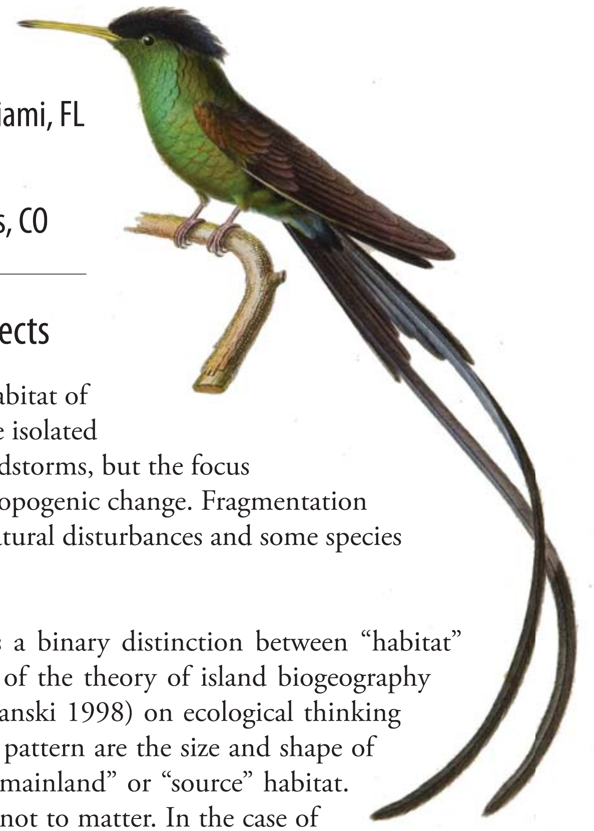
Does the Matrix Matter? Testing the Influence of Matrix Type on Bird Responses to Forest Fragmentation

by
John C. Withey
Department of Biological Sciences, Florida International University, Miami, FL

Christina M. Kennedy
Development by Design Program, The Nature Conservancy, Fort Collins, CO



Part I – Introduction to Habitat Fragmentation and Matrix Effects

Habitat fragmentation is the process whereby previously contiguous habitat of a certain type (for example, forest) is subdivided into smaller and more isolated fragments. Fragmentation occurs naturally due to fire, floods, and windstorms, but the focus of most ecological research is on fragmentation that results from anthropogenic change. Fragmentation caused by humans is not as regular in intensity, scale, or duration as natural disturbances and some species can be more vulnerable to such changes as a result.

The traditional approach to studying habitat fragmentation includes a binary distinction between "habitat" and "non-habitat." This distinction arose in part from the influence of the theory of island biogeography (MacArthur and Wilson 1967), and later, metapopulation theory (Hanski 1998) on ecological thinking and research. In both theories the important parameters of landscape pattern are the size and shape of habitat patches, as well as their isolation from each other and from "mainland" or "source" habitat. The non-habitat surrounding habitat patches was ignored or assumed not to matter. In the case of island biogeography, this was literally true since islands are separated from the mainland by water. In metapopulation theory, habitat occurs in discrete patches that have been assumed to be separated by matrix hostile to focal species.

Box 1. Key Definitions

Patch (or Habitat Patch): Distinct ecological communities with definable boundaries. The patch is usable as habitat by one or more species of interest.

Matrix: In a given landscape, the areas surrounding habitat patches. This includes the different types of non-habitat in a given landscape.

Landscape: An area of land containing a mosaic of different types of habitat and non-habitat. Landscapes generally occupy a spatial scale intermediate between an organism's normal home range and its regional distribution.

A growing body of research, however, finds that the type and the quality of land cover surrounding isolated patches of primary habitat—that is, the matrix itself—can determine species occupancy, abundances, and behavioral and community responses to fragmentation (Kupfer et al. 2006). In a recent meta-analysis, Prugh et al. (2008) found that "patch area and isolation were surprisingly poor predictors of occupancy across species" and concluded that "improving matrix quality may lead to higher conservation returns than manipulating the size and configuration of remnant patches…" Of course these findings do not mean that patch size, isolation, or quality are irrelevant to most species' behavior or population dynamics, but rather that understanding species' responses to different types of matrix land cover is critical for developing effective conservation plans.

For this case study, we focus on the effects of matrix land cover on terrestrial birds. Birds are an ideal group to use as a model to understand how complex communities respond to human-modified landscapes. Birds have been a focus of many landscape studies because they are effective biological indicators of landscape degradation. They respond to habitat changes at multiple spatial scales (e.g., responding to local and regional resources); perform important ecological functions in forests (e.g., as predators, pollinators, and seed dispersers); and many species are easily detected with well-established survey techniques. Birds also exhibit a wide range of habitat associations and ecological characteristics, so they tend to show divergent responses to landscape change.

Matrix land cover has been hypothesized to influence the response of birds to habitat fragmentation through a number of mechanisms (Kennedy et al. 2010), including:

1) inter-patch movement (the *dispersal hypothesis*): matrix type mediates species' ability to move between primary habitat patches.
2) supplemental or complementary resources (the *habitat compensation hypothesis*): different matrix types provide additional or alternative food sources or nest sites, supporting greater abundances than expected if a species were limited to primary habitat patches alone.
3) vegetation structure of edges (the *edge contrast hypothesis*): matrix types that are more dissimilar to primary habitat increase the negative impacts of edges (e.g., through nest predation or parasitism), and may alter within-patch vegetation structure, composition, and microclimates.
4) anthropogenic land use (the *disturbance hypothesis*): different matrix types have different levels of human activity (e.g., hunting, logging, burning, noise, and traffic) that can impact birds in their primary habitat.

Part II – Designing a Study of Matrix Impacts

You work for a conservation non-profit called Bird Protection International (BPI), which is interested in funding applied ecological research. One of BPI's research priorities is to understand the response of birds to anthropogenic habitat fragmentation in forested landscapes. You are in a staff meeting to complete the following task from the Science Director of BPI:

> *Dear BPI Colleagues:*
>
> *As you know, we will soon receive a number of research proposals that set out to study the response of birds to forest fragmentation. To help evaluate proposals, I would like you to brainstorm ways that studies could be designed to evaluate the influence of matrix land cover on how birds respond to forest fragmentation. Thank you for doing this important work!*
>
> *Yours,*
> *Jim Bullock*

Questions

With one of the four mechanisms listed in Part I that have been hypothesized to explain the influence of matrix land cover on birds, please answer the following questions. For forest-dependent birds, forest is considered "primary habitat" and any non-forested area is "non-habitat." In addition to non-habitat, the matrix may include elements such as shade-grown coffee or other agroforestry with some trees but lacking native understory plants.

1. What types of bird data could be considered effective response variables to detect and understand bird responses to forest fragmentation and matrix land cover? (List as many response variables as you can think of and be prepared to discuss which response variable might be preferred.)
2. What forest patch and/or landscape characteristics would be important to measure as independent variables to determine the effects of habitat fragmentation on birds?
3. What types of matrix land cover could be useful to test the specific hypothesis from Part I that you are currently considering?
4. What could be the sample unit(s) of a potential study?

Part III – A Proposal on Matrix Effects on Birds in Jamaica

Based on your input, BPI decides to fund a research project with the following objective:

"...to investigate how forest-dependent Neotropical resident birds in Jamaica respond to habitat patches in landscapes that are similar in structural habitat fragmentation but that are surrounded by different human-modified land cover types."[1]

You now receive another memo from Science Director Jim Bullock:

> *Dear BPI Colleagues:*
>
> *I'm excited to announce that we will fund a study on birds in Jamaica. Please read the following information about the proposed study and then answer the questions on the next page. Thank you for providing feedback to the researchers who will conduct this important study!*
>
> *Yours,*
> *Jim Bullock*

Landscape Data

The study will take place largely in Manchester Parish, Jamaica, where about 30% of native forest remains. Most of the forest clearing occurred over 200 years ago (typically for agriculture). Forest patches that remain tend to be less than 100 hectares (ha) and occur as hilltop remnants, surrounded by agriculture (primarily cattle pasture, see Figure 2), residential (peri-urban) development, or bauxite mining (mining for aluminum).

The researchers will sample forest patches within three human-dominated landscape types, as well as "control" patches within continuous forest. In total, 20 landscapes will be sampled (delineated as 1-km^2 areas): six comprising continuous forest cover, and 14 in which forest has been fragmented by agriculture (N = 5), by suburban development (N = 4), or by bauxite mining (N = 5), i.e., surrounded by a human-dominated matrix (Figure 1 and 2). Patches will be embedded in landscapes with a similar proportion and spatial configuration of forest cover (except for the control sites), so the amount and extent of forest fragmentation among the three human-dominated landscape types will be similar. Surveyed landscapes also have similar environmental conditions (e.g., elevation, climate, soil substrate), but vegetation structure may differ. Patches in agricultural landscapes, and to a lesser extent in continuous forest, tend to have greater stand basal area, leaf area index, tree diameter, tree canopy height, and tree cover than patches in peri-urban and bauxite landscapes. Forest fragments embedded in bauxite and peri-urban matrices have lower and relatively more open canopies and a greater proportion of herbaceous cover and low shrubs.

Bauxite landscapes are former agricultural lands that have been converted to mining within the past 10 years where remnant forests are largely surrounded by exposed bauxitic soils (Figure 2). Suburban and agricultural matrices contain greater foliage cover and vertical complexity than bauxite lands, and thus may provide greater potential resources (e.g., food or nesting sites) or enhance structural connectivity to aid movement outside forest remnants relative to bauxite landscapes. Peri-urban and bauxite landscapes are exposed to more ongoing human disturbance, including hunting, selective logging, noise, road and surface-mining impacts, fire ignition sources, and domestic animals than are agricultural landscapes that tend to be large private land holdings.

Bird Data

Across all 20 landscapes and matrix types, a total of 99 forest patches will be surveyed for resident birds using point counts during three breeding seasons. Both the number of species (richness) and their abundances will be calculated as response variables. About 40 species are expected to be commonly found in these landscapes.

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1 Unless otherwise noted, all quotes, site descriptions, and results are from Kennedy, C.M., Marra, P.P., Fagan, W.F. & Neel, M.C. (2010). Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs* 80: 651–669.

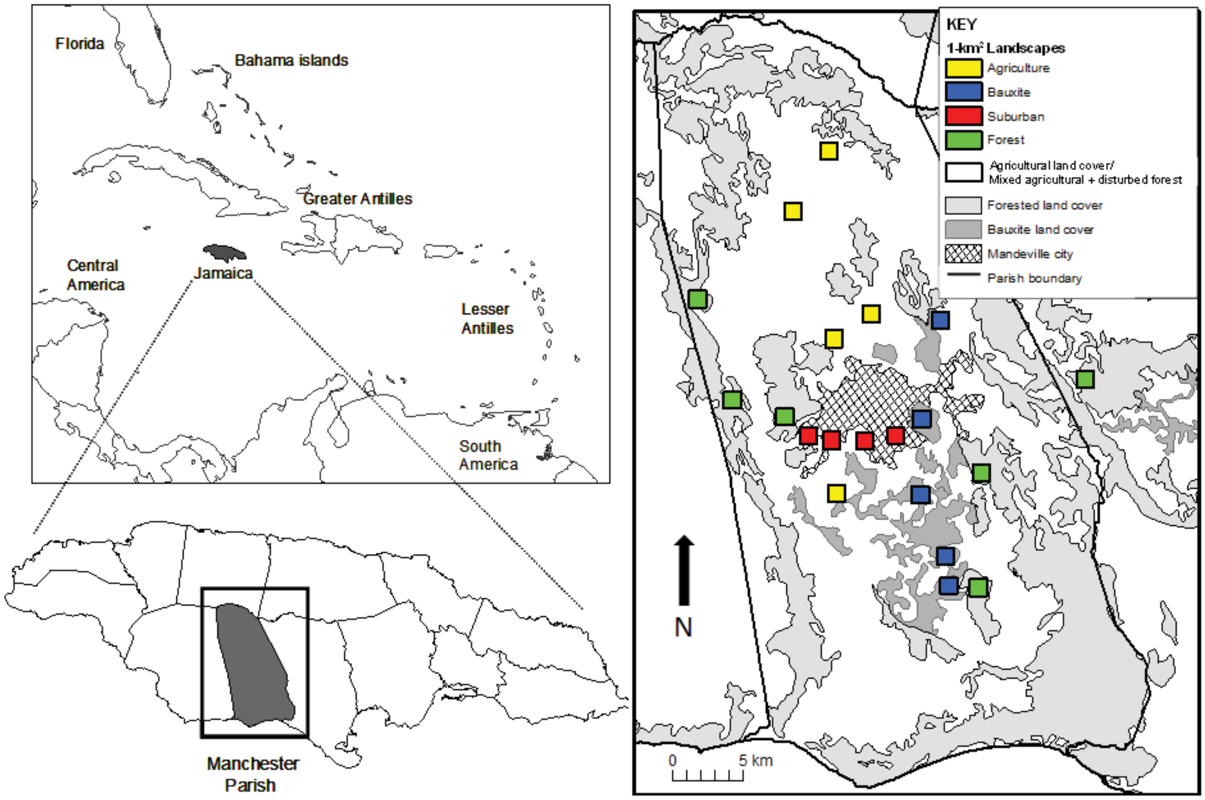

Figure 1. Locations of the twenty 1-km^2 landscapes surveyed for birds on the island of Jamaica. Modified from *Ecological Monographs*, 80(4), 2010, pp. 651–669. Copyright 2010 by the Ecological Society of America. Used with permission.

Figure 2. Aerial view of representative landscapes surveyed in Jamaica: upper left, landscape of continuous forest cover; upper right, landscape fragmented by agriculture; lower left, landscape fragmented by peri-urban development; lower right, landscape fragmented by bauxite mining. Forest cover appears in dark green and is surrounded by pasture, tree-lined fencerows, and paddock trees in agricultural landscapes; by houses, roads, ornamental lawns and gardens, and roadside vegetation in suburban landscapes; and exposed bauxitic (terra rossas) soil and early growth of ferns and Acacia stands in bauxite mining landscapes. Reproduced with permission from *Ecological Applications*, 21(5), 2011, pp. 1837–1850. Copyright 2010 by the Ecological Society of America.

The following 11 ecological and life history traits will also be gathered for all resident bird species, for use as potential independent (explanatory) variables:

1) Taxonomic order (one of 7 orders)
2) Body mass (average weight in grams)
3) Clutch size (average number of eggs laid during a single nesting period)
4) Rarity (mean density of birds within their primary habitat)
5) Geographic range (worldwide distribution of a species: Jamaican endemic, Caribbean, neotropical, or temperate-tropical)
6) Altitudinal range (elevational distribution of a species: low to mid, mid to high, or low to high elevation)
7) Diet guild (dominant food source of a species: frugivore, nectarivore, insectivore, omnivore, granivore, or carnivore)
8) Foraging strata (dominant height zone where a species forages: ground, understory, canopy, or multiple)
9) Nest height (dominant height zone where a species nests: ground, understory, canopy, or multiple)
10) Nest type (type of nest that a species constructs: nest type with large openings ["open"] or with partially closed openings ["closed"])
11) Habitat association (habitat preference of a species: forest-restricted, open-associated, or generalist)

Questions

5. Given the study design and the data collected, what are some of the landscape and matrix influences on birds that *can* and *cannot* be tested for in this study?
6. In your opinion which, if any, of the hypotheses listed in Part I (as mechanisms that explain matrix impacts) can be evaluated in this study, and why or why not?
7. List any doubts or questions you have about the design of this study.

Part IV – Data Analysis and Interpretation

Three years later, the results come in from the research team. They have written up their findings in a report to BPI, and your Science Director now asks you to evaluate some of their findings.

Below are a series of figures from the study in Jamaica. Questions follow each figure for your interpretation.

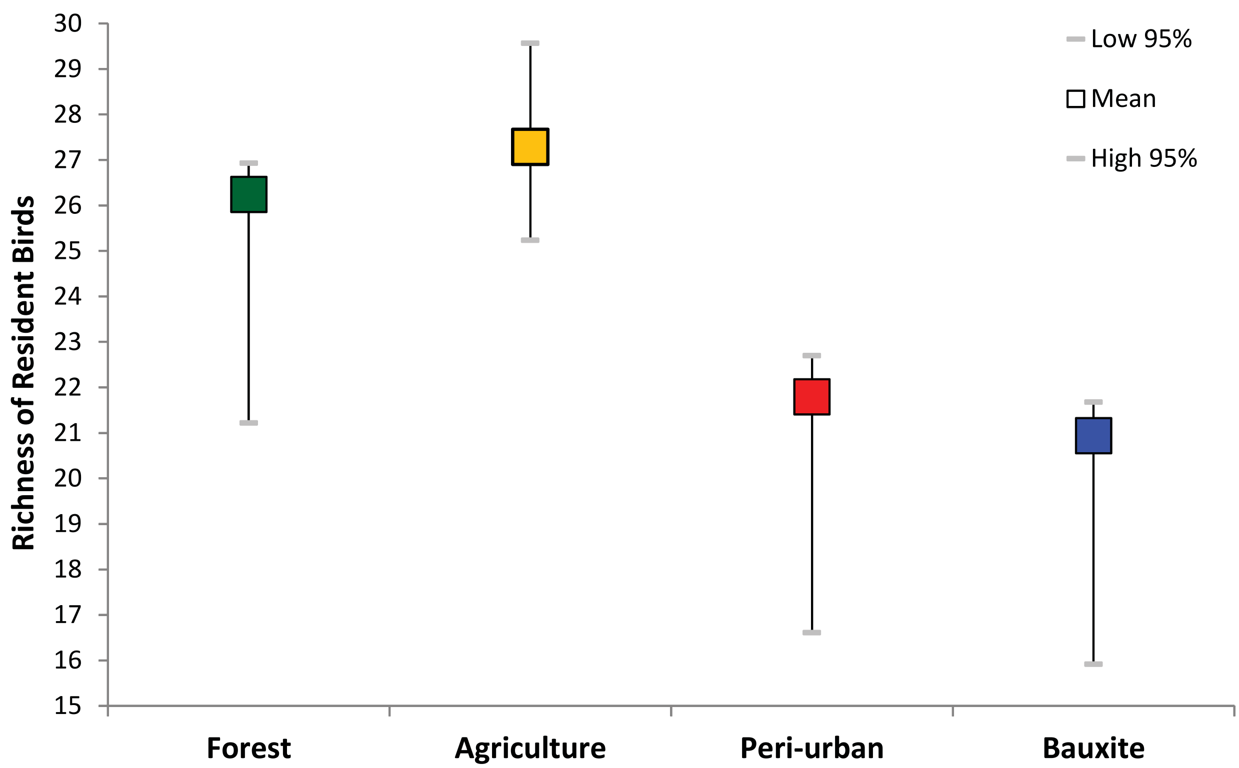

Figure 3. Richness of resident birds in forest patches by landscape matrix type. Bird richness was estimated based on Chao1 estimator, which adjusts for bias due to missed species (Chao 1984). Means and 95% credible intervals are provided based on linear mixed models.

Question

8. How does overall species richness vary by landscape matrix type (use the credible intervals as an indicator of statistical significance)? Does this match with what you would have expected? Is overall richness the best response variable to consider?

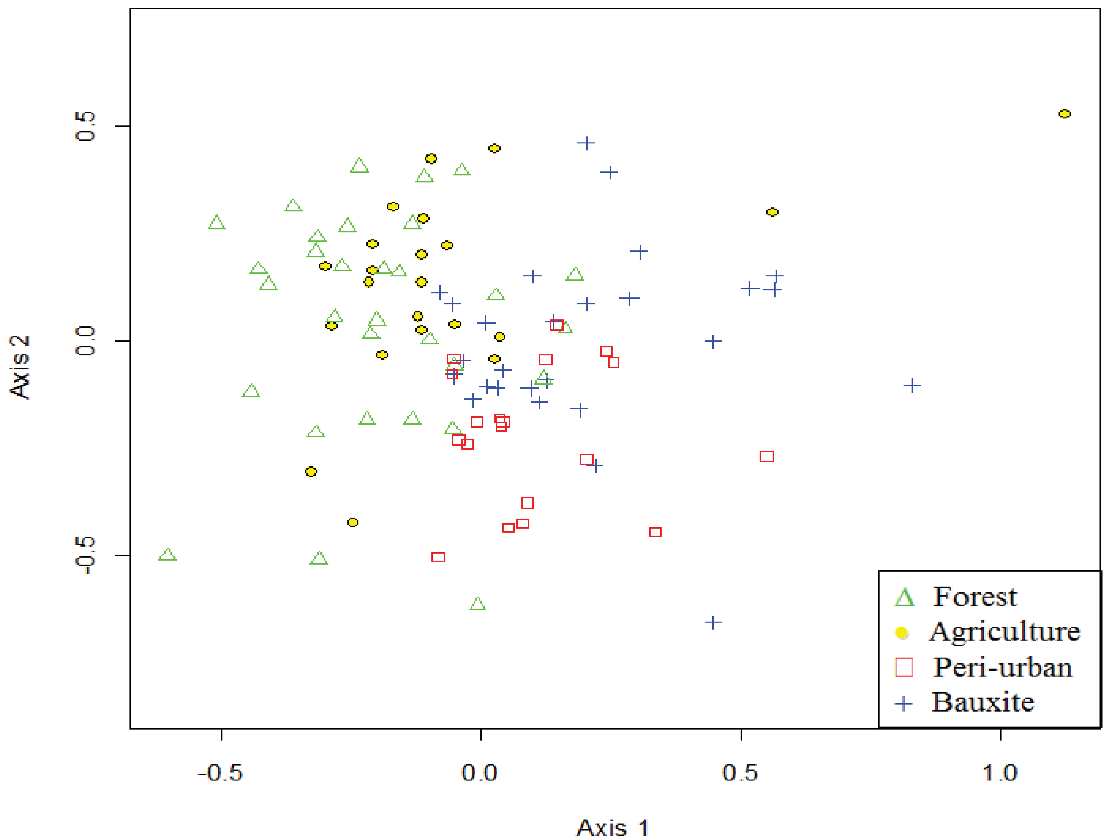

Figure 4. Resident bird communities of each forest patch in nonmetric multidimensional scaling (NMDS) ordination space as coded by landscape matrix type. Modified from *Ecological Monographs,* 80(4), 2010, pp. 651–669. Copyright 2010 by the Ecological Society of America.

Interpreting Figure 4

Here are the key concepts to know about "NMDS," one type of ordination:

- Each point in the figure represents the bird community (both species identity and abundance) in a single forest patch.
- The axes don't have specific units attached to them, but you can potentially work out an interpretation of one or both axes.
- Points that are closer together by linear distance on this figure (and in ordination space) represent bird communities more similar to each other.
- One way to help answer the questions below is to draw a line around all the points in a single group—in this case, by landscape matrix type.

Questions

9. How similar do the bird communities surrounded by different matrix types appear to be to each other? Are there identifiable differences by matrix type?
10. Which landscape type(s) appear to have greater variability in its bird community assemblages, and which to have less variability?
11. What would account for the overlap between different landscape types? How can you relate the overlap to the results shown in Figure 3?

Below are some additional results that help explain the strong or significant associations shown in Table 1:

- *Diet Guild:* About two-thirds of species that were insectivores or frugivores were more abundant in the forested landscapes than human-dominated landscapes, while *all* nectarivores and omnivores and 86% of species that were granivores were more abundant or had similar abundances in human-dominated matrix types relative to continuous forest.
- *Nest Height:* Most canopy-nesting species (86%) were more abundant in the forest landscape, while all ground-nesters had similar abundances across landscape types (75%) or were more abundant in one or more of the human-dominated matrix types (25%).
- *Habitat Association:* Thirty percent of forest-restricted species had similar abundances across landscape types and 70% were more abundant in the forest landscapes. In contrast, 90% of birds associated with open habitats and approximately 80% of generalist birds had equal or higher abundances in human-dominated landscapes as compared to continuous forest.

Trait	*Variable Importance*	*P-value*
Diet Guild	100.00	**0.0105**
Nest Height	72.93	**0.0113**
Habitat Association	67.57	**0.0092**
Foraging Strata	45.12	0.0788*
Taxonomic Order	30.45	0.2135
Geographic Range	28.93	0.3944
Rarity	25.54	0.4888
Nest Type	19.29	0.1566
Clutch Size	18.26	0.1621
Altitudinal Range	8.46	0.2639
Body Mass	2.61	0.7461

Table 1. A measure of the association of species traits with landscape matrix responses. Variable Importance is based on classification tree analysis, and P-values are based on randomized χ^2 tests (values in boldface significant at $P < 0.05$ and by * at $P < 0.10$). The variable with the greatest prediction accuracy is attributed the highest value (100), and the variable with the lowest prediction accuracy is attributed the lowest value (0).

- *Foraging Strata:* Canopy foragers, and to a lesser extent understory foragers, had lower abundances in fragmented landscapes than did ground foragers. Two-thirds of canopy foragers and 56% of understory foragers were lower in abundance in fragments in human-dominated landscapes than intact forest.

Questions

12. Although this study does not experimentally test any of the hypotheses listed in Part I, consider the results shown in Table 1 and assess whether certain mechanisms are more supported than others. If so, how?

    Hint: Relate each trait listed in Table 1 with potential mechanisms that may affect species' vulnerability to land cover change as informed by life history and biogeographic theories and empirical findings from fragmentation research. (For example, body size and taxonomic order are correlated with dispersal distance, and geographic and altitudinal range sizes are correlated with the ability of a species to establish in new areas.) Then see how significant traits predominately relate to mechanisms and how this might inform which of the mechanisms may drive bird responses to fragmentation and matrix type. Refer again to hypotheses listed in Part I.
13. As BPI staff, what conservation implications would you learn from this study? For example, what are the consequences of classifying habitat as "forest" vs. "human-dominated" in central Jamaica? What could be future outcomes of on-going conversion of pasture lands to residential or mining areas? Are there any other conservation implications?
14. What types of future research would you recommend as follow-up to this study? For example, since overall richness and community analyses such as NMDS do not show the responses of individual species, are there certain species you might focus on in the future? Are there ways to confirm mechanisms of the underlying bird responses to forest conversion in this region? How could you manipulate the system for experimental landscape research? Other ideas?

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Credit: Image in title block, *L'Oiseau-mouche a tete noire,* illustration of *Trochilus polytmus Linnaeus*, 1758. From: *Histoire naturelle des Oiseaux-Mouches* (Paris 1829). http://teylers.sterna-project.eu/18d%2067_0086.jpg. Image from the collection of Teylers Museum, Haarlem, Netherlands, used with permission. This hummingbird, the national bird of Jamaica, is also known as the Red-billed Streamertail.