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Using stable isotopes to measure the dietary responses of Costa Rican forest birds to agricultural countryside

Çağan H. Şekercioğlu[1,2,3,4]*, Melissa J. Fullwood[5], Thure E. Cerling[1,6], Federico Oviedo Brenes[7], Gretchen C. Daily[2], Paul R. Ehrlich[2], Page Chamberlain[8] and Seth D. Newsome[9]

[1]School of Biological Sciences, University of Utah, Salt Lake City, UT, United States, [2]Center for Conservation Biology, Department of Biology, Stanford University, Stanford, CA, United States, [3]Department of Molecular Biology and Genetics, Koç University, Sarıyer, Istanbul, Türkiye, [4]KuzeyDoğa Society, Kars, Türkiye, [5]Cancer Science Institute of Singapore, National University of Singapore, Singapore, Singapore, [6]Department of Geology, Geophysics College of Mines and Earth Sciences, University of Utah, Salt Lake City, UT, United States, [7]300m Norte de la Escuela de Buena Vista, Barva, Heredia, Costa Rica, [8]Department of Geological Sciences, Doerr School of Sustainability, Stanford University, Stanford, CA, United States, [9]Department of Biology, University of New Mexico, Albuquerque, NM, United States

How human modification of native habitats changes the feeding patterns and nutritional ecology of tropical birds is critical to conserving avian biodiversity, but tropical bird diets are laborious to investigate using the traditional methods of diet analysis. Stable isotope analysis provides a cost-effective and efficient proxy to identify general foraging patterns, especially when dietary shifts spanning multiple trophic levels have occurred due to ecosystem disturbance or transformation. To characterize the diets of forest bird species that persist in tropical agricultural countryside, we compared feather carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values of four species caught and radio-tracked in a 270 hectare forest reserve, smaller forest remnants (including mature forest, secondary forest, and riparian strips), and coffee plantations in mid-elevation (*ca.* 800–1,400m) southern Costa Rica. Bird habitat choice had a significant effect on diet composition as revealed by δ^{13}C and δ^{15}N values. Three of the four species studied showed evidence of significantly reduced consumption of invertebrates in coffee plantations, with the isotope values of two species (*Tangara icterocephala* and *Mionectes oleaginous*) indicating, by comparison, nearly a doubling of invertebrate consumption in forest remnants. Our results suggest that coffee plantations are deficient in invertebrates preferred by forest generalist birds that forage in both native forest remnants and coffee plantations. In this region, typical of mountainous American tropics, small forest remnants and a larger forest reserve provide critical dietary resources for native forest birds that utilize the agricultural countryside.

Introduction

Forests worldwide are being reduced to biologically-impoverished remnants (Laurance and Bierregaard, 1997) embedded in agricultural countryside (Daily et al., 2001; Şekercioğlu et al., 2019) – croplands, pasture, gardens, open second growth, and a scattering of forest fragments, riparian strips, and remnant trees. Even though human-dominated areas are the preferred

habitat of fewer than 1% of the world's ~ 11,000 avian species (Şekercioğlu et al., 2004), about a third make some use of such habitats (Şekercioğlu et al., 2007), including many temperate-tropical migratory birds (Blount et al., 2021) that are increasingly threatened with extinction (Horns and Şekercioğlu, 2018). Tropical agricultural countryside can even favor generalist species by providing them with additional food resources (Clough et al., 2011; Fahrig et al., 2011). Given the high rate of tropical deforestation, the extent and ecological qualities of deforested countryside will determine whether some forest species can persist in the absence of large, intact forest patches.

Nitrogen is an essential component of protein synthesis but is found in limited quantities in most ecosystems (White, 1993). Compared to tropical fruits, which average ~ 5% dry mass as protein (Bosque and Pacheco, 2000), invertebrates have substantially higher protein content (~60% of dry mass; Bell, 1990) and are key sources of nitrogen for most tropical bird species.

A limitation of protein-rich food sources could have large-scale effects on avian communities because the relative level of protein intake has important impacts on bird growth and reproduction (Izhaki, 1998; Gill et al., 2019). Proteins are critical in many cellular processes, and the growth, development and consequently the fitness of organisms may be limited by a deficiency of nitrogen in their dietary resources. The underappreciated research frameworks of ecological stoichiometry and ionomics address how such changes in the environmental nutritional supply affect the ecophysiology, behavior, health, and fitness of individuals, influencing their ecological interactions, population functioning and conservation biology (Kaspari, 2021; Filipiak and Filipiak, 2022).

Stoichiometric mismatch between metabolic demands and nutritional supply can be especially critical for juveniles (Filipiak and Filipiak, 2022). For example, even for bird species that predominantly eat fruits as adults, invertebrates are preferentially caught by adults and fed to offspring during critical periods of growth and development (Izhaki, 1998), enabling chicks to rapidly fledge in an environment full of nest predators, with some exceptions in granivorous birds (Díaz, 1996). Some tropical forest birds time their breeding with increased insect availability (Hau et al., 2000). Declines in protein sources can thus lead to reduced growth rates, increased chick mortality, declines in population recruitment, and other limitations on the growth rate and overall size of a bird population.

We used stable isotope analysis (SIA) to test the hypothesis that the breeding season diets of native forest birds that continue to persist in and adjacent to coffee plantations in southern Costa Rica are deficient in nitrogen (protein) in coffee plantations when compared to their diets in native forest remnants. Because birds have higher energy and protein needs during reproduction (Klasing, 1998) and songbirds tend to consume more arthropods during this period (Izhaki, 1998), we conducted our study to coincide with the main breeding season of our study species between March and June. By examining the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of feathers ($n = 170$) collected from four resident bird species, we tested the hypothesis that individual birds foraging in southern Costa Rican human-modified habitats dominated by coffee plantations consume fewer invertebrates in comparison to individuals of the same species foraging in native forest vegetation. We also collected and analyzed samples of common sources of food (fruits and invertebrates) consumed by our focal bird species (Şekercioğlu et al., 2007). We sampled birds and dietary items from two primary habitats,

partially shaded coffee plantations and forest remnants that include primary forest, secondary forest, and riparian strips; hereafter referred to as "coffee" and "non-coffee" habitats, respectively. We also used radiotelemetry data to assess the overall habitat use of each individual bird and to understand the level of use of coffee versus non-coffee habitats. A total of 49 individuals from three species were intensively radio-tracked and their habitat use patterns were documented in detail (Şekercioğlu et al., 2007), which allowed for a unique coupling of isotopically derived dietary information with information on individual movement patterns.

Based on *a priori* knowledge of the birds' habitat and dietary preferences, we hypothesized that there would be significant isotopic differences among bird species related to their degree of insectivory, which would mirror those recorded from field observations (Şekercioğlu et al., 2007). Coffee plantations in our study area have depauperate invertebrate communities (Goehring et al., 2002; Ricketts et al., 2002), so we also predicted that birds that spend a greater amount of time in these areas should consume fewer invertebrates than do the birds spending more time in forest remnants. The unique coupling of extensive radio-tracking data with isotopically derived dietary information on resource use and assimilation provides a rare perspective on the potential effects of landscape modification on the nutrient uptake of a tropical bird community. This is one of the few ornithological studies that combines radio tracking and SIA to address a critical conservation issue for tropical avian species.
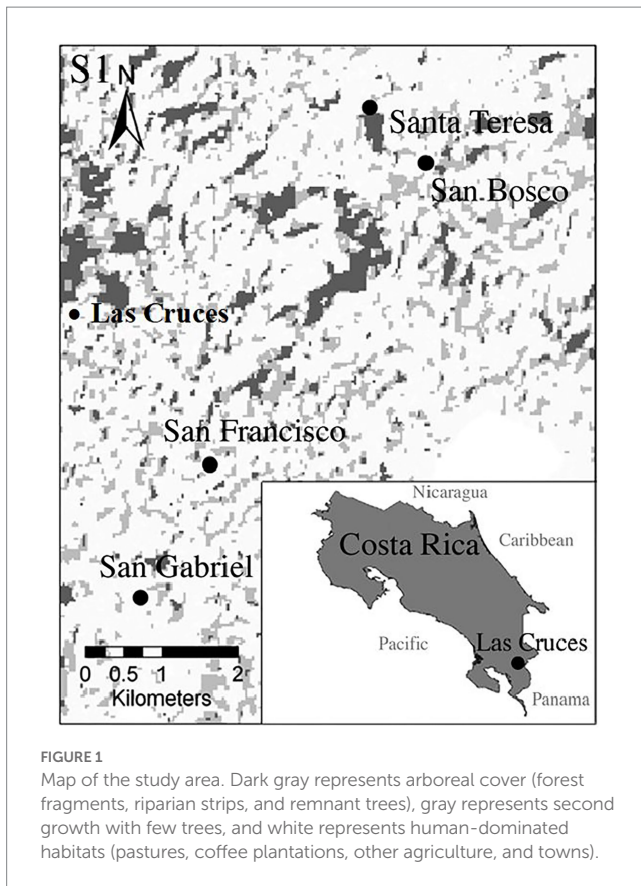
Materials and methods

Study site

Our study area in southern Costa Rica (Figure 1), near the Las Cruces Biological Station, is a formerly forested region now dominated by coffee plantations (~50% of land cover), cattle pastures (~20%), and other human-modified environments (~10%). In these agricultural areas, large quantities of chemicals in the form of fungicides, pesticides, and fertilizers are applied on coffee plantations, and the regulations restricting the use of pesticides are not adequately enforced (Stiles and Skutch, 1989). Thus, the conversion of forests to agricultural countryside may not only reduce the abundance of invertebrates *via* decreases in vegetation structure and botanical diversity, but the elimination of invertebrates with pesticides can lead to the poisoning of birds and other non-target species while directly decreasing the amount of protein available to the resident bird species. Previous studies at our study site found significant decreases in the numbers of invertebrates such as Blatteria, Coleoptera, Diptera, Lepidoptera, and Orthoptera in coffee plantations in comparison to the forest remnants (Goehring et al., 2002; Ricketts et al., 2002). These insect orders are major components of local bird diets (Şekercioğlu, 2002) and such reductions could result in nitrogen limitation for birds that spend a considerable amount of their time foraging in coffee plantations.

Study species

Catharus aurantiirostris (Orange-billed Nightingale-thrush, hereafter *Catharus*) is a species with low forest dependence and

FIGURE 1
Map of the study area. Dark gray represents arboreal cover (forest fragments, riparian strips, and remnant trees), gray represents second growth with few trees, and white represents human-dominated habitats (pastures, coffee plantations, other agriculture, and towns).

prefers forest edge, second growth, thickets, plantations, and gardens (Stiles and Skutch, 1989). *Tangara icterocephala* (Silver-throated Tanager, hereafter *Tangara*) has intermediate forest dependence and is a common species of forest canopy, forest edge and agricultural habitats in the study area. *Tangara* was the most common seed disperser visiting *Miconia* trees (a major food source analyzed in this study) isolated in the pastures surrounding the intact Las Cruces forest (Luck and Daily, 2003). *Turdus assimilis* (White-throated Thrush, hereafter *Turdus*) is most often found in moist forests, but also enters bordering thickets, riparian corridors, second growth and isolated fruiting trees, especially outside the breeding season (Stiles and Skutch, 1989). Finally, *Mionectes oleaginous* (Ochre-bellied Flycatcher, hereafter *Mionectes*) is most often found in the lower levels of humid forest, secondary growth, and clearings (Stiles and Skutch, 1989). *Mionectes* was the only species that was not radio-tracked. All four species are regularly found in forest and open countryside, feed on fruits and invertebrates, and are likely to be important dispersers of forest plants into non-forested areas. *Catharus* is mostly insectivorous, whereas the others are mostly frugivorous (Stiles and Skutch, 1989; Şekercioğlu et al., 2007).

We analyzed a subset of feathers from 170 individuals of these four bird species (Table 1). The feathers were part of a collection of contour and tail feathers from over 6,000 individuals of 211 Costa Rican bird species obtained during a long-term bird banding and radio telemetry study centered around the Las Cruces Biological Station in the Coto Brus canton of southern Costa Rica (Şekercioğlu et al., 2002, 2007, 2015, 2019).

Radio tracking

For three of these four species, we collected extensive radiotelemetry data on 49 individuals (Şekercioğlu et al., 2007). We used radiotelemetry data to assess the habitat use of each individual bird, especially the use of forest habitats (the mostly intact primary forest of the Las Cruces Forest Reserve, small forest remnants, and riparian strips) versus agricultural habitats (mostly coffee plantations). Various studies have shown that radio tags have minimal to no impact on bird physiology and behavior (Kenward, 2001; Wells et al., 2003), and the radio tags in this study had no observable effects on our study species (Şekercioğlu et al., 2007).

From the average radio-tracked individual, we collected ≥55 Global Positioning System (GPS) points during more than 45 h of radio-tracking distributed across 11 days. To assess the level of confidence we could place on bird capture locations for understanding habitat use, we analyzed the fit between 97 capture site data points, each of which describes the location where an individual bird was caught, and each bird's radio tracking locations, which give detailed information on habitat use by the same individual bird. For each bird, we calculated the ratio of the number of telemetry data points collected in coffee plantations to all telemetry data points. To assess whether the capture location of the bird could predict the habitat where the bird spent most of its time according to radiotelemetry, the vegetation cover of the study area was classified as "coffee" versus "non-coffee," each of which had ~50% cover based on extensive vegetation surveys (Şekercioğlu et al., 2007).

If an individual bird spent more than 50% of its time in coffee plantations, we interpreted it as a preference for that habitat type and vice versa for non-coffee areas. We divided the number of times capture data and radio-tracking data assigned an individual to the same habitat (coffee or non-coffee) by the total number of radio-tracked birds. A *z*-test was performed to see if this was significantly different than the 50% value that would be expected by chance alone. We expected the fit between the capture locations and the corresponding telemetry data points to be better than that expected by chance alone. As the coffee and non-coffee areas each represent ~50% of the study site, the expected agreement rate due to chance alone was ~50%.

For the purposes of the isotope mixing models and statistical analyses, percent agricultural use was calculated for each bird by dividing the number of telemetry points from agricultural habitats by the total number of telemetry points. An index value of 34% or less was arbitrarily taken to indicate light use of agricultural countryside, between 34 and 67% moderate use, and above 67%, heavy use. For birds that were not radio-tracked, capture data was used instead, and 0% was assigned to a bird captured in a non-coffee site, while 100% was assigned to a bird captured in a coffee site. We also calculated the percent of each bird's home range that was covered by trees and used linear regression to analyze the relationship between percent tree cover and the isotopic composition of each bird's feathers.

We assumed that the location of each bird during the time of feather formation (and reflected in its isotopic signatures) corresponds to the location in which the bird was caught or to the locations in which the bird spent most of its time as revealed by radio tracking studies. In addition, we assumed that a bird's diet during the period of feather formation is representative of its typical diet. This might not

be true because feather formation requires high amounts of protein and thus, during this time, birds may be preferentially consuming more protein (Earle and Clarke, 1991; Wolf et al., 2003). Nevertheless, even if an individual does modify its foraging behavior to consume more protein during the molting/re-growth period, a bird impoverished in protein post-formation was likely even more nutrient impoverished during feather formation.

Stable isotopes as avian dietary proxies

SIA has yielded important insights into the life history, ecology, migration, and evolution of birds (Hobson and Clark, 1992; Chamberlain et al., 1997; Hobson, 1999a; Rubenstein et al., 2002; Smith et al., 2002; Hobson and Bairlein, 2003; Pain et al., 2004). Specifically, carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analyses of bird tissues have been used to investigate trophic relationships (Hobson, 1999b; Kelly, 2000; Herrera et al., 2003) and to characterize avian diet composition (Mizutani et al., 1990; Thompson et al., 1995; Thompson and Furness, 1995; Bearhop et al., 1999; Hocking and Reimchen, 2002). The use of SIA to analyze diet has several advantages. Traditionally, the examination of regurgitates, feces, and pellets, and other laborious means have been necessary to study avian diets (Rosenberg and Cooper, 1990; Şekercioğlu et al., 2002). These techniques provide a snapshot of dietary information and typically represent food ingested over a few days prior to capture. These techniques are also highly invasive, may create intolerable levels of stress for study subjects, and can even lead to mortality (Poulin et al., 1994). Isotopic analysis of feathers, easily collected during any study that involves mist netting (Smith et al., 2002), removes the need for the laborious and invasive processes involved in obtaining regurgitates and feces, and provides direct insights into the diet of an individual bird recorded in its feathers during the period of feather growth (Mizutani et al., 1990).

Finally, quantitative estimates of dietary sources can sometimes be made with SIA by applying trophic discrimination factors to consumer tissue isotope values to account for isotopic sorting during metabolic and biosynthetic processes, and then using mixing models designed to calculate the relative proportion of dietary sources in consumer diets (Phillips and Koch, 2002; Phillips and Gregg, 2003; Parnell, 2019). In most cases, consumers are enriched in the rare heavy isotope (^{13}C or ^{15}N) relative to their diets by ~1–2‰ for δ^{13}C and 3–5‰ for δ^{15}N for each increase in trophic level (Kelly, 2000; Caut et al., 2009).

Fruit and invertebrate samples

We conducted SIA of commonly consumed fruit and invertebrate samples from the sites where the birds were captured. We sampled the fruits of *Miconia trinervia* (family Melastomataceae; hereafter *Miconia*), a regular food resource of all the study species and a plant that is commonly found in natural and human-dominated habitats in the study area. We also collected the fruits of *Cecropia* spp. (family Cecropiaceae; hereafter *Cecropia*), also fruits commonly consumed by our study species. For invertebrates, we sampled predaceous arachnids (spiders) and grazing Orthoptera (grasshoppers), which represent two trophic levels and are two of the four invertebrate groups (others

include Coleoptera and Formicidae) that are most frequently encountered in the diet samples of birds from our study area we collected *via* regurgitation (Şekercioğlu et al., 2002). We collected and analyzed 4–25 samples of each dietary item from coffee and non-coffee areas to compare the isotopic differences between these treatments.

Stable isotope analyses

Bird tail feathers were prepared for isotope analysis by washing in a 2:1 chloroform/methanol mixture to remove surface contaminants, followed by drying for at least 8 h in a fume hood to remove solvents (Kelly, 2000). Fruits and invertebrates were freeze-dried and homogenized using a mortar and pestle. Dried samples of feathers (0.5 mg) and potential food items (invertebrates: ~0.5 mg; fruits: ~5.0 mg) were sealed in tin capsules, and δ^{13}C or δ^{15}N values were measured using a Costech elemental analyzer interfaced with a Finnegan Delta Plus gas source mass spectrometer in the Department of Geological and Environmental Sciences at Stanford University (Palo Alto, CA). Results are expressed as δ values, δ^{13}C or $\delta^{15}N = 1,000$ $[(R_{sample}/R_{standard}) - 1]$, where R_{sample} and $R_{standard}$ are the ^{13}C/^{12}C or ^{15}N/^{14}N ratios of the sample and standard, respectively; units are expressed as parts per thousand or per mil (‰). The standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. Repeated within-run measurements of a gelatin standard yielded an average standard deviation of <0.2‰ for both δ^{13}C and δ^{15}N values. Duplicate isotopic measurements were performed on ~20% of all unknown samples and yielded an absolute difference of 0.2‰ for both δ^{13}C and δ^{15}N values. We also measured the weight percent carbon and nitrogen concentrations of all samples, which are presented as nitrogen concentrations and C/N ratios in Table 1.

An analysis of variance (ANOVA) with a Tukey-HSD *post hoc* comparison test was used to test for significance among groups (bird species or prey types), which was assessed at an α-value of 0.05. In addition, we used a Bayesian concentration-dependent mixing model, Stable Isotope Mixing Models in R (simmr; Parnell, 2019), to estimate the relative contribution of four prey types to the diet of each bird species. Based on the results of a controlled feeding experiment on an omnivorous passerine (Pearson et al., 2003), we varied δ^{13}C and δ^{15}N trophic discrimination factors (TDF) among prey types to account for the differences in assimilation due to prey protein (nitrogen) content. For δ^{13}C, we applied mean (±SD) TDFs of 3.0 ± 0.5‰ for invertebrates (spiders and grasshoppers) and 2.0 ± 0.5‰ for fruits (Cecropia and Miconia). For δ^{15}N, we applied mean (±SD) TDFs of 3.5 ± 0.5‰ for invertebrates (spiders and grasshoppers) and 3.0 ± 0.5‰ for fruits (Cecropia and Miconia). The model also included elemental concentration data and we used mean weight percent [C] and [N] for each prey type reported in Table 1. Gelman diagnostics for all model runs produced values of one, indicating model convergence. We used a two-tailed t-test to assess the significant differences in prey contributions between habitats within species, and significance was assessed using an α-value of 0.05. The dietary percentages presented in Table 2 represent the mean source contributions (SD in parentheses) of all individuals within a species versus habitat type based on telemetry data or capture location (coffee versus non-coffee).

TABLE 1 Mean (±SD) δ^{13}C and δ^{15}N values and the sample sizes of tail feathers of four bird species and potential food sources collected in coffee and non-coffee habitats.

Species/prey type	Coffee					Non-coffee					Forest dependence
	n	δ^{13}C	δ^{15}N	[N]	C/N	n	δ^{13}C	δ^{15}N	[N]	C/N	
Catharus aurantiirostris	28	−23.9 ± 1.5	8.3 ± 1.3	–	–	35	−24.1 ± 0.8	7.8 ± 1.0	–	–	Low
Turdus assimilis	5	−23.5 ± 0.5	6.7 ± 0.7	–	–	33	−24.4 ± 0.7	6.6 ± 1.1	–	–	High
Tangara icterocephala	15	−23.7 ± 0.8	5.6 ± 1.1	–	–	19	−24.0 ± 0.4	4.5 ± 1.2	–	–	Medium
Mionectes oleaginous	5	−23.3 ± 0.5	7.8 ± 1.4	–	–	31	−23.0 ± 1.4	6.6 ± 1.4	–	–	Medium
Spiders	7	−23.1 ± 1.7	8.9 ± 1.6	12.6 ± 0.4	3.9 ± 0.3	9	−24.8 ± 0.6	5.8 ± 1.1	11.6 ± 1.1	4.2 ± 0.4	–
Grasshoppers	20	−26.3 ± 2.8	3.9 ± 2.8	11.1 ± 1.4	4.2 ± 0.2	22	−26.5 ± 2.6	4.1 ± 1.5	10.7 ± 0.5	4.3 ± 0.4	–
Miconia Fruits	4	−27.0 ± 0.7	1.3 ± 1.7	1.9 ± 0.3	23.3 ± 4.7	33	−28.2 ± 1.4	0.5 ± 1.0	1.9 ± 0.3	24.7 ± 4.5	–
Cecropia Fruits	8	−26.7 ± 1.3	4.2 ± 0.9	1.9 ± 0.4	25.0 ± 4.6	10	−26.9 ± 0.9	4.4 ± 1.6	2.0 ± 0.3	23.4 ± 3.6	–

Mean (±SD) weight percent nitrogen [N] concentration and [C]/[N] ratios are also provided for potential food sources. Estimates of forest dependence are from Şekercioğlu et al. (2007, 2019).

TABLE 2 Mean (±SD) contributions of potential prey to the diets of four bird species collected in coffee and non-coffee habitats.

Species	Habitat	Spiders	Grasshoppers	*Miconia*	*Cecropia*
Catharus	Coffee (*28*)	11.5 ± 3.2***	17.7 ± 8.0	35.3 ± 20.1*	35.6 ± 21.8
	Non-coffee (*35*)	25.8 ± 5.8	19.2 ± 5.4	24.7 ± 12.2	30.4 ± 17.0
Turdus	Coffee (*5*)	9.8 ± 6.5	20.5 ± 13.5	42.4 ± 21.6*	27.3 ± 19.5
	Non-coffee (*33*)	8.4 ± 3.9	21.8 ± 5.2	28.1 ± 11.1	41.8 ± 15.4
Tangara	Coffee (*15*)	3.1 ± 2.1***	12.7 ± 10.6	70.8 ± 18.5***	13.3 ± 12.2***
	Non-coffee (*19*)	22.9 ± 11.3	15.9 ± 9.0	28.5 ± 20.8	32.7 ± 15.3
Mionectes	Coffee (*5*)	16.1 ± 7.6*	23.2 ± 12.8***	33.3 ± 18.0***	27.4 ± 18.0
	Non-coffee (*31*)	22.8 ± 6.0	52.6 ± 7.8	11.5 ± 7.0	13.1 ± 8.3

The numbers in italics next to the habitat designations denote the number of individuals captured in each habitat. Results of two-tailed t-tests of prey contributions between habitats within species are indicated by superscripts; $p < 0.001$***, $p < 0.01$**, $p < 0.05$*.

Results

Habitat use

The agreement between 97 capture site data points and telemetry data points was 68%. This was significantly higher ($z = 3.70$; $p = 0.0002$) than would be expected based on chance alone, meaning that the capture location was a good predictor of the habitat use of an individual bird over time. Hence, capture location data were used in data analyses for birds that were not radio-tracked. We also calculated the average percent (±SD) agricultural use of radio-tracked birds to determine the extent of use of agricultural countryside. Percent agricultural use was 14% (±5.9%) for Mionectes, 22% (±5.0%) for Turdus, 33% (±4.9%) for Catharus, and 34% (±6.9%) for Tangara, indicating that these species made relatively low use of the agricultural countryside. Percent agricultural use for Mionectes was calculated using only the capture locations since this species was not radio-tracked.
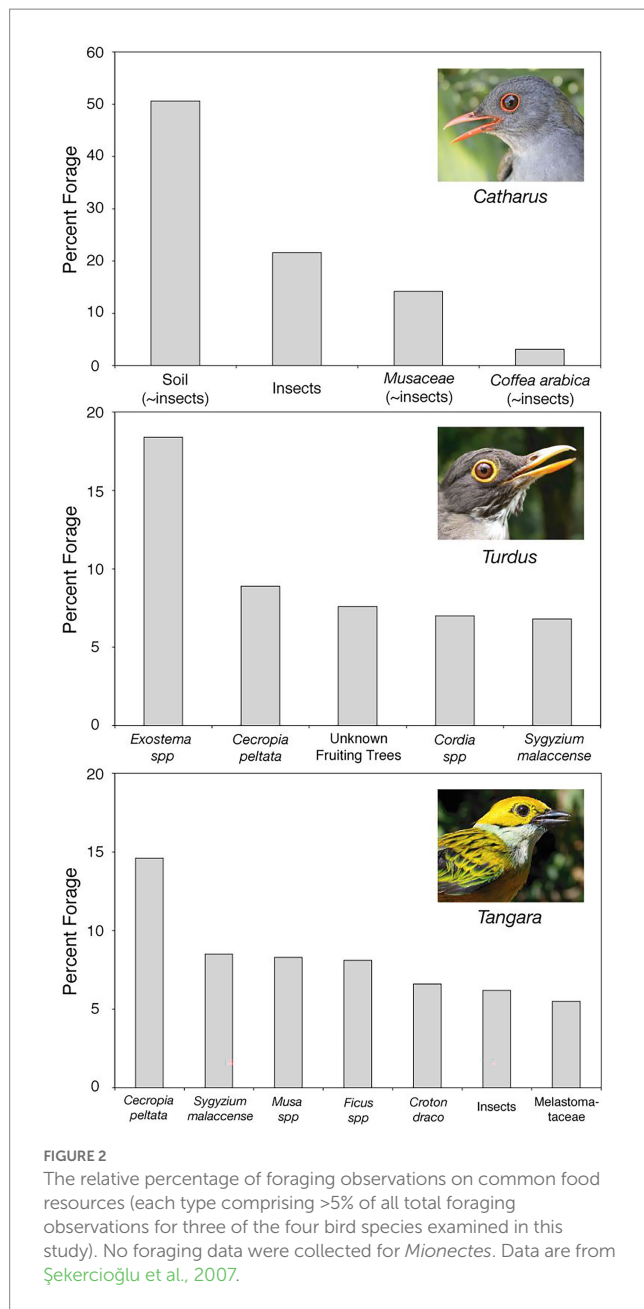
Foraging observations

Each species differed from the other two in its resource use (Figure 2), based on the proportion of foraging observations on the resources that each species was observed to exploit (all $\chi^2 > 120$; all $p < 0.001$; Figure 2). *Catharus* (Figure 2), although observed to forage on 14 plant taxa, foraged predominantly on invertebrates, either directly or on substrates (i.e., soil, rotting fruit) where invertebrates are commonly found. *Turdus* (Figure 2) and *Tangara* (Figure 2) were more frugivorous and foraged on 71 and 45 plant taxa, respectively. Fruits of *Cecropia peltata*, *Ficus* spp., and *Syzygium malacanse* were favorite dietary items for both species.

Isotopic composition of dietary sources

There were significant differences between δ^{15}N values, δ^{13}C values, and weight percent carbon:nitrogen (C/N) concentrations among potential food sources (Tukey HSD, $p < 0.01$; Table 1; Figure 3). Spiders collected within coffee habitats had significantly higher δ^{15}N values than any other food source (Figure 3). Miconia fruits collected in non-coffee habitats had significantly lower δ^{15}N values than any other food source. δ^{15}N and δ^{13}C values of Cecropia fruits were not statistically distinguishable from those of grasshoppers in either habitat. For both habitats, spiders had significantly higher values than did grasshoppers, but only grasshoppers collected in non-coffee habitats had significantly higher δ^{15}N values than non-coffee Miconia

FIGURE 2
The relative percentage of foraging observations on common food resources (each type comprising >5% of all total foraging observations for three of the four bird species examined in this study). No foraging data were collected for *Mionectes*. Data are from Şekercioğlu et al., 2007.

FIGURE 3
Mean $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values of the four bird species and common dietary resources collected in coffee versus forested non-coffee habitats. Error bars denote one standard deviation from the mean. Refer to Table 1 for the sample sizes. Lowercase letters signify results of a one-way ANOVA comparing mean values among prey types and uppercase letters signify ANOVA results for the comparisons of a single prey type between habitats.

$\delta^{15}N$) had higher $\delta^{13}C$ values in coffee versus non-coffee habitats (Figure 3B).

Grasshoppers had significantly higher variance in $\delta^{13}C$ and $\delta^{15}N$ values than any other food source type (Table 1; Figure 3). There were no differences in the concentrations of carbon [C] and nitrogen [N] between samples of particular food types collected in coffee versus non-coffee habitats (Table 1). Invertebrates (spiders and grasshoppers) had significantly higher [N] than fruits, resulting in significant differences in C/N ratios between these two general types of food (Table 1).

Isotopic composition of bird feathers

We measured the $\delta^{13}C$ and $\delta^{15}N$ values of feathers collected from 63 *Catharus*, 38 *Turdus*, 34 *Tangara*, and 36 *Mionectes* individuals (Table 1). At the species level, sex, wingspan, and body mass did not have significant effects on $\delta^{13}C$ and $\delta^{15}N$ values (ANOVA, $p > 0.05$). For intraspecific comparisons (uppercase letters, Figure 3), the location of capture had a significant effect on feather $\delta^{15}N$ values for *Catharus, Mionectes,* and *Tangara*, where individuals captured in coffee habitats had significantly higher $\delta^{15}N$ values than individuals from non-coffee habitats (Figure 3; ANOVA). For $\delta^{13}C$, intraspecific comparisons showed significant effects of habitat for only one species. *Turdus* individuals captured in coffee plantations had significantly higher $\delta^{13}C$ values than those caught in non-coffee habitats (Figure 3).

fruits. $\delta^{15}N$ values of grasshoppers were indistinguishable from $\delta^{15}N$ values of Miconia fruits in coffee plantations. Lastly, spiders collected in coffee habitat had significantly higher $\delta^{15}N$ values than spiders from non-coffee habitats.

Like $\delta^{15}N$ results, spiders collected within coffee habitats also had significantly higher $\delta^{13}C$ values than any other food source (Figure 3), with the only exception being spiders collected from non-coffee habitats. The $\delta^{13}C$ composition of grasshoppers collected in coffee or non-coffee habitats was indistinguishable from that of *Cecropia* fruits. The mean $\delta^{13}C$ value of *Cecropia* fruits from either habitat was indistinguishable from that of *Miconia* fruits. However, *Miconia* fruits collected from non-coffee habitats had significantly lower $\delta^{13}C$ values than grasshoppers from either habitat. Lastly, within-type comparisons of food sources collected in coffee versus non-coffee habitats showed no significant differences in $\delta^{13}C$ values except for spiders, which (like

FIGURE 4
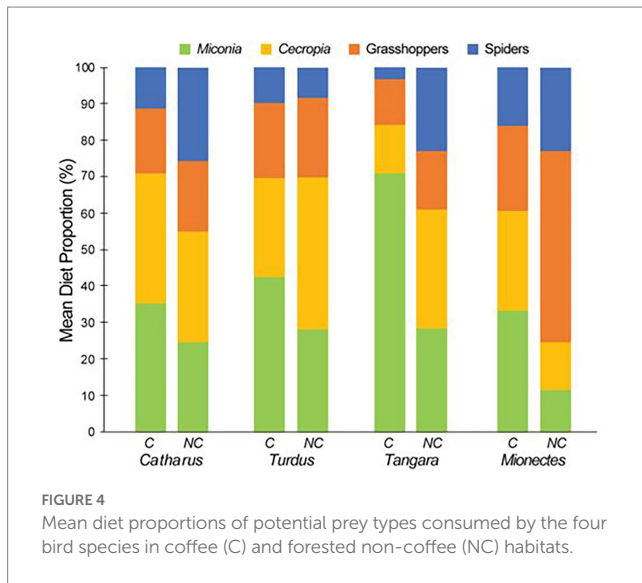Mean diet proportions of potential prey types consumed by the four bird species in coffee (C) and forested non-coffee (NC) habitats.

FIGURE 5
Effect of percent tree cover in radio-tracked birds' home ranges on the nitrogen **(A)** and carbon **(B)** isotopic composition of bird feathers. Regression statistics for the entire bird community (rather than single species) are provided because bivariate analyses of isotopic composition versus percent tree cover for each species were similar ($r^2 < 0.10$; $p > 0.05$ for both $\delta^{13}C$ and $\delta^{15}N$).
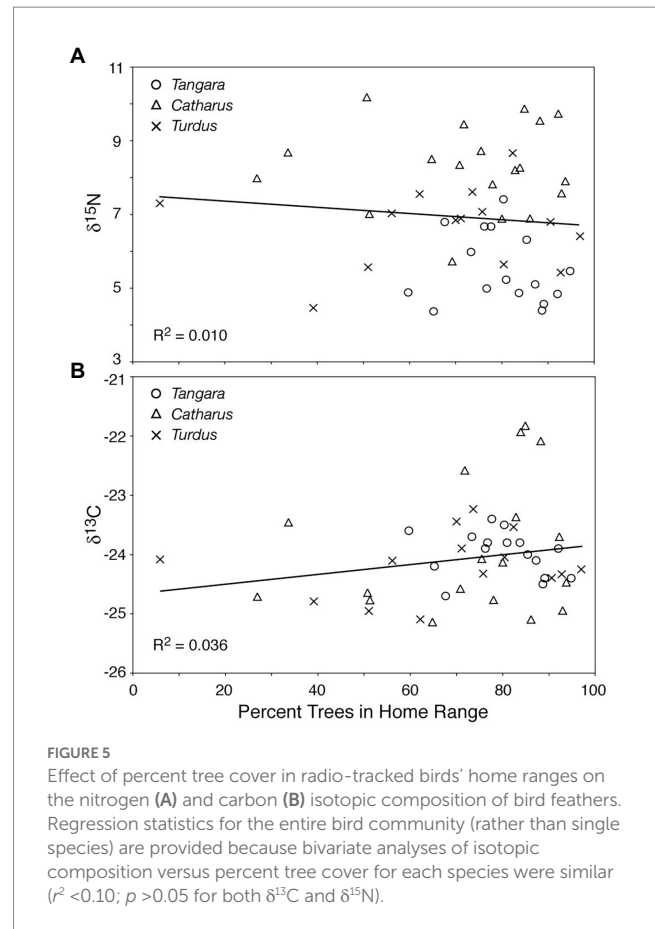
Interspecific ANOVA comparisons (lower case letters, Figure 3) show significant differences in mean $\delta^{15}N$ but not mean $\delta^{13}C$ values among species. *Catharus* and *Mionectes* have significantly higher $\delta^{15}N$ values than do *Tangara*. Furthermore, *Turdus* captured in non-coffee habitats have significantly lower $\delta^{15}N$ values than *Catharus* captured in either habitat type. Likewise, *Tangara* captured in non-coffee habitats have lower $\delta^{15}N$ values than *Turdus* caught in either habitat type.

Results of the $\delta^{13}C$ and $\delta^{15}N$ concentration-dependent mixing model are presented in Table 2. Consumption of invertebrates was higher in forested versus coffee habitats for three of the four focal bird species (Figure 4). Specifically, the mean contribution of spiders to the diets of *Catharus*, *Tangara*, and *Mionectes* was higher in forested versus coffee habitats. The mean contribution of grasshoppers to the diet of *Mionectes* was higher in forested versus coffee habitats. Conversely, the consumption of *Miconia* fruits was higher in coffee versus forested habitats for all four bird species, but the consumption of *Cecropia* fruits by *Tangara* was higher in forested versus coffee habitats. These results mostly confirm our hypotheses. All species except *Turdus* consume substantially more invertebrates in forested non-coffee habitats than they do in coffee plantations, with *Tangara* and *Mionectes* consuming nearly double the invertebrates in forest remnants than they do in coffee plantations (Figure 4). Patterns among species are similar; overall, *Mionectes* has the highest invertebrate consumption and *Turdus* and *Tangara* have the lowest (Figure 4).

Of the 170 individual birds sampled for isotopes, 19 *Catharus*, 16 *Tangara*, and 14 *Turdus* were radio-tracked. The percentage of trees in their home ranges had no significant effect ($r^2 < 0.10$; $p > 0.05$ for both isotope systems) on feather $\delta^{13}N$ (Figure 5A) or $\delta^{13}C$ values (Figure 5B) for any of the species that were radio-tracked.

Discussion

Our results indicate that three of the four bird species examined in this study fed on fewer invertebrates in coffee plantations than in forested habitats comprised mostly of forest remnants as well as riparian strips and a larger (270 ha) forest reserve. In the mosaic of habitat types in our study area, extensive coffee plantations and other human-modified habitats have a significant negative effect on the diet composition of the four frugivore-insectivore bird species we examined in this study. Individual birds that were captured in coffee plantations, or known (*via* radiotelemetry data) to spend a considerable portion of time in coffee plantations, may be able to make up for some of their resulting deficiency in invertebrates because their mobility allows them to move among coffee plantations and the surrounding forest remnants, including primary forests, small forest fragments, secondary forest, and/or riparian strips adjacent to coffee-dominated habitat. This explanation is supported by our radio-tracking data, which showed that *Tangara* and *Turdus* were highly mobile and remained in coffee plantations for relatively short periods of time in comparison to the amount of time spent in forest remnants (Şekercioğlu et al., 2007). Moreover, we were able to capture a greater number of *Tangara* and *Turdus* individuals in non-coffee habitats versus coffee plantations in comparison to *Catharus*. Of the species radio tracked, *Tangara* and *Turdus* have significantly larger home ranges than *Catharus*. Average home range estimates for *Tangara* range from ~16–22 ha and between ~30–70 ha for *Turdus* (Şekercioğlu et al., 2007), but only ~1.7–3.6 ha for *Catharus*, depending on whether minimum convex polygon versus kernel densities were used to calculate home range size. This suggests that highly mobile birds that can rapidly move between forest remnants in agricultural countryside may have greater access to nitrogen-rich foods (invertebrates), but less mobile species such as *Catharus* may be stuck between paying a high

energetic cost by constantly moving between forest remnants or getting less invertebrate protein in coffee plantations.

Catharus has relatively low forest dependence compared to most other forest birds in the region (Stiles, 1985), and its natural preference for forest gaps, edges, and second growth has resulted in its successful adaptation to coffee plantations (Şekercioğlu et al., 2007). Most other insectivorous birds in the region are more forest dependent (e.g., *Lophotriccus pileatus, Platyrinchus mystaceus, Thamnophilus bridgesi*) and generally avoid the nonforest matrix dominated by coffee plantations (Şekercioğlu, 2002; Şekercioğlu et al., 2015, 2019). Future tracking and dietary studies should focus on these species, although capturing sufficient numbers of more forest-dependent species in coffee plantations will remain a challenge.

While our isotopic results show differences in the percentages of invertebrates consumed among species, all the species examined are generalist omnivores and likely have broader dietary tolerances than do the more specialist species. In comparison to many tropical forest insectivore specialists that are particularly sensitive to habitat disturbance and fragmentation and are rarely found outside forested areas (Şekercioğlu and Sodhi, 2007; Sherry et al., 2020), the relatively mobile and omnivorous bird species we examined here are more capable of using the agricultural countryside effectively to obtain the protein they require. Nonetheless, our results show that even these more adaptable species consume substantially fewer invertebrates in coffee plantations than they do in forest remnants.

Intraspecific comparisons showed that capture habitat sometimes had a significant effect on $\delta^{15}N$ values. This effect appears to be mainly driven by the differences in spider $\delta^{15}N$ values (Figure 3) and not in the differences in the proportion of dietary items consumed in different habitats. We do not know why spiders captured in coffee plantations have significantly higher $\delta^{15}N$ values than do the spiders in non-coffee habitats. However, it is unlikely to be due to the influence of anthropogenic nitrogenous inputs (e.g., fertilizers, atmospheric deposition) in agricultural areas because other dietary items (grasshoppers, *Cecropia*, and *Miconia*) at lower trophic levels collected in coffee plantations do not have significantly higher $\delta^{15}N$ values than those collected in forested habitats. Spiders are generalist insectivores (Sanders and Platner, 2007) and could forage at multiple trophic levels, so the observed differences in mean $\delta^{15}N$ values could relate to the differences in their diet composition in coffee versus forested habitats.

Our results indicate significant differences in diet composition among species that agree with these birds' foraging preferences based on our observational evidence (Şekercioğlu et al., 2007). These results mostly confirm our hypotheses. All species except *Turdus* consume substantially more invertebrates in forested non-coffee habitats than they do in coffee plantations, with *Tangara* and *Mionectes* consuming nearly double the invertebrates in forest remnants than they do in coffee plantations (Figure 4). Patterns among species are similar; overall, *Mionectes* has the highest invertebrate consumption and *Turdus* and *Tangara* have the lowest (Figure 4).

One limitation of our study was that we were only able to analyze four food sources that likely represent a small subset of possible resources consumed by these bird species, especially in southern Costa Rica's very diverse tropical habitats. Although *Cecropia* and *Miconia* fruits are consumed by these species regularly, and spiders and grasshoppers make up two of the top four invertebrate types eaten by these species in our study area (Şekercioğlu et al., 2002), these

generalist bird species likely feed on a wide range of fruits and invertebrates in this diverse landscape mosaic. When dealing with omnivorous species inhabiting diverse ecosystems, it is sometimes difficult to isotopically characterize all potential food sources. Thus, we designed our sampling protocol to capture potential items representative of three trophic levels, including primary producers (fruits), primary consumers (grasshoppers), and secondary consumers (spiders) to specifically evaluate the relative proportion of nitrogen-rich (invertebrates) versus nitrogen-poor (fruits) resources in individual bird diets.

The second potential source of error in our analyses is associated with the precision of our habitat use classifications for individual birds that were not radio-tracked, especially in relation to the timing of feather formation in the species examined. While our statistical analysis suggests that the location of capture is a dependable indicator of individual habitat use, the high mobility of some species may bias our coffee versus non-coffee classification scheme if all individuals (within a species) are utilizing habitats in equal proportion to the average habitat use reflected in the radio-tracking data (Şekercioğlu et al., 2007). A comparison of habitat use data derived from radiotelemetry, however, suggests a considerable amount of variance in the types of habitats utilized and the home range sizes of individual birds. For instance, some *Catharus* and *Turdus* individuals spend a lot of time in agricultural areas even though average habitat use at the species level suggests low use of this habitat type in comparison to forested habitats (Figure 5). Furthermore, just how persistent individual movement patterns are over the course of feather growth remains unresolved. For individuals that were radio-tracked, each bird was followed for an average of 45 h distributed across an average of 11 days. We must consider the possibility that the temporal persistence of individual habitat preferences is shorter than the average duration of feather growth. For the four resident tropical forest bird species examined, feather molt and regrowth occur from June to September, which coincides with the wet season in southern Costa Rica. The radiotelemetry data and the dietary samples for isotopic analysis were collected during the months of March–June. If the individual habitat preferences, as recorded in the radio-tracking data, are more ephemeral than the duration of time required to regrow tail feathers during the molting period, than it is possible that the telemetric and isotopic data do not correlate in time (as seen in Figure 5).

Conclusion

Our results indicate that coffee plantations in southern Costa Rica may be deficient in the invertebrates preferred by generalist birds that use both forest remnants and coffee plantations. Forest remnants surrounding coffee plantations in our study area provide important dietary resources for native forest birds that utilize the agricultural countryside. At least three of the four species examined in this study may be obtaining most of their food from forest remnants and spending time in coffee plantations only while moving between remnants. This interpretation is supported by our extensive radio-tracking data (Şekercioğlu et al., 2007), which showed that most of these same forest species have persisted in agricultural landscapes by being highly mobile foragers that feed on dozens of different native plant and invertebrate species scattered in small forest remnants.

Landscape context is increasingly shown to be of paramount importance for biodiversity conservation in human-dominated, agricultural landscapes (Kati and Şekercioğlu, 2006; Concepción et al., 2008; Şekercioğlu, 2009; Martin et al., 2019; Meier et al., 2022) and our findings support this. Conservation strategies should focus on increasing the connectivity of forest remnants – intact forest, secondary growth, riparian strips – in tropical agricultural countryside, and it is urgent to prioritize the conservation and regeneration of forest remnants in increasingly human-dominated agricultural areas that continue to replace the world's most biodiverse tropical forests.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was reviewed and approved by Stanford University IACUC.

Author contributions

ÇŞ developed the idea for the paper, conceptualized and designed the study, with support from SN, PC, GD, and PE. GD, PE, and ÇŞ acquired funding and resources for the field work. ÇŞ and FB conducted the field work and collected the radio tracking data, feather and diet samples. ÇŞ analyzed the radio tracking and habitat use data. MF conducted isotopic analyses on the diet and feather samples, with help from SN and PC. PC provided the mass spectrometer and other resources for isotopic analyses. ÇŞ, MF, and SN and led the writing of the manuscript. PC, TC, GD, and PE reviewed the manuscript and provided intellectual insights. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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