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COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Distinct carbon sources indicate strong differentiation between tropical forest and farmland bird communities

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Abstract The conversion of forest into farmland has resulted in mosaic landscapes in many parts of the tropics. From a conservation perspective, it is important to know whether tropical farmlands can buffer species loss caused by deforestation and how different functional groups of birds respond to land-use intensification. To test the degree of differentiation between farmland and forest bird communities across feeding guilds, we analyzed stable C and N isotopes in blood and claws of 101 bird species comprising four feeding guilds along a tropical forest-farmland gradient in Kenya. We additionally assessed the importance of farmland insectivores for pest control in C_4 crops by using allometric relationships, C stable isotope ratios and estimates of bird species abundance. Species composition differed strongly between forest and farmland bird communities. Across seasons, forest birds primarily relied on C_3 carbon sources, whereas many farmland birds also assimilated C_4 carbon. While C sources of frugivores and omnivores did not differ between forest and farmland communities, insectivores used more C_4 carbon in the farmland than in the forest. Granivores assimilated more C_4 carbon than all other guilds in the farmland. We estimated that insectivorous farmland birds consumed at least 1,000 kg pest invertebrates km^{-2} $year^{-1}$. We conclude that tropical forest and farmland understory bird communities are strongly separated and that tropical farmlands cannot compensate forest loss for insectivorous forest understory birds. In tropical farmlands, insectivorous bird species provide a quantitatively important contribution to pest control.

Keywords Stable isotopes · Habitat fragmentation · Pest control · Feeding guilds · Foraging movements

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Introduction

The conversion of tropical forests into agricultural land has resulted in mosaic landscapes of forest and farmland in many parts of the tropics (Bierregaard et al. 1992; Skole and Tucker 1993). Both habitats, tropical forests and farmland, can harbor high bird diversities (Balmford et al. 2001; Waltert et al. 2005; Mulwa et al. 2012). If the two

habitat types harbor similar bird communities and if birds frequently pass habitat boundaries when foraging, tropical farmlands may buffer species loss caused by forest destruction to a certain degree (Daily et al. 2001; Hughes et al. 2002). Hence, from a conservation perspective it is important to assess the value of tropical farmlands for the maintenance of tropical bird diversity (Hughes et al. 2002; Sekercioglu et al. 2007).

Habitat destruction and fragmentation may not influence all feeding guilds within a bird community in the same way (Waltert et al. 2005; Burney and Brumfield 2009). Insectivorous understory species appear to be more vulnerable to forest destruction and fragmentation (Newmark 1991; Laurance et al. 2004; Mulwa et al. 2012) than other feeding guilds, such as frugivores (Luck and Daily 2003; Burney and Brumfield 2009). As different feeding guilds offer different ecosystem services (e.g., seed dispersal by frugivores and agricultural pest control by insectivores), forest destruction and fragmentation may differently affect these ecosystem services (Sekercioglu et al. 2004). However, the foraging patterns of bird communities providing different ecosystem services in mosaic landscapes of tropical forests and farmlands are largely unknown.

In the last decades, stable isotope analysis (SIA) has proved to be a powerful tool in the study of the foraging patterns and the dietary composition of birds (reviewed by Hobson 1999; Kelly 2000; Rubenstein and Hobson 2004; West et al. 2006; Inger and Bearhop 2008). In contrast to traditional methods like field observations or feces analyses that usually provide insights into the diet of a bird over short time scales (Inger and Bearhop 2008), stable isotopes can integrate dietary information in animal tissues over various time scales, ranging from hours (e.g., breath; Hatch et al. 2002) to years (e.g., bone collagen; Hobson and Clark 1992). Moreover, the traditional methods can only detect ingested and undigested food items, whereas SIA provides information on assimilated nutrients and therefore reflects the nutritional value of a particular food source (Peterson and Fry 1987; Herrera et al. 2006).

Common applications of SIA in trophic studies are the assessment of the trophic position of a species in a food web and the contribution of different food sources to a species' diet. The assessment of the trophic position relies on the increase of the N stable isotope ratio ($^{15}N/^{14}N$) in a consumer relative to its diet (Post 2002). In contrast, the C stable isotope ratio changes little between trophic levels, but consumers usually reflect the C stable isotope ratio of their diet, allowing one to trace the C back to its primary source (Peterson and Fry 1987; Post 2002). The identification of primary C sources (hereafter called "C sources" or "C_3/C_4 sources") is particularly informative in terrestrial systems because C of plants with the C_4 photosynthetic pathway is enriched in ^{13}C compared to C from plants with the C_3 pathway (Peterson and Fry 1987). This approach is particularly valuable in tropical landscapes consisting of a mosaic of forest and farmland as most woody and herbaceous species are C_3 plants (e.g., trees, shrubs, herbs) whereas many crops and grasses in tropical farmlands are C_4 plants (e.g., sugar cane). Additionally, SIA can allow the assessment of the pest control service of predators foraging on pest invertebrates that rely on isotopically distinct crops (Ostrom et al. 1997; Prasifka and Heinz 2004).

The majority of dietary studies on birds using SIA were conducted in temperate systems (reviewed by Kelly 2000), but isotopic foraging studies on birds in tropical forests are rare and restricted to Neotropical species (Herrera et al. 2003, 2005, 2006, 2009; Herrera and Reyna 2007; Hardesty 2009). Moreover, most of the foraging studies on tropical forest birds focus on single bird species rather than on bird communities (but see Herrera et al. 2003, 2006) and on patterns within a distinct habitat rather than on differences between habitat types in a mosaic landscape.

Here, we use SIA to assess the conservation value of farmland for bird diversity in tropical forest-farmland mosaics. We test whether birds of different feeding guilds differ in their utilization of food resources from farmland habitats and thereby evaluate whether feeding guilds are differently affected by land-use change. Furthermore, we quantify the importance of insectivorous birds for agricultural pest control in tropical farmlands.

In particular, the objectives of this study were to:

1. Study the C sources of understory bird communities of tropical rainforest and farmland and to evaluate to which extent these communities are isolated from each other.
2. Test whether feeding guilds differ in their C sources between forest and farmland and thus rely on distinct foraging habitats.
3. Test the applicability of SIA in quantifying pest control services by insectivorous birds.

We hypothesize that:

1. Forest birds depend mostly on C from C_3 sources and that the importance of C_4 sources for birds increases with distance from the forest edge into farmland.
2. Insectivorous forest birds hardly use farmland C sources, while granivorous species predominantly assimilate C from farmland food resources.
3. Insectivorous farmland bird species play an important role in pest control in tropical agro-ecosystems.

We analyzed blood and claw tissues of birds to test these hypotheses on a short (days to weeks) and on a long (months) time scale.

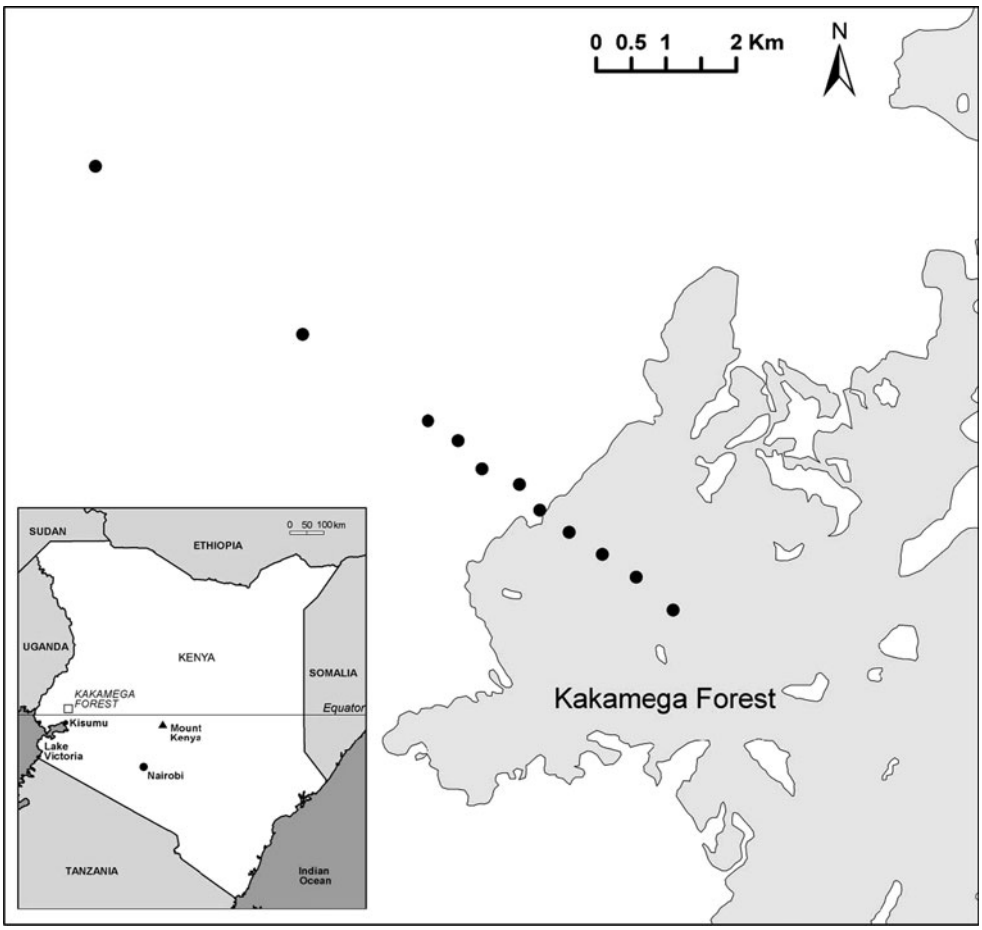

Fig. 1 Location of the 11 study sites in the northwestern part of the Kakamega Forest region, western Kenya

Materials and methods

Study area

We conducted this study in Kakamega Forest (0°08′–0°22′N, 34°46′–34°57′E) and its adjacent farmland in western Kenya. Kakamega Forest is the only remaining mid-altitude tropical rain forest in Kenya (1,500–1,700 m a.s.l.) and is considered to be the easternmost remnant of the lowland Congo basin rain forests of Central Africa (Kokwaro 1988). Mean annual precipitation is about 1,960 mm and is seasonally distributed with a long rainy season from April to November and a short dry season from December to March (Forest Department records at Isecheno Forest Station 1982–2005). The agricultural land surrounding Kakamega Forest has a very high population density of 600 inhabitants km^{-2} and is one of the most densely populated rural areas of the world (Blackett 1994).

The avifauna of Kakamega Forest includes species of the Guinea-Congo Forests biome and of the Afrotropical Highlands biome (BirdLife International 2009). A total of 410 bird species has been recorded in the forest (Shanni and de Bruijn 2006) and the surrounding farmland also harbors an exceptional bird species richness and abundance (Laube et al. 2008). Kakamega Forest is listed as an Important Bird Area (BirdLife International 2009).

The study area was located at the northwestern edge of Kakamega Forest (Fig. 1). All study sites inside the forest were placed in near-natural forest. This part of the forest has been managed by the Kenya Wildlife Service since 1986 and experiences low levels of human disturbance (Bleher et al. 2006). Most forest plant species in Kakamega Forest are C_3 plants. The farmland northwest of Kakamega Forest is little to moderately structured and is composed of a mixture of C_3 plants (e.g., isolated trees, hedgerows) and C_4 plants, like sugar cane, the local cash crop (>25 % land cover in the study area, Schaab et al. 2010). There is almost no transition zone between forest and farmland in Kakamega.

Collection and preservation of samples

We carried out field work during the dry season from the end of January to mid March 2009. We caught birds at 11 sites along a 10-km transect from the forest interior to the adjacent farmland (Fig. 1). Nine sites were established at a

Table 1 Effects of habitat, distance to forest edge and site on the proportion of C_4 carbon (arcsin square root transformed) in blood and claw samples of birds caught at five forest and six farmland sites along a 10-km forest-farmland transect

	df	SS	MS	*F*	*P*
Response: $\%C_4$ blood					
Habitat	1	8.28	8.28	14.26	0.005
Distance to forest edge	1	0.03	0.03	0.05	0.834
Site	8	4.65	0.58	5.74	<0.001
Residuals	541	54.83	0.10		
Response: $\%C_4$ claws					
Habitat	1	4.27	4.27	10.14	0.013
Distance to forest edge	1	0.01	0.01	0.02	0.878
Site	8	3.37	0.42	4.46	<0.001
Residuals	551	51.99	0.09		

Habitat and distance to forest edge were tested against the variation among sites

distance of 500 m from each other ranging from 2 km inside to 2 km outside the forest, including one site at the forest edge that was considered as a forest site in all analyses. Two additional sites were located in the farmland at 4 km and 8 km distance to the forest edge. At each site, we trapped birds with ten mist nets (each 2.5 m high and 6 m long) on 3 subsequent days. Nets were opened before dawn and closed around 12:00. The sequence of data collection at the 11 study sites was randomized. Captured birds were identified using Zimmermann et al. (1999), measured and ringed with rings of the Ringing Scheme of East Africa. Recaptured birds were not sampled again. Overall, we sampled 567 birds of 101 species, 250 individuals of 44 species in the forest and at the forest edge, and 317 individuals of 66 species in the farmland. Only two species were trapped both inside the forest and in the farmland and another seven species both at the forest edge and in the farmland, whereas all other species were clearly restricted to one type of habitat.

We collected 20–100 µl of blood from the antebrachial vein and 1–2 mm of the tips of both middle claws of each bird. Whole blood of birds integrates dietary information over several days to a few weeks (Hobson and Bairlein 2003; Pearson et al. 2003) whereas the first 1–2 mm of a claw integrate this information for the 2–5 months prior to sampling (Bearhop et al. 2003). Claw samples were stored in sealed paper envelopes, which in turn were stored in sealed plastic containers with silica gel to keep them dry. Blood samples were stored in locked glass vessels containing 70 % ethanol because freezing and air drying were not feasible. Ethanol preservation has been shown to have a negligible effect on stable C and N isotope values of tissues of various taxa (reviewed by Sarakinos et al. 2002), including birds (Hobson et al. 1997).

We also determined the isotopic composition of the potential plant and invertebrate diet of the birds (Table 1 in ESM). We collected ripe fruits of the most common fleshy fruiting plant species at each capture site (overall 28 individuals of 16 morphospecies). At farmland sites, we also collected leaves of sugar cane (*Saccharum sp.*) because it comprises the great majority of C_4 plants there and is therefore the major source of C_4 carbon in our study area northwest of Kakamega Forest (Schaab et al. 2010). We collected whole invertebrate communities at each site using beating and direct searching (Sutherland 1996). At the farmland sites, we collected invertebrate communities separately from shrubs in hedgerows and from sugar cane fields. In forest and farmland, most invertebrates belonged to the following taxa: Araneae, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera, all of which are bird food (Sekercioglu et al. 2002; Gámez-Virués et al. 2007). Different taxa were not analyzed separately in the following analyses because we were interested in the isotopic composition of the entire invertebrate community. Plant and invertebrate samples were stored in paper envelopes and sun-dried on a black tarp for a number of days.

Plant and invertebrate samples were collected at the same time as blood and claw samples from birds. Therefore their isotopic signal has been integrated over roughly the same time period as those of the blood samples of the birds. Our baseline samples are not detailed enough to identify exact food resources of single bird species but they are sufficiently resolved to differentiate C sources and trophic positions of birds in a community study such as this.

Sample preparation and isotopic analysis

Blood samples were oven-dried at 60 °C until they reached constant weight and were then powdered with a hand mortar (Cherel et al. 2007). Due to the low lipid content of blood, lipid extraction was not necessary (Bearhop et al. 2000). We washed claw samples in 2:1 chloroform:methanol for 30 min to remove surface contaminants and adherent oils (Dobush et al. 1985). Washed claw samples

were air-dried under a fume hood for 48 h. Samples of fruits, leaves and invertebrate communities were also oven-dried at 60 °C to constant weight and powdered. All samples were stored dry until SIA.

Samples of blood (0.1–3 mg, $n = 553$), claws (0.1–2.5 mg, $n = 563$), plant material (6–11 mg, $n = 35$) and invertebrate communities (0.8–3 mg, $n = 36$, with two replicate measurements per sample) were weighed into tin boats and combusted at 1,150 °C in a VarioEL III elemental analyzer (Elementar Analysensysteme, Hanau, Germany) in the laboratory of the Geographic Institute of the Johannes Gutenberg-University Mainz, Germany. The resulting gases were separated and analyzed for the isotope composition of C and N using a continuous flow isotope ratio mass spectrometer (IsoPrime, GVI, Manchester, UK). All stable isotope ratios are expressed in per mill (‰) using the δ notation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1{,}000 \quad (1)$$

where X refers to ^{13}C or ^{15}N and R is the corresponding ratio between ^{13}C/^{12}C and ^{15}N/^{14}N, respectively. In every run, we used 57 samples together with four international standards (each with three samples). Standards were IAEA-CH-6 and IAEA-CH-7 (referenced against Vienna Pee Dee belemnite) for δ^{13}C and IAEA-N-1 and IAEA-N-2 [referenced against Air (atmospheric N)] for δ^{15}N. To refer our measurements to the international reference materials Vienna Pee Dee belemnite for C and Air for N, we used the following two-point linear normalization (Coplen et al. 2006) advocated by Paul et al. (2007):

$$\delta^{\text{T}}_{\text{sample}} = \frac{\delta^{\text{T}}_{\text{standard1}} - \delta^{\text{T}}_{\text{standard2}}}{\delta^{\text{M}}_{\text{standard1}} - \delta^{\text{M}}_{\text{standard2}}} \times \left(\delta^{\text{M}}_{\text{sample}} - \delta^{\text{M}}_{\text{standard2}}\right) + \delta^{\text{T}}_{\text{standard2}} \quad (2)$$

where δ^{M}_{Y} is the measured δ value of the material Y (i.e., sample or standard) relative to the working gas and δ^{T}_{Y} is the true δ value of the material Y. Repeated analyses of the four international standards ($n = 99$ for each standard) showed that δ^{13}C and δ^{15}N were measured with a precision of ±0.1 and 0.2 ‰ (SD), respectively. We determined δ^{13}C and δ^{15}N values of the 18 samples of invertebrate communities in duplicate and found only a minor variation in replicate measurements (average SD = 0.2 for both δ^{13}C and δ^{15}N, $n = 2$ replicate measurements per sample).

Plant and invertebrate diet of birds

We compared the different types of baseline samples ($n = 53$, Table 1 in ESM), averaged at the site level, with pair-wise multivariate ANOVAs (MANOVAs), using δ^{13}C and δ^{15}N as response variables. To control for type 1 errors, P-values were corrected using a sequential Bonferroni correction (Holm 1979). Farmland invertebrates collected from hedgerows and sugar cane did not differ in their C and N stable isotope composition (pairwise MANOVA: Pillai's trace = 0.08, $F_{1,11} = 0.42$, $P = 0.667$) and were pooled for further analyses. Differences between invertebrates and fruits in the forest were only marginally significant (pairwise MANOVA: Pillai's trace = 0.53, $F_{1,8} = 3.98$, $P = 0.070$); all other sources strongly differed in their C and N stable isotope ratios (all P-values <0.05; Fig. 2).

Application of stable isotope discrimination factors

Community-wide studies using SIA require some generalizations that potentially lead to minor inaccuracies at the species level (Gannes et al. 1997; Post 2002). One of these generalizations is the application of discrimination factors (Δ^{13}C, Δ^{15}N) which are not species specific. We minimized this inaccuracy by applying discrimination factors that are specific for the type of tissue analyzed. For blood samples, we calculated mean tissue-specific discrimination factors for δ^{13}C and for δ^{15}N with values derived from experimental studies that dealt only with passerines (Table 2 in ESM). We did not consider the numerous studies of aquatic and pelagic bird species (reviewed by Caut et al. 2009) because they are hardly comparable to the terrestrial bird community of Kakamega Forest. Due to the lack of experimental studies on the enrichment of ^{13}C and ^{15}N in claws, we used tissue-specific enrichment factors for feathers of passerine species (Table 2 in ESM). Both claws and feathers consist mainly of keratin and C and N stable isotope ratios of claws and feathers were closely correlated in former studies (Bearhop et al. 2003; Clark et al. 2006). We also found a strong correlation of stable isotope ratios between feather and claw samples of species that were collected in this study (δ^{13}C, $r = 0.95$, $P < 0.001$, $n = 99$; δ^{15}N, $r = 0.82$, $P < 0.001$, $n = 99$).

We did not apply different discrimination factors for bird species belonging to different feeding guilds (but see Herrera et al. 2006) because few previous studies have determined guild-specific discrimination factors for birds and the differences in discrimination factors between feeding guilds was not consistent across studies (Table 2 in ESM). Our approach is conservative because it reduces potential systematic errors due to imprecise guild-specific discrimination factors (Bond and Diamond 2011). However, applying guild-specific discrimination factors (as given in Table 2 in ESM) resulted in qualitatively very similar results (not shown).

Feeding guild classification and tropic levels

We used a database of the diet of all sub-Saharan breeding bird species compiled from a detailed literature survey (W. D. Kissling and K. Böhning-Gaese, unpublished data) to classify

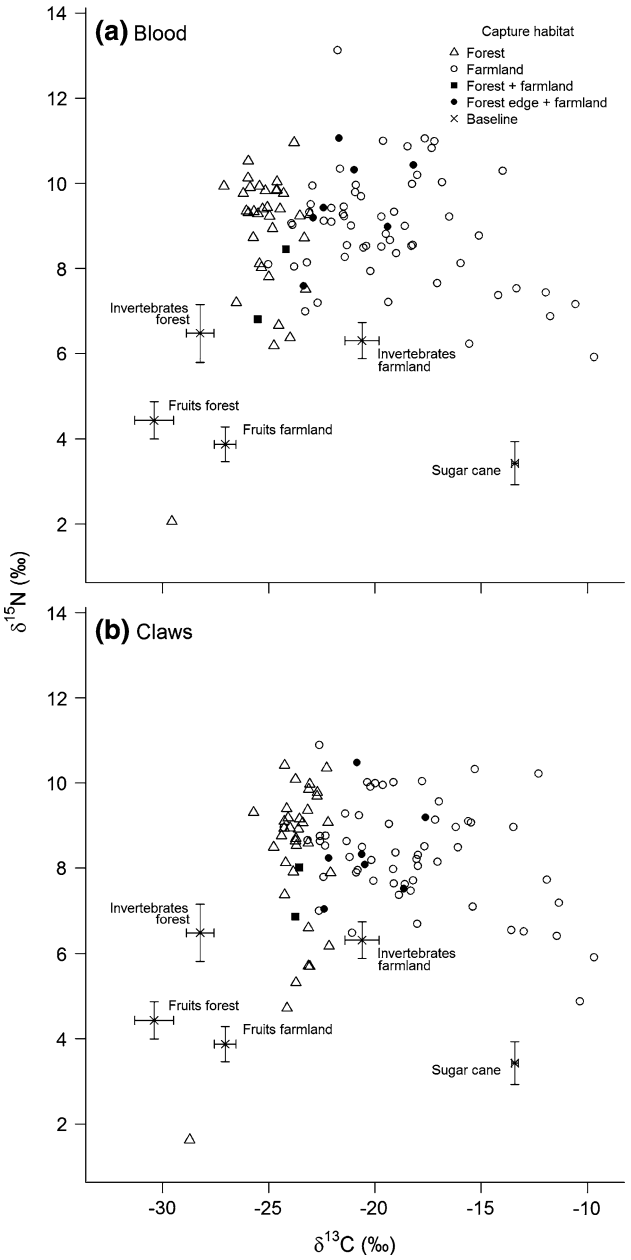

Fig. 2 Mean C stable isotope ratio (δ^{13}C) and N stable isotope ratio (δ^{15}N) of blood (**a**) and claw samples (**b**) of 101 bird species of the forest and farmland communities. For clarity, *error bars* (±1 SE) are only shown for the plant and invertebrate baselines. For exact values and sample sizes see Tables 1 and 3 in ESM

bird species into four different feeding guilds according to their major food items (for methodological details see Kissling et al. 2007). Feeding guilds were: insectivores (feeding on invertebrates and/or small vertebrates), frugivores (fruits and/or other plant material), omnivores (invertebrates and any plant material), and granivores (only seeds). Most species were classified as insectivorous (60 species) or omnivorous (22), nine species as frugivorous and ten as granivorous (Table 3 in ESM). Granivorous species were caught exclusively in the farmland. We calculated the trophic levels for each bird species using δ^{15}N signatures of the sampled birds according to the equation:

$$\mathrm{TL}_{\mathrm{consumer}} = \lambda + \frac{\left(\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{base}}\right)}{\Delta^{15}\mathrm{N}} \quad (3)$$

with $\delta^{15}\mathrm{N}_{\mathrm{base}} = 4.0$ ‰ (=the mean δ^{15}N ratio of all plant material) and $\lambda = 1$ (=the trophic level of primary producers; for details see Post 2002). The application of constant bird tissue-specific discrimination factors (Δ^{15}N) could introduce a minor bias in estimates for species from higher trophic levels, as discrimination factors could be different at lower levels in the food web. Detailed information on the isotopic food web structure would be needed to correct for this bias which is beyond the scope of this study.

Contribution of C_4 sources to diet

We determined the relative contribution of C_4 sources to the birds' diets using a two-end-member linear mixing model (Phillips and Gregg 2001). To control for the trophic position (Eq. 3) of the birds, we used Eq. 4 to correct their δ^{13}C values before running the model:

$$\delta^{13}\mathrm{C}_{\mathrm{corrected}} = \delta^{13}\mathrm{C}_{\mathrm{consumer}} - \Delta^{13}\mathrm{C} \times (\mathrm{TL}_{\mathrm{consumer}} - 1) \quad (4)$$

Because C isotope ratios of C_3 plants differed between forest and farmland, we used separate mixing models for the forest and farmland bird communities, respectively. For forest birds and for two species that were caught in both habitats, the end members of the model were the mean δ^{13}C values of C_3 forest plants and sugar cane. For farmland birds and for seven species that were caught in the farmland and at the forest edge, the mean δ^{13}C signatures of C_3 farmland plants and sugar cane were used. Since our estimates of the endpoints of the model are means across fruiting plant species (not minima and maxima), relative contributions of C_4 sources were slightly negative or larger than 100 % for some consumer species (see Table 3 in ESM for original values). We set the respective values to 0 and 100 %, respectively. This approach is conservative as it reduces the relative differences in C_4 contributions to the diet of different bird species. For further analyses, we used the common arcsin square root transformation of the proportions of C_4 C to improve normality of residuals and homogeneity of variances.

Birds as pest control agents

To estimate the annual invertebrate biomass production in Kakamega farmland we used sweep net samples from a

Table 2 Estimated pest control services of 20 insectivorous farmland bird species around Kakamega Forest, Kenya

Species	Weight (g)	Food (g day^{-1})	C_4 (%)	Pest control per individual (g day^{-1})	Individuals km^{-2}	Pest control per species (g km^{-2} day^{-1})	Percentage of sum
Northern black flycatcher	30	18	46	8	111	930	35
Baglafecht weaver	30	18	39	7	61	430	16
African blue flycatcher	9	8	35	3	120	324	12
Yellow white-eye	10	8	8	1	216	147	5
Tawny-flanked prinia	9	8	32	2	58	141	5
Brown babbler	66	31	51	16	9	138	5
Tropical boubou	51	26	20	5	20	106	4
White-browed robin-chat	39	22	39	8	12	97	4
Brown-crowned tchagra	36	20	35	7	12	82	3
African pygmy kingfisher	13	10	39	4	20	77	3
Singing cisticola	14	11	41	4	15	63	2
White-headed saw-wing	11	9	39	3	9	29	1
Cardinal woodpecker	25	16	19	3	9	26	1
White-browed scrub robin	19	13	65	9	3	25	1
African paradise flycatcher	15	11	22	2	9	21	1
African dusky flycatcher	9	7	47	4	6	21	1
Common wattle-eye	14	11	19	2	6	12	0
Spectacled weaver	22	15	5	1	12	9	0
Pale flycatcher	18	13	9	1	6	7	0
Copper sunbird	9	8	16	1	3	3	0
Sum						2,687	100

Pest control was estimated as the product of mean feeding rate (as derived from Eq. 5), mean percentage of C_4 carbon in claw samples and mean species density (calculated from point count data from Laube et al. 2008). All values are rounded averages

12-month study in 60 permanent plots (R. K. Mulwa and K. Böhning Gaese, unpublished data). We assumed that 50 sweeps translate into a sampled area of 1 m^2 (Witsack 1975), that the mean biomass turnover ratio of invertebrates is 3.5 (Waters 1969) and that the mean generation time is 4 months (e.g. for grasshoppers; Meyer et al. 2002).

To estimate the proportion of pest invertebrates of the biomass of the invertebrate community we used the two-end-member linear mixing model (Phillips and Gregg 2001) described above. We corrected the $\delta^{13}C$ signature (Eq. 4) of the farmland invertebrate community samples before we ran the model by using averaged discrimination factors ($\Delta^{13}C = 0.18$ and $\Delta^{15}N = 3.1$) from studies dealing with terrestrial invertebrates (reviewed by Caut et al. 2009). We used the mean $\delta^{13}C$ signatures of C_3 farmland plants and sugar cane as baseline.

To estimate the pest control service of insectivorous bird species, we used allometric relationships, C stable isotope ratios and independent estimates of bird abundances. We used the mean weight of a bird species, as measured in the field, to calculate the daily feeding rates of insectivorous farmland bird species as grams fresh matter intake (FMI) of invertebrates per day with the following equation (Nagy 2001):

$$\frac{\text{FMI}}{\text{day}} = 1.633(\text{grams body mass})^{0.705} \quad (5)$$

We estimated the mean contribution of FMI to pest control by multiplying FMI by the mean proportion of C_4

carbon in claws because claws integrate dietary information over a larger time scale than blood and are thus more suitable for the estimation of average pest control. We assumed that the consumption of plant material or other pest control species (e.g., carnivorous invertebrates) by insectivorous birds is negligible and that the majority of assimilated C_4 carbon in bird tissues is derived from pest invertebrates feeding on agricultural crops, especially sugar cane. By combining stable isotope data and mean densities of farmland bird species around Kakamega Forest (published in Laube et al. 2008), we were able to estimate the pest control service of 20 insectivorous farmland bird species in the study area.

Statistical analyses

In order to compare short- and long-term foraging patterns, all analyses were performed separately for blood and claw samples. Nine species that were caught in both habitats (i.e., forest and farmland) were not included in analyses at the species level that included habitat as a factor because these species could not be assigned to a single habitat type. Because samples of the green-backed twinspot ($n = 1$ individual; see Table 3 in ESM for scientific species names) differed strongly in their C and N isotopic composition from all other birds (bottom left, Fig. 2a, b), this species was excluded from all analyses.

We analyzed the spatial gradient of C sources of bird individuals along the forest-farmland transect in a nested linear model. In this model, the effects of habitat (i.e. forest or farmland) and distance to forest edge (of the respective study site) were tested against variation among sites and the site effect against variation among individuals per site. The variance in the proportion of C_4 carbon between the forest and farmland bird communities was compared with Fligner–Killeen tests (Conover et al. 1981).

We tested differences in C sources of bird species between habitats within separate feeding guilds with ANOVAs. *P*-values were corrected with a sequential Bonferroni correction (Holm 1979). Accordingly, we used ANOVAs and Tukey's honest significant difference (HSD) post hoc tests to analyze whether C sources of species differed among feeding guilds within forest and farmland habitats, respectively. All statistical analyses were performed with R 2.12.2 (R Development Core Team 2011).

Results

Feeding guilds and trophic levels

According to the strong differences in $\delta^{15}N$ values among bird species (Fig. 2), the feeding guilds differed significantly in their trophic levels (ANOVA: blood, $F_{3,96} = 9.58$, $P < 0.001$; claws, $F_{3,95} = 7.97$, $P < 0.001$). Granivores occupied a significantly lower trophic position than insectivores and omnivores (Tukey's HSD: all *P*-values <0.01; Fig. 1 in ESM) and a marginally significantly lower position than frugivores (all *P*-values <0.1). Insectivores and omnivores tended to have slightly higher trophic levels than frugivores but these differences were not significant (Tukey's HSD: all *P*-values >0.05; Fig. 1 in ESM).

C sources of forest and farmland birds

Forest species had much lower $\delta^{13}C$ values in blood and claws than farmland species (Fig. 2) and derived significantly less of their C from C_4 sources than farmland species (ANOVA: blood, $F_{1,89} = 16.11$, $P < 0.001$; claws, $F_{1,88} = 11.29$, $P = 0.001$). Many forest species derived their C almost exclusively from C_3 sources [e.g., equatorial akalat, 3 ± 5 % (mean ± SE) C_4 carbon in blood samples; blue-shouldered robin-chat, 5 ± 5 %; little greenbul, 7 ± 5 %; Table 3 in ESM]. In the farmland, both mainly C_3 feeding (e.g., pale flycatcher, 3 ± 5 % C_4 carbon in blood samples; Table 3 in ESM) and C_4 feeding species (e.g., yellow-mantled widowbird, 95 ± 7 %) occurred. Accordingly, forest species spanned a much smaller range in C sources than the farmland bird community (Fig. 2; Fligner-Killeen test: blood, $\chi^2 = 10.93$, $P < 0.001$, $n = 91$; claws, $\chi^2 = 17.47$, $P < 0.001$, $n = 90$).

Despite the strong differences between forest and farmland, distance to the forest edge did not affect the proportion of C_4 carbon for both blood and claws (Table 1; Fig. 3). However, the proportion of C_4 carbon in blood and claw samples differed among sites (within habitat). The site effect was attributable to a higher proportion of C_4 carbon in birds at the forest edge compared to those in the forest interior (Fig. 3).

C sources of different feeding guilds

Frugivorous species obtained similar amounts of C from C_4 sources in forest and farmland (ANOVA: blood, $F_{1,6} = 1.03$, $P = 0.700$; claws, $F_{1,6} = 2.64$, $P = 0.310$; Fig. 4). Omnivorous species also showed an equal utilization of C_4 sources in both habitats (ANOVA: blood, $F_{1,18} = 0.37$, $P = 0.700$; claws, $F_{1,18} = 0.52$, $P = 0.481$; Fig. 4). In contrast, insectivorous species obtained a significantly lower amount of C from C_4 sources in the forest than in the farmland (ANOVA: blood, $F_{1,52} = 21.16$, $P < 0.001$; claws, $F_{1,51} = 15.38$, $P < 0.001$; Fig. 4).

In the forest, feeding guilds differed in the proportion of C_4 carbon (ANOVA: blood, $F_{2,31} = 4.78$, $P = 0.016$; claws, $F_{2,31} = 2.98$, $P = 0.065$) because insectivores assimilated a lower proportion of C from C_4 sources than omnivores (Tukey's HSD: blood, $P = 0.013$; claws, $P = 0.071$; Fig. 4).

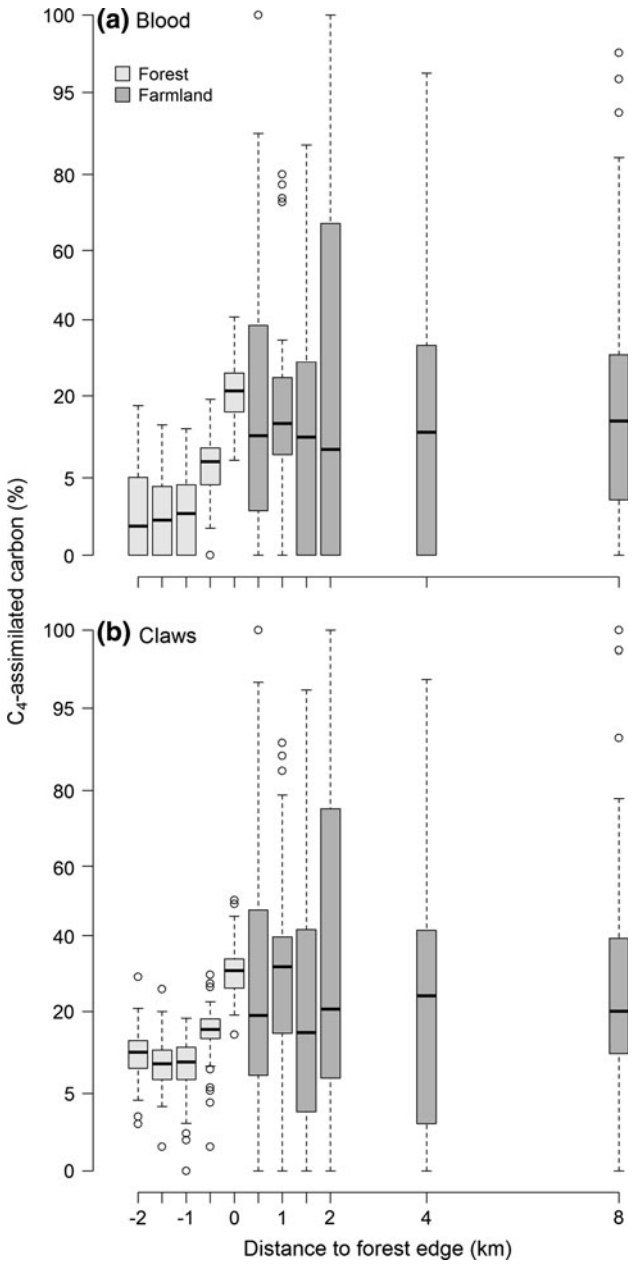

Fig. 3 Proportion of C_4 carbon in blood (**a**) and claw samples (**b**) of birds at five forest and six farmland sites; note that the *y*-axis is arcsin square root transformed. The *horizontal lines* show the median percentage of C_4 carbon of all individuals per plot, the *upper hinge* is the first quartile and the *lower hinge* the third quartile; the *whiskers* are either the maximum value or 1.5 times the interquartile range, whichever is the smaller. Calculation of $\%C_4$ is based on average discrimination factors; variation among bird species could thus be slightly underestimated

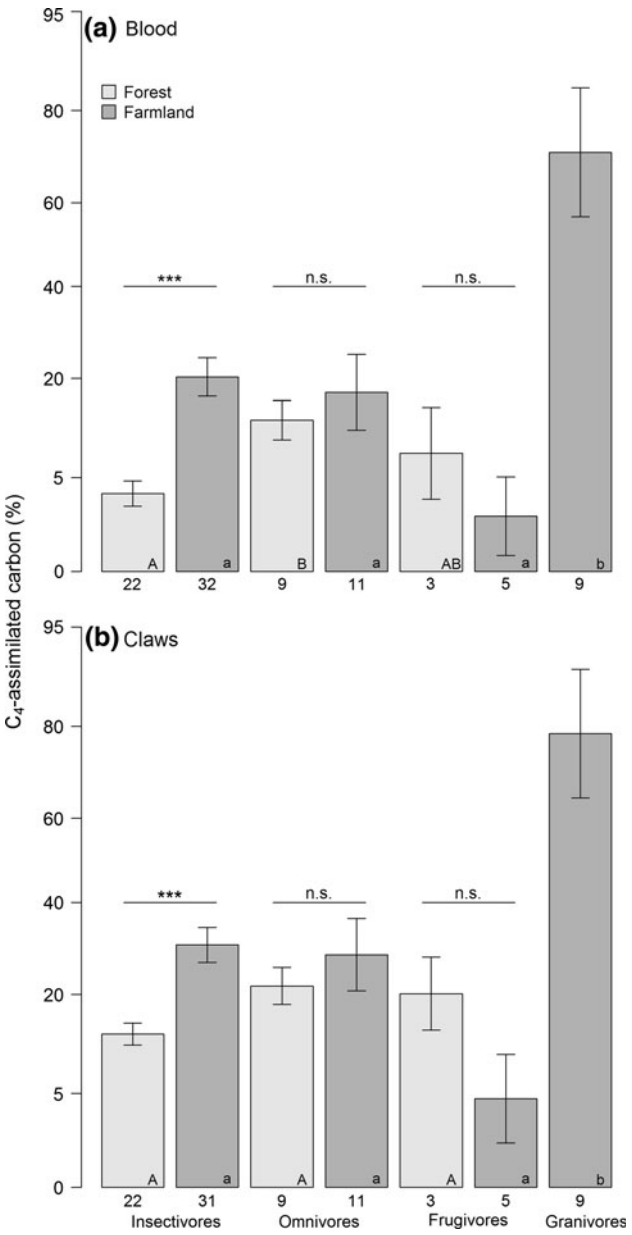

Fig. 4 Mean proportion of C_4 carbon in blood (**a**) and claw samples (**b**) of species of different feeding guilds in forest and farmland (±SE); note that the *y*-axis is arcsin square root transformed. Significant differences within feeding guilds between habitats are indicated by *asterisks* (ANOVA: $P \leq 0.05$). Differences between feeding guilds were tested separately for each habitat, as indicated by *lower case* (farmland) and *upper case letters* (forest). *Different letters* indicate that feeding guilds differ significantly from each other (Tukey's honest significant difference: $P \leq 0.05$). *Numbers below bars* indicate the number of species in each guild; no granivores were sampled in the forest. Calculation of $\%C_4$ is based on average discrimination factors; variation among bird species could thus be slightly underestimated

Differences between feeding guilds in the forest were more pronounced for blood than for claw samples.

Feeding guilds in the farmland strongly differed in the proportion of C_4 carbon in samples of blood (ANOVA: $F_{3,53} = 11.05$, $P < 0.001$) as well as claws (ANOVA: $F_{3,52} = 11.35$, $P < 0.001$). The granivorous species in the farmland obtained a much higher proportion of their C from C_4 sources than the farmland frugivores, omnivores and insectivores (Tukey's HSD: blood and claws, all *P*-values ≤ 0.01; Fig. 4; Table 3 in ESM). Granivorous farmland

species fed mainly on seeds of C_4 plants (e.g., grey-headed sparrow, 90 ± 5 % C_4 carbon in blood samples), whereas frugivorous farmland species mainly foraged on fleshy fruits of C_3 plants (e.g., common bulbul, 3 ± 5 %). Both omnivores and insectivores spanned a wide range of C_3 and C_4 sources in the farmland, ranging from mainly C_3-feeding to mainly C_4-feeding species (Fig. 2; Table 3 in ESM).

Seasonality of foraging patterns

Both $\delta^{13}C$ ($r = 0.98$, $P < 0.001$, $n = 99$) and $\delta^{15}N$ ($r = 0.79$, $P < 0.001$, $n = 99$) were correlated between blood and claws. The amount of C_4-assimilated C of bird species did not differ between blood and claw samples (paired t-test: $t_{98} = -15.94$, $P = 1$). In contrast, the trophic levels of bird species differed strongly between the two tissues (paired t-test: $t_{98} = 28.00$, $P < 0.001$), with claw samples being, on average, 0.99 trophic levels lower than blood samples.

Birds as pest control agents

We estimated an annual invertebrate biomass production of about 17,000 kg km^{-2} in Kakamega farmland. On average 54 % of the C in our farmland invertebrate community samples originated from C_4 sources, suggesting an annual biomass production of pest invertebrates of about 9,000 kg km^{-2}. We estimated the pest control service of 20 species of insectivorous farmland birds to account for about 1,000 kg year^{-1} km^{-2} (Table 2), suggesting that the populations of these 20 species consume about 10 % of the pest invertebrate biomass per year in Kakamega farmland.

Different insectivorous farmland species contributed very differently to agricultural pest control, depending on the daily feeding rate of a species, the proportion of pest invertebrates in the diet and the abundance of the species in the study area (Table 2). The pest control services per species did not differ from a log-normal distribution (Shapiro Wilk's normality test: $W = 0.98$, $P = 0.937$, $n = 20$), indicating that only a few species provided a large proportion of the overall contribution to pest control. The most effective pest control species, the northern black flycatcher, accounted for about 35 % of the overall pest control service; this was more than the collective contribution of the 16 species with the lowest impact (Table 2).

Discussion

Feeding guilds and trophic levels

Trophic levels derived from SIA reflected literature-based feeding guilds. However, except for the trophic separation of granivorous birds, differences in trophic levels between feeding guilds were not significant. This suggests dietary overlap among feeding guilds, which could be due to seasonal fluctuations in food resources in Kakamega. Fruit abundance in Kakamega Forest is high between October and March (R. K. Mulwa, K. Böhning-Gaese, M. Schleuning, unpublished data). During this time of the year, some insectivorous species might have supplemented their diet with fruits. This is consistent with findings from previous work showing that insectivorous species occasionally feed on fruits in the forest understory (Schleuning et al. 2011). In turn, frugivores might also have supplemented their diet with invertebrates, especially in the period from January to March, when invertebrate abundance peaks in Kakamega. Seasonal shifts in the birds' diets are thus a likely explanation for why differences in trophic levels were so weak. The differences in trophic levels between feeding guilds could also be blurred by the fact that N in avian blood and claws is mostly routed from dietary protein (Herrera et al. 2006), which is mostly derived from invertebrate and not from fruit resources. Therefore, the estimation of trophic levels could overestimate the invertebrate portion of the diet. We based our feeding guild classification only on the birds' major food items and did not include supplementary food items (Kissling et al. 2007). Thereby, we deliberately did not consider seasonal dietary fluctuations within feeding guilds.

C sources of forest and farmland birds

In line with our hypothesis, the two bird communities in forest and farmland strongly differed in their sources of C. In the forest, many birds relied almost exclusively on C from C_3 sources (e.g., green hylia; Table 3 in ESM), whereas many farmland birds used a high proportion of C_4 carbon (e.g., grey-headed sparrow), probably because of the high proportion of C_4 crops cultivated there. Other studies in a tropical rain forest (Herrera et al. 2003) and a tropical dry forest (Herrera et al. 2006) also found a high dependency of forest bird communities on C_3 sources. In these studies, only some bird individuals obtained a significant contribution of C from CAM or C_4 plants, but there were no consistent differences among different forest habitats.

In Kakamega, forest and farmland habitats border one another. Nevertheless, contrary to our hypothesis, the distance to the forest edge did not affect the C sources of birds. Only at the forest edge site, some individuals of five insectivorous and two omnivorous farmland species (e.g., African blue flycatcher, African pygmy kingfisher), had foraged on C_4 sources. This indicates a strong isolation of the two bird communities and only a low level of exchange and energy flow between forest and farmland. This result is

also supported by the hardly overlapping species composition of the two communities, with only two of 101 species caught in both habitats.

Differences in C sources among feeding guilds

Corresponding to our hypothesis, C sources differed among feeding guilds. Insectivorous forest species assimilated significantly less C from C_4 sources than insectivorous farmland species, indicating a strong dietary separation between insectivorous forest and farmland communities. In contrast, omnivores and frugivores did not differ in their C sources between forest and farmland. This dietary overlap could derive from isotopically similar food resources of these feeding guilds in forest and farmland habitats and/or from occasional movements of omnivorous and frugivorous species between forest and farmland foraging habitats. While the nearly complete separation of species in the capture data suggests the former, the significant isotopic separation of forest and farmland fruits collected in this study suggests the latter. Thus, we do not rule out either possibility.

Results of other studies on tropical rainforest birds suggest that the strength of isolation between habitats depends on forest stratum and diet (e.g., Newmark 1991; Westcott and Graham 2000; Laurance et al. 2004; Burney and Brumfield 2009; Schleuning et al. 2011). These studies found a higher reluctance to cross or enter open habitats and a lower dispersal propensity in understory and insectivorous species than in canopy and frugivorous species. In contrast to our study, previous studies in Kakamega Forest actually recorded farmland species in the forest (Farwig et al. 2006, 2008; Kirika et al. 2008a, b) and forest species in the adjacent farmland (Eshiamwata et al. 2006; Berens et al. 2008; Laube et al. 2008). However, these studies used point count observations and focused mostly on frugivorous species from higher forest strata. In contrast, mist netting samples primarily understory species (Bibby et al. 2000) and the proportion of obligate frugivores is low in tropical forest understory bird communities (Laurance et al. 2004; Schleuning et al. 2011). Correspondingly, most of the species sampled in this study were insectivorous (Table 3 in ESM). Our findings are thus consistent with the notion that insectivorous forest understory birds possess narrower habitat and foraging niches than mostly frugivorous species, highlighting the importance of forest habitats for insectivorous bird species.

In contrast to insectivores, granivorous bird species can benefit from land-use intensification in tropical agro-ecosystems (Waltert et al. 2005). Consistently, we found that granivorous species assimilated significantly more C from C_4 sources than insectivorous, omnivorous and frugivorous species in the farmland. Apart from granivores, feeding guilds did not differ in their C sources in the farmland. The main reason for this overlap among feeding guilds was the strong variation of $\delta^{13}C$ values within the insectivorous (e.g., pale flycatcher 0 ± 5 % C_4 carbon in blood samples vs. African pied wagtail 59 ± 6 %) and omnivorous farmland bird communities (e.g., double-toothed barbet 0 ± 5 % vs. black-headed weaver 77 ± 2 %). The strong differences in C sources among insectivorous and omnivorous bird species could derive from a species-specific invertebrate diet and the possibility that different invertebrate species specialize on either C_3 or C_4 sources. However, in our study, we did not find differences in $\delta^{13}C$ between invertebrate communities that were sampled in hedgerows (C_3) and sugar cane fields (C_4). For a more precise test of invertebrate specialization on C sources, invertebrates need to be sampled and analyzed with a higher taxonomic resolution than in this study.

Seasonality of foraging patterns

We found that trophic levels based on claws were on average one trophic level lower than those based on blood. The absolute difference in trophic levels between claws and blood might be altered by the application of feather-specific discrimination factors to claw tissues. Because of the lack of studies providing claw-specific discrimination factors we were unable to correct for possible differences in blood- and claw-specific discrimination factors. However, trophic levels calculated from feather samples (Table 3 in ESM) were also significantly lower (on average 0.47) than those of blood (paired t-test: $t_{100} = 15.50$, $P < 0.001$). These differences in trophic levels between different tissues hint towards seasonal changes in the ratio of invertebrate to plant food in the entire bird community. Kakamega experiences seasonal changes in rainfall and accordingly in fruit and insect availability (R. K. Mulwa, K. Böhning-Gaese, M. Schleuning, unpublished data). Fruit abundance in Kakamega forest and farmland is high during the time periods over which blood and claw samples from our study integrate dietary information (i.e. January–March for blood, and September–January for claw samples). In contrast, invertebrate abundance in Kakamega peaks from January to March (i.e. during the time period integrated by blood samples). An increase in invertebrates in the diet of birds during this time of the year would thus be consistent with the high trophic levels derived from blood samples. Strong seasonal shifts between plant and invertebrate diets in response to resource availability have previously been confirmed for a temperate bird community (Carnicer et al. 2008), calling for more studies of this phenomenon also in tropical systems (see also Herrera et al. 2005).

In contrast to the seasonal fluctuations in trophic levels, we did not find changes in the sources of C between both tissues, indicating a lack of temporal variation in C sources of the birds. This suggests that the separation of forest and farmland bird communities as well as the guild-specific utilization of C sources persist across seasons. These findings clearly illustrate that understory bird species in our study area react to seasonal fluctuations in resources primarily by a switch in dietary composition rather than by changing their foraging grounds.

Birds as pest control agents

Our results suggest an opposite role of different feeding guilds as pests or pest control agents. Granivorous species are generally considered to increase crop damage (Basili and Temple 1999), which is supported by the significantly higher utilization of C_4 carbon in blood and claw samples of granivores in our study. In contrast, insectivorous birds are generally considered to be pest control agents in agricultural systems (Philpott et al. 2001). This is corroborated by the increase in C_4 carbon uptake in farmland insectivores compared to forest insectivores.

In line with our hypothesis, many insectivorous farmland bird species obtained a considerable proportion of their C from C_4 sources (e.g., African pied wagtail: 67 ± 5 % C_4 carbon in claw samples). According to our estimations, insectivorous birds consumed about 10 % of the pest invertebrates in Kakamega farmland per year and thus may play an important role as pest control agents. This estimation is conservative and may underestimate the true service, because we did not have independent abundance data for all insectivorous bird species and did not include omnivorous species that also feed on pest invertebrates.

The contribution to agricultural pest control strongly differed among species and depended not only on feeding preferences, but also on feeding rates and abundances (Table 2). The multiplicative effects of these factors resulted in a lognormal distribution of species' contributions to the overall pest control service with a dominance of a few species. The northern black flycatcher turned out to be a key species for agricultural pest control in our study area, providing about 35 % of the service of the whole community (Table 2). The lognormal distribution of species' contributions to agricultural pest control is consistent with species' contributions to other ecosystem services like seed dispersal or pollination (Bascompte et al. 2003; Vázquez et al. 2009).

In tropical farmlands, bird species richness and abundance are much higher in three-dimensionally structured habitats such as hedgerows than in agricultural fields (Laube et al. 2008), suggesting that insectivorous farmland birds forage mostly in structurally rich microhabitats. Interestingly, the invertebrates that were caught on C_3 plants in hedgerows carried a similarly high $\delta^{13}C$ signal to invertebrates caught in fields of sugar cane. This strongly suggests that invertebrates regularly move between different habitat structures in the farmland. Thus, even if insectivorous birds in the farmland probably forage mostly in hedgerows and not in agricultural fields (Laube et al. 2008) they still contribute to agricultural pest control. Former studies have typically used exclosure experiments to measure avian pest control which does not record the consumption of pest insects on other plant individuals and species (Kremen et al. 2007). The morphological analysis of avian gut or stomach samples may control for this bias, but is hindered by the differential digestion of prey items (Gámez-Virués et al. 2007), although molecular-based methods can partly overcome this constraint (O'Rorke et al. 2012). SIA can correct for both disadvantages and, as exemplified by our study, may be a useful tool for future studies on agricultural pest control.

Conclusion

We conclude that understory bird communities in tropical forests hardly utilize farmland food resources, even in farmland habitats in close proximity to their forest habitats. Differences in C sources among avian feeding guilds, however, show guild-specific responses to land-use change: insectivorous forest birds are negatively affected by land-use intensification, while granivorous farmland species can benefit from such changes. Thus, despite their high bird diversity, tropical farmlands do not provide foraging niches for insectivorous forest understory birds. The insectivorous farmland bird community, however, comprises several key species that provide a quantitatively important contribution to agricultural pest control.

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