Bird assemblages of forested and human-modified countryside habitats in the Pacific lowlands of southern Costa Rica

Grupos de aves de hábitat boscosos y rurales en las tierras bajas del Pacífico del sur de Costa Rica

Christian H. SCHULZE & Isabell RIEDL

Abstract: We surveyed birds of the forest interior, forest margin and human-dominated countryside habitats in the Pacific lowlands of the Golfo Dulce region in the vicinity of the "Tropenstation La Gamba". Species richness was significantly higher at the forest margin compared to forest interior and human-modified habitats. Only a small proportion of species (8.8%) were recorded in all three habitat types. The majority of species were recorded only in one (41.9%) or two habitat types (49.3%). The lowest faunal similarity and thereby highest beta diversity was observed between forest interior and human-dominated habitats. The higher similarities between forest margins and the two other habitat types emphasised their role as ecotones characterised by a pronounced overlap of species from forested and (semi-)open habitats. As demonstrated by various examples, all three habitat types have characteristic species reaching their highest abundances in the forest interior, at forest edges and in human-dominated habitats, respectively. Relative species richness and abundance of range-restricted species (Central and northern South American distribution or smaller ranges) was highest in the forest interior and decreased towards forest margins and human-dominated habitats. Extremely widespread species (e.g. New World distribution) were not recorded in the forest interior but represented a substantial proportion of species and individuals recorded at the forest margin and particularly in human-dominated habitats. While winter visitors were regularly recorded at the forest margin and in human-dominated habitats, they were completely absent from the forest interior. The relative importance of feeding guilds differed between the three different habitats. The most obvious changes were observed in purely insectivorous birds, in birds feeding predominantly on seeds, in omnivores, and in scavengers. While the relative abundance of insectivorous birds was 2-3 times higher in the forest than in human-dominated habitats and at the forest margin, the mean number of recorded insectivores per observation unit was lowest at the forest margin but reached similar values in forest interior and human-dominated habitats. The abundance of granivores, omnivores and scavengers increased conspicuously from forest interior towards forest margin and (semi-)open habitats. Although human-dominated habitats of the humid Pacific lowlands in Costa Rica can be characterised by a species-rich avifauna, their potential conservation value is limited because they do not support the majority of range-restricted species. Furthermore, our data indicate that ecological services provided by birds most likely change significantly as response to deforestation.

Key words: avifauna, conservation, Costa Rica, countryside habitats, ecological services, guild structure, habitat specificity, Pacific lowland rainforest, species richness.

Resumen: Se investigaron las aves del interior del bosque, margenes del bosque y hábitat rurales en las tierras bajas del Pacífico de la región de Golfo Dulce, en las cercanías de la "Estación Tropical La Gamba". La riqueza de especies fue significativamente mayor en los márgenes del bosque comparada con el interior del bosque y hábitat rurales. Sólo una pequeña proporción de especies (8.8%) fue encontrada en los tres tipos de hábitat. La mayoría de las especies fue encontrada sólo en uno (41.9%) o dos tipos de hábitat (49.3%) respectivamente. La baja similitud en la fauna y, por consiguiente, la mayor diversidad beta fue observada entre los hábitat de bosque de interior y rurales. La alta similitud entre márgenes del bosque y los otros dos tipos de hábitat enfatizan su rol como ecotono, caracterizado por una pronunciada sobreposición de especies desde hábitat forestados y (semi-) abiertos. Como ha sido demostrado por varios ejemplos, los tres hábitat tienen especies características, alcanzando su mayor abundancia en el bosque de interior, borde de bosque y en hábitat rurales respectivamente. La riqueza de especies relativa y la abundancia de especies de rango restringido (distribución en la zona central y norte de Sudamérica o pequeños rangos) fue mayor en el bosque de interior y disminuyó hacia los márgenes del bosque y hábitat de dominio humano. Especies con una amplia distribución (distribución en el Nuevo Mundo) no fueron registradas en el interior del bosque, pero representan una proporción subtancial de especies e individuos registrados en el margen del bosque y particularmente en hábitat rurales. Mientras que los visitantes invernales fueron frecuentemente registrados en los márgenes del bosque y en hábitat rurales, ellos estuvieron completamente ausentes del interior del bosque. La importancia relativa de los gremios alimentarios difieren entre los tres diferentes hábitat. El cam-

Stapfia **88**,
zugleich Kataloge der
oberösterreichischen
Landesmuseen
Neue Serie **80** (2008):
395-408

bio más obvio que observamos fue en aves insectívoras, en aves que se alimentan principalmente de semillas, en omnívoras y en carroñeras. Mientras que la abundancia relativa de aves insectívoras fue 2 a 3 veces mayor en el bosque que en los hábitat rurales y en el margen del bosque, el número medio de insectivoras registradas por unidad de observación fue inferior en el márgen del bosque, pero alcanzó valores similares en el interior del bosque y hábitat rurales. La abundancia de granívoras, omnívoras y carroñeras incrementó conspicuamente desde el interior del bosque hacia los márgenes del bosque y hábitat (semi-) abiertos. Aunque los hábitat rurales de las tierras bajas húmedas del Pacífico en Costa Rica se caracterizan por una riqueza de las especies de avifauna, su valor de conservación potencial es limitado, porque ellos no soportan la mayoría de las especies de rango restringido. De esta manera, nuestros datos indican que los servicios ecológicos proporcionados por las aves probablemente cambiarían significativamente como respuesta a la deforestación.

Palabras clave: avifauna, conservación, Costa Rica, hábitat rurales, servicios ecológicos, estructura de gremios, especificidad de hábitat, bosque lluvioso de las tierras bajas del Pacífico, riqueza de especies.

Introduction

In contrast to most other tropical countries, a large body of published information is available on Costa Rican birds covering a large variety of different aspects ranging from studies on the structure of understorey (Young et al. 1998) and canopy forest bird communities (Loiselle 1988), changes of species richness along elevational gradients (Blake & Loiselle 2000, Young et al. 1998), altitudinal migration (Powell & Bjork 1994), foraging ecology (Tramer & Kemp 1980), frugivory and seed dispersal (Blake & Loiselle 1992, Loiselle & Blake 1991, Wheelwright et al. 1984, Wheelwright 1991, Mazer & Wheelwright 1993), species richness and ecology of hummingbirds (Borgella et al. 2001, Stile 1975), occurrence of bird species wintering in Costa Rica (Tramer & Kemp 1982), habitat use (Sekercio lu et al. 2007), effects of forest disturbance and fragmentation on bird assemblages (Blake & Loiselle 2001, Borgella et al. 2001, Daily et al. 2001) and avian blood parasites (Young et al. 1993).

The large number of ornithological studies in Costa Rica, compared to other tropical countries, can be related to the availability of several research stations with a good infrastructure and which have been successfully operated for many years. This is demonstrated particularly by the many studies conducted in the close vicinity of Las Cruces Biological Field Station (Borgella et al. 2001, Daily et al. 2001, Sekercio lu et al. 2002, Stiles 1996) and La Selva Biological Station (Blake 1992, Blake & Loiselle 2000, 2002, Loiselle 1988). Additionally, many studies certainly profit from the large areas of nearly pristine forest remaining in Costa Rica. In most other tropical countries, the increasing demand for land by their growing human population causes a continuing loss and increasing fragmentation and isolation of rainforest. Today, in many tropical regions such remaining forest remnants are often situated on steep slopes and remote areas which are difficult to access. Only in a few countries such as Costa Rica and Brazil is deforestation nowadays negligible at least in protected areas (Sánchez-Azofeifa 2003, Schwartzman et al. 2000), while in most others forest loss is going on with enormous speed even inside national parks (e.g. Curran et al. 2004).

Generally, most groups of plants and animals show a strong negative response to rainforest disturbance and conversion (Dunn 2004, Lawton et al. 1998, Schulze et al. 2004), including birds (e.g. Estrada et al. 1997, Fjeldså 1999, Kofron & Chapman 1995, Naidoo 2004, Sodhi et al. 2005, Waltert et al. 2004). So far, few studies have quantified the effects of habitat disturbance on bird assemblages in Costa Rica (Daily et al. 2001, Sekercio lu et al. 2002, 2007) and the effects of forest conversion on the avifauna of the humid Pacific lowlands of southern Costa Rica are completely unknown, a gap which will be partly filled by our study from the Golfo Dulce region.

In this study we compare the importance of three different habitats – forest interior, forest margin and human-dominated habitats – for Pacific lowland birds in southwestern Costa Rica. Human-dominated habitats in southern Costa Rica include active agricultural plots, plantation or managed forest, fallow land, gardens, and small remnants of native vegetation embedded in landscapes devoted primarily to human activities (Daily et al. 2001).

Particularly the following questions are addressed:

(1) How do forest conversion and edge effects influence the abundance and species richness of birds?

(2) How pronounced is habitat specificity in resident and migratory birds wintering in the Pacific lowlands?

(3) How does the importance for range-restricted species differ between habitats?

(4) Does forest modification and transformation affect the abundance of individual feeding guilds?

Material and methods

Study area and surveyed habitats

Our study was conducted in close proximity to the “Tropenstation La Gamba”. The area is characterised by an extremely species-rich avifauna (SAUBERER et al. 2007) with a total of 319 recorded bird species (TEBB 2007a). Its high conservation value is underlined by the occurrence of the black-cheeked ant-tanager *Habia atrimaxillaris*, which is endemic to the Golfo Dulce lowlands of southwestern Costa Rica (TEBB 2007b).

The study area covered three different habitat types: forest interior, forest margin, and human-dominated countryside habitats (Fig. 1). Surveyed forest represented humid lowland forest predominately located within the “Regenwald der Österreicher” and the protected Esquinas forest. A more detailed description of the lowland rainforests of the Golfo Dulce region as well as regional climate, geography and geological history of the study area is provided by WEBER et al. (2001). The forest margin zone was defined as the transition zone between forest interior and (semi-)open human-dominated countryside habitats. It included parts of the forest up to ca. 50 m inwards from the edge of the old grown forest. Additionally, disturbed forests or strips of artificially planted trees (e.g. garden areas of the Tropenstation La Gamba and Esquinas lodge) attached to the forest margin were classified as forest margin habitats when located within a distance to the natural forest edge of less than ca. 50 m. Human-dominated habitats included settlements, village gardens, planted rows of trees along roads, forested riparian strips (≤ 20 m wide) along rivers, oilpalm plantations, fallows with dense herbaceous vegetation (often overgrown with vines), shrubs and small trees, paddy fields, recently abandoned and active cattle pastures.

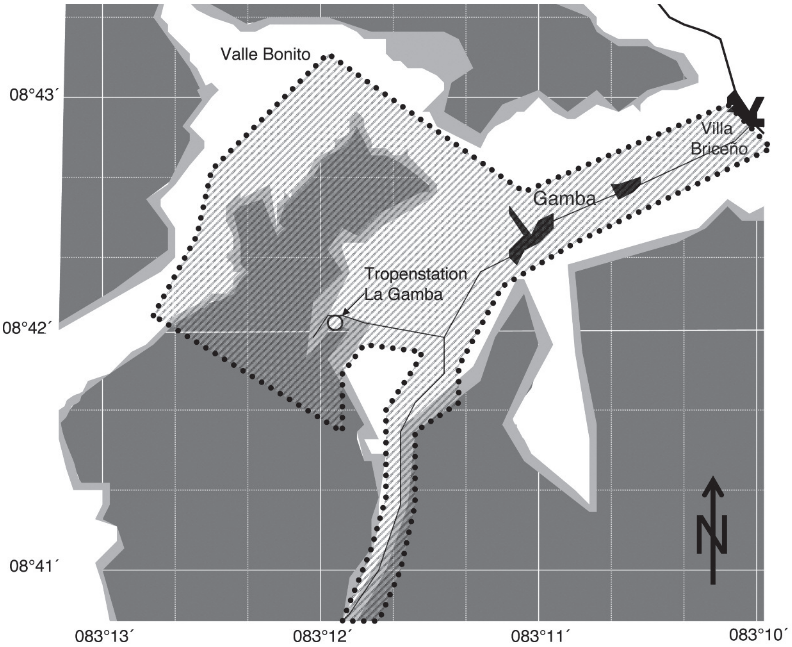

Fig. 1: Study area showing the three different surveyed habitat types: forest interior (dark grey), forest margin (pale grey) and human-dominated countryside habitats (white). Hatching indicates the approximate area in which bird surveys were conducted.

Bird surveys

Bird observations were conducted during the following time periods: 15-18 January, 26 January-2 February and 22 June-7 July 2007. Birds were recorded visually and acoustically during 10-minute observation units within a radius of approximately 50 m. Unfamiliar birds songs and calls were tape-recorded using a digital voice recorder and compared later with recordings by ROSS (2001, Costa Rican Bird Songs) or own recordings of identified birds made earlier. Bird abundance estimates provided by this point census method are far from being accurate and are biased by factors such as vegetation density. Despite this, however, they are probably more precise than abundance estimates based on observation frequencies as provided by surveys using the “MacKinnon species lists method” (e.g. O‘DEA et al. 2004). Point counts were conducted along existing trails and roads through forested and (semi-)open areas. Sampling effort was 66, 162 and 82 observation units for human-dominated habitats, forest margin and forest interior, respectively. To use the limited time as efficiently as possible we did not follow common recommendations to restrict point censuses to the first three hours of the morning (e.g. BLAKE 1992), but conducted bird surveys from dusk to dawn.

Birds were identified using available field guides (STILES et al. 1989, GARRIGUES & DEAN 2007) and voice recordings (Naturesongs and Von GAUSIG 1998-2001, ROSS 2001). Nomenclature and taxonomy follow CALDERÓN et al. (2007). Referring to STILES et al. (1989), bird species were assigned to seven feeding guilds by their primary diet: granivores, frugivores, nectarivores, insectivores, predators (of vertebrates), scavengers and omnivores.

Recorded species of the bird families Anatidae, Ardeidae, Rallidae, Jacanidae, Scolopacidae and Alcedinidae were excluded from all analyses because the majority depend on freshwater habitats (e.g. STILES et al. 1989), which we did not take into consideration. Swifts (Apodidae) were excluded from the analysis because it is often difficult to link them to a certain habitat type due to their exclusively insectivorous aerial-hawking feeding mode (e.g. STILES et al. 1989).

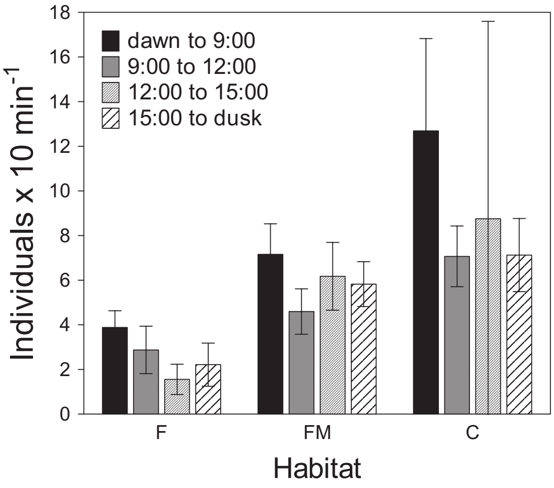

Fig. 2: Effects of habitat (F – forest interior, FM – forest margin, C – human-dominated countryside habitats) and survey time on mean number of birds counted per 10-min observation unit.

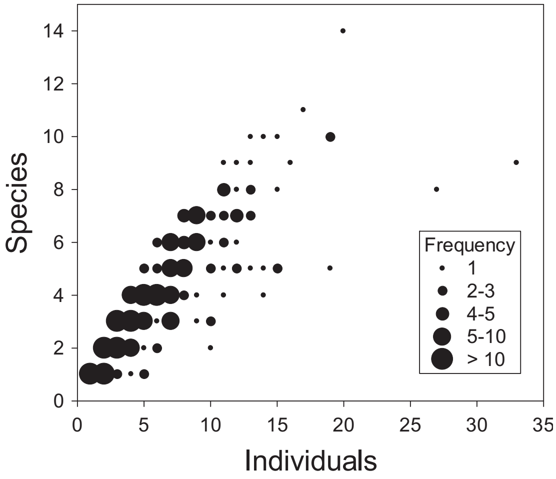

Fig. 3: Relationship between number of counted birds and species recorded per 10-min observation unit.

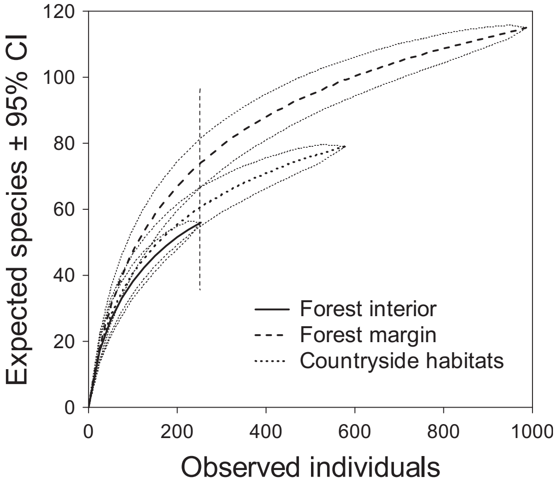

Fig. 4: Species accumulation curves ± 95% confidence intervals for bird assemblages of forest interior, forest margin and human-dominated countryside habitats. The vertical dashed line indicates the largest shared sample size of 253 birds.

Table 1. Results of two-way ANOVA testing effects of habitat and survey time on number of birds detected per 10-min observation unit. Significant effects printed bold.

Dependent variable	Independent factor	DF	*F*	*p*
Abundance	**Habitat**	**3**	**33.41**	**<0.001**
	Time	**2**	**10.61**	**<0.001**
	Habitat x time	6	2.06	0.057

Statistical analysis

Differences of mean and median numbers of birds between habitats were tested for significance by two-way ANOVAs and Kruskal-Wallis ANOVAs. All ANOVAs were calculated with the software Statistica 7.1 (StatSoft 2005). Although activity of lowland birds shows a conspicuous temporal variation (BLAKE 1992; this study), we do not expect our survey design to bias the results in favour of an individual habitat, because temporal distribution of sampling effort of surveys were similar in all habitat types.

Additional programs (KREBS 1989) were used to estimate expected species numbers for a largest shared sample size (= largest number of counted birds), to construct species accumulation curves, and to obtain variance estimates necessary to calculate 95% confidence intervals for expected species numbers according to SIMBERLOFF (1978). Total species richness was estimated for the incomplete species inventories of the three habitat types by the extrapolation methods abundance-based coverage estimator (ACE), Chao 1, first-order jackknife (Jack 1) and Michaelis-Menten richness estimator (MMeans) with 100 repetitions (COLWELL 2006). For subsequent analyses, the median of the four different estimates was used as measure for avian species richness of the three habitats and to estimate completeness of species inventories (= recorded species/median of estimates).

Similarity of species compositions between habitats was quantified by Sørensen's similarity index, which is regarded as one of the most effective presence/absence similarity measures (e.g. SOUTHWOOD & HENDERSON 2000). However, the classic Sørensen index of compositional similarity is highly sensitive to sample size and completeness of species inventories. In addition to the classical Sørensen similarities, therefore, we calculated an estimator for the number of shared species proposed by CHAO et al. (2005). This Chao's Sørensen raw abundance-based similarity index proved to be considerably less biased than the classic similarity indices (COLWELL 2006) and reduces the negative bias which potentially undermines the usefulness of the traditional Sørensen similarity index when rich species ensembles are incompletely sampled (CHAO et al. 2005).

Results

Abundance and species richness

A total of 1.803 birds belonging to 148 species were recorded visually or acoustically during the 310 surveys, excluding 15 additional species related to aquatic habitats and two species of swift. The number of bird individuals counted per 10 min observation unit was

Table 2. Survey effort (number of 10-min observation units), recorded and estimated species richness (ACE, Chao 1, Jack 1, MMMean; see text), median of species richness estimates, and completeness of species inventories (= recorded species/median of estimated species) for forest interior (F), forest margin (FM) and countryside habitats (C).

Habitat	Observ. units	Recorded species	ACE	Chao 1	Jack 1	MMMean	Median estimate	Completeness of inventories [%]
F	82	56	73.6	66.2	79.7	80.5	76.7	73.1
FM	162	115	138.3	146.1	152.8	134.8	142.2	80.9
C	66	79	96.4	95.2	106.6	97.3	96.9	81.6

significantly affected by observation time and habitat (Table 1). Bird activity was highest in the morning, but on the whole only slightly decreased towards midday and afternoon (Fig. 2). The highest numbers of birds counted per 10 min observation unit were reached at human-dominated habitats, lowest bird abundances were observed in the forest interior (Fig. 2). As expected, the number of species recorded per observation unit was significantly related to the number of counted individuals (r = 0.84, p < 0.001; Fig. 3).

Species accumulation curves indicated a significantly higher species richness at the forest margin compared to forest interior and human-dominated countryside habitats. Curves for the latter two habitats did not differ significantly from each (Fig. 4). Expected numbers of species for a largest shared samples size of 253 birds were 56, 74 and 61 species for forest interior, forest margin and human-dominated habitats, respectively (Fig. 4).

Estimates of total species richness showed an identical ranking of habitats with respect to species richness. Highest species richness (142 species) was estimated for forest margins, a total species richness of 77 and 97 species was predicted for forest interior and human-dominated habitats, respectively (Table 2). The estimated completeness of species inventories was similar for forest margins and cultivated area (ca. 81% of estimated species total) while it was slightly lower for forest interior (73%) (Table 2).

Habitat specificity

Many bird species showed clear habitat specificity (see examples in Fig. 5). While some species such as *Habia atrimaxillaris* (Thraupidae) and *Crax rubra* (Cracidae) were predominantly restricted to the forest interior, other species such as *Patagioenas nigrirostris* (Columbidae), although most frequently recorded inside the forest, also occurred at forest margin and even rarely at human-dominated habitats (Fig. 5), where they visited strips of gallery forest. Other species, which were most abundant at the forest margin, were seen only seldom in forest interior and could not be reported at human-dominated habitats (e.g. *Tangara larvata*, Thraupidae; Fig. 5) or occurred but rarely outside forested habitats. Particularly several hummingbird species appeared to occupy a wide variety of different habitats ranging from the forest interior to highly disturbed secondary vegetation within cultivated areas, but reaching highest densities at the forest margin (e.g. *Amazilia tzacatl*, Trochilidae; Fig. 5). Some species appeared to reach similar abundances at the forest margin and within the cultivated area as demonstrated by the tanager (Thraupidae) *Ramphocelus costaricensis* (Fig. 5). A last group of species occurred predominantly in human-dominated habitats as demonstrated by *Thraupis episcopus* (Thraupidae) and *Pitangus sulphuratus* (Tyrannidae) (Fig. 5).

Table 3: Similarity between bird assemblages surveyed at forest interior (F), forest margin (FM) and countryside habitats (C) quantified by classic Sørensen Similarity indices (lower left) and Chao's Sørensen Raw Abundance-Based Similarity indices (upper right, printed in bold).

	F	FM	C
F	-	**0.62**	**0.34**
FM	0.49	-	**0.76**
C	0.24	0.57	-

Only a small proportion of species (8.8%) was recorded in all three habitat types (Fig. 6). The majority of species were recorded in only one (41.9%) or two habitat types (49.3%) (Fig. 6). The lowest faunal similarity was found between forest and human-dominated habitats. The higher similarity between forest margin and the two other habitat types emphasized the status of forest margins as ecotones 'linking' forest interior and human-dominated habitats. However, Sørensen similarities indicated a higher faunal overlap between forest margin and adjacent human-dominated habitats than between forest margin and forest interior (Table 3). As expected, classical Sørensen similarities severely underestimated the predicted fraction of shared species.

Range-restricted species

Relative species richness and abundance of range-restricted species (Central and northern South American distribution or smaller) was highest in forest interior and decreased towards forest margins and human-dominated habitats. The most widespread species with a distribution range covering large parts of the New World were not recorded in the forest interior, but rep-

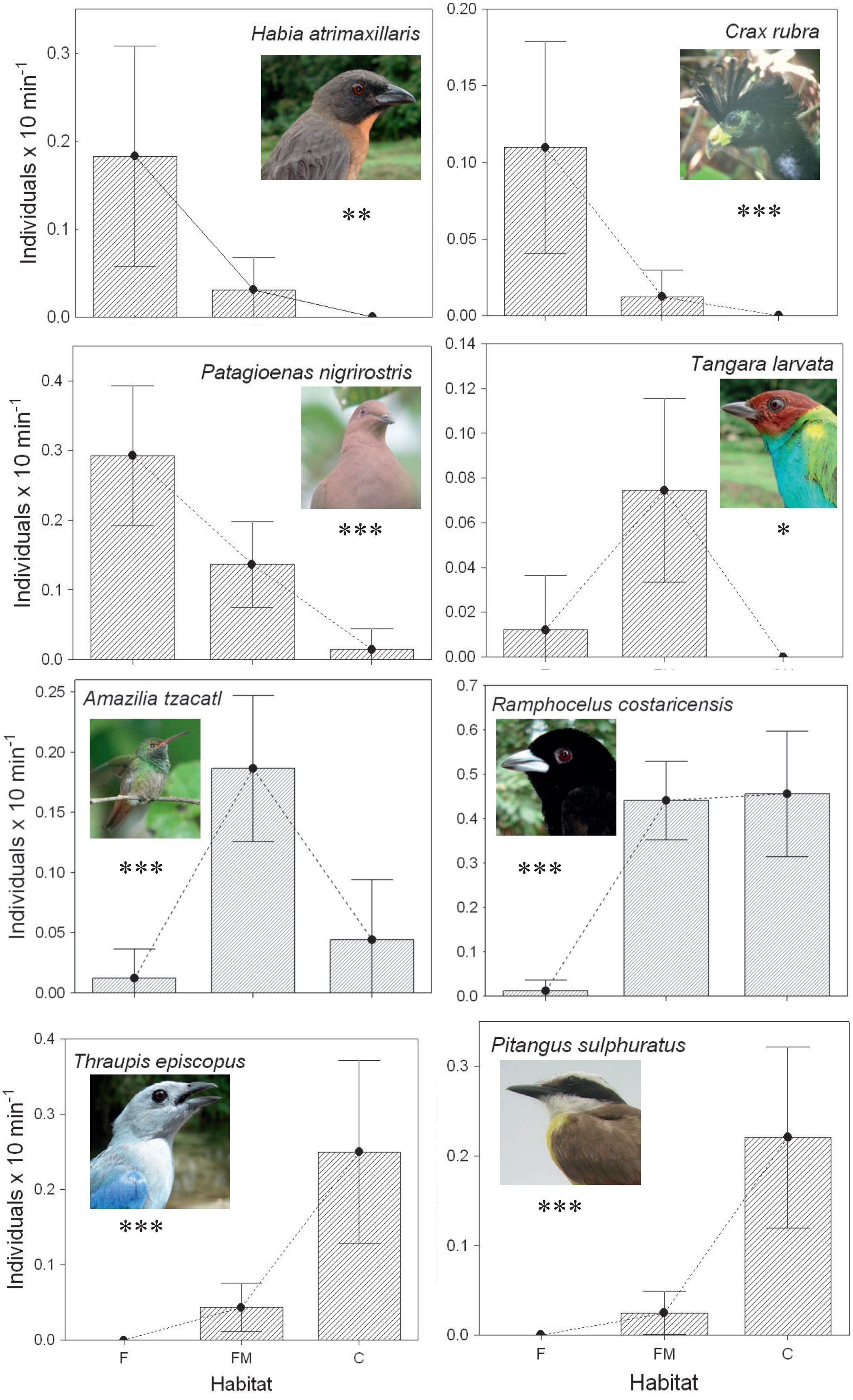

Fig. 5: Habitat specificity of selected species quantified as mean number of individuals counted per 10-min observation unit at forest interior (F), forest margin (FM) and human-dominated countryside habitats (C). Error bars represent 95% confidence intervals. Asterisks indicate statistical significance (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) of Kruskal-Wallis test. Total numbers of counted individuals: *Habia atrimaxillaris* – 20 individuals, *Crax rubra* – 11, *Patagioenas nigrirostris* – 63, *Tangara larvata* – 18, *Amazilia tzacatl* – 36, *Ramphocelus costaricensis* – 226, *Thraupis episcopus* – 35, *Pitangus sulphuratus* – 23.

resented a substantial proportion of the species and individuals recorded at the forest margins and particularly in the cultivated landscape (Fig. 7).

Winter visitors

Nine migratory bird species wintering in Costa Rica were recorded between 15 January and 2 February. The mean number of winter visitors counted per observation unit during that survey period differed significantly between habitat types (Kruskal-Wallis ANOVA: H_2 = 12.04, p = 0.002). While winter visitors were regularly recorded at the forest margin (total of 23 individuals and 8 species) and in the cultivated area (total of 11 individuals and 6 species), no such birds were observed in the forest interior (Fig. 8).

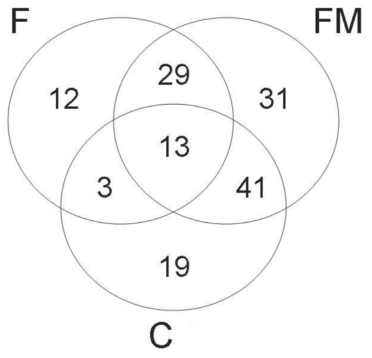

Fig. 6: Faunal overlap between the three surveyed habitat types (F – forest interior, FM – forest margin, C – human-dominated countryside habitats) quantified as number of species recorded in individual habitats only, recorded in two habitat types and all habitat types.

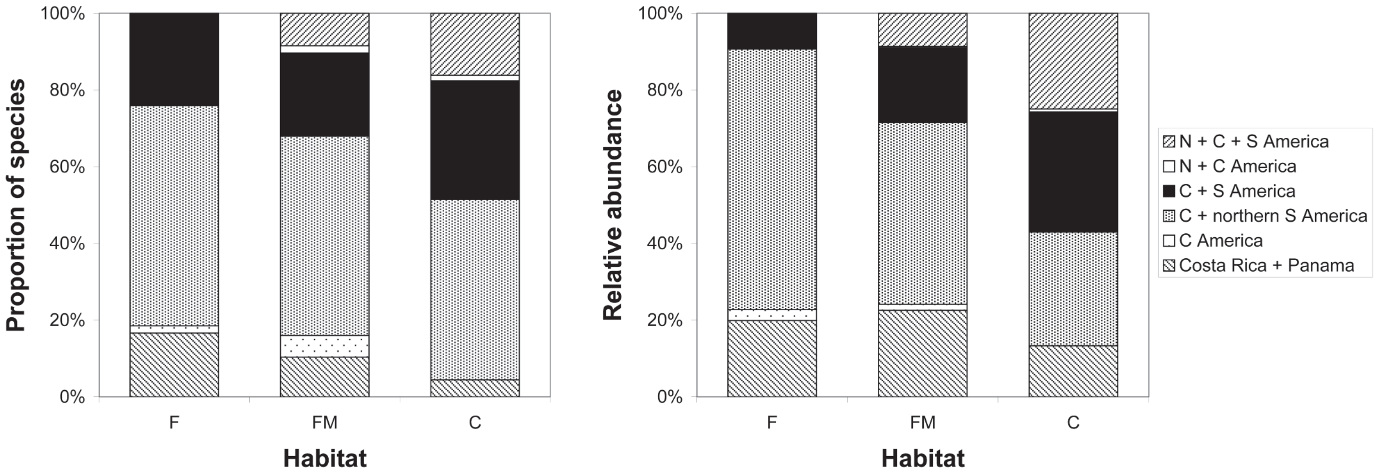

Fig. 7: Relative species richness and abundance of species with different distribution ranges at forest interior (F), forest margin (FM) and human-dominated countryside habitats (C). Species with smallest ranges represent birds endemic to Costa Rica and Panama, species with largest ranges occur over large parts of the New World.

Feeding guilds

The structure of feeding guilds differed between the three surveyed habitat types (Fig. 9). The most conspicuous changes were observed in purely insectivorous birds, birds feeding predominantly on seeds, and scavengers. The relative abundance of insectivores was 2-3 times higher in forest interior (22.9% of total number of observed bird individuals) than in human-dominated habitats (10.4%) and at forest margins (7.7%). While granivores only represented a minor proportion (0.7%) in the forest interior, they increased significantly towards the forest margins (4.0%) and human-dominated habitats (12.5%). The relative abundance of scavengers also increased significantly from the forest interior (0.4%) towards the forest margin (3.9%) and human-dominated habitats (6.3%). Nectarivores (predominantly hummingbirds) reached their highest relative abundance at the forest margin (8.3%), while their importance was particularly low in human-dominated habitats (2.7%).

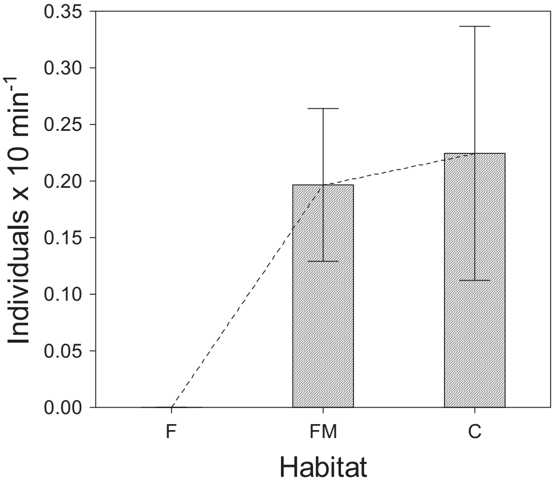

Fig. 8: Differences of abundance of migratory birds between forest interior (F), forest margin (FM) and human-dominated countryside habitats (C) quantified by mean number of individuals counted per 10-min observation unit. Error bars represent 95% confidence intervals.

A comparison of the absolute abundances proved that insectivorous birds were rarest at forest margin sites. Abundances of granivores, scavengers and omnivores increased significantly from forest interior towards forest margin and human-dominated habitats. Nectarivorous birds reached a significantly higher abundance at forest margin than at forest interior and human-dominated habitats. The abundance of frugivorous birds did

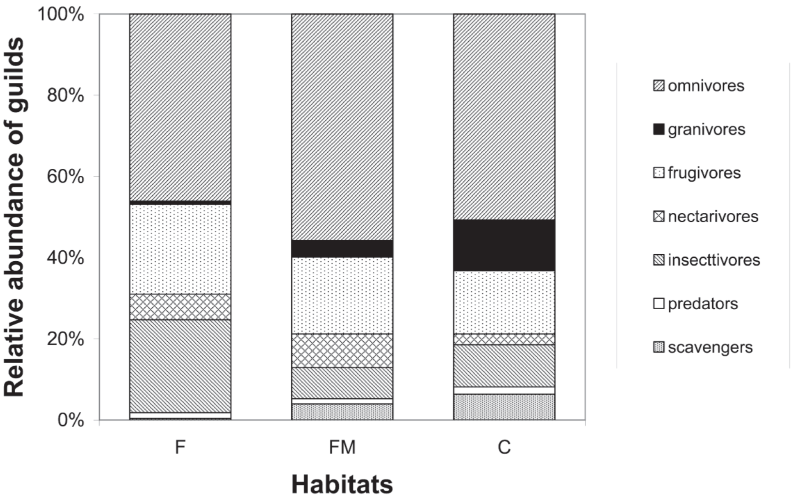

Fig. 9: Relative abundance of feeding guilds at forest interior (F), forest margin (FM) and human-dominated countryside habitats (C).

not differ significantly between the three habitat types (Fig. 10). The guild of predators was not considered due to its generally low abundance (n = 27 individuals).

Discussion

Temporal and spatial variation of bird activity

As expected, bird activity was highest in the early morning in all habitat types. Therefore, it is often suggested to restrict point counts to the first three hours of the morning (BLAKE 1992), and most bird surveys follow this recommendation (e.g. DAILY et al. 2001, SODHI et al. 2005, WALTERT et al. 2004). However, some authors also conducted surveys until midday and again in the late afternoon (e.g. ESTRADA et al. 1997), particularly when the primary aim was to achieve relatively complete species inventories in short periods of time (e.g.

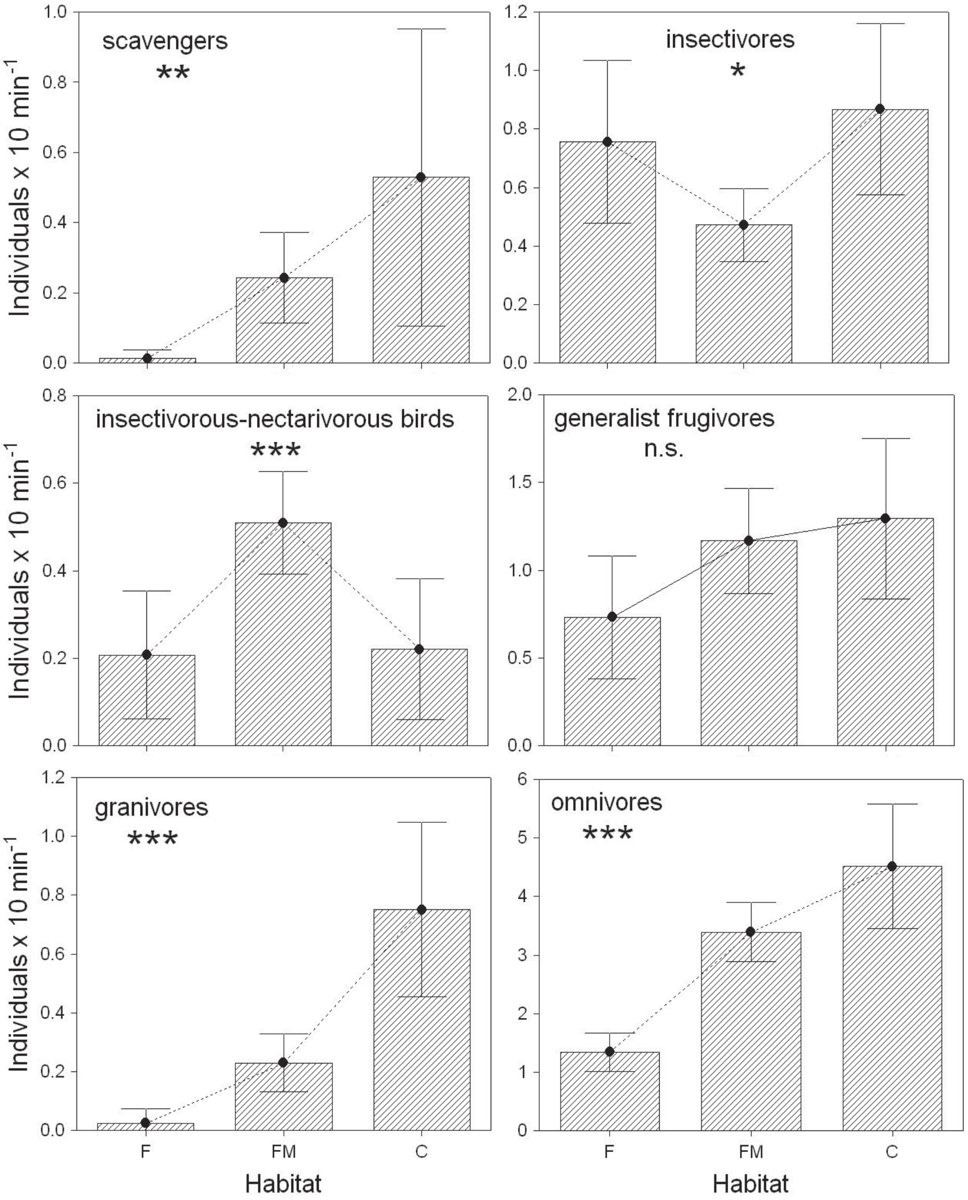

Fig. 10: Differences in abundance of feeding guilds between forest interior (F), forest margin (FM) and human-dominated countryside habitats (C) quantified by mean numbers of individuals counted per 10-min observation unit. Error bars represent 95% confidence intervals. Asterisks indicate statistical significance (* = p < 0.05, ** = p < 0.01, *** = p < 0.001) of Kruskal-Wallis test.

HERZOG et al. 2005). Our data indicate that particularly during rapid bird assessments surveys should be conducted from dawn to dusk because even during midday and afternoon, bird activity in Costa Rica was high enough that bird counts contributed significantly to achieving a high completeness of species lists. Also for comparing the abundance of species and guilds between habitats, additional counts during midday and afternoon may be valuable by increasing the number of point census replicates. When temporal distribution of point census replicates does not differ between habitats and therefore a systematic bias can be avoided, there is no reason to restrict bird counts exclusively to the early morning, particularly when available time for fieldwork is limited.

The number of birds counted per observation unit differed conspicuously between habitats. Highest bird counts were obtained in human-dominated habitats. However, it has to be considered that recorded bird density in human-dominated habitats may be inflated to an unknown extent by a better detectability of birds in such mostly open and semi-open habitats. This does not affect comparisons of relative abundance and species richness between habitats, but may bias comparisons of means and medians of counted birds. Therefore, apparent differences between habitats should be judged with caution if corresponding tests just reached the level of statistical significance.

The importance of human-dominated habitats for maintaining bird diversity

Because the number of counted birds per observation unit may be influenced by a better detectability of birds in (semi-)open countryside habitats than forested habitats, as mentioned above, we constructed species accumulation curves by plotting accumulative species numbers against accumulative numbers of counted birds and not against survey effort (= number of observation units). Rarefaction analysis as well as the estimates of total species richness ranked the habitat types according to species richness in the following order: forest margin > human-dominated habitats > forest interior.

A similar study comparing species richness of forests and human-dominated countryside habitats was conducted in the vicinity of the Las Cruces Biological Field Station situated close to the border between Costa Rica and Panama (DAILY et al. 2001). Although the study was conducted at a significantly higher elevation (760-1420 m a.s.l.) and included highly fragmented forests (area: 0.3-25 ha), the authors draw some similar conclusions from their results. At Las Cruces, the avifauna of countryside habitats also proved to be extremely species rich. A total of 123 species were recorded in human-dominated habitats compared to 79 species found in human-dominated habitats at La Gamba. The higher species richness reported for non-forested habitats for Las Cruces by DAILY et al. (2001) may be due to the higher sampling effort. For our study area the achieved species inventory for countryside habitats was still incomplete. However, also the estimated total species richness for countryside habitats at La Gamba (97 species) is still conspicuously lower compared to Las Cruces. This may be related to altitudinal differences or differences of habitat diversity or matrix heterogeneity of countryside habitats between study areas.

Habitat specificity in Pacific lowland birds

In our study, only a small number of species (8.8%) were recorded in all three habitat types, with the lowest faunal similarity existing between forest interior and human-dominated habitats. The forest edge proved to be intermediate between both habitats. Of the 272 bird species recorded at Las Cruces (southern Costa Rica), 55% were only reported from forested habitats and 23% only in open habitats; the remaining 22% occurred in both habitats (DAILY et al. 2001). When combing forest and forest margin into a category of forested habitats (comparable to the habitat category in DAILY et al. 2001), we found a slightly different pattern of faunal overlap between forest (including forest edge) and human-dominated habitats in our study. Of the 148 recorded species 49% were only recorded from forested habitats, 13% occurred only in human-dominated habitats, and a relatively large proportion of 39% was found in both habitat types. However, it has to be considered that species richness estimates for our surveyed habitats showed that species inventories are incomplete. Therefore, faunal overlap may be even underestimated as indicated by Sørensen similarities based on estimated shared number of species (Table 2).

In our study area, migratory birds wintering in Costa Rica were frequently recorded at forest edges and human-dominated habitats, but could not be recorded in forest interior. Remarkably, lowland forests in southern Mexico proved to be of much higher importance for migrants from North America (ESTRADA & COATES-ESTRADA 2005). However, these forests were highly fragmented and, therefore, likely to be more strongly influenced by edge effects.

The high overlap of species assemblages between habitats as documented by our study emphasises the potential of the diverse human-dominated countryside at La Gamba for maintaining a large proportion of the local species richness. The higher similarity of bird assemblages between human-dominated habitats and forested habitats compared to Las Cruces (Daily et al. 2001) may be due to the high density of strips of gallery forest and rows of roadside trees. A large proportion of forest species recorded within the human-dominated landscape matrix was observed in this countryside habitat typical for the close vicinity of La Gamba (unpublished data). However, while some forest species such as *Patagioenas nigrirostris* at least rarely visited such small forested strips within the anthropogenically modified landscape, other forest species such as *Habia atrimaxillaris* and *Crax rubra* appeared to be not capable of using such habitats at all (Fig. 5).

Implications for bird conservation

As shown for other tropical regions (e.g. Sodhi et al. 2005), in southern Costa Rica a substantial fraction of forest-affiliated bird species occur in human-dominated countryside habitats (Daily et al. 2001, this study). However, as emphasised by Daily et al. (2001), such conclusions exclusively based on temporally restricted surveys may convey a misleading impression of the capacity of such countryside habitats to support bird species over the long run. Many bird species, particularly frugivorous canopy species frequently exploit seasonal fruit resources in forest edge and (semi-)open habitats, but depend on forest habitats most of the year. The supply of important resources, such as food and nesting locations secure from predation, may not be sustainable in human-dominated countryside habitats. For instance, when long-lived trees and other plant species with poor recruitment in human-dominated habitats die off, this may cause a substantial decrease in species richness of (semi-)open areas (Daily et al. 2001).

Species commonly attending mixed-species foraging flocks may be at particular risk. Daily et al. (2001) found associations among some species in human-dominated countryside habitats in southern Costa Rica, but not the species richness or individual abundance characteristic of foraging flocks in forest habitats. A similar conclusion can be drawn by our unfortunately rather sparse data. Mixed species flocks appear to be relatively rare in the area of the Esquinas forest. During the whole period of field work, we recorded only five mixed-species flocks, but all in forested habitats (unpublished data).

The extent and intrinsic quality of human-dominated habitats will largely determine the future of life on the planet (Daily 1997, Daily et al. 2001). However, our study showed that even diverse human-dominated countryside habitats are only of limited conservation value for range-restricted species. From a conservation aspect, perhaps the black-cheeked ant-tanager *Habia atrimaxillaris*, represents the most important bird species of our study area La Gamba (Tebb 2007b). This tanager species is restricted to the lowlands of a small area in southwestern Costa Rica around Golfo Dulce and the Osa Peninsula and strictly depends on old-grown forests. Due to forest loss, it may well become confined to the Corcovado National Park and Golfito Faunal Refuge (Collar et al. 1994, BirdLife International 2007). However, populations appear to be stable in these protected areas, and the species remains common in Corcovado (BirdLife International 2007) and in the Esquinas forest reserve (own observations).

Other range-restricted birds (occurring on the Pacific slope of Costa Rica and parts of western Panama) recorded during our study were Cherrie's tanager *Ramphocelus costaricensis*, the charming hummingbird *Amazilia decora*, Baird's trogon *Trogon bairdii*, the black-hooded antshrike *Thamnophilus bridgesi*, the fiery-billed aracari *Pteroglossus frantzii*, the golden-naped woodpecker *Melanerpes chrysauchen*, the riverside wren *Thryothorus semibadius* and the spot-crowned euphonia *Euphonia imitans*. Only Cherrie's tanager reached a high abundance in human-dominated countryside habitats (see also Daily et al. 2001), while all other range-restricted species were exclusively found in forested habitats (*T. bairdii*: N = 10 birds; *T. bridgesi*: N = 9; *Pteroglossus frantzii*: N = 6; *M. chrysauchen*: N = 10; *E. imitans*: N = 6) or only a minor proportion of the total number of individuals was recorded in human-dominated habitats (*A. decora*: 25% of total of N = 12 birds; *T. semibadius*: 8%, N = 25). Additional range-restricted species recorded from the study area such as the turquoise cotinga *Cotinga ridgwayi* and yellow-billed cotinga *Carpodectes antoniae* were only recorded from forest habitats or such as the garden emerald *Chlorostilbon assimilis* and orange-collared manakin *Manacus aurantiacus* at least appear to be more abundant in old-grown forest than secondary habitats (Tebb 2007a. b). This clearly emphasises that a sustainable protection of remaining forest areas is the only option to maintain high bird species richness.

Potential effects of forest modification on ecosystem services provided by birds

Birds are important but ecologically little known actors in many ecosystems (Sekercioğlu et al. 2006) and a decrease of bird diversity as result of habitat modification can cause a decline of important ecosystem processes such as pollination and seed dispersal (Sekercioğlu et al. 2004). Our data indicated a pronounced change of feeding guild structure related to forest conversion. The increase of scavengers, omnivores and granivores from forest interior towards forest margin and (semi-)open countryside habitats was particularly conspicuous. These three feeding guilds apparently profited from forest conversion. For carrion feeders such as New World vultures it may be easier to detect carcasses in open areas than in closed forest. Additionally, human-dominated habitats may offer better food availability (carcasses of domestic animals such as cattle). The higher abundance of granivores in such countryside habitats is most likely related to an increased abundance of seeds in open habitats such as annual cultures (e.g. paddy fields).

Neotropical insectivorous birds appeared to respond extremely sensitively to habitat disturbance and fragmentation in other studies (CANADAY 1997, SEKERCIOĞLU et al. 2002, STRATFORD & STOUFFER 1999). Particularly insectivores of the forest interior are more likely to be absent from impacted forest and non-forest habitats than non-insectivores (CANADAY 1997). Also our study reported a conspicuously higher relative abundance of insectivores in forest (23%) compared to forest margin (8%) and human-dominated habitats (10%). However, the mean number of insectivorous birds per observation unit did not confirm this pattern, but showed a similar abundance in forest interior and human-dominated habitats. The unexpectedly high number of counted birds in human-dominated habitats is probably an artefact of higher detectability, but this remains to be explicitly tested.

With the exception of *Icterus galbula* (Icteridae), all the nectarivores at La Gamba were hummingbirds. They reached their highest abundance at the forest margin which corresponds well to the subjective impression of a higher availability of flowers at the forest edge. A similar abundance of nectarivores was found in forest interior and human-dominated habitats. Our results are consistent with previous studies reporting that hummingbirds may be less affected by deforestation and forest fragmentation than other guilds (BORGELLA et al. 2001).

Relative species richness of frugivores did not differed significantly between forest interior, forest edge and coffee plantations at a lowland site in Ecuador (CANADAY 1997). We also did not found a significant difference of the relative importance of frugivorous birds between habitat types at our lowland site. However, further studies are needed to analyse the effects of habitat modification on rates of visitation by birds to fruiting trees and seed dispersal efficiency, which may influence plant composition in fragmented landscapes (GRAHAM et al. 2002).

While CANADAY (1997) did not find a response of omnivorous birds to forest disturbance, our data showed a significant increase of omnivores from forest interior towards forest margin and human-dominated habitats as expected when assuming that it should be easier for generalists than specialists to adapt to highly disturbed landscapes.

Conclusions

Worldwide habitat loss, fragmentation and degradation are operating on a massive scale and have shown or predicted dire consequences for the future of global biodiversity including birds (SODHI & SMITH in press). Habitat loss in the tropics especially is unprecedented, which is of particular concern because the tropics have the greatest diversity and are centres of endemism. Major causes of bird endangerment are habitat loss and degradation (86% of threatened species), over-exploitation (ca. 33%), and invasive species (ca. 33%) (SODHI & SMITH in press, www.birdlife.org/action/ science/species/global_species_programme/red_list.html). Habitat loss also represents the major threat to birds in the neotropics (GARCÍA-MORENO et al. in press).

Only a small proportion of land can realistically be protected as nature reserves and thus conservation efforts also must focus on the ecological value of agroecosystems and developed areas surrounding nature reserves (PETIT et al. 1999). Although forest clearance does not necessarily spell doom for all forest species and indeed many can probably persist in human-dominated countryside landscapes that maintain forest fragments (DAILY et al. 2001) or strips of gallery forest, a future agricultural intensification may dramatically change the entire landscape matrix. This could cause not only a decrease of bird species richness in human-dominated habitats, but also may result in the development of more pronounced barriers for forest birds to move between remaining highly isolated forest fragments.

Further studies are needed to evaluate in detail the importance of individual habitat structures for maintaining bird species richness within Pacific lowland countryside landscapes of Costa Rica. A study in the lowlands of Panama showed that species of moderate and high vulnerability were primarily those categorised as forest specialists or forest generalists and even species-rich non-forest habitats provided little conservation value for the most vulnerable species (PETIT & PETIT 2003). Range-restricted species appeared to be more sensitive to forest modification also in our study area. This points to a similar situation for the Pacific lowland avifauna, because species with smaller ranges are mostly more vulnerable than widespread ones.

First preliminary observations from our study site indicated that particularly strips of gallery forests along streams contribute significantly to overall species richness (unpublished data). This habitat type common in the Golfo Dulce region is also mentioned by DAILY et al.

(2001) for Valle de Coto Brus located close to the border between Costa Rica and Panama. However, it remains unknown for a large proportion of species recorded from small forest strips within the matrix of (semi-) open countryside habitats if they are capable of reproducing in this habitat, if they only visit it to exploit temporarily available food sources, or if they use such habitat structures during dispersal. Species regularly observed in disturbed habitats not necessarily reproduce there as shown for the white-plumed antbird *Pithys albifrons* (Thamnophilidae). At an Ecuadorian lowland site, the species occurred in a variety of forested habitats, but individuals with bare, rugose brood patches were only found in undisturbed forest interior, indicating that habitats with greater human impact were suboptimal for reproduction (CANADAY 1997).

The landscape matrix structure can have a strong effect on recolonisation by birds (STOUFFER & BIERREGAARD 1995) and the maintenance of species richness in forest fragments may depend on the permeability of the matrix (ANTONGIOVANNI & METZGER 2005). Particularly patches of secondary vegetation (e.g. strips of secondary forests beside rivers) could represent an important component for improving the condition for birds in remaining forest remnants and for revitalising metapopulation dynamics by weakening barrier effects between forest fragments in human-dominated landscapes (e.g. STOUFFER et al. 2006).

Acknowledgements

We like to thank the Ministerio del Ambiente y Energía for granting the research permit for conducting this study. We are also grateful to Werner Huber and Anton Weißenhofer for their help in applying for necessary documents and for organising our first visit to La Gamba. Finally, we thank all students and colleagues who joined us during bird surveys: Florian Hofhansl, Dr. Werner Huber, Florian Karolyi, Hella Klosius, David Roderus, Dr. Norbert Sauberer, Benjamin Seaman, Stefan Schneeweihs, Elisabeth Vogel and Günther Wöss. We are grateful to Prof. Dr. Konrad Fiedler, who provided valuable statistical advice, and to Dr. Graham Tebb for providing many helpful comments on a former version of our manuscript. The fieldwork of CHS was supported by a travel grant from the University of Vienna. IR received a KWA grant of the University of Vienna.

References

ANTONGIOVANNI M. & J.P. METZGER (2005): Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. — Biol. Conserv. **122**: 441-451.

BIRDLIFE INTERNATIONAL (2007): Species factsheet: Habia atrimaxillaris. — http://www.birdlife.org (last accessed: 1 October 2007).

BLAKE J.G. (1992): Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. — The Condor **94**: 265-275.

BLAKE J.G. & B.A. LOISELLE (1992): Fruits in the diets of neotropical migrant birds in Costa Rica. — Biotropica **24**: 200-210.

BLAKE J.G. & B.A. LOISELLE (2000): Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. — The Auk **117**: 663-686.

BLAKE J.G. & B.A. LOISELLE (2001): Bird assemblages in second-growth and old-growth forests, Costa Rica: Perspectives from mist net and point counts. — The Auk **118**: 304-326.

BLAKE J.G. & B.A. LOISELLE (2002): Manakins (Pipridae) in second-growth and old-growth forests: patterns of habitat use, movement and survival. — The Auk **119**: 132-148.

BORGELLA R., SNOW A.A. & T.A. GAVIN (2001): Species richness and pollen loads of hummingbirds using forest fragments in Southern Costa Rica. — Biotropica **33**: 90-109.

CALDERÓN G.O., SANDOVAL L., CHAVES CAMPOS J., ORIAS J.V. & W.A. CERVANTES (2007): Official list of the birds of Costa Rica 2006. — Zeledonia **11**: 1-76.

CANADAY C. (1997): Loss of insectivorous birds along a gradient of human impact in Amazonia. — Biol. Conserv. **77**: 63-77.

CHAO A., CHAZDON R.L., COLWELL R.K. & T.-J. SHEN (2005): A new statistical approach for assessing similarity of species composition with incidence and abundance data. — Ecol. Lett. **8**: 148-159.

COLWELL R.K. (2006) EstimateS: Statistical estimation of species richness and shared species from samples. Version 8. http://www.purl.oclc.org/estimates (last accessed: 1 October 2007).

CURRAN L.M., TRIGG S.N., MCDONALD A.K., ASTIANI D., HARDIONO Y.M., SIREGAR P., CANIAGO I. & E. KASISCHKE (2004): Lowland forest loss in protected areas of Indonesian Borneo. — Science **303**: 1000-1003.

DAILY G.C. (1997): Countryside biogeography and the provision of ecosystem services. — In: RAVEN P. (ed.), Nature and human society: The quest for a sustainable world. National Research Council, National Academy Press, Washington D.C.: 104-113.

DAILY G.C., EHRLICH P.R. & G.A. SANCHEZ-AZOFEIFA (2001): Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. — Ecol. Appl. **11**: 1-13.

DUNN R.R. (2004): Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds, and Lepidoptera. — For. Ecol. Manage. **191**: 215-224.

ESTRADA A., COATES-ESTRADA R. & D.A. MERITT Jr. (1997): Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. — Biodiv. Conserv. **6**: 19-43.

FJELDSÅ J. (1999): The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. — Bird Conserv. Internat. **9**: 47-62.

García-Moreno J., Clay R.P. & C.A. Ríos-Muñoz (in press): The importance of birds for conservation in the neotropical region. — J. Ornithol., DOI 10.1007/s10336-007-0194-5.

Garrigues R. & R. Dean (2007): The Birds of Costa Rica: A Field Guide. — Cornell University Press, New York.

Graham C., Martínez-Leyva J.E. & L. Cruz-Paredes (2002): Use of fruiting trees by birds in continuous forest and riparian forest remnants in Los Tuxtlas, Veracruz, Mexico. — Biotropica **34**: 589-597.

Henle K., Lindenmayer D.B., Margules C.R., Saunders D.A. & C. Wissel (2004): Species survival in fragmented landscapes: where are we now? — Biodiv. Conserv. **13**: 1-8.

Herzog S.K., Kessler M. & K. Bach (2005): The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. — Ecography **28**: 209-222.

Kofron C.P. & A. Chapman (1995): Deforestation and bird species composition in Liberia, West Africa. — Trop. Zool. **8**: 239-256.

Krebs C.J. (1989): Ecological Methodology. — Harper Collins Publishers, New York.

Lawton J.H., Bignell D.E., Bolton B., Bloemers G.F., Eggleton P., Hammond P.M., Hodda M., Holt R.D., Larsen T.B., Mawdsley N.A., Stork N.E., Srivastava D.S. & A.D. Watt (1998): Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. — Nature **391**: 72-76.

Loiselle B.A. (1988): Bird abundance and seasonality in a Costa Rican lowland forest canopy. — The Condor **90**: 761-772.

Loiselle B.A. & J.G. Blake (1991): Temporal variation in birds and fruits along an elevational gradient. — Ecology **72**: 180-193.

Mazer S. & N.T. Wheelwright (1993): Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. — Evol. Ecol. **7**: 556-575.

Naidoo R. (2004): Species richness and community composition of songbirds in a tropical forest-agricultural landscape. — Anim. Conserv. **7**: 93-105.

Naturesongs & D. Von Gausig (1998-2001): — http://www.naturesongs.com/CRsounds.html#birds (last accessed: 10 September 2007).

O'Dea N., Watson J.E.M. & R.J. Whittaker (2004): Rapid assessment in conservation research: a critique of avifaunal assessment techniques illustrated by Ecuadorian and Madagascan case study data. — Divers. Distrib. **10**: 55-63.

Petit L.J., Petit D.R., Christian D.G. & H.D.W. Powell (1999): Bird communities of natural and modified habitats in Panama. — Ecography **22**: 292-304.

Petit L.J. & D.R. Petit (2003): Evaluating the importance of human-modified lands for neotropical bird conservation. — Conserv. Biol. **17**: 687-694.

Powell G.V.N. & J. Bjork (1994): Implications of altitudinal migration for conservation strategies to protect tropical biodiversity: a case study of the resplendent quetzal *Pharomachrus mocinno* at Monteverde, Costa Rica. — Bird Conserv. Int. **4**: 161-174.

Ross D.L. Jr. (2001): Costa Rican bird songs. — Distribuidores Tropical S.A., San José.

Sánchez-Azofeifa G.A., Daily G.C., Pfaff A.S.P. & C. Busch (2003): Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. — Biol. Conserv. **109**: 123-135.

Sauberer N., Tebb G., Huber W. & A. Weissenhofer (eds) (2007): The birds of the Golfo Dulce Region. — Verein zur Förderung der Tropenstation La Gamba, Wien.

Schulze C.H., Waltert M., Kessler P.J.A., Pitopang R., Shahabuddin, Veddeler D., Steffan-Dewenter I., Mühlenberg M., Gradstein S.R. & T. Tscharntke (2004): Biodiversity indicator taxa of tropical landuse systems: comparing plants, birds and insects. — Ecol. Appl. **14**: 1321-1333.

Schwartzman A., Moreira A. & D.C. Nepstad (2000): Rethinking tropical forest conservation: Perils in parks. — Conserv. Biol. **14**: 1351-1357.

Sekercioğlu C.H. (2006): Increasing awareness of avian ecological function. — Trends Ecol. Evol. **21**: 464-471.

Sekercioğlu C.H., Ehrlich P.R., Daily G.C., Aygen D., Goehring D. & R.F. Sandi (2002): Disappearance of insectivorous birds from tropical forest fragments. — Proc. Natl. Acad. Sci. USA **99**: 263-267.

Sekercioğlu C.H., Daily G.C. & P.R. Ehrlich (2004): Ecosystem consequences of bird declines. — Proc. Natl. Acad. Sci. USA **101**: 18042-18047.

Sekercioğlu C.H., Loarie S.R., Brenes F.O., Ehrlich P.R. & G.C. Daily (2007): Persistence of forest birds in the Costa Rican agricultural countryside. — Conserv. Biol. **21**: 482-494.

Simberloff D. (1978): Use of rarefaction and related methods in ecology. — In: Dickson K.L., Cairns J. Jr. & R.J. Livingston (eds), Biological data in water pollution assessment: Quantitative and statistical analyses. American Society for Testing and Materials, Philadelphia: 150-165.

Sodhi, N.S. & K.G. Smith (2007): Conservation of tropical birds: mission impossible? — Journal of Ornithology **148**: 305-309.

Sodhi N.S., Koh L.P., Prawiradilaga D.M., Darjono, Tinulele I., Putra D.D. & T.H.T. Tan (2005): Land use and conservation value for forest birds in Central Sulawesi (Indonesia). — Biol. Conserv. **122**: 547-558.

Southwood R. & P.A. Henderson (2000): Ecological methods. — Blackwell Science, Oxford.

StatSoft (2005): STATISTICA for Windows, 7.1. — StatSoft Inc., Tulsa, Oklahoma.

Stiles F.G. (1975): Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. — Ecology **56**: 285-301.

Stiles F.G., Skutch A.F. & D. Gardner (1989): A Guide to the Birds of Costa Rica. — Cornell University Press, New York.

Stouffer P.C. & R.O. Bierregaard Jr. (1995): Use of Amazonian forest fragments by understory insectivorous birds. — Ecology **76**: 2429-2445.

Stouffer P.C., Bierregaard Jr. R.O., Strong C. & T.E. Lovejoy (2006): Long-term landscape change and bird abundance in Amazonian rainforest fragments. — Conserv. Biol. **20**: 1212-1223.

Stratford J.A. & P. Stouffer (1999): Local exctinction of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. — Conserv. Biol. **13**: 1416-1423.

Tebb G. (2007a): Bird list for La Gamba. — In: Sauberer N., Tebb G., Huber W. & A. Weissenhofer (eds), The birds of the Golfo Dulce Region. Verein zur Förderung der Tropenstation La Gamba, Wien: 68-77.

Tebb G. (2007b): "Very important birds" of the Esquinas forest. — In: Sauberer N., Tebb G., Huber W. & A. Weissenhofer (eds), The birds of the Golfo Dulce Region. Verein zur Förderung der Tropenstation La Gamba, Wien: 65–66.

TRAMER E.J. & T.R. KEMP (1980): Foraging ecology of migrant and resident warblers and vireos in the highlands of Costa Rica. — In: KEAST A. & E.S. MORTON (eds), Migrant birds in the neotropics: Ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C.: 285-296.

TRAMER E.J. & T.R. KEMP (1982): Notes on migrants wintering at Monteverde, Costa Rica. — Wilson Bull. **94**: 350–354.

WALTERT M., MARDIASTUTI A. & M. MÜHLENBERG (2004): Effects of land use on bird species richness in Sulawesi, Indonesia. — Conserv. Biol. **18**: 1339–1346.

WEBER A., HUBER W., WEISSENHOFER A., ZAMORA N. & G. ZIMMERMANN (2001): An introductory field guide to the flowering plants of the Golfo Dulce rainforests, Costa Rica. — Stapfia **78**: 1-462.

WHEELWRIGHT N.T. (1991): How long do fruit-eating birds stay in the plants where they feed? — Biotropica **23**: 29-40.

WHEELWRIGHT N.T., HABER W.A., MURRAY K.G. & C. GUIDON (1984): Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. — Biotropica **16**: 173-192.

YOUNG B.E., GARVIN M.C. & D.B. MCDONALD (1993): Blood parasites in birds from Monteverde, Costa Rica. — J. Wildlife Diseases **29**: 550–560.

YOUNG B.E., DEROSIER D. & G.V.N. POWELL (1998): Diversity and conservation of understorey birds in the Tilarán Mountains, Costa Rica. — The Auk **115**: 998-1016.

Address of authors:

Christian H. SCHULZE
Isabell RIEDL
Department of Population Ecology
Faculty of Life Sciences
University of Vienna
Althanstraße 14
A-1090 Vienna, Austria
E-mail: christian.schulze@univie.ac.at
isabellR@gmx.net

Zeitschrift/Journal: Stapfia

Jahr/Year: 2008

Band/Volume: 0088

Autor(en)/Author(s): Schulze Christian H., Riedl Isabell

Artikel/Article: Bird assemblages of forested and human-modified countryside habitats in the Pacific lowlands of southern Costa Rica 395-408