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DISSERTATION / DOCTORAL THESIS

Titel der Dissertation /Title of the Doctoral Thesis

„Gallery forests in the lowlands of Costa Rica: ecological traps or suitable breeding sites and dispersal corridors for forest birds?“

verfasst von / submitted by

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1. Acknowledgements

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In particular, I want to thank my parents Brigitte Riedl-Milan and Christoph Riedl who raised me as an independent and hard-working woman, enabled me to study and always encouraged me to continue my education.

2. Curriculum vitae

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Education

2017	Doctoral thesis in partial fulfilment of the requirements for the degree of Dr. rer. nat.
2011	Degree in Business economics of Berufsförderungsinstitut (BFI) Austria
Since 06/2008	Doctoral studies of biology at the University of Vienna, Ecology
27/05/2008	Master's Degree with distinction (Mag. rer. nat.) at University of Vienna, Ecology
2003	Matriculation with distinction at BG/BRG Perchtoldsdorf, Perchtoldsdorf

Professional Career

07/2016-07/2017	Maternity leave
Since 06/2012	Assistant at Werner Lampert BeratungsGmbH, 1010 Vienna
Spring 2011	Research for WWF
06/2008-10/2010	Stay abroad at Costa Rica for Doctoral thesis
06-09/2007	Stay abroad at Costa Rica for Master thesis
07/2006	Laboratory at the department of Microbial Ecology, University of Vienna
02/2005-06/2006	Contract for work: Austrian Research Centers/ Biotechnology Seibersdorf

Publications

Cornils, J. S., Riedl, I., Fricke, J., Katz, M. & Schulze, C. H. (2015). Population density and habitat preferences of the Black-cheeked Ant-tanager *Habia atrimaxillaris*. Bird Conservation International, 25(3), 306-321.

Riedl, I. G., Fricke, J., Katz, M. & Schulze, C. H. (2010). Un caso extremo de ectoparasitismo de moscardón del género *Philornis* en tangara hormiguera carinegra *Habia atrimaxillaris*, endémica del Golfo Dulce, Costa Rica. Zeledonia, 14(2), 39.

Riedl, I. G. & Schulze, C. H. (2010). Observación de manguito de veragua *Anthracothorax veraguensis* (Reichenbach 1855) en las tierras bajas del Pacífico sur de Costa Rica. Zeledonia (Costa Rica), 14(1), 21-27.

Schulze, C. H. & Riedl, I. (2008). Bird assemblages of forested and human-modified countryside habitats in the Pacific lowlands of southern Costa Rica. Natural and cultural history of the Golfo Dulce Region, Costa Rica. Stapfia, 88, 395-408.

3. Abstract

Recordings of an exceptionally rapid loss of biodiversity over the last few centuries indicate that we are in the middle of the sixth mass extinction. In birds, habitat fragmentation is well-known for its negative effect on diversity. Due to growth of human population, agricultural and settlement areas are especially expanding in tropical zones, which leads to the increasing fragmentation of natural habitats such as lowland rainforests.
Human-modified habitats often act as effective barrier for forest species impeding movement between remaining forest fragments. Gallery forests embedded in such landscapes may provide structures used as biological corridors or stepping stones by forest species. However, their importance for facilitating the use of anthropogenically altered landscapes by forest species is only incompletely known.
In my study, I examined the composition and structure of bird communities as well as temporal changes and nest predation rates in gallery forests and their surroundings in La Gamba, in the Pacific lowlands of Costa Rica. La Gamba is situated near the Esquinas Rainforest. The region is extremely species rich and is upvalued by the occurrence of the Black-cheecked Ant-Tanager *Habia atrimaxillaris*. This range-restricted species only was observed in forest interior and margin.
Nevertheless, gallery forests turned out to inhabit a high bird richness comparable to pristine forests. However, richness of forest specialists decreased significantly from forest interior towards gallery forests. Their strip width and connectivity to the closed forest affected forest specialists positively.
Most of the feeding guilds were favoured or not affected by the highly fragmented habitat gallery forest and only insectivores declined significantly from forest interior towards gallery forests.
Temporal changes in bird species composition between survey periods could hardly be related to seasons (wet vs. dry season). For example frugivores, nectarivores, omnivores and granivores were higher abundant in the wet and dry season 2009, than in the dry season 2008 and wet season 2010. Instead, insectivores were less abundant in gallery forest habitats in the dry seasons, but the highest recorded abundance was at forest margin in the dry season 2009. Therefore, I suggest that seasonal changes of resource availability in the area are not strong enough to lead to significant changes in bird assemblages.
Studying clutch predation using artificial nests, nest predation was found being significantly higher at gallery forests than at forest interior. Hence, small strips of gallery forests may act as ecological traps for forest birds, when utilizing them as breeding habitat.
Still, my research indicates that gallery forests could maintain a substantial fraction of lowland forest birds, which may revitalise metapopulation dynamics by acting as corridors and stepping stones.

4. Zusammenfassung

Der außergewöhnlich hohe Artenverlust in den letzten Jahrhunderten deutet darauf hin, dass wir uns inmitten des sechsten Massensterbens befinden. Bei Vögeln ist es bekannt, dass die Fragmentierung von Habitaten negative Auswirkungen auf die Diversität hat. Das starke Wachstum der menschlichen Bevölkerung führt dazu, dass sich Siedlungen und landwirtschaftlich genutzte Flächen vor allem in tropischen Gebieten ausbreiten, was zur Fragmentierung von natürlichen Habitaten wie Tieflandregenwäldern führt.
Menschlich beeinflusste Gebiete wirken oft als effektive Ausbreitungsbarrieren für Waldarten und verhindern einen Artenaustausch zwischen Waldfragmenten. In solche Landschaften eingebettete Galeriewälder könnten als biologische Korridore oder Trittsteine für Waldarten dienen. Dennoch ist die Bedeutung solcher mehr oder weniger linearen Waldstreifen für Waldarten, indem sie die Permeabilität der anthropogen veränderten Landschaften erhöhen, nur sehr unzureichend bekannt.
In meiner Studie untersuchte ich die Zusammensetzung und Struktur von Vogelzönosen, deren zeitliche Veränderung sowie Nestprädationsraten in Galeriewäldern und deren Umgebung in La Gamba, im pazifischen Tiefland von Costa Rica. La Gamba befindet sich nahe des Esquinas Regenwaldes. Die Region ist extrem artenreich und wird durch das Vorkommen der Schwarzwangen-Ameisentangare *Habia atrimaxillaris* zusätzlich naturschutzfachlich aufgewertet. Diese Art, deren Verbreitungsgebiet auf die Golfo-Dulce-Region beschränkt ist, konnte nur im Waldinneren beobachtet werden.
Dennoch, beherbergten Galeriewälder einen ähnlich hohen Vogelartenreichtum wie die unberührten Wälder.
Der Artenreichtum von Waldspezialisten nahm jedoch signifikant vom Waldinneren in Richtung Galeriewälder ab. Deren Breite und eine direkte Verbindung zu geschlossenen Waldflächen beeinflusste Waldvogelarten positiv.

Die meisten Nahrungsgilden wurden positiv oder gar nicht durch das stark fragmentierte Habitat Galeriewald beeinflusst, nur Insektivore nahmen signifikant vom Waldinneren zu den Galeriewäldern ab.
Zeitliche Veränderungen bei den Vogelgesellschaften konnten kaum auf die Trocken- und Regenzeit zurückgeführt werden. Zum Beispiel waren Frugivore, Nektarivore, Omnivore und Granivore in der Regen- und Trockenzeit 2009 häufiger als in der Trockenzeit 2008 und der Regenzeit 2010. Stattdessen, waren Insektivore in den Galeriewäldern in beiden Trockenzeiten am seltensten, und die größte Abundanz fand ich am Waldrand in der Trockenzeit 2009. Daher, vermute ich, dass die saisonalen Unterschiede in der Nahrungsverfügbarkeit zu gering sind, um zu signifikanten Veränderungen in den Vogelgesellschaften zu führen.

Bei der Untersuchung der Prädation auf Vogelgelege mittels Kunstnestern, konnte eine signifikant höhere Nestprädation in den Galeriewäldern im Vergleich zum Waldinneren festgestellt werden. Dies lässt vermuten, dass Galeriewälder für Waldvogelarten als ökologische Fallen fungieren könnten.

Dennoch zeigte meine Studie, dass Galeriewälder einen nicht unbeträchtlichen Teil der Tieflandwaldvogelarten beherbergen und daher möglicherweise als Korridore und Trittsteine dienen, welche die Metapopulationsdynamik zumindest mancher Arten aufrechterhalten könnten.

5. List of manuscripts with statement of personal contribution

a. Schulze, C. H. & Riedl, I. (2008). Bird assemblages of forested and human-modified countryside habitats in the Pacific lowlands of southern Costa Rica. Natural and cultural history of the Golfo Dulce Region, Costa Rica. Stapfia, 88, 395-408.

Status: published

Personal Contribution:

- Field work (partly)
- Data preparation

b. Riedl, I., Schütz C. & Schulze, C. H. (2017). The importance of gallery forests for forest birds in the lowland countryside of Costa Rica

Status: submitted to *Nature Conservation* (Rejected 31/08/2017, Resubmission is encouraged after a thorough revision.)

Personal Contribution:

- Planning and conception of the field work together with C. H. Schulze
- Field work
- Data and data preparation
- Analyses together with C. Schütz and C. H. Schulze
- Literature survey, drafting and writing of the manuscript

c. Riedl, I. & Schulze, C. H. (2017). Indistinct effects of season on the composition of bird species assemblages in forest habitats in the Pacific lowlands of Costa Rica

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Personal Contribution:

- Planning and conception of the field work together with C. H. Schulze
- Field work
- Data and data preparation
- Analyses together with C. H. Schulze
- Literature survey, drafting and writing of the manuscript

d. Riedl, I. & Schulze, C. H. (2017). Understory forest birds facing higher clutch predation risk in linear gallery forest strips compared to old-growth forest areas: a case study using artificial nests

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Personal Contribution:

- Planning and conception of the field work together with C. H. Schulze
- Field work
- Data and data preparation
- Analyses together with C. H. Schulze
- Literature survey, drafting and writing of the manuscript

e. Cornils, J. S., Riedl, I., Fricke, J., Katz, M. & Schulze, C. H. (2015). Population density and habitat preferences of the Black-cheeked Ant-tanager *Habia atrimaxillaris*. Bird Conservation International, 25(3), 306-321.

Status: published

Personal Contribution:

- Planning and conception of the field work together with C. H. Schulze
- Field work together with J. Cornils, J. Fricke, M. Katz
- Part of data, data preparation
- Analyses together with J. Cornils, J. Fricke, M. Katz, C. H. Schulze
- Literature survey and Co-Author

f. Riedl, I. G. & Schulze, C. H. (2010). Observation of Veraguan Mango *Anthracothorax veraguensis* (Reichenbach, 1855) in the southern Pacific lowlands of Costa Rica/ Observación de manguito de veragua *Anthracothorax veraguensis* (Reichenbach 1855) en las tierras bajas del Pacífico sur de Costa Rica. Zeledonia (Costa Rica) 14(1): 21-27.

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Personal Contribution:

- Planning and conception of the field work together with C. H. Schulze
- Field work
- Data, Photos
- Literature survey, drafting and writing of the manuscript

6. General introduction

The loss of tropical forests is widely discussed in the context of climate change, the expansion of crops like soybean and oil palm, and the conversion of forest to permanent pastures. The disappearance of tropical pristine forests is especially of concern, because they have been determined as the most species-rich biome on Earth, inhabiting astonishingly 50% of species on just 7% of the land area (Wilson 1988). Although the annual rate of net loss of forest has slowed from 0.18 percent in the 1990s to 0.08 percent over the last five-year period, the largest forest area loss occurred in the tropics (MacDicken et al. 2015). Unfortunately, deforestation in tropical hotspots is projected to result in the extinction of at least 18% of the species by 2100 or even 40% if natural habitats are only retained in currently protected areas (Pimm & Raven 2000). Considering that widespread taxonomical and functional erosion of biodiversity even happens in protected areas (Laurance et al. 2012), this predicted extinction rate may be widely underestimated. The main factors pushing extinction in the remaining forest fragments are human disturbance, the reduction of population sizes, reduction of immigration rates, forest edge effects (e.g. resulting in a higher predation risk), changes in community structure and the immigration of exotic species (Turner 1996, Tabarelli et al. 2012, Hufbauer et al. 2015). Hence, it is crucial to conserve protected areas, but also to pay attention to their surroundings, like establishing buffer zones and increasing connectivity to other forest areas (Laurance et al. 2012). A term always arising in this context are biological corridors.

To maintain viable regional populations the connectivity to other populations is elemental (Cushman et al. 2013, Hufbauer et al. 2015). Regrettably, many forest species avoid clearings even smaller than 100 m (Laurance et al. 2012). Biological corridors aid isolated populations to spread and re-colonize remaining forest fragments (Beier & Noss 1998). For example, forest birds cross open areas preferentially along wooded connecting corridors (Haas 1995). Corridors typically are linear patches, such as streamside riparian areas, shelter belts, forest remnants remaining from tree harvest, living fences and, hedgerows (Rosenberg et al. 1997). Further, remnant trees may increase metapopulation dynamic functioning as “stepping stones” (Guevara et al. 1998, Harvey and Haber 1998, Harvey et al. 2006, Manning et al. 2006).

For my doctoral thesis, I conducted a broadly based ornithological research about the importance of gallery forests in the surroundings of the Tropical Station La Gamba (www.lagamba.at), in the Pacific lowlands of Costa Rica. This small country in Central America is a model-state in nature conservation, where forest cover augmented 0.5% per year between 1998 and 2013 (Minae, Sinac & Conagebio 2013). Furthermore, a forestry law in Costa Rica (Ministerio de Ambiente y Energía, 1996) prohibits felling trees beside rivers

since 1996. The resulting network of gallery forest strips within a landscape matrix dominated by strongly human-modified habitats may increase the connectivity between forest remnants by acting as corridors and stepping stones (Gillies & Clair 2008, Seaman & Schulze 2010, Fagan et al. 2016).

Gallery forests in our study area are surrounded by settlements (Fig. 1a) and agricultural areas such as pastures (Fig. 1b), oil palm plantations and rice fields. Two types have been defined — gallery forests connected (GC, Fig. 1c) to forest and isolated (GI, Fig. 1d) from forest. The mean width (± SD) of forest strips was 62.05 (± 40.33) m for my GC sites and 21.77 (± 10.66) m for my GI sites. Mean tree height for all gallery forest types was between 10 and 15 m and the understorey density was comparable with those of forest margins and the forest interior.

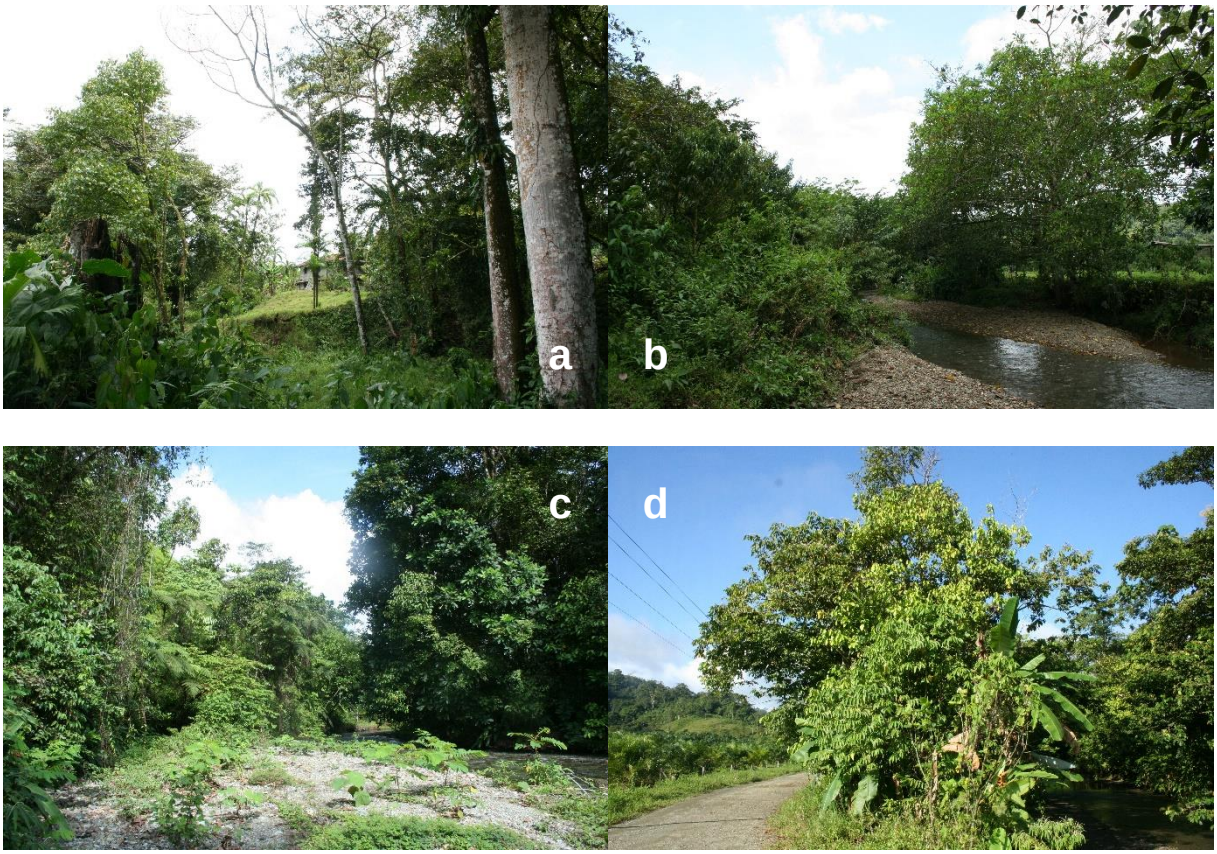

Figure 1. Examples of studied gallery forests in vicinity of the Tropical Station La Gamba. **a**: gallery forest isolated from closed forest and bordering on a settlement. **b**: gallery forest connected to closed forest and bordering on a pasture. **c**: connected gallery forest. **d**: isolated gallery forest.

The study area is a very species rich region with closed forests, gallery forests and strongly human-modified habitats like settlements, pastures and oil palm plantations. So far, more than 330 bird species, including 55 migrants, were recorded (Tebb 2007), and the number rose by more than 20 species during my surveys. One those observed species, the Veraguan Mango *Anthracothorax veraguensis* (Reichenbach, 1855), even represented the

first record for the country Costa Rica (Riedl & Schulze 2010, Chapter 7f). The high conservation value of the area is underlined by the occurrence of the Black-cheeked Ant-Tanager *Habia atrimaxillaris* (Fig. 2), which is endangered and endemic to the Golfo Dulce lowlands of southwestern Costa Rica and its population seems to be declining (IUCN Red List 2017).

Therefore, gathering information about the area is of big interest for conservation management plans.

In my thesis, I particularly addressed following questions:

a) How do bird assemblages change from forested towards human-modified countryside habitats? (Chapter 7a)
b) Can gallery forest strips serve as corridors and stepping stones for tropical forest birds within a landscape matrix consisting of strongly human-dominated habitats? (Chapter 7b)
c) Are composition and structure of bird assemblages affected by seasonal climate changes? And does the strength of such effects differ between habitats? (Chapter 7c)
d) Are understory forest birds facing higher clutch predation risk in linear gallery forest strips compared to old-growth forest areas? Are gallery forests a suitable breeding site or ecological trap for forest birds? (Chapter 7d)
e) Which are the habitat preferences of the Black-cheeked Ant-Tanager *Habia atrimaxillaris* in the lowland forest area of the Golfo Dulce region? How dense is its population? (Chapter 7e)

Figure 2. Black-cheeked Ant-Tanager *Habia atrimaxillaris*, range-restricted species to Golfo Dulce lowlands

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7. Publications and unpublished manuscripts

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

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

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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, márgenes 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 comparado 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 hábitats 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) fueron 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 sustancial 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 difiere entre los tres diferentes hábitat. El cambio 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 insectívoras registradas por unidad de observación fue inferior en el margen 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 hábitats 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, hábitats 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 (Şekercioğlu 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, Şekercioğlu 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, Şekercioğlu 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.

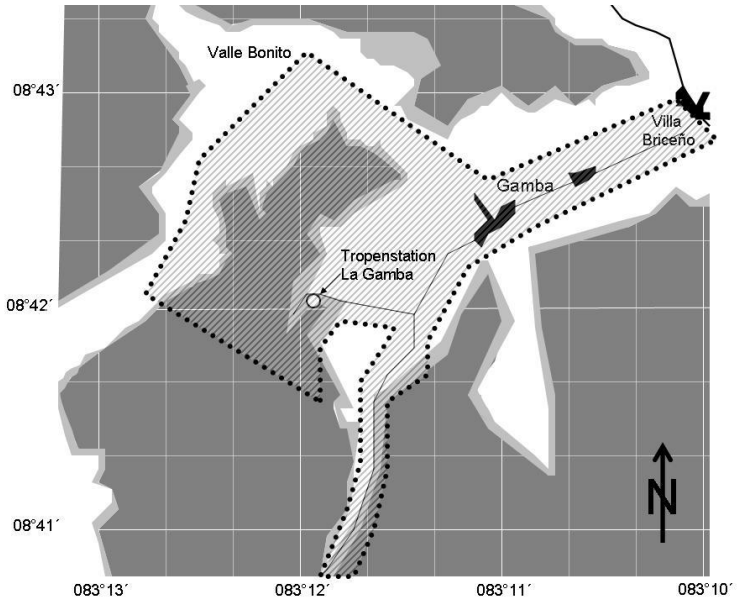

Fig. 1: Study area showing the three different surveyed habitat types: forest interior (dark grey), forest margin (pale grey) and human-dominated countryside habitats (white). Hatching indicates the approximate area in which bird surveys were conducted.

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).

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 significantly affected by observation time and habitat (Tab. 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).

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

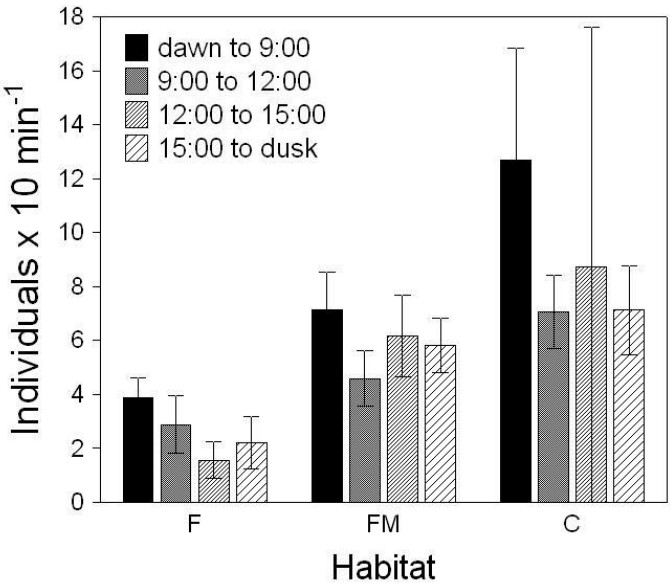

Fig. 2: Effects of habitat (F – forest interior, FM – forest margin, C – human-dominated countryside habitats) and survey time on mean number of birds counted per 10-min observation unit.

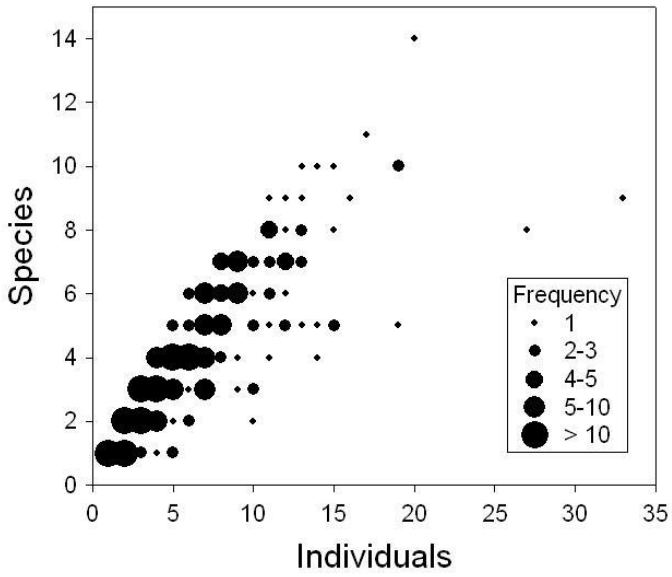

Fig. 3 Relationship between number of counted birds and species recorded per 10-min observation unit.

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).

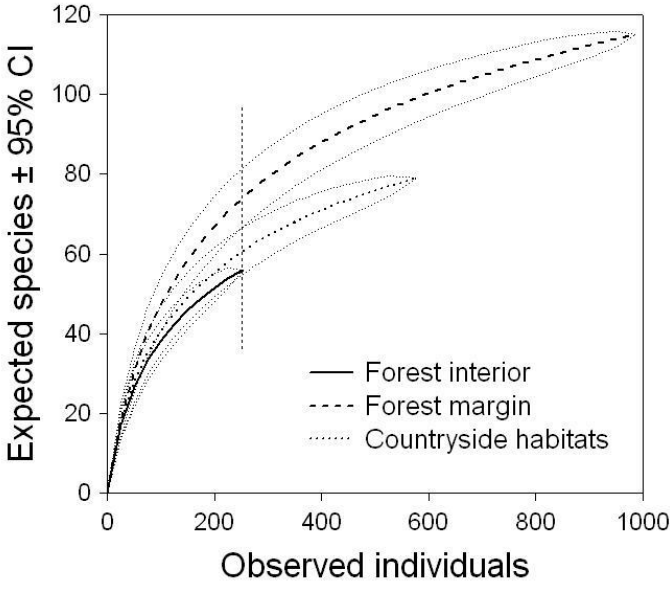

Fig. 4: Species accumulation curves ± 95% confidence intervals for bird assemblages of forest interior, forest margin and human-dominated countryside habitats. The vertical dashed line indicates the largest shared sample size of 253 birds.

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 (Tab. 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%) (Tab. 2).

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 human-modified 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

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).

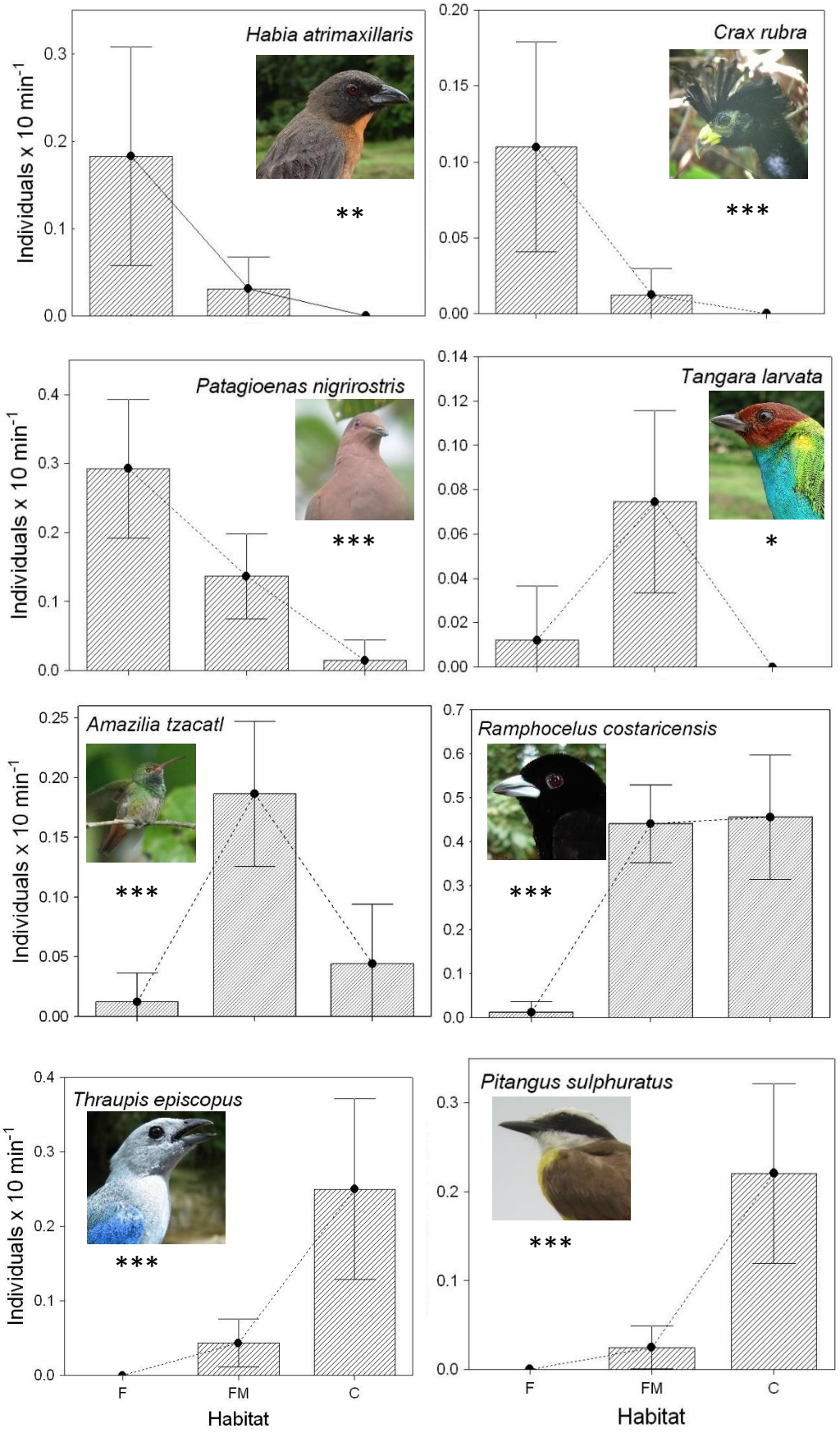

Fig. 5: Habitat specificity of selected species quantified as mean number of individuals counted per 10-min observation unit at forest interior (F), forest margin (FM) and human-dominated countryside habitats (C). Error bars represent 95% confidence intervals. Asterisks indicate statistical significance (*

= 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.

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 (Tab. 3). As expected, classical Sørensen similarities severely underestimated the predicted fraction of shared species.

Table 3. Similarity between bird assemblages surveyed at forest interior (F), forest margin (FM) and human-modified 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	–

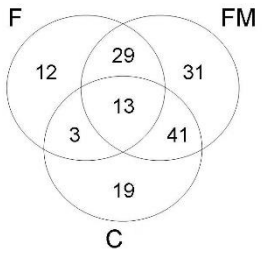

Fig. 6 Faunal overlap between the three surveyed habitat types (F – forest interior, FM – forest margin, C – human-dominated countryside habitats) quantified as number of species recorded in individual habitats only, recorded in two habitat types and all habitat types.

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

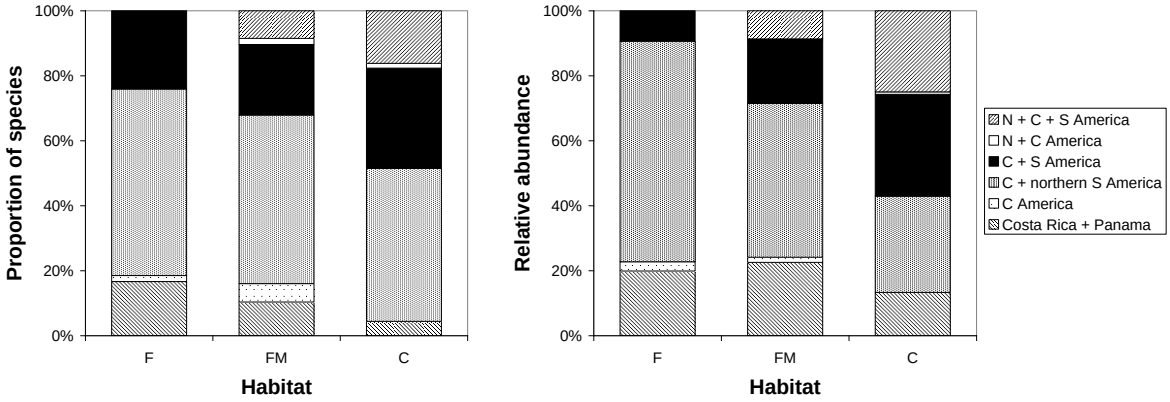

Fig. 7 Relative species richness and abundance of species with different distribution ranges at forest interior (F), forest margin (FM) and human-dominated countryside habitats (C). Species with smallest ranges represent birds endemic to Costa Rica and Panama, species with largest ranges occur over large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

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).

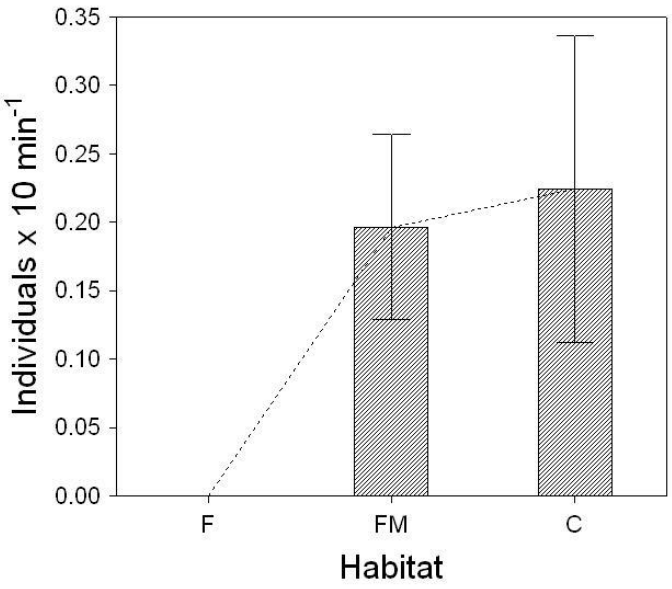

Fig. 8: Differences of abundance of migratory birds between forest interior (F), forest margin (FM) and human-dominated countryside habitats (C) quantified by mean number of individuals counted per 10-min observation unit. Error bars represent 95% confidence intervals.

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%).

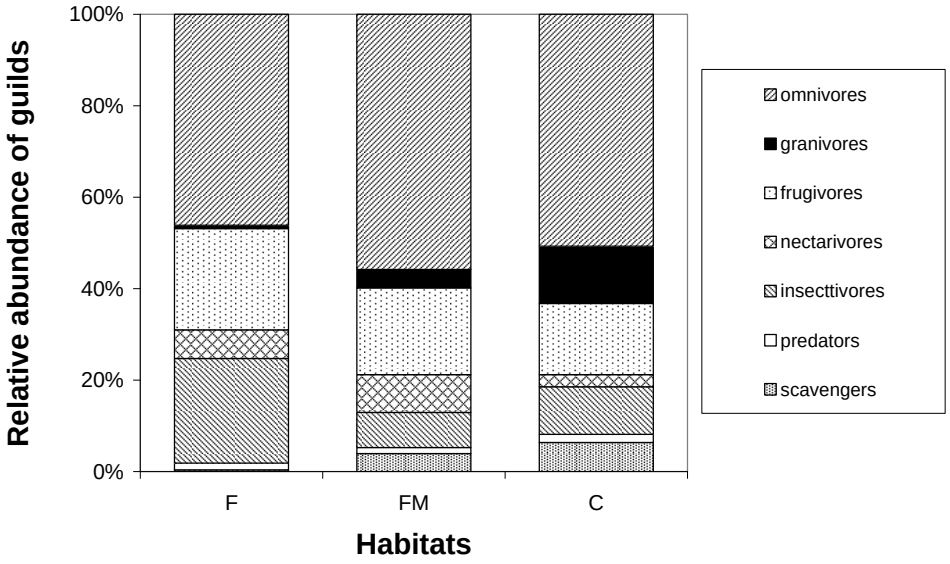

Fig. 9 Relative abundance of feeding guilds at forest interior (F), forest margin (FM) and human-dominated countryside habitats (C).

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 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).

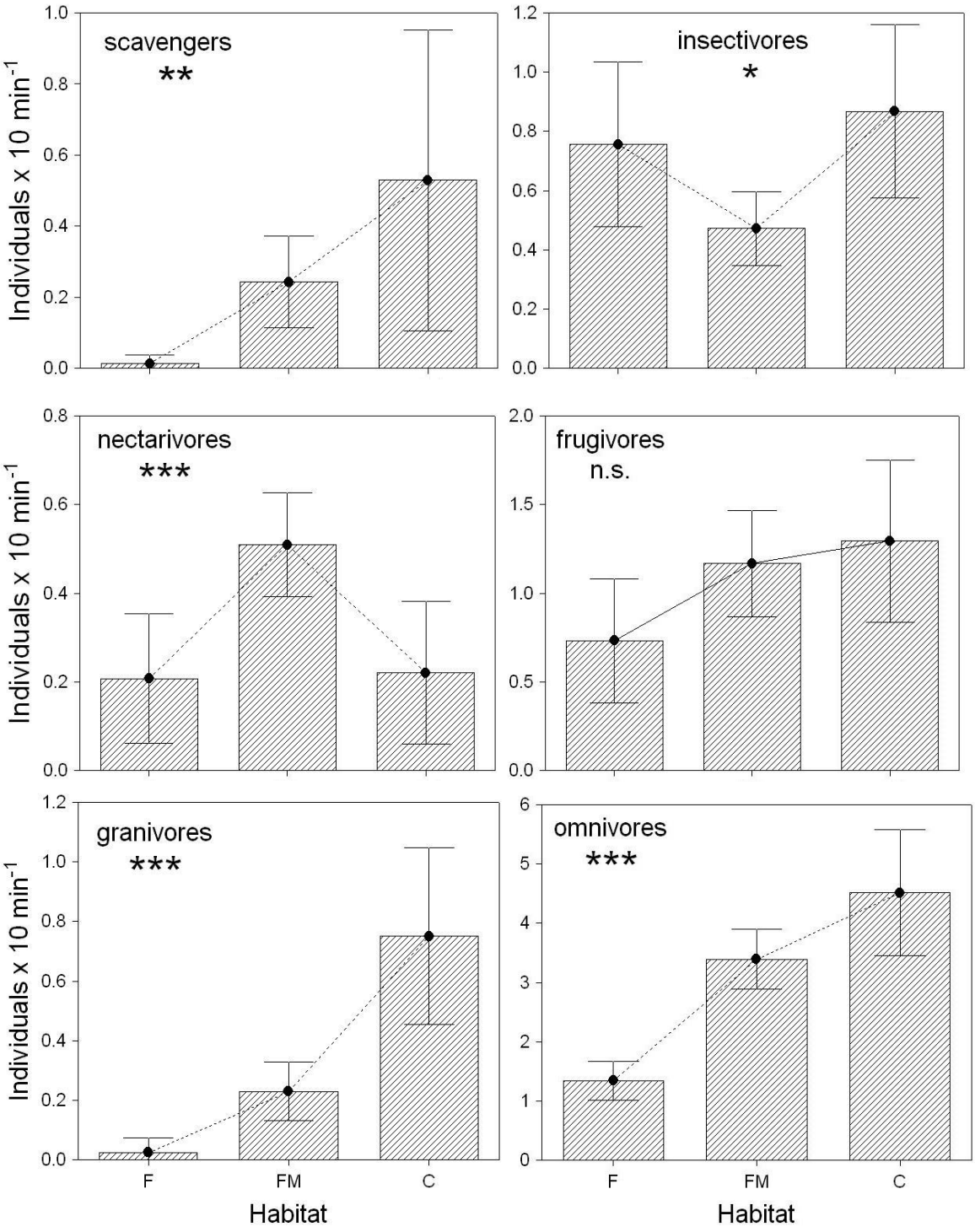

Fig. 10 Differences in abundance of feeding guilds between forest interior (F), forest margin (FM) and human-dominated countryside habitats (C) quantified by mean numbers of individuals counted per 10-min observation unit. Error bars represent 95% confidence intervals. Asterisks indicate statistical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

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. Herzog et al. 2005). Our data indicates 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 (Tab. 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 (Şekercioğlu 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 (Şekercioğlu 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 1996, Şekercioğlu 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 1996).

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 1996). 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 1996).

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).

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b. The importance of gallery forests for forest birds in the lowland countryside of Costa Rica

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Abstract

As result of a forestry law implemented in 1996 a dense network of narrow gallery forests interspersed throughout the landscape may develop in Costa Rican lowlands. This study investigated the importance of such gallery forest strips within a landscape matrix consisting of strongly human-dominated habitats to serve as corridors and stepping stones for tropical forest birds. Birds were surveyed in forest interior (FI), forest margin (FM), gallery forest connected to (GC), and gallery forest isolated from closed forest (GI) in the Pacific lowlands of the Golfo Dulce region. Richness of forest specialists decreased significantly from FI towards FM, GC and GI. While gallery forest strip width affected forest specialists positively, the percentage cover of gardens and settlements within a radius of 200 m around census points had a negative effect. However, high connectivity of gallery forest strips to remaining larger forest areas is most likely of prime importance for maintaining a high suitability for forest species. Our study underlines the importance of gallery forests for maintaining high species richness in human-dominated landscapes and their potential capability of increasing the survival for forest specialist birds in nowadays highly fragmented patches of lowland forest, particularly when they are connected to remaining blocks of closed forest.

Keywords: forest specialists, landscape matrix, lowland rainforest, riparian forest, species composition, species richness, tropical forest birds

Introduction

Negative effects of forest fragmentation and isolation on tropical biodiversity can be dampened by biological corridors that connect remaining forest islands (Laurance and Laurance 1999, Pardini et al. 2005, Fagan et al. 2016). Such corridors can increase the exchange of individuals by facilitating dispersal between forest fragments (Haas 1995, Gillies and St. Clair 2008, Kormann et al. 2016), thereby improving the persistence of metapopulation dynamics (Machtans et al. 1996, Beier and Noss 1998, De Lima and Gascon 1999, Sieving et al. 2000).

In Costa Rica the government prohibits the felling of trees along streams and rivers since the year 1996. The resulting narrow gallery forests are declared as protected areas according to forestry law. They are defined as a 15 m strip of land in rural areas and a 10 m strip in urban areas, measured horizontally on both sides of rivers, ravines or streams banks, if the land is flat. The forest strip has to be 50 m wide in undulating terrain (Asamblea Legislativa de la Republica de Costa Rica, 1997, No. 7575 Ley Forestal).

Natural riparian forest corridors belong to the most diverse terrestrial habitats (Naiman et al. 1993) and, particularly in more open landscapes (such as savannas), can contribute significantly to the regional species richness (Woinarski et al. 2000). This study analysed to what extent small riparian forest strips, which just emerged in the cultivated landscape of south-western Costa Rica due to the forestry law, contribute to maintaining forest bird diversity within a landscape matrix dominated by land-use systems and other man-made habitats. We particularly addressed the following questions:

(1) How do bird species richness and composition of forest specialists and generalists differ between gallery forest strips and closed forest? Gallery forest strips in Costa Rica can be characterized by remarkably rich bird communities (Matlock et al. 2002, Seaman and Schulze 2010). However, species richness is expected to differ between gallery forests isolated and connected to closed forest as documented for riparian forests in the temperate zone (Machtans et al. 1996) and in the tropics (Lees and Peres 2008, Seaman and Schulze 2010). Particularly for forest specialists – depending on closed old-growth forest – the conservation value of gallery forest strips may be limited.

(2) How do vegetation parameters and the landscape matrix affect the forest bird species richness in gallery forests? Little is known about the effects of the vegetation structure of gallery forests on its bird species assemblages. Therefore, we tested for effects of several vegetation parameters on species richness and composition of forest birds. We also analysed if the width of the riparian forests influence species assemblages as demonstrated for various terrestrial animal groups including birds (Lees and Peres 2008, Marczak et al. 2010, Bueno et al. 2012, De Oliveira and Dos Anjos 2014). Furthermore, the landscape matrix is known to play an important role for the conservation of bird species in forest remnants, especially for forest specialists (Gascon et al. 1999, Kennedy and Marra 2010, Kennedy et al. 2010). Beside gallery forest connectivity, we tested for effect of landscape cover on forest species in the riparian forest strips.

Methods

Study area, surveyed habitats and study sites

The study was conducted at the southern Pacific slope of Costa Rica at the edge of the Piedras Blancas National Park, in proximity to the village La Gamba (8° 42" 61' N, 83° 12' 97" W) located in the Golfo Dulce region (Figure 1). A more detailed description of the lowland rainforests of the Golfo Dulce region as well as the regional climate, geography and geological history of the study area was provided by Weber et al. (2001). The avifauna of the study area is extremely species-rich with a total of 326 recorded bird species (Tebb 2007).

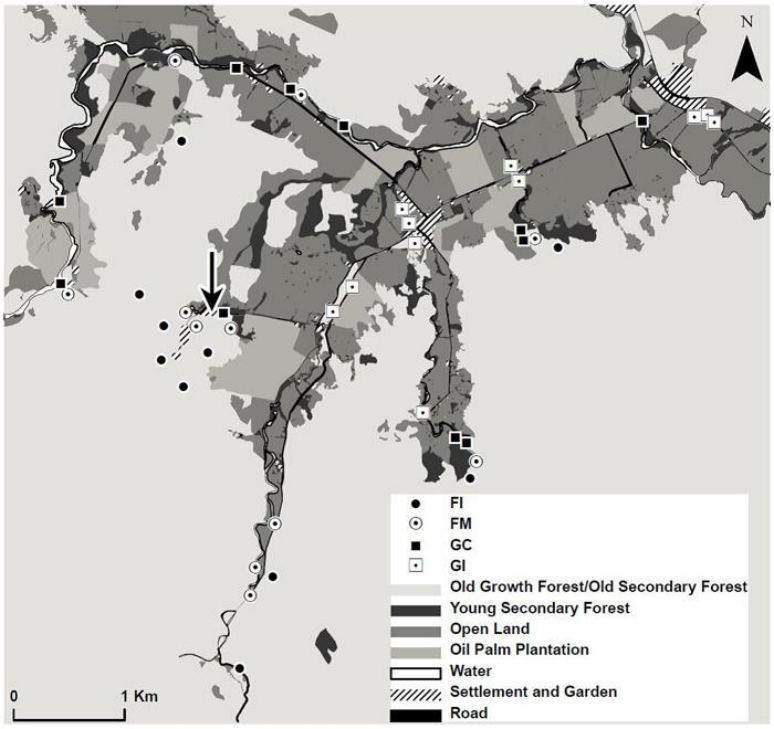

Figure 1. Schematic map of the study area. The map indicates all bird census points at forest interior (FI), forest margin (FM), and gallery forest sites connected to (GC) and isolated from closed forest (GI) as well as areas covered by old forest, young secondary forest, open land, oil palm plantations, settlements and gardens, water courses and roads. The arrow marks the location of the Tropical Research Station La Gamba (8° 42' 61" N, 83° 12' 97" W).

Birds were surveyed in four different habitat types: forest interior (FI), forest margin (FM), gallery forest connected to closed forest (GC), and isolated (GI). For each habitat type, eleven sites were selected for standardized bird counts expect for FI, where only ten were chosen (Figure 1). FI sites were located within a larger forest block (Piedras Blancas National Park) and in a distance of >100 m to the nearest forest edge. Selected FM sites were situated within the transition zone between (semi-) open human-modified habitats and up to ca 50 m towards the forest interior. Tree strips along streams crossing open areas were defined as gallery forests. They were classified as “connected“, when being in direct contact to closed forest, otherwise were categorized as “isolated”. Mean distances ± SD (min.-max.)

between census points were 2,374 ± 1,287 m (310–4,813 m) for FI, 2,585 ± 1,204 m (161–4,903 m) for FM, 2,705 ± 1,2011 m (92–5,439 m) for GC and 1,869 ± 1,152 m (87–3,843 m) for GI sites.

Bird counts

To assess bird assemblages at study sites, point counts were conducted during four survey periods representing two dry seasons (1 November 2008–20 February 2009, 2 November 2009–27 February 2010) and two wet seasons (30 May–30 September 2009, 31 May–4 October 2010). Due to decreasing bird activity during the course of the day, point counts were performed only from dawn 0500 h to 1000 h (e.g. Blake 1992). Further, no bird counts were conducted during strong rain showers or strong wind. Birds were recorded during 10-min observation units within a radius of ca 25 m around the observer. Each day bird counts were done at 8–12 census points, which were visited in a rotating order to avoid bias by temporal differences in detection rates of birds (Blake 1992). Each census point was visited 10 to 12 times per survey period.

An 8x40 binocular was used for bird observation during point censuses, which were made exclusively by the first author, who acquired identification skills during 4 months of experience in the study area prior to conducting standardized bird counts. Birds were identified using available field guides (Stiles et al. 1989, Garrigues and Dean 2007). Unfamiliar bird songs and calls were tape-recorded using a digital voice recorder (Olympus VN 480-PC with external microphone) and compared later with voice-recordings by Ross (2001) or own recordings of identified birds made earlier. Unidentified individuals were not considered in further analyses. Nomenclature and taxonomy of birds follow BirdLife International (2017).

The bird families Anatidae, Ardeidae, Pandionidae, Jacanidae, Rallidae, Charadriidae, Scolopacidae and Alcedinidae were excluded from all analyses because most species depend on freshwater habitats (e.g. Stiles et al. 1989), but not all observation points (several FI and FM sites) were situated next to a river. Swifts (Apodidae) were excluded from analysis because they usually cannot be related to a certain habitat type due to their insectivorous aerial-hawking feeding mode (e.g. Stiles et al. 1989). Also other birds such as soaring raptors or swallows were not considered when flying high above the canopy and did not show a direct “interaction” with the vegetation structure of the respective census point. We also did not consider records of nocturnal birds (Caprimulgidae, Strigidae) accidentally recorded during our daytime point counts.

Habitat preferences

All forest species recorded during this study were classified into three groups according to their habitat preferences: (1) forest specialists, (2) forest generalists and (3) openland species (Appendix 1). The classification of bird species' habitat preferences was based on information provided by Stiles et al. (1989). Species were categorized as forest specialists when their habitat preferences are described as forest, wet forest, and old secondary growth. When habitat preferences were given as broken forest, semi-open woodland, young secondary forest, forest edges, tree plantations and gardens species were defined as forest generalists. Birds were classified as openland species, when they occur in pastures, fallows and annual cultures. The latter group was not further considered in this study.

Habitat variables

To evaluate, which environmental variables affect species richness of forest birds in gallery forest strips, we measured at each GC and GI census point two variables characterizing forest structure within circular plots of 25 m radius: (1) height of all trees with a diameter in breast height (DBH) >10 cm and (2) the total number of trees with a DBH > 10 cm. Furthermore, we measured (3) the total width of the gallery forest strips on both sides of the river and (4) the distance of the census points to next intact closed forest using a digital map of the study area. The height of trees and total number of trees are reliable parameters to describe age and tree cover of forests affecting richness, abundance and composition of forest bird assemblages (Vilchez et al. 2014).

Several studies showed that the capability of linear forest strips to serve as suitable corridors is related to the width of these landscape structures (Lees and Peres 2008, Martensen et al. 2008, Bueno et al. 2012, De Oliveira and Dos Anjos 2014) and their isolation from closed forest (Martensen et al. 2008, Uezu et al. 2008). Therefore, the total width of gallery forest strips and the nearest distance to closed forest was measured at every gallery forest census point.

Finally, based on an available digital vegetation map of the area (Weissenhofer et al. 2008), which was updated and modified using aerial photographs of 2009 (OpenLayers plugin of Quantum GIS 1.7.2) and ground survey experiences, (5) old growth/old secondary forests, (6) settlements and gardens and (7) young secondary forests were digitised for the study area (scale 1:10,000) in the Geographical Information System Quantum GIS 1.7.2 (Quantum GIS Development Team 2011). For further analyses the percentage cover of these three habitat types within a 200 m radius around the census points was calculated using the software package ArcMap 9.0 (ESRI).

Statistical analysis

Coverage of tropical bird communities after 40–48 point counts per site is expected to be incomplete. Therefore, the use of raw data on observed species may be misleading (Gotelli and Colwell 2001). Consequently, we used species accumulation curves (not shown) calculated with the software EstimateS Version 7.5.2 (Colwell 2006) to evaluate differences in species richness between habitats. As a standardized measurement for species richness at census points we used species numbers estimated for the largest shared number of 40 counts per census point.

To analyse effects of habitat on species richness of forest specialists and forest generalists at census points (calculated for a largest shared sample size of 40 point counts) we calculated one-way ANOVAs. Statistical significance ($p < 0.05$) was accepted when remaining significant after applying Bonferroni correction. If habitat type proved to have a significant effect, we used Scheffé tests to analyse, which habitats differed significantly from each other.

To test for effects of habitat and landscape variables on species richness of forest specialists and generalists, we conducted univariate correlations between habitat variables and the number of species of forest specialists and generalists estimated for the largest shared sample size. Only habitat or landscape variables, which proved to be significantly related to species richness of forest birds after applying Bonferroni correction, were further considered. However, the remaining predictor variables proved to differ significantly between GC and GI sites, when applying Mann-Whitney *U* tests. Therefore, univariate correlations were calculated again separately for both gallery forest types to differentiate clearly between effects of habitat and landscape variables and effects of gallery forest connectivity. Unless mentioned otherwise, all statistical tests were computed with the software Statistica 7.1 (StatSoft Inc., Tulsa).

Similarity of species assemblages between FI, FM, GC and GI census points was quantified by the abundance-based Bray-Curtis similarity index (using square-root transformed abundance data) calculated with the software Primer version 5.2.9 (PRIMER-E Ltd., Plymouth) separately for forest specialists and generalists. Multidimensional scaling (NMDS) ordinations based on the resulting Bray-Curtis similarities were used to visualize differences of species composition between census points for both groups of birds. Accompanying stress values lower than 0.20 indicate a good poorness-of-fit of the representation of the original distance matrix values by the ordination (Clarke 1993). One-way ANOSIMs and subsequent ANOSIM pairwise tests were used to test for effects of habitat on species composition (Clarke and Gorley 2001). Subsequently, NMDS ordinations were constructed for forest

generalists and specialists only considering GC and GI sites. Extracted Dimension 1 and 2 values were related to habitat and landscape variables using Spearman rank correlations.

Results

Species richness in different forest types

During a total of 1753 point counts 20,481 individuals belonging to 208 bird species were counted at the 43 census points. Of these recorded birds 31.3 percent of the individuals and 43.8 percent of the species represented forest specialists, while 50.8 percent of the individuals and 44.2 percent of the species belonged to the group of forest generalists. Mean species richness of forest specialists per census point calculated for a largest shared number of 40 point counts differed significantly between the four forest types (one-way ANOVA: $F_{3,39} = 53.68$, $p < 0.001$). It decreased continuously from FI and FM towards GC and GI sites (Figure 2a). Also forest generalists richness per census point estimated for a largest shared sample size of 40 point counts was significantly affected by habitat type (one-way ANOVA: $F_{3,39} = 32.74$, $p < 0.001$). Richness was significantly lower at FI sites compared to all other three forest types, which were characterized by a rather similar mean number of species (Figure 2b).

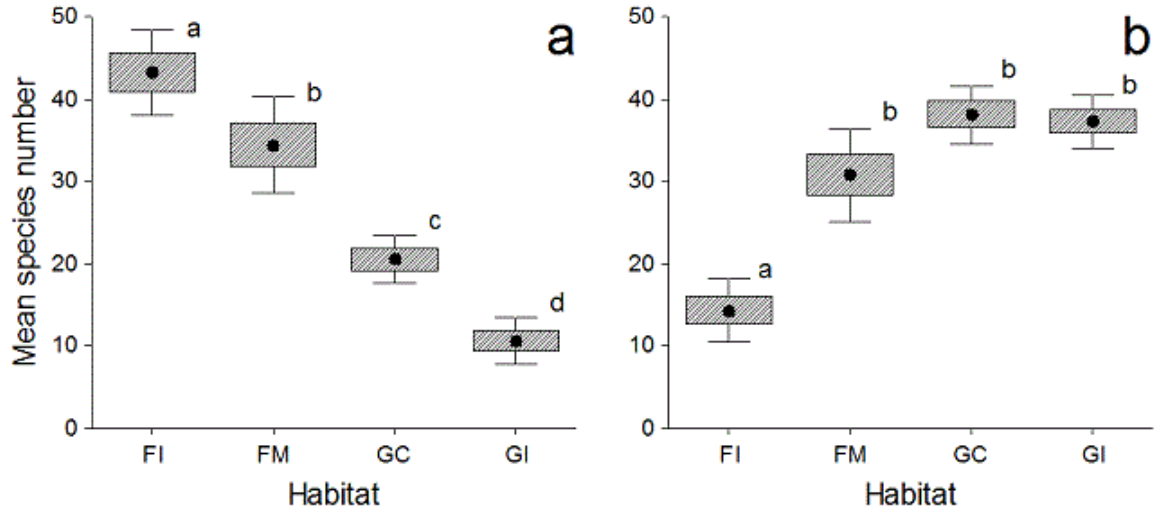

Figure 2. Species richness of forest birds. Mean species richness ± standard error (box) and 95% CI (whiskers) per census point of (a) forest specialists and (b) forest generalists in forest interior (FI), forest margin (FM), gallery forest connected to (GC) and isolated from closed forest (GI). *N* = 10–11 sites per habitat type. As standardized measurement for species richness at census points we used species numbers estimated for a largest shared number of 40 counts per census point. Significant differences (Scheffé test) between habitat types are indicated by different letters.

Effects of habitat and landscape variables on bird richness in gallery forests

After applying Bonferroni correction, univariate correlations between richness of forest specialists and habitat and landscape variables indicate significant effects of the cover of

settlements and gardens and gallery forest strip width (Table 1). Increasing cover of settlement and gardens had a negative effect on species richness of forest specialists (Figure 3a). An increase of forest species richness was found with increasing width of gallery forest strips (Figure 3b). As indicated by the correlation coefficients, width of gallery forest strips had the highest explanatory power (Table 1). However, *U* tests indicate significant differences between GC and GI sites for settlement + garden cover (U = 19.00, p = 0.0064) and width of gallery forest strips (U = 14.00, p = 0.0023). The mean percentage of settlement + garden cover (± SD) was 1.98 (± 3.08) percent and 12.19 (± 11.25) percent for GC and GI sites, respectively. The mean width (± SD) of forest strips was 62.05 (± 40.33) m for GC sites and 21.77 (± 10.66) m for GI sites. Therefore, it is difficult to separate between effects of both predictor variables and connectivity of gallery forest to closed old-growth forest on richness of forest specialists. When testing for relationships between the both predictor variables cover of settlements + gardens and width of gallery forest strips and species richness of forest specialists separately for both gallery forest types, no significant levels were achieved (results not shown). This may indicate that forest connectivity is more important for explaining richness of forest specialists (compare Figure 2a) than any of these two predictor variables. For forest generalists, no significant effect of any forest structure or landscape variable on species richness was found (Table 1).

Table 1. Effects of habitat and landscape variables on species richness. Results of Spearman rank correlations relating bird richness recorded at gallery forest census points to habitat variables and landscape measures, separately calculated for forest specialists and forest generalists. Results printed bold remained significant after Bonferroni correction.

Variables	Forest specialists	Forest generalists
Old-growth forest cover	r = 0.341, p = 0.1195	r = -0.053, p = 0.8152
Settlement and garden cover	r = -0.613, p = 0.0024	r = -0.300, p = 0.1750
Young secondary forest cover	r = 0.363, p = 0.0973	r = -0.017, p = 0.9419
Distance to forest margin	*r* = -0.536, *p* = 0.0102	*r* < 0.001, *p* > 0.9999
Tree density	*r* = 0.176, *p* = 0.4340	*r* = 0.009, *p* = 0.9688
Mean tree height	r = 0.342, p = 0.1198	r = -0.178, p = 0.4293
Gallery forest width	r = 0.829, p < 0.0001	r = 0.135, p = 0.5478

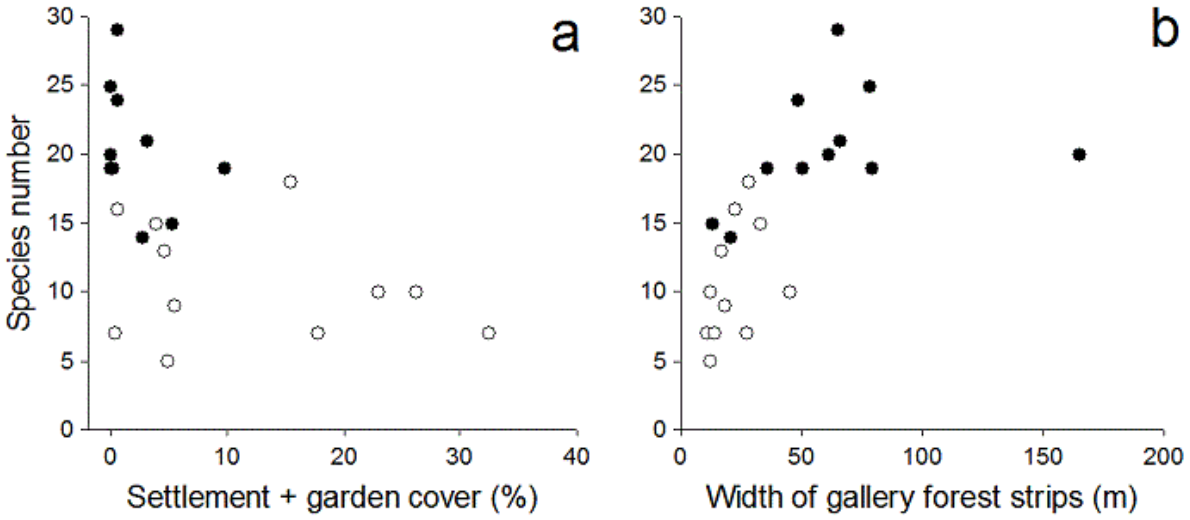

Figure 3. Effects of habitat cover on forest birds. Relationship between richness of forest specialists and (a) settlement + garden cover within a radius of 200 m around the census points and (b) the width of gallery forest strips. Species richness was quantified as number of species expected for a largest shared sample size of 40 10-min counts per census point. Filled circles indicate GC, open circles indicate GI sites.

Species composition

A high extent of differentiation between habitats regarding species composition was found for forest specialists. NMDS plots based on Bray-Curtis similarities indicate a clear segregation of census points into habitats (Figure 4a). A significant effect of habitat type on species composition was indicated by the computed one-way ANOSIM (global R = 0.51, p = 0.001). Pairwise tests distinguished significantly between species composition for all possible pairs of habitats (Appendix 2).

In forest generalists, grouping of gallery forest habitats was not as clear as for forest specialists; GC and GI sites overlapped to a large extent in the resulting NMDS plot based on Bray-Curtis similarities (Figure 4b). A significant effect of habitat type on species composition was indicated by a one-way ANOSIM (global R = 0.35, p = 0.001), but pairwise tests demonstrate that species composition of the two gallery forest habitats did not differ significantly (Appendix 2).

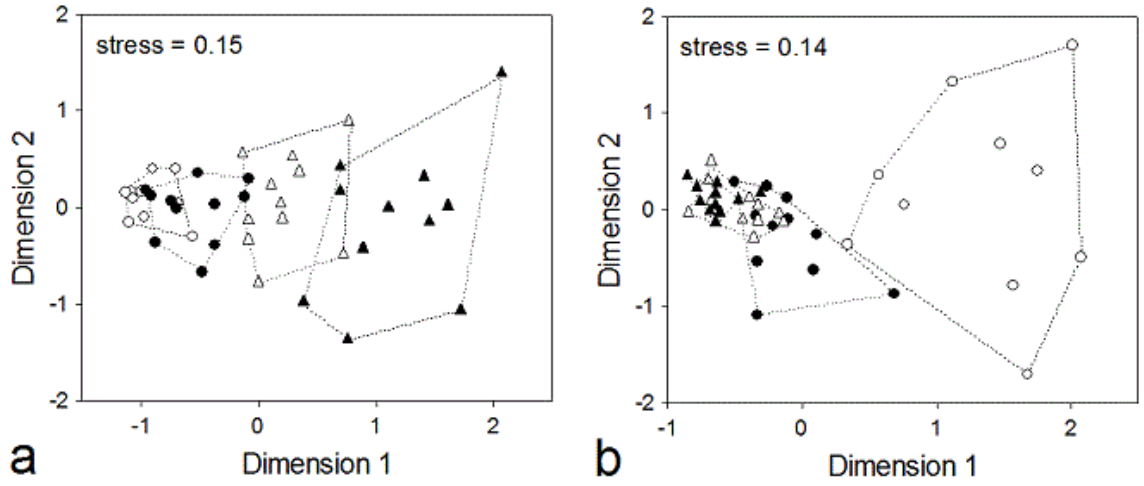

Figure 4. Species composition in different habitat types. Similarity of species composition of (a) forest specialists and (b) forest generalists between census points belonging to four different habitat types FI, FM, GC and GI visualized by multidimensional scaling ordinations based on Bray–Curtis similarities (calculated using square-root transformed abundance data).

To test for effects of landscape and habitat variables on species composition of forest specialists and generalists in gallery forests we constructed NMDS plots based on Bray-Curtis similarities only including GC and GI sites. While composition of species assemblages did not differ between GC and GI sites in forest generalists (one-way ANOSIM: Global R = 0.10, p = 0.071), a significant difference was confirmed for forest specialists (Global R = 0.33, p = 0.001). However, no significant relationship between habitat/landscape variables and extracted Dimension 1 and 2 values (Spearman rank correlations) remained significant after Bonferroni correction, neither in forest specialists nor in forest generalists (results not shown).

Discussion

Species richness and species composition of forest birds in gallery forests

Forest disturbance and deforestation generally have a strong negative effect on tropical biodiversity (Lawton et al. 1998, Dunn 2004, Schulze et al. 2004, Aratrakorn et al. 2006, Alroy 2017), including birds (Şekercioğlu et al. 2002, Dunn 2004, Waltert et al. 2004, Mammides et al. 2015). However, tropical human-dominated landscapes in Costa Rica can be characterized by relatively rich bird assemblages (Daily et al. 2001), particularly in landscapes with remaining strips of tall shrubs and trees along streams (Warkentin et al. 1995, Schulze and Riedl 2008). As shown for lowlands of Costa Rica, such gallery forests can support a rich avifauna (Matlock et al. 2002, Seaman and Schulze 2010). The occurrence of forest birds in such linear patches of woody vegetation embedded in a

landscape matrix consisting predominately of human-dominated habitats does not necessarily imply that these species maintain sustainable populations there. Rather, many forest species have little prospect of surviving outside of closed forest (Daily et al. 2001).

Small gallery forest strips in the Golfo Dulce region even can reach bird species richness similar to that of forest interior and forest margin, but they are characterized by a distinct species composition (Seaman and Schulze 2010). This is partly due to the decrease of forest specialists and the increase of birds with habitat preferences for forest edges, secondary growth, fallows and land-use system as demonstrated by our study. Forest specialists of particular conservation relevance decreased dramatically from closed forest towards gallery forests and even less forest specialists were found in gallery forest isolated from larger forest blocks. Very similar results were found for understory birds in the same study area (Seaman and Schulze 2010) and for birds in remnant riparian forest corridors in the Brazilian Amazon (Lees and Peres 2008). All these studies indicate that a substantial proportion of forest birds are not capable of crossing the matrix of agricultural habitats in which isolated gallery forests are embedded. Matrix permeability plays a major role in the efficiency of corridors and stepping stones. In a Brazilian Atlantic Forest region, only a small subset of forest species was present in gallery forests or small forest remnants. Highly forest-dependent species did not benefit from forest structures outside primary forests at all, most likely because of a high matrix resistance (Uezu et al. 2008). Also in our study corridors (gallery forest connected to closed forest) and stepping stones (isolated gallery forest strips) were embedded in a landscape dominated by agroecosystems with a simple vegetation structure not resembling any forest-like structures, hence, generating a high matrix resistance for forest specialist birds.

Effects of habitat and landscape variables on forest bird species in gallery forests

Considering the relatively high species richness and abundance of forest specialists in gallery forests connected to the margin of large forest areas, these forest strips can be proposed as important landscape structures with a potentially high value as corridors for bird movements between forest fragments in the Pacific lowlands of Costa Rica. While settlement and gardens negatively influenced the richness of forest specialists in gallery forests, the width of the forest strips showed a positive effect. However, both variables were not independent of gallery forest type and relationships could not be confirmed when analysed separately for both gallery forest types. This could either indicate that connectivity is the prime factor explaining differences in richness and composition of forest birds or that the remaining variability of gallery forest width and the relative area coverage by settlements and gardens is too small in both remaining data sets.

Also for several other vertebrate taxa riparian forests proved to be an important habitat. For example, forest strips along streams of 140 to 190 m in width in Brazil inhabited a species richness, composition, and abundance of small mammals and litter-frogs not significantly different to the adjacent continuous rainforest. Further, many frogs and small mammals were reproducing and moving in the remnants (De Lima and Gascon 1999). For birds a high importance of linear forest corridors with a width between 25 and 100 m was reported for species occurring in Atlantic rainforest fragments in Brazil, particularly for understory species with low capability to move through human-modified landscape matrix (Martensen et al. 2008). Bird richness and abundance are higher in riparian forest with mean width of 50 m in each margin and lower anthropogenic disturbance (De Oliveira and Dos Anjos 2014). Even more, to protect forest birds efficiently at least 200 m of riparian forest on each side of streams are needed in the Brazilian Amazonas (Lees and Peres 2008, Bueno et al. 2012). In addition, our data indicate that the much smaller width of gallery forest strips at La Gamba is only sufficient for a certain fraction of forest species.

Conclusion

Connectivity of forest remnants is known to be very important for forest birds in highly fragmented areas (Martensen et al. 2008). Therefore, corridors facilitating bird movements between forest fragments (Haas 1995, Gillies and St. Clair 2008, Gillies et al. 2011, Şekercioğlu et al. 2015), thereby supporting exchange of individuals (De Lima and Gascon 1999, Sieving et al. 2000), and lowering inbreeding, play an important role. Strips of gallery forests may represent such corridors or stepping stones at least for some forest specialists. Additionally, riparian vegetation can have a high proportionate positive influence on woodland birds in anthropogenic environments. Hence, the protection and restoration of gallery forests should have high priority (Bennett et al. 2014). In most regions, including the lowlands of Costa Rica, particularly the connectivity of gallery forests to source areas (remaining forest fragments) and their current width (too small to facilitate a large proportion of forest birds) have to be improved.

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Appendix 1. Classification of all recorded bird species. Classified as forest specialists (FS), forest generalists (FG) or openland species (OL) according to information on habitat preferences provided by Stiles *et al.* (1989) and their frequency of occurrence (= number of sites from which the species was recorded) in different habitats (FI = forest interior, FM = forest margin, GC = gallery forest connected to forest, GI = gallery forest isolated from forest). Species were categorized as forest specialists when their habitat preferences are described as forest, wet forest, and old secondary growth. When habitat preferences were given as broken forest, semi-open woodland, young secondary forest, forest edges, tree plantations and gardens species were defined as forest generalists. Birds were classified as openland species, when they occur in pastures, fallows and annual cultures.

Family Species	Common Name	Habitat preference	**Habitat** Frequency of occurrence			
			FI	FM	GC	GI
Tinamidae						
Tinamus major	Great Tinamou	FS	5	2		
Crypturellus soui	Little Tinamou	FS	6	7	5	
Cracidae						
Ortalis cinereiceps	Gray-headed Chachalaca	FS			4	3
Penelope purpurascens	Crested Guan	FS	7	4	2	
Crax rubra	Great Curassow	FS	7	6		
Odontophoridae						
Odontophorus gujanensis	Marbled Wood-Quail	FS	1			
Cathartidae						
Coragyps atratus	Black Vulture	OL	1	2	4	4
Cathartes aura	Turkey Vulture	FG		2	3	2
Accipitridae						
Gampsonyx swainsonii	Pearl Kite	FG			1	
Pseudastur albicollis	White Hawk	FS	1			
Buteogallus urubitinga	Great Black- Hawk	FG		2		
Rupornis magnirostris	Roadside Hawk	OL	1	4	9	9
Buteo nitidus	Grey-lined Hawk	FG			2	1
Falconidae						
Micrastur semitorquatus	Collared Forest-Falcon	FS	1			
Caracara cheriway	Northern Crested Caracara	OL			1	
Milvago chimachima	Yellow-headed Caracara	OL	1	2	4	5
Herpetotheres cachinnans	Laughing Falcon	FG	1	2	2	2
Columbidae						
Patagioenas cayennensis	Pale-vented Pigeon	OL	3	3	8	11
Patagioenas nigrirostris	Short-billed Pigeon	FS	9	11	10	2
Columbina talpacoti	Ruddy Ground-Dove	OL		4	10	11
Claravis pretiosa	Blue Ground-Dove	FG	7	11	11	6
Leptotila verreauxi	White-tipped Dove	FG	4	11	1	11
Leptotila cassinii	Grey-chested Dove	FS	9	10	9	
Geotrygon montana	Ruddy Quail-Dove	FS	7	7	1	
Psittacidae						
Psittacara finschi	Finsch's Parakeet	OL			1	
Eupsittula pertinax	Brown-throated Parakeet	OL			1	1
Brotogeris jugularis	Orange-chinned Parakeet	OL	1	4	6	7
Pyrilia haematotis	Brown-hooded Parrot	FS	3		2	
Pionus menstruus	Blue-headed Parrot	FG	1	3	5	8
Pionus senilis	White-crowned Parrot	FG		1	2	2
Amazona autumnalis	Red-lored Parrot	FG	5	1	2	5
Amazona farinosa	Mealy Amazon	FS		1	1	

Cuculidae						
Piaya cayana	Squirrel Cuckoo	FG	6	6	6	3
Crotophaga ani	Smooth-billed Ani	OL			2	3
Trochilidae						
Glaucis aeneus	Bronzy Hermit	FG	4	7	5	4
Threnetes ruckeri	Band-tailed Barbthroat	FS	8	10	9	5
Phaethornis longirostris	Long-billed Hermit	FS	10	6	3	1
Phaethornis striigularis	Stripe-throated Hermit	FG	8	8	6	3
Eutoxeres aquila	White-tipped Sicklebill	FS	3			
Campylopterus cuvierii	Scaly-breasted Sabrewing	FG		4	10	10
Florisuga mellivora	White-necked Jacobin	FG	2	7	11	10
Anthracothorax veraguensis	Veraguan Mango	OL			1	1
Klais guimeti	Violet-headed Hummingbird	FG	2			
Thalurania colombica	Crowned Woodnymph	FS	9	6	2	
Hylocharis eliciae	Blue-throated Sapphire	FG	2	3	2	4
Amazilia decora	Charming Hummingbird	FG	5	8	7	7
Amazilia tzacatl	Rufous-tailed Hummingbird	FG	3	10	11	1
Heliothryx barroti	Purple-crowned Fairy	FG		4	4	2
Heliomaster longirostris	Long-billed Starthroat	FG		1	3	2
Trogonidae						
Trogon massena	Slaty-tailed Trogon	FS	6	4	5	2
Trogon bairdii	Baird's Trogon	FS	6	9	4	2
Trogon violaceus	Violaceous Trogon	FS	1	1	1	1
Trogon rufus	Black-throated Trogon	FS	8	6	2	
Momotidae						
Momotus lessonii	Blue-diademed Motmot	FS	8	7		
Bucconidae						
Malacoptila panamensis	White-whiskered Puffbird	FS	2	1		
Galbulidae						
Galbula ruficauda	Rufous-tailed Jacamar	FS	8	7		
Ramphastidae						
Pteroglossus frantzii	Fiery-billed Aracari	FS	8	2	3	2
Ramphastos ambiguus	Black-mandibled Toucan	FS	10	7	9	7
Picidae						
Picumnus olivaceus	Olivaceous Piculet	FG			3	5
Melanerpes chrysauchen	Golden-naped Woodpecker	FS	9	4	3	
Melanerpes rubricapillus	Red-crowned Woodpecker	FG	1	9	11	11
Veniliornis kirkii	Red-rumped Woodpecker	FS	1	4	7	4
Piculus simplex	Rufous-winged Woodpecker	FS	5	6		
Hylatomus lineatus	Lineated Woodpecker	FS	3	5	6	7
Campephilus guatemalensis	Pale-billed Woodpecker	FS	3	2		
Furnariidae						
Synallaxis albescens	Pale-breasted Spinetail	OL		1		
Synallaxis brachyura	Slaty Spinetail	OL			1	1
Automolus ochrolaemus	Buff-throated Foliage-gleaner	FS	6	5		
Xenops minutus	Plain Xenops	FS	4	3	2	
Dendrocincla anabatina	Tawny-winged Woodcreeper	FS	4	4	2	1
Deconychura longicauda	Long-tailed Woodcreeper	FS	2	1	2	
Glyphorynchus spirurus	Wedge-billed Woodcreeper	FS	5	6	2	3

Dendrocolaptes sanctithomae	Northern-barred Woodcreeper	FS	3	3		
Xiphorhynchus susurrans	Cocoa Woodcreeper	FS	10	10	11	9
Xiphorhynchus lachrymosus	Black-striped Woodcreeper	FS	7	6	2	
Lepidocolaptes souleyetii	Streak-headed Woodcreeper	FS	3	7	11	10
Campylorhamphus pusillus	Brown-billed Scythebill	FS	1	1		
Thamnophilidae						
Taraba major	Great Antshrike	FS		1	2	
Thamnophilus doliatus	Barred Antshrike	FG	1			1
Thamnophilus bridgesi	Black-hooded Antshrike	FS	10	8	4	
Thamnistes anabatinus	Russet Antshrike	FS	3	1		
Microrhopias quixensis	Dot-winged Antwren	FS	6	6		
Cercomacroides tyrannina	Dusky Antbird	FS	2	3		
Poliocrania exsul	Chestnut-backed Antbird	FS	10	11	8	2
Gymnopithys bicolor	Bicolored Antbird	FS	1			
Formicariidae						
Formicarius analis	Black-faced Antthrush	FS	10	9	1	
Tyrannidae						
Ornithion semiflavum	Yellow-bellied Tyrannulet	FS	3	5	5	1
Camptostoma obsoletum	Southern Beardless-Tyrannulet	FG		1	4	5
Capsiempis flaveola	Yellow Tyrannulet	FG		4	8	8
Tyrannulus elatus	Yellow-crowned Tyrannulet	FG			1	2
Elaenia flavogaster	Yellow-bellied Elaenia	OL	1	3	9	10
Mionectes oleagineus	Ochre-bellied Flycatcher	FG	8	5	6	7
Zimmerius vilissimus	Paltry Tyrannulet	FG	3	8	11	11
Lophotriccus pileatus	Scale-crested Pygmy-Tyrant	FS	2			
Oncostoma cinereigulare	Northern Bentbill	FG	7	7	4	1
Poecilotriccus sylvia	Slate-headed Tody-Flycatcher	FG	4	9	8	4
Todirostrum cinereum	Common Tody-Flycatcher	FG		10	11	11
Rhynchocyclus brevirostris	Eye-ringed Flatbill	FS	5			
Tolmomyias sulphurescens	Yellow-olive Flatbill	FG	3	3	5	4
Platyrinchus coronatus	Golden-crowned Spadebill	FS	5	2		
Myiobius sulphureipygius	Sulphur-rumped Myiobius	FS	7	5		
Contopus sordidulus	Western Wood Pewee	FG		1		
Contopus virens	Eastern Wood Pewee	FG		4	3	1
Contopus cinereus	Tropical Pewee	FG		1		3
Empidonax flaviventris	Yellow-bellied Flycatcher	FG		1	1	
Empidonax alnorum	Alder Flycatcher	FG		3	1	
Empidonax minimus	Least Flycatcher	FG		4	2	1
Attila spadiceus	Bright-rumped Attila	FS	9	11	11	8
Rhytipterna holerythra	Rufous Mourner	FS	4	3		
Myiarchus tuberculifer	Dusky-capped Flycatcher	OL	1	4	3	7
Myiarchus crinitus	Great Crested Flycatcher	FG		2	2	1
Pitangus sulphuratus	Great Kiskadee	OL	3	10	11	11
Megarynchus pitangua	Boat-billed Flycatcher	FG	4	8	7	5
Myiozetetes cayanensis	Rusty-margined Flycatcher	OL		1		1
Myiozetetes similis	Social Flycatcher	OL	1	7	11	11

Myiozetetes granadensis	Grey-capped Flycatcher	FG	1	10	11	11
Myiodynastes maculatus	Streaked Flycatcher	FG		2	4	2
Myiodynastes luteiventris	Sulphur-bellied Flycatcher	FG			1	1
Legatus leucophaius	Piratic Flycatcher	FG	2	8	7	8
Tyrannus melancholicus	Tropical Kingbird	OL	3	8	11	11
Pipridae						
Manacus aurantiacus	Orange-collared Manakin	FS	9	10	7	2
Lepidothrix coronata	Blue-crowned Manakin	FS	3	1		
Ceratopipra mentalis	Red-capped Manakin	FS	7	7	2	
Cotingidae						
Lipaugus unirufus	Rufous Piha	FS	6	3		
Tityridae						
Onychorhynchus mexicanus	Northern Royal Flycatcher	FG	1	2	2	2
Terenotriccus erythrurus	Ruddy-tailed Flycatcher	FS	2	1		
Schiffornis veraepacis	Northern Mourner	FS	1			
Pachyramphus cinnamomeus	Cinnamon Becard	FG		1		1
Pachyramphus polychopterus	White-winged Becard	FG		4	6	2
Pachyramphus aglaiae	Rose-throated Becard	FS	3	6	4	4
Tityra semifasciata	Masked Tityra	FG	3	2	4	3
Tityra inquisitor	Black-crowned Tityra	FG			7	5
Vireonidae						
Vireo flavifrons	Yellow-throated Vireo	FG	1	2	4	4
Vireo philadelphicus	Philadelphia Vireo	FG		2		
Hylophilus flavipes	Scrub Greenlet	FG		1	8	7
Hylophilus ochraceiceps	Tawny-crowned Greenlet	FS	6	1		
Hylophilus decurtatus	Lesser Greenlet	FS	8	8	6	3
Vireolanius pulchellus	Green Shrike- Vireo	FS	4	2		
Corvidae						
Cyanocorax morio	Brown Jay	FG				1
Hirundidae						
Progne chalybea	Grey-breasted Martin	OL				1
Stelgidopteryx serripennis	Northern Rough-winged Swallow	OL			1	
Stelgidopteryx ruficollis	Southern Rough-winged Swallow	OL		2	7	2
Troglodytidae						
Pheugopedius fasciatoventris	Black-bellied Wren	FS	5	9	7	1
Cantorchilus semibadius	Riverside Wren	FS	10	11	10	7
Cantorchilus modestus	Plain Wren	OL	1	2	8	10
Troglodytes aedon	House Wren	OL		3	6	1
Microcerculus marginatus	Southern Nightingale-Wren	FS	8	2		
Polioptilidae						
Ramphocaenus melanurus	Long-billed Gnatwren	FS	4	2		
Polioptila plumbea	Tropical Gnatcatcher	FS	4	2	5	3
Turdidae						
Catharus ustulatus	Swainson's Thrush	FG	1	1		
Turdus grayi	Clay-colored Thrush	OL	1	10	10	11
Turdus assimilis	White-throated Thrush	FG	3	2		
Parulidae						
Vermivora chrysoptera	Golden-winged Warbler	FS				1

Leiothlypis peregrina	Tennessee Warbler	FG	2	5	4	9
Setophaga petechia	Mangrove Warbler	FG	2	3	6	10
Setophaga pensylvanica	Chestnut-sided Warbler	FG	8	10	11	11
Mniotilta varia	Black-and-white Warbler	FG	1	2	1	2
Parkesia noveboracensis	Northern Waterthrush	FG	3	3	8	11
Parkesia motacilla	Louisiana Waterthrush	FS	1	1		
Geothlypis philadelphia	Mourning Warbler	FG		3	6	9
Myiothlypis fulvicauda	Buff-rumped Warbler	FS	5	7	3	1
Thraupidae						
Coereba flaveola	Bananaquit	FG	3	11	11	11
Eucometis penicillata	Gray-headed Tanager	FS	2	3	1	
Piranga rubra	Summer Tanager	FG	4	6	9	8
Lanio leucothorax	White-throated Shrike-Tanager	FS	4	1		
Islerothraupis luctuosa	White-shouldered Tanager	FS	4	2		
Tachyphonus rufus	White-lined Tanager	FG	1		1	2
Ramphocelus costaricensis	Cherrie's Tanager	FG	3	10	11	11
Habia atrimaxillaris	Black-cheeked Ant-Tanager	FS	9	9		
Tangara episcopus	Blue-grey Tanager	OL	2	10	11	11
Tangara palmarum	Palm Tanager	OL		3	5	7
Tangara larvata	Golden-hooded Tanager	FG	6	10	10	9
Tangara gyrola	Bay-headed Tanager	FS	8	6	2	1
Tangara icterocephala	Silver-throated Tanager	FS				2
Dacnis venusta	Scarlet-thighed Dacnis	FG			3	2
Dacnis cayana	Blue Dacnis	FS	3	5	2	3
Chlorophanes spiza	Green Honeycreeper	FS	3	5	3	1
Cyanerpes lucidus	Shining Honeycreeper	FS	5	3	5	6
Cyanerpes cyaneus	Red-legged Honeycreeper	FG	3	2	8	9
Volatinia jacarina	Blue-black Grassquit	OL		2	5	7
Sporophila schistacea	Slate-colored Seedeater	OL	2	6	9	8
Sporophila corvina	Black Seedeater	FG	1	7	11	11
Sporophila torqueola	Cinnamon-rumped Seedeater	OL			1	4
Sporophila nigricollis	Yellow-bellied Seedeater	OL			1	3
Sporophila funerea	Thick-billed Seed-Finch	OL	2	5	7	8
Saltator maximus	Buff-throated Saltator	FG	8	11	11	11
Saltator striatipectus	Streaked Saltator	FG		5	6	4
Passerellidae						
Arremon aurantiirostris	Orange-billed Sparrow	FS	10	11	9	9
Arremonops conirostris	Black-striped Sparrow	FG	1	8	11	11
Cardinalidae						
Pheucticus ludovicianus	Rose-breasted Grosbeak	FG			1	1
Cyanoloxia cyanoides	Blue-black Grosbeak	FS	8	3	5	2
Icteridae						
Dives dives	Melodious Blackbird	FG				1
Quiscalus mexicanus	Great-tailed Grackle	OL		1	4	9
Molothrus aeneus	Bronzed Cowbird	OL			4	3
Icterus spurius	Orchard Oriole	FG				2
Icterus galbula	Baltimore Oriole	FG	1	2	5	7
Amblycercus holosericeus	Yellow-billed Cacique	FS		6	7	1
Cacicus microrhynchus	Scarlet-rumped Cacique	FS	10	9	9	8
Psarocolius decumanus	Crested Oropendola	FG			1	1
Fringillidae						

Euphonia luteicapilla	Yellow-crowned Euphonia	FG	3	5	7	7
Euphonia laniirostris	Thick-billed Euphonia	FG	3	9	8	11
Euphonia elegantissima	Elegant Euphonia	FS			1	
Euphonia imitans	Spot-crowned Euphonia	FS	9	9	5	7
Euphonia minuta	White-vented Euphonia	FS		1	1	

Appendix 2. Results of ANOSIMs testing for differences in species composition of forest specialists and forest generalists. Similarity of species composition was quantified by abundance-based Bray–Curtis and incidence-based estimated Sørensen similarities. Significant differences are printed bold.

Pairwise tests	Forest specialists	Forest generalists
FI vs. FM	***R* = 0.17, *p* = 0.015**	***R* = 0.48, *p* = 0.001**
FI vs. GC	***R* = 0.77, *p* = 0.001**	***R* = 0.63, *p* = 0.001**
FI vs GI	***R* = 0.86, *p* = 0.001**	***R* = 0.70, *p* = 0.001**
FM vs. GC	***R* = 0.42, *p* = 0.001**	***R* = 0.10, *p* = 0.036**
FM vs. GI	***R* = 0.74, *p* = 0.001**	***R* = 0.36, *p* = 0.001**
GC vs. GI	***R* = 0.33, *p* = 0.001**	*R* = 0.10, *p* = 0.079

c. Indistinct effects of season on the composition of bird species assemblages in forest habitats in the Pacific lowlands of Costa Rica

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Abstract

Higher latitudes are characterized by strong seasonal changes in climatic conditions forcing plants to be dormant and a substantial number of animals to migrate or hibernate. Although seasonality is less pronounced in tropical regions, they typically still show seasonal changes in precipitation with at least one more or less pronounced wet and dry season. As the availability of important food sources for birds, such as insects, fruits, seeds and flower nectar, has been observed to correlate with the amount of rain and available sunlight, this consequently also may affect the composition and structure of bird communities.

In this study, we examined the impact of seasonal changes on bird species assemblages in the Pacific lowlands of Costa Rica. Hence, birds were assessed by point counts in four different forest habitats (forest interior, forest margin, gallery forest connected and isolated from forest) between November 2008 and October 2010, a time period covering two dry and two wet seasons.

Seasonal changes in bird assemblages were indistinct. Whereas species composition differed significantly between habitats, the season had no clear effect. Nevertheless, temporal changes did occur as survey periods showed significant effects.

Frugivores, nectarivores, omnivores and granivores were more abundant in the wet and dry season 2009, than in the dry season 2008 and wet season 2010. Otherwise, the abundance of insectivores during survey periods was different. In gallery forest habitats, insectivores were less abundant in the dry seasons than in the following wet seasons, but the highest recorded abundance was at forest margins in the dry season 2009. Temporal differences were not habitat-specific for all feeding guilds. We suggest that seasonal changes of resource availability in the area are not strong enough to lead to significant changes in bird assemblages. Regarding the changes due to habitat, all feeding guilds except insectivores were more common and species rich in gallery forests than at forest interior and margin, for insectivores the opposite was true.

As the abundance and species richness of feeding guilds even showed opposite patterns during two consecutive wet and dry seasons, we highly recommend interpreting recorded seasonal changes, just if observations were conducted throughout multiple years.

Keywords: seasonality, feeding guilds, abundance, species richness, tropical birds, insectivorous birds, resource, species composition

Introduction

Tropical rain forests have been determined as the most species-rich biome on Earth, inhabiting astonishingly 50% of species on just 7% of the land area (Wilson 1988, Myers et al. 2000). Regarding birds, all the global hotspots are situated in the tropical zone (Orme et al. 2005). The reason for the high species richness especially in rainforests is not settled yet (Hill & Hill 2001). A possible explanation is that this biome is characterized by no winter and dormancy, generally showing very poor seasonal changes in insolation and temperature compared to temperate zones.

Nevertheless, the abundance of insects, fruits, seeds, and flowers in nearly all tropical forests varies seasonally (Frith & Frith 1985, van Shaik et al. 1993). Fluctuations occur due to seasonal changes in insolation and precipitation over the year, which can result in a more or less pronounced dry and wet season. Studies show that there is almost no water shortage in tropical rainforests (Kato et al. 2000, Nemani et al. 2003, Huete et al. 2006, Williams & Middleton 2008), but that plant productivity is light-limited. That is the reason why leaf flushes occur during drier periods when cloud cover is less dense (Wright & van Schaik 1994, Huete et al. 2006). Fruit peaks happen afterwards at the end of dry season or during periods of low photosynthetic activity (French 1992, Jordano 2000). In addition, changes in insect abundance in tropical rainforests appear to be related closely to rainfall. Highest insect abundances will be typically reached in the wettest months (Frith & Frith 1985, Develey & Peres 2000). Wetter habitats (Janzen & Schoener 1968, Janzen 1973), as well as the availability of young leaves, flowers, and fruits (Wolda 1978, van Schaik et al. 1993) seem to affect insect abundance positively.

Arthropods are an important energy source for raising nestlings. Hence, the reproductive periods of insectivorous birds are often closely associated with peaks in arthropod abundances (Develey & Peres 2000, Wikelski et al. 2000). In Panama, the amount of rainfall, which correlated with insect abundance, increased the growth rate of gonads of various birds (Wikelski et al. 2000, 2003). Thus, seasonal resource availability may lead to fluctuations in bird assemblages due to growth of population.

In addition, higher resource availability also attracts birds from other habitats and altitudes influencing bird composition, which was frequently observed for frugivores (Levey 1988, Loiselle & Blake 1991, Poulin et. al 1993, Şekercioğlu et al. 2007). For example, for Keel-billed Toucans food resources played an important role in spatial movement decisions (Graham 2001). For three Costa Rican understory birds (*Myadestes melanops, Phainoptila melanoxantha*, and *Semnornis frantzii*) radiotelemetry data indicated that paths were directly chosen because of fruit sources (Murray 1988).

Yet, not only vertical, but also latitudinal migrants possibly affect bird communities seasonally. For example, resident species have been observed to forage in higher vegetation layers during the occurrence of migratory birds, probably because of food competition (Rabøl 1987, Waide 1981, Moore & Yong 1991, Jedlicka et al. 2006). The aspect, that the departure of migrants to their breeding grounds correlates with higher rainfalls and food availability in the tropical habitats (Balbontín et al. 2009, Saino et al. 2004), may intensify seasonal fluctuations in bird communities even more.

In this study, we examine the effect of wet and dry season on resident bird communities and feeding guilds in four different habitats (forest interior, forest margin, gallery forest connected, and gallery forest isolated) in the Pacific lowlands of Costa Rica. Based on previous studies, we especially expect to find a seasonal effect on insectivores and frugivores, namely a higher abundance in the wet season (Levey 1988, Poulin et. al 1993, Moegenburg & Levey 2003). The changes in species composition could also occur habitat-specific. Closed forests are known to buffer changes in humidity and temperature showing lower annual and seasonal variability than the adjacent habitats (Didham & Lawton 1999, Ewers & Banks-Leite 2013). Instead, forest edges and forest fragments are characterized by altered microclimate conditions (Ewers & Banks-Leite 2013). Therefore, seasonal effects on bird species assemblages may be clearer in gallery forest than at forest interior.

Methods

Study area, surveyed habitats and study sites

The study was carried out at the Esquinas Rainforest and its close vicinities at the southern Pacific slope of Costa Rica (8°42'61" N, 83°12'97" W). The Esquinas Rainforest is situated in the Golfo Dulce region next to the village La Gamba, bordering the National Park Piedras Blancas. A very detailed description of the Golfo Dulce region and its regional climate, geography, geological history, flora and fauna is provided by Weissenhofer et al. (2008).

The area belongs to the wettest lowland forests in Central America with an annual precipitation of c. 5800mm. Rainy season generally is from May to November and dry season from December to April, with the heaviest rainfalls occurring in October and November and the driest months from January to March (Weissenhofer & Huber 2008).

The area is characterized by an extremely species-rich avifauna (Sauberer et al. 2007) with more than 330 (includes 55 migrants) recorded bird species (Tebb 2007) and the number is still rising (e.g. Riedl & Schulze 2010).

Bird surveys were conducted in four different habitat types: forest interior (FI), forest margin (FM), and gallery forests connected (GC) or isolated (GI) from closed forest. FM was defined as the transition zone between (semi-) open countryside habitats and up to c. 50 m towards the forest interior. Tree strips along streams crossing open areas were defined as gallery forests. In total, eleven census points were surveyed in each habitat (FM, GC, GI), except for FI, where only ten points were selected (Fig. 1).

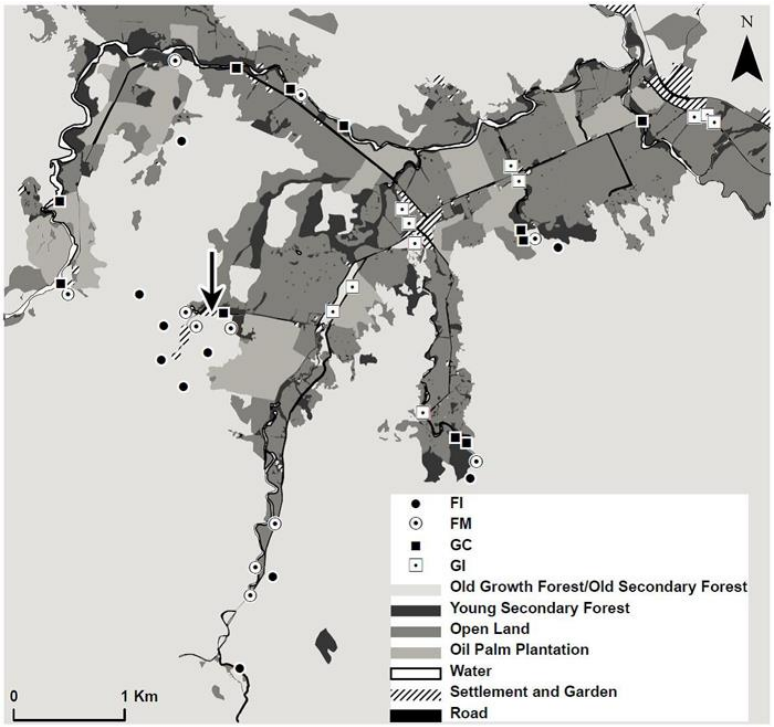

Figure 1. Schematic map of the study area. The map indicates all bird census points at forest interior (FI), forest margin (FM), and gallery forest sites connected to (GC) and isolated from closed forest (GI) as well as areas covered by old forest, young secondary forest, open land, oil palm plantations, settlements and gardens, water courses and roads. The arrow marks the location of the Tropical Research Station La Gamba (8° 42' 61" N, 83° 12' 97" W).

Bird counts

Fieldwork was conducted exclusively by the first author, which acquired essential skills during four month of experience in the study area prior to conducting standardized bird counts. Survey periods represented two dry seasons (1 November 2008–20 February 2009, 2 November 2009–27 February 2010) and two wet seasons (30 May–30 September 2009, 31 May–4 October 2010).

Mean precipitation per month amounted to 558 mm/m² and 753 mm/m² in the wet seasons 2009 and 2010, respectively. In the dry seasons 2008/09 and 2009/10 the mean monthly precipitation reached 291 mm/m² and 328 mm/m² , respectively (data of climate station at the Tropical Research Station La Gamba; 8°42'61" N, 83°12'97" W; 70 m a.s.l.).

As bird activity is highest in the morning, point counts were performed only from dawn (5:00) to 10:00 (e.g. Blake 1992). Each of the 43 census points was visited 10 to 12 times. During each visit all birds were recorded for 10min within a radius of c. 25 m around the observer. The census points were visited in a rotating order to avoid bias by temporal differences in detection rates of birds (Blake 1992).

Birds were observed using an 8x40 Zeiss binocular during point censuses. For identification available field guides were used (Stiles et al. 1989, Garrigues and Dean 2007). Unfamiliar bird songs and calls were tape-recorded using a digital voice recorder (Olympus VN 480-PC) and compared later with voice-recordings by Ross (2001) or own recordings of identified birds made earlier. Nomenclature and taxonomy of birds follow BirdLife International (2017).

Species depending on freshwater habitats (e.g. Stiles et al. 1989) like birds of the families Anatidae, Ardeidae, Jacanidae, Scolopacidae and Alcedinidae were excluded from all analyses because not all observation points (several FI and FM sites) were located at a river. As swifts (Apodidae) usually cannot be related to a certain habitat type due to their insectivorous aerial-hawking feeding mode over wide ranges (e.g. Stiles et al. 1989), they were excluded from our analysis as well. Also long-distance migrants (only Northern migrants were recorded) were omitted, because they only appear in the dry season.

Assignment to feeding guilds

Referring to Stiles et al. (1989), bird species were assigned to feeding guilds according to their primary diet (Appendix: Tab. A). Species feeding on seeds, berries, fruits and/or nuts were categorized as frugivores; on insects as insectivores; on a mixture of plant parts and small animals (mostly insects) as omnivores; and species frequently visiting flowers to feed on nectar as nectarivores, although they additionally may take insects as is known for hummingbirds (Stiles et al. 1989). Birds feeding predominantly on seeds were classified as being granivorous. Scavengers feeding on carrion and carnivores feeding on vertebrates or a mixture of vertebrates and invertebrates were not included into the analysis because of their small abundance at the observation points.

Statistical analysis

Similarity of species assemblages assessed during the four survey periods at FI, FM, GC and GI census points was quantified by the abundance-based Bray-Curtis similarity index (using square-root transformed abundance data) calculated with the software Primer version 5.2.9 (PRIMER-E Ltd., Plymouth). Multidimensional scaling (NMDS) ordinations based on the resulting Bray-Curtis similarities were used to visualize differences of species composition at census points between the two pairs of wet and dry seasons as well as the two pairs of subsequent dry and wet seasons, respectively. Accompanying stress values lower than 0.20 were assumed indicating a good poorness-of-fit of the representation of the original distance matrix values by the ordination (Clarke 1993). To test for effects of habitat and differences between the two wet and dry seasons, respectively, as well as between subsequent dry and wet seasons two-way crossed ANOSIMs were calculated with Primer version 5.2.9 (PRIMER-E Ltd., Plymouth). To account for multiple testing, we calculated false discovery rate (FDR) adjusted *p* values (Pike 2011).

Generalized linear mixed models (GLMMs; with log normal error distribution and log-link function) were calculated (with the software package SPSS version 20, IBM) to evaluate effects of habitat type, survey period and the interaction term habitat type x survey period on the abundance and species richness of feeding guilds. As species richness estimates and abundances of feeding guilds were assessed at the same census points during all four survey periods, census point ID was included as random effect. Again, to account for multiple testing, FDR adjusted *p* values were calculated (Pike 2011).

Results

Species composition

NMDS ordinations visualizing similarity relationships of species assemblages recorded at census points between habitats and observation periods do only indicate a clear effect of habitat but do not show any pronounced seasonal effects. The comparisons across all habitat types between the two wet seasons (Fig. 2a) and dry seasons (Fig. 2b), respectively, do not differ obviously from the NMDS ordinations comparing the two pairs of successive dry and wet seasons (Fig. 2c-d).

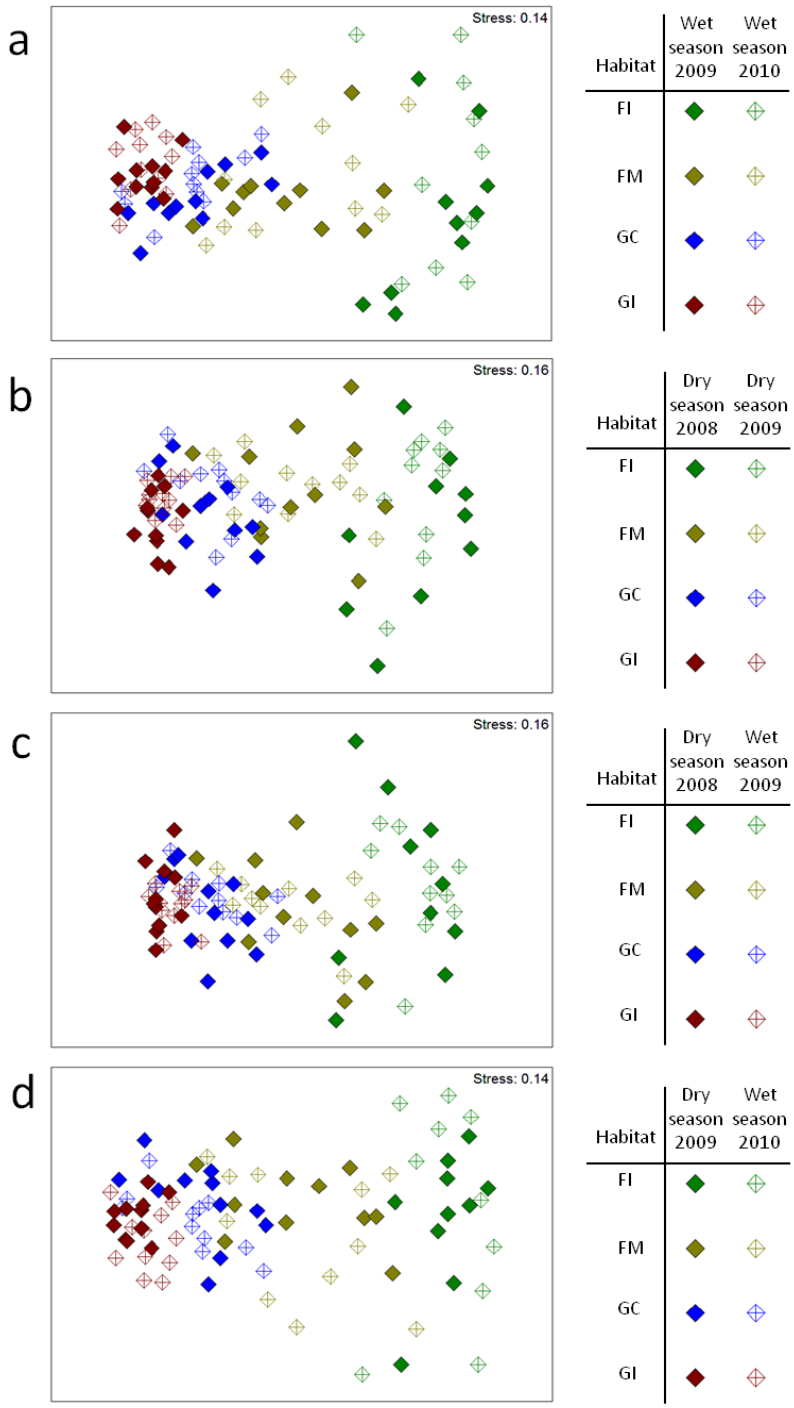

Figure 2. NMDS ordinations visualizing similarity relationships of species assemblages recorded at census points between habitats and different pairs of survey periods. Shown are comparisons across all habitat types (a) between the two wet seasons, (b) between the two dry seasons, and (c, d) between the two pairs of successive dry and wet seasons.

Pairwise ANOSIM tests showed that habitat types had a distinctive species composition in all possible pairs of survey periods. Species composition also differed significantly between the survey periods except for the pair of wet season 2009 vs. 2010 (Tab. 1).

Table 1. Results of two-way crossed ANOSIMs testing for effects on species composition between different dry and wet seasons, between successive dry and wet seasons, and between habitats. *p*

values represent FDR-adjusted values. Effects remaining significant after FDR correction are printed bold.

Comparison	Survey period		Habitat	
	Global *R*	FDR adjusted *p*	Global *R*	FDR adjusted *p*
Wet season 2009 vs. 2010	0.049	0.084	**0.533**	**<0.001**
Dry season 2008 vs. 2009	**0.068**	**0.035**	**0.565**	**<0.001**
Dry season 2008 vs. wet season 2009	**0.067**	**0.026**	**0.537**	**<0.001**
Dry season 2009 vs. wet season 2010	**0.084**	**0.016**	**0.561**	**<0.001**

Differences of species richness and abundance of feeding guilds between forest habitats and survey periods

While abundances of frugivorous, insectivorous and nectarivorous birds were only affected by survey period, granivores were affected exclusively by habitat. Only the abundance of omnivores differed significantly between habitats and survey periods. The interaction term habitat x season did not affect any of the feeding guilds significantly (Tab. 2).

Table 2. Results of GLMMs (normal error distribution, log-link function) testing for effects of habitat, survey period and the interaction term habitat x survey period on the mean number of individuals of different feeding guilds counted at census points during different survey periods. Census point ID was included as random effect. *p* values represent FDR-adjusted values. Effects remaining significant after FDR correction are printed bold.

Feeding guilds	Habitat	Survey period	Habitat x survey period
Frugivores	$F_{3,156}$ = 2.911, p = 0.077	**$F_{3,156}$ = 9.373, p = 0.025**	$F_{9,156}$ = 0.957, p = 0.552
Insectivores	$F_{3,156}$ = 2.528, p = 0.098	**$F_{3,156}$ = 17.887, p < 0.001**	$F_{9,156}$ = 1.834, p = 0.099
Nectarivores	$F_{3,156}$ = 2.277, p = 0.112	**$F_{3,156}$ = 7.106, p = 0.025**	$F_{9,156}$ = 1.018, p = 0.535
Omnivores	**$F_{3,156}$ = 16.934, p < 0.001**	**$F_{3,156}$ = 13.787, p < 0.001**	$F_{9,156}$ = 0.559, p = 0.829
Granivores	**$F_{3,156}$ = 14.374, p < 0.001**	$F_{3,156}$ = 2.747, p = 0.084	$F_{9,156}$ = 0.676, p = 0.782

The abundance of frugivores was higher in gallery forests than in FM and FI (but no significant effect of habitat detected by GLMMs; see Tab. 2; Fig. 3). Also the omnivores reached a higher abundance in GC and GI than FI, while abundances at FM were intermediate. Granivores showed a particularly low mean abundance at FI sites (Fig. 3). Although the abundance of all feeding guilds, except granivores, was affected by survey period (Tab. 2), no clear pattern emerged which could be related to a wet-dry seasonality. In

fact, all feeding guilds, except insectivores, showed lowest mean abundances in the dry season 2008 and the wet season 2010 in at least three of the four surveyed habitats (Fig. 3).

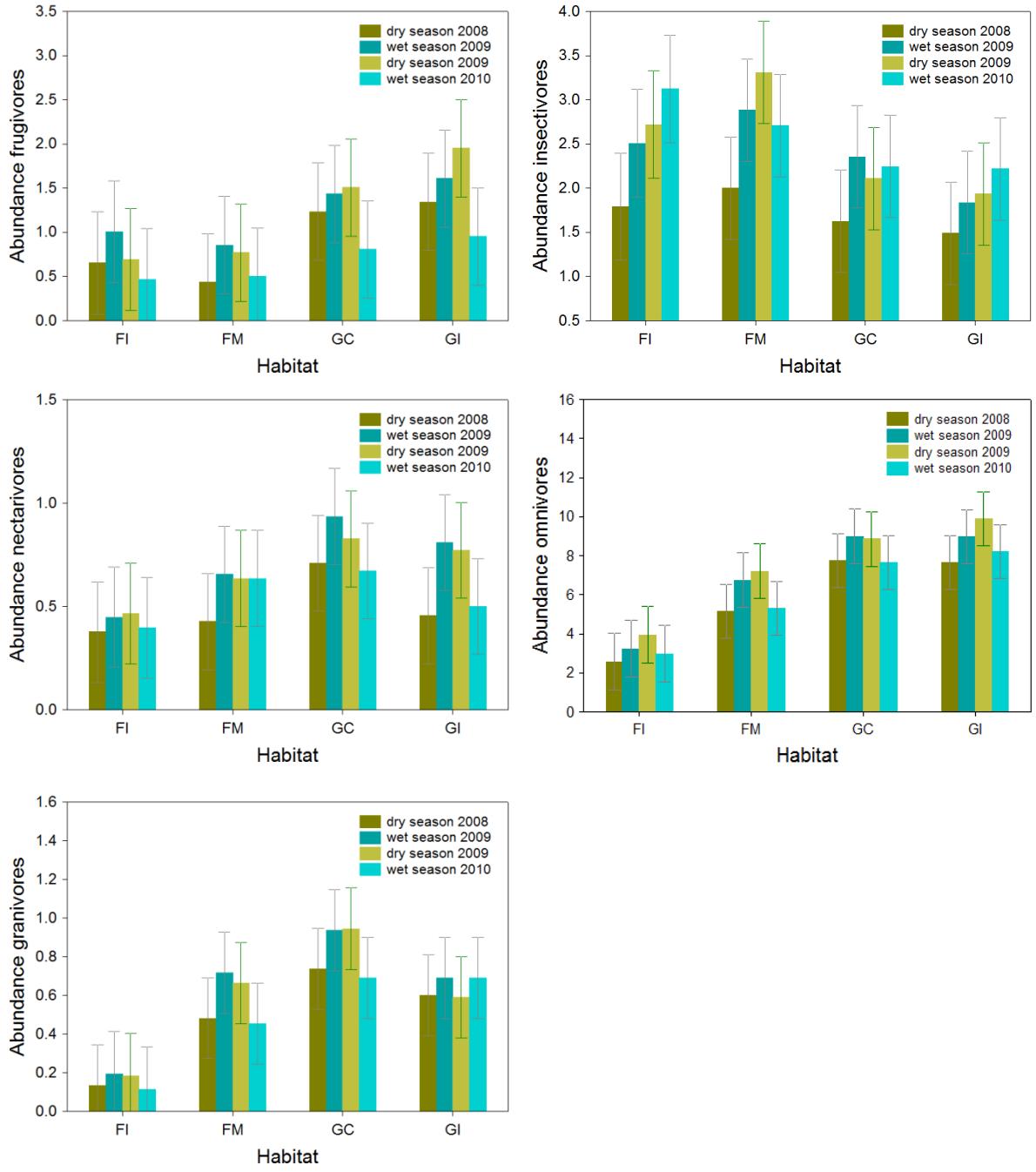

Fig. 3. Estimated means of birds (± 95% CI) counted at census points in four different habitats (FI – forest interior, FM – forest margin, GC – gallery forest strips connected to closed forest, GI – isolated gallery forest strips) during for different survey periods (two wet and two dry seasons), separately analyzed for five different feeding guilds.

Species richness of all feeding guilds except granivores differed significantly between survey periods. A significant effect of the habitat type on species richness could be shown for all feeding guilds except nectarivores. The interaction term habitat x season did not affect any of the feeding guilds significantly (Tab. 3).

Table 3. Results of GLMMs (normal error distribution, log-link function) testing for effects of habitat, survey period and the interaction term habitat x survey period on the number of recorded species of different feeding guilds at census points during different survey periods. Census point ID was included as random effect. *p* values represent FDR-adjusted values. Effects remaining significant after FDR correction are printed bold.

Feeding guilds	Habitat	Survey period	Habitat x survey period
Frugivores	**$F_{3,156}$ = 13.519, p < 0.001**	**$F_{3,156}$ = 12.850, p < 0.001**	$F_{9,156}$ = 1.058, p = 0.397
Insectivores	**$F_{3,156}$ = 12.401, p < 0.001**	**$F_{3,156}$ = 7.826, p < 0.001**	$F_{9,156}$ = 1.797, p = 0.073
Nectarivores	$F_{3,156}$ = 1.007, p = 0.391	**$F_{3,156}$ = 6.669, p < 0.001**	$F_{9,156}$ = 0.985, p = 0.455
Omnivores	**$F_{3,156}$ = 15.369, p < 0.001**	**$F_{3,156}$ = 17.331, p < 0.001**	$F_{9,156}$ = 0.384, p = 0.941
Granivores	**$F_{3,156}$ = 10.121, p < 0.001**	$F_{3,156}$ = 1.451, p = 0.230	$F_{9,156}$ = 1.482, p = 0.159

Richness of frugivores was lowest at FI, intermediate at FM and highest at the two gallery forest types. The number of insectivorous bird species declined continuously from FI to FM, GC and GI. Omnivorous and granivorous birds both showed a lower species richness at FI sites compared to the three other habitat types with a relatively similar richness. Only the guild of nectarivores was characterized by a similar richness in all four habitat types (Fig. 4). Species richness of four feeding guilds was affected by survey period (Tab. 3). However, again no clear pattern emerged which appeared being associated to wet-dry seasonality (Fig. 4).

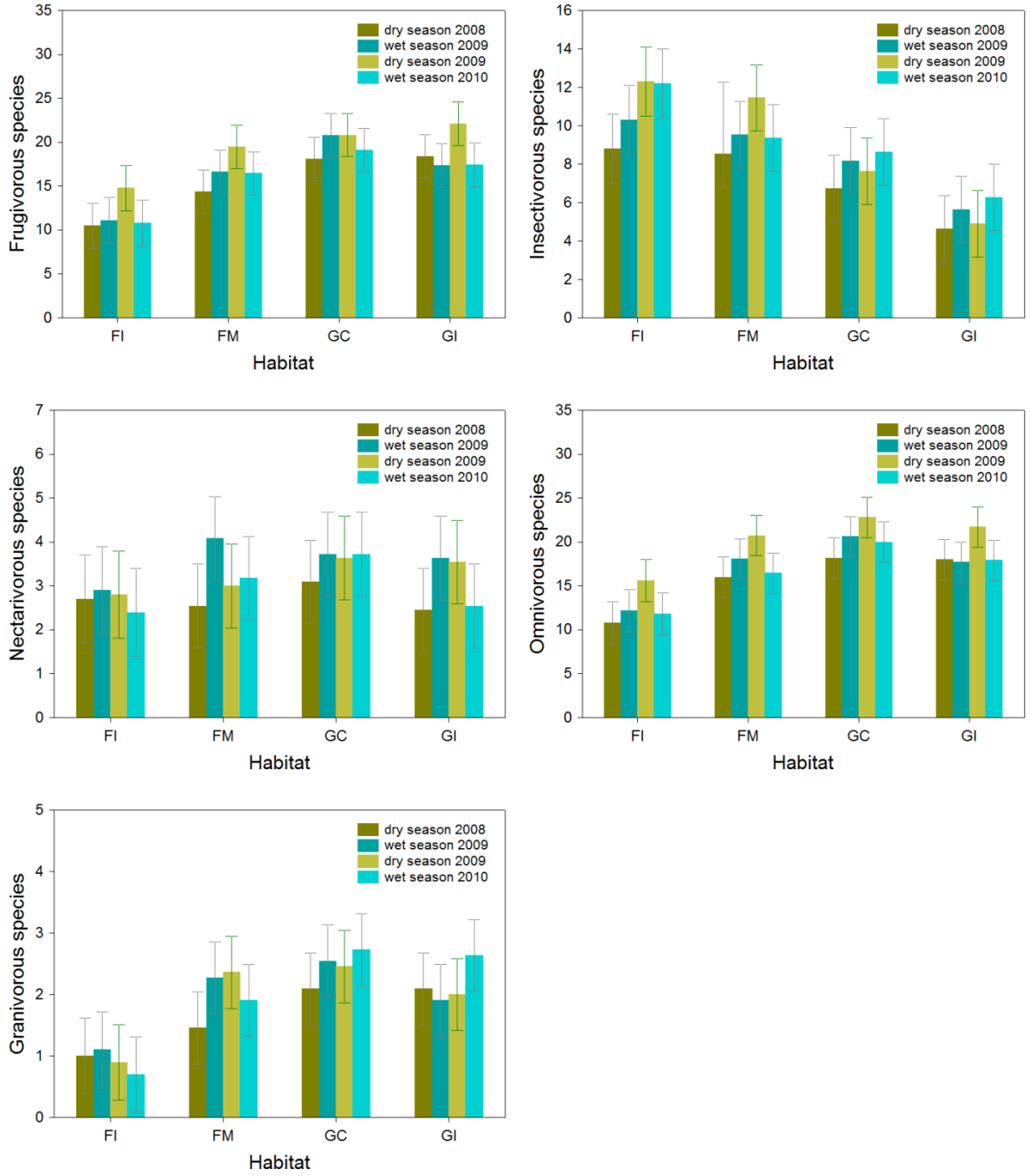

Fig. 4. Estimated means of bird species (± 95% CI) recorded at census points in four different habitats (FI – forest interior, FM – forest margin, GC – gallery forest strips connected to closed forest, GI – isolated gallery forest strips) during four different survey periods (two wet and two dry seasons), separately analyzed for five different feeding guilds.

Discussion

Changes in bird composition can be found due to reproduction, migration, and moult (Weise 1974), which all are energy-intensive events and must be timed with resource availability, which typically fluctuates seasonally. Nevertheless, we failed to find seasonal changes in bird species assemblage structure in our study area, although temporal changes did occur as we

found significantly different species composition between survey periods. The reason for not finding seasonal changes may be the beginning of our dry season-surveys in November, although the driest months are from January to April and November appears to be one of the wettest months in La Gamba (Weissenhofer & Huber 2008). However, mean precipitation per month differed significantly between our wet and dry seasons accounting to 291 mm/m² vs. 558 mm/m² in the dry season 2008 vs. wet season 2009 and to 328 mm/m² vs. 753 mm/m² in the dry season 2009 vs. wet season 2010. Thus, difference was more striking during the second survey period. Wet and dry season do seem to have a small effect on bird composition in the area, but the effect can be neglected.

Although a correlation between seasonal changes in food resource and abundance of tropical birds is common in frugivores and insectivores (Levey 1988, Loiselle & Blake 1991, Poulin et. al 1993, Wikelski et al. 2000, 2003, Şekercioğlu et al. 2007), in our study area there were no distinguishable changes triggered by wet and dry seasons. For example, the abundance of frugivores and omnivores was higher in the wet season 2009 than in the dry season 2008, but during the next wet and dry season the opposite pattern was observed.

Probably the amount of rain did not cause any water shortage during dry seasons, which could have limited the resource availability leading to clearer seasonal changes. This has been observed in tropical regions with high annual precipitation before (Nemani et al. 2003, Huete et al. 2006). At La Selva, in the north of Costa Rica the fruit scarcity could not be related to precipitation either, and the rainfall did not seem to be meaningful for fruit development (Frankie et al. 1974, Opler et al. 1980, Levey 1988). Another Costa Rican study even found a higher abundance of insects in the dry season than in the wet season (Janzen 1973) contradicting other studies, where the opposite was true (Frith & Frith 1985, Develey & Peres 2000). Thus, maybe in our study area insect and fruit abundances did not show significant seasonal changes either. Further, flowering and leaf flushing might not have occurred during the dry season only either, contradicting former researches (Wright & van Schaik 1994, Rivera et al. 2002, Huete et al. 2006). That no clear habitat-specific seasonality in abundance and species richness was observed for any feeding guild may support this assumption.

Interestingly, most of the feeding guilds showed higher abundances in all habitats in the wet and dry season 2009, than in the dry season 2008 and wet season 2010. Otherwise, the abundance of insectivores during survey periods was indistinct. In gallery forest habitats, insectivores were less abundant in the dry seasons than in the following wet seasons, but the highest recorded abundance was at FM in the dry season 2009. Insectivorous species richness at both gallery forest types was lowest during the dry seasons.

Probably, the occurrence of migratory species had a main impact on residential insectivores. Scientists often mentioned the paradox, how tropical communities support such an influx of consumers in the dry season, when insect abundance is supposed to be lowest (Janzen & Schoener 1968; Janzen 1973; Young 1994; Greenberg 1995). As the occurring migratory species at our study site were half insectivores, half omnivores (unpublished data), maybe the residential insectivores of our study site foraged in higher vegetation layers during dry season (Rabøl 1987, Waide 1981, Jedlicka et al. 2006), making them more difficult to detect during the observations in the dry seasons. Shifts in foraging niche seems to be a mechanism for insectivorous residents to avoid seasonal competition with abundant migrant species (Jedlicka et al. 2006).

However, that does not explain the higher abundance at FM sites, and the higher species richness at FI and FM sites during the dry season 2009, where trees were higher and denser (unpublished data), which would have even further decreased the detectability of resident birds there compared to the gallery forest sites.

A highly speculative assumption would be that residential insectivores moved to forest margins to avoid the migratory species preferring fragmented and human-dominated habitats like gallery forests for overwintering (Robbins et al. 1989, Petit & Petit 2003, Jedlicka et al. 2006, Schulze & Riedl 2008, unpublished data). Still, all those hypotheses do not explain why the change could only be observed in the dry season 2009 but not in the dry season 2008. To clarify the circumstance, further studies should be considered.

Besides the temporal effects on feeding guilds, habitat played a major role in feeding guild composition. Abundance of frugivores, nectarivores, granivores and omnivores increased from closed forest towards gallery forest types. The higher abundance and species richness of granivores in gallery forest types and at forest margins, is most likely related to their proximity to cultivated areas (e.g. annual cultures such as paddy fields) offering higher amounts of seeds than the surroundings of other habitat types (Schulze & Riedl 2008). In contradiction, no clear seasonal effects could be detected. Probably, the resource availability of cultivated grasslands like rice or other crops, which may affect granivores, did not differ seasonally (Butler et al. 2009, Chamberlain et al. 2000).

Usually, frugivores are reported to be sensitive to forest fragmentation (Canaday 1996, Schulze & Riedl 2008), what could potentially affect seed dispersal efficiency and plant composition in fragmented landscapes (Graham et al. 2002). However, abundance and species richness of frugivorous birds was higher at gallery forests than at FM and FI, why seed dispersal in riparian forests may not be affected. An explanation for higher frugivorous abundance at gallery forests could be a higher availability of fruits there. Higher densities of

fruiting plants are known to be found at fresh forest gaps due to higher plant productivity because of elevated photosynthesis (Levey 1988). Nevertheless, Restrepo et al. (1999) failed to find higher fruit abundance at old edges of forest fragments.

Hummingbirds represented all nectarivores recorded during our study at La Gamba. The highest abundance of nectarivores was achieved at gallery forests and forest margin, the species richness only differed slightly. This result is consistent with previous studies, reporting that hummingbirds may be less affected by deforestation and forest fragmentation than other guilds (Borgella et al. 2001, Gray et al. 2007). Here as well, flower resources could influence the abundance as it was recorded to be higher at forest edges and in forest fragments (Borgella et al. 2001, Brosi et al. 2008). This may therefore also count for gallery forest strips.

Omnivorous species richness and abundance was significantly higher at gallery forest types than at FM and FI, which enforces that omnivores are less sensitive to forest conversion (Aratrakorn et al. 2006, Renner et al. 2006, Gray et al. 2007). Another study conducted in La Gamba, Costa Rica, also found a significant increase in the abundance of omnivores from forest interior towards cultivated areas (Schulze & Riedl 2008). However, a mist-netting study in the same research area failed to find a significant difference in abundance of understory omnivores between gallery forests, FI and FM (Seaman & Schulze 2010).

Neotropical insectivorous birds appear to respond extremely sensitive to habitat disturbance and fragmentation (Canaday 1996, Stratford & Stouffer 1999, Şekercioğlu et al. 2002). Particularly forest insectivores are more likely to be absent from impacted forest and non-forest habitats (Canaday 1996, Şekercioğlu et al. 2002). Our study also reported a significant decrease of abundance and species richness in insectivores from FI and FM, towards the fragmented gallery forests.

Summing up, we observed temporal but no clear seasonal changes in the bird assemblages of La Gamba. Hence, it seems that seasonal effects in resource availability may be too indistinct that they could cause a detectable change in bird assemblages. Instead, habitat differences affect species richness and abundance of all feeding guilds and most of them significantly.

Taking into account that some feeding guilds showed opposite patterns in abundance during the first pair of wet and dry season and the second pair of wet and dry season, we advise against using results of seasonal effects observed within one year for any interpretation. Fluctuations in bird populations regularly occur as reproductive success differs between years (Marone 1992, Morrison & Bolger 2002). Hence, studies testing for seasonal effects

should be conducted in multiple consecutive years and our results have to be treated as being preliminary.

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Appendix 1. Classification of all recorded bird species. Feeding guild affiliation (O = omnivores, I = insectivores, C = carnivores, S= scavengers, F = frugivores, G = granivores, N = nectarivores) according to information on feeding preferences provided by Stiles *et al.* (1989) and their frequency of occurrence (= number of sites where the species was recorded) in different habitats (FI = forest interior, FM = forest margin, GC = gallery forest connected to forest, GI = gallery forest isolated from forest).

Family Species	Common Name	Habitat preference	**Habitat** Frequency of occurrence			
			FI	**FM**	**GC**	**GI**
Tinamidae						
Tinamus major	Great Tinamou	O	5	2		
Crypturellus soui	Little Tinamou	O	6	7	5	
Cracidae						
Ortalis cinereiceps	Gray-headed Chachalaca	F			4	3
Penelope purpurascens	Crested Guan	F	7	4	2	
Crax rubra	Great Curassow	O	7	6		
Odontophoridae						
Odontophorus gujanensis	Marbled Wood-Quail	O	1			
Cathartidae						
Coragyps atratus	Black Vulture	S	1	2	4	4
Cathartes aura	Turkey Vulture	S		2	3	2
Accipitridae						
Gampsonyx swainsonii	Pearl Kite	C			1	
Pseudastur albicollis	White Hawk	C	1			
Buteogallus urubitinga	Great Black- Hawk	C		2		
Rupornis magnirostris	Roadside Hawk	C	1	4	9	9
Buteo nitidus	Grey-lined Hawk	C			2	1
Falconidae						
Micrastur semitorquatus	Collared Forest-Falcon	C	1			
Caracara cheriway	Northern Crested Caracara	C			1	
Milvago chimachima	Yellow-headed Caracara	C	1	2	4	5
Herpetotheres cachinnans	Laughing Falcon	C	1	2	2	2
Columbidae						
Patagioenas cayennensis	Pale-vented Pigeon	F	3	3	8	1 1
Patagioenas nigrirostris	Short-billed Pigeon	F	9	11	10	2
Columbina talpacoti	Ruddy Ground-Dove	G		4	10	1 1
Claravis pretiosa	Blue Ground-Dove	O	7	11	11	6
Leptotila verreauxi	White-tipped Dove	G	4	11	1	1 1
Leptotila cassinii	Grey-chested Dove	G	9	10	9	
Geotrygon montana	Ruddy Quail-Dove	G	7	7	1	
Psittacidae						
Psittacara finschi	Finsch's Parakeet	F			1	
Eupsittula pertinax	Brown-throated Parakeet	F			1	1
Brotogeris jugularis	Orange-chinned Parakeet	F	1	4	6	7
Pyrilia haematotis	Brown-hooded Parrot	F	3		2	
Pionus menstruus	Blue-headed Parrot	F	1	3	5	8
Pionus senilis	White-crowned Parrot	F		1	2	2
Amazona autumnalis	Red-lored Parrot	F	5	1	2	5
Amazona farinosa	Mealy Amazon	F		1	1	
Cuculidae						

Piaya cayana	Squirrel Cuckoo	I	6	6	6	3
Crotophaga ani	Smooth-billed Ani	I			2	3
Trochilidae						
Glaucis aeneus	Bronzy Hermit	N	4	7	5	4
Threnetes ruckeri	Band-tailed Barbthroat	N	8	10	9	5
Phaethornis longirostris	Long-billed Hermit	N	10	6	3	1
Phaethornis striigularis	Stripe-throated Hermit	N	8	8	6	3
Eutoxeres aquila	White-tipped Sicklebill	N	3			
Campylopterus cuvierii	Scaly-breasted Sabrewing	N		4	10	10
Florisuga mellivora	White-necked Jacobin	N	2	7	11	10
Anthracothorax veraguensis	Veraguan Mango	N			1	1
Klais guimeti	Violet-headed Hummingbird	N	2			
Thalurania colombica	Crowned Woodnymph	N	9	6	2	
Hylocharis eliciae	Blue-throated Sapphire	N	2	3	2	4
Amazilia decora	Charming Hummingbird	N	5	8	7	7
Amazilia tzacatl	Rufous-tailed Hummingbird	N	3	10	11	1
Heliothryx barroti	Purple-crowned Fairy	N		4	4	2
Heliomaster longirostris	Long-billed Starthroat	N		1	3	2
Trogonidae						
Trogon massena	Slaty-tailed Trogon	O	6	4	5	2
Trogon bairdii	Baird's Trogon	O	6	9	4	2
Trogon violaceus	Violaceous Trogon	O	1	1	1	1
Trogon rufus	Black-throated Trogon	O	8	6	2	
Momotidae						
Momotus lessonii	Blue-diademed Motmot	O	8	7		
Bucconidae						
Malacoptila panamensis	White-whiskered Puffbird	I	2	1		
Galbulidae						
Galbula ruficauda	Rufous-tailed Jacamar	I	8	7		
Ramphastidae						
Pteroglossus frantzii	Fiery-billed Aracari	O	8	2	3	2
Ramphastos ambiguus	Black-mandibled Toucan	O	10	7	9	7
Picidae						
Picumnus olivaceus	Olivaceous Piculet	I			3	5
Melanerpes chrysauchen	Golden-naped Woodpecker	I	9	4	3	
Melanerpes rubricapillus	Red-crowned Woodpecker	O	1	9	11	11
Veniliornis kirkii	Red-rumped Woodpecker	I	1	4	7	4
Piculus simplex	Rufous-winged Woodpecker	I	5	6		
Hylatomus lineatus	Lineated Woodpecker	I	3	5	6	7
Campephilus guatemalensis	Pale-billed Woodpecker	I	3	2		
Furnariidae						
Synallaxis albescens	Pale-breasted Spinetail	I		1		
Synallaxis brachyura	Slaty Spinetail	I			1	1
Automolus ochrolaemus	Buff-throated Foliage-gleaner	I	6	5		
Xenops minutus	Plain Xenops	I	4	3	2	
Dendrocincla anabatina	Tawny-winged Woodcreeper	I	4	4	2	1
Deconychura longicauda	Long-tailed Woodcreeper	I	2	1	2	

Glyphorynchus spirurus	Wedge-billed Woodcreeper	I	5	6	2	3
Dendrocolaptes sanctithomae	Northern-barred Woodcreeper	I	3	3		
Xiphorhynchus susurrans	Cocoa Woodcreeper	I	10	10	11	9
Xiphorhynchus lachrymosus	Black-striped Woodcreeper	I	7	6	2	
Lepidocolaptes souleyetii	Streak-headed Woodcreeper	I	3	7	11	10
Campylorhamphus pusillus	Brown-billed Scythebill	I	1	1		
Thamnophilidae						
Taraba major	Great Antshrike	I		1	2	
Thamnophilus doliatus	Barred Antshrike	I	1			1
Thamnophilus bridgesi	Black-hooded Antshrike	I	10	8	4	
Thamnistes anabatinus	Russet Antshrike	I	3	1		
Microrhopias quixensis	Dot-winged Antwren	I	6	6		
Cercomacroides tyrannina	Dusky Antbird	I	2	3		
Poliocrania exsul	Chestnut-backed Antbird	I	10	11	8	2
Gymnopithys bicolor	Bicolored Antbird	I	1			
Formicariidae						
Formicarius analis	Black-faced Antthrush	I	10	9	1	
Tyrannidae						
Ornithion semiflavum	Yellow-bellied Tyrannulet	O	3	5	5	1
Camptostoma obsoletum	Southern Beardless-Tyrannulet	O		1	4	5
Capsiempis flaveola	Yellow Tyrannulet	O		4	8	8
Tyrannulus elatus	Yellow-crowned Tyrannulet	O			1	2
Elaenia flavogaster	Yellow-bellied Elaenia	O	1	3	9	10
Mionectes oleagineus	Ochre-bellied Flycatcher	O	8	5	6	7
Zimmerius vilissimus	Paltry Tyrannulet	O	3	8	11	11
Lophotriccus pileatus	Scale-crested Pygmy-Tyrant	I	2			
Oncostoma cinereigulare	Northern Bentbill	I	7	7	4	1
Poecilotriccus sylvia	Slate-headed Tody-Flycatcher	I	4	9	8	4
Todirostrum cinereum	Common Tody-Flycatcher	I		10	11	11
Rhynchocyclus brevirostris	Eye-ringed Flatbill	O	5			
Tolmomyias sulphurescens	Yellow-olive Flatbill	I	3	3	5	4
Platyrinchus coronatus	Golden-crowned Spadebill	I	5	2		
Myiobius sulphureipygius	Sulphur-rumped Myiobius	I	7	5		
Contopus sordidulus	Western Wood Pewee	I		1		
Contopus virens	Eastern Wood Pewee	I		4	3	1
Contopus cinereus	Tropical Pewee	I		1		3
Empidonax flaviventris	Yellow-bellied Flycatcher	O		1	1	
Empidonax alnorum	Alder Flycatcher	O		3	1	
Empidonax minimus	Least Flycatcher	I		4	2	1
Attila spadiceus	Bright-rumped Attila	O	9	11	11	8
Rhytipterna holerythra	Rufous Mourner	O	4	3		
Myiarchus tuberculifer	Dusky-capped Flycatcher	O	1	4	3	7
Myiarchus crinitus	Great Crested Flycatcher	O		2	2	1

Pitangus sulphuratus	Great Kiskadee	O	3	10	11	11
Megarynchus pitangua	Boat-billed Flycatcher	O	4	8	7	5
Myiozetetes cayanensis	Rusty-margined Flycatcher	I		1		1
Myiozetetes similis	Social Flycatcher	O	1	7	11	11
Myiozetetes granadensis	Grey-capped Flycatcher	O	1	10	11	11
Myiodynastes maculatus	Streaked Flycatcher	O		2	4	2
Myiodynastes luteiventris	Sulphur-bellied Flycatcher	O			1	1
Legatus leucophaius	Piratic Flycatcher	O	2	8	7	8
Tyrannus melancholicus	Tropical Kingbird	O	3	8	11	11
Pipridae						
Manacus aurantiacus	Orange-collared Manakin	O	9	10	7	2
Lepidothrix coronata	Blue-crowned Manakin	O	3	1		
Ceratopipra mentalis	Red-capped Manakin	O	7	7	2	
Cotingidae						
Lipaugus unirufus	Rufous Piha	I	6	3		
Tityridae						
Onychorhynchus mexicanus	Northern Royal Flycatcher	I	1	2	2	2
Terenotriccus erythrurus	Ruddy-tailed Flycatcher	I	2	1		
Schiffornis veraepacis	Northern Mourner	O	1			
Pachyramphus cinnamomeus	Cinnamon Becard	I		1		1
Pachyramphus polychopterus	White-winged Becard	O		4	6	2
Pachyramphus aglaiae	Rose-throated Becard	O	3	6	4	4
Tityra semifasciata	Masked Tityra	O	3	2	4	3
Tityra inquisitor	Black-crowned Tityra	O			7	5
Vireonidae						
Vireo flavifrons	Yellow-throated Vireo	I	1	2	4	4
Vireo philadelphicus	Philadelphia Vireo	O		2		
Hylophilus flavipes	Scrub Greenlet	O		1	8	7
Hylophilus ochraceiceps	Tawny-crowned Greenlet	I	6	1		
Hylophilus decurtatus	Lesser Greenlet	O	8	8	6	3
Vireolanius pulchellus	Green Shrike- Vireo	O	4	2		
Corvidae						
Cyanocorax morio	Brown Jay	O				1
Hirundidae						
Progne chalybea	Grey-breasted Martin	I				1
Stelgidopteryx serripennis	Northern Rough-winged Swallow	I			1	
Stelgidopteryx ruficollis	Southern Rough-winged Swallow	I		2	7	2
Troglodytidae						
Pheugopedius fasciatoventris	Black-bellied Wren	I	5	9	7	1
Cantorchilus semibadius	Riverside Wren	I	10	11	10	7
Cantorchilus modestus	Plain Wren	I	1	2	8	10
Troglodytes aedon	House Wren	I		3	6	1
Microcerculus marginatus	Southern Nightingale-Wren	I	8	2		

Polioptilidae						
Ramphocaenus melanurus	Long-billed Gnatwren	I	4	2		
Polioptila plumbea	Tropical Gnatcatcher	I	4	2	5	3
Turdidae						
Catharus ustulatus	Swainson's Thrush	O	1	1		
Turdus grayi	Clay-colored Thrush	O	1	10	10	11
Turdus assimilis	White-throated Thrush	O	3	2		
Parulidae						
Vermivora chrysoptera	Golden-winged Warbler	O				1
Leiothlypis peregrina	Tennessee Warbler	O	2	5	4	9
Setophaga petechia	Mangrove Warbler	I	2	3	6	10
Setophaga pensylvanica	Chestnut-sided Warbler	I	8	10	11	11
Mniotilta varia	Black-and-white Warbler	I	1	2	1	2
Parkesia noveboracensis	Northern Waterthrush	I	3	3	8	11
Parkesia motacilla	Louisiana Waterthrush	I	1	1		
Geothlypis philadelphia	Mourning Warbler	I		3	6	9
Myiothlypis fulvicauda	Buff-rumped Warbler	I	5	7	3	1
Thraupidae						
Coereba flaveola	Bananaquit	O	3	11	11	11
Eucometis penicillata	Gray-headed Tanager	I	2	3	1	
Piranga rubra	Summer Tanager	O	4	6	9	8
Lanio leucothorax	White-throated Shrike-Tanager	I	4	1		
Islerothraupis luctuosa	White-shouldered Tanager	O	4	2		
Tachyphonus rufus	White-lined Tanager	O	1		1	2
Ramphocelus costaricensis	Cherrie's Tanager	O	3	10	11	11
Habia atrimaxillaris	Black-cheeked Ant-Tanager	O	9	9		
Tangara episcopus	Blue-grey Tanager	O	2	10	11	11
Tangara palmarum	Palm Tanager	O		3	5	7
Tangara larvata	Golden-hooded Tanager	O	6	10	10	9
Tangara gyrola	Bay-headed Tanager	O	8	6	2	1
Tangara icterocephala	Silver-throated Tanager	O				2
Dacnis venusta	Scarlet-thighed Dacnis	F			3	2
Dacnis cayana	Blue Dacnis	O	3	5	2	3
Chlorophanes spiza	Green Honeycreeper	O	3	5	3	1
Cyanerpes lucidus	Shining Honeycreeper	O	5	3	5	6
Cyanerpes cyaneus	Red-legged Honeycreeper	O	3	2	8	9
Volatinia jacarina	Blue-black Grassquit	G		2	5	7
Sporophila schistacea	Slate-colored Seedeater	G	2	6	9	8
Sporophila corvina	Black Seedeater	O	1	7	11	11
Sporophila torqueola	Cinnamon-rumped Seedeater	G			1	4
Sporophila nigricollis	Yellow-bellied Seedeater	G			1	3
Sporophila funerea	Thick-billed Seed-Finch	G	2	5	7	8
Saltator maximus	Buff-throated Saltator	O	8	11	11	11
Saltator striatipectus	Streaked Saltator	O		5	6	4

Passerellidae						
Arremon aurantiirostris	Orange-billed Sparrow	O	10	11	9	9
Arremonops conirostris	Black-striped Sparrow	O	1	8	11	11
Cardinalidae						
Pheucticus ludovicianus	Rose-breasted Grosbeak	F			1	1
Cyanoloxia cyanoides	Blue-black Grosbeak	O	8	3	5	2
Icteridae						
Dives dives	Melodious Blackbird	O				1
Quiscalus mexicanus	Great-tailed Grackle	O		1	4	9
Molothrus aeneus	Bronzed Cowbird	O			4	3
Icterus spurius	Orchard Oriole	O				2
Icterus galbula	Baltimore Oriole	O	1	2	5	7
Amblycercus holosericeus	Yellow-billed Cacique	I		6	7	1
Cacicus microrhynchus	Scarlet-rumped Cacique	O	10	9	9	8
Psarocolius decumanus	Crested Oropendola	O			1	1
Fringillidae						
Euphonia luteicapilla	Yellow-crowned Euphonia	O	3	5	7	7
Euphonia laniirostris	Thick-billed Euphonia	O	3	9	8	11
Euphonia elegantissima	Elegant Euphonia	F			1	
Euphonia imitans	Spot-crowned Euphonia	O	9	9	5	7
Euphonia minuta	White-vented Euphonia	F		1	1	

d. Understory forest birds facing higher clutch predation risk in linear gallery forest strips compared to old-growth forest areas: a case study using artificial nests

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ABSTRACT

Habitat loss and change are major threats to biodiversity. Especially in the tropics, forest areas are falling victim to agricultural and human settlement expansion, which leads to more and more forest fragments and remnants. In Costa Rica, a forestry law prohibits to fell trees beside rivers, resulting in a net of gallery forests, which shall connect forest fragments and diminish forest species loss. Actually, gallery forests are very species rich, even inhabiting a fraction of forest birds. However, they border on highly modified habitats and forest birds are possibly facing typical edge effects like higher predation risk.

Hence, we tested the difference in nest predation with artificial nests and Styrofoam eggs between two seasons and four habitats – forest interior, forest margin, gallery forests connected and isolated from forest. Nest predation was significantly higher at isolated gallery forests than in forest interior. There was no significant difference between wet and dry season. Main predators, identified by their marks left on the Styrofoam balls, were birds accounting for c. 65% of predated eggs. Other predators were mammals and reptiles. The relative importance of birds, reptiles and mammalian predators did not differ significantly between habitats.

If predation risk on real nests in our study area exhibits the same pattern like observed for artificial nests, gallery forests may act as ecological trap for forest birds. However, they still may be have a conservation value by facilitating movements of forest birds between remaining larger forest fragments.

Las aves de sotobosque están enfrentadas a un mayor riesgo de depredación de nidadas en bosques de galería en comparación con áreas de bosques primarios: un estudio de caso usando nidos artificiales

RESUMEN

El cambio y la pérdida del hábitat representan mayores riesgos para la biodiversidad. Especialmente en los trópicos, las áreas forestales son arrasados por la expansión de la agricultura y la urbanización, lo que provoca más y más remanentes y bosques fragmentados. En Costa Rica la ley forestal prohíbe la tala de árboles al lado de ríos, lo que da como resultado una red de bosques de galería, que conecta fragmentos de bosques y disminuye la pérdida de especies forestales. Efectivamente, los bosques de galería están caracterizados por una alta diversidad de especies, a tal punto que llegan a albergar una fracción de aves forestales. Sin embargo, están limitando con hábitats altamente modificados y probablemente las aves forestales están confrontadas con efectos típicos de las áreas limítrofes como un alto riesgo de depredación.

Por lo tanto, examinamos la diferencia de depredación en nidales con nidos artificiales y huevos de poliestireno entre dos estaciones y cuatro hábitats - interior del bosque, margen del bosque, bosques de galería conectados y aislados del bosque. La depredación en nidales fue significativamente más alta en bosques de galerías aislados que en el interior de la selva. No se encontró una diferencia significativamente entre la temporada seca y la de lluvias. Los principales predadores, identificados por las marcas dejadas en los huevos de poliestireno, eran aves, las cuales robaron aprox. 65% de los huevos. Los otros depredadores fueron mamíferos y reptiles. La importancia relativa de las aves, los reptiles y los mamíferos predadores no se diferenció significativamente entre los hábitats.

Si el riesgo de depredación en nidos reales de nuestra área de estudio exhibe el mismo patrón que el observado en los nidos artificiales, los bosques de galería pueden actuar como trampa ecológica para aves forestales. Sin embargo, pueden tener un valor de conservación al facilitar los movimientos de aves forestales entre grandes fragmentos de selva.

Key words: artificial nests, nest predation, tropical birds, gallery forest, habitat loss, forest fragmentation, ecological trap

INTRODUCTION

Deforestation at a high rate resulting in forest fragmentation is a well-known problem in tropical regions. Seven million hectares of tropical forest were lost per year over the period of 2000 to 2010 (FAO 2016). Hence, tropical forest birds are severely threatened by increasing habitat change and loss (Turner 1996, Brooks et al. 2002). Corridors and stepping stones like linear gallery forest strips are supposed to counteract negative effects of forest fragmentation and isolation on tropical biodiversity (Laurance & Laurance 1999, Pardini et al. 2005, Fagan et al. 2016). For example, in Costa Rica gallery forest strips are specified by remarkable high bird species richness, although, forest bird richness decreases significantly from forest interior towards gallery forests (Matlock et al. 2002, Seaman & Schulze 2010). Furthermore, the occurrence of forest birds in such linear riparian structures does not necessarily indicate that these species maintain sustainable populations there.

Most likely, birds have to deal with higher edge effects in smaller forest fragments like gallery forests than in large closed forest areas (Lees & Peres 2008, Banks-Leite et al. 2010). One well-known edge effect is a higher nest predation rate (Martin 1993, Hartley & Hunter 1998, Söderström 1999, Vetter et al. 2013) because of greater diversity of predators and their better foraging efficiency along edges (Bayne & Hobson 1997, Larivière 2003). Therefore, habitat disturbance may affect native fauna negatively (Posa et al. 2007), especially if the forest edge borders strongly human-modified landscape (Lahti 2001). Interestingly, inverse edge effects may occur as well due to forest-dependent small

mammals or snakes as it has been observed in the East African tropical forests, where ground nests faced a higher predation rate in the forest interior than at the edges (Spanhove et al. 2009).

Either way, nest predation is recognized as a serious threat to the survival of bird populations (Ricklefs 1969, Smith et al. 2010). Namely, birds only return to a breeding site if successful, using their reproductive performance as a guide to future habitat selection (Chalfoun & Martin 2010; Pakanen et al. 2014), also known as the "win–stay: lose–switch" strategy (Hildén 1965; Greig-Smith 1982). Indeed, this strategy has been confirmed by predator removal experiments, where birds responded to the presence of predators by altering settlement decisions (Fontaine & Martin 2006, Hua et al. 2013, Ibáñez-Álamo et al. 2015).

Considering the recent and fast progressing deforestation and fragmentation in the tropics, it is important to learn more about predation rates in tropical forest edges. In addition, unsuitable habitats for reproduction represent a major concern for nature conservation, because they may become ecological traps (Schlaepfer et al. 2002).

In this study we compare bird nest predation using artificial shrub nests in forest interior (FI), forest margin (FM), gallery forest connected to (GC), and gallery forest isolated from closed forest (GI) in a study area in the Pacific lowlands of the Golfo Dulce region. Basically, we want to test if understory forest birds are facing higher clutch predation risk in linear riparian forests than in closed forest.

By identifying the marks on the predated artificial eggs, we also compare the composition of predators (mammals, birds, reptiles) between the four habitats. A higher amount of small mammals like rodents was documented to operate on shrub nests on forest edges (Pangau-Adam et al. 2006), maybe due to the "mesopredator release hypothesis" (Terborg 1974, Crooks & Soulé 1999; Söderström 1999). It predicts an increased abundance of small nest predators in fragmented habitats, because of the absence of top predators.

As our experiment was conducted in the wet and dry season, which could affect overall food availability and hence nest predation rates, we considered potential seasonal effects too.

We are aware of the problems in interpreting artificial nest predation studies, e.g. that affected artificial nests may not reflect the lost egg quantity of natural nests (Berry & Lill 2003, Robinson et al. 2005b). Nevertheless, studies confirmed that nest predators seek, find and respond in the same manner to artificial nests like to natural nests (Martin 1987; Carlson & Hartman 2001, Pangau-Adam et al. 2006). Hence, predation on artificial nests

could predict the predation pressure on real nests (Pangau-Adam et al. 2006) or at least relative differences between habitats. Furthermore, useful information for addressing some conservation questions can be gained (Villard & Pärt 2004; Ibáñez-Álamo et al. 2015). Besides, finding nests in the tropical thicket to record clutch predation proves to be very difficult (Oniki 1979, Roper 2003, Robinson et al. 2005a, b).

Based on previous studies, we expect to find higher predation rates at more disturbed habitats like gallery forests, which are embedded in a landscape matrix containing mostly human-modified habitats at our study area.

METHODS

Study area, surveyed habitats and study sites

The study was conducted near La Gamba in the Golfo Dulce region, a small village bordering on the Piedras Blancas National Park (8°42'61" N, 83°12'97" W) at the southern Pacific slope of Costa Rica. La Gamba has a typical equatorial climate with high day temperatures (between 19 and 39 °C) and an average relative humidity of over 90%. It belongs to the wettest lowland forests in Central America with a mean annual precipitation of c. 5800 mm (Weissenhofer & Huber 2008).

More than 326 bird species have been recorded in the area (Tebb 2007), and this number is rising continually (e.g. Riedl & Schulze 2010). An endemic species to the Golfo Dulce lowlands of southwestern Costa Rica, the Black-cheeked Ant-Tanager *Habia atrimaxillaris*, upvalues the distinctive avifauna of this region (Cornils et al. 2015).

Using artificial nests, clutch predation was quantified for four different habitat types: forest interior (FI), forest margin (FM), gallery forest connected to closed forest (GC), and isolated (GI). For FM, GC and GI eleven replicate sites and for FI ten were chosen (Figure 1). FI sites were selected within a larger forest block (Piedras Blancas National Park) and FM sites at its edge. FM sites were located within the transition zone between (semi-) open countryside habitats and up to c. 50 m towards the forest interior. Riparian forest strips crossing open areas were defined as gallery forests. If the strips were in direct contact to closed forest, they were classified as "connected", otherwise as "isolated". The mean width and length (± SD) of forest strips was 62.05 (± 40.33) m and 923 (± 1154.37) m for GC sites and 21.77 (±40.33) m and 1974.55 (± 1568.10) m for GI sites, respectively. The mean distance (±SD) to the forest margin was 173.73 (± 154.70) m for GC sites and 543.00 (± 141.13) m for GI sites.

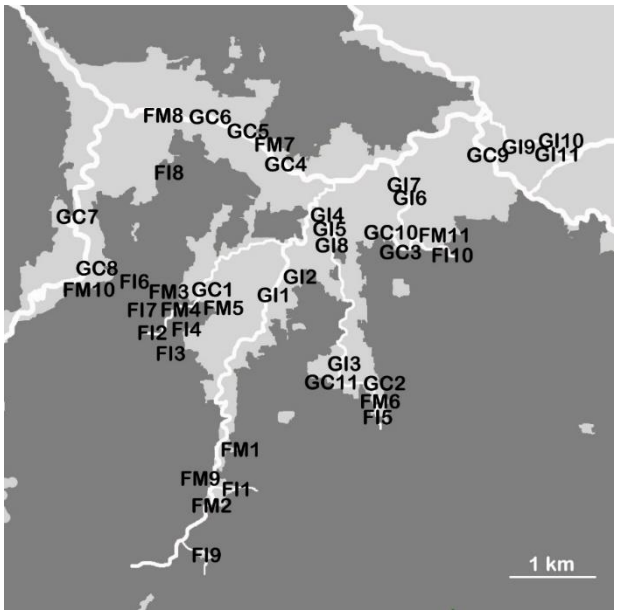

Figure 1. Schematic map of the study area indicating all bird census points at forest interior (FI), forest margin (FM), and gallery forest sites connected to (GC) and isolated from closed forest (GI). White lines represent rivers, the dark grey areas primary forests and forest remnants, while the light grey shows human-dominated areas like agriculture and settlements.

Experimental design of artificial nests

Predation tests were conducted at every site of all four habitats one time in the wet season (22 July–23 October 2008) and once in the dry season (3 October 2009–18 February 2010). Altogether 10 nests were placed in two linear transects (five nests on each transect) at each study site. Nets were situated 10 m apart and 1–1.5m above the grounds in forked branches of plants to resemble nests of understorey shrub-nesting birds. If a stream crossed the site, the two transects were separated by it, hence five nests were placed on each side of the stream.

All nests were made of wire netting, 10 (±2) cm (diameter) x 5 cm (in depth). To give them a more natural look, the wire baskets were covered with leaves of *Cecropia* sp., a very common tree in this region. In each nest we put three small white Styrofoam balls (25 mm), which were tied to the wire with a thin dark brown thread. To imitate real eggs, small black dots were painted on the balls with a waterproof marker (Figure 2). In order to avoid any odours during all operations gloves and rubber boots were worn (Laurance et al. 1993).

Figure 2: Dummy nests made of wire covered in a Cecropia sp. leaf with three white Styrofoam balls tied to the nest. Nests were placed into shrubs at study sites.

Artificial nests were exposed for seven days. A nest was considered as predated, if either the entire nest or its eggs were missing, if eggs were kicked out of the nest or showed tracks (beak or bite marks) of predators.

Identification of predators

Pointed angled holes or chopped eggs were interpreted as beak marks of birds. Squashed eggs were linked to snakes and semi circled imprints without teeth marks to lizards, later summarized as reptiles. If the eggs showed marks of incisors, the predator was defined as rodent, pointed thin holes were specified as marks of canine teeth. Marks of such teeth and claw marks on eggs were defined as predated by mammals.

The predator was classified as unknown, when the total nest went missing, or eggs were thrown outside but without any marks.

Statistical analysis

Records of egg predators were pooled on the level of habitat types. To test for differences in the proportion of eggs with signs of the identified predators between habitat types, Chi-Square tests were calculated. Results did not have to be adapted for multiple testing using a Bonferroni correction as no test indicated a significant difference between habitats (see Results section).

Overall nest predation per site was quantified separately for dry and wet season as the percentage of nests with any signs of predation. A GLM (with log normal error distribution and log-link function) was calculated to test for effects of habitat type, season and the interaction term habitat type X season on the percentage of predated nests.

RESULTS

Nest predation was generally very high reaching a mean percentage of predated clutches per site (± SD) of 60.45 (± 16.13) & during the wet season and 55.00 (± 23.77) % during the dry season. The GLM indicated a significant effect of habitat on the percentage of predated nests. Instead, clutch predation was not significantly affected by season and the interaction habitat X season (Table 1). In both seasons the percentage of predated nests increased from FI and FM towards the gallery forest sites, reaching highest values at GI sites (Figure 3).

Table 1. Results of GLM (with log normal error distribution and log-link function) testing for effects of habitat type, season and the interaction term habitat type X season on the percentage of predated nests.

Variables included	df	MS	*F*	*P*
Constant	1	293254.5	790.64	<0.0001
Habitat	3	1518.2	4.09	0.0093
Season	1	654.5	1.76	0.1878
Habitat X Season	3	421.2	1.14	0.3398
Error	80	370.9		

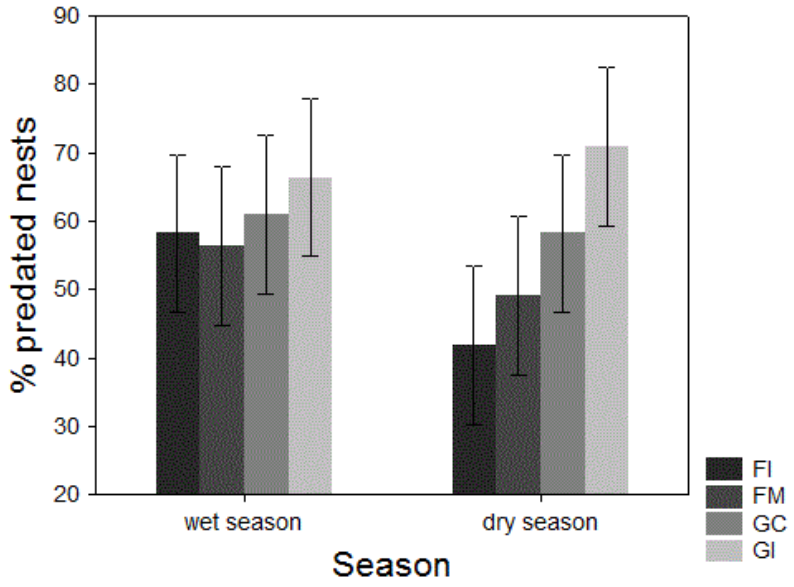

Figure 3. Least square means of percentage of predated nests per site, separately figured for wet and dry season.

Most of the recorded egg predators (84.08 %) represented birds (Figure 4-5). The relative importance of birds, reptiles and mammalian predators did not differ significantly between habitats (all Chi-Square tests: $P > 0.05$).

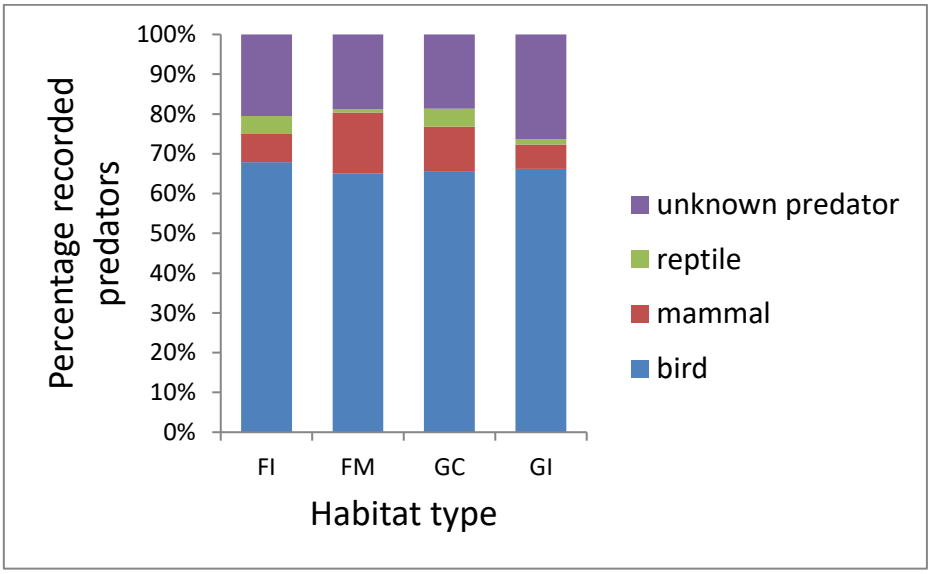

Figure 4. Percentage of recorded egg predators at different habitats. FI– forest interior, FM– forest margin, GC– gallery forests connected to closed forest, GI– gallery forest isolated from closed forest.

Figure 5. Example of predated nest, where Styrofoam balls show clear marks of a bird beak and two balls were thrown out of the nest

DISCUSSION

Formerly, the international ornithological community accepted that breeding success primarily depends on food availability, when in the 1990s the immense impact of predation became clear (Birkhead et al. 2014, Guppy et al. 2017). Today it is well-known, that nest predation has a major impact on nest failure (Hanski et al. 1996, Flaspohler et al. 2001). Monitoring real bird nests showed very high predation all over the world on various bird species' nests, being higher in tropical regions (Snow & Snow 1963, Willis 1974, Robinson et al. 2000), although Gibbs (1991) supposed that the last fact might be an artefact because tropical birds were mostly studied in disturbed or isolated forests. Anyway, the loss of tropical nests can even reach up to 100% as it was recorded in Central Panama for Chestnut-backed Antbirds (Robinson et al. 2005a).

Especially high nest predation, likewise if tested with artificial nests or observed on real ones, occurs in forest fragments and at forest edges in deforested landscapes (Hartley & Hunter 1998, Wilson et al. 1998, Batary & Baldi 2004, Sosa & de Casenave 2017). This may be due to predation-related edge effects as predators profit from a higher detection rate of nests at edges (Bayne & Hobson 1997, Chalfoun et al. 2002, Larivière 2003). Predators may also influx more easily from the surrounding matrix into forest patches and forest edges or could use them as forage and travel lane (Chalfoun et al. 2002). These results are underlined by our experiments documenting an increased clutch predation along linear forest strips, namely the isolated gallery forests.

A further reason, why predation rates rise in fragmented forests is that top predators are particularly vulnerable to fragmentation and go extinct. The absence of top predators subsequently leads to an increase of typical nest predators like small mammals (Crooks & Soulé 1999, Dijak & Thompson 2000). Somehow, at our study site the distribution of predator classes did not differ significantly. At all habitats, birds, followed by mammals and reptiles, predated the vast majority of artificial eggs.

Regarding other studies, it becomes clear, that there is no homogenous pattern of main nest predators, neither for any climatic zone nor for any habitat. In two studies in the temperate zone, the importance of avian predators declined in larger areas away from the forest edge and concurrently mammals took over (Nour et al. 1993, Haskell 1995). Evaluating various researches main predators can range from birds (Robinson & Robinson 2001, Rodewald & Kearns 2011, Cockle et al. 2016) to mammals (Laurance & Grant 1994, Thompson & Burhans 2004, Pangau-Adam et al. 2006, Michalski & Norris 2014) and reptiles like snakes (Weatherhead & Blouin-Demers 2004, Robinson et al. 2005a) not showing any pattern or dependence to habitat or climatic zone. Hence, case studies are highly recommended when aiming to identify the main predators for a specific target area.

Besides classifying predators, we also tested for seasonal effects on predation rate. The increase of predated nests from FI towards GI was clearer in the dry season, but the total nest predation was slightly higher in the wet season. Comparing the two seasons no significant difference could be detected.

According to Skutch (1950) Costa Rican bird species normally breed in the beginning of the wet season from April to June when food, both vegetable and insects, is most abundant and migratory species have left. As our nest predation experiment of the wet season started in July and ended in October, no tests were made during highest breeding rate, although it could have delivered interesting results. The second survey period took place from October, when migratory birds arrived, until February. October and November are one of the wettest months of the year (Weissenhofer & Huber 2008) at La Gamba, hence the dry season was not well defined, which might be the cause that we failed to find a seasonal effect. However, other studies did not find clear seasonal changes in predation rates on artificial nests either (Gibbs 1991, Young 1994, Zanette 2002).

A major question arising when discussing results of artificial nests is if artificial nests can be compared with real ones. Some researches claim that inferences about predation on natural nests based on artificial nest experiments should be avoided (Zanette 2002, Robinson et al. 2005b). Others suggest that survival rates of artificial eggs are lower because of the lack of bird parents defending and camouflaging them (Wilson et al. 1998, King 1999, Remeš 2005). Further, the amount of predated nests may not be equivalent if the eggs used in artificial nests are different to natural ones.

Commonly used eggs for experiments are quail eggs, which are bigger than those of most tropical understorey birds. The difference in size and the hardness of the shell affects the type of predators (Thompson & Burhans 2004). Hence, trends in predation rates on artificial nests may not be a good index for actual rates (Haskell 1995, Maier & DeGraaf 2000, Robinson et al. 2005b, Michalski & Norris 2014).

Nevertheless, well-designed experiments do provide valuable information, as it was shown by Roos (2002) in Sweden, where the predation risk measured on artificial nests could be used as a relative index of spatial and temporal variation in real nest predation risk. Although artificial nests should not be used to measure the actual amount of affected eggs, there is evidence that overall predation rates are similar among real and artificial nests (Wilson et al. 1998, Thompson & Burhans 2004). Therefore, results of artificial nests can be regarded as representative and valuable to detect trends in predation pressure, even if the percentage of attacked fake nests may not predict the real breeding success (Wilson et al. 1998).

If predation on real nests in our study area exhibit the same pattern like that we observed on artificial nests, birds face a very high predation risk in gallery forests. Considering that concentration of resources may be high at those habitats (Fogden 1972, Ries & Sisk 2004), gallery forests attract even some forest birds. Hence, gallery forests may appear as suitable breeding site to them while high nest predation leads to nest failure. This situation is referred to as an ecological trap (Misenhelter & Rotenberry 2000, Schlaepfer et al. 2002). Increased nest predation in forest fragments and at forest edges may tighten the pressure on forest species beside habitat loss and change in tropical regions even more. However, gallery forest strips may be of conservation value by facilitating spatial movements of forest birds between remaining forest fragments (Seaman & Schulze 2010), hence buffering smaller fragments against local extinctions. This potential conflict may only be reduced when increasing the width of (gallery) forest strips, thereby further increasing the permeability of human-dominated landscapes for forest birds on the one hand and decreasing predator-related edge effects on the other hand.

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e. Population density and habitat preferences of the Black-cheeked Ant-tanager *Habia atrimaxillaris*

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Summary

The lowland forest on the southern Pacific slope of Costa Rica has an extremely diverse avifauna, including the Black-cheeked Ant-tanager *Habia atrimaxillaris*. The only known remaining populations of this highly range-restricted species occur in the areas of Piedras Blancas and Corcovado National Park. It is assumed that the population is decreasing due to habitat loss and fragmentation. We assessed the species' population density in a part of the Piedras Blancas National Park using distance sampling (in February–April 2009 and November 2010–January 2011) and territory mapping (November 2010–January 2011). We also examined habitat preferences based on vegetation structure at point count locations. Black-cheeked Ant-tanagers were exclusively found in old-growth forest. The species' likelihood of occurrence at census points increased with forest cover (within a radius of 200 m around census points), canopy closure, and density of trees (with diameter at breast height >10 cm). Average population density estimated by distance sampling was 24–27 individuals per km², which is in accordance with the population size estimated by territory mapping (17–25 birds per km²). Based on these estimates, an overall population size of 12,432–20,720 birds is predicted for the remaining 592 km² lowland forest area of the Golfo Dulce region. The Black-cheeked Ant-tanager was only recorded in old-growth forest, but not in gallery forests embedded in a human-dominated landscape matrix. Since the species appears to avoid forest edges, further forest degradation and fragmentation will have a strong negative impact and should be rapidly reduced by adequate conservation measures.

Keywords: Costa Rica, distance sampling, forest cover, forest structure, Piedras Blancas National Park, population size estimate, tropical lowland forest, territory mapping

Introduction

Habitat loss and fragmentation are major threats to rainforest biodiversity (Terborgh 1992, Lawton et al. 1998, Curran et al. 2004, Huang et al. 2007), including birds (Fjeldså 1999, Sodhi and Smith 2007). For 50% of all threatened bird species in the Americas, it is the only threat that needs to be managed and prevented (Collar et al. 1997). Habitat loss in the tropics is of particular concern given that 70% of all threatened bird species occur in tropical forests (Sodhi and Smith 2007).

Mesoamerica with its character as a melting pot for northern and southern American species was ranked as one of the 25 primary biodiversity hotspots by Myers et al. (2000). It houses a high percentage of endemic vertebrates and plants. A total of 9% (29) of the 327 threatened

bird species in the Americas have a distribution restricted to Central America, which only represents a small proportion of the whole continent. In terms of range-restricted birds, Costa Rica and Panama have the most diverse species assemblages in the Neotropics (Collar et al. 1997) and they belong among the 15 countries with the most restricted-range bird species in the world (García-Moreno et al. 2007). One of the region's endemic birds, the Black-cheeked Ant-tanager *Habia atrimaxillaris* (Dwight et al. 1924), has a particularly small distribution range. It only occurs in the lowlands of the Golfo Dulce Region in the south-western part of Costa Rica (Slud 1964, Stiles and Skutch 1989, Garrigues and Dean 2007). Due to its extremely small distribution range of only c.500 km^2 the species is classified as 'Endangered' (Aubrecht 2008, BirdLife International 2014). The poor knowledge on the species' biology is emphasised by the fact that the first nests of Black-cheeked Ant-tanager were found and described only recently (Huber et al. 2008, Sandoval and Gallo 2009). Furthermore, information on the species' actual conservation status and its habitat preferences is very limited (Aubrecht 2008, Aubrecht and Schulze 2008, Sandoval and Gallo 2009).

Negative effects of human disturbance on forest birds have been reported for many tropical regions (Thiollay 1992, Schulze et al. 2004, Waltert et al. 2005, Gray et al. 2007, Maas et al. 2009, Mordecai et al. 2009). Range-restricted understorey birds are particularly sensitive to anthropogenic forest disturbance (Gray et al. 2007). Therefore, we expect that with ongoing fragmentation of the Pacific lowland forest, remaining populations of the endemic Black-cheeked Ant-tanager will further decline in the next few years. Even well-protected areas such as Corcovado National Park are still strongly affected by deforestation close to their boundaries (Sánchez Azofeifa et al. 2003), which is increasing their isolation from other remaining forest fragments, a phenomenon found to negatively affect most tropical protected areas (Laurance et al. 2012). The range of the Black-cheeked Ant-tanager has declined by approximately 50% since 1960 (BirdLife International 2014). The only remaining populations are found in Corcovado National Park and in the vicinity of Golfito, particularly in the Esquinas Forest (Piedras Blancas National Park) and the Golfito Faunal Refuge (Schulze and Riedl 2008, Seaman and Schulze 2010, BirdLife International 2014).

Published information on habitat preferences of the Black-cheeked Ant-tanager indicates that the species is restricted to the understorey of dense lowland rainforest (Stiles and Skutch 1989), where it occurs in undisturbed, older secondary and selectively logged forest areas (e.g. Aubrecht 2008). In contrast to other *Habia* species (e.g. *H. gutturalis* and *H. fuscicauda*), the Black-cheeked Ant-tanager forages higher up in the undergrowth and prefers more mature forest (Willis 1966). However, so far no studies have quantitatively analysed the species' habitat preferences, using a standardised survey design. In this study

we tried to identify important habitats and forest vegetation structures preferred by the Black-cheeked Ant-tanager. In particular, we addressed the following questions:

(1) Does Black-cheeked Ant-tanager prefer mature and old-growth secondary forest, although it can occasionally be observed in other habitats (e.g. beachfront scrub, palms adjacent to forest) (Stiles and Skutch 1989, Capper et al. 1998, Aubrecht 2008)? Slud (1964) noted that they live more in tall secondary growth and broken forests than in the interior of unbroken forests.
(2) Does the species avoid forest edges? and
(3) to what extent is the species' occurrence related to forest structure (tree density, canopy closure and understorey density)?

Depending on the information used for estimating the species' current population size, the total number of birds is between c.10,000 and 20,000 individuals (BirdLife International 2014). In this study, two different methods – territory mapping and distance sampling – are used to estimate population density in part of the Esquinas Forest. So far such data are missing for this forest reserve. Furthermore, these are the first precise population density estimates, which we use to estimate the species' current total population size.

Methods

Study area

The study area is situated in the Golfo Dulce region in the south-western part of Costa Rica. The remaining lowland forests in this region are relatively well protected by the Corcovado National Park (established in 1975) located on the Osa Peninsula and the Piedras Blancas National Park (established in 1994) on the eastern side of Golfo Dulce. These two protected areas are connected through the Golfo Dulce Forest Reserve (established in 1979). Furthermore, a corridor project to improve connectivity between these two National Parks and other protected areas in the vicinity is in progress as part of the project for a Mesoamerican Biological corridor.

Our study sites were located near La Gamba village (8°42′30”N, 83°11′0”W) and the La Gamba Tropical Research Station (8°42′61”N, 83°12′97”W; Figure 1). Here, most areas of flat terrain are covered by human-dominated habitats (pastures, annual cultivation, oil palm plantations, settlements) and secondary forest. On hilly terrain, large parts of the study area are still covered with almost pristine forest (Figure 1; for a more detailed description of habitat types see Höbinger et al. 2011).

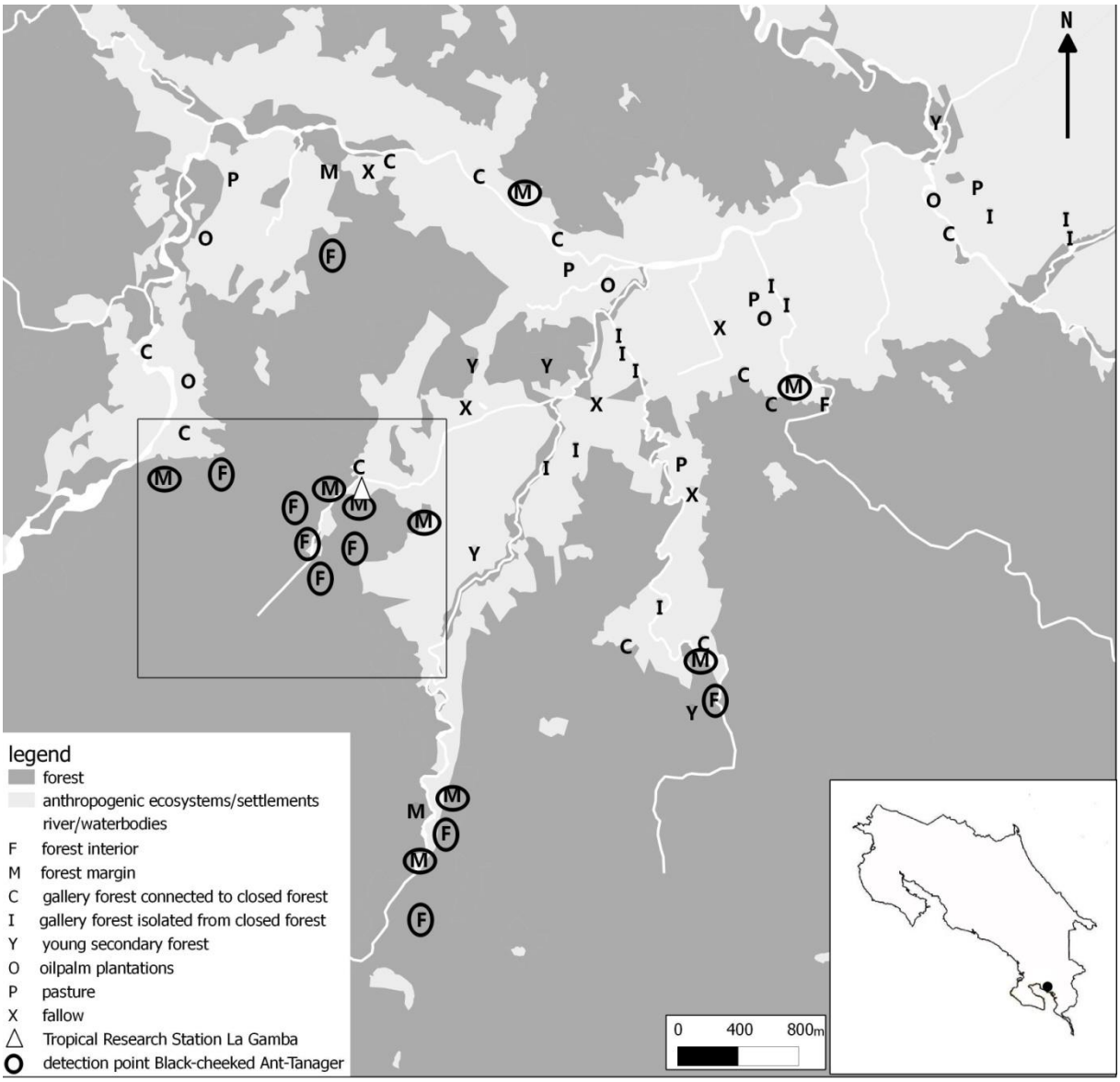

Fig. 1: Maps indicating the location of our study area (inset) and the location of census points used for conducting bird surveys in eight different habitats: FI – interior of old-growth forest, FM – margin of old-growth forest, YSF – young secondary forest, GC – gallery forest strips connected to closed forest, GI – gallery forest strips isolated from closed forest, PP – oil palm plantations, FA – fallows, PA – pastures. Different shading indicates old-growth forest (dark grey), human-dominated habitats (pale grey) and rivers and streams (white). The Tropical Research Station La Gamba is marked by a white triangle. Furthermore, points are indicated at which Black-cheeked Ant-tanagers were recorded. The black square marks the area for which distance sampling was used to quantify population density using a dense trail system (compare Figure 2).

The forest area in the immediate vicinity of the Tropical Research Station La Gamba is located between elevations of 75 and 350 m and belongs to the Piedras Blancas National Park. It is easily accessible via an existing trail system (Figure 2) with a total length of 9.2 km. The trails are mainly situated in primary forest (76% of total trail length). The rest of the trails are situated in old-growth secondary forest (with canopy trees > 15 m high and single

emergent trees > 25 m high) logged > 30 years ago. The classification of forest types is based on Weissenhofer et al. (2008).

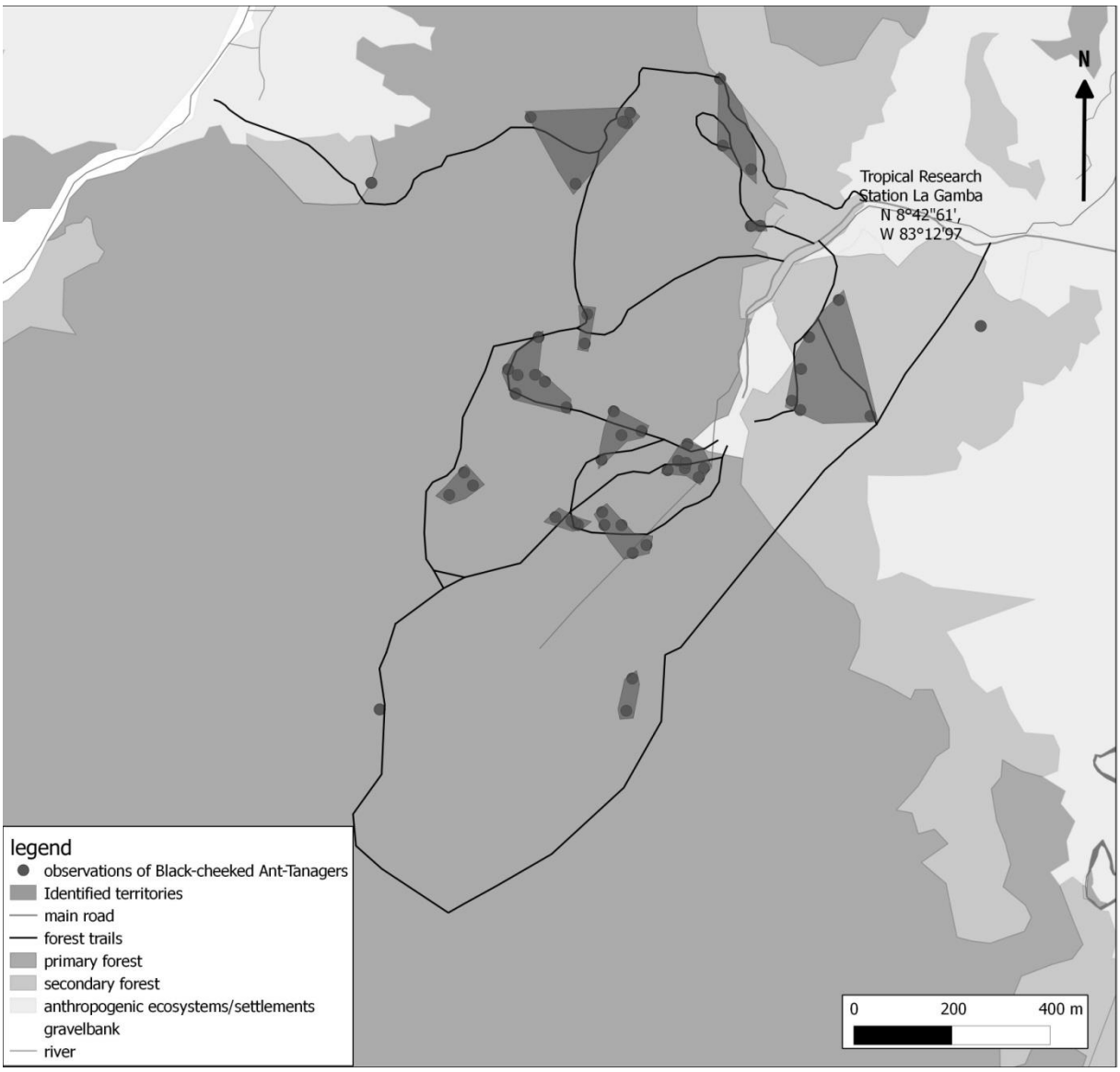

Fig. 2: Trail system used for distance sampling and observations of Black-cheeked Ant-tanagers as well as their affiliation to identified territories in the vicinity of the Tropical Research Station La Gamba in 2010/2011.

The study area has a mean daily temperature of 28.5°C; the annual precipitation is about 6,000 mm. The rainy season lasts from August to November; a drier period usually lasts from January to March (Weissenhofer and Huber 2008). Knowledge of the avifauna of the Golfo Dulce region is summarised in an annotated up-to-date checklist (Tebb 2008).

Point counts

We established point count locations in eight different habitats: forest interior (FI) and forest margin (FM) of old-growth forest, young secondary forest (YSF), gallery forest connected to closed forest (GC) and isolated (GI), oil palm plantations (PP), fallows (FA) and pastures (PA). For forest types, 10 (FI) and 11 replicate sites (FM, GC, GI) were selected for standardised bird counts (Figure 1). All FI sites were located > 50 m from forest edges within the large forest block of Piedras Blancas National Park. FM sites were located within the transition zone between c.50 m inside the forest and (semi-)open human-dominated habitats. This distance was chosen because edge effects quantified by abiotic parameters (e.g. air temperature, light) and various vegetation features (e.g. tree stem density, canopy closure, understorey density) mostly do not penetrate further into the forest (reviewed by Murcia 1995). In addition, many forest birds apparently do not respond to edge effects at distances > 50 m from the forest edge (e.g. examples in Restrepo & Gómez 1998).

Gallery forests were defined as strips of trees along streams crossing open areas. When in direct contact to closed forest, they were classified as “connected“ (GC), otherwise they were defined as “isolated” (GI). The mean length and width (± SD) of forest strips was 923 (± 1,154.37) m and 62.05 (± 40.33) m for GC sites and 1,974.55 (± 1568.10) m and 21.77 (± 40.33) m for GI sites, respectively. The mean distance (± SD) to the forest margin was 173.73 (± 154.70) m for GC sites and 543.00 (± 141.13) m for GI sites. For all other habitat types (YSF, PP, FA, PA) five replicate sites were selected (Figure 1). All sites were selected based on a vegetation map of the study area (Weissenhofer et al. 2008).

Field work was conducted by IR between 1 November 2008 and 4 October 2010. At each study site, 10-min point counts were performed from dawn (05h00) until 10h00 (e.g. Blake 1992) using 8 x 40 binoculars. All Black-cheeked Ant-tanagers seen or heard within a radius of c.25 m around the census point were recorded. Each day, bird counts were carried out at 8–12 census points. To avoid temporal bias in detection rates of birds with time of day, census points were visited in a rotating order (Blake 1992). Each census point was visited 10–12 times in October–February 2008/2009 and 2009/2010 (both dry season) and in June-September 2009 and 2010 (both rainy season).

Habitat variables

To evaluate the importance of edge effects on the occurrence of Black-cheeked Ant-tanager in old-growth forest sites, forest cover at all FI, FM and YSF sites was quantified within a radius of 200 m around census points. We used a digital vegetation map of the study area (Weissenhofer et al. 2008) which was updated using aerial photographs from 2009 (OpenLayers plugin of Quantum GIS 1.7.2) and ground surveys to calculate the percentage

of old-growth forest within the 200 m radius around the census points using the software package ArcMap 9.0 (ESRI). We prefer to use the term “old-growth forest” (classified as primary forest in Weissenhofer et al. 2008) because it cannot be excluded that individual trees were selectively extracted at some of our sites some decades ago.

To describe vegetation structure at FI, FM and YSF census points, we measured or estimated tree density, canopy closure and understorey density. Tree density was measured as the number of trees (with diameter at breast height > 10 cm) within a radius of 25 m around the census point. To estimate canopy closure, four photographs were taken of the canopy in four different directions from the census point at the margin of the 25 m radius. Canopy closure was estimated for each photograph to an accuracy of 10% and then quantified for every census point as the mean of the four estimates. To estimate understorey density, a photograph was taken from breast height towards the ground at eight randomly selected points within the radius of 25 m around census points. For each of the eight points, understorey density was estimated as the percentage (to an accuracy of 10%) of the photograph covered by vegetation. Understorey density at census points was then quantified as the mean of the eight values.

Distance sampling

We used distance sampling to estimate the population density of Black-cheeked Ant-tanager within old-growth forest. In contrast to traditional bird survey methods, distance sampling is a rather simple approach to estimate population density in a defined area (Thomas et al. 2010). We recorded birds along line transects and measured the perpendicular distance between the transect line and all birds detected visually and acoustically with a rangefinder (Nikon Laser 800 S). There are three main assumptions that have to be fulfilled to achieve reliable density estimates: (1) objects on the transect line are detected with certainty, (2) objects are detected before moving and (3) distance measurements are exact (Thomas et al. 2010).

Transects for distance sampling should be random and straight and distance sampling is based on the assumption that the location of detected animals is independent of the positions of the transect lines, which becomes critical if transects are placed along trails (Thomas et al. 2010). We had to use the network of narrow (c.1 m) trails (Figure 2) for the bird survey due to the steep terrain in our study area (Hiby and Krishna 2001, Gale and Thongaree 2006). When conducting distance sampling along transect lines, usually 5% of the measured distances are truncated, because they contribute little to the abundance estimate (Buckland et al. 2001). We truncated our distance measurements of detected birds

at 60 m. In fact, only seven (4.5%) of all detections of all detections during the two survey periods were beyond 60 m.

There were two surveys to estimate the population density of Black-cheeked Ant-tanagers in the study area. The first survey was conducted from February to April 2009 by JF and MK, the second survey from November 2010 to January 2011 by JSC. The whole trail network was divided in subunits which were each surveyed 9–28 times in 2009 and 8–12 times in 2010/2011. This resulted in a total of 168 km transects walked in 2009 and 95 km in 2010/2011. Surveys were done between dawn (05h30) and 12h00 and between 15h00 and dusk (18h00).

Territory mapping

For all Black-cheeked Ant-tanagers detected during transect walks between November 2010 and January 2011, location was determined with a GPS device. Quantum GIS map (Quantum GIS 1.7.3; Quantum GIS Development Team 2011) was then used to visualise the spatial distribution of records and define territories based on spatially clustered observations. When clustered observations were over 50 m apart from each other and/or individuals were detected on the same transect at approximately the same time in different locations, observations were assigned to two different territories. Single observations of solitary birds were not classified as territories. They may represent juvenile birds still searching for new territories or non-breeding “floaters” rather than birds occupying a territory. However, although we additionally considered behaviour indicating a territory border (e.g. where birds stopped moving in their initial direction), a partly arbitrary interpretation of the spatial distribution of territories cannot be avoided when using such an approach without marking the birds (e.g. by colour rings).

Data analysis

To compare preferences of Black-cheeked Ant-tanager for different habitats (FI, FM, YSF, GC, GI, PP, FA, PA), we compared the mean number of birds detected per point between all habitats. Abundance per point was quantified as the mean number of birds recorded per 10-min count. Because birds were only recorded at FI and FM sites (see Results), a t-test calculated with the software Statistica 7.1 (Statsoft Inc. 2005) was used to test for differences in abundance only between these two forest types.

To test for effects of forest cover, tree density, canopy closure and understorey density on the presence of Black-cheeked Ant-tanager, univariate logistic regressions were calculated with the software Statistica 7.1. Subsequently, generalised linear models (GLMs) with binomial error distribution and logit-link function were used to evaluate effects of habitat variables on the species’ occurrence at points. Variables were first tested for multicollinearity.

In case of significant correlations between habitat variables, only the variables that proved to have a stronger effect on Black-checked Ant-tanager occurrence were considered in univariate logistic regressions. Then GLMs including all remaining variables (standardised) and possible subsets, their corrected Akaike information criterion (AIC_c) values, Δ AIC_c values and AIC_c weights (a relative measure of support for a model) were calculated with the software R (Barton 2013, R Development Core Team 2013). A higher AIC_c weight indicates a higher relative likelihood of a model compared to alternative models (Wagenmakers and Farrell 2004). Subsequently, a model averaging was calculated for the `top model set` (models with Δ $AIC_c < 4$). We did not consider the small gallery forest strips (GC, GI) and all non-forest habitats (PP, FA, PA), where we never recorded Black-cheeked Ant-tanagers, to avoid zero inflation in our models.

Based on the measured perpendicular distances between detected birds and the transect lines, the population density of the Black-cheeked Ant-tanager was estimated by the software Distance 6.0, which fits a detection function to the observed distances (Bibby et al. 1998, Thomas et al. 2002). The analysis started with a truncation of the data at a distance of 60 m from the transect line. Due to the topography and the dense forest understorey, visual and acoustical detections are very unlikely at distances > 60 m and resulting distance measurements are too inaccurate.

We used four of the models provided by Distance 6.0 (uniform key with cosine adjustments, half-normal key with cosine adjustments, half-normal key with Hermite polynomial adjustments, hazard-rate key with simple polynomial adjustments) which perform best in many studies (Thomas et al. 2010). To select the two models that best fit our data, quantil-quantil plots were used by comparing the detection functions of the models with the actual distribution of our distance data (Thomas et al. 2010). Selected models showed the best fit of the data points with the detection function based on a visual evaluation. This model selection was additionally crosschecked using the ranking of models according to the Akaike information criterion (Thomas et al. 2010). The population density was estimated separately for the two survey periods 2009 and 2010/2011, and by combining data from both survey periods. Because differences in the size of Black-cheeked Ant-tanager groups between both survey periods could potentially result in a difference in detectability, we tested if the number of birds per observation differed between both survey periods using a Mann-Whitney U-test, calculated with Statistica 7.1 (Statsoft Inc. 2005).

Results

Habitat preferences

Our point census data from different habitats ranging from forest interior towards highly modified land-use systems clearly demonstrate that the Black-cheeked Ant-tanager is restricted to the interior and the margin of old-growth forest. No birds were detected at YSF, GC, GI, PP, FA and PA sites. Although the mean number of birds counted per census point was nearly twice as high at FI (mean number of birds per 10 min count ± SD = 0.32 ± 0.28 birds) than at FM sites (0.19 ± 0.19 birds), it did not differ significantly between habitats (t = 1.26, df = 19, P = 0.223).

Effects of forest cover and vegetation structure at old-growth forest sites

Calculated logistic regressions indicate that the likelihood of Black-cheeked Ant-Tanager occurrence at forest census points increased significantly with increasing forest cover (χ^2 = 6.23, p = 0.013; Figure 3a), increasing tree density (χ^2 = 7.16, p = 0.007; Figure 3b) and increasing canopy closure (χ^2 = 5.46, p = 0.019; Figure 3c). Only understorey density did not affect the species' occurrence (χ^2 = 2.28, p = 0.131).

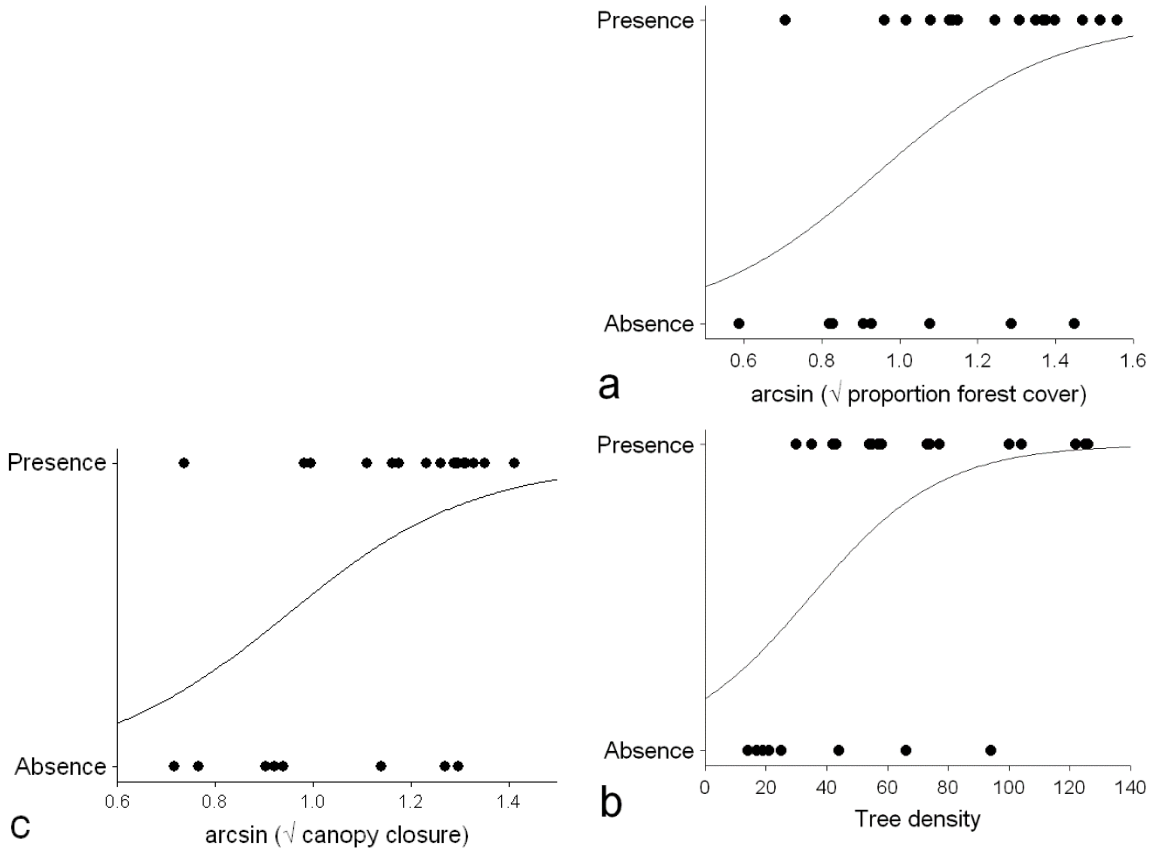

Fig. 3: Univariate logistic regressions showing effects of (a) forest cover, (b) tree density and (c) canopy closure on the occurrence of Black-cheeked Ant-tanager at forest census points (FI and FM sites).

Because tree density and canopy closure were highly correlated (r = 0.75, p < 0.001), canopy closure was excluded from the subsequent GLMs due to its weaker effect on the occurrence of Black-cheeked Ant-Tanager according to univariate logistic regressions. GLMs calculated with the three remaining habitat parameters and all possible subsets indicate a prominent effect of forest cover on Black-cheeked Ant-Tanager occurrence. This variable remained in all three best models (Table 1) and was the variable with the highest explanatory power according to the model averaging approach (Table 2).

Table 1. Results of GLMs (with binomial error distribution and logit-link function) calculated to evaluate effects of forest cover, tree density and understorey density (all standardised) on the occurrence of Black-checked Ant-Tanagers at forest census points (FI, FM and YSF sites). GLMs were calculated including all predictor variables and all possible subsets and then ranked according to their corrected Akaike values (AIC_c). Furthermore, the **Δ** AIC_c values and the AIC_c weights are provided for each model.

Included variables	**AIC_c**	**Δ AIC_c**	**AIC_c weight**
tree density, forest cover	**26.2**	**0.00**	**0.389**
tree density, understorey density, forest cover	**26.7**	**0.58**	**0.291**
understorey density, forest cover	**28.0**	**1.85**	**0.154**
tree density	**29.5**	**3.30**	**0.075**

Table 2. Results of model averaging to quantify effects of each variable on the occurrence of Black-cheeked Ant-Tanagers at census points.

Included variables	**Estimate**	**SE**	***z***	***P***
forest cover	1.624	0.828	1.962	0.0498
tree density	1.920	1.128	1.702	0.0887
understorey density	-1.068	0.751	1.423	0.1548

Estimating Black-cheeked Ant-Tanager density by distance sampling

During distance sampling, Black-cheeked Ant-tanagers were detected 101 times with 185 birds in 2009 and 53 times with 102 birds in 2010/2011. The mean group sizes of 1.85 (SD ± 0.96) birds in 2009 and 1.93 (± 0.83) birds in 2010/2011 did not differ significantly (Mann-Whitney U-test: U = 2433.50, P = 0.407) between the two survey periods.

The two distance sampling models pre-selected through the quantil-quantil plots and the Akaike information criterion (AIC) are the hazard rate simple polynomial model and the half normal cosine model; only the difference between AIC values of both models for the 2009

survey was > 2 (Table 3). Some of the resulting detection probability curves underestimated the number of observed birds close to the transect line and overestimated the number of detected birds in the next distance band (Figure 4a -b, e-f). Only the distribution of the detection distances of the 2010/2011 survey is predicted very precisely by the calculated detection probability curves (Figure 4c-d).

Table 3. Akaike information criterion (AIC) values for two different models used to estimate the population density (birds/km^2) of Black-cheeked Ant-Tanager for the survey periods 2009 and 2010/2010 and for both survey periods combined.

Model	Survey 2009		Survey 2010/2011		Both surveys	
	AIC	birds/km²	AIC	birds/km²	AIC	birds/km²
Hazard rate simple polynomial model	740.52	21.08	354.42	27.04	1106.96	24.34
Half normal cosine model	737.75	24.43	352.42	35.59	1105.26	26.51

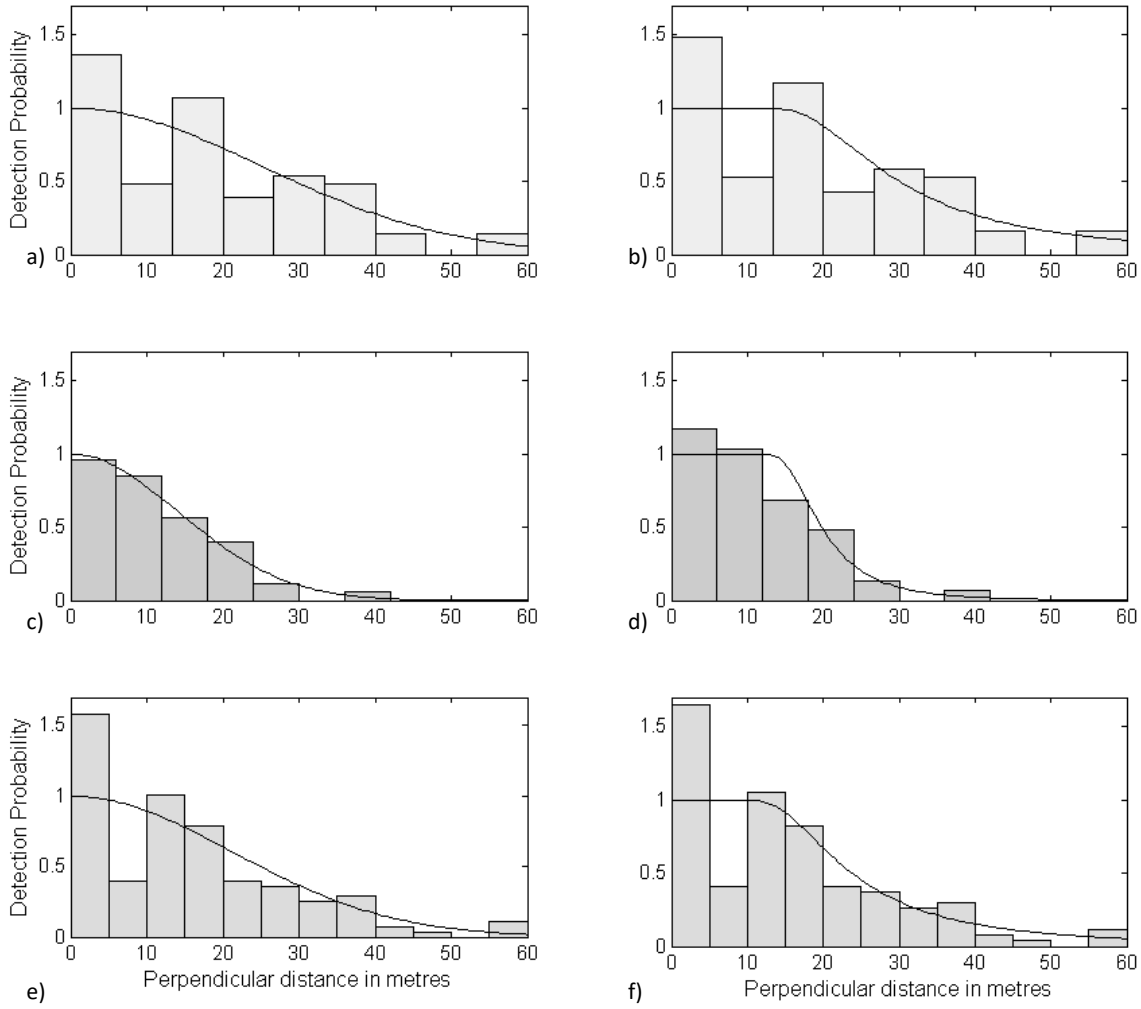

Fig. 4: Histograms of detection distances for the transect surveys conducted in (a-b) 2009 and (c-d) 2010/2011 and (e-f) for a combination of both survey periods. Also shown are the corresponding fits of models predicting the detection probability with increasing distance from the transect line using a truncation at 60 m distance from the transect line. Detection curves in graphs on the left side are predicted by hazard rate simple polynomial model and on the right side by half normal cosine model.

Predicted densities were 22.0% (hazard rate simple polynomial model) and 31.4% (half normal cosine model) higher for 2010/2011 than 2009. When data from both survey periods were combined, population densities reached values intermediate between the densities estimated for the first and second survey periods. Five of the six models estimated Black-cheeked Ant-tanager densities between c.21 and 27 individuals per km^2. A much higher density of c.35.6 birds per km^2 was estimated for 2010/2011 by the half normal cosine model (Table 3).

Estimating Black-cheeked Ant-Tanager density by territory mapping

In total 12 territories were identified in our study area. Three single observations were not assigned to a territory (Figure 2). Assuming that territories are occupied by a pair or a pair and at least one juvenile bird, population densities of 17 and 25 birds per km^2, respectively, were estimated by territory mapping for our study area of 1.45 km^2 (100 m buffer zone on both sides of the transects). Only one territory and one single observation were located in old-growth secondary forest, all other observations of Black-cheeked Ant-tanager were from the interior of old-growth forest or its margin (Figure 2).

Discussion

The Black-cheeked Ant-Tanager – a forest interior species

As emphasised earlier (Aubrecht 2008, BirdLife International 2014), our study clearly showed that the occurrence of the Black-cheeked Ant-tanager is restricted to the interior and margin of primary and old-growth secondary forest. The species does not move into younger secondary forests and gallery forest strips, even when they are connected to closed forest. Although the Black-cheeked Ant-tanager can be frequently found close to the forest margin (this study; Seaman and Schulze 2010), our data showed that its occurrence at forest census points was positively related to the percentage of forest cover within a radius of 200 m. This indicates that the species tends to avoid forest edges. The species' preference for old-growth, largely undisturbed forest is further emphasised by our finding that its likelihood of occurrence increased with increasing canopy closure. However, a preference for forest sites with a higher density of trees (> 10 cm dbh), typical for forest areas or sites disturbed some decades ago, could indicate a weak preference for slightly disturbed sites. This would be partly in accordance with Slud (1964) who noted that the species prefers tall secondary growth and broken forests to the interior of unbroken forests. In our study at least one territory could be located in old secondary forest. If occasional observations of birds in beachfront scrub and palms adjacent to Corcovado National Park (Capper et al. 1998) or in other disturbed habitats at the margin of closed forests (e.g. the botanical garden of the Tropical Research Station La Gamba; pers. obs.) refer to territorial birds. More likely such records may refer to dispersing birds or individuals only occasionally exploiting attractive resources in habitats at the forest margin, which otherwise may be unsuitable for the species.

Population density estimates using distance sampling

Distance sampling is a method widely used to estimate the population density of species in challenging field conditions (Thomas et al. 2010). It is frequently applied to estimate the population density of endangered low density species (e.g. Heydon and Bulloh 1997, Morrogh-Bernard et al. 2003, Hoekman et al. 2011) including understorey forest birds (e.g. Jiménez et al. 2003, Shankar Raman 2003). During both of our survey periods the number of Black-cheeked Ant-tanager observations was higher than the minimum number of 50 detections recommended for estimating population densities with the software Distance (Buckland et al. 1993; but see Oostra et al. 2008).

Our distance sampling data from the survey period 2010/2011 do not indicate that the number of detected birds in the first distance band was affected by the forest trails which were used as transect lines. Additionally, the trail did not obviously act as a barrier to bird movements. Frequently, Black-cheeked Ant-tanagers were observed crossing the small paths (pers. obs.). In contrast, the distribution of measured detection distances from the survey in 2009 (and in consequence the data combining distances sampled in 2009 and 2010/2011) is characterised by an overrepresentation of records in the first distance band and fewer birds observed than expected in the second distance band. However, we do not believe that the unexpectedly high number of Black-cheeked Ant-tanagers detected in the first distance band during the 2009 distance sampling is caused by using forest trails as transect lines. Rather, it may be a result of territorial behaviour during the breeding season, which lasts from mid- January to May (Sandoval and Gallo 2009), the time period of our 2009 survey (February- April). During the breeding season, birds may approach an observer entering their territory more frequently and, therefore, may move more often towards the transect line before detection. The difference between the two surveys cannot be explained by a higher number of singing birds detected close to the transect line during the breeding season. In fact, only nine detections (of 101) during the breeding season in 2009 refer to singing birds only detected acoustically. Furthermore, all of these birds were detected at distances of more than 10 m from the transect line. However, the number of acoustically detected singing birds was obviously too small to affect the shape of the detection curve. The 2010/2011 detection curves had a high detection rate from the zero line up to over 10 m and then decreased rapidly. The resulting relatively broad shoulder is a feature essential for the accuracy of population density estimation (Buckland et al. 1993). For this reason, the population density estimated by distance sampling for the 2010/2011 survey may be more reliable. However, in fact, both estimates for 2010/2011 and 2009 correspond well to the densities estimated by the number of territories identified in our study area in 2010/2011 (this study) and 2009 (Fricke and Katz unpubl. data).

Population density estimated by territory mapping

Based on territory mapping in 2010/2011, a total of 12 breeding pairs was estimated for our study area, which corresponds to 17–25 individuals in our 1.45 km^2 study area when assuming 2–3 birds per family group (Aubrecht 2008). In 2009 the density predicted by distance sampling (21–24 birds) was similar to that achieved by territory mapping (eight territories ≈ 16–24 individuals; Fricke and Katz unpubl. data).

Other studies (e.g. Gale et al. 2009, Gottschalk and Huettmann 2011, Shankar Raman 2003) comparing territory mapping with point or line distance sampling methods in tropical forests, as well as in forests and open landscapes in the temperate zone, showed that territory mapping produced similar results to the less labour-intensive line distance sampling (Gottschalk and Huettmann 2011, Shankar Raman 2003).

The spatial distribution of territories identified in 2009 (Fricke and Katz unpubl. data) and 2010/2011 (this study) was remarkably similar. Several 2009 and 2010/2011 territories overlapped or were located close to each other. This could indicate a minor turnover of territory owners or that territory sites have to fulfill specific requirements. A low turnover of territory owners and a rather stable spatio-temporal pattern of territories was already recorded for other understorey rainforest birds (Greenberg and Gradwohl 1986, Stouffer 2007).

Comparison with previous population size estimates

Based on the assessment of known records, descriptions of abundance and range size, the current population size estimated by IUCN for the Black-cheeked Ant-tanager is 10,000–19,999 individuals (BirdLife International 2014). However, on the distribution map the species is marked as possibly extinct in the area of the Piedras Blancas National Park (IUCN 2012). In fact, our study documented that the species appears to be still abundant in Piedras Blancas National Park. Therefore, when assuming that the species occurs in any old-growth forest in all three protected areas, Corcovado National Park, Golfito Faunal Refuge and Piedras Blancas National Park, the actual distribution range may cover an area of about 592 km^2. Considering an average density of 24–27 individuals per km^2 (as estimated by our distance sampling study), the current population size may be between 12,432 and 20,720 birds.

Conservation implications

The remaining distribution range of the Black-cheeked Ant-tanager is exclusively located within protected areas of Pacific lowland rainforest. Therefore, we do not expect an ongoing decline in range and population area (but see BirdLife International 2014). However, in particular the species' actual status in the Golfito Faunal Reserve should be assessed (Wege

and Long 1995). Further sites, which should be surveyed for remaining populations, include the forest area of the Golfo Dulce Forest reserve (IUCN protection category V). Although the species' population size may be currently stable, its small distribution still justifies its current classification as ´Endangered` (BirdLife International 2014).

As documented by our study, Black-cheeked Ant-tanagers tend to avoid forest edges and do not appear to move into highly disturbed forests, but can occasionally be found in old secondary forest. This emphasises that any significant forest disturbance and fragmentation within its remaining distribution will most likely result in local extinctions, which can hardly be compensated for by re-colonisation. Gallery forest strips connecting remaining forest fragments can improve landscape connectivity for several forest species (Seaman and Schulze 2010). Although Black-cheeked Ant-tanagers were not recorded in these forest strips by our study, it remains to be proved whether they facilitate movements on a landscape scale. Even very rare movements of perhaps non-territorial dispersing birds, which may remain largely undetected in such matrix habitats, can facilitate the re-colonisation of small isolated forest patches as indicated for small rainforest fragments in Brazil (Stouffer et al. 2011).

However, full protection of the remaining lowland forest at the southern Pacific slope will remain the only way to successfully protect its unique avifauna. There are still opportunities to expand the existing protected forest areas in the Golfo Dulce Region (e.g. compare forested areas indicated on vegetation map in Weissenhofer et al. 2008) and thereby improve the conservation status for the Black-cheeked Ant-tanager and other lowland forest birds. Costa Rica has a high reputation for preserving its biodiversity and is setting standards for conservation networks (13.74% of the country is strictly protected), which play an important role for the protection of threatened species (Sánchez et al. 2009). Hopefully, the endemic Black-cheeked Ant-tanager will also benefit from this exemplary conservation policy. Considering that the Black-cheeked Ant-tanager apparently represents a key species in mixed species flocks, other bird species may benefit too, which would otherwise face the risk of local extinction as documented for Red-crowned Ant-tanager *Habia rubica*, a key species for maintaining cohesion and stability of mixed-species flocks in coastal Atlantic forest of southern Brazil (Develey and Peres 2000). The disappearance of this species of ant-tanager seems to extirpate this type of association locally. Therefore, conservation plans for nuclear species (such as the Black-cheeked Ant-tanager) and their habitats should be a high priority (Maldonado-Coelho and Marini 2004).

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f. Observation of Veraguan Mango *Anthracothorax veraguensis* (Reichenbach, 1855) in the southern Pacific lowlands of Costa Rica

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Abstract

On 15th December 2008, male and female individuals of Veraguan Mango (*Anthracothorax veraguensis*) were observed in the southern Pacific lowlands of Costa Rica at the Tropical Research Station La Gamba (vicinity of Golfito). At the same location, subsequently at least 2 females could be observed visiting flowers of an *Erythrina gibbosa* tree until the 26th February 2009. Again, a male and female were seen near La Gamba from December 2009 until February 2010. This hummingbird species was included in the Official List of the Birds of Costa Rica in November 2009. Here, first observations and records of this hummingbird species are summarized and documented by photographs and detailed descriptions of the observed birds.

Resumen

El 15 de Diciembre 2008 un individual macho y una hembra de Manguito de Veragua (*Anthracothorax veraguensis*) estaban observados en las tierras bajas en el sur pacífico de Costa Rica a la Estación Tropical La Gamba (proximidad de Golfito). En el mismo lugar, al menos 2 hembras podían estar observadas visitando flores de *Erythrina gibbosa* hasta el 26 de Febrero 2009. De nuevo, un macho y una hembra estaban vistos cerca de La Gamba el de diciembre 2009 hasta febrero 2010. Esta especie de colibrí estaba incluida a la lista oficial de Costa Rica en noviembre 2009. Aquí están sumados las primeras observaciones y comprobantes documentados por fotos y una descripción detallada de los pájaros observados.

Keywords: Trochilidae, *Anthracothorax veraguensis* (Reichenbach, 1855), Veraguan Mango, new record, Costa Rica, range expansion

Introduction

Of the nine recognized Mango species, three occur in Central America, the Black-throated Mango *Antharcothorax nigricollis* (Vieillot, 1817), the Veraguan Mango *A. veraguensis,* and the Green-breasted Mango *A. prevostii* (Lesson, 1832). Only *A. veraguensis* is exclusively restricted to Central America, so far classified as being endemic to Panama (Schuchmann 1999). However, the species has been included to the Official List of the Birds of Costa Rica (November 2009), due to documentation by Kevin and Steven Easley, but it is still questionable if this species is resident (Obando-Calderón et al. 2009).

The taxon *veraguensis* was first described in 1855, and is often considered as a subspecies of the Green-breasted Mango *Anthracothorax prevostii* (e.g. Ridgely and Gwynne Jr. 1989). The Veraguan Mango was considered as endemic to Panama with a very restricted range (Schuchmann 1999), nevertheless it is classified as Least Concern by BirdLife International (2007) and in the Red List of IUCN (2009). There are recent records of individuals from the southern Pacific lowlands of Costa Rica that were either Green-breasted or Veraguan Mangos (Garrigues and Dean 2007).

Here we describe records of the Veraguan Mango from the vicinity of La Gamba located in the southern Pacific lowlands of Costa Rica. These observations represent reliable records for Costa Rica and possibly indicate a recent northward range expansion of the species. Other range expansions of this species have been recorded in Bocas del Toro, Panama (Olson 1993), which was the first record of the Veraguan Mango on the Caribbean Slope. Olson (1993) also reported the Green- breasted Mango in this region and noteed the difficulty distinguishing between these two Mango species. New investigations by Miller (2009) indicate that the Veraguan Mango shows a very subtle difference in DNA to Green-breasted Mango. This little difference in DNA means that there is no genetic barrier to inter-breeding between the two forms. If Veraguan Mango and Green-breasted Mango are two species, separation took place about 100 000 years ago, therefore, characterizing the Mangos of western Panama as either Veraguan or Green-breasted is problematic. However, more genetic material is necessary to solve this scientific question (Miller 2009). Nevertheless, the Scientific Committee of AOCR (Comité Científico de la AOCR) follows the taxonomic classification of AOU (2009), which separates them into two distinct species.

Although intensive ornithological surveys were conducted in the area around the village La Gamba (Golfo Dulce Region) during recent years (e.g. Sauberer et al. 2007, Schulze and Riedl 2008), Veraguan Mangos were first recorded here in December 2008, when at least 3 individuals (1 male, 2 females) were observed visiting flowers of an *Erythrina gibbosa* tree at the entrance of the Tropical Research Station La Gamba. The species was observed for the first time on 15th December 2008 at 9:40 am by the first author, when one male and one female – seen from a distance of about 6 m – visited flowers at a height of 3 m above ground. Light conditions were very good (cloudless) and both individuals could be observed with a 10x42 binocular for at least 5 min. The record was documented by photographs (with digital camera and 300 mm zoom lense; Fig. 1a, 3a) and video recordings. But the Scientific Committee of AOCR (Comité Científico de la AOCR) considered that hummingbird of Figure 1a represents Sapphire-throated Hummingbird *Lepidopyga coeruleogularis* and photos of females were not clear enough to distinguish between *A. veraguensis* and *A. prevostii*. Around the 23rd of December 2008 Steven Easely was able to take better photographs (Fig. 2) of a male at the same tree (Costa Rican Forum 2008), which led to accepting this

species for the Official List of the Birds of Costa Rica (Obando-Calderón et al. 2009). Additional to these first observations, one female was seen again on 18th December 2008 and on 13th February 2009. Subsequently, two females were observed on 22th, 24th and 26th February 2009 feeding on *Erythrina* flowers during the whole day and defending these nectar sources against other hummingbird species (*Amazilia decora, Amazilia tzacatl, Heliomaster longirostris, Heliothryx barroti*). A female was seen again at the same place on 5th December 2009.

Another tree of *Erythrina gibbosa* near La Gamba was visited by a female and male and they could be observed feeding on nectar on 7th December 2009 and again on 8th January and on 12th February 2010. During these observations better photos were taken of the male (Fig. 1b) and were accepted by some members of Scientific Committee as *A. veraguensis* (pers. comm., Gerardo Obando-Calderón).

Description of the recorded *A. veraguensis* individuals

Size and shape

The species was much bigger than the abundant Rufous-tailed Hummingbird *Amazilia tzacatl* (de la Llave, 1833). Its shape appeared to be similar to that of the White-necked Jacobin *Florisuga mellivora* (Linnaeus, 1758) but with a longer beak.

Plumage

Upperparts of the females and males observed by the first author were emerald green. The females had white underparts with a black central stripe from the bill down to the lower part of the belly to the base of the tail (compare Fig. 3). The tail of females had white tips on the outer rectrices, which were colored rufous on their basal half and could be easily seen in flight (compare Fig. 3).

The male individuals observed on 15 December 2008, 7th December 2009, 8th January and 12th February 2010 had a blue chest and an olive-green belly without any black on the throat and breast (Fig. 1), which differentiates it from the Green-breasted Mango. In males of the subspecis *A. prevostii gracilirostris* (Ridgway, 1910), whose range extends from El Salvador and Honduras south to Costa Rica, the centre of throat and breast is extensively black bordered laterally with deep blue (Schuchmann et al. 1999). In the *A. veraguensis* males no black could be recognized on the throat or belly, although the birds were seen from various angles and under different light conditions. The tail of the males was partly violet rufous, but not as brightly colored as in the much smaller Rufous-tailed Hummingbird.

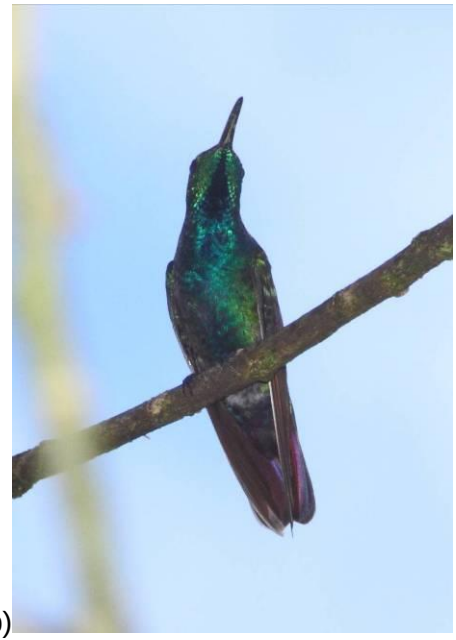
a)  b) 

Figure 1: Male Veraguan Mango *Anthracothorax veraguensis* seen on 15th December 2008 (considered as Sapphire- throated Hummingbird *Lepidopyga coeruleogularis* by Comité Científico) (a); and male seen on 7th December 2009 (photo sent to Comité Científico) (b), La Gamba, Golfo Dulce Region, Costa Rica (photographs by Isabell G. Riedl).

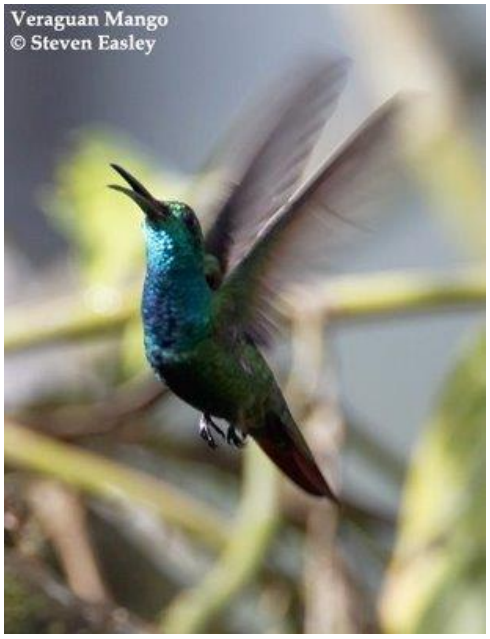


Figure 2: Male Veraguan Mango *Anthracothorax veraguensis* photographed by Steven Easely at La Gamba around the 23rd of December 2008. First proven record of this species in Costa Rica.

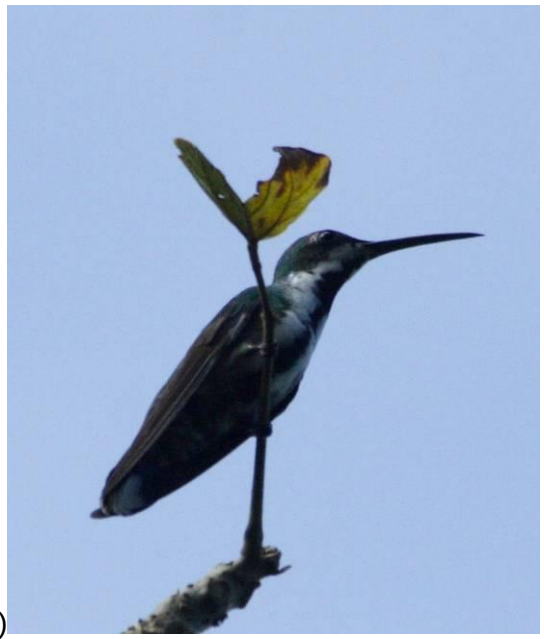
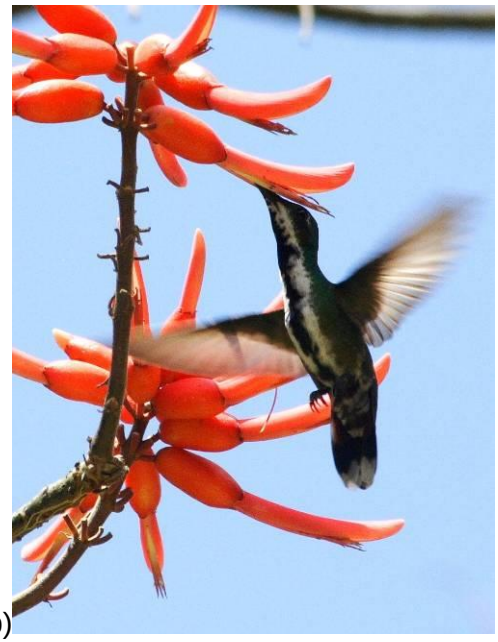
a)  b) 

Figure 3: Two different females, most likely representing Veraguan Mangos *Anthracothorax veraguensis* recorded at La Gamba, Golfo Dulce Region, Costa Rica between 15th December 2008 (a) and 24th February 2009 (b).

Discussion

As females of *A. veraguensis* and *A. prevostii* are not properly separable in the field, the sightings of females alone are not sufficient to prove a range expansion of the Veraguan Mango into the Pacific lowland of southern Costa Rica. However, because females were seen visiting flowers of the *Erythrina gibbosa* trees together with males of *A. veraguensis*, they most likely belonged to the same Mango hummingbird species.

The males could be confused with male Sapphire-throated Hummingbirds *Lepidopyga coeruleogularis* (Gould, 1851), a species which was seen near the Tropical Research Station on 23rd December 2008 (Costa Rica Bird Forum 2008) as well. Furthermore, males of Sapphire-throated Hummingbird have a distinctive forked tail and a pale lower mandible (Stiles et al. 1989). Both characteristics were not visible in the observed males, which had a totally black bill and a round tail.

Already 20 years ago, Stiles et al. (1989) assumed that *A. veraguensis* might eventually be found at the Southern Pacific slope of Costa Rica. However, Garrigues and Dean (2007) still described its status in Costa Rica as uncertain, though also speculating that the species might expand its range from Panama northwards into the southern Pacific lowlands of Costa Rica. The records of two male individuals and about three additional females, also most likely belonging to this species, and the fact that the birds were observed over a period of about 2 months from December 2008 and again in December 2009, January and February 2010 indicate that the species presumably has expanded its range into southern Costa Rica, as

predicted by Stiles et al. (1989), at least to La Gamba, which is located ca. 40 km north of the border to Panama.

After the withering of the *Erythrina* flowers, the only recorded nectar source visited by the Veraguan Mangos at La Gamba, the birds were not recorded until *Erythrina* flowered again. Besides flowering *Calliandra* shrubs and *Inga* trees, flowering *Erythrina* trees are also mentioned as a nectar source by Schuchmann (1999), who furthermore emphasized that the species is territorial at mass-flowering trees, a behaviour also observed in the La Gamba birds.

As in other Central American bird species, forest clearing may also facilitate range expansion of the Veraguan Mango. The species occurs in open vegetation habitats such as pastures and stream edges with shrubs and scattered trees (Schuchmann 1999), habitats typical of the human-dominated landscape at La Gamba. Further bird surveys in the area will confirm if these records of *A. veraguensis* remain an exception or indeed indicate a northward range shift of this enigmatic hummingbird species.

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8. Synopsis

In this final section, I will give a brief summary of the results I achieved in the framework of my doctoral thesis. Further, I will draw some conclusions on how to improve bird conservation in today's tropical landscapes.

Tropical rainforests unfortunately are characterized by rapid loss and alteration of pristine or little intervened habitats and fragmenting of closed forest areas (Laurance et al. 2014). Bird communities respond in different ways to forest fragmentation; there are highly sensitive species, which go extinct rapidly, and others, which are capable of colonizing even small wooded patches, gaps and secondary growths (Antongiovanni & Metzger 2005). Insectivorous birds are known to be particularly sensitive against anthropogenic disturbances and consequently show a substantial decline in many areas of greater human impact. In contrast, granivores and omnivores sometimes even profit from anthropogenic land use intensification, while the response of nectarivores is not always clear (Canaday 1996, Schulze & Riedl 2008, Gray et al. 2007, Tscharntke et al. 2008, Mulwa et al. 2012).

Although some species seem to adapt easily to open land, it was shown by radio tracking, that they were highly dependent on the remaining trees and spent nearly the whole time in them, especially in the dry season when trees were fruiting and if birds were breeding (Şekercioğlu et al. 2007). Generally, remnant trees represent a very important landscape structure for the conservation of biodiversity of birds, they maybe even act as "stepping stones" (Guevara et al. 1998, Harvey & Haber 1998, Harvey et al. 2006, Manning et al. 2006). Further, corridors are known for their positive effect on biodiversity, being used by forest wildlife as movement corridors, conduits through which animals can disperse or commute between forest patches, and habitat linkages (Haas 1995, Beier & Noss 1998, Lees & Peres 2008). Hence, biological corridors shall dampen negative effects of forest fragmentation and isolation (De Lima & Gascon 1999, Sieving et al. 2000). Streamside riparian areas represent an example for biological corridors (Rosenberg et al. 1997, Manning et al. 2006). In Costa Rica, since 1996 a forestry law prohibits felling trees beside streams, resulting in a network of gallery forests in a highly modified landscape, which could act as corridors.

To address various questions, I observed the bird composition of the Golfo Dulce region near the "Tropenstation La Gamba" by standardized bird counts between 2007 and 2010. Point counts of birds are the most widely used quantitative method to measure bird populations. It means that an observer records birds from a single point for a standardized time period, in my case 10 minutes (Ralph et al. 1995). Bird counts are discussed to be biased by the observer (Cunningham et al. 1999, Johnson 2008) and due to the learning curve of the

observers (Jiguet 2009). Therefore, all observations, which were compared to each other, were exclusively made by me. I acquired identification skills during 4 months of experience in the year 2007 prior to starting the longer survey periods in 2008. Census points were chosen randomly and visited in a rotating order to avoid bias by temporal differences in detection rates of birds (Blake 1992, Ralph et al. 1995). Further, artificial nests were used to quantify differences in clutch predation between the studied forest types.

a. How do bird assemblages change from forested towards human-modified countryside habitats?

Comparing the bird assemblages of the pristine forest and the human-modified countryside in the region, it became clear, that a very high species richness of openland species and even a small fraction of forest birds populated the altered habitats. Nevertheless, range-restricted species could not be supported by these habitats and mostly occurred in closed forests. Extremely widespread species and winter migrants instead were not recorded in the forest interior, but frequently appeared in human-dominated habitats and at forest margin. Regarding the relative importance of feeding guilds, insectivores were 2–3 times higher abundant in the forest interior than in human-dominated habitats, whilst granivores, omnivores and scavengers preferred the modified landscapes.

b. Can gallery forest strips serve as corridors and stepping stones for tropical forest birds within a landscape matrix consisting of strongly human-dominated habitats?

After knowing, that human-dominated habitats around La Gamba only support a minority of forest species, they may even be an effective dispersal barrier for them.

With my observations, I aimed to answer the question if gallery forests are capable of increasing the permeability of human-dominated landscapes for forest birds, hence providing a management tool for re-connecting remaining forest areas. Although I did not follow spatial movements of forest birds, the results provide at least indirect evidence for the importance of such linear forest structures as dispersal corridors.

Forest specialists decreased significantly from forest interior, towards the gallery forests, suggesting that the conservation value of gallery forests might be limited. However, some gallery forests sites inhabited more of these bird species than others did. The richness of forest bird assemblages proved being positively related to gallery forest strip width and direct connection to closed forests. In contrast, the percentage cover of gardens and settlements within a radius of 200 m around census points influenced them negatively.

Therefore, widening of gallery forest strips could improve their conservation value as corridors and stepping stones for at least a certain fraction of forest birds.

c. Are composition and structure of bird assemblages affected by seasonal climate changes? And does the strength of such effects differ between habitats?

As closed forests are known to show lesser annual and seasonal changes conserving humidity and temperature (Didham & Lawton 1999, Ewers & Banks-Leite 2013), gallery forest may particularly show changes in the bird community during dry season. However, I could not find any clear seasonal changes. Species composition was affected significantly by survey period but not by wet and dry season. Highest abundance for frugivores, nectarivores, omnivores and granivores was recorded in the wet and dry season 2009. In the dry season 2008 and wet season 2010 lesser individuals were counted.

Interesting was the unclear pattern of recorded insectivores in the four habitats. They were significantly lower species rich and abundant at gallery forests, but the temporal changes were chaotic. Thus, in gallery forests they were less abundant and species rich in the dry seasons, but most abundant in the dry season 2009 and most species rich during dry seasons at FM sites.

Probably, insectivores tried to avoid migratory birds overwintering in gallery forests (Fig. 1) during the dry seasons by moving to FM sites (Schulze & Riedl 2008).

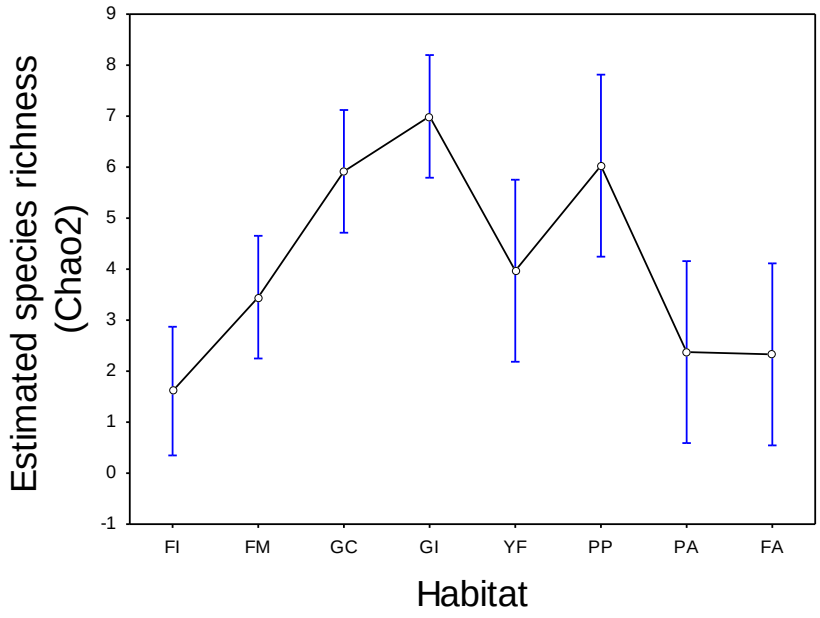

Figure 1: Estimated species richness of migratory birds in dry season 2008 and dry season 2009 at the study area at forest interior (FI), forest margin (FM), gallery forest connected (GC) and isolated (GI) from forest, young secondary forest (YF), palm plantation (PP), pastures (PA) and fallows (FA).

Indistinct trends in species richness and abundance of feeding guilds during the four survey periods propose that other factors than season influence the bird compositions of La Gamba. Maybe the high amount of rainfall throughout the year did not limit resource availability

seasonally (Nemani et al. 2003, Huete et al. 2006), hence not resulting in detectable seasonal changes in bird assemblages.

Besides temporal changes, all feeding guilds except insectivores were more common and species rich in gallery forests than at forest interior and margin. For insectivores the opposite was true.

d. Are understory forest birds facing higher clutch predation risk in linear gallery forest strips compared to old-growth forest areas? Are gallery forests a suitable breeding site or ecological trap for forest birds?

Examining the importance of gallery forest, a major question was if they could represent ecological traps. Gallery forests could be suitable breeding sites for a small fraction of forest bird species due to offering a high concentration of resources (Ries & Sisk 2004). But, high predation risk may outweigh the positive aspects. Testing the predation risk by artificial nests, the recorded nest predation was highest in the gallery forests suggesting that they could act as ecological traps for forest birds.

e. Which are the habitat preferences and how dense is the population of the Black-cheeked Ant-Tanager *Habia atrimaxillaris* in the lowland forest area of the Golfo Dulce region?

A species of conservational high interest in the region is the Black-cheeked Ant-Tanager *Habia atrimaxillaris,* an endemic species to the southwestern lowland rainforests of Costa Rica. It is not just endemic, but highly range-restricted only occurring in the areas of Piedras Blancas and Corcovado National Park. We estimated the population at 12,432–20,720 individuals for the lowland forest area of the Golfo Dulce region (592 km²). During all surveys, we could never observe it outside primary forests. Hence, for this species gallery forests appear to be neglectable for facilitating dispersal movements. Studying the vegetation structure c. 25 m around the census points, we could show that the Black-cheeked Ant-Tanager prefers high forest cover, canopy closure, and density of trees.

f. Conclusion

Forest strips like hedgerows, living fences, or riparian forests are popular objects to nature conservation for enhancing biodiversity (Naiman et al. 1993, Hinsley & Bellamy 2000, Zahawi 2005).

Gallery forests in my study area inhabit a high bird diversity and even a fraction of forest birds. Nevertheless, high forest species turnover (unpublished data) and predation risk in gallery forests suggest that these habitats may not be suitable breeding sites for forest birds and may even act as ecological trap (Holmes & Sherry 2001, Şekercioğlu et al. 2007).

The two variables influencing forest species richness within gallery forests the most were their width and the connectivity to closed forest. Therefore, I recommend implementing reforestation measures improving the connectivity between gallery forests and closed forest and planting trees beside the existing forest strips in the region. Wider forest strips could decrease edge effects and consequently nest predation as well, upvaluing gallery forests as breeding site for forest birds.

Since the Black-cheeked Ant-tanager avoids forest edges and appears not to leave forest interior, further forest degradation and fragmentation would have a strong negative impact. Conservation measures for this species should aim to protect remaining intact forests.

However, for other forest species gallery forests could serve as corridors, stepping stones and even useful habitats enhancing metapopulation dynamics.

After implementing the measures suggested above, their positive impact would even increase, maybe facilitating movements between forest remnants of a wider range of forest specialists.

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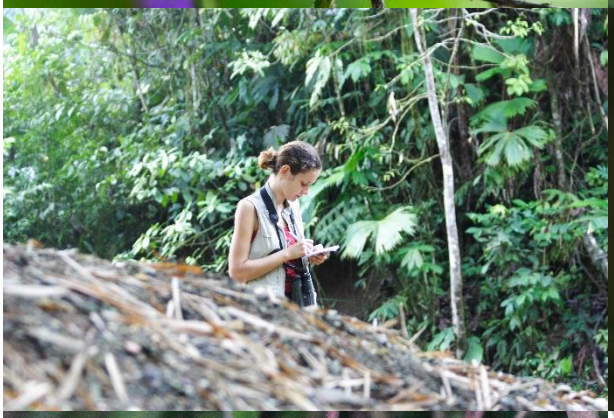
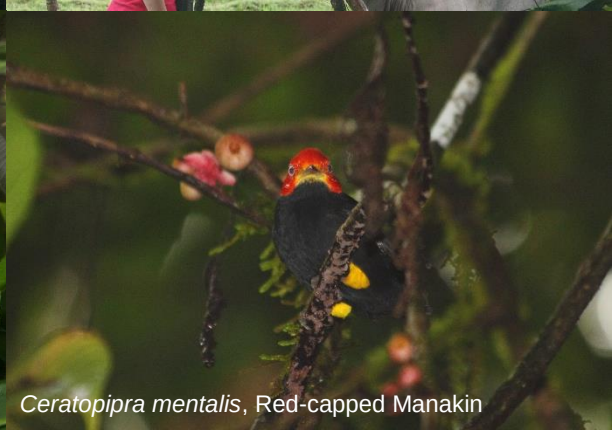


Poliocrania exsul, Chestnut-backed Antbird

Trogon rufus, Black-throated Trogon



Ceratopipra mentalis, Red-capped Manakin