Forest Ecology and Management 329 (2014) 384–392

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The response of birds and mixed-species bird flocks to human-modified landscapes in Sri Lanka and southern India

Eben Goodale[a,*], Sarath W. Kotagama[b], T.R. Shankar Raman[c], Swati Sidhu[c], Uromi Goodale[a], Samuel Parker[d], Jin Chen[a]

[a] Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China
[b] Field Ornithology Group of Sri Lanka, Department of Zoology, University of Colombo, Colombo 3, Sri Lanka
[c] Nature Conservation Foundation, 3076/5, 4th Cross, Gokulam Park, Mysore 570 002, Karnataka, India
[d] Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford St., Cambridge, MA 01238, USA

ARTICLE INFO

Article history:
Available online 9 September 2013

Keywords:
Agroforestry
Anthropogenic disturbance
Biodiversity loss
Bird diversity
Buffer zones
Countryside biogeography

ABSTRACT

While there is no substitute for undisturbed forest, secondary forests and agroforests are increasingly common in tropical areas and may be critical to conservation plans. We compared the diversity and abundance of birds and the characteristics of mixed-species bird flocks in forests inside protected reserves to "buffer" areas, consisting of degraded forests and non-native timber plantations at reserve boundaries, and to agricultural areas. We monitored a network of 57 transects placed over an altitudinal gradient (90–2180 masl) in Sri Lanka and southern India, collecting 398 complete flock observations and 35,686 observations of birds inside and outside of flocks over two years. Flocks were rarely found in agricultural areas. However, the density of flocks in buffer areas was similar to that in forests, although buffer flocks were smaller in average flock size and differed significantly in composition, as measured by the proportion of species that were classified, from the literature, as forest interior or open-landscape species. While flock composition was distinct between agricultural, buffer and forest areas, the differences in the composition of flocks was not as great as the differences between the overall communities in these different habitats. Considering buffer transects alone, pine plantations retained fewer forest interior species in flocks than did forests, and small areas of agriculture and abandoned agriculture attracted open-landscape species. Though clearly not equivalent to protected forests, degraded forests and agroforests in buffer areas still hold some conservation value, with forest species found particularly in mixed-species flocks in these human-modified habitats.

1. Introduction

Biodiversity loss is a global problem (Butchart et al., 2010), particularly in the tropics where biodiversity is highest. While relatively undisturbed forests are essential for conservation (Gibson et al., 2011), they are not sufficient given that protected areas cover less than 10% of the world's forests globally (Schmitt et al., 2009). The study of how animals live and reproduce in landscapes of human-modified ecosystems, including agricultural areas (Daily et al., 2001), agroforests (Bhagwat et al., 2008) and secondary forests (Chazdon et al., 2009), is thus essential to conservation (Gardner et al., 2009).

Birds are useful taxa to study for understanding the response of animals to anthropogenic disturbance because, besides being predominantly diurnal and readily identified, they are quite sensitive to disturbance, especially for highly mobile animals (Chazdon et al., 2009; Gibson et al., 2011). Birds also extensively interact with other taxa, providing important ecosystem benefits, such as insect control, seed dispersal and pollination (Sekercioglu, 2006). Besides studying the total bird community, it is useful to investigate mixed-species flocks of birds, which incorporate a large proportion of the avifauna in the tropics (Powell, 1985; Greenberg, 2000). Birds that participate in such flocks have been reported to be more vulnerable to anthropogenic disturbance (Stouffer and Bierregaard, 1995; Van Houtan et al., 2006).

Here we investigate how mixed-species flocks, and the total bird community, respond to different land-use types in Sri Lanka and the Western Ghats. Sri Lanka and the Western Ghats represent one of the earth's biodiversity hotspots (Myers et al., 2000; Gunawardene et al., 2007), and of all the hotspots, have the most dense human population (Cincotta et al., 2000). Although mixed-species bird flocks have been extensively studied in the region (Goodale et al., 2009), most of these studies were inside protected reserves, and did not quantitatively relate flock characteristics to land-use. In the present study, we sampled birds inside and outside

* Corresponding author. Tel.: +86 18008819305.
E-mail address: egoodale@xtbg.org.cn (E. Goodale).

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.08.022

of flocks in three '***broad***' land-use types: inside protected forests, in buffer areas containing degraded forest or tree plantations, and in agricultural areas. Transects were also mapped as to the '***specific***' land-use types (e.g., *Eucalyptus* plantation) found nearby them. Here we report how flock characteristics such as density, size and composition (by which we specifically mean the proportion of forest interior and open-landscape species) were affected by (1) the broad land-uses (the comparison between forest, buffer, and agriculture) and (2) the specific types of land-use, focusing on those found on buffer transects. Further, we look at the response of the overall bird community to these same types of land-uses, in terms of species richness, bird abundance and composition, to trace the implications of differing types of land-use for tropical bird conservation in countryside landscapes.

2. Materials and methods

2.1. Study area

We worked in areas of moist evergreen forest in Sri Lanka and southern India (Fig. 1). The reserves that we sampled in these areas have either not been systematically logged during the last half century (although roads may have been cut through them, $n = 15$ transects), or were selectively logged during the 1970s ($n = 4$ transects) and 1980s ($n = 2$); they are currently relatively well protected, although some small-scale extraction (e.g., polewood and firewood) occurs in some areas. Forests are largely confined to protected areas, but fragments do exist in areas of intensive agriculture (Anand et al., 2010). The Forest Departments of the respective countries, and to a lesser extent private agencies, have planted land bordering forests with timber crops, including *Eucalyptus* sp. in montane Sri Lanka and mid-elevation India, *Pinus caribaea* in lowland and mid-elevation Sri Lanka, and *Tectona grandis* and *Swietenia* sp. in lowland India.

2.2. Sampling

Between December 2006 and December 2007, we sampled three sites in Sri Lanka: the Sinharaja World Heritage Reserve, western sector (300–500 masl), Sinharaja eastern sector (900–1100 m), and the Nuwara Eliya region (1800–2000 m). For each site, we laid down eight 2-km transects: three transects were placed in relatively undisturbed forest inside protected reserves, three transects in "buffer zones" near the borders of protected reserves, and two transects in areas of intensive agriculture (Fig. 1, sites A–C). Between April 2007 and June 2008, we sampled two sites in southern India: the Thattekad Reserve in Kerala (40–80 m) and the Anamalai Hills in Tamil Nadu (850–1000 m). At each site, we laid down eight 2-km transects following the same methodology as in Sri Lanka (Fig. 1, sites D and E). Finally, between January 2008 and January 2009, we sampled the altitudinal gradient from the Gillimalle Forest Reserve (90 m) to the Horton Plains Reserve (2180 m) in Sri Lanka. Seventeen 1-km transects were placed over this gradient, again attempting to match transects of one type of land-use with nearby transects of the other types, although for logistical reasons such matching was not perfect (Fig. 1, these transects are between the A, B and C sites).

For transects we chose pre-existing paths or small roads that were relatively straight, and ensured that transects were at least 250 m away from each other at all points. Detailed maps were constructed for the area 25 m to each side of each transect, classifying the specific land-use type that was the majority of that area

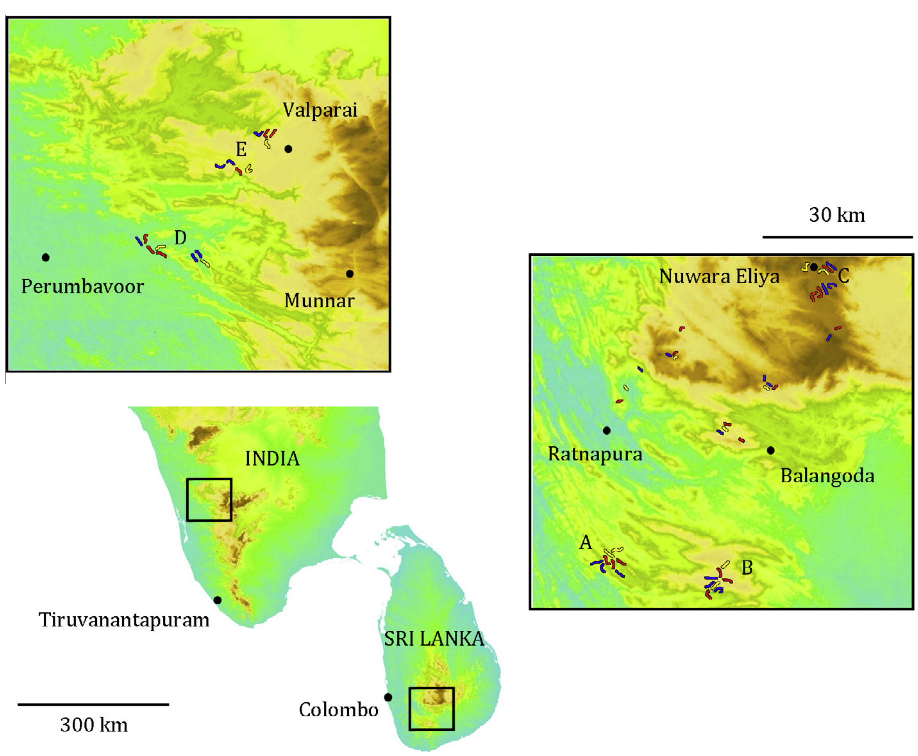

Fig. 1. Transects ($n = 57$) from which observations were made in Sri Lanka and India over an altitudinal gradient. Transects through forests are blue, those in "buffer" lands (degraded forests or plantations) at the border of forests are red, and those in agricultural lands are yellow. Beige colored areas are between 1000 and 1500 masl, with dark brown above that and green and blue below. The width of the transect is not to scale. Topographical data are void-filled seamless SRTM data V1, 2004, from International Center for Tropical Agriculture (CIAT), available from the CGIAR-CSI SRTM 90 m database at_http://srtm.csi.cgiar.org. (A) Western sector of the Sinharaja World Heritage Reserve; (B) eastern sector of Sinharaja; (C) Nuwara Eliya region; (D) Thattekad Reserve; and (E) Anamalai Hills.

(see Table 1 for classification scheme). Visits to the transects were rotated throughout the year. Each day the observers conducted one transect in the morning (8:00–10:00), and another in the afternoon (15:00–17:00). The average transect was visited 7.2 times over a year (SD = 4.0).

When walking a transect, two observers took records on every bird encountered and how far it was from the transect. The bird was recorded as being inside or outside of a flock, defined as two or more species definitively moving the same direction (Goodale et al., 2009). When a flock was encountered, we stopped to record its composition for a minimum of 5 min and a maximum of 15 min, and noted the distance from the transect to the closest member of the flock. If the composition of the flock was observed well, the flock was considered complete. For complete flocks, we believe that 80–100% of the individuals were counted, with canopy species being the most difficult to detect. We also noted the presence of flocks not seen well (incomplete flocks). Additional flock records were taken when walking back on the transect, if a flock had not been seen previously that day within 500 m.

We took records on all birds and mammals observed, but analyze only birds, as they accounted for 98% of observations within 25 m of the transect (see Appendix 1; Funambulus squirrels were the only mammals seen in flocks, Kotagama and Goodale, 2004). Bird taxonomy follows Gill and Donsker (2013).

2.3. Analysis

We used DISTANCE software to calculate detection functions for flocks and for individuals outside of flocks, and thereby estimate densities (Buckland et al., 2001). For flocks, land-use was included as a co-variate in the models, as well as the presence of a noisy leading species, the Sri Lankan endemic Orange-billed Babbler (*Turdoides rufescens*), which significantly increased detection rates. Following Buckland et al. (2001) recommendations, we only ran analyses on individuals outside of flocks if there were at least 40 observations per species. Land-use was included as a covariate if the species had at least 40 observations in all three land-use types. Distance-adjusted data was used in the analysis of flock density, and in all the analyses of the total bird community.

We conducted two major kinds of analyses of the effect of land-use. Broad land-use analyses investigated differences between forest, buffer and agricultural transects. Here the transect was the unit of replication and response variables (e.g. flock size) were averaged for all observations on a transect. Specific land-use analyses investigated how birds were affected by different specific kinds of land-uses (see Table 1) in the buffer transects. Since all buffer transects were placed at the boundaries of reserves, they tended to be at similar distances from the forest, and thus different specific land-uses on buffer transects were comparable to each other (in contrast, specific land-uses on agricultural transects were not comparable to those on buffer transects, because they tended to be much further away from the forest). In these analyses, the transect/specific land-use combination was the unit of replication, and thus response variables like flock size were averaged for all observations in the specific land-use in question on a transect. For both broad and specific land-use analyses, we investigated the effects of land-use separately on mixed-species flocks and on the total bird community, and hence we present four analyses in the "Results" section (broad land-use/flocks, broad land-use/total community, specific land-use/flocks, specific land-use/total community).

For each of these four analyses, we looked at both summary statistics for the flock system or community as a whole and the composition of that community (which species were where). Summary statistics investigated for flocks included flock density (using information from complete and incomplete flocks), and flock size (in terms of species and individuals, using information from complete flocks only). Summary statistics for the total bird community included species richness and the total number of individual observations, a measure of bird abundance. To adjust for differences between transects in their sampling, we divided the total number of individual observations by sampling effort (calculated in hectares, incorporating both the length and 50 m width of the transect and the number of times the transect was walked). For species, we used the rarefaction program *rrarefy* in the *vegan* package of R (Oksanen et al., 2008) to estimate how many species would have been found if the number of individual observations made on a transect was the minimum number of individual observations made on any one transect. To investigate species composition, we first classified 'forest interior' and 'open-landscape' species from the literature, and then determined what proportion of species in complete flocks belonged to these different groups. We used Ali and Ripley (1987) and Grimmett et al. (1999) to make these classifications; if a species did not fall clearly into either of the two groups, it was not used in the analysis.

Statistical models for broad land-use analyses included the three fixed factors of land-use (forest, buffer, agriculture), elevation (coded as low = 0–500 m; medium = 800–1300 m; and high = 1500–2180 m), and country. For the specific land-use analyses, we only used data from Sri Lanka, as it was most consistent in the land-use categorization system. Statistical models for the specific land-use analyses were mixed models, with land-use and elevation as fixed factors, and transect as a random factor. For most response variables, we used general linear models (the function aov in R, or, for mixed models, the function lmer in the package lme4, Bates et al., 2011). For the variables of the proportion of species that were forest interior or open-landscape, we used generalized linear models with a binomial distribution (the function *glm*, or, for mixed models, the function *glmer*). Response variables were transformed to improve normality and homoscedasticity. All

Table 1
Classification of specific land-use types. Only buffer transects in Sri Lanka were used in this analysis (see text). The number of such transects for specific land-use types with complete flocks, or with more than five hectares sampled, is shown; we only included a specific land-type in the analysis if there it was found in complete flocks on more than three transects, or sampled more than five hectares on three transects.

Major type	Minor type	Description	# Buffer transects with complete flocks	# Buffer transects with 5 hectare or more sampled
I	Relatively undisturbed forest		4	5
II	Relatively disturbed forest			
	a	Forest heavily disturbed for firewood or for enrichment (e.g., cardamom)	5	5
	b	Forest completely cut, but regenerated for >20 yrs	7	6
III	Plantations			
	a	Pine plantation	8	9
	b	Eucalyptus plantation	8	8
IV	Agriculture			
	a	Tea	2[a]	6
	b	Home gardens	2[a]	4
V	Abandoned agriculture			
	a	Shrubland (regenerated <20 yrs)	8	7
	Total analyzed		40	50

[a] Found on too few transects for analysis.

models were progressively simplified, dropping interaction terms and factors that did not significantly (α = 0.05) explain the variance. The final reduced model was followed by multiple comparisons, reducing the alpha level for the number of tests made by the Tukey procedure, and using the package *multcomp* (Bretz et al., 2010). All analyses were conducted using R, version 2.12.2.

In preparing for the specific land-use analyses, we summed together different stretches of the same specific land-use on a transect to calculate the total amount of that land-use type within 25 m of the transect. We then calculated a sampling effort in hectares for that specific land-use type, incorporating both the size of the specific land-use type and the number of times that the transect was walked. The total number of individual observations was divided by sampling effort and the number of species observed was estimated by rarefaction analysis, as above, to estimate the number of species that would have been observed had the number of individual observations been the same as the minimum number of individual observations made on any one transect/specific land-use combination. For the analysis of the effect of specific land-use on flock size and the proportion of forest interior and open-landscape species in flocks, we analyzed only specific land-use types that had complete flocks seen in them on at least three transects. For all other analyses, we used those specific land-use types that had at least five hectares sampled on at least three transects. When multiple comparisons between a forest category and a non-forest category were significant or close to significant, we conducted an additional analysis in which all forest categories (I, II-a, II-b; see Table 1) were lumped together, to better compare the non-forest specific land type to "remnant forests" in these buffer areas.

3. Results

3.1. Data collected

We collected 35,686 observations of birds over the sampling period, inside and outside of flocks. We encountered 206 bird species, with 57 species classified as forest interior species and 52 as open-landscape species (the rest were classified as both; Appendix S1). There were 21 bird species listed as Near Threatened or more endangered on the IUCN Red List (IUCN, 2013). For flocks, we collected 329 complete and 159 incomplete observations while walking transects, and an additional 69 complete observations that were made on transects, but not while walking a transect.

3.2. Broad land-use type analysis (forests, buffer, agriculture) for flocks

Land-use strongly affected flock density (Fig. 2A). Flock density was much higher in forest and buffer transects than in agricultural ones (Table 2A). A land-use/country interaction was due to buffer transects in India having higher flock densities than forest ones, while in Sri Lanka, the opposite was true. Buffer flocks were smaller than forest flocks in terms of species (Fig. 2B, Table 2B) and agricultural flocks tended to be smaller than forest flocks in terms of individuals (Fig. 2C, Table 2C).

The percentage of interior forest species that participated in flocks was significantly higher in forest transects than in buffer or agricultural transects (Fig. 3, Table 2D). In contrast, the percentage of open-landscape species participating in flocks increased from forest to buffer to agricultural transects (Table 2E).

3.3. Broad land-use type analysis (forests, buffer, agriculture) for the total bird community

Land-use was not a strong influence on the species richness of a transect (Table 3A), or the bird abundance (Table 3B). A land-use country interaction for both these factors was caused by agricultural transects in Sri Lanka having similar levels of species or individual observations with the other treatments, but agricultural transects in India having significantly fewer species than other land-uses (less than buffers or forests, *Z*-scores > 3.40, $P < 0.013$), and lower bird abundance (*Z*-scores > 2.87, $P < 0.033$).

Unsurprisingly, in the total community analysis, forest interior species were most abundant in the forest (Fig. 3, Table 3C), and open-landscape species were most abundant in agriculture (Table 3D). These differences among the broad categories were much more striking for the total community analysis than for flocks (for forest interior species, total bird community $X_2^2 = 90.45$, whereas for flocks it was 18.69; for open-landscape species, total bird community $X_2^2 = 191.09$, whereas for flocks it was 50.67). This is because flocks outside of forests include more forest interior birds than would be expected based on the total bird community (see Fig. 3): agricultural flocks were composed of 22.1% forest interior species, whereas only 15.7% of the total bird community in the agricultural transects were forest interior species. Similarly, flocks do not include many open-landscape species: agricultural flocks contained only 19.3% of these species, although they made up 33.5% of the total bird community.

3.4. Specific land-use type analysis for flocks

Specific land-uses did not strongly influence flock characteristics, when we analyzed only flocks seen on buffer transects. Analyzing eight specific land-uses (I, II-a, II-b, III-a, III-b, IV-a, IV-b, and V-a) for both complete and incomplete flock data, we found no effect of land-use on flock density ($X_7^2 = 6.33$, $P = 0.50$). Analyzing six specific land-uses for complete flock data (I, II-a, II-b, III-a, III-b, V-a; there were too few complete flocks on agricultural land-use types), there was no effect of land-use on the average number of species per flock ($X_5^2 = 8.37$, $P = 0.14$), or the number of individuals ($X_5^2 = 5.75$, $P = 0.33$).

However, specific land-use did affect the composition of flocks. Specific land-use (including the six types analyzed for complete flocks) influenced the number of forest interior species (Fig. 4, $X_5^2 = 14.55$, $P = 0.012$), with pine plantations having fewer species than regenerated forests ($Z = 3.22$, $P = 0.016$). This result was retained if one lumps together all forest classes into a "remnant forest" category: specific land-type influences the proportion of forest interior species ($X_3^2 = 10.12$, $P = 0.018$), and pine plantations have lower proportions of forest interior species than remnant forest ($Z = 2.73$, $P = 0.031$). For open-landscape species, the effect of specific land-use was significant when analyzing six categories ($X_5^2 = 14.51$, $P = 0.013$), but none of the multiple comparisons had a *P*-value less than 0.10. However, a subsequent four category analysis (remnant forest, III-a, III-b, V-a), also showed a strong effect of specific land-use ($X_3^2 = 13.20$, $P = 0.0042$), with abandoned agriculture having a higher proportion of open-landscape species than remnant forest ($Z = 2.99$, $P = 0.014$).

3.5. Specific land-use type analysis for the total bird community

Specific land-uses also did not have large effects on the species richness of the bird community or the abundances of birds. An analysis with eight land-uses (I, II-a, II-b, III-a, III-b, IV-a, IV-b, and V-a) showed no effect of specific land-use on species richness ($X_7^2 = 3.13$, $P = 0.87$) or bird abundance ($X_7^2 = 10.52$, $P = 0.16$).

The effect of specific land-use on species composition was also muted. Specific land-use tended to influence the proportion of forest interior species ($X_7^2 = 13.29$, $P = 0.066$), but no multiple comparisons had a *P*-value less than 0.10. A six category analysis that lumped together forest classes (remnant forest, III-a, III-b, Iv-a, Iv-b, and V-a) showed no influence of specific land-use on the

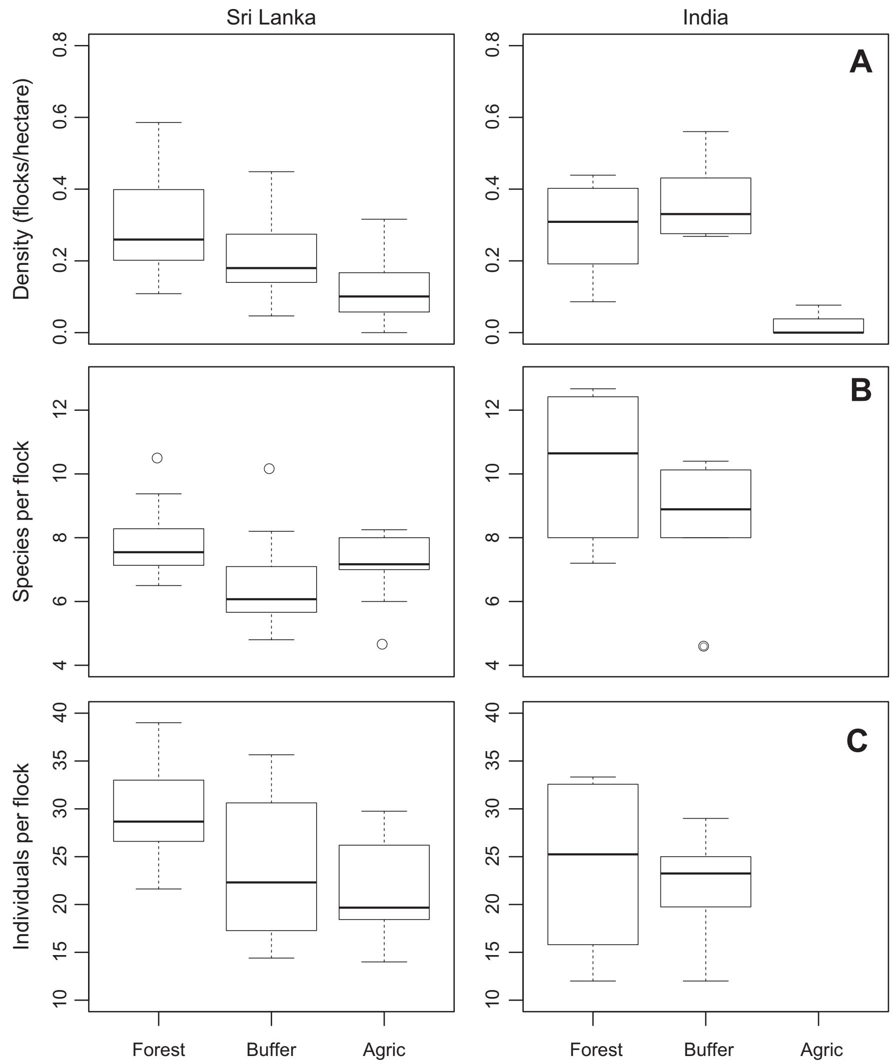

Fig. 2. The effect of the land-use type of the transect (forest, buffer or agriculture) on characteristics of mixed-species bird flocks. The left column shows Sri Lankan data, and the right column Indian data. (A) The density of flocks per hectare. (B) The average number of species per flock. (C) The average number of individuals per flock. There were no complete flocks observed on village Indian transects. For statistics, see Table 2A–C.

proportion of forest interior species ($X_5^2 = 4.40$, $P = 0.49$). As to open-landscape species, the full eight category analysis showed a significant effect of specific land-use ($X_7^2 = 23.46$, $P = 0.0014$), with regenerated forests having fewer open-landscape species than the home gardens ($Z = 3.27$, $P = 0.023$) or tea gardens ($Z = 3.08$, $P = 0.042$) in the buffer areas. However, when forests were lumped together in a six category analysis, the effect of specific land-use was not strong ($X_5^2 = 9.45$, $P = 0.092$), with no multiple comparisons having a P-value less than 0.10.

4. Discussion

We found strong differences when comparing flocks and total bird communities between forests, buffer, and agricultural areas in Sri Lanka and southern India. Mixed-species flocks were very rare in agricultural areas. Buffer areas, however, had as high densities of flocks as did forests, although the flocks were smaller in average size and had significantly different composition than forest flocks. Compared to these dramatic differences at different distances from the forest, the effect of specific land-uses in the buffer areas (all placed at the boundaries of forest reserves) was relatively small. Nonetheless, there were detectable differences in species composition, with pine plantations not retaining forest interior species in flocks compared to forests, and agriculture and abandoned agriculture being more amenable habitats than forests for open-landscape species. Comparing mixed-species flocks to the total bird community, we found that flocks outside of forests retained a greater percentage of forest interior species, and included a lower percentage of open-landscape species, than did the overall bird community.

Any study of how biodiversity changes due to human disturbance has difficulty distinguishing between the effects of different variables associated with anthropogenic change, such as degradation of habitat (Mortelliti et al., 2010), fragmentation (Laurance et al., 2002), distance to the remaining forest (Anand et al., 2010), quality of the matrix (Perfecto and Vandermeer, 2002), and edge effects (Murcia, 1995). Our sampling method of line transects, which we chose because it is suitable to surveying relatively rare phenomena like flocks, is not well-suited to study the effects of fragmentation, and we largely ignore these effects in our analysis. For example, in investigating the effects of specific land-uses, we summed together patches of the same land-use, without considering the effect of the size of those patches, or any related edge effects. Another major limitation of this study is that we are

Table 2
Flock characteristics, by broad land-use type (forest, buffer, agriculture) country and elevation. Factor is only included in final model if it was significant ($\alpha = 0.05$), or if it was included in a significant interaction.

Comparison	Factor	F or X^2 [a]	df	P	Posthoc tests	T or Z [b]	p
A. Density (ANOVA)							
	Land-use	15.46	2,51	<0.001	A vs. B	−4.87	<0.001
					A vs. F	−5.07	<0.001
					B vs. F	−0.24	0.97
	Country	0.13	1,51	0.72			
	Land-use:Country	4.78	2,51	0.01			
B. Size: species (ANOVA) [c]							
	Land-use	5.37	2,48	0.008	A vs. B	1.12	0.5
					A vs. F	−1.32	0.39
					B vs. F	−3.28	0.005
	Country	17.02	1,48	<0.001	I > SL		
C. Size: individuals (ANOVA) [c]							
	Land-use	2.53	2,49	0.09	A vs. B	−0.91	0.64
					A vs. F	−2.10	0.10
					B vs. F	−1.56	0.27
D. Proportion of forest interior species (GLM – binomial)							
	Land-use	18.69	2	<0.001	A vs. B	−1.95	0.23
					A vs. F	−3.75	<0.001
					B vs. F	−2.86	0.02
	Elevation	9.41	2	0.009	L vs. M	−0.03	1
					L vs. H	2.72	0.034
					M vs. H	2.76	0.030
E. Proportion of open-landscape species (GLM – binomial)							
	Land-use	50.67	2	<0.001	A vs. B	3.28	0.006
					A vs. F	6.55	<0.001
					B vs. F	4.31	<0.001
	Elevation	13.28	2	0.001	L vs. M	−2.37	0.09
					L vs. H	1.40	0.56
					M vs. H	3.51	0.003

[a] *F* statistics for ANOVA, χ^2 statistics for binomial GLM. *F*-tests for multifactor ANOVA use Type III sum of squares.
[b] *T* statistics for ANOVA and *Z* statistics for GLM. Positive figures are shown when the value for the first treatment level is greater than for the second in the posthoc test. Abbreviations: A = Agriculture, B = Buffer, F = Forest; L = Low, M = Middle, H = High; I = India, and SL = Sri Lanka.
[c] Response variable square-root transformed to improve normality.

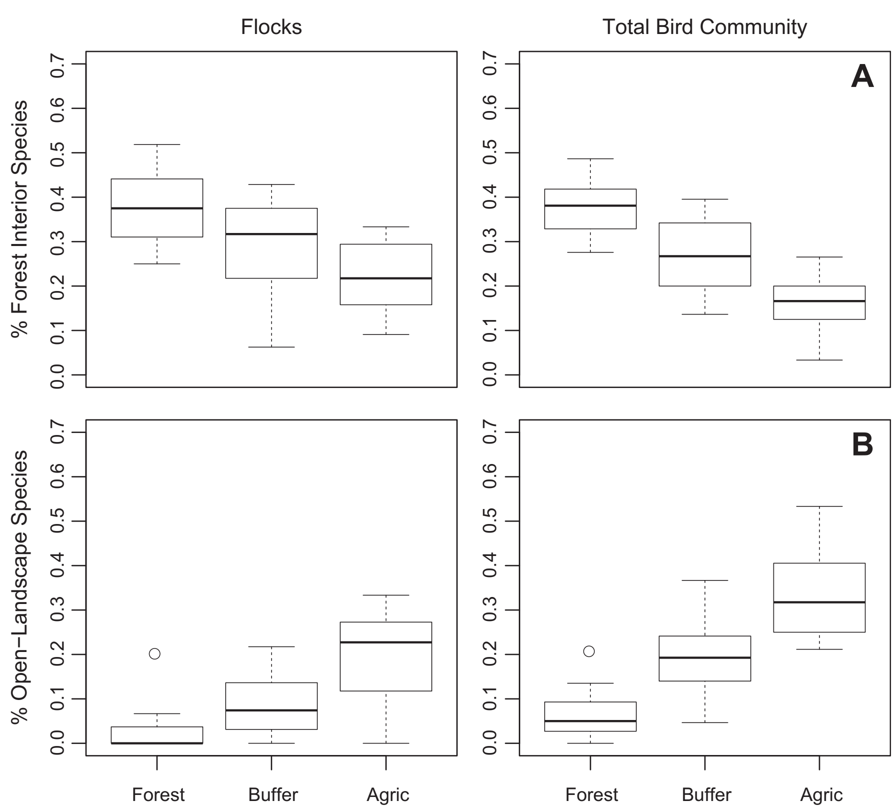

Fig. 3. The proportion of species that were (A) forest interior species or (B) open-landscape species for flocks (left column) and for the total bird community (right column) in the broad land-use analysis. For statistics, see Table 2D and E for flocks, and Table 3C and D for the total bird community.

Table 3
Bird community characteristics, by broad land-use type (forest, buffer, agriculture) country and elevation. Factor is only included in final model if it was significant (α = 0.05), or if it was included in a significant interaction.

Comparison	Factor	F or X^{2}[a]	df	P	Posthoc tests	T or Z[b]	p
A. Total species (ANOVA)[c,d]							
	Land-use	0.85	2,49	0.43			
	Elevation	27.26	2,49	<0.001	L vs. M	3.97	<0.001
					L vs. H	7.36	<0.001
					M vs. H	4.25	<0.001
	Country	0.30	1,49	0.59			
	Landuse:Country	6.18	2,49	0.0040			
B. Total individual observations/sampling effort (ANOVA)[d]							
	Land-use	0.08	2,51	0.92			
	Country	0.02	1,51	0.88			
	Landuse:Country	3.81	2,51	0.029			
C. Proportion of forest interior species (GLM – binomial)							
	Landuse	90.45	2	<0.001	A vs. B	−4.65	<0.001
					A vs. F	−8.94	<0.001
					B vs. F	−5.40	<0.001
	Elevation	14.04	2	<0.001	L vs. M	−1.00	0.57
					L vs. H	2.88	0.011
					M vs. H	3.65	<0.001
D. Proportion of open-landscape species							
	Landuse	191.09	2	<0.001	A vs. B	5.70	<0.001
					A vs. F	12.39	<0.001
					B vs. F	8.39	<0.001
	Elevation	18.79	2	<0.001	L vs. M	1.37	0.36
					L vs. H	−3.25	0.0032
					M vs. H	−4.36	<0.001

[a] *F* statistics for ANOVA, X^2 statistics for binomial GLM. *F*-tests for multifactor ANOVA use Type III sum of squares.
[b] *T* statistics for ANOVA and *Z* statistics for GLM. Positive figures are shown when the value for the first treatment level is greater than for the second in the posthoc test. Abbreviations: A = Agriculture, B = Buffer, F = Forest; L = Low, M = Middle, H = High; I = India, and SL = Sri Lanka.
[c] So control for variance in sampling effort, we recalculated the number of species through rarefaction, using the minimum number of individuals seen on a transect.
[d] Response variable square-root transformed to improve normality.

measuring the presence of birds, and not their fitness in the different environments. Even areas where animals persist can actually be found to be population sinks when fitness is measured (Robinson et al., 1995; Battin, 2004).

Keeping these caveats in mind, we draw two conclusions about the response of birds to varying intensities of land-use from this data. First, distance from the forest, as reflected by the differences we found between forest, buffer and agricultural transects, is a very strong influence on biodiversity, as also found for our region by the review of Anand et al. (2010). In comparison, the effect of specific land-use types – measured on the buffer transects, which were all placed at relatively similar distances to the forest – is weaker. The different patches of specific land-uses were small in these buffer areas, and birds can thus 'spill-over' from one habitat to another, obscuring which habitat they prefer: for example, flocks might be observed moving across habitats that they do not prefer to stay in.

Our second conclusion is that the data paints a picture of relatively high persistence of biodiversity in buffer habitats. Flocks in buffers retained 78.0% of the forest interior species that were found in forest flocks, and the total community retained 71.4% of the forest interior species found in forests. The best buffer transects for flocks were in India, and consisted of plantations where the native canopy trees were retained, and the crop (coffee or cardamom)

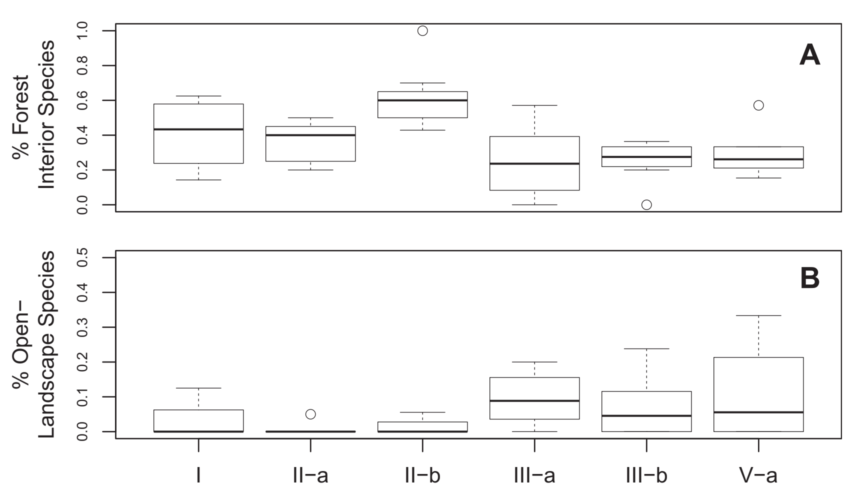

Fig. 4. The proportion of species in flocks that were (A) forest interior species or (B) open-landscape species for the different specific land-uses found on buffer transects. Forest types: I, relatively undisturbed; II-b, heavily disturbed; II-c, regenerated. Timber plantations: III-a, deciduous; III-b, coniferous. Abandoned agriculture: V-a, shrubland. See Table 1 for sample sizes, and text for statistics.

planted in the understory. Deciduous, hardwood plantations also performed quite well in both countries, although pine plantations in Sri Lanka retained fewer forest interior species. Our results are comparable to those of Lee et al. (2005), who found flock size to be similar between forest interior and forest edge sites. This persistence of birds in these areas is undoubtedly related to the structure of the vegetation of these habitats (Raman, 2006), and decisions as to how to manage agroforests or shade plantations, such as how many shade trees to retain, will be important in retaining their value for biodiversity (such considerations even influence how tea plantations retain or attract birds, see Chetana and Ganesh, 2012).

How do our results fit with the accumulating literature on the responses of animals to human modified habitats? There is a current controversy between those studies that stress the importance of modified environments to conservation (e.g., Dent and Wright, 2009), and those who stress how such environments do not compare to undisturbed forest (e.g., Gibson et al., 2011). Sometimes authors disagree as to how to interpret the same data (e.g., Ranganathan et al., 2008; Sridhar, 2009). In our view, this is a "is the glass half full or half empty?" argument: clearly these modified habitats are not as good for animal conservation as undisturbed forests, but they do conserve some aspects of biodiversity. For example, while shade coffee can contain high diversities and abundances of birds (Greenberg et al., 1997), some forest interior species may not be able to use these environments (Tejeda-Cruz and Sutherland, 2004). Although we believe it is vital to stop the conversion of forest to transitional habitats like timber plantations or degraded forests (see Tejeda-Cruz et al., 2010 about pitfalls in which "environmentally friendly" agriculture leads to forest loss), once these habitats exist they do retain some bird species, more than they would if they, in turn, were converted to agricultural lands. Further, there are methods for restoring such forests back towards more complex vegetative structure and a higher level of floristics (Ashton et al., 2001; Raman et al., 2009).

A final conclusion from our data is that more forest interior species, and fewer open-landscape species, were found in flocks than in the overall bird community. Mixed-species flocks are known to be a forest phenomenon and open-landscape species may simply not forage in ways amenable to flocking, or may have completely different ways of dealing with predation risk (Terborgh, 1990). Further research is necessary to determine exactly what vegetation structure and fragment sizes enable/facilitate flocks to exist in fragments or to move through corridors in the countryside.

Acknowledgements

We thank A. Jayarathna, R.M. Pathiraja, G. Ramachandran, W. Ranjith, M.V.I. Sanjeewanie and H. Sathischandra for collecting the data, and R.T. Corlett, R.D. Harrison, D.I. King, R. Sreekar, H. Sridhar and two anonymous reviewers for helping improve the analyses and manuscript. We appreciate the assistance of the Sri Lanka Forest Department and Wildlife Conservation Department, and the Tamil Nadu and Kerala Forest Departments. This study was supported by the Conservation, Food and Health Foundation and the American Institute for Indian Studies. EG is grateful to the National Science Foundation (International Research Fellowship Program grant 0601909) for support during data collection and the 1000 Plan Recruitment Program of Global Experts of the People's Republic of China for support during analysis and write-up.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.08.022.

References

Ali, S., Ripley, S.D., 1987. Compact Handbook of the Birds of India and Pakistan, Together with those of Bangladesh, Nepal, Bhutan and Sri Lanka. Oxford University Press, New Delhi.

Anand, M.O., Krishnaswamy, J., Kumar, A., Bali, A., 2010. Sustaining biodiversity conservation in human-modified landscapes in the Western Ghats: remnant forests matter. Biol. Conserv. 143, 2363–2374.

Ashton, M.A., Gunatilleke, C.V.S., Singhakumara, B.M.P., Gunatilleke, I.A.U.N., 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. Forest Ecol. Manage. 154, 409–430.

Bates, D., Maechler, M., Bolker, B., 2011. Linear Mixed-Effects Models Using S4 Classes. <http://cran.r-project.org/web/packages/lme4/index.html> (accessed December 2012).

Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv. Biol. 18, 1482–1491.

Bhagwat, S.A., Willis, K.J., Birks, H.J.B., Whittaker, R.J., 2008. Agroforestry: a refuge for tropical biodiversity? Trends Ecol. Evol. 23, 261–267.

Bretz, F., Hothorn, T., Westfall, T., 2010. Multiple Comparisons Using R. CRC Press, Boca Raton.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundances of Biological Populations. Oxford University Press, Oxford.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global biodiversity: indicators of recent declines. Science 328, 1164–1168.

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–1417.

Chetana, H.C., Ganesh, T., 2012. Importance of shade trees (*Grevillea robusta*) in the dispersal of forest tree species in managed tea plantations of southern Western Ghats, India. J. Trop. Ecol. 28, 187–197.

Cincotta, R.P., Wisnewski, J., Engelman, R., 2000. Human population in the biodiversity hotspots. Nature 404, 990–992.

Daily, G.C., Ehrlich, P.R., Sánchez-Azofeifa, G.A., 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. Ecol. Appl. 11, 1–13.

Dent, D.H., Wright, S.J., 2009. The future of tropical species in secondary forests: a quantitative review. Biol. Conserv. 142, 2833–2843.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–383.

Gill, F., Donsker, D. (Eds.), 2013. IOC World Bird List (v. 3.3). <http://www.worldbirdnames.org/> (accessed May 2013).

Goodale, E., Nizam, B.Z., Robin, V.V., Sridhar, H., Trivedi, P., Kotagama, S.W., Padmalal, U.K.G.K., Perera, R., Pramod, P., Vijayan, L., 2009. Regional variation in the composition and structure of mixed-species bird flocks in the Western Ghats and Sri Lanka. Curr. Sci. India 97, 648–663.

Greenberg, R., 2000. Birds of many feathers: the formation and structure of mixed-species flocks of forest birds. In: Boinski, S., Garber, P.A. (Eds.), On the Move: How and Why Animals Travel in Groups. Univ. of Chicago Press, pp. 521–558.

Greenberg, R., Bichier, P., Sterling, J., 1997. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, Mexico. Biotropica 29, 501–514.

Grimmett, R., Inskipp, C., Inskipp, T., 1999. A Guide to the Birds of India, Pakistan, Bangladesh, Bhutan, Sri Lanka and the Maldives. Princeton University Press, Princeton.

Gunawardene, N.R., Daniels, A.E.D., Gunatilleke, I.A.U.N., Gunatilleke, C.V.S., Karunakaran, P.V., Nayak, K.G., Prasad, S., Puyravaud, P., Ramesh, B.R., Subramanian, K.A., Vasanthy, G., 2007. A brief overview of the Western Ghats – Sri Lanka hotspot. Curr. Sci. India 93, 1567–1572.

IUCN, 2013. IUCN Red List of Threatened Species. <www.iucnredlist.org> (accessed January 2013).

Kotagama, S.W., Goodale, E., 2004. The composition and spatial organization of mixed-species flocks in a Sri Lankan rainforest. Forktail 20, 63–70.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16, 605–618.

Lee, T.M., Soh, M.C.K., Sodhi, N., Koh, L.P., Lim, S.L.-H., 2005. Effects of habitat disturbance on mixed species bird flocks in a tropical sub-montane rainforest. Biol. Conserv. 122, 193–204.

Mortelliti, A., Amori, G., Boitani, L., 2010. The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163, 535–547.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10, 58–62.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., de Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.
Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2008. The Vegan Package: Community Ecology Package. <http://vegan.r-forge.r-project.org/> (accessed November 2012).
Perfecto, I., Vandermeer, J., 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in Southern Mexico. Conserv. Biol. 16, 174–182.
Powell, G.V.N., 1985. Sociobiology and adaptive significance of interspecific foraging flocks in the Neotropics. Ornithol. Monogr. 36, 713–732.
Raman, T.R.S., 2006. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. Biodivers. Conserv. 15, 1577–1607.
Raman, T.R.S., Mudappa, D., Kapoor, V., 2009. Restoring rainforest fragments: survival of mixed-native species seedlings under contrasting site conditions in the Western Ghats, India. Restor. Ecol. 17, 137–147.
Ranganathan, J., Daniels, R.J.R., Chandran, M.D.S., Ehrlich, P.R., Daily, G.C., 2008. Sustaining biodiversity in ancient tropical countryside. Proc. Natl. Acad. Sci. USA 105, 17852–17854.
Robinson, S.K., Thompson III, F.R., Donovan, T.M., Whitehead, D., Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267, 1987–1990.
Schmitt, C.B., Burgess, N.D., Coad, L., Belokurov, A., Besançon, C., Boisrobert, L., Campbell, A., Fish, L., Gliddon, D., Humphries, K., Kapos, V., Louks, C., Lysenko, I., Miles, L., Mills, C., Minnemeyer, S., Pistorius, T., Ravilious, C., Steininger, M., Winkel, G., 2009. Global analysis of the protection status of the world's forests. Biol. Conserv. 142, 2122–2130.
Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.
Sridhar, H., 2009. Are arecanut plantations really suitable for biodiversity conservation? Proc. Natl. Acad. Sci. USA 106, E34.
Stouffer, P.C., Bierregaard Jr., R.O., 1995. Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76, 2429–2445.
Tejeda-Cruz, C., Sutherland, W.J., 2004. Bird responses to shade coffee production. Anim. Conserv. 7, 169–179.
Tejeda-Cruz, C., Silva-Rivera, E., Barton, J.R., Sutherland, W.J., 2010. Why shade coffee does not guarantee biodiversity conservation. Ecol. Soc. 15, 13.
Terborgh, J., 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. Am. J. Primatol. 21, 87–100.
Van Houtan, K.S., Pimm, S.L., Bierregaard Jr., R.O., Lovejoy, T.E., Stouffer, P.C., 2006. Local extinctions in flocking birds in Amazonian forest fragments. Evol. Ecol. Res. 8, 129–148.