscape variables. (a) Factor map of variables (identified by two-letter codes); (b) factor map of the urban–rural gradient classes. See the text for axis definition.

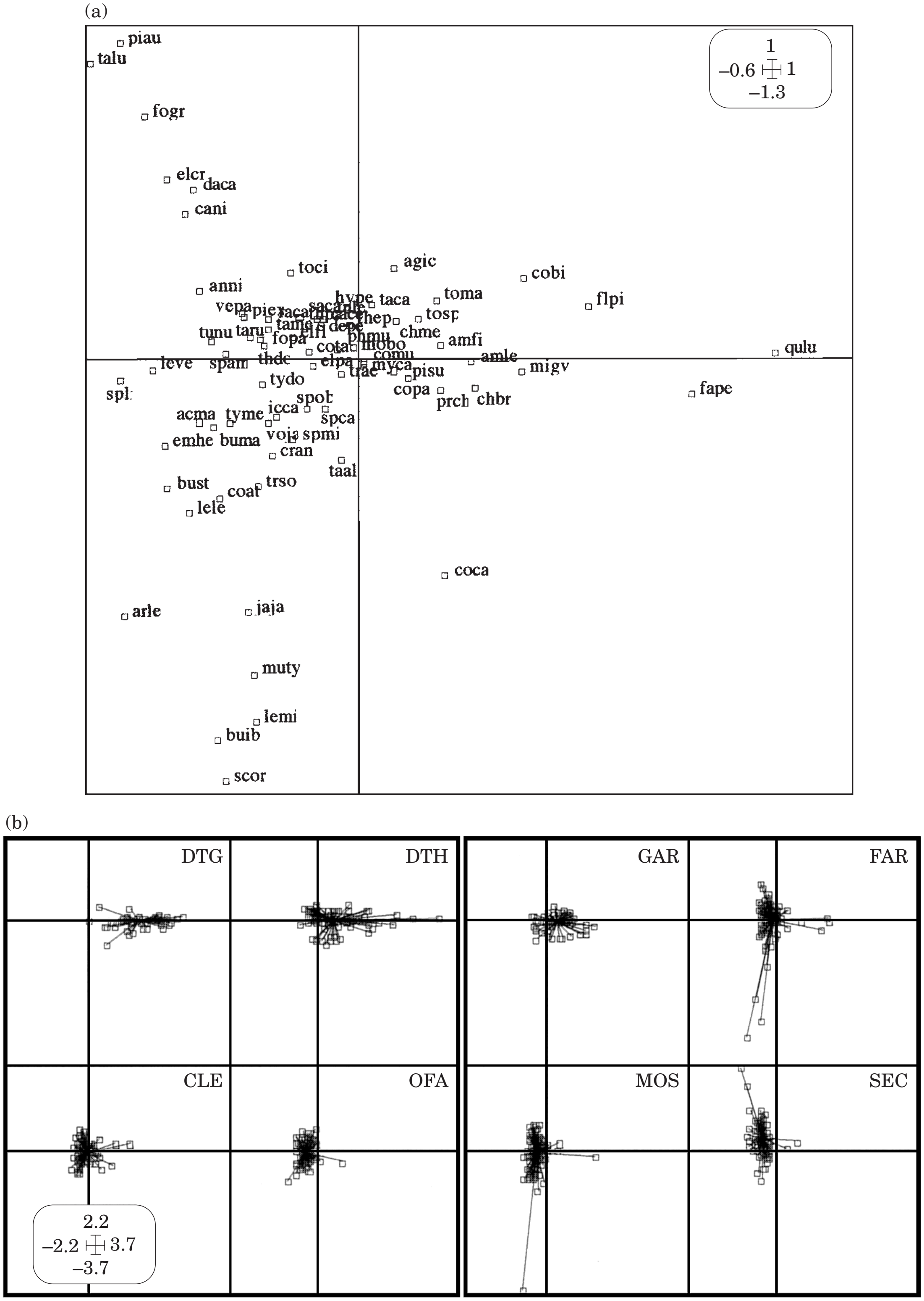

Figure 4. First factor map of the co-inertia analysis for the different bird species. (a) Factor map of the species (identified by four-letter codes; see the Appendix for the full names); (b) factor map of the urban–rural gradient classes (axis as in Figure 2).

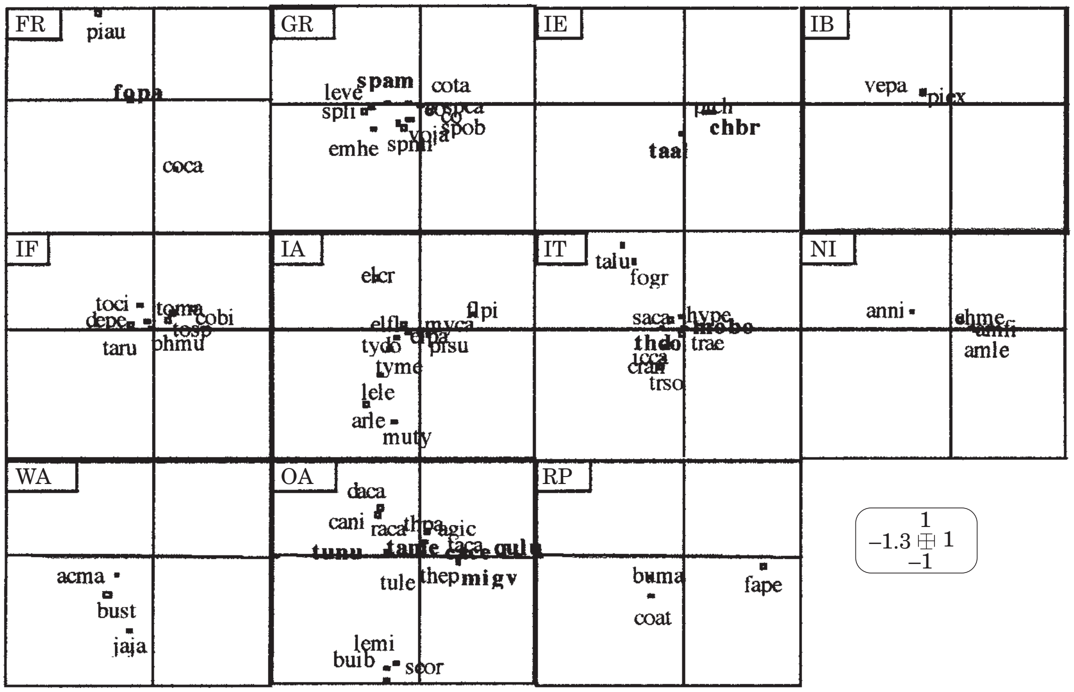

Figure 5. First factor map of the co-inertia analysis for the different bird species. Bird species of a given guild are grouped together, with guilds and birds markers in bold characters (see Table 3 for guild abbreviations and definitions, and the Appendix for the full names of bird species).

Table 3. Definition of the trophic guilds and distribution of the bird species in Cayenne

Definition	abbr.	Total no. of species	No. of main species
Frugivores (manakins, parrotlets)	FR	7	3
Arboreal, terrestrial and grass granivores (finches, ground-doves)	GR	15	10
Aerial insectivores (swallows and swifts)	IE	9	3
Bark-dwelling insectivores feeding in trunk interior (woodpeckers) or superficially (woodcreepers)	IB	6	1
Arboreal, gleaning insectivores (tody-flycatchers, tyrannulets)	IF	24	7
Arboreal, sallying insectivores (species that hawk, hover, snatch or strike: becards, tyrants)	IA	20	11
Gleaning terrestrial and ant-following insectivores (wrens, antbirds)	IT	15	10
Nectarivore-insectivores (hummingbirds, honeycreepers)	NI	6	4
Waterbirds (sandpipers, jacanas, herons)	WA	7	3
Predominant omnivores (icterids, thrushes, tanagers)	OA	17	16
Raptors (hawks, falcons, vultures)	RP	11	3

species were found in each class during the first 10 point-counts, and were thus taken into account only if some drastic upheaveal (e.g. major pollution, or climatic change) occurred in the urban–rural gradient during the study period.

Screening was then carried out on the accessory species, some of which were also ubiquitous; e.g. among the granivores, *Sporophila castaneiventris, Columbina minuta, Columbina passerina*, and *Columbina talpacoti*. We selected 11 species which, on account of their relatively high density and ease of detectability, were used as biological markers of the urban–rural gradient (Table 5). In the omnivore guild, for example, the dominant feather pattern was: black for *Quiscalus lugubris*; light gray for *Mimus gilvus*; browner for *Turdus nudigenis*; cobalt-blue for *Tangara mexicana* and black and golden-yellow for *Cacicus cela*. They were found along the urban–rural gradient in the

Table 4. Distribution of the dominant species along the urban–rural gradient: minimum number of point-counts required to find a bird of a particular species in a given habitat

Species	Abbr.	Guilds	Relative density (%)	Frequency %	DTG	DTH	GAR	FAR	CLE	OFA	MOS	SEC
Thraupis episcopus	thep	OA	9·20	80	1	1	1	1	1	1	1	1
Pitangus sulphuratus	pisu	AN	8·25	88	1	1	1	1	1	1	1	1
Thraupis palmarum	thpa	OA	6·11	61	1	1	1	1	1	1	1	1
Troglodytes aedon	trae	IT	5·38	69	2	1	1	1	1	1	1	1
Phaeomyias murina	phmu	IF	5·36	64	2	1	1	1	1	1	1	1
Turdus leucomelas	tule	OA	5·09	58	2	1	1	1	1	1	1	1
Elaenia flavogaster	elfl	AN	4·79	61	3	1	1	1	1	1	1	1
Progne chalybae	prch	IE	3·94	45	1	1	2	1	1	1	1	1
Myozetetes cayannensis	myca	AN	3·51	45	4	1	1	1	1	1	1	2

Table 5. Distribution of species markers among the habitat classes: minimum number of point-counts required to find a bird of a particular species in a given class in the urban–rural gradient in Cayenne

Species	Abbr.	Guilds	Total no.	Frequency (%)	Point-counts per habitat							
					DTG	DTH	GAR	FAR	CLE	OFA	MOS	SEC
Forpus passerinus	fopa	FR	204	15	n	3	8	6	4	1	3	2
Sporophila americana	spam	GR	90	9	n	27	9	6	10	3	9	4
Chaetura brachyura	chbr	IE	125	11	2	6	2	3	12	5	7	18
Tachycineta albiventer	taal	IE	88	9	6	5	12	6	10	4	7	14
Thamnophilus doliatus	thdo	IT	145	17	22	20	5	3	3	4	3	2
Molothrus bonariensis	mobo	IT	79	2	n	7	n	n	2	5	6	14
Quiscalus lugubris	qulu	OA	792	26	1	1	1	3	1	10	7	10
Mimus gilvus	migv	OA	126	13	6	2	2	8	3	15	9	24
Cacicus cela	cace	OA	101	5	n	3	12	22	n	12	2	14
Tangara mexicana	tame	OA	82	7	n	13	n	9	6	4	4	8
Turdus nudigenis	tunu	OA	79	10	n	80	7	6	20	5	4	5

n, never seen in the given class.

following order: qulu, migv, cace, tame, tunu (Figure 5(a)). Table 6 can be given either a vertical or a horizontal reading. The vertical reading is associated with the investment that may be needed to differentiate between two given habitats. With 10 point-counts, each of the 11 species was found along the banks of freshwater channels (MOS), but at different densities; in the secondary forest, one *C. cela* was found in every 14 point-counts, whereas it took 24 point-counts to find a *M. gilvus*, but only two to find a *Thamnophilus doliatus*. In downtown garden areas, the chances of finding *C. cela* were slim; on the other hand, it took six point-counts to find a *M. gilvus*, and 22 for a *T. doliatus*. Each omnivore marker was specific to a given anthropization step, while each insectivorous marker was associated with a particular type of vegetation structure (Figure 5).

The horizontal reading shows the probability of a given species being associated with a given habitat. For the five omnivorous species, with 10 point-counts it was impossible to find a *M. bonariensis* or a *M. gilvus* in SEC, *Turdus nudigenis* in DTG, DTH or CLE, *C. cela* in DTG, GAR, CLE or FAR, and *T. mexicana* in DTG, DTH or GAR. With an investment of only five point-counts for each class, the observation of the first five species shown in Table 5 was enough to characterize the classes as a whole.

As regards bird knowledge and investment cost, the characterization of the degree of anthropization was feasible for five guilds

Table 6. Minimum number of point-counts required to observe a bird of a particular guild

Guilds		DTG	DTH	GAR	FAR	CLE	OFA	MOS	SEC
Frugivores	FR	22	2	8	4	3	1	3	1
Granivores	GR	1	1	1	1	1	1	1	1
Aerial insectivores	IE	1	1	1	1	1	1	1	1
Bark-dwelling insectivores	IB	N	10	9	18	7	12	10	5
Gleaning insectivores	IF	N	8	8	4	12	11	8	2
Sallying insectivores	IA	1	1	1	1	1	1	1	1
Terrestrial insectivores	IT	1	1	1	1	1	1	1	1
Nectarivores	NI	1	1	3	1	2	2	1	2
Waterbirds	WA	N	40	9	15	59	15	4	18
Omnivores	OA	1	1	1	1	1	1	1	1
Raptors	RP	22	7	N	11	12	4	10	24

A sighting of an individual bird of a particular guild in four observations (120 mn) signifies a relative density of 1%. Possible marker are shown in bold.

of low relative density (using interguild markers), and also for five guilds of high density if marker species of medium relative density (interspecies markers) were taken into consideration. At the species level, five point-counts were enough to obtain the set of markers of the habitat classes. And it might be noted that interspecies markers are preferable to interguild markers in terms of accurancy and ease of interpretation.

Discussion

The study of urban–rural gradients provides a context in which human activities must be taken into consideration as crucial components of ecological systems. The interaction between anthropogenic and natural variables means that urban–rural gradients are complex, and our choice of variables for the location of survey stations took this fact into account. In our data, there are four variables that relate to human activities: AN, HU, IP and BC. MCA was used to classifiy the habitats into eight classes, and the co-inertia analysis brought out the main relationships and differences between these classes. Distinctions between classes were due more to human impact on the original landscape than to the diversification of the landscape itself. Day-to-day human activities and understory density are the main components of axis 1 (Figure 3(a)). The distribution of bird species was firstly related to the anthropization gradient (Figure 4(b)), but many species were mainly associated with the understory–open country gradient.

To assess the value of birds as biological markers along the urban–rural gradient, we first took into account the least costly sampling level (the density-dependent effect). The assumption is that the study of guilds is less time-consuming than that of species. The analysis of the avian response guilds showed which groups of species were most sensitive to habitat perturbations, and which benefited from, or at least were not affected by, environmental disturbance. This analysis, carried out either individually or in combinations, reflected the patterns of disturbance of the landscape.

Six guilds were ubiquitous: in other words, a bird belonging to one of these guilds was seen in a maximum of three point-counts in each habitat (Table 6). There are two possible explanations for this. The first is that the guilds contained many species which exist at high density, each bound to a particular group of habitat classes: e.g. among the omnivores, *Q. lugubris* in downtown areas (35% of the birds being found in DTG, and 16% in DTH), *M. bonariensis* in new clear-cuts, and *C. cela* in old fallow areas (OFA). The second is that there was only one ubiquitous species, for the nectarivores, i.e. *Amazilia fimbriata*, which was found in 39% of the samples, and accounted for 77% of all nectarivores. The five guilds that were most sensitive to anthropogenic disturbance were also among those that had specific habitat requirements; they provided most of the information that was used for characterizing the urban–rural gradient classes (in bold characters in Table 6).

The only easy way of differentiating between downtown gardens and other habitats is to utilize the fact that no bird belonging to any of the indicator guilds was seen in the course of 20 observations (400 min). Frugivores were less abundant in parks and stadia than in old house gardens, due to the fact that the fruit resources were lower there, but bark-dwelling insectivores were more numerous in parks and stadia than in old house gardens, and therefore also in traditional farming areas, because the density of mature trees was higher. Water birds were able to be used as markers for two habitats—the riparian corridors, and the parks and stadia—because they often forage in waterlogged lawns. They were not present in downtown parks because of the high level of disturbance—gleaning insectivores need patches of dense understory such as is found in the remote secondary forest areas, whereas species such as *Troglodytes aena* are well acclimatized to anthropic vegetation, which is why they are numerous in old house gardens, parks and stadia, and traditional farming areas. The raptor guild includes the scavengers, which are numerous downtown, but some raptors remain at the edge of the forest (Jullien, 1992) and hunt in less disturbed areas which provide them with rodents and chickens (Traditional farming, Mimosa clearing) or reptiles (Riparian corridors). The 10 point-counts in each of the urban–rural gradient classes proved to be enough to characterize the habitats of these five guilds. With 10 point-counts, for instance, frugivores were not found in downtown gardens, but were found in all the other habitats, with diverse efforts: for secondary forest areas and old fallows, in every point-count; for riparian corridors and mimosa clearing, in one in three point-counts; but for traditional farming areas, in only one in eight point-counts. For habitats with 10 point-counts, gleaning insectivores and raptors were found in old house gardens, water birds in parks and stadia, gleaning insectivores alone in traditional farming areas, bark-dwelling insectivores in mimosa clearing, raptors in old fallows, water birds and raptors in riparian corridors, and gleaning and bark-dwelling insectivores in secondary forest. At the level of 10 point-counts per class, there were species of high relative density that could also be used as markers, given that each habitat possessed a characteristic bird population composed of specialists, generalists and incidental species.

For breeding birds in sagebrush steppe areas, species richness and dominance showed little overlap between values for the extremes of impact class, and thus had some potential as indicators of biological integrity (Bradford *et al.*, 1998). The fact that some species were more easily detectable than others, and that there was no assumption of random sampling, meant that no comparison between species could be made (Blake and Karr, 1987). Priority had to be given to the most easily detectable species if the observation cost was to be as low as possible; comparisons were established, for these same species, between the different habitats.

Lawton *et al.* (1998), in their general study on indicator taxa, show that it takes an average of 50 scientist-hours to sample, sort, and identify a bird species, compared with 150 for a butterfly species, and 2000 for a termite species. In the present study, the number of scientist hours was between 2 and 10, depending of the degree of accuracy aimed at; and it took 33 scientist hours (100 point-counts) to record more than 80% of the species in a given habitat type.

Ecosystem structure and function along urban–rural gradients are currently being studied by a number of researchers (see, for example, McDonnell and Pickett, 1990). The present study shows that it is possible to use small bird assemblages as indicators of anthropization levels; the fact that, in the different habitat classes, the number of bird species varied between 31 and 91, with a total of 136 species, suggests that the method could be used for identifying indicator species in forested areas such as those found in Europe (Lescourret and Genard, 1994), the USA (Turchi *et al.*, 1995), and in rain forests (Reynaud, 1998). As the number of species decreases, it becomes more difficult to distinguish between different habitat classes (Bradford *et al.*, 1998).

The integration of this intensive small-scale habitat selection study and an extensive study of bird population changes is very fruitful for predicting and interpreting the impacts of different land-use practice on wildlife, and in management decision-making processes. First, the methodology proposed for the identification of the habitats of small bird assemblages that can serve as bioindicators is not complex, and requires little ornithological skill to put into practice, given that the indicator species are not numerous and are easy to observe. Second, the constitution of a mosaic of habitats comprising nine classes meant that areas of high species richness were easy to identify. These habitats were at the edge of the largest urbanized area under study, but, like the cottage garden areas and riparian corridors, they formed a fine tissue with high biodiversity, whose equilibrium was fragile because the disturbance factors associated with residential development outweighed the habitat value of ornamental yard planting (Smith and Schaeffer, 1992). In Cayenne, the protection of these habitats would favor the preservation of biodiversity, as well as a continuum of habitats which ranges from the remains of the rain forest almost to the center of the city.

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Appendix

Population data for 136 species observed along the urban–rural gradient in Cayenne. N, number of birds; *d*, relative density. The checklist follows Meyer de Schauensee and Phelps (1978) and Tostain *et al*. (1992). Guilds are from Terborgh *et al*. (1990), Thiollay (1986), Blake and Loiselle (1991), and our own observations: FH, piscivores; CN, raptors; FA, arboreal frugivores; GR, arboreal, terrestrial and grass granivores; IA, arboreal, sallying insectivore species that hawk, hover, snatch or strike (Fitzpatrick, 1981); IB, bark-dwelling insectivores feeding in trunk interiors (e.g. woodpeckers) or superficially (e.g. some dendrocolaptids and furnariids); IF, arboreal, gleaning insectivores; IT: gleaning terrestrial and ant-following insectivores; NI, nectarivore-insectivores (and not only hummingbirds); OA, predominant omnivores.

For habitat types, see Results: DTG, downtown gardens; DTH, old house gardens; GAR, parks and stadia; FAR, traditional farming; CLE, mimosa clearing; MOS, mosaics of cottages and riparian corridors; OFA, old fallows; SEC, secondary forest.

	Abbr.	Guild	Frequency %	N	Total *d*	Relative density (%)							
						DTG	DTH	GAR	FAR	CLE	MOS	OFA	SEC
ARDEIDAE													
Egretta thula	egth	WA	1	2	0·01							0·09	
Butorides striatus	bust	WA	13	16	0·12			0·15				0·52	0·11
Bubulcus ibis	buib	OA	5	11	0·08				0·47		0·04	0·04	
CATHARTIDAE													
Coragyps atratus	coat	RP	5	14	0·10		0·05		0·26	0·14	0·13	0·13	
ACCIPITRIDAE													
Chondrohierax uncinatus	chun	RP	2	3	0·02						0·09	0·04	
Harpagus bidentatus	habi	RP	1	1	0·01								0·05
Accipiter bicolor	acbi	RP	1	1	0·01				0·05				
Buteo magnirostris	buma	RP	16	19	0·14		0·05		0·10	0·07	0·49	0·17	
Asturina nitida	buni	RP	6	6	0·04		0·27			0·07			
Buteogallus urubitinga	buur	RP	1	2	0·01						0·09		
FALCONIDAE													
Micrastur gilvicollis	migi	RP	3	4	0·03						0·09	0·04	0·05
Falco peregrinus	fape	RP	6	8	0·06	0·27	0·22					0·04	0·05
Falco deiroleucus	fade	RP	2	2	0·01					0·07	0·04		
RALLIDAE													
Aramides axillaris	arax	WA	3	3	0·02							0·13	
JACANIDAE													
Jacana jacana	jaja	WA	7	11	0·08			0·23	0·26		0·09	0·04	

(*Continued overleaf*)

Appendix

Continued

	Abbr.	Guild	Frequency %	N	Total *d*	Relative density (%)							
						DTG	DTH	GAR	FAR	CLE	MOS	OFA	SEC
CHARADRIIDAE													
Pluvialis squatarola	plsq	WA	1	4	0·03							0·17	
SCOLOPACIDAE													
Tringa solitaria	trso	IT	12	15	0·11		0·05	0·08	0·05	0·14	0·04	0·39	
Tringa macularia	acma	WA	8	8	0·06				0·05	0·07	0·09	0·17	
Calidris minutilla	cami	WA	3	6	0·04		0·11				0·09		0·11
COLUMBIDAE													
Columba cayennensis	coca	FR	7	13	0·10	0·27			0·31	0·35			
Columbina passerina	copa	GR	171	333	2·44	2·03	4·21	3·36	1·92	2·73	1·75	1·74	2·23
Columbina minuta	comu	GR	127	210	1·54	2·17	0·82	1·91	1·56	1·12	2·60	1·09	1·33
Columbina talpacoti	cota	GR	119	221	1·62	0·95	0·71	0·92	1·71	2·03	2·37	1·65	1·91
Leptotila verreauxi	leve	GR	13	15	0·11				0·10		0·13	0·22	0·27
Leptotila rufaxilla	leru	GR	1	2	0·01	0·27							
PSITTACIDAE													
Forpus passerinus	fopa	FR	89	204	1·49		1·64	0·46	0·83	1·12	2·91	1·39	2·07
Pionus fuscus	pifu	FR	3	7	0·05		0·38						
Amazone amazonica	amam	FR	2	3	0·02					0·14		0·04	
CUCULIDAE													
Coccyzus minor	comi	IF	2	2	0·01		0·11						
Piaya minuta	pimi	IF	2	2	0·01						0·04		0·05
Crotophaga major	crma	IT	3	3	0·02		0·16						
Crotophaga ani	cran	IT	110	326	2·39	0·41	1·31	2·21	2·59	1·61	2·42	5·34	1·06
APODIDAE													
Chaetura brachyura	chbr	IE	66	125	0·91	2·71	0·76	1·83	1·40	0·35	0·72	0·65	0·21
Chaetura spinicauda	chsp	IE	2	3	0·02		0·05	0·15					
Panyptila cayennensis	paca	IE	5	6	0·04		0·11		0·05		0·09	0·04	
Tachornis squamata	resq	IE	2	3	0·02		0·05					0·09	
TROCHILIDAE													
Glaucis hirsuta	glhi	NI	6	7	0·05		0·11		0·05			0·04	0·16
Anthracothorax nigricollis	anni	NI	12	18	0·13			0·15	0·10	0·07		0·09	0·58
Chlorestes notatus	chno	NI	10	11	0·08		0·11		0·05	0·21	0·09	0·09	0·05
Chlorostilbon melisugus	chme	NI	34	42	0·31		0·38	0·23	1·19		0·18	0·17	0·05
Amazilia fimbriata	amfi	NI	225	308	2·25	4·87	2·51	0·76	3·16	2·38	1·43	2·61	1·54
Amazilia leucogasterc	amle	NI	12	14	0·10	0·41	0·16		0·10		0·04	0·22	
GALBULIDAE													
Galbula galbula	gaga	IA	1	2	0·01								0·11
CAPITONIDAE													
Capito niger	cani	OA	10	13	0·10				0·05		0·09	0·17	0·32
PICIDAE													
Picumnus exilis	piex	IB	8	9	0·07			0·23	0·05	0·07			0·21
Veniliornis passerinus	vepa	IB	26	31	0·23		0·16		0·21	0·35	0·27	0·30	0·32
Veniliornis cassini	veca	IB	2	3	0·02					0·07			0·11
Piculus rubiginosus	piru	IB	3	3	0·02						0·04	0·09	
Colaptes punctigula	copu	IB	6	7	0·05		0·27	0·15					
FURNARIDAE													
Synallaxis albescens	syal	IT	7	13	0·10						0·58		
Certhiaxis cinnamomea	ceci	IF	5	6	0·04		0·22		0·05	0·07			
Xenops milleri	xemi	IT	1	1	0·01							0·04	
DENDROCOLAPTIDAE													
Deconychura longicauda	delo	IB	5	6	0·04					0·07		0·04	0·21

(*Continued overleaf*)

Appendix

Continued

	Abbr.	Guild	Frequency %	N	Total *d*	Relative density (%)							
						DTG	DTH	GAR	FAR	CLE	MOS	OFA	SEC
THAMNOPHILIDAE													
Sakesphorus canadensis	saca	IT	6	8	0·06		0·11					0·22	0·05
Thamnophilus doliatus	thdo	IT	100	145	1·06	0·27	0·22	0·69	1·40	1·26	0·90	1·39	1·75
Thamnophilus amazonicus	tham	IF	1	1	0·01								0·05
Formicivora grisea	fogr	IT	12	14	0·10				0·05			0·04	0·64
PIPRIDAE													
Pipra aureola	piau	FR	11	15	0·11				0·05			0·04	0·69
Manacus manacus	mama	FR	2	3	0·02								0·16
TYRANNIDAE													
Zimmerius gracilipes	zigr	IF	2	2	0·01							0·09	
Ornithion inerme	orin	IF	5	10	0·07				0·10				0·42
Camptostoma obsoletum	caob	IF	9	17	0·12			0·08	0·31				0·53
Phaeomyias murina	phmu	IF	370	732	5·36	2·57	5·13	5·11	6·74	4·12	6·49	5·17	5·25
Tyrannulus elatus	tyel	IA	8	10	0·07				0·16			0·09	0·27
Elaenia flavogaster	elfl	IA	349	654	4·79	2·03	3·39	3·43	4·98	3·70	6·27	4·47	7·43
Elaenia parvirostris	elpa	IA	20	25	0·18		0·11	0·08	0·26	0·35	0·22	0·13	0·21
Elaenia cristata	elcr	IA	18	27	0·20		0·05		0·05		0·09	0·39	0·74
Lophotriccus galeatus	coga	IA	1	1	0·01								0·05
Todirostrum maculatum	toma	IF	7	10	0·07			0·38	0·16	0·14			
Todirostrum cinereum	toci	IF	11	16	0·12		0·05		0·41		0·13	0·17	
Todirostrum pictum	topi	IF	1	2	0·01							0·09	
Tolmomyias sp	tosp	IF	34	50	0·37		0·71	0·15	0·57	0·56	0·18	0·30	0·27
Myiophobus fasciatus	myfa	IF	3	3	0·02						0·09	0·04	
Ochthoeca littoralis	ocli	IF	1	1	0·01								0·05
Fluvicola pica	flpi	IA	17	20	0·15	0·41	0·49		0·05	0·28	0·04	0·04	0·05
Arundinicola leucocephala	arle	IA	7	9	0·07				0·21		0·22		
Sirystes sibilator	sisi	IA	2	2	0·01			0·08					0·05
Myiarchus ferox	myfe	IA	3	3	0·02							0·09	0·05
Myiarchus tyrannulus	myty	IA	6	6	0·04				0·10	0·07	0·04	0·09	
Pitangus sulphuratus	pisu	IA	506	1127	8·25	12·72	7·65	11·75	9·33	8·04	7·92	6·73	5·94
Megarynchus pitangua	mepi	IA	1	1	0·01						0·04		
Myozetetes cayannensis	myca	IA	257	480	3·51	1·62	4·31	5·19	4·35	3·56	3·45	3·00	2·12
Legatus leucophaius	lele	IA	12	19	0·14				0·05	0·07	0·13	0·61	
Empidonomus varius	emva	IA	1	1	0·01							0·04	
Tyrannus melancholicus	tyme	IA	24	32	0·23		0·16	0·23	0·05	0·21	0·45	0·43	0·11
Tyrannus savana	muty	IA	5	11	0·08				0·31	0·14		0·13	
Tyrannus dominicensis	tydo	IA	51	72	0·53	0·27	0·22	0·15	0·31	0·14	1·12	0·83	0·64
Pachyramphus rufus	paru	IF	3	5	0·04		0·16						0·11
Tityra cayana	tica	OA	4	5	0·04						0·13	0·09	
HIRUNDINIDAE													
Tachycineta albiventer	taal	IE	51	88	0·64	0·95	0·82	0·31	0·73	0·42	0·98	0·65	0·27
Phaeoprogne tapera	phta	IE	1	2	0·01							0·09	
Progne chalybae	prch	IE	261	538	3·94	7·44	6·17	1·91	3·11	5·24	3·54	3·26	2·97
Riparia riparia	riri	IE	1	4	0·03						0·18		
Hirundo rustica	hiru	IE	1	2	0·01							0·09	
TROGLODYTIDAE													
Donacobius atricapillus	doat	IT	2	2	0·01		0·05			0·07			
Thryothorus leucotis	thle	IT	1	1	0·01						0·04		
Troglodytes aedon	trae	IT	395	735	5·38	3·65	5·84	3·36	5·50	6·36	4·57	6·86	5·31
MIMIDAE													
Mimus gilvus	migv	OA	77	126	0·92	0·95	2·46	1·83	0·57	1·33	0·27	0·48	0·16

(*Continued overleaf*)

Appendix

Continued

	Abbr.	Guild	Frequency %	N	Total *d*	Relative density (%)							
						DTG	DTH	GAR	FAR	CLE	MOS	OFA	SEC
TURDIDAE													
Turdus leucomelas	tule	OA	336	695	5·09	3·11	3·00	6·33	6·64	5·94	4·34	4·60	6·26
Turdus nudigenis	tunu	OA	59	79	0·58		0·05	0·53	0·73	0·21	0·72	1·00	0·80
SYLVIIDAE													
Polioptila plumbea	popl	IF	4	6	0·04						0·09		0·21
VIREONIDAE													
Vireo olivaceus	viol	IF	1	2	0·01								0·11
Hylophilus pectoralis	hype	IT	23	31	0·23		0·22	0·61	0·21	0·28	0·18	0·17	0·16
Hylophilus ochraceiceps	hyoc	IF	1	1	0·01								0·05
PARULIDAE													
Dendroica petechia	depe	IF	112	144	1·05	0·41	0·71	1·45	1·24	1·47	0·81	1·00	1·22
Geothlypis aequinoctialis	geae	IF	3	5	0·04							0·17	0·05
ICTERIDAE													
Molothrus bonariensis	mobo	IT	22	79	0·58		0·66			1·75	0·85	0·78	0·27
Scaphidura oryzivora	scor	OA	2	20	0·15				0·52			0·43	
Cacicus cela	cace	OA	31	101	0·74		1·75	0·31	0·21		0·31	2·13	0·27
Quiscalus lugubris	qulu	OA	151	792	5·80	35·18	15·84	10·30	1·45	3·42	0·40	0·61	0·37
Agelaius icterocephalus	agic	OA	5	24	0·18		0·33			0·63		0·39	
Icterus cayanensis	icca	IT	19	30	0·22			0·15	0·26	0·56	0·27	0·30	0·11
Icterus nigrogularis	icni	OA	9	10	0·07	0·14	0·22			0·14	0·04	0·09	
Leites militaris	lemi	OA	5	13	0·10				0·57			0·09	
EMBERIZIDAE													
Coereba flaveola	cofl	IA	4	5	0·04				0·05			0·04	0·16
Dacnis cayana	daca	OA	23	36	0·26				0·16	0·14	0·27	0·48	0·74
Chlorophanes spiza	chsi	IF	1	2	0·01				0·10				
Conirostrum bicolor	cobi	IF	15	27	0·20	0·27	0·71			0·42	0·27		
Tangara mexicana	tame	OA	40	82	0·60		0·33		0·52	0·70	1·03	1·04	0·48
Tangara cayana	taca	OA	20	29	0·21			0·84	0·36		0·36		0·16
Euphonia violacea	euvi	FR	1	1	0·01								0·05
Thraupis episcopus	thep	OA	459	1257	9·20	7·71	9·23	9·38	8·35	8·67	7·48	10·42	11·46
Thraupis palmarum	thpa	OA	349	835	6·11	4·19	5·08	3·81	6·32	5·38	6·36	7·38	7·96
Ramphocelus carbo	raca	OA	246	527	3·86	0·41	1·97	2·21	5·13	4·05	4·16	4·26	5·89
Tachyphonus rufus	taru	IT	158	273	2·00		1·04	1·60	2·23	2·03	2·28	2·34	2·97
Tachyphonus luctuosus	talu	IF	6	10	0·07					0·14			0·42
Spiza americana	spam	GR	4	9	0·07				0·36	0·14			
Oryzoborus angolensis	oran	GR	1	1	0·01				0·05				
Sporophila americana	spam	GR	52	90	0·66		0·16	0·38	0·83	0·42	1·39	0·48	0·95
Sporophila lineola	spli	GR	26	52	0·38				0·21	0·14	0·67	0·39	1·17
Sporophila minuta	spmi	GR	20	40	0·29		0·22		0·93		0·67	0·09	0·05
Sporophila castaneiventris	spca	GR	241	628	4·60	0·68	3·33	9·31	3·37	8·46	5·15	3·00	3·71
Volatinia jacarina	voja	GR	248	556	4·07	0·68	2·02	5·26	2·49	5·59	6·54	4·04	4·14
Emberizoides herbicola	emhe	GR	5	19	0·14				0·05		0·76	0·04	
Zonotrichia capensis	zoca	GR	3	6	0·04								0·32
Spinus cucullatus	spcu	GR	1	1	0·01						0·04		