ABSTRACT

Title of dissertation: MATRIX EFFECTS ON INDIVIDUAL AND COMMUNITY-LEVEL RESPONSES OF BIRDS TO FOREST FRAGMENTATION IN JAMAICA

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Land cover between habitat patches (“matrix”) can impact species persistence in fragmented landscapes by altering resource availability, edge effects, or inter-patch movement. This thesis examines how the matrix affects the Neotropical bird community in central Jamaica in landscapes where forest is embedded in three human-dominated matrix types (agriculture, peri-urban development, and bauxite mining) and one natural “matrix” (continuous forest).

First, I examine whether richness, community composition, and abundances of resident birds differ in ~ 100 forest patches within the four matrix types, and relate species responses to traits influencing dispersal, resource acquisition, and/or population growth. Agricultural landscapes were found to retain avian diversity and community assemblages most similar to intact forest relative to peri-urban and bauxite landscapes.

Traits related to resource acquisition best predicted species responses, indicating that resource limitation driven by the matrix may be a primary factor driving bird responses to fragmentation.

Next, I determine the relative influence of patch area, isolation, vegetation structure, and matrix type on the occupancy dynamics of resident insectivorous birds. Within-patch vegetation and matrix type were the most important determinants of colonization and extinction, but the effects of patch area, isolation, and vegetation on occupancy dynamics were matrix- and species-dependent. Across the community, the matrix influenced extinction probabilities more than colonization, indicating that extinction processes likely drive population dynamics.

Finally, I examine the relative permeability of peri-urban, bauxite, and forested landscapes on the movement of the migrant American Redstart (*Setophaga ruticilla*) and the resident Jamaican Tody (*Todus todus*) by experimentally translocating > 140 birds 0.6–4 km from their territories across landscape treatments. Redstarts returned with greater success and faster speed than Todies. Return success was not impacted by landscape treatment, but both species returned more rapidly in forest relative to bauxite matrix, with return times intermediate in a peri-urban matrix. These findings indicate that bird mobility in fragmented landscapes is mediated by the landscape matrix.

This research is among few empirical studies to discern the impacts of different matrix types on species patterns and processes. These results inform theory on fragmentation as well as bird conservation in an understudied system.

MATRIX EFFECTS ON INDIVIDUAL AND COMMUNITY-LEVEL RESPONSES OF BIRDS TO FOREST FRAGMENTATION IN JAMAICA

By

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2009

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Preface

This dissertation contains an overall abstract and introduction, three chapters, and nine supporting appendices. Each chapter is presented in manuscript form; therefore, background and methods may be repeated, pronouns reflect manuscript authorship, and tables and figures appear at the end. A single reference section occurs at the end for literature cited throughout the dissertation, and appendices are labeled in the order of citation in the text. All research was conducted under applicable permits and approved animal care/use protocols (University of Maryland IACUC protocol #R-06-83, Smithsonian National Zoological Park CRC-IACUC proposal #06-25, and Jamaica NEPA Ref. No. 18/27).

Dedication

To my husband, John – who, with endless encouragement and support, made possible my education, fieldwork, and research pursuits. I am grateful beyond words.

And to our son, Aidan – who, with each glance and smile, reminds me why I embarked on a career that is intended to honor, respect, and improve the world in which we live.

Acknowledgments

On my dissertation journey, I have been blessed with a vast network of people who have made my education and research possible. I would like to start by thanking Dr. Maile Neel, Dr. Peter Marra, and Dr. William Fagan, who collectively supported me during all stages of my doctoral dissertation. Dr. Neel provided extensive guidance on the landscape-level design and analysis of my research as well as offered generous professional and personal support. Dr. Marra is the reason I chose to work in Jamaica; he introduced me to the system, imparted his ornithological insights, and facilitated in-country logistics and funding. Dr. Fagan welcomed me into his lab, which shaped my university experience and broadened my exposure to spatial and theoretical ecology. I also thank my committee members: Dr. Taylor Ricketts for challenging me to address fundamental questions in conservation even when I was unsure how to do so; Dr. David Inouye for input on my proposal, chapters, and talks; and Dr. Eric Kasischke for stepping in at the final hour to ensure completion of my dissertation.

I received essential in-country support from many researchers, nonprofit and governmental organizations, and private landowners in Jamaica. I thank Ann Hayes-Sutton for sharing her knowledge of the study region and providing logistical assistance during field seasons; Owen Evelyn (Jamaica Forest Department) and Steve Schill (The Nature Conservancy) for GIS and remote sensing data; O. Evelyn for help in vegetation identification; and Susan Koenig (Windsor Research Centre) for her expert consultation on all issues involving Jamaican birds. I extend a special debt of gratitude to my field assistants who endured long hours and grueling field conditions. Thank you, Mathew Podolsky, Marlon Beale, Stephan Lorenz, and Matthew White, for your much-

appreciated help and company in the field and back at Marshall's Pen. I am also grateful to the Jamaica Forestry Department; Windalco, Alpart Mining Venture, and Jamalco bauxite mining companies; S&G Road Surfacing Materials Ltd.; and many private farmers and Mandeville citizens who graciously permitted access to their lands. Finally, I recognize three people who embody the true spirit of Jamaica to me: Herlitz Davis, Chris Samuels, and James Godfrey. Thank you, Herlitz, for guiding me in bird identification in my first season and for acclimating me to Jamaica. Thank you, Chris, for sticking it out with me for three years in the field, even during challenging personal times. Thank you, James, for opening up your home during hurricane warnings or when I was without water or electricity, for allowing me to routinely sneak behind your properties at 5 am to look for birds, and for your companionship when I felt alone in a strange land. To you all, I am grateful for your unconditional generosity and kindness.

In addition to community-wide support in Jamaica, I received generous funding from NASA Earth System Science Program (Doctoral Fellowship), Smithsonian Institution (James Bond Trust), Fulbright U.S. Scholarship Program, Washington Explorer's Club, Cosmos Club Foundation, and the University of Maryland (UMD) (Behavior, Ecology, Evolution, and Systematics Graduate Program and an Ann G. Wylie Dissertation Fellowship). I thank Jamaica National Environment and Planning Agency (NEPA), Smithsonian National Zoological Park, and UMD for research permits/approval.

I am grateful to many friends and colleagues who enriched my experience when I was back at home in Maryland. I thank Fagan and Neel Lab members, past and present, who provided advice on statistical problems, critiqued preliminary practice talks, and simply offered their friendship. I especially thank Holly Martinson, Katie Schneider, Eric Lind, Jamie Pettengill, Paula Casanovas, Elise Larsen, James Gilbert, Sara Zeigler, David Luther, Allison Leidner, Thomas Mueller, Chris Che-Castaldo, Heather Lynch, and Sarah Kingston. I appreciate the unique contributions of the following people: Leslie Ries, who was a positive mentor and close friend, neighbor, and childcare partner; Shannon Franks, whose late nights at NASA Goddard resulted in a land-cover classification of my study region that otherwise would not have manifested; and Evan Grant, who guided me through the complex maze of occupancy modeling.

Numerous undergraduates performed mundane data entry and GIS mapping tasks in good humor and often without pay, including Shelly Gupta, Rohan Verma, Adam Pyle, Nelson Sofoluke, Mark Thomas, Maureen Loman, Piyali Kundu, Elsa Abraham, Dan Fink, Jana Lovell, Chibale Chanza, David Harris, Leslie Wells, and Vy Tran.

Finally, I thank those who supported me from the beginning. I am especially grateful to Maria Bieberich and Brandie Fariss, whose enduring friendship has carried me through many difficult days; and to my mother-in-law, Fran Hamilton, whose willingness to fly in on a second's notice helped me meet many deadlines and field obligations. Deserving of all my gratitude is my mother, Antigone Kennedy, whose consistent financial and moral support allowed me to pursue many years of graduate education.

Last but definitely not least, this dissertation would not have been possible without the unwavering support of my husband, John Hamilton. Thank you for your optimism, your infinite patience, and your willingness to support my journey even when it took us to Jamaica. And to our beloved son, Aidan, who inspired me to keep everything in perspective and not take life (or at least the dissertation) too seriously. To you both, I am forever indebted.

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Introduction

Around the world, natural areas are being converted to and fragmented by human-dominated land uses, a change that is threatening global biodiversity (Sala et al. 2000; Foley et al. 2005). Consequently, habitat fragmentation has become a major research theme (Fazey et al. 2005). Despite such attention, we still have limited understanding and ability to predict how species will respond to habitat conversion, particularly in non-temperate areas (Ford et al. 2001; Laurance 2008). A major reason may be that research has been largely guided by patch-based models that assume landscapes can be simplistically reduced to habitat and undefined non-habitat. Island biogeographic theory and metapopulation models (MacArthur and Wilson 1967; Hanski 1998), which provide the theoretical foundation for fragmentation research, focus on the effects of reducing habitat patch size (area effects) and increasing inter-patch distance (isolation effects), while often ignoring the potential role of land cover between primary habitat (Haila 2002; Fahrig 2003; Kupfer et al. 2006). In reality, the process of fragmentation occurs not at the individual-patch but among multiple patches in a landscape (McGarigal and Cushman 2002; Fahrig 2003), which are often surrounded by complex mosaics of different land-cover types. Species may be affected not only by the size and spatial location of primary habitat, but also by the structure and composition of the intervening land cover, termed the “matrix” (Haila 2002; Ewers and Didham 2006; Kupfer et al. 2006). The matrix can affect inter-patch movement of animals (e.g., Revilla et al. 2004; Bender and Fahrig 2005), can alter the resource base within a landscape by providing alternative or supplemental resources (e.g., Perfecto and Vandermeer 2002; Brotons et al. 2003), and can impact the type and magnitude of edge effects (e.g., habitat quality, microclimate, predation rates) (e.g., Chalfoun et al. 2002; Ries et al. 2004).

Despite the potential importance of the landscape matrix, its effects remain poorly understood. The relative importance of multiple human-modified land-cover types has rarely been examined in one study, and matrix types are often lumped together in a single “matrix” category or are assumed to be of subordinate importance to habitat components (i.e., patch area and isolation). Given the small number of empirical studies that have disentangled the effects of the matrix from those of habitat area or isolation (Rodewald 2003; Laurance 2008), the unique impacts of matrix types on species processes are only beginning to be discerned.

The central aim of my research was to determine the effects of the landscape matrix on the Neotropical bird community in fragmented forests in central Jamaica. This island was once almost entirely covered by forests, but now less than 30% remains (NRCA 1995; FAO 2001; Forestry Department 2001). Despite such extensive loss, remnant forests are essential to protecting the island’s unique biodiversity. Jamaica is in one of the top four global biodiversity hotspots, with one of the highest rates of endemism (Myers et al. 2000) and the greatest number of endemic bird species in the Caribbean, including five endemic avian genera (*Pseudoscops*, *Trochilus*, *Loxipasser*, *Euneornis* and *Nesopsar*) (BirdLife International 2003). Despite Jamaica’s legacy of forest loss and the potential threat to its endemic species (Brooks et al. 2002), this is the first study to examine the effects of forest fragmentation on avian assemblages in different landscape contexts.

Most of the human land conversion in Jamaica occurred by the eighteenth century (Eyre 1987b), when native forests were converted historically for cultivation of cash crops (e.g., sugar, bananas, and coffee), and more recently for cattle pasture (Eyre 1987a; Eyre 1987b). Since the 1950s, land-cover change in Jamaica (Evelyn and Camirand 2003) and on other Caribbean islands (Lugo 2002) has resulted largely from the conversion of agriculture to residential development and to mining for bauxite. In a classic island biogeographic or metapopulation framework, these land uses would fail to be distinguished, given that they equally result in the creation of non-native land cover. Treating these three anthropogenically modified lands as a single cover type (i.e., non-habitat), however, has the potential to lead to erroneous decision-making. To better inform conservation planning and restoration efforts in the region, we need to understand the unique impacts of each of these three human land uses on forest-dependent birds.

Study area

My research sites were located in Manchester and Clarendon Parishes (latitude: 17 56'24"-18 11'6" N; longitude: 77 23'13"- 77 37'5" W). This region lies in the premontane moist forest climatic zone (Holdridge 1967), with mean annual temperature of 26° C. Rainfall is bimodal, peaking in May/June and September/October, with 1000 mm per year average (Jamaican Meteorological Service, *unpublished data*). The landform is karst topography with white limestone hills and plateaus, ranging between 400 and 800 m elevation (Porter 1990). In pre-Columbian times, this region was covered in wet limestone forest (Asprey and Robbins 1953) composed of evergreen and semi-deciduous trees, referred to as Evergreen Season Forest formation (Beard 1944; Beard 1955). Forest is now restricted to small hilltop remnants on limestone outcrops (often <

10 ha) surrounded by a matrix dominated by agriculture, residential (peri-urban) development, or bauxite mining. Given the karst topography, the habitat fragmentation pattern is similar among landscapes subject to these different human land-use pressures. Spatial locations and extent of forest fragments in this region have remained fairly stationary in recent time but are embedded within a changing matrix. Thus, this setting provided a unique opportunity to investigate the influence of matrix land cover on the Neotropical bird community.

Over a three-year period (2005-2007), I surveyed birds in 20 landscapes that captured the land-cover patterns in the region: 14 landscapes in which remnant forest had been fragmented and converted to three dominant land-cover types (5 agriculture, 4 peri-urban development, 5 bauxite mining), and 6 landscapes with intact forest cover. To isolate the potential influence of matrix context, agricultural, peri-urban, and bauxite landscapes were selected such that they were similar in the major components of fragmentation. I sampled ~100 forest patches similar in patch area (mean ± 1 SE: 3.89 ± 0.45 ha) and inter-patch isolation (33.58 ± 3.48 m, 160.80 ± 19.79 m, and 2381.75 ± 147.07 m to the nearest fragment > 0.5 ha, 5 ha, and 100 ha, respectively). Patches were also embedded in landscapes with a similar proportion (35.84 ± 1.59) and spatial configuration of forest cover (i.e., shape complexity, inter-patch connectivity).

Research objectives and dissertation format

The main goals of my research were to determine (1) the effects of forest fragmentation and the landscape matrix on the Neotropical bird community, (2) the extent to which species responses are driven by intrinsic factors (i.e., life history and ecological traits) and extrinsic factors (i.e., patch area, isolation, within-habitat quality, and matrix conditions), and (3) the relative importance of potential underlying mechanisms (i.e., resource limitation, dispersal limitation, and reproductive growth/predation).

My first chapter examines the effects of forest fragmentation and the landscape matrix on the resident (non-migratory) Neotropical bird assemblage. I determine how species richness, community composition, and relative abundances of birds differ in forest patches embedded in the three human-dominated matrix types (agriculture, peri-urban development, bauxite mining) relative to sites in a natural "matrix" (continuous forest). Individual bird responses are categorized into matrix response types, depending upon whether species abundances were higher, lower, or similar among the fragmented matrix types relative to continuous forest. Species matrix responses were then related to eleven life history and ecological traits that affect dispersal ability, resource acquisition, and/or population growth potential to tease out plausible mechanisms underlying bird responses to anthropogenically modified landscapes.

In my second chapter, I move beyond inferring potential mechanisms based on species abundance patterns and directly assess the role of local colonization and local extinction in driving differential occupancy dynamics of resident Neotropical insectivorous birds among the four landscape types. I selected insectivorous birds because this guild is disproportionately declining in fragmented tropical forests worldwide (e.g., Stratford and Stouffer 1999; Castelletta et al. 2000; Ribon et al. 2003; Sodhi et al. 2004). To ensure unbiased inferences, I apply recently developed multi-season patch-occupancy models to account for the fact that species are often imperfectly and/or differentially detected (MacKenzie et al. 2003; MacKenzie et al. 2006). I investigate the relative effects of patch area, patch isolation, within-patch habitat structure, and matrix type based on an information-theoretic approach, which allows for the examination of alternative hypotheses and multi-model inference (Burnham and Anderson 2002). I specifically examine (1) how patch area and within-patch habitat (vegetation) structure affect the probabilities of local extinction, (2) how patch isolation affects the probabilities of local colonization, and (3) whether and how matrix conditions mediate isolation-, area-, and habitat-relationships.

In my third chapter, I focus directly on the role of the landscape matrix in mediating dispersal abilities of two insectivorous bird species – a habitat generalist, the Nearctic-Neotropical migrant American Redstart (*Setophaga ruticilla*) and a resident forest specialist, the Jamaican Tody (*Todus todus*). These species were targeted given their divergent life history traits, which I predicted would impose differential constraints on their ability to respond to forest fragmentation. I experimentally translocated > 140 birds an average of 1.7 ± 0.60 km (± 1 SE) from their territories across three landscape treatments: landscapes fragmented by either peri-urban or bauxite mining development (i.e., peri-urban or bauxite matrix types) versus continuous forest. I test whether return success or return time differ among landscape treatments as well as among species. Additional factors beyond landscape structure can affect both site fidelity and dispersal ability of birds (Bowler and Benton 2005); thus, I consider the relative influence of sex, body condition, territory habitat quality, and translocation distance. Experimental manipulations, in particular translocations, can be an effective way to measure functional connectivity at a landscape scale for vagile species like birds (Desrochers et al. 1999; Bélisle et al. 2001).

By integrating research on community- and individual-level patterns, occupancy dynamics, and movement experiments, this dissertation provides a novel synthesis of the role of the landscape matrix in mediating effects of forest fragmentation on Neotropical bird communities. This research is among few empirical studies to discern the relative impacts of different matrix types on species patterns and processes in fragmented systems and to evaluate the relative importance of alternative mechanisms. These results inform general conservation theory on fragmentation and also Neotropical bird conservation in an understudied system.

Chapter 1: Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica

Abstract

Land cover surrounding fragmented habitat can greatly impact species persistence by altering resource availability, edge effects, or the movement of individuals throughout a landscape. Despite the potential importance of the landscape matrix, we still have limited understanding of differential effects of intensive land uses in empirical systems. Here, we investigated whether Neotropical resident bird communities differed in limestone forest patches embedded in three different human-dominated matrix types (agriculture, peri-urban development, and bauxite mining) relative to sites in continuous forest in central Jamaica. We found that species richness, community composition, and abundances were matrix-dependent, with agricultural landscapes supporting greater avian diversity and more intact community assemblages than either peri-urban or bauxite landscapes. Seventy percent of resident bird species had abundances that differed in forest embedded in the different landscape matrix types. Traits related to resource use best predicted species responses, lending support to the hypothesis that resource availability may be a primary factor driving Neotropical bird responses to fragmentation. Insectivores, frugivores, canopy nesters, understory and canopy foragers, and forest-restricted species rarely observed in matrix habitats had lower abundances in forest fragments embedded in human-modified matrix types than in continuous forest. In contrast, nectarivores, omnivores, granivores, ground and multi-strata nesters, ground foragers, and species regularly in matrix habitats were least sensitive to forest

fragmentation. Results suggest that structure, composition, and land use disturbance in matrix areas impact overall habitat quality in landscapes by potentially mediating resource availability inside as well as outside forest habitat. This study reinforces the importance of differentiating among land uses in fragmentation research.

Introduction

Around the world, forests are being converted to and fragmented by human-dominated land uses, a change that is threatening global biodiversity (Sala et al. 2000; Foley et al. 2005). Despite substantial research attention to fragmentation (Fazey et al. 2005), we remain unable to predict how most species will respond to forest conversion (Henle et al. 2004; Ewers and Didham 2006). A major reason for this inability could be that landscapes are often simplistically reduced to inadequate binaries of habitat and undefined non-habitat in fragmentation studies. This conceptualization likely stems from the application of island biogeography and metapopulation theories (MacArthur and Wilson 1967; Hanski 1998) to human-dominated systems. These theories have emphasized the impacts of reducing forest patch size (i.e., area effects) and increasing inter-patch distance (i.e., isolation effects) on species diversity and persistence, while often ignoring the role of land cover between forest remnants (Haila 2002; Fahrig 2003). In reality, landscapes are complex mosaics of different land-cover types under varying intensities of use. Species are thus affected not only by the size, shape, and spatial location of forest habitat, but also by surrounding non-forested areas, which we collectively refer to as the “landscape matrix.”

The matrix is broadly defined as the portion of the landscape that has at some point in time undergone anthropogenic perturbation, such as logging or conversion of native forest to human land uses such as silviculture, agricultural fields, pasture, and development (*sensu* Lindenmayer and Franklin 2002; Kupfer et al. 2006). Despite what the term may imply, the matrix is neither homogeneous nor entirely inhospitable or inert to forest-dwelling species. Rather, the landscape matrix can differentially mediate processes that influence species-area and -isolation relationships (Ewers and Didham 2006; Prugh et al. 2008) and edge effects (Ries et al. 2004; Ries and Sisk 2004). Different matrix types may provide alternative or supplemental resources (e.g., food or nesting sites) to support greater species abundances than would be expected based on primary habitat alone (i.e., habitat compensation hypothesis) (e.g., Gascon et al. 1999; Norton et al. 2000; Brotons et al. 2003; Luck and Daily 2003; Cook et al. 2004). Inter-patch movement of animals may also differ in landscapes with varying matrix structure, thus influencing functional landscape connectivity in varying degrees (i.e., dispersal hypothesis) (e.g., Bélisle et al. 2001; Ricketts 2001; Gobeil and Villard 2002; Revilla et al. 2004; Bender and Fahrig 2005). The type and extent of contrast between matrix habitats and forest remnants can also mediate the magnitude of edge effects, such as nest predation and parasitism (Donovan et al. 1997; Chalfoun et al. 2002; Driscoll and Donovan 2004) or the alteration of within-patch conditions (e.g., vegetation structure, microclimate) (Saunders et al. 1991; Ries et al. 2004) (i.e., edge effects hypothesis). Lastly, land-use pressures may vary in different landscape contexts (Friesen et al. 1995; Rodewald and Bakermans 2006), with hunting pressures, logging, noise, and spread of fire or invasives likely to increase in areas with greater human access (i.e., disturbance hypothesis) (Lugo et al. 1981; Laurance 2008). Collectively, these hypotheses outline mechanisms by which "matrix effects" may ultimately drive colonization-extinction dynamics in fragmented landscapes (e.g., Vandermeer and Carvajal 2001).

Despite the potential importance of the matrix, its effects remain poorly understood. Most studies examining the impact of the landscape matrix have compared forest fragments surrounded by intensely human-modified matrix (in particular, agriculture) to other fragments surrounded by matrix types that are more similar structurally to once-contiguous forest. For example, researchers have compared forest patches embedded in pasture to patches embedded in secondary forest growth (Laurance et al. 2002), exotic tree plantations (Estades and Temple 1999; Hobson and Bayne 2000; Renjifo 2001; Lindenmayer et al. 2002; Wethered and Lawes 2003), or silvicultural forests (Andren 1992; Aberg et al. 1995; Bayne and Hobson 1997; Norton et al. 2000). These studies reveal that species movement and persistence are best maintained when matrix areas are similar in structure, floristic composition, and microclimate to once-contiguous forest. This finding has led to matrix effects being predominately based on gross structural characteristics. Matrix types that have high structural contrast (i.e., divergent in vegetation structure) to remnant habitat are thus predicted to be less permeable to movement and more hostile to species than matrix types with low-contrast boundaries (e.g., Stamps et al. 1987; Forman 1995; Strayer et al. 2003). Thus, in forested landscapes, human land uses that create "open" deforested habitats, such as for agricultural or residential development, may be considered equally hostile to forest-dwelling species. This simplification, however, ignores other potential important and less obvious impacts of human land uses.

By focusing on the differential effects of agricultural landscapes versus forested landscapes, previous research has failed to identify the unique impacts of matrix land cover because the amount of forest is inseparable from the type of land use. Despite a few notable exceptions (e.g., Renjifo 2001; Rodewald and Yahner 2001; Rodewald and Bakermans 2006), forest amount and spatial configuration are commonly confounded with one another in fragmentation research and then further confounded with matrix composition (Rodewald 2003; Laurance 2008). Avoiding such conflation of factors is essential, because the influence due to habitat elements is likely to outweigh the influence due to any matrix elements (Goodwin and Fahrig 2002); thus, matrix effects are more likely to go undetected. Only a few studies have disentangled the effects of human land uses from the effects due to forest amount, and multiple human-modified land-cover types with similar structural “edge contrast” (Strayer et al. 2003) are rarely examined in conjunction; thus, few empirical data exist to evaluate the relative impact of different human activities on fauna within forest remnants.

In Jamaica, as well as on other Caribbean islands, agriculture, residential development, and mining for bauxite are dominant land uses. Land cover is increasingly being converted from subsistence agriculture to more intensive development (i.e., urbanization and mining) in the Caribbean (Lugo 2002; Evelyn and Camirand 2003) and in many other regions of the world (DeFries et al. 2004). Despite their pervasiveness, intensively developed landscapes that result in more structurally “open” habitat types have seldom been compared to understand whether they differentially impact species existing in fragmented forest remnants. The goals of this study were (1) to evaluate whether Neotropical bird communities in Jamaica respond similarly to fragmentation when forest is surrounded by three different but intensive land uses and (2) to determine to what extent differential species responses are governed by life history and ecological traits. Specifically, we examined whether species richness, community composition, or abundances of Neotropical resident birds differ in forest fragments embedded in agriculture (i.e., pasture), residential (peri-urban) development, or mining for bauxite (i.e., human-dominated matrices) relative to sites in continuous forest (natural "matrix"). We surveyed human-dominated landscapes that were similar in the major components of fragmentation (i.e., forest amount and configuration) to isolate the influence of the matrix. When different landscape matrices are examined, species responses to habitat fragmentation are seemingly idiosyncratic (e.g., Watson et al. 2005; Mac Nally 2007; Ries and Sisk 2008). To elucidate potential mechanistic explanations behind why groups of species may respond in a similar manner to forest conversion, we selected a suite of traits proposed to influence species persistence in fragmented systems (Ewers and Didham 2006). We consider phylogenetic relatedness, body size, rarity, geographic and altitudinal ranges, clutch size, nest type, nest height, diet guild, foraging strata, and habitat association. Each of these traits can affect dispersal ability, resource acquisition, and/or population growth potential (Henle et al. 2004); thus, we predicted these traits would relate to species responses to human-altered forest. Although researchers have addressed associations between species traits and species responses to fragmentation (e.g., Laurance 1991; Hansen and Urban 1992; Pereira et al. 2004; Lampila et al. 2005; Sigel et al. 2006), a clear consensus has yet to emerge on which traits govern divergent responses and why (Henle et al. 2004). Moreover, patterns detected are contingent upon which landscape matrix types are examined (Bender et al. 1998; Debinski and Holt 2000; Ewers and Didham 2006), a factor that is not often explicitly addressed.

Methods

Study area

We conducted research in Manchester and Clarendon Parishes in central Jamaica (latitude: 17 56'24"-18 11'6" N; longitude: 77 23'13"- 77 37'5" W). This region lies in the premontane moist forest climatic zone (Holdridge 1967), with mean annual temperature of 26° C. Rainfall is bimodal, peaking in May/June and September/October, with 1000 mm per year average (Jamaican Meteorological Service, *unpublished data*). The landform is karst topography with white limestone hills and plateaus, ranging between 400 and 800 m elevation (Porter 1990).

In pre-Columbian times, this region was covered in wet limestone forest (Asprey and Robbins 1953) composed of evergreen and semi-deciduous trees, referred to as Evergreen Season Forest formation (Beard 1944; Beard 1955). Dominant canopy species included broadleaf (*Terminalia latifolia*), Jamaican cedar (*Cedrela odorata*), sweetwoods (*Nectandra* spp.), and bulletwoods (*Daphnopsis* spp.) (Asprey and Robbins 1953). Today, less than 30% of native forest remains (Evelyn and Camirand 2003), which is within the range where the effects of fragmentation are postulated to occur (Fahrig 2003). Forest is now restricted to small hilltop remnants on limestone outcrops, surrounded by valleys cleared for three dominant land uses: agriculture (i.e., primarily cattle pastureland), residential development, and mining for bauxite. The vast majority of forest fragments are ≤ 100 ha, with only a few large forest tracts remaining along inaccessible hilltop ridges. Large-scale deforestation occurred by the eighteenth century (Eyre 1987a; Eyre 1987b). The exact rate of deforestation in the region is unknown but is estimated to be as low as 0.1% annually for the country; with current land-use change largely occurring among human-modified matrices (i.e., agricultural areas converted to urbanization or mining) (Evelyn and Camirand 2003). We are thus investigating the role of the matrix in a region that has undergone historic rather than contemporary forest loss and fragmentation, but where the character of the matrix continues to shift. Locations and extent of forest fragments in this region have remained fairly stationary in recent time but are embedded within a changing matrix. This setting provided a unique opportunity to investigate the influence of matrix land cover on Neotropical birds in fragmented forests.

Site selection

We surveyed 20 landscapes that were typical of land-cover patterns in central Jamaica: 6 landscapes comprising continuous forest and 14 landscapes in which forest has been fragmented by agriculture (N = 5), by peri-urban development (N = 4), or by bauxite mining (N = 5) (Figure 1.1). Landscapes were delineated as 1-km squared areas, which is a biologically relevant scale given known territory sizes of forest songbirds (Robbins et al. 1989a; Terborgh et al. 1990) and movement patterns for Jamaican birds (Cruz 1981). To increase the probability that birds were independently sampled, replicate landscapes were separated by > 1 to 26 km, with the exception of peri-urban landscapes due to logistical constraints. This distance range should be sufficient to prevent overlap in territories or daily movement of the majority of Jamaican forest birds within our sampling periods (Chapter 3, A. M. Haynes-Sutton, *personal communication,* S. E.

Koenig, Windsor Research Centre, *unpublished data*). We identified landscapes based on 2001-2002 IKONOS imagery, land-cover maps (Forestry Department 1999), and field verification. To assess the spatial characteristics of forest habitat, we digitized forest cover from IKONOS multispectral pan-sharpened imagery (1-m resolution, Space Imaging 2002) and ground-truthing surveys using ArcGIS 9.3 (ESRI 2008) (LCC, WGS 84 projection). Forest habitat was categorized by a closed canopy and visual dominance of native broadleaf trees; producer's and user's accuracy for this cover type were estimated at 92% and 84%, respectively. Accuracy was based on 1,983 reference points collected across our study region: 536 forest reference points and 1446 non-forest reference points (493 points of scattered trees, 415 points of agricultural fields, 229 of cleared land, and 310 points of development) (see Appendix I for definitions). We selected fragmented landscapes that contained a similar proportion and spatial configuration of remnant forest, but that were dominated by only one of the three target matrix types. Human-modified landscapes contained ~ 36% of forest cover and ~ 20 fragments that were an average of 4 to 6 ha. Shape complexity of forest fragments (1.3 to 1.4 perimeter-area fractal dimension), inter-patch distances (20 to 30 m), and patch connectivity (~ 34% of patches inter-connected) were also similar among the different landscape matrix types. (Comparisons of patch- and landscape-level patterns of forest fragmentation in agricultural, peri-urban, and bauxite landscapes are detailed in Appendix A.) To serve as reference sites, we selected landscapes in the largest intact forested areas in the region (Figure 1.1).

Land-cover composition and vegetation structure in matrix areas differed substantially among the three human-modified landscape types. We conducted > 700 vegetation surveys documenting both land-cover composition and foliage structure in matrix areas (see Appendix B for full detail). Agricultural landscapes were dominated by introduced pasture and herbaceous gardens (~ 60%), followed by treelined fencerows (18%), paddock trees (9%), and secondary growth of *Acacia* stands (10%) that were interspersed in valleys between forested hilltops. Peri-urban landscapes consisted mainly of low-density residential housing and roads that were surrounded by lawns (~ 10%), herbaceous gardens (9%), fruiting tree gardens (25%), ornamental shrubbery (20%), ornamental trees (12%), and mixed woodlands (11%). Bauxite landscapes were former agricultural lands that had been converted to mining within the past ten years; relictual forests were surrounded by exposed bauxitic soils with vegetation cover dominated by planted grassland or ferns (~ 78%) and recent growth of *Acacia* trees (19%). Peri-urban and agricultural matrices had greater foliage cover and vertical complexity than bauxite lands, largely due to the presence of scattered trees in peri-urban areas (i.e., ornamental tree gardens, vacant woodlots) and in agricultural pasture (i.e., paddock trees, live fences, fencerows).

We surveyed an average of five forest fragments per replicate landscape using stratified random sampling to represent the size distribution. Twenty-two of these fragments were sampled in an agricultural matrix, 19 in a peri-urban matrix, and 27 in a bauxite mining matrix. Qualitative assessment based on aerial photographs taken in 1968 indicated that sampled fragments have been in existence for at least forty years (Evelyn 1997), although the nature of matrices may have changed within this time period. Within forested landscapes, we selected 31 “pseudo-patches” by randomly accumulating consecutive samples along transects that were located in intact forest, such that sampled areas were approximately equal in size to patches in fragmented landscapes. We refer to both pseudo-patches sampled in a natural "matrix" and forest fragments sampled in human-modified matrices as "patches." In total, 99 forest patches were sampled across 20 landscapes.

Sampled patches had similar forest area (mean ± 1 SE = 3.89 ± 0.45 ha) and isolation (33.58 ± 3.48 m, 160.80 ± 19.79 m, and 2381.75 ± 147.07 m to the nearest fragment > 0.5 ha, 5 ha, and 100 ha, respectively) (Appendix A). Vegetation structure in patches did differ, however, among the four landscape matrix types (comparisons are detailed in Appendix C). Patches in agricultural landscapes, and to a lesser extent in continuous forest, had 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 had lower and relatively more open canopies and a greater proportion of herbaceous cover and low shrubs (Appendix C). We did not exclude patches where selective logging or moderate human use has occurred, because (1) all forest in the region is unprotected secondary forest that is subject to on-going human encroachment, and (2) we wanted to document bird richness and abundance patterns in landscapes undergoing disturbance that was representative of each landscape matrix type.

Sampling of resident bird communities

We conducted a total of 286 point counts on two or three separate occasions from early February to mid-June during the height of breeding activity (Raffaele et al. 1998), each year for three consecutive breeding seasons (2005-2007). Point counts were conducted along a centrally placed transect in each of the 68 forest patches in human-modified landscapes, and along one to three randomly placed transects (averaging 1500 m in length) in forested landscapes. We surveyed an average of 12 to 15 stations per replicate landscape per occasion. We conducted sampling proportional to forest area to ensure representative coverage, typically adding one station for each additional hectare (conditional on the terrain). To minimize double-counting, stations were located 100 m apart and > 25 m from a matrix-forest boundary. Surveying intensity was uniform among landscapes and sufficient in representing resident bird diversity in the region based on species accumulation curves that reached definitive asymptotes in all four landscape types (Gotelli and Colwell 2001) (Appendix D).

At each point-count station, we recorded the number of individuals per species seen or heard within a 10-minute period (conducted between 0600-1000 hrs on clear days without rain) and in a 25-m fixed-radius area (Hutto et al. 1986). We selected a 25-m radius because it provided reliable detection across all of our sites based on field tests, as found by other researchers in the Caribbean (Wunderle and Waide 1993). Each site was visited by one of three trained observers for repeat counts within a season, and the order of site visitation was rotated throughout each field season. Thus, potential bias due to heterogeneity in detection due to observer and time-of-day effects and differential effort was diminished with our sampling scheme, lending confidence in the reliability of our abundance estimates.

To determine species occurrence in and potential use of matrix habitats, we conducted 241 point counts in 2005 in matrix land cover surrounding forest patches in fragmented landscapes. Two to four point-count stations were located midway between adjacent forest fragments (when logistically feasible) and > 100 m from a matrix:forest boundary in at least two cardinal directions. We conducted matrix point counts using a protocol similar to that used in the forest point counts (i.e., 10-min fixed radius point count) during a similar time span (early March to mid June). Matrix surveys were used to determine bird-habitat associations for trait analyses (as described below).

Species traits

We considered the influence of 11 traits on bird responses to landscape matrix type. Trait values for each species were determined from published information in field guides and primary literature, consultation with ornithological experts, and personal field observations (Appendix E). We recorded species taxonomic order and derived body mass and clutch size based on averaged published estimates. Species were classified into diet guilds based on dominant food sources consumed (i.e., frugivore, nectarivore, insectivore, omnivore, granivore, and carnivore). We categorized where a species is found to forage or nest into four height zones: ground (< 0.5 m), understory (shrub layer to midstory canopy, up to 5 m), canopy (upper forest layer, > 5 m), or multiple strata (commonly using more than one height zone). Nest type was classified as open or closed, with the former containing large openings (i.e., cup, saucer, and platform nests) and the latter being partially enclosed (i.e., cavity, burrow, sphere, and pendant nests). Geographic range was based on whether species distributions were restricted to Jamaica, the Caribbean, the New World Tropics, or spanned both Nearctic and Neotropical regions. Altitudinal range was based on species distributions among lowland, mid-elevation, and montane regions in Jamaica.

We determined species rarity and habitat associations based on our own field data. Rarity was based on the average density of each species in continuous forest over the three-year sampling period except for birds classified as open-associated (see below), for which we relied on average densities in matrix habitats. We classified species as forest-restricted, generalist, or open-associated by comparing their average densities in continuous forest to their average densities in matrix habitats. Species were classified as restricted to forest habitat if their average densities were at least three times greater in forest than in matrix areas. In contrast, species were classified as associated with open habitats if their average densities were at least three times greater in matrix areas than in continuous forest. Species with densities within a factor of three between forest and matrix habitats were classified as generalist species. We chose this cutoff to ensure that species categorized as forest and open-associated had a strong affinity for respective cover types. This somewhat arbitrary cut-off was necessary, because no standard exists in the literature to delineate habitat-specificity. Our resulting classifications, however, closely matched habitat associations published in field guides (e.g., Downer and Sutton 1995; Raffaele et al. 1998), and with the expert opinion of local ornithologists (P. P. Marra, A. M. Haynes-Sutton, and H. A. Davis, *personal communication*). Based on those convergences, we are very confident in our habitat classifications

Statistical analyses

All resident native birds detected in our study region are included in analyses, with the exception of nocturnal and aquatic birds, vultures, swifts, and swallows. Species richness estimates were based on all detections at forest point-count stations (i.e., within the 25-m fixed radius and beyond). Abundance estimates for community and individual species analyses (as described below) were restricted to detections within the 25-m radius to minimize potential double-counting of individual birds.

Community composition

We used non-metric multidimensional scaling (NMDS) to describe variation in the composition of resident bird communities in forest patches embedded in the four matrix types. NMDS is a non-parametric ordination technique effective for graphically depicting multivariate relationships in ecological data, via maximizing the rank correlation between calculated distances in an original matrix and distances in reduced ordination space (Kruskal 1964; Clarke 1993). NMDS was performed using a Bray-Curtis dissimilarity matrix derived from species relative abundances at the patch-level, where patches were standardized by dividing species abundances by the total number of point counts conducted within each patch across all years. To avoid spurious effects of rare species, we excluded species that occurred in less than 5% of samples and standardized community matrices by species maximum. Overall statistical significance of the ordination was determined based on a Monte Carlo unrestricted permutation test with 100 randomizations. Standardized avian species composition was compared among matrix types using multiresponse permutation procedure (MRPP) (based on Bray-Curtis distance matrix), which compares distances among samples within *a priori* groups from those derived from a randomization procedure (Mielke and Berry 2001; McCune and Grace 2002). To determine the importance of spatial dependence among sampled patches, we tested for the overall correlation between the standardized species community matrix with a corresponding matrix of geographic distance between patches using a Mantel test (Bray-Curtis distance matrix, N = 9999 randomizations) (Legendre and Legendre 1998).

Species richness and individual species abundances

The influence of the landscape matrix on species richness and individual abundances was analyzed using linear and generalized linear mixed models, respectively. Both richness and abundances were based on total point counts in each forest patch for each sampling occasion. Species richness was estimated based on Chao1, a nonparametric estimator that accounts for detectability using species abundance distributions (Chao et al. 2005) and that is more robust than other richness estimators (Walther and Moore 2005). Based on model diagnostics (e.g., histograms and plots of residuals versus fitted values) and dispersion scores, we modeled richness via a normal distribution and abundances via a Poisson probability distribution using a log link function.

Because sampling was conducted hierarchically (i.e., patches sampled within landscapes) and over multiple time intervals (i.e., within and across three years), we examined eight models that captured three distinct error structures that were logical based on our sample design: (1) correlations among repeat observations of a patch (temporal correlation); (2) correlations among patches within a landscape (spatial correlation); and (3) correlations among patches within a landscape across different sampling occasions (temporal and spatial correlations) (Pinheiro and Bates 2002). Based on the lowest Akaike's information criterion, corrected for small sample sizes (AIC_c), and using maximum likelihood estimation (Burnham and Anderson 2002), the most supported model for species richness and for ~ 60% of species accounted for within-patch correlation due to repeated measures but lacked explicit correlation among years and due to patch location. Our final models therefore included landscape matrix type as the fixed effect and patch identity as a random effect, using a Laplace likelihood approximation, which is considered more accurate for count data with small means (Bolker et al. 2009).

Significance of differences in species richness and relative bird abundances among forest patches embedded in the four matrix types was determined based on ANOVA F tests and Wald χ^2 tests, respectively. Posthoc pairwise comparisons were conducted using Tukey's multiple comparison procedure to separate treatment means (Westfall and Young 1993). We used a familywise $\alpha = 0.10$ to indicate a biologically relevant response. Failing to detect an effect when species were in fact differing in abundance by landscape matrix type (making a Type II error) had as severe a consequence as falsely detecting an effect (making a Type I error). Using a familywise $\alpha < 0.10$ would have led us to substantially under-predict species that were responding to forest fragmentation given stronger evidence to the contrary, which would have had repercussions for a subsequent analysis (see below).

Matrix response and species traits

We categorized species into one of four response classes based on differences in relative abundance in forest patches among the human-dominated matrix types relative to a continuous forest matrix, as detected by mixed models and posthoc tests: (1) lower abundance(s) in patches embedded in one or more of the human-dominated matrix types (Type L); (2) higher abundance(s) in patches embedded in one or more of the human-dominated matrix types (Type H); (3) opposite matrix response, with higher abundance in patches in at least one human-dominated matrix type and lower abundance in patches in a different human-dominated matrix type (Type O); and (4) no significant difference in abundance in patches among any of the three human-dominated matrix types relative to intact forest (Type N).

We used a classification decision tree analysis to assess whether species traits predicted how species grouped within response types. This non-parametric method determines membership in pre-defined groups based on a suite of characteristics using recursive data partitioning. This technique is well suited for non-normal, inter-correlated, multivariate data characteristic of life history traits (De'ath and Fabricius 2000). We selected the final model based on a series of 1000 10-fold cross-validations, using the 1-SE rule and Gini index of impurity, and prior probabilities proportional to sample sizes. Overall statistical significance of the final tree was determined based on Monte Carlo resampling (N = 1000 randomizations) (Breiman et al. 1993).

We tested the relative importance of each trait with regard to species sensitivity to forest fragmentation and landscape matrix type in two ways. First, we calculated the ability of each trait to distinguish among matrix response types as determined by the decrease in impurity attributable to the best surrogate split for each variable on the final classification tree (Breiman et al. 1993). We also conducted goodness-of-fit tests to determine the statistical significance of each trait in relation to matrix response. These univariate tests complement the tree-based approach by detecting important variable(s) that may be masked in a tree-based framework (McCune and Grace 2002; Maindonald and Braun 2003). For both the classification decision tree analysis and the goodness-of-fit tests, we excluded the one species with an opposite matrix response, given this was a unique response and thus insufficient to analyze independently. To increase the reliability of the contingency table analyses, we increased cell counts by combining the seven species with higher abundances in patches in fragmented landscapes with species that lacked an abundance response. This contrast provided a distinct comparison between birds likely to be negatively affected by forest fragmentation (i.e., exhibit lower abundances, Type L) versus those that may not (i.e., exhibit higher or constant abundances in human-modified landscapes relative to intact forest, Types H + N). Due to multicollinearity among traits, separate tests were conducted on each trait and based on randomized chi-square tests using Monte Carlo simulations (N = 1,000,000 randomizations), which are more accurate for sparse cell counts (Sokal and Rohlf 1995). We examined adjusted residuals from chi-square tests to determine classes that were driving significant overall differences (Everitt 1992).

Statistical packages

Statistical analyses were performed using the *R* statistical system (v 2.8.1) (R Development Core Team 2008) and SAS (v 9.2) (SAS Institute, Cary, NC). Richness (Chao) estimation, NMDS, MRPP, and Mantel tests were performed using the *R* 'vegan' package (v 1.13.1) (Oksanen et al. 2008). Model selection for linear and generalized linear mixed models was conducted using 'nlme' (Pinheiro et al. 2008) and 'lme4' (Bates et al. 2008) packages, respectively. The final linear mixed model was implemented using 'nlme' and multiple comparisons performed via 'multcomp' package (Hothorn et al. 2008) in *R*; final generalized linear mixed models were implemented using PROC GLIMMIX in SAS. Chi-square tests were performed using 'stats' package and classification regression trees using 'rpart' package in *R* (Therneau and Atkinson 2009).

Results

Species richness and community composition

In total we detected 16,996 resident birds in forest patches among all landscapes, and captured 44 resident species, of which 23 were endemic to Jamaica. Estimated richness of resident birds significantly differed in patches embedded in the four different matrix types (mixed model ANOVA, $F_{3,95} = 6.29$ $P = 0.0006$). Based on pairwise comparisons, forest patches in an agricultural matrix had greater richness than did patches in peri-urban and bauxite matrices ($P = 0.0225$ and $P = 0.0027$, respectively). Patches embedded in a continuous forest matrix exhibited richness greater than patches in a bauxite matrix ($P = 0.0075$) and marginally greater than patches in a peri-urban matrix ($P = 0.0595$). Avian richness did not differ in patches embedded in forest and agricultural matrices ($P = 0.9341$), nor did it differ in patches in peri-urban and bauxite matrices ($P = 0.9665$) (Table 1.1).

We retained 41 of the 44 resident species detected in the community analyses based on the > 5% detection rule. NMDS ordination resulted in a 3-axis solution, with a final stress of 17.702, which is within the range reliable for community data and unlikely to have been obtained by chance (Monte Carlo test, $P < 0.001$) (McCune and Grace 2002). The three axes together represented 96.9% of the variance in resident bird communities, using a fit-based R^2 measure (Oksanen et al. 2008). Patches within the same matrix type tended to group together in ordination space, indicating a similarity in bird community composition (Figure 1.2). Substantial overlap in patches in forest and agricultural matrices in ordination space indicated shared species assemblages. Despite these similarities, the MRPP analyses confirmed that forest bird communities differed significantly among all matrix types ($A = 0.0587$, $P < 0.0001$) (Figure 1.2). Differences in community assemblage among matrix types cannot be attributed to mere spatial correlation among patches (Mantel test, $r = 0.0869$, $P = 0.102$).

Individual species responses

Thirty-six species that were detected in > 15% of patches had sufficient occurrences to model via Poisson regressions (i.e., likelihood functions converged with reliable model fit and parameter estimates). Relative abundances of 69.4% of these species differed significantly in forest patches among the four matrix types, which is greater than would be expected by chance (binomial test, $P = 0.014$). Thirteen species had lower abundances in one or two of the human-dominated matrix types (agriculture, peri-urban, bauxite) (Table 1.1). Six of these species had abundances that were lower in forest fragments in peri-urban and bauxite matrices relative to a forest matrix; but their abundances in fragments in an agricultural matrix were similar to in intact forest. Seven species had reduced abundances in only one human-dominated matrix type; for all but one of these species, abundances were lowest in peri-urban forest fragments. The Black-faced Grassquit was the exception, being least abundant in fragments in a bauxite matrix, but as equally abundant in fragments embedded in a peri-urban matrix as in a forest matrix (Table 1.1; scientific names listed). No species was consistently lower in abundance in fragments in all three human-dominated matrix types. Two species, however, showed trends suggesting this response, but were too scarce for statistical analyses: the Stolid Flycatcher was detected 86% of the time in continuous forest (12 times) and the Rufous-throated Solitaire was detected only in continuous forest (8 times).

No species exhibited abundances that were consistently higher in forest fragments in all three human-dominated matrix types, but seven species were higher in abundance in one or two of the human-dominated matrix types relative to continuous forest. Of these species, five were higher in abundance in fragments in an agricultural matrix but lower in abundance in fragments in peri-urban and bauxite matrices. Two species were more abundant in two types of human-dominated landscapes relative to continuous forest: the Loggerhead Kingbird was higher in abundance in forest embedded in both agriculture and bauxite, and the Smooth-billed Ani was higher in abundance in forest embedded in both bauxite and peri-urban development. Only one species, the Vervain Hummingbird, was more abundant in patches in a peri-urban matrix than in all other matrix types.

The White-eyed Thrush was the only species that exhibited an opposite matrix response, with abundances higher in agricultural patches but lower in bauxite patches. The remaining fifteen species did not differ in abundance in forest patches in human-dominated matrix types relative to a forest matrix. Four of these species, however, had abundances that varied among the three human-dominated landscape types.

Overall, peri-urban and bauxite landscapes had the highest frequency of resident birds with reduced abundances relative to continuous forest: 8 species were lower in abundance in bauxite patches, and 12 species were lower in abundance in peri-urban patches (Figure 1.3). No species was less abundant in patches in agricultural landscapes relative to forested landscapes. Six species were more abundant in patches in an agricultural matrix whereas only three species were more abundant in patches in bauxite and/or peri-urban matrices relative to a forest matrix.

Role of species traits

The most parsimonious classification tree model (with the greatest prediction accuracy) included only 1 of 11 traits (diet guild) and predicted two response types (Type L and Type N). Sixty-six percent of observed bird responses to landscape matrix were correctly classified based on diet guild alone, which is greater than expected by chance (Monte Carlo simulation, $P = 0.0079$) (Figure 1.4). The model correctly classified 84.6% of species with observed lower abundances, and 80.0% with observed similar abundances in patches in human-dominated matrices compared to a forest matrix. Misclassifications largely stemmed from the erroneous categorization of the seven species with higher abundances in fragmented landscapes (Type H). Five of these species were incorrectly predicted to have no difference in abundance (i.e., misclassified as Type N); and two of these species were incorrectly predicted to have lower abundances in fragmented forest relative to continuous forest (i.e., misclassified as Type L).

The decision tree analysis and chi-square tests provided complementary support that diet guild, nest height, habitat association, and to a lesser extent foraging strata, were strongly associated with bird responses to landscape matrix (Table 1.2). Taxonomic order, geographic and altitudinal range, body size, rarity, clutch size, and nest type had weak prediction power and lacked any statistical association.

Diet Guild: A total of 70% of insectivores and 67% of frugivores had lower abundances in patches in human-dominated matrices than a forest matrix. In contrast, 100% of nectarivores and omnivores and 86% of granivores had higher or similar abundances in fragments (Figure 1.4, Figure 1.5a). Carnivores lacked a consistent response, with the Jamaican Lizard-Cuckoo exhibiting lower abundances, and the

Chestnut-bellied Cuckoo and the Mangrove Cuckoo exhibiting similar abundances, between human-dominated and forested landscapes.

Habitat association: The extent to which a species was known to be a forest specialist rather than to use matrix habitats impacted its response to fragmentation. Forest-restricted species exhibited the greatest reductions in abundance, with 70% lower, 30% similar, and none higher in abundance in patches in human-dominated matrices than in a forest matrix (Figure 1.5b). In contrast, ~ 90% of birds associated with open habitats and ~ 80% of generalist birds had greater (38% and 29%, respectively) or equal abundances (50% each) in fragments as compared to continuous forest.

Nest height: The dominant height at which a species nested also impacted its fragmentation response. Eighty-six percent of canopy-nesting species were less abundant and 14% were equally abundant in forest patches in human-dominated matrices relative to a forest matrix (Figure 1.5c). In contrast, 100% of ground-nesting species either had similar abundances (75%) or had higher abundances (25%); and 80% of multi-strata nesters had similar or higher abundances in patches in human-dominated matrices (60 percent and 20 percent, respectively) than in a forest matrix. Understory nesters failed to exhibit a consistent response, with roughly one third of species with higher (31%), lower (38%), or equal abundances (31%) in patches in human-dominated landscapes relative to intact forest.

Foraging strata: Canopy foragers, and to a lesser extent understory foragers, had abundances that were lower in fragmented landscapes than did ground foragers (Figure 1.5d). Two thirds of canopy foragers were lower in abundance in fragments; whereas 17% were higher abundance and another 17% were equal in abundance in fragments as intact forest. Fifty-six percent of understory foragers were lower in abundance, 33% were equal in abundance, and only 11% (one species) were more abundant in patches in human-dominated matrices than in a forested matrix. In contrast, all but one ground-foraging species had greater (30%) or similar (60%) abundances in human-dominated landscapes as compared to forested landscapes. Species that foraged among multiple strata failed to exhibit a strong response, with 20% higher, 30% lower, and 50% exhibiting no change in abundance among fragmented versus forested landscapes.

Discussion

Richness, community composition, and abundances of birds mediated by landscape matrix

Landscapes in Jamaica would seem to adhere to the classic binary habitat versus non-habitat model in that historically forested areas have been converted to an intensely modified matrix that is superficially similar in being comprised of novel habitats with relatively little or no forest cover. This study demonstrates, however, that such a simplistic model of habitat fragmentation does not adequately reflect responses of Neotropical bird communities in Jamaica. Suites of species were profoundly affected by whether once-continuous forest was converted to agricultural, peri-urban, or bauxite mining development. Almost 70% of bird species differed in abundance in patches among the four landscape matrix types. Over 36% of species had lower abundances in forest fragments embedded in peri-urban and bauxite mining matrices relative to a forested matrix. Another 20% had higher abundances in fragments embedded in an agricultural matrix than in a forest matrix. One species had mixed responses, with abundances greater in forest in one human-modified matrix type (agriculture) but lower in another (bauxite). No species exhibited a consistently higher or lower abundance response in all human-modified landscape types. The agricultural matrix had seemingly little effect even on forest-restricted species and some generalist species, and species associated with open habitats actually increased in this landscape type. In contrast, peri-urban and mined landscapes had lower native bird diversity and had communities that were strikingly different from those in forested landscapes; in these intensely developed landscapes, many insectivores and frugivores were absent or in reduced abundance. These matrix-specific responses were detected despite similar climate, geology, elevation, and forest type, and despite controlling for the amount and configuration of forest cover among anthropogenically fragmented landscapes.

Role of species traits and possible mechanisms mediating responses to forest fragmentation

Three proximate mechanisms have been proposed to explain divergent responses to forest fragmentation by species in different landscape contexts: (1) differential impedence or facilitation of inter-patch movement in varying composition and configuration of matrix land cover (e.g., Bélisle et al. 2001; Renjifo 2001; Ricketts 2001; Gobeil and Villard 2002; Revilla et al. 2004; Bender and Fahrig 2005); (2) differential alteration of inter-species interactions, in particular predation (Rodewald and Yahner 2001; Chalfoun et al. 2002); and (3) differential mediation of resources either via habitat compensation by the addition of alternative or supplemental resources (e.g., food or nesting sites) in certain matrix areas (e.g., Gascon et al. 1999; Norton et al. 2000; Brotons et al. 2003; Cook et al. 2004) or the disparate reduction of within-patch habitat quality (i.e., microclimate and vegetation structure) due to dissimilar edge effects (Saunders et al.

1991; Ries et al. 2004) or uneven human disturbances (Friesen et al. 1995; Rodewald and Bakermans 2006).

Collectively, our results suggest that resource availability may be the more important driver of bird community changes in Jamaica's fragmented landscapes. Although we cannot tie any single trait to a particular mechanistic explanation, the combination of traits that emerged as important provides key insights. Diet guild, habitat association, nest height, and foraging strata best predicted the variation in bird responses to forest fragmentation in the different landscape matrices. These four traits strongly relate to a species ability to acquire and use resources in human-modified landscapes. Jamaica's insectivorous birds had lower abundances in fragmented landscapes relative to other guilds. This finding supports growing research that insectivorous birds are declining disproportionately in tropical forest remnants (e.g., Castelletta et al. 2000; Ribon et al. 2003; Sodhi et al. 2004; Sigel et al. 2006; Stouffer et al. 2009). One hypothesis is that such declines may be due to the interdependent effects of loss of microhabitats and decline of prey availability (e.g., Burke and Nol 1998; Zanette et al. 2000). The fact that forests in agricultural landscapes supported a greater number of insectivores may be due to greater leaf area indices (Appendix C) that could translate to greater foraging substrates. Frugivores also exhibited lower abundances in human-modified landscapes in the region. Survival of birds in this guild has been shown to be jeopardized in fragmented forests (Kattan et al. 1994; Ribon et al. 2003; Ruiz-Gutierrez et al. 2008), potentially due to lack of year-round fruit in deforested tropical areas (Sodhi et al. 2004). Understory and canopy foragers and canopy nesters also had lower abundances, which may be due to the reduction in the vertical complexity of forest structure and the loss of canopy and emergent trees in peri-urban and bauxite mining landscapes (Appendix C); an effect that has also been shown to accompany tropical forest fragmentation (Tabarelli et al. 2004). In contrast, nectarivores, omnivores, and granivores were insensitive to fragmentation, particularly in agricultural matrices. Edge- and matrix-foraging birds are increasingly shown to persist and even thrive in fragmented tropical systems (e.g., Stouffer and Bierregaard 1995; Renjifo 1999; Sigel et al. 2006) due to potential cross-boundary subsidies (Fagan et al. 1999; Cantrell et al. 2001). A species tolerance of forest conversion is increasingly linked to its ability to utilize resources in matrix habitats (e.g., Laurance 1991; Gascon et al. 1999; Henle et al. 2004).

Many studies examining the role of the matrix have focused on how matrix habitats impact dispersal or movement (e.g., Renjifo 2001; Ricketts 2001; Gobeil and Villard 2002; Revilla et al. 2004). Dispersal limitation is often invoked to explain bird responses to forest fragmentation in temperate (e.g., Bélisle et al. 2001; Bélisle and Clair 2002) and tropical regions (e.g., Robinson 1999; Renjifo 2001; Laurance et al. 2002; Sekercioglu et al. 2002; Stratford and Robinson 2005). This mechanism, however, may not be of overriding importance in Jamaica. This assertion is based on the fact that traits linked to species dispersal abilities were not associated with bird-landscape associations. Body size and taxonomic order, which are found to correlate significantly with potential dispersal power of birds (Sutherland et al. 2000), did not emerge as important predictors. Geographic and altitudinal range sizes, which relate in part to species dispersal and establishment abilities (Gaston 1996), also failed to predict landscape matrix responses. Moreover, frugivores had disproportionately lower abundances in forest remnants than in intact forest; but we would not predict that these species would be dispersal-limited due to their adaptations to search for resources that are patchily distributed in both space and time (Bowler and Benton 2005). The karst countryside in central Jamaica is characterized by small forest hilltops, often < 10 ha, which are separated by other land uses but remain in close spatial proximity (e.g., hundreds of meters apart) relative to potential bird dispersal. Such small distances between forest patches may not prohibit frequent movement of many bird species. Moreover, the evolutionary history of Caribbean avifauna has likely promoted selection of species with stronger dispersal abilities and fewer physiological or morphological limitations than mainland counterparts; these characteristics have allowed them to (re)colonize and (re)establish in island habitats and to withstand large-scale natural disturbance events like hurricanes (Lack 1976; Ricklefs and Bermingham 2008).

Other frequently cited causes of forest bird declines are increased nest parasitism and predation (e.g., Robinson et al. 1995; Lampila et al. 2005), the impact of which can vary by landscape context (Donovan et al. 1997; Rodewald and Yahner 2001; Chalfoun et al. 2002; Driscoll and Donovan 2004). Traits such as nest type and nest height may affect a species susceptibility to nest predation, with open- and ground-nesting species found to be at greater risk (Ford et al. 2001; Chalfoun et al. 2002; Lampila et al. 2005) (but see Martin 1993). Abundance differences between fragmented and intact forest, however, were not related to nest type. Moreover, species predicted to be most sensitive to nest predation (ground nesters) were least likely to exhibit lower abundances; and species predicted to be least sensitive to nest predation (canopy nesters) were more likely to exhibit lower abundances in human-modified landscapes. Traits related to reproductive potential (i.e., rarity and clutch size) also failed to predict bird abundance patterns. Thus, differential functional connectivity (i.e., via altering species dispersal and recolonization events) and differential population growth potential (i.e., via population sinks due to higher predation) may not be dominant mechanisms underlying bird responses to forest fragmentation in Jamaica.

Impacts of land uses in the matrix interacting with forest fragmentation effects

In contrast to findings from other temperate and mainland tropical studies, birds in Jamaica may be influenced more by the extent to which the landscape matrix mediates the availability of critical resources. This mediation could occur through resource supplementation in matrix habitats, or differential reduction of within-patch forest quality, or some combination of both. In many cases, matrix habitats may be hospitable for native species, and may provide supplemental or additional resources that allow for population maintenance or growth in fragmented systems (Norton et al. 2000; Brotons et al. 2003; Cook et al. 2004). In comparison to bauxite lands, peri-urban and agricultural matrices contained greater vegetation cover and complexity (Appendix B). Vegetation in agricultural matrices (e.g., pasture, paddock trees, and live fences) may have provided additional resources for omnivores and granivores, which were more abundant in these landscapes than in other matrix types. Similarly, nectarivores may have benefited from residential gardens, given these birds were equally or more abundant in peri-urban landscapes as compared to other human-modified matrix types.

Human land uses not only modify external matrix habitats but also can impact internal forest conditions. Surface-mining activities in bauxite areas involve large-scale removal of vegetation and topsoil, and the creation of open pits of exposed earth, all of which could alter soil water retention, create dust pollution, and lead to biogeochemical and hydrologic changes (Bell and Donnelly 2006). Bauxite development also introduces extensive noise and road development. All of these factors likely impact within-forest microclimate and structure, and can alter the composition of fauna, but the degree and direction of these changes are largely unknown (Simmons et al. 2008). Even after post-mining restoration, ecological communities may not fully recover to their original state (Parrotta and Knowles 1999; Parrotta and Knowles 2001). Bird species in peri-urban landscapes may be disproportionately affected by forest disturbance from human activities (e.g., hunting, selective logging, noise, spread of fire or invasives) (e.g., Theobald et al. 1997; Marzluff et al. 2001; Miller et al. 2003; Rodewald and Bakermans 2006). Forest remnants in bauxite and peri-urban matrices have low stature and more open canopies, less structural complexity, and greater percent shrub layer (Appendix C); these factors indicate that these forests may have undergone greater disturbance and/or be in earlier successional stages than forests in agricultural matrices (Asprey and Robbins 1953). Agricultural areas tend to be in large private land holdings, which afford a greater level of forest protection than commonly found in bauxite and peri-urban areas.

Even though landscapes we surveyed had similar environmental conditions (e.g., elevation, climate, soil substrate), we were unable to disentangle the effects of forest structure from matrix type because they were inter-dependent. Rarely will alterations to the surrounding landscape matrix proceed without associated changes internal to forest habitat (Laurance et al. 2002; Laurance 2008). Forest conditions were closely tied to land-cover and land-use practices in matrix areas; thus, they were part of the collective matrix effects in Jamaica. Avian community structure could be driven as much by the degree of disturbance to internal properties of remnant forest as by the external properties of the matrix. These findings are consistent with an edge model that predicts that species responses in complex landscapes are determined both by changes to internal habitat quality and by changes to the availability of matrix resources (Sisk et al. 1997; Ries and Sisk 2004; Ries and Sisk 2008).

Conservation implications

Treating all anthropogenically modified lands as a single cover type (i.e., non-habitat) in fragmentation research and/or conservation planning has consequences for biodiversity. All matrix types examined in our study could be classified as having a similar "edge contrast" (Strayer et al. 2003) in that they differed dramatically in structure, composition, and microclimate from the once-contiguous native forest. Consequently, matrix areas could be considered equally hostile to native species. Bird communities, however, did not respond evenly to the three human-modified matrix types. Patches surrounded by an agricultural matrix maintained greater native bird diversity and more intact community assemblages than did patches embedded in a peri-urban or a bauxite mining matrix. Treating all modified lands equally, and categorizing Jamaica's landscapes into "matrix" versus "forest" components would have hidden these important patterns. The trajectory of land conversion in many regions of the world is from subsistence agriculture to increasing urbanization (DeFries et al. 2004). Since the 1950s, land-cover change in Jamaica (Evelyn and Camirand 2003) and on other Caribbean islands (Lugo 2002) results largely from conversion of agriculture to residential development and mining for bauxite. This study strongly suggests that such land conversion could cause loss of a large proportion of the Neotropical bird community, even without additional forest loss or fragmentation. Although we have not experimentally confirmed the mechanism, evidence suggests that human land-use practices in the matrix may be driving differential abundance patterns via mediating resource availability both within the forest and in external matrix habitats.

Historic declines and temporal differences among land uses must also be considered when interpreting trends. Examination of current-day abundance patterns may underestimate the effects of forest fragmentation on species persistence in regions like the West Indies, where flora and fauna have been altered by a long history of habitat conversion, human disturbance, and introductions of novel predators (e.g., rats, mongoose) (Ricklefs and Bermingham 2008). Abundance patterns detected in Jamaica's fragmented landscapes may be gross underestimates, given that the reference baseline is itself unprotected secondary forest that has been have been altered by decades of selective logging, fuelwood collection, and human-caused fire (Forestry Department 2001; Tole 2001). Moreover, the full extent of species responses may not have been captured uniformly among landscapes due to the temporal differences among land practices. Bauxite matrices were more recently converted (< 10 years); therefore, their full impacts may not yet be fully manifest. Thus, we recommend continued research to document the long-term effects of land-use practices and the relative importance of extinction versus colonization processes on species persistence in the Caribbean. This study, however, provides key insights into potential mechanisms that may underlie the role of the landscape matrix on Neotropical avian communities in fragmented forests.

Table 1.1. Estimated means (± 1 SE) of linear and generalized linear mixed models for richness and abundances of native resident birds in forest patches in agricultural (N = 22), peri-urban development (N = 19), or bauxite mining (N = 25) landscapes, or sites in continuous forest (N = 31) in central Jamaica. *P*-values are based on ANOVA F tests and Wald χ^2 tests (values in bold significant at $P < 0.05$ and * for $P < 0.10$). Letters indicate pairwise comparisons among matrix types based on posthoc Tukey's HSD tests. Species are categorized based on abundance differences among human-dominated matrix types relative to intact forest.

	Forest		Agriculture		Peri-urban		Bauxite			Diet†	Habitat assoc.§	Nest ht.‖	Foraging strata‖
Species & Response Type	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P*- value				
Species Richness	26.25^{a}	1.76	27.30^{a}	1.35	21.79^{b}	1.92	20.94^{b}	1.81	**0.0006**				
Lower abundance in peri-urban & bauxite landscapes													
Arrow-headed Warbler (*Dendroica pharetra*) (e)	0.48^{a}	0.10	0.76^{a}	0.18	0.06^{b}	0.02	0.14^{b}	0.04	**<.0001**	I	FR	U	M
Jamaican Becard (*Pachyramphus niger*) (e)	0.23^{a}	0.06	0.29^{a}	0.09	0.02^{b}	0.01	0.01^{b}	0.01	**<.0001**	I	FR	C	C
Jamaican Elaenia (*Myiopagis cotta*) (e)	0.28^{a}	0.07	0.39^{a}	0.11	0.02^{b}	0.01	0.11^{c}	0.04	**<.0001**	I	FR	C	C
Jamaican Pewee (*Contopus pallidus*) (e)	0.36^{a}	0.10	0.25^{a}	0.09	0.00^{b}	0.00	0.01^{b}	0.01	**0.0001**	I	FR	C	U
Jamaican Woodpecker (*Melanerpes radiolatus*) (e)	0.67^{a}	0.11	0.68^{a}	0.14	0.31^{b}	0.07	0.22^{b}	0.05	**0.0001**	I	G	C	M
Rufous-tailed Flycatcher (*Myiarchus validus*) (e)	0.28^{a}	0.07	0.36^{a}	0.10	0.05^{b}	0.02	0.04^{b}	0.02	**<.0001**	I	FR	C	C
Lower abundance in peri-urban landscapes													
Greater Antillean Bullfinch (*Loxigilla violacea*)	1.04^{a}	0.15	1.12^{a}	0.19	0.61^{b}	0.12	0.95^{ab}	0.15	0.0834*	F	FR	M	U
Jamaican Lizard-Cuckoo (*Saurothera vetula*) (e)	0.06^{a}	0.03	0.04^{ab}	0.02	0.00^{b}	0.00	0.03^{ab}	0.02	**0.0482**	C	FR	U	U
Jamaican Vireo (*Vireo modestus*) (e)	1.41^{a}	0.22	1.49^{a}	0.28	0.45^{b}	0.10	0.84^{ab}	0.16	**0.0001**	I	FR	U	U
Olive-throated Parakeet (*Aratinga nana*)	0.15^{a}	0.05	0.13^{a}	0.06	0.02^{b}	0.01	0.14^{a}	0.06	**0.0294**	F	G	C	M
White-crowned Pigeon (*Columba leucocephala*)	0.68^{a}	0.12	0.83^{a}	0.17	0.28^{b}	0.07	0.60^{a}	0.12	**0.0074**	F	FR	M	C
Yellow-shouldered Grassquit (*Loxipasser anoxanthus*) (e)	0.34^{a}	0.06	0.26^{a}	0.06	0.09^{b}	0.03	0.42^{a}	0.09	**0.0008**	F	G	U	U
Lower abundance in bauxite landscapes													
Black-faced Grassquit (*Tiaris bicolor*)	0.13^{ab}	0.04	0.06^{bc}	0.02	0.25^{a}	0.06	0.019^{c}	0.01	**0.0001**	G	OA	U	G
Higher abundance in agricultural & bauxite landscapes													
Loggerhead Kingbird (*Tyrannus caudifasciatus*)	0.19^{b}	0.04	0.46^{a}	0.10	0.30^{ab}	0.07	0.44^{a}	0.09	**0.0100**	O	OA	M	M
Higher abundance in peri-urban & bauxite landscapes													
Smooth-billed Ani (*Crotophaga ani*)	0.00^{b}	0.00	0.03^{ab}	0.02	0.05^{a}	0.03	0.05^{a}	0.03	**0.0455**	O	OA	M	G

Higher abundance in agricultural landscapes													
Jamaican Spindalis (*Spindalis nigricephala*)‡ (e)	0.68^{b}	0.13	1.33^{a}	0.27	0.64^{b}	0.14	0.54^{b}	0.11	**0.0125**	F	G	U	C
Jamaican Oriole (*Icterus leucopteryx*)	0.57^{b}	0.08	0.99^{a}	0.14	0.55^{b}	0.09	0.75^{ab}	0.11	**0.0188**	I	G	U	M
White-Bellied Dove (*Leptotila jamaicensis*)	0.13^{b}	0.03	0.36^{a}	0.08	0.14^{b}	0.04	0.26^{ab}	0.06	**0.0093**	G	G	G	G
White-winged Dove (*Zenaida asiatica*)	0.03^{b}	0.01	0.22^{a}	0.07	0.04^{b}	0.02	0.06^{b}	0.03	**0.0004**	G	OA	U	G
Higher abundance in peri-urban landscapes													
Vervain Hummingbird (*Mellisuga minima*)	0.15^{b}	0.04	0.21^{ab}	0.06	0.37^{a}	0.10	0.15^{b}	0.04	0.0616*	N	G	U	U
Higher abundance in agricultural & lower abundance in bauxite landscapes													
White-eyed Thrush (*Turdus jamaicensis*) (e)	0.29^{b}	0.07	0.72^{a}	0.19	0.12^{bc}	0.04	0.06^{c}	0.03	**<.0001**	O	FR	M	M
No difference in abundance in anthropogenic landscapes than intact forest													
Bananaquit (*Coereba flaveola*)	2.28	0.28	2.39	0.35	2.19	0.34	2.12	0.29	0.9382	N	G	M	M
Chestnut-bellied Cuckoo (*Hyetornis pluvialis*) (e)	0.12	0.03	0.09	0.03	0.13	0.04	0.06	0.02	0.2974	C	G	M	M
Common Ground-Dove (*Columbina passerina*)	0.08	0.03	0.06	0.03	0.06	0.03	0.05	0.02	0.7754	G	G	U	G
Jamaican Euphonia (*Euphonia jamaica*) (e)	0.54	0.10	0.75	0.16	0.47	0.11	0.52	0.11	0.4265	F	G	M	C
Jamaican Mango (*Anthracothorax mango*) (e)	0.02	0.01	0.06	0.03	0.01	0.01	0.04	0.02	0.1648	N	OA	C	U
Jamaican Tody (*Todus todus*) (e)	0.92	0.13	1.25	0.21	1.08	0.19	0.84	0.14	0.3179	I	FR	G	M
Mangrove Cuckoo (*Coccyzus minor*)	0.04^{ab}	0.02	0.03^{ab}	0.02	0.00^{b}	0.00	0.07^{a}	0.03	0.0408*	C	FR	U	U
Northern Mockingbird (*Mimus polyglottos*)	0.01	0.01	0.03	0.02	0.06	0.03	0.05	0.02	0.2325	O	OA	M	G
Orangequit (Euneornis campestris) (e)	2.63^{ab}	0.31	3.33^{a}	0.46	2.27^{ab}	0.34	2.08^{b}	0.28	0.0857*	N	FR	NA	M
Red-billed Streamertail (*Trochilus polytmus*) (e)	1.65	0.23	2.18	0.35	1.82	0.31	1.74	0.26	0.6130	N	G	U	M
Ruddy Quail Dove (*Geotrygon montana*)	0.15^{ab}	0.05	0.32^{a}	0.10	0.07^{b}	0.03	0.12^{ab}	0.04	**0.0275**	G	FR	G	G
Sad Flycatcher (*Myiarchus barbirostris*) (e)	0.26^{ab}	0.05	0.48^{a}	0.10	0.17^{b}	0.04	0.14^{b}	0.04	**0.0007**	I	G	U	U
White-chinned Thrush (*Turdus aurantius*) (e)	0.99	0.12	1.26	0.18	1.34	0.19	1.41	0.18	0.1974	O	G	M	G
Yellow-faced Grassquit (*Tiaris olivacea*)	0.11	0.03	0.08	0.03	0.09	0.03	0.15	0.05	0.5329	G	OA	G	G
Zenaida Dove (*Zenaida aurita*)	0.08	0.02	0.19	0.06	0.12	0.04	0.17	0.05	0.1446	G	OA	M	G

(e) Indicates species endemic to Jamaica

‡ Previously named Jamaican Stripe-headed Tanager (*Spindalis nigricephalus*) (Banks et al. 2000)

† Primary diet guild: (C) carnivore, (F) frugivore, (G) granivore, (I) insectivore, (N) nectarivore, (O) omnivore

§ Primary habitat association: (FR) forest-restricted, (G) generalist, (OA) open-associated

‖ Primary nesting height or foraging strata: (G) ground, (U) understory, (C) canopy, (M) multiple strata

Species included in community analyses, but with insufficient detections for Poisson mixed models were: American Kestrel (*Falco sparverius*), Jamaican Crow (*Corvus jamaicensis*) (e), Red-tailed Hawk (*Buteo jamaicensis*), Rufous-throated Solitaire (*Myadestes genibarbis*), and Stolid Flycatcher (*Myiarchus stolidus*).

Species detected in the study region, but with insufficient detections to include in any analyses were: Crested Quail Dove (*Geotrygon versicolor*) (e); Yellow-billed Parrot (*Amazona collaria*) (e); and Greater Antillean Grackle (*Quiscalus niger*).

Table 1.2. The strength of association among the 11 traits with landscape matrix responses by resident birds in central Jamaica. Variable importance was determined by calculating the change in impurity (i.e., Gini index) when a trait was substituted for the original variable on the final decision tree (i.e., diet), and is expressed as the relative magnitude of the total decrease in impurity (based on normalized quantiles). 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). *P*-values from randomized chi-square tests are provided with values in bold significant at $P < 0.05$ and * for $P < 0.10$.

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

† Variable importance based on continuous distribution; chi-square test based on classified groups (< 0.25 and > 0.25 density)

‡ Variable importance based on continuous distribution; chi-square test based on classified groups (< 3 and > 3 eggs)

§ Variable importance based on continuous distribution; chi-square test based on classified groups (< 15, 15-50, and > 50g)

‖ One bird with unknown nest height excluded from chi-square test

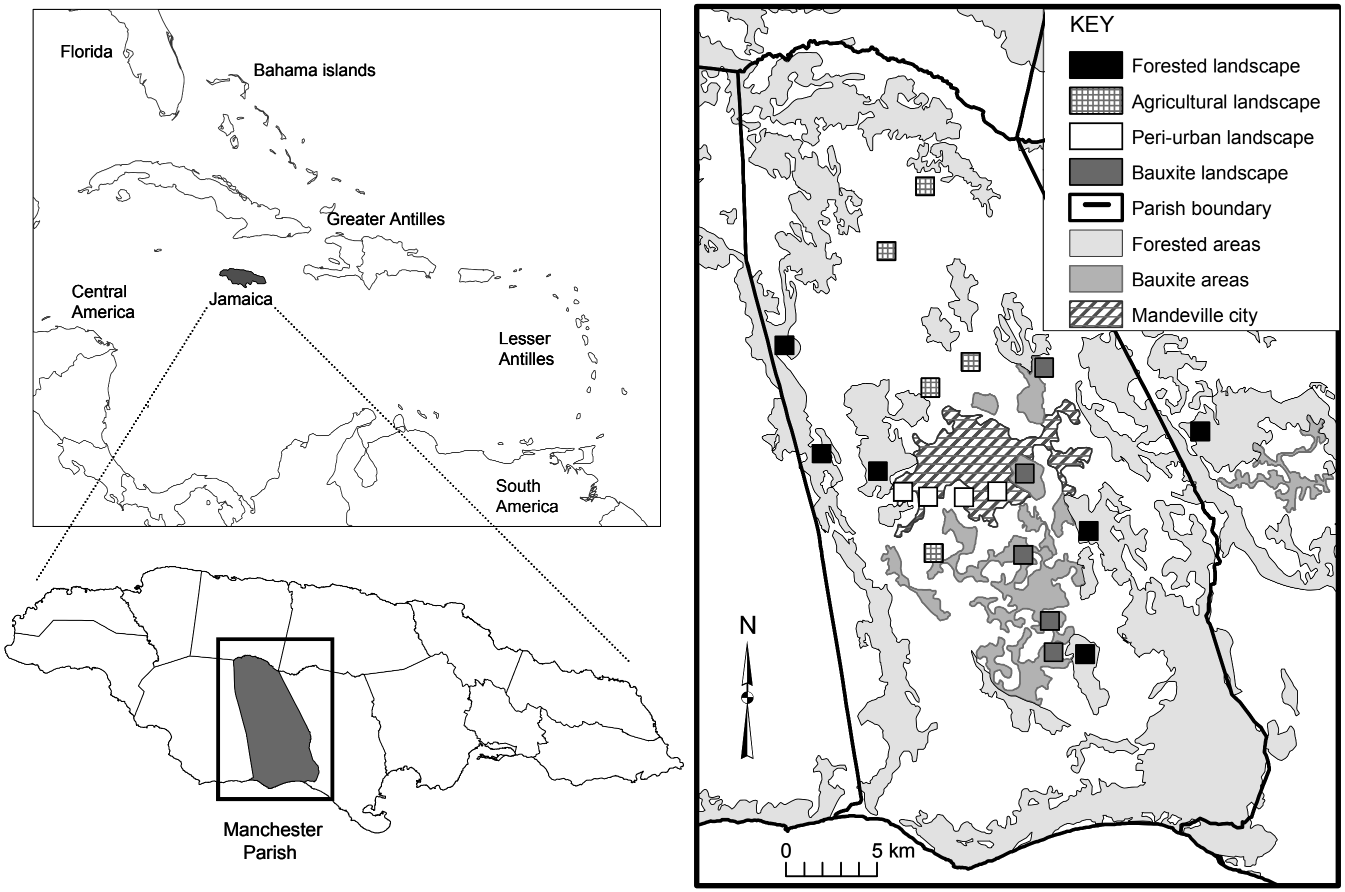
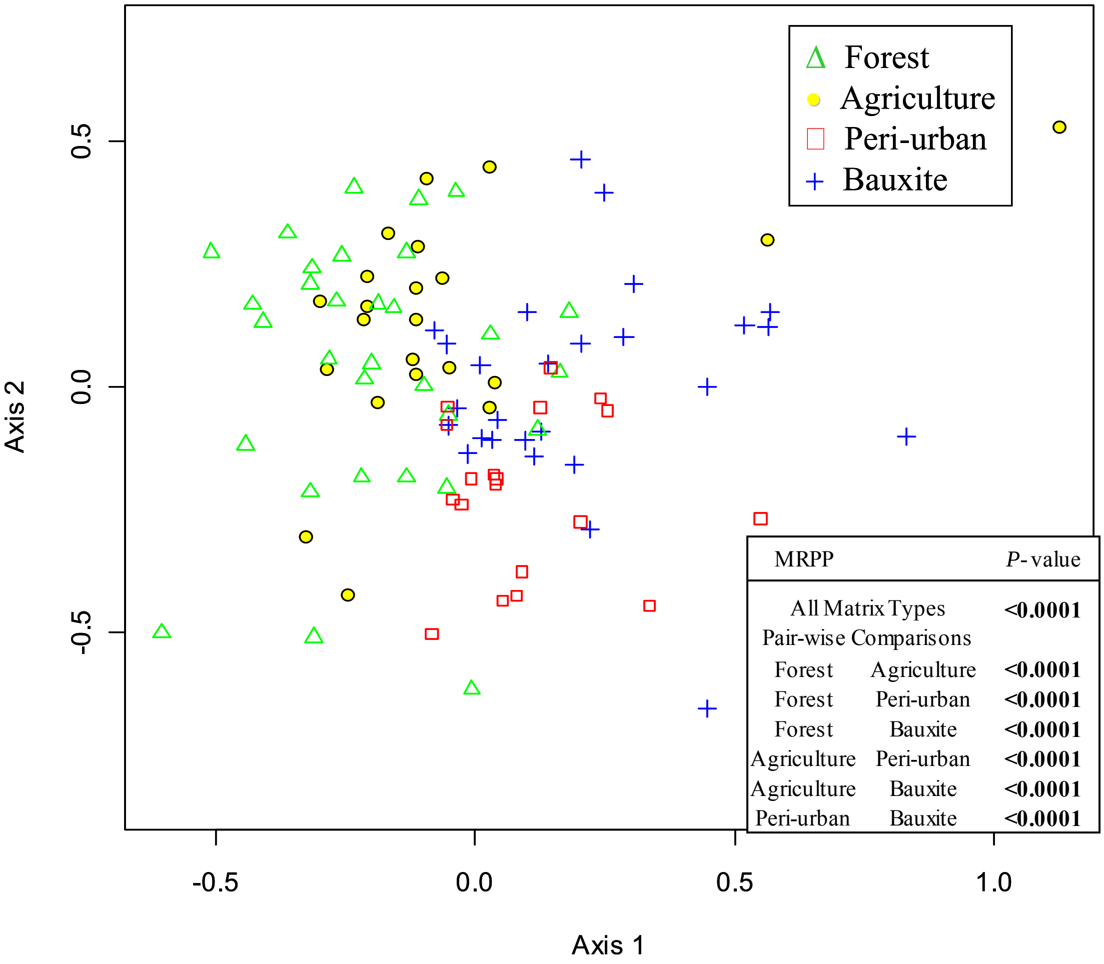


Figure 1.1. Locations of the 20, 1-km^2 landscapes surveyed in the Manchester Parish on the island of Jamaica as shown in the context of the West Indies.



MRPP		*P*-value
All Matrix Types		**<0.0001**
Pair-wise Comparisons		
Forest	Agriculture	**<0.0001**
Forest	Peri-urban	**<0.0001**
Forest	Bauxite	**<0.0001**
Agriculture	Peri-urban	**<0.0001**
Agriculture	Bauxite	**<0.0001**
Peri-urban	Bauxite	**<0.0001**

Figure 1.2. Non-metric dimensional scaling ordination (stress = 17.0170) of resident bird communities in the 99 forest patches in the four matrix types over the study period (2005-2007). For illustration purposes NMDS axis 1 and axis 2 (of a 3-dimensional solution) are presented, which capture most of the variation in community structure and depict the overall pattern in 3-dimensional ordination space. Dimensions represent the relative position among sampled patches based on species assemblages, with patches with similar avian composition containing similar scores in multidimensional space. Community composition among the four landscape matrix types significantly differed (based on familywise $\alpha = 0.05$) based on overall and pairwise comparisons based on MRPP results (inset).

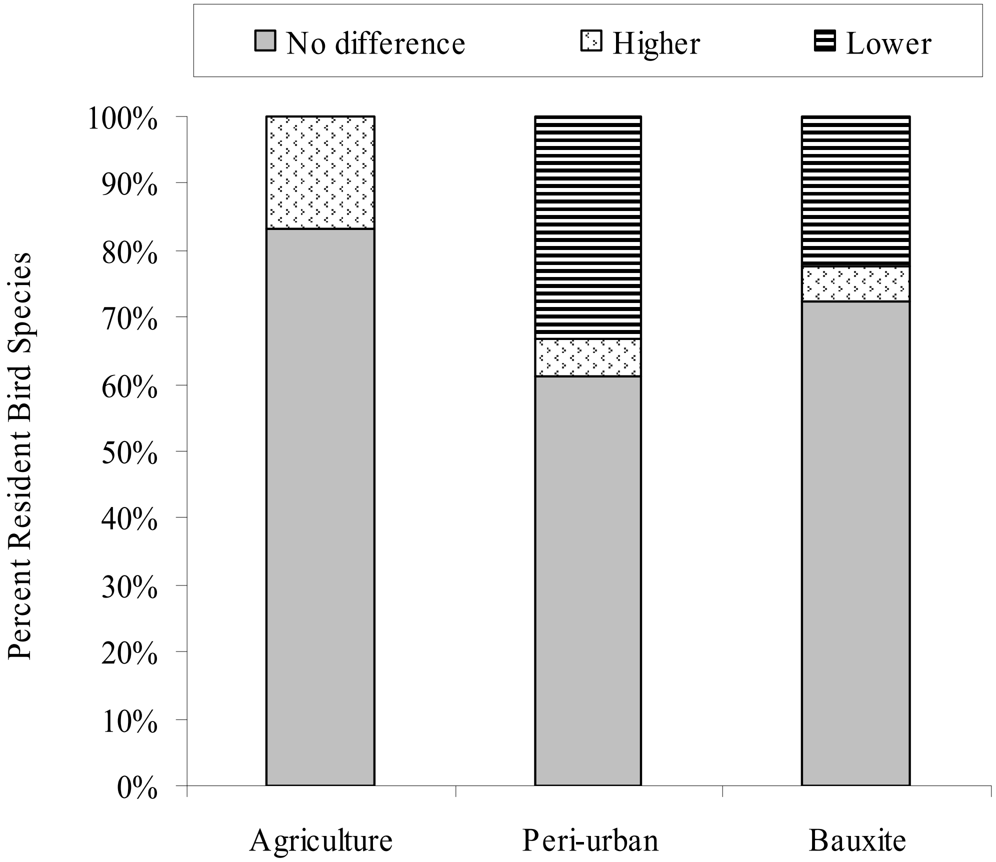


Figure 1.3. Percent of resident bird species in agricultural, peri-urban, or bauxite mining landscapes that exhibited significantly lower abundance, higher abundance, or no abundance difference relative to forested landscapes over the study period (N = 36 species).

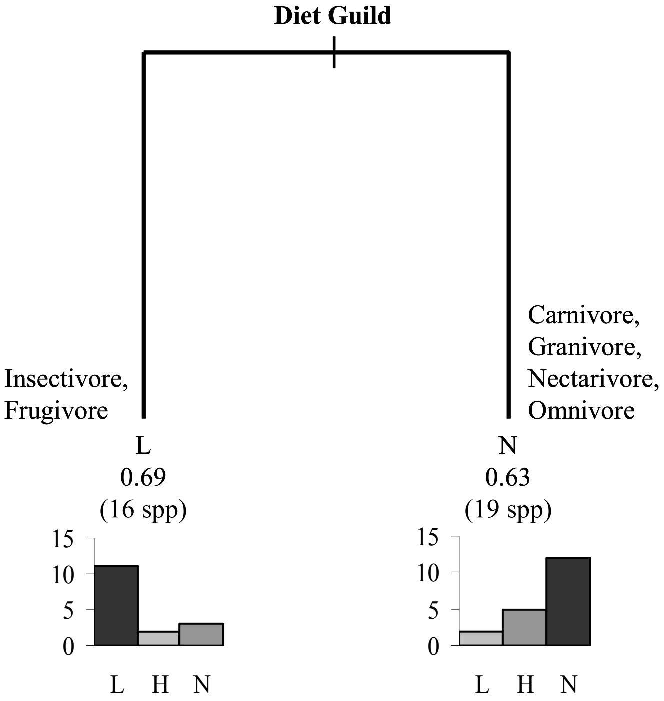
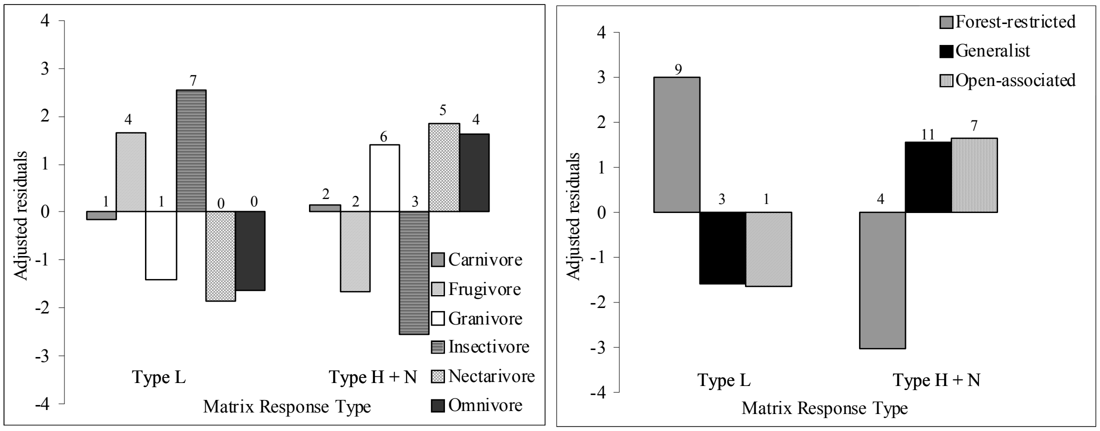


Figure 1.4. Predicted response type, percentage of observations correctly classified per response type, the number of species (in parentheses), and the distribution of the observed responses per group based on classification tree analysis of the responses by resident birds in central Jamaica to landscape matrix in relation to 11 life history or ecological traits. Species responses were categorized as: (1) Type L: lower in abundance in any of the human-dominated matrix type(s) relative to intact forest; (2) Type H: higher in abundance in any of the human-dominated matrix type(s) relative to intact forest; and (3) Type N: no difference in abundance in fragmented landscapes relative to intact forest. Diet guild was the only trait retained in the final model, with two matrix types predicted (Type L and Type N) (with 34% misclassification rate).

a. Diet guild b. Habitat association



c. Nest height d. Foraging strata

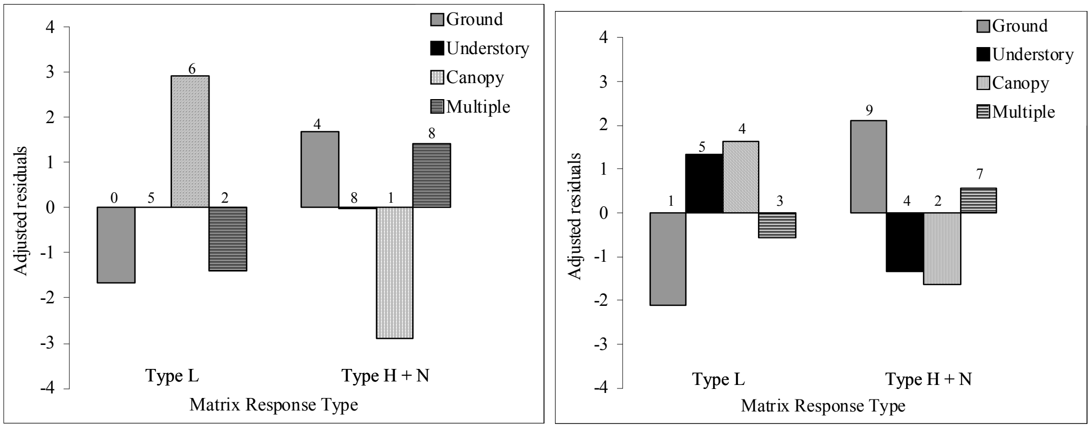


Figure 1.5. Adjusted residuals of the chi-square analyses relating the number of resident bird species exhibiting two matrix responses types to (a) diet guild, (b) habitat association, (c) nest height, and (d) foraging strata. The two response types were classified as (1) Type L: lower in abundance in any of the human-dominated matrix type(s) relative to intact forest, and (2) Type H + N: higher in abundance or similar in abundance among human-modified landscapes relative to intact forest. The number above each bar represents the number of species observed to exhibit the respective matrix response type and trait class combination. Adjusted residuals with the largest absolute values indicate the class driving overall significant differences among matrix response and the trait in question.

Chapter 2: Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores

Abstract

Fragmentation research has traditionally focused on how patch-level attributes (i.e., patch area and isolation) affect animal communities, while ignoring the landscape context. The nature of land cover between habitat patches, the "matrix," may drive colonization and extinction dynamics in fragmented landscapes more than patch area or isolation. We employed multi-season patch-occupancy models to determine the relative influence of patch area, patch isolation, within-patch vegetation structure, and matrix type on the occupancy dynamics of nine Neotropical insectivorous birds in almost 100 forest patches embedded in four matrix types (agriculture, peri-urban development, bauxite mining, and forest) in central Jamaica. We found that within-patch vegetation structure and matrix type between patches were more important than patch area and isolation in determining local colonization and extinction, and that the effects of patch area, isolation, and vegetation structure on occupancy dynamics were matrix- and species-dependent. Across the community, the matrix influenced extinction probabilities more than colonization, indicating that extinction processes, rather than movement, likely drive interspecific differences in population dynamics. This suggests that the nature of human land use surrounding primary habitat strongly impacts avian communities. These findings lend crucial empirical support to the hypothesis that species occupancy dynamics in fragmented systems depend greatly upon the landscape context.

Introduction

Island biogeography theory (MacArthur and Wilson 1967) and metapopulation models (Hanski 1994; Hanski 1998) predict that the processes of extinction and colonization, as influenced by island/habitat area and isolation, determine species distributions and persistence patterns. These conceptual models have been frequently extended to understand species patterns and processes in fragmented landscapes (e.g., Laurance 2008). As forests become fragmented, patch size decreases and patch isolation increases; this process is predicted to alter natural extinction and colonization rates (e.g., Fahrig 2003). Smaller fragments are expected to exhibit increased species extinction, and more isolated fragments to have reduced colonization. The occupancy and richness patterns expected, based on these theoretical predictions, are not always observed in real systems. Empirical relationships of species responses to patch size and isolation have been found to be weak or absent in fragmented systems; this discrepancy may be attributed to the simplification of habitat fragments as islands separated by an inhospitable matrix (Bender et al. 1998; Debinski and Holt 2000; Prugh et al. 2008). In reality, habitat is often embedded in complex mosaics of different land-cover types. Species may be affected not only by the size and spatial location of primary habitat, but also by the structure and composition of the intervening land cover, termed the "matrix" (Haila 2002; Ewers and Didham 2006; Kupfer et al. 2006). The matrix can affect inter-patch movement of animals (e.g., Revilla et al. 2004; Bender and Fahrig 2005), can alter the resource base within a landscape by providing alternative or supplemental resources (e.g., Perfecto and Vandermeer 2002; Brotons et al. 2003), and can impact the type and magnitude of edge effects (e.g., habitat quality, microclimate, predation rates) (e.g., Chalfoun et al. 2002; Ries et al. 2004). Expected species-isolation relationships may be altered if species inter-patch movements differ based on varying composition and configuration of matrix land cover (e.g., Bélisle et al. 2001; Ricketts 2001; Gobeil and Villard 2002; Bender and Fahrig 2005). The type of matrix could directly influence local extinction within primary habitat if patch-resident species commonly obtain resources from certain matrix areas; this behavior has been observed of birds in the field (e.g., Graham et al. 2002; Luck and Daily 2003). This phenomenon could result in higher extinction rates in smaller patches embedded in a "hospitable" matrix than in larger patches embedded in an "inhospitable" matrix (Sisk et al. 1997; Estades 2001). Species-area relationships may also be obscured if habitat quality is differentially altered due to land-use practices in the matrix (Donovan et al. 1997; Rodewald and Yahner 2001; Rodewald and Bakermans 2006). For example, hunting pressures, selective logging, or spread of fire or invasives may disproportionately increase in landscapes with greater human access (Lugo et al. 1981; Laurance 2008). Thus, the matrix may obscure commonly assumed relationships among species occupancy and patch size and isolation, and may ultimately mediate colonization-extinction dynamics in fragmented systems (e.g., Vandermeer and Carvajal 2001).

Despite the potential importance of the landscape matrix, its effects remain poorly understood. The relative importance of multiple human-modified land-cover types is rarely examined in one study, and matrix types are often lumped together in a single category or assumed to be of subordinate importance to habitat components (i.e., patch area and isolation). The unique impacts of matrix types on species processes are only beginning to be understood, given the small number of empirical studies that have disentangled the effects of the matrix from those of habitat area or isolation (Rodewald 2003; Laurance 2008). Further, most inferences about fragmentation and matrix effects are based solely on species diversity, abundance, or occurrence patterns, rather than directly addressing the underlying processes of extinction or colonization (Fahrig 2003; Lampila et al. 2005); and studies rarely account for detection biases which may lead to false inference (Moilanen 2002; MacKenzie et al. 2006).

In this paper, we seek to understand the relative effects of patch area, patch isolation, within-patch habitat structure, and matrix type on occupancy dynamics in fragmented landscapes. We examine (1) how patch area and within-patch habitat (vegetation) structure affect the probabilities of local extinction, (2) how patch isolation affects the probabilities of local colonization of avian insectivores, and (3) whether and how matrix conditions mediate isolation-, area-, and habitat-relationships. We chose to investigate resident (non-migratory) Neotropical insectivorous birds because this guild is disproportionately declining in fragmented tropical forests worldwide (Ribon et al. 2003; Sodhi et al. 2004; Sigel et al. 2006; Stouffer et al. 2009). To ensure unbiased inferences, we apply recently developed multi-season patch-occupancy models to account for the fact that species are often imperfectly and/or differentially detected (MacKenzie et al. 2003; MacKenzie et al. 2006). Models were based on repeat surveys conducted over a three-year period (2005–2007) in forest patches embedded in three common human-modified matrix types in the Caribbean (agricultural, peri-urban development, and bauxite mining) and in sites in a natural “matrix” (i.e., continuous forest). To our knowledge, this is the first study to use estimation methods that explicitly incorporate detection bias to test whether occupancy dynamics differ across landscapes that are similar in structural habitat fragmentation but that vary in surrounding human-modified land cover.

Methods

Study area and site selection

Our study sites were located in Manchester and Clarendon Parishes in central Jamaica (latitude: 17 56'24"-18 11'6" N; longitude: 77 23'13"- 77 37'5" W). This region lies within the premontane moist forest climatic zone (Holdridge 1967), and was once covered in predominantly wet limestone forest (Asprey and Robbins 1953). Less than 30% of native forest currently remains, with most of the human land conversion occurring by the eighteenth century (Eyre 1987b). Forest is now largely restricted to small hilltop remnants on limestone outcrops, with surrounding valleys cleared for agriculture (i.e., primarily cattle pasture), residential development, and mining for bauxite (Evelyn and Camirand 2003).

We sampled a total of 20 landscapes (delineated as 1-km^2 areas). In 14 of those landscapes, remnant forest patches were embedded in the three dominant land-cover types (5 agriculture, 4 peri-urban development, 5 bauxite mining), and 6 landscapes were located in continuous forest cover (see Chapter 1). Forest remnants were surrounded by introduced pasture, treelined fencerows, paddock trees, and herbaceous garden plots in agricultural areas and by low-density residential housing, ornamental gardens, abandoned woodlots, and roadside secondary growth in peri-urban landscapes. Bauxite landscapes were former agricultural lands that had been converted to mining within the past ten years, where relictual forests were surrounded by exposed bauxitic soils, with some recent growth of ferns, *Acacia* trees, or planted grassland. Peri-urban and agricultural matrices contained greater foliage cover and vertical complexity than bauxite lands, and thus are expected to provide greater potential resources (e.g., food or nesting sites) and to enhance structural connectivity to aid movement outside forest remnants relative to bauxite landscapes. Beyond direct effects on movement among patches, land-cover composition and structure in the matrix can affect species extinction processes within remnant forest patches through human land-use practices associated with particular matrix types (Rodewald 2003; Rodewald and Bakermans 2006). For example, peri-urban and bauxite landscapes are exposed to more ongoing human disturbance, including increased hunting pressures, selective logging, noise, road and surface-mining impacts, fire ignition sources, and escape of domestic animals or spread of invasive species than are agricultural landscapes that tend to be large private land holdings. Thus, we predicted that agricultural and peri-urban landscapes would have colonization rates most similar to intact forest relative to bauxite landscapes, and that agricultural landscapes would have extinction rates most similar to intact forest relative to both peri-urban and bauxite landscapes.

We surveyed an average of five forest patches per replicate landscape using stratified random sampling of patches to represent the size distribution. Twenty-two of these patches were sampled in an agricultural matrix, 19 in a peri-urban matrix, and 27 in a bauxite mining matrix. Within forested landscapes, we selected 31 “pseudo-patches” by randomly accumulating consecutive samples along transects that were located in intact forest, such that sampled areas were approximately equal in size to patches in fragmented landscapes. We refer to both pseudo-patches sampled in forested landscapes and forest remnants sampled in anthropogenic landscapes as “patches.” In total, 99 forest patches were sampled across 20 landscapes. To increase the probability that birds were independently sampled, patches within replicate landscapes were separated by > 1 to 26 km (with the exception of a few peri-urban patches), which is believed to prevent overlap in territories for target species (Cruz 1981, A. M. Haynes-Sutton, *personal communication,* C. M. Kennedy, *unpublished data*). Previous analyses revealed no significant spatial correlation between bird communities and the spatial configuration of sampled patches (Chapter 1).

To isolate the potential influence of matrix type, agricultural, peri-urban, and bauxite landscapes were selected such that they were similar in the major components of fragmentation. Sampled patches had similar forest area (mean ± 1 SE = 3.89 ± 0.45 ha) and isolation (33.58 ± 3.48 m, 160.80 ± 19.79 m, and 2381.75 ± 147.07 m to the nearest fragment > 0.5 ha, 5 ha, and 100 ha, respectively). Patches were also embedded in landscapes with a similar proportion (35.84 ± 1.59) and spatial configuration (i.e., shape complexity, inter-patch connectivity) of forest cover (Appendix A).

Target species

We modeled occupancy dynamics for 9 of the 11 native resident insectivorous bird species found in our region (Chapter 1) (Table 2.1). These species are ideal for an investigation of multi-patch dynamics because they are specialized in Jamaica's limestone forests, which allows for the spatial delineation of primary habitat. They are also sensitive to forest fragmentation in the region (Chapter 1). Although these species are in the same broad diet guild, they are taxonomically and ecologically diverse in that they represent six families and a range of body masses (~ 7−100 g) with different (but overlapping) altitudinal ranges (Table 2.1). Species represented both foraging and nesting specialists and generalists, and exhibited a variety of foraging behaviors. The two species we did not include in the study were either too common (Jamaican Oriole, *Icterus leucopteryx*) or too rare (Stolid Flycatcher, *Myiarchus stolidus*) to model. Overall, we were able to fit models to > 80% of the central Jamaican insectivorous bird community.

Sampling methods

We conducted a total of 286 point counts on two to three separate occasions from early February to mid-June during the height of breeding activity (Raffaele et al. 1998), each year for three consecutive breeding seasons (2005-2007). Point counts were conducted along a centrally placed transect within each of the 68 forest patches in anthropogenic landscapes, and along one to three randomly placed transects (averaging 1500 m in length) in forested landscapes. We surveyed an average of 12 to 15 stations per replicate landscape per occasion, proportional to patch area. To minimize double-counting, stations were located 100 m apart and > 25 m from a matrix-forest boundary.

At each sampling station, we recorded the number of individuals per species seen or heard within a 10-minute period (conducted between 0600-1000 hrs on clear days without rain) and in a 25-m fixed-radius area (Hutto et al. 1986). We selected a 25-m radius because it provided reliable detection across all of our sites based on field tests, as found by other researchers in the Caribbean (Wunderle and Waide 1993). Each site was visited by one of three trained observers for repeat counts within a season, and the order of site visitation was rotated throughout each field season.

Patch-level covariates

We considered four patch-level covariates: matrix type, patch area, patch isolation, and local vegetation structure. Matrix type was determined categorically based on 2001-2002 IKONOS imagery and field verification as to whether each sampled patch was embedded in a landscape dominated by agriculture, peri-urban development, or bauxite mining or in continuous forest. To quantify patch area and isolation, we first digitized forest cover from multispectral pan-sharpened IKONOS imagery (1-m resolution, Space Imaging 2002) and 2007 ground-truthing surveys using ArcGIS 9.3 (ESRI 2008) (LCC, WGS 84 projection). Forest habitat was categorized by a closed canopy and visual dominance of native broadleaf trees; producer's and user's accuracy for this cover type were estimated at 92% and 84%, respectively (Chapter 1). We then used FRAGSTATS 3.3 (McGarigal et al. 2002) to obtain area and isolation measures for forest patches using a 4-m raster cell size and an eight-neighbor rule for patch delineation. Patch area was the size of a forest patch in hectares. Patch isolation was calculated as the nearest-neighbor distance from each sampled patch to a forest patch greater than 100 ha (variable ENN_100ha), reflecting the distance a bird would travel to reach a potential source population. Euclidean nearest-neighbor distance is the simplest and most widely used metric to approximate isolation (Moilanen and Hanski 2001; Bender et al. 2003), and was selected because of its clear interpretation and because it captured the spatial variation of forest habitat. The variable ENN_100ha was significantly correlated ($P < 0.001$) with several other measures of habitat isolation: distance to the nearest forest patch of any size (Spearman's rank correlation, $\rho = 0.6211$), distance to a patch greater than the average size found in landscapes (≥ 5 ha) ($\rho =$

0.6520), as well as distance to a ≥ 10-ha patch ($\rho = 0.7768$), and a "proximity index" ($\rho = -0.6534$) that incorporates the amount and proximity of habitat within a patch neighborhood (based on a 100-m search radius) (Gustafson and Parker 1992). Given the lack of data on dispersal abilities of Caribbean birds and of tropical birds in general (Walters 2000), we were unable to use connectivity measures that scale the effect of inter-patch distance to known dispersal distances (e.g., Moilanen and Hanski 2001; Moilanen and Nieminen 2002).

To quantify vegetation structure, we measured 12 variables in a 10-m radius plot centered at each point-count station between April 27 and July 2, 2005: tree diameter, basal area, canopy height, leaf area index, leaf litter depth, abundance of woody and herbaceous vines, and percent herbaceous cover (0-0.5-m height class), low shrub (0.5-2 m), tall shrub (2-6 m), trees (> 6 m), and open canopy. Each plot was divided into four equal quadrats based on 10-m transects in each cardinal direction. We measured tree basal area using a 10-factor prism at each plot center. Within each quadrat we measured diameter breast height (DBH) and canopy height of the largest tree, and we estimated the abundance of herbaceous and woody vines based on a categorical scale (0 = absent, 1 = solitary, 2 = few, scattered individuals, 3 = common, 4 = abundant). At 2-m intervals along each transect, we measured leaf litter depth and foliage structure. Foliage structure was scored based on foliage touches along a pole at four height classes (0-0.5 m, 0.5-2 m, 2-6 m, > 6 m), with percent cover calculated as the percent of all points at a given height interval with ≥ 1 touch (after Schemske and Brokaw 1981). Percent canopy openness and effective leaf area (Stenberg et al. 1994) were estimated using the Gap Light Analyzer (GLA) program (v 2.0) (Frazer et al. 1999) based on hemispherical canopy photographs taken at 5-m intervals along two randomly selected transects with a Nikon Coolpix 950 Camera and FC-E8 Nikon Fisheye lens. All measurements were calibrated between two observers. Patch-level vegetation structure was estimated by averaging all plots within patches. To distill the variation in the 12 patch-level vegetation variables into fewer non-correlated components, we conducted a principal component analysis (PC). The averaged PC axis 1 score was used as proxy for patch-level vegetation structure in models.

A major difficulty in discerning the relative influence of components of fragmentation (e.g., habitat amount, configuration, and quality) and the role of the matrix, is that effects are often highly inter-correlated (Fahrig 2003; Rodewald 2003; Laurance 2008). Thus, we examined whether the continuous covariates of patch area, isolation, and vegetation structure were inter-correlated and whether they differed by matrix type based on Spearman's rank correlation (ρ) and one-way ANOVA, respectively. Statistical analyses were performed using the 'stats' package in the *R* statistical system (R Development Core Team 2008). All variables were tested for normality and homogeneity of variances, and transformations were performed where necessary. Untransformed means ±1 SE are reported.

Occupancy analyses

We used multi-season patch-occupancy models to estimate initial occupancy (ψ_{2005}), local colonization (γ), and local extinction (ε) probabilities for each bird species separately from 2005 to 2007 (MacKenzie et al. 2003; MacKenzie et al. 2006). In contrast with other occupancy models (Moilanen 2002), this modeling framework explicitly incorporates detection probability into the estimation of initial occupancy and the rate parameters (i.e., colonization and extinction probabilities), which reduces bias in the parameter estimation (MacKenzie et al. 2003; MacKenzie et al. 2006). A detection history was constructed for each species and patch, where a presence indicated that at least one individual of a species was detected during any point-count survey event, and an absence indicated a failure to detect a species. To overcome difficulties in separating true absence (i.e., species not occupying a site) from false absence (i.e., failure to detect a species that is truly present during a survey event), we used multiple surveys conducted over a short enough period to meet the assumption of population closure (no births, deaths, immigration or emigration from the patch). Local colonizations and extinctions are allowed between seasons, and are adjusted for false absences by using repeat surveys within a season where closure is assumed. Colonization and extinction probabilities were determined based on between-year detection histories via likelihood maximization (MacKenzie et al. 2003; MacKenzie et al. 2006).

We developed a candidate model set to test the main effects of patch isolation, patch area, vegetation structure, and matrix type; we predicted all of these factors would influence local colonization and local extinction processes of birds in our region (28 models, Table F1 in Appendix F). In all models, initial occupancy was modeled without any covariates to focus our investigation on rate parameters (after Ferraz et al. 2007). Following classic island biogeography and metapopulation models (MacArthur and Wilson 1967; Hanski 1994), we predicted that the process of colonization depended upon the spatial isolation of forest habitat (i.e., patch isolation), and extinction processes depended upon patch size. To expand upon these traditional models, we tested whether local vegetation structure covaried with local extinction, given that this environmental feature is known to influence habitat quality for birds due to its effects on the availability of food resources, perching/nesting sites, predation, and shelter against abiotic conditions (e.g., Wiens 1989).

To test how species colonization and extinction dynamics were influenced by the landscape matrix, we modeled both extinction and colonization as a function of the type of matrix in which forest patches were embedded (referred to as "matrix type"). One might hypothesize that the matrix may interact with patch area, isolation, and habitat structure; however, we only considered additive relationships for all covariates, because complex models with several interaction parameters could not be reasonably supported by our data, particularly in a multi-season occupancy modeling framework.

Prior to modeling occupancy and associated rate parameters, we determined the best covariance structure on detection probability (p). We predicted that survey month and number of point counts were the two most important factors influencing potential variability in bird detection (Appendix F). Other covariates, such as observer and time of day, might influence species detection (Ralph and Scott 1981), but their effects were diminished by rotating observers and the temporal order of sampling. We modeled p without a covariate relationship (i.e., constant) and as a function of survey month, sampling effort, or the additive effect of both (Table F2 in Appendix F). Using the most general model structure for occupancy (i.e., the global model), we selected the covariance structure on p with the lowest Akaike's Information Criterion (AIC), and then fit the 28 occupancy models separately for each bird species, including the global model with all patch-level covariates on γ and ε, as well as reduced model forms. We standardized all covariates to their z-scores, and fit models in the program PRESENCE (Hines and

MacKenzie 2008). Models that failed to converge or that contained nonsensical parameter estimates were eliminated from the model set for the appropriate species, and were not used for inference. We ranked models based on AIC and identified top models (i.e., ΔAIC < 2.0) for each species, and calculated the associated model weights (*w*) (Burnham and Anderson 2002). To determine the most supported model structure for the avian insectivore community, we averaged the weight of each model across all species. To assess the relative effects of patch area, isolation, vegetation structure, and matrix type, we calculated model-averaged estimates of the coefficients for each of these covariates based on the 95% confidence set per species (Burnham and Anderson 2002). Model averaging combines parameter estimates from each model using their associated AIC weights to provide an estimate that incorporates both within- and across-model uncertainty. This approach reduces model bias and allows for more robust inferences than those based on a single selected best model (Burnham and Anderson 2002). We calculated model-averaged colonization $\left(\hat{\bar{\gamma}}\right)$ and extinction $\left(\hat{\bar{\varepsilon}}\right)$ for each species by matrix type (when all other covariates were held constant to their average values). Interpreting model-averaged point estimates of colonization and extinction as a function of landscape matrix was of primary interest in our study; therefore, we tested whether they differed based on ANOVA F tests (based on $P < 0.05$ and 0.10) with posthoc comparisons based on Benjamini-Hochberg adjustments (Benjamini and Hochberg 1995). We were unable to test for differences in rate parameters based on the generalized chi-square statistic (Sauer and Williams 1989), because associated model-averaged variance-covariance matrices could not be calculated for all species due to boundary problems (i.e., parameter estimation at 0 or 1). Finally, we graphed model-averaged covariates against $\hat{\bar{\gamma}}$ and $\hat{\bar{\varepsilon}}$ to assess the direction and strength of relationships.

Results

Patch-level covariates

Sampled pseudo-patches in continuous forest ranged from 1.2 to 25 ha, and sampled patches in fragmented landscapes ranged from 0.6 to 19.6 ha in agricultural, 1.0 to 8.3 ha in peri-urban, and 0.6 to 13.3 ha in bauxite landscapes. Overall, patch area did not differ among matrix types (ANOVA, $F_{3,95} = 0.389$, $P = 0.761$) (Table 2.2). Patches in agricultural, peri-urban, and bauxite landscapes were on average 2381.75 (± 147.07) m from a ≥100 ha fragment, with isolation distances not differing among matrix types ($F_{2,65} = 1.435$, $P = 0.246$).

Local vegetation structure, as determined by PC1, was strongly positively associated with percent open canopy, herbaceous and low shrub cover, and abundance of herbaceous vines. PC1 was strongly negatively associated with proportion of tree cover, canopy height, leaf area index, tree basal area, tree diameter, and leaf litter depth (Appendix G). Vegetation structure differed significantly by matrix type ($F_{3,95} = 4.616$, $P = 0.005$). Forest and agricultural patches tended to have greater forest cover and vertical structure, larger and more abundant trees, and more leaf litter (i.e., more negative PC1 values) than forest in bauxite, and to a lesser extent, in peri-urban landscapes. Bauxite and peri-urban landscapes tended to have greater low shrub and herbaceous cover and more vines (i.e., more positive PC1 values). Only patches within bauxite landscapes, however, significantly differed from those in other landscape types ($P < 0.05$). None of the continuous covariates were significantly inter-correlated (Patch area:PC1 $\rho = 0.043$, $P = 0.672$; Patch area:ENN_100ha $\rho = -0.101$, $P = 0.320$; PC1: ENN_100ha $\rho = 0.032$, $P = 0.756$).

Estimated species occupancy and detection

Initial occupancy estimates ($\hat{\psi}_{2005}$) ranged from < 1 to 1, and estimated species detection was always < 1 across species based on top models (Tables H1 and H2 in Appendix H). For all species, detection probability was best modeled with sampling effort, with detection increasing with the number of point counts surveyed. For five species, the most supported model structure on detection included both survey month and sampling effort, with the greatest detection earlier in the breeding season rather than later for all species except one (Jamaican Tody) (Table H2 in Appendix H) (refer to Table 2.1 for scientific names). We used the best covariate structures on detection probability for each species to investigate covariate relationships with the rate parameters, which were of primary interest in our study.

Relative importance of patch-level covariates for colonization and extinction

Patch isolation was an important covariate on local colonization probabilities for five of the nine species, and matrix type was important for six of them (Table 2.3). Matrix type was included as a covariate in top-ranking models with higher AIC weights ($w > 0.20$), indicating it is a better predictor for colonization than is patch isolation. Patch area was an important covariate on local extinction probabilities for about half of the species, but was included in models with lower weights. Extinction was most consistently predicted by both vegetation structure and matrix type; these patch-level covariates entered in high-ranking models with higher weights for almost all species. The most commonly supported model structures were ones in which colonization was either a function of matrix type or modeled as constant, and covariates on extinction probability included an additive function of matrix type and vegetation structure (Table H1 in Appendix H). When weights for each model were averaged across all species, the best model structure was one in which local colonization was a function of matrix type only, and local extinction was a function of both vegetation structure and matrix type. This model structure had an average weight of 34%, which was three times higher than that of any other model. Thus, matrix type and vegetation structure were the two most important covariates influencing the occupancy dynamics of the insectivorous bird community in our study system.

Effects of patch isolation, area, vegetation structure on colonization and extinction

Patch isolation had no effect on colonization probabilities for four species: Jamaican Becard, Jamaican Elaenia, Jamaican Pewee, and Sad Flycatcher. When models included patch isolation on colonization probability, increasing isolation had a negative effect as predicted by theory (except for one species), but the effect was often estimated near zero (based on approximated 95% CIs) (Table 2.4). The magnitude and slope of the relationship between colonization and isolation was similar across the different matrix types for the majority of species with a detected effect (Figure H1 in Appendix H). However, increasing patch isolation negatively affected colonization only in peri-urban and bauxite mining landscapes for the Jamaican Tody, and only in bauxite landscapes for the Rufous-tailed Flycatcher (Figure 2.1a).

Also according to theoretical expectations, local extinction probabilities generally declined with increasing patch area (Table 2.4, Figure H2 in Appendix H), but there was no effect for four of the nine species (Jamaican Becard, Jamaican Elaenia, Jamaican Pewee, and Rufous-tailed Flycatcher). Patch area had a strong influence on local extinction for only two species: the Arrow-headed Warbler, for which patch area had a uniformly negative effect across all matrix types; and the Jamaican Woodpecker, for which patch area had a negative effect only in bauxite and peri-urban landscapes (Figure 2.1b).

The effect of vegetation structure on extinction probabilities was greater than the effect of patch area. For all species except the Jamaican Vireo, the probability of extinction increased with greater percent herbaceous cover and low shrubs and abundance of vines, and decreasing canopy cover and height, tree diameter and basal area, and leaf area index (i.e., increasing PC1 value). For five species, the slope of this relationship was consistent among matrix types, but the rate of increase in extinction probability was matrix-dependent (Figure H3 in Appendix H). For example, the probability of extinction reached 100% for the Jamaican Becard at negative PC values in both bauxite and peri-urban landscapes but at positive PC values in forested and agricultural landscapes. For the remainder of the species, the relationship between vegetation structure and local extinction was matrix-dependent, demonstrating an increase in extinction probabilities for some matrix types but a decrease for others. For example, vegetation structure affected extinction probabilities for the Jamaican Pewee only in agricultural and forested landscapes, and affected extinction probabilities for the Jamaican Woodpecker largely in bauxite and peri-urban landscapes (Figure 2.1c). Large standard errors for many of the estimated coefficients for patch isolation and area, and to a lesser extent vegetation structure, may suggest these relationships are not significant or that our sample size was too small (Table 2.4); but model selection results clearly support the influence of vegetation structure and matrix type on occupancy dynamics across species (Table H1 in Appendix H).

Estimated colonization and extinction by matrix type – holding patch area, isolation, and vegetation structure constant

The Jamaican Elaenia, Jamaican Pewee, and Jamaican Woodpecker had higher model-averaged estimates of colonization probabilities in forested and agricultural landscapes; the Jamaican Becard and Rufous-tailed Flycatcher had higher estimated colonization in agricultural landscapes; and the Jamaican Tody in all fragmented landscape types (Table 2.5). The remainder of species (Arrow-headed Warbler, Jamaican Vireo, and Sad Flycatcher) exhibited a weak relationship between colonization and matrix types. On average, model-averaged colonization probabilities were highest in agricultural landscapes (0.60 ± 0.12), followed by forested (0.37 ± 0.12), bauxite (0.24 ± 0.10), and peri-urban landscapes (0.18 ± 0.11) (Table 2.5). Lower colonization probabilities in forested landscapes were due to consistent occupancy of patches for several species (e.g., Jamaican Becard, Jamaican Pewee, Jamaican Tody). Although they are supported by model selection, these estimates only differed statistically at $P < 0.10$ (ANOVA, $F_{3,32} = 2.542$, $P = 0.074$), with colonization higher in only agricultural relative to both peri-urban and bauxite landscapes.

In contrast, model-averaged extinction probabilities differed more strongly among matrix types ($F_{3,32} = 5.201$, $P = 0.005$), with the insectivore community as a whole having significantly higher extinction in both peri-urban (0.43 ± 0.15) and bauxite (0.53 ± 0.13) landscapes than in either forested (0.09 ± 0.03) or agricultural (0.07 ± 0.04) landscapes ($P < 0.05$). All species consistently had higher model-averaged point estimates of extinction in peri-urban and/or bauxite landscapes: two species with higher extinction in peri-urban (Jamaican Elaenia, Jamaican Vireo), four higher in bauxite (Arrow-headed Warbler, Jamaican Tody, Jamaican Woodpecker, and Rufous-tailed Flycatcher), and three higher in both peri-urban and bauxite landscapes (Jamaican Becard, Jamaican Pewee, and Sad Flycatcher).

Discussion

Occupancy dynamics mediated by landscape matrix

Although it is widely recognized that land cover surrounding primary habitat can affect species occupancy dynamics, to our knowledge this is the first study to test the effects of several different types of human-modified landscapes similar in structural habitat fragmentation (i.e., amount and configuration of habitat) and to compare them with continuous forest. We found that the landscape matrix, regardless of patch isolation, best explains local colonization, and the additive effect of within-patch vegetation structure and matrix type, regardless of patch area, best explains local extinction of Neotropical avian insectivores. Thus, occupancy dynamics in Jamaica are driven more by matrix conditions than by the commonly assumed patch area and isolation, and local extinction rates are driven more by within-patch habitat structure than by patch area. Moreover, the effects of patch area, isolation, and vegetation structure on occupancy dynamics were contingent upon matrix context. These relationships were detected even though patch area, isolation, and vegetation structure were uncorrelated, and despite similar climate, geology, forest type, and controlling for the amount and configuration of forest cover among anthropogenically fragmented landscapes.

Although individual species responded differently, a general community-wide pattern emerged. Local extinction of resident avian insectivores was substantially higher and local colonization marginally lower in peri-urban and bauxite mining landscapes relative to agricultural and forested landscapes, suggesting an eventual population decline. As predicted, species colonization was higher in agricultural relative to bauxite landscapes, but not in peri-urban landscapes as was expected, perhaps due to higher mortality during movement (e.g., predation). Colonization patterns, however, were variable across species. The same number of species had similar colonization probabilities among matrix types as exhibited differences. In many cases, there was low to moderate uncertainty as to whether matrix type was an important covariate on colonization, and constant colonization rates among patches were supported for some species. In contrast, there was unequivocal support that extinction probabilities across the community were influenced by both vegetation structure and matrix type. All species exhibited extinction estimates that were consistently higher in bauxite mining and/or peri-urban landscapes in accordance with our predictions. Kennedy et al. (*unpublished manuscript*) found lower abundances of resident avian insectivores in forest remnants in peri-urban and bauxite mining landscapes than in agricultural or forested landscapes in the region (Chapter 1). We suggest that such differential abundance patterns are driven more by extinction than colonization dynamics.

Potential mechanisms underlying differential occupancy patterns among matrix types

Three broad mechanisms have been proposed to explain the decline of avian insectivores in fragmented forests, the impact of which may vary by landscape matrix: (1) impedence of inter-patch movement, which reduces functional landscape connectivity (e.g., Stratford and Stouffer 1999; Sekercioglu et al. 2002; Moore et al. 2008); (2) increased nest parasitism and predation of birds (e.g., Rodewald and Yahner 2001; Chalfoun et al. 2002; Lampila et al. 2005); and (3) reduction of habitat quality, including the interdependent effects of loss of microhabitats and decline of prey availability (e.g., Burke and Nol 1998; Zanette et al. 2000).

Sekerciouglu (2002) found that the best determinant of the persistence of understory insectivorous birds in small fragments in Cost Rica is the ability to disperse through deforested matrix habitats. Consequently, he argued that dispersal limitation is the dominant factor underlying the decline of insectivores in fragmented tropical forests. Likewise, Amazonian forest-dependent insectivores have been found averse to crossing even small gaps, such as road clearings (e.g., 30-40 m) (Laurance et al. 2004); and experiments have indicated that insectivores are the most dispersal-limited terrestrial avian guild in lowland Panama and disproportionately more likely to become extinct (Robinson 1999; Moore et al. 2008). These studies support the hypothesis that insectivores, particularly understory specialists, have low mobility due to their relatively localized habitats and potential physiological or morphological limitations (Harris and Reed 2002; Laurance et al. 2002; Stratford and Robinson 2005), which could explain their extinction vulnerability. However, the reverse pattern has also been found. Based on long-term data at the Biological Dynamics of Forest Fragments Project in Brazil, bird species previously assumed to be dispersal-limited were found to frequently move distances of 150 to 900 m from continuous forest post-fragmentation (Van Houtan et al. 2007). Species that dispersed more widely were also found more extinction-prone (Van Houtan et al. 2007), and for some of these tropical birds, isolation did not influence their occupancy (Ferraz et al. 2007), suggesting that connectivity may not be the limiting factor determining long-term population dynamics in fragmented landscapes. Species that dispersed more widely were also found more extinction-prone, suggesting that connectivity may not be the limiting factor determining long-term population dynamics in fragmented landscapes (Van Houtan et al. 2007).

In light of our findings and given the nature of Jamaica's topography and the evolutionary history of its species, we believe that dispersal limitation is not the primary mechanism explaining bird distributions among forest patches. The karst countryside in central Jamaica is characterized by small forest hilltops, often < 10 ha, which are separated by other land uses but remain in close spatial proximity (e.g., hundreds of meters apart) relative to potential bird dispersal. Such small distances between forest patches may not prohibit frequent movement of bird species, as supported by high probabilities of local colonization of several of our target species in fragmented landscapes (Table 2.5). Further, the evolutionary history of Caribbean avifauna has likely promoted selection of species with stronger dispersal abilities and fewer physiological or morphological limitations than mainland counterparts; these characteristics have allowed them to (re)colonize and (re)establish in island habitats and to withstand large-scale natural disturbance events like hurricanes (Lack 1976; Ricklefs and Bermingham 2008).

Other commonly cited causes of forest bird declines are increased nest parasitism and predation (e.g., Robinson et al. 1995; Lampila et al. 2005), the impact of which may vary by landscape matrix (Donovan et al. 1997; Rodewald and Yahner 2001; Driscoll and Donovan 2004). Nest predation has been identified as the key cause of nest failure throughout the world (Martin 1993; Ford et al. 2001). Although nest predation has yet to be studied for the vast majority of birds in the West Indies, traits such as nest type and nest height may affect susceptibility, with open- and ground-nesting species found to suffer greater predation (Chalfoun et al. 2002; Lampila et al. 2005) (but see Martin 1993). We found no detectable association between nest type and differential bird abundances between continuous and fragmented forest in Jamaica; and species predicted to be most sensitive to nest predation (ground nesters) were least likely to exhibit lower abundances in fragmented landscapes (Chapter 1). Moreover, insectivores in this study showed no differences in local extinction patterns in relation to either nest type or nesting height (Table 2.1). Brood parasitism, particularly by cowbirds (*Molothrus* spp), has been shown to increase in disturbed landscapes in North America (Brittingham and Temple 1983; Robinson et al. 1995). This threat is currently considered minimal in Neotropical systems (Stratford and Robinson 2005). The generalist brood parasite, Shiny Cowbird (*M. bonariensis*), has only recently arrived in the West Indies and was detected on only 6 of 1681 occasions in our study region. Lastly, predation of juvenile or adult birds by raptors has been proposed as an additional source of mortality for certain insectivores (e.g., those in mixed-species flocks) (e.g., Canaday 1996; Ford et al. 2001); such predation may increase with increasing forest disturbance (Thiollay 1992). Given the lack of diversity and density of raptors in Jamaica, this is not a plausible explanation for differential extinction patterns. Only two raptor species likely pose a predation threat (American Kestrel, *Falco sparverius*; Red-tailed Hawk, *Buteo jamaicensis*), and they were detected infrequently and in essentially equal numbers among landscapes in our region.

Rather, evidence suggests that occupancy dynamics in Jamaica are driven by local extinctions, likely as a function of differential habitat quality among landscapes and its essential components (e.g., food, cover). This assertion is based on the fact that area and isolation of forest patches did not vary among fragmented landscapes, but within-patch vegetation structure did. Forest remnants in bauxite and peri-urban matrices had low stature and more open canopies, less structural complexity, reduced leaf litter, and greater percent shrub layer (Table 2.2), thus indicating they may be in earlier successional stages and/or have been subject to greater disturbance than forests in agricultural matrices (Asprey and Robbins 1953). Bird species in peri-urban landscapes may be disproportionately affected by human-induced forest disturbance, including selective harvesting, road impacts, and/or spread of fire or invasive species (Theobald et al. 1997; Marzluff et al. 2001). Surface-mining activities in bauxite areas involve the large-scale removal of vegetation and topsoil, as well as the creation of roads and open pits of exposed earth, which could alter soil water retention, create dust pollution, and lead to biogeochemical and hydrologic changes (Bell and Donnelly 2006). Even after post-mining restoration, ecological communities may not fully recover to their original state (Parrotta and Knowles 1999; Parrotta and Knowles 2001). All of these factors likely alter within-forest vegetation structure and microclimate, and may have led to a reduction in invertebrate biomass, thereby affecting insectivorous birds (e.g., Burke and Nol 1998;

Zanette et al. 2000). Given enhanced foraging specializations of insectivorous tropical birds on specific microhabitats (e.g., Remsen and Parker 1984; Rosenberg 1990; Marra and Remsen 1997), slight perturbations in a resource base could cause increased cascading effects on local extinction dynamics.

Even though surveyed landscapes had similar environmental conditions (e.g., elevation, climate, soil substrate), we were unable to disentangle the effects of habitat structure from matrix type on occupancy dynamics of birds, because land-use practices in the matrix are driving the internal forest changes. The nature of within-patch vegetation structure, however, does not fully capture the effects of the landscape matrix on habitat quality, because matrix type was an additional predictor of bird occupancy dynamics and mediated the influence of local vegetation (Figure 2.2, Appendix H). The role of forest fragmentation and disturbance on prey availability is unclear, given its effects may differ across arthropod taxa, with some species increasing in abundance post-fragmentation (Didham 1997). Thus, additional research is needed to identify impacts of fragmentation in different landscape contexts on invertebrate communities and its repercussions for avian insectivores.

The landscape matrix may itself mediate resource availability, both within the primary habitat and in the surrounding matrix areas. In many cases, matrix habitats may be hospitable for native species and may provide supplemental or additional resources that allow for population maintenance or growth in fragmented habitats (Norton et al. 2000; Brotons et al. 2003; Cook et al. 2004). In fact, the ability to utilize resources within matrix areas has been identified as a key determinant of species tolerance to forest conversion for many taxa (e.g., Laurance 1991; Gascon et al. 1999; Henle et al. 2004).

Abundances of edge- and matrix-foragers, such as nectarivores, omnivores, and granivores, have been found relatively insensitive to fragmentation in Jamaica, likely due to potential cross-boundary subsidies (Chapter 1), as also found in other systems (e.g., Stouffer and Bierregaard 1995; Renjifo 1999; Sigel et al. 2006). Compared to most avian foraging guilds, insectivores exhibit enhanced forest specialization; thus, we suspect that resource supplementation in matrix areas is not driving differential occupancy dynamics as much as is the reduction in forest habitat quality. Nonetheless, resource supplementation may play a role in buffering against local extinction. Based on sampling conducted within matrix areas (Chapter 1), the disproportionate use of matrix habitats in particular landscapes coincides with a reduction in local extinction probabilities for certain species. For example, the Sad Flycatcher and the Jamaican Becard were disproportionately detected in agricultural matrix habitats (e.g., foraging in grasslands and using hedgerows/paddock trees as perching and/or nesting habitat) relative to other matrix types, which may have reduced their local extinction in agricultural landscapes (Table 2.5). Similarly, the Jamaican Tody and the Jamaican Woodpecker were rarely detected in bauxite relative to peri-urban or agricultural matrices, and exhibited comparatively higher estimates of extinction in forests embedded in bauxite. The Jamaican Vireo and the Jamaican Eleania had lower extinction probabilities in agricultural and bauxite landscapes, and were observed less often in peri-urban matrix habitats relative to agricultural and bauxite matrices (Chapter 1). Further research is needed to identify the specific mechanism(s) driving differential long-term survival of birds among landscapes in Jamaica.

Conservation implications

The different matrix types in our region study could be simplistically classified as equally hostile to native species, given they differ dramatically in vegetation structure, composition, and microclimate from once-contiguous native forest. The insectivorous bird community, however, was profoundly affected by whether once-continuous forest was converted to agricultural, peri-urban, or bauxite mining development. Agricultural landscapes had occupancy dynamics more similar with continuous forest, with bird species in peri-urban or mining landscapes having higher extinction and marginally lower colonization rates. Thus, occupancy patterns not only differed between human-dominated versus natural matrix types as more typically found (e.g., Prugh et al. 2008), but also among the different human land-use types. Treating all modified lands equally, and categorizing Jamaica's landscapes into "matrix" versus "forest" components would have hidden these important patterns. The trajectory of land conversion in many regions of the world is from subsistence agriculture to increasing urbanization (DeFries et al. 2004). Since the 1950s, land-cover change in Jamaica (Evelyn and Camirand 2003) and on other Caribbean islands (Lugo 2002) has resulted largely from conversion of agriculture to residential development and mining for bauxite. This study strongly suggests that this conversion of agricultural lands to more intensive development will result in further losses of avian insectivores even without increased forest loss or fragmentation. Although we have not experimentally confirmed the mechanism, our evidence suggests that local extinction, rather than local colonization, is causing differential occupancy dynamics of insectivores among fragmented landscapes in Jamaica via the mediation of resource availability by human land uses and practices within the matrix. This finding is in contrast to several other tropical bird studies and the prevailing thought in the field. Thus, we recommend greater attention be given to the potential role of resource provisioning in different landscape contexts as a potential selective mechanism driving the decline of insectivores in fragmented landscapes.

Table 2.1. Life history and ecological traits of the nine resident insectivorous bird species included in analyses. All species were endemic to the island of Jamaica and known to breed in mid-elevation limestone forests within the study region.

Order: Family & Species	Body mass (1)	Altitudinal range (2)	Foraging strata (3)	Foraging mode (4)	Nest height (5)	Nest type (6)
Coraciiformes: Todidae						
Jamaican Tody (*Todus todus*)	6.8	L-M-H	M	S, G	G	C
Passeriformes: Cotingidae						
Jamaican Becard (*Pachyramphus niger*)	38.6	M-H	C	S, G	C	C
Passeriformes: Parulidae						
Arrow-headed Warbler (*Dendroica pharetra*)	10.3	M-H	M	G	U	O
Passeriformes: Tyrannidae						
Jamaican Elaenia (*Myiopagis cotta*)	12.8	L-M-H	C	S	C	O
Jamaican Pewee (*Contopus pallidus*)	9.9	M-H	U	S	C	O
Rufous-tailed Flycatcher (*Myiarchus validus*)	41.4	M-H	C	S	C	C
Sad Flycatcher (*Myiarchus barbirostris*)	13.4	L-M-H	U	S	U	C
Passeriformes: Vireonidae						
Jamaican Vireo (*Vireo modestus*)	10.5	L-M-H	U	G	U	O
Piciformes: Picidae						
Jamaican Woodpecker (*Melanerpes radiolatus*)	99.8	L-M-H	M	BP	C	C

(1) Estimated body mass (g), averaged across male, female, and unknown sexes (Lack 1976, Windsor Research Centre 2009).

(2) Altitudinal distribution on the island of Jamaica. (M-H) found in mid-elevation (300-1200 m) up to montane forests (600-2000m); (L-M-H) found in lowland, mid-elevation, and montane forest (0-2000 m) (Lack 1976).

(3) Foraging height most commonly observed. (U) understory in lower to mid forest or shrub layer (0.5 to < 5 m); (C) upper canopy (> 5 m); (M) among multiple heights (i.e., undergrowth up to canopy) (Cruz 1974, Cruz 1980, Raffaele et al. 1998, P. P. Marra, A. M. Haynes-Sutton, and H. A. Davis, *personal communication*).

(4) Foraging behavior most commonly observed. (BP) pecking/excavating in bark; (G) glean from nearby substrate (e.g., leaves, twigs); (S) sally from a perch to perch to attack prey (Lack 1976, Downer and Sutton 1995, Raffaele et al. 1998) (definitions from Remsen and Robinson 1990).

(5) Nesting height most commonly observed. (G) ground-level (< 0.5 m); (U) understory (0.5 to < 5 m); (C) upper canopy (> 5 m) (Bond 1993, Downer and Sutton 1995, Raffaele et al. 1998, P. P. Marra, A. M. Haynes-Sutton, and H. A. Davis, *pers. comm.*).

(6) Nest structure typically constructed. (C) partially closed, including cavity, burrow, sphere, and pendant nests; (O) nests with large openings, including cup, saucer, and platform nests (Downer and Sutton 1995, Raffaele et al. 1998) (definitions from Ehrlich et al. 1998).

Table 2.2. Means (± 1 SE) of patch area, isolation, and vegetation structure (PC1 scores) of sampled sites in intact forest (N = 31) and sampled patches in agriculture (N = 22), peri-urban (N = 27), or bauxite mining (N = 19) landscapes. *P*-values from one-way ANOVAs are provided (values in bold significant at $P < 0.05$). Letters indicate pairwise comparisons among matrix types based on posthoc Benjamini-Hochberg adjustments.

	Forest		Agriculture		Peri-urban		Bauxite		
Covariate	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P*- value
AREA	4.29	0.85	4.86	1.12	3.46	0.50	3.39	0.59	0.7612§
ENN_100ha	0	0	2362.34	222.76	2794.84	346.69	2106.87	204.05	0.2456‡
PC1	-0.29^a	0.31	-0.43^a	0.36	0.55^a	0.26	0.94^b	0.28	**0.0047***

AREA = Area of sampled forest patch or size of sampled plot within intact forest in hectares

ENN_100ha = Euclidean nearest-neighbor distance between sampled patch and forest fragment ≥100 ha in meters

PC1 = Measure of vegetation structure of sampled patch based on axis 1 of a principal component analysis

§ Based on log transformation of response variable (including sites within forested landscapes)

‡ Based on square root transformation of response variable (excluding sites within forested landscapes)

* Based on untransformed response variable (including sites within forested landscapes)

Table 2.3. Contribution of patch-level covariates to top models (i.e., ΔAIC < 2) of local colonization and extinction dynamics of nine resident insectivorous birds in Jamaica. √ indicates a covariate included in a top model with $w > 0.20$; (√) indicates a covariate included in a top model with $w < 0.20$. Results were qualitatively similar with other breakpoints (i.e., $w < 0.10$ or $w < 0.30$) (see Appendix H for individual model results). "Isolation" is the nearest-neighbor distance from each sampled patch to a forest fragment ≥ 100 ha. "Area" is the size of a forest patch. "Vegetation" is the Principal Component Score that is a composite index of 12 variables measuring forest vegetation structure (see Appendix G). "Matrix type" identifies whether a patch was in an agricultural, peri-urban development, bauxite mining, or forested matrix.

	Colonization (γ)		**Extinction (ε)**		
Species	Isolation	Matrix Type	Area	Vegetation	Matrix Type
Arrow-headed Warbler	√	√	√	√	
Jamaican Becard		√		√	√
Jamaican Elaenia		√		√	√
Jamaican Pewee		√		√	√
Jamaican Tody			(√)	(√)	√
Jamaican Vireo	(√)		(√)	√	√
Jamaican Woodpecker	(√)	(√)	(√)	(√)	(√)
Rufous-tailed Flycatcher	√	√		√	√
Sad Flycatcher	(√)		(√)	(√)	√

Table 2.4. Model-averaged slope parameter estimates (i.e., Beta coefficients) (± 1 SE) for each species based on z-transformed variables on the logit scale. Refer to Table 2.3 for explanations of covariates. Slope estimates close to 0 and 1 (based on normal scale) are indicated in parentheses.

	Slope Parameters $\left(\hat{\bar{\beta}}\right)$					
	Colonization $\left(\bar{\gamma}\right)$		Extinction $\left(\bar{\varepsilon}\right)$			
Species	$\hat{\bar{\beta}}$ (isol)	SE	$\hat{\bar{\beta}}$ (area)	SE	$\hat{\bar{\beta}}$ (veg)	SE
Arrow-headed Warbler	-0.18	0.23	-6.92	3.32	5.69	3.32
Jamaican Becard	–		–		(412.61)	–
Jamaican Elaenia	–		(-31.65)	–	(629.15)	–
Jamaican Pewee	–		–		2.33	0.97
Jamaican Tody	-0.45	2.05	-0.16	0.22	0.10	0.14
Jamaican Vireo	-0.21	0.56	0.02	0.50	-0.83	1.02
Jamaican Woodpecker	0.28	1.81	-1.50	4.73	1.34	0.86
Rufous-tailed Flycatcher	-0.83	1.14	–		2.34	1.93
Sad Flycatcher	-0.72	2.94	-0.01	0.16	0.14	0.22

(–) indicates either effect was not included in 95% confidence set or model-averaged SEs were nonsensical (i.e., unestimatable due to boundary problems). SEs calculated based on model-averaged Betas, using delta method (Williams et al. 2002), including only models with estimatable variance-covariance matrices.

Large (+) Beta estimates equal slope ~ 1; large (-) estimates equal slope ~ 0 (e.g., Beta > ±10) (as indicated in parantheses).

Table 2.5. Model-averaged estimates for local colonization and local extinction probabilities (± 1 SE) by landscape matrix type for each species. Estimates were determined when all other patch-level covariates (i.e., area, isolation, vegetation structure) were held constant at mean value.

	Local Colonization $\left(\hat{\gamma}\right)$ †								Local Extinction $\left(\hat{\varepsilon}\right)$ §							
Species	Forest	SE	Agriculture	SE	Peri-urban	SE	Bauxite	SE	Forest	SE	Agriculture	SE	Peri-urban	SE	Bauxite	SE
Arrow-headed Warbler	0.41	0.37	0.24	0.27	0.13	0.27	0.29	0.26	0.16	0.46	0.17	0.49	0.18	0.50	0.57	0.85
Jamaican Becard	0.00	–	1.00	–	0.00	–	0.00	–	0.00	–	0.00	–	1.00	–	1.00	–
Jamaican Elaenia	1.00	–	0.44	–	0.00	–	0.00	–	0.00	–	0.00	–	1.00	–	0.00	–
Jamaican Pewee	0.18	0.12	0.30	0.28	0.00	–	0.03	0.05	0.17	0.11	0.35	0.35	1.00	–	1.00	–
Jamaican Tody	0.00	–	0.99	0.03	0.86	0.44	0.80	0.58	0.10	0.06	0.00	–	0.00	–	0.28	0.21
Jamaican Vireo	0.78	0.30	0.81	0.24	0.66	0.36	0.65	0.36	0.00	–	0.00	–	0.23	0.34	0.08	0.16
Jamaican Woodpecker	0.69	1.65	0.64	1.49	0.00	–	0.00	–	0.01	0.03	0.00	–	0.05	0.25	0.31	0.92
Rufous-tailed Flycatcher	0.26	1.95	1.00	–	0.00	–	0.39	1.79	0.10	19.12	0.00	–	0.00	–	1.00	–
Sad Flycatcher	0.00	–	0.00	–	0.00	–	0.00	–	0.27	0.34	0.10	0.23	0.42	0.39	0.51	0.34
Average	0.37	0.12	0.60	0.12	0.18	0.11	0.24	0.10	0.09	0.03	0.07	0.04	0.43	0.15	0.53	0.13

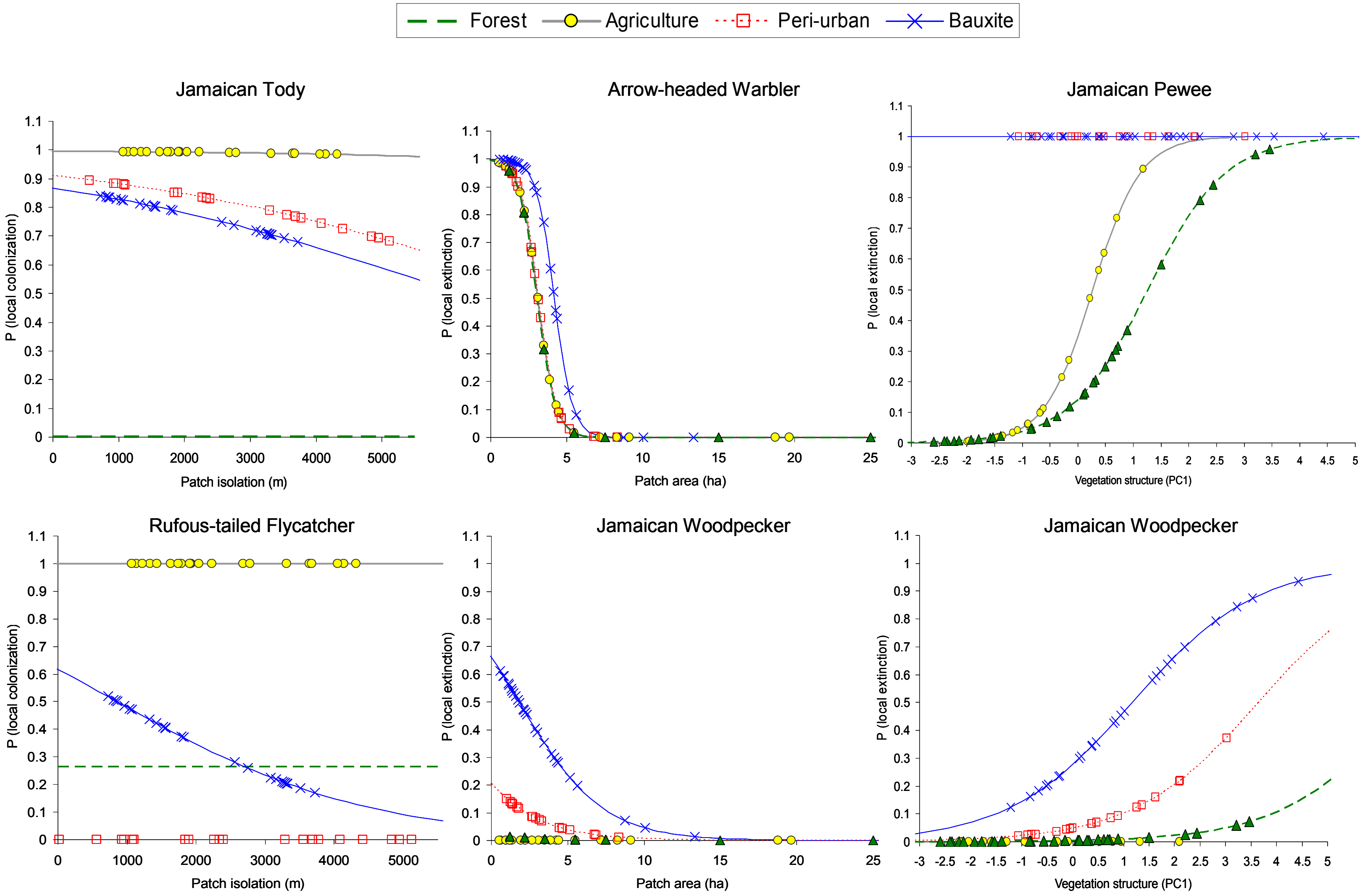
† Local colonization probabilities estimated at mean value of isolation for all fragmented landscapes and at 0 isolation for forested landscapes.

§ Local extinction probabilities estimated at mean value of patch area and mean value of vegetation structure (PC1) for all landscapes.

(–) indicates variances that could not be estimated due to estimation of Beta at boundary (i.e., 0 or 1) and/or due due to variance-covariance errors.

SEs calculated based on model-averaged Betas, using delta method (Williams et al. 2002), when covariances are assumed to be 0 and only including models with estimatable variance-covariance matrices.

Figure 2.1. Model-averaged point estimates of occupancy parameters for representative bird species in relation to a) local colonization probabilities as a function of patch isolation by matrix type; b) local extinction probabilities as a function of patch area by matrix type; and c) local extinction probabilities as a function of within-patch vegetation structure by matrix type. All patch-level covariates were modeled via additive relationships. Species presented exhibited rate parameters strongly influenced by patch-level covariates (refer to Table 2.4, 2.5 for unconditional standard errors, and Appendix H for additional species graphs).



a) Patch isolation b) Patch area c) Patch vegetation structure

Chapter 3: Landscape matrix mediates movements of generalist and specialist avian insectivores in fragmented tropical forest

Abstract

Maintaining species movement among habitat patches in fragmented landscapes is essential to maintaining functional connectivity. Dispersal abilities may depend in large part upon the landscape matrix in which habitat is embedded, but few empirical tests have been conducted to discern the role of the matrix on species movement. We examined the relative permeability of three landscape types in central Jamaica on the movement of the forest generalist, a Nearctic-Neotropical migrant, the American Redstart (*Setophaga ruticilla*); and a forest specialist, the endemic Jamaican Tody (*Todus todus*). We experimentally translocated > 140 birds 0.6–4 km from their territories across three landscape treatments: (1) landscapes fragmented by peri-urban development, (2) landscapes fragmented by bauxite mining, and (3) continuous forest. We investigated the relative influence of sex, body condition, territory habitat quality, translocation distance, and landscape matrix on return success and return time of individual birds. Redstarts returned with greater success and quicker return time than todies across all landscape types, with 95% of redstarts returning in an average of 2.5 days versus 60% of todies in an average of >20 days. Return success was best predicted by translocation distance for redstarts and by sex for todies, with a trend of fewer returns of redstarts and todies released in a bauxite matrix relative to other treatments. Return time was strongly affected by landscape type, with both redstarts and todies returning more rapidly in forest relative to a bauxite matrix and with return times intermediate in a peri-urban matrix.

Landscapes fragmented by peri-urban development were thus more permeable to bird dispersal than those fragmented by bauxite mining; this enhanced permeability is attributed to greater matrix vegetation cover in peri-urban areas. These findings provide crucial empirical support to the hypothesis that the nature of human land use surrounding primary habitat influences bird mobility within fragmented landscapes.

Introduction

Insectivorous birds are disproportionately declining in fragmented forests worldwide, with Neotropical-Nearctic migrants (e.g., Robbins et al. 1989a; Robbins et al. 1989b; Askins et al. 1990) and Neotropical residents (e.g., Sodhi et al. 2004; Sigel et al. 2006; Stouffer et al. 2009) being particularly impacted. Dispersal limitation is increasingly identified as a dominant mechanism underlying their demise (Lampila et al. 2005; Stratford and Robinson 2005). As forests become fragmented and converted to other habitat types, natural dispersal patterns may be disrupted, leading to a loss in connectivity among populations (e.g., Fahrig 2003). Understanding this potential reduction in the functional connectivity of landscapes (*sensu* Bélisle 2005) is essential for predicting species losses due to forest loss or alteration. Even for well-studied taxa like birds, movement responses to forest fragmentation are poorly known, because information on bird dispersal capabilities is lacking, particularly in the tropics (Walters 2000). Moreover, dispersal success and movement rates may be contingent upon the structure and composition of the intervening land cover in which habitat is embedded (termed the “matrix”) (Ricketts 2001; Revilla et al. 2004; Bender and Fahrig 2005).

Despite the potential importance, actual effects of the landscape matrix on bird dispersal remain poorly understood. The majority of research on bird movement has been conducted in landscapes of varying amounts of forest cover (e.g., Bélisle et al. 2001) or landscapes solely dominated by an agricultural matrix (e.g., Bayne and Hobson 2001; Castellon and Sieving 2006; Gillies and Clair 2008; Hadley and Betts 2009). These studies reveal that dispersal of forest-dependent birds is generally more successful in landscapes with greater forest cover, and that certain species avoid venturing into open pasture even at the energetic cost of greater travel time. Few studies, however, have compared bird dispersal in other human-modified matrix types or in multiple matrix types simultaneously. Further, when alternative matrix types have been considered, the effects of habitat amount and configuration could not be disentangled from effects due to other matrix features (e.g., Gobeil and Villard 2002). Given that the trajectory of land conversion in many regions of the world is from subsistence agriculture to urbanization (DeFries et al. 2004), a better understanding of bird mobility in these more intensively developed landscapes is sorely needed.

Our central aim was to determine whether matrix type influences dispersal abilities of two insectivorous bird species – a habitat generalist, Nearctic-Neotropical migrant, the American Redstart (*Setophaga ruticilla*); and a resident forest specialist, the Jamaican Tody (*Todus todus*). This study is the first in which a Nearctic-Neotropical migrant was translocated on its wintering grounds in comparison with a Neotropical resident bird. These species were targeted given their divergent life history traits and evolutionary trajectories (see Methods), which we predicted would impose differential constraints on their ability to respond to forest fragmentation. We experimentally translocated 142 birds an average of 1.7 ± 0.60 km (± 1 SE) from their territories across three landscape types: landscapes fragmented by peri-urban or bauxite mining development (i.e., peri-urban or bauxite matrix types) or landscapes comprising continuous forest (i.e., natural “matrix”). Understanding bird mobility in landscapes where forests were embedded in either a peri-urban or a bauxite matrix was important because land-cover change in Jamaica as well as on other Caribbean islands is increasingly due to these human land uses (Lugo 2002), and their effects on animal dispersal are not well documented. Experimental manipulations, particularly translocations, can be an effective way to measure functional connectivity for vagile species like birds (Desrochers et al. 1999; Bélisle et al. 2001), because they allow for dispersal motivation to be standardized across individuals, for probable return pathways to be predicted, and for landscape features of interest to be isolated (i.e., intervening matrix types) (Bélisle 2005).

We tested whether the probability with which birds returned (i.e., return success) or the time it took for them to return (i.e., return time) to territories differ among matrix types as well as among species. We predicted that birds would travel more successfully and more quickly through continuous forest relative to the fragmented landscapes, with intermediate return success and return time in peri-urban landscapes. Bird movement was expected to be enhanced in peri-urban landscapes because matrix areas contained greater vegetation cover that could act as stepping stones to aid movement while bauxite landscapes lacked this vegetation structure (see Study Area). Tropical non-migratory specialists, particularly understory insectivores, are expected to be more dispersal-inhibited than temperate generalist birds (e.g., Paradis et al. 1998; Harris and Reed 2002; Stratford and Robinson 2005); thus, we predicted that the American Redstart would have greater return success and quicker return time than the Jamaican Tody across all landscape types.

Additional factors beyond landscape structure can influence both site fidelity and dispersal ability and may in turn impact homing propensity (i.e., return of birds) (Bowler and Benton 2005). Female birds are typically more dispersive than males (Greenwood and Harvey 1982; Clarke et al. 1997). Birds inhabiting lower quality habitats may be less site-tenacious (e.g., Holmes et al. 1996), and individuals with reduced fitness may be less prone to return to territories (e.g., Marra and Holmes 2001) or less able to withstand physiological costs associated with translocation. Because homing abilities of our study species are unknown, we investigated the potential influence of sex, body condition, and territory habitat quality on return patterns.

Methods

Study area

We conducted our experiments in Manchester and Clarendon Parishes in central Jamaica, an area that was once covered in predominantly wet limestone forest (Asprey and Robbins 1953). Less than 30% of native forest currently remains, with most of the conversion occurring by the eighteenth century (Eyre 1987b). Forest is largely restricted to small hilltop remnants on limestone outcrops, with low lying areas converted for agriculture (i.e., historically for cultivation of cash crops, and later for cattle pasture) (Eyre 1987b; Eyre 1987a) and more recently for residential development and mining for bauxite (Evelyn and Camirand 2003). Given the karst topography, the habitat fragmentation pattern is similar among landscapes subject to these different human land-use pressures. Locations and extent of forest fragments in this region have remained fairly stationary in recent time but are embedded within a changing matrix. This setting provided a unique opportunity to investigate the influence of matrix land cover on movement patterns of forest-dependent birds.

We targeted three landscapes types in the region: (1) landscapes in which forest has been fragmented by residential (peri-urban) development, (2) landscapes in which forest has been fragmented by bauxite mining, and (3) landscapes comprising continuous forest (Figure 3.1). Open areas surrounding forest patches differed substantially in these peri-urban and bauxite matrices. Forest remnants in peri-urban landscapes were surrounded by low-density housing, ornamental gardens, abandoned woodlots, and roadside secondary growth. Bauxite landscapes were former agricultural lands that had been converted to mining within the past ten years, where relictual forests were surrounded by exposed bauxitic soils, with some recent growth of ferns, *Acacia* trees, or planted grassland (Figure 3.2). Relative to bauxite landscapes, peri-urban matrices contained greater foliage cover and vertical complexity (Appendix A).

Target species

We translocated the Jamaican Tody (*Todus todus*) and the American Redstart (*Setophaga ruticilla*) (hereafter tody and redstart). Both species are common insectivores in the region. The former species is endemic to Jamaica and the latter species is a migrant that winters in Jamaica from late August through May (Marra et al. 1998; Studds et al. 2008). The tody occurs in several forest types in Jamaica (e.g., dry to wet montane tropical forest), but it is most abundant in mid-elevation limestone forests (Raffaele et al. 1998). It is an understory forest specialist that forages commonly < 5 m from the ground, taking large insects from leaf undersides (Lack 1976). The redstart is a habitat generalist that is found in forest, woodland, and non-forested habitats in the Caribbean, where it forages for a wide variety of insect prey on a diversity of substrates over the full vertical range of habitats (Sherry and Holmes 1997).

The biology of the Jamaican Tody has yet to be rigorously studied but is known to breed and to hold territories between December and July (Raffaele et al. 1998, C. M. Kennedy, *unpublished data*), similar to congeners in Puerto Rico (*T. subulatus*, *T. angustirostris,* and *T. mexicanus*) (Kepler 1977; Latta and Wunderle 1996). Redstarts return annually to the same territory on their non-breeding, wintering grounds in Jamaica; both males and females vigorously defend these territories (Holmes et al. 1989; Marra 2000). Given their presumed similar motivation to return to capture sites, todies and redstarts were model subjects for our experiment. Both species were found in fragmented landscapes in the region (Chapter 1, C. M. Kennedy, *unpublished data*) and were relatively easy to detect and capture, thus, they provided an excellent means of comparing bird movements between human-altered versus forested matrices.

Capture and release sites

We captured birds from 17 forest fragments embedded in 4 bauxite mining landscapes, 12 forest fragments embedded in 4 peri-urban landscapes, and in sites in 4 intact forested landscapes (Figure 3.2). Capture patches in fragmented landscapes were similar in forest area (mean ± 1 SE: peri-urban: 4.24 ± 0.64 ha; bauxite: 3.10 ± 0.56 ha) and isolation (31.76 ± 7.72 m and 48.88 ± 7.60 m to nearest fragment > 0.5 ha and 2280.00 ± 485.44 m and 2139.47 ± 251.29 m to > 100-ha fragment in peri-urban and bauxite landscapes, respectively) as determined from an object-based classification of 2001-2002 multispectral pan-sharpened IKONOS imagery (1-m resolution) (Appendix I) using ArcGIS 9.3 (ESRI 2008). Patches were also embedded in landscapes with a similar proportion (35.84 ± 1.59) and spatial configuration of forest cover (i.e., shape complexity, inter-patch connectivity) (Appendix A).

To standardize the stimulus for dispersal, we also released birds in forest patches of similar size (peri-urban: 2.01 ± 0.48 ha; bauxite: 2.92 ± 0.71 ha) and isolation (112.46 ± 14.92 m and 103.49 ± 9.73 m to nearest fragment > 0.5 ha and 2866.20 ± 352.60 m and 2456.92 ± 481.65 m to > 100 ha fragment in peri-urban and bauxite landscapes, respectively). Thus, the landscape matrix was the primary difference among our experimental translocations. Release locations were predetermined from imagery, land-cover maps (Forestry Department 1999), and our previous field research, such that individuals were translocated in one of three treatments: peri-urban matrix (N = 46: 35 todies and 11 redstarts), bauxite mining matrix (N = 50: 25 todies and 25 redstarts), or forested "matrix" (N = 46: 31 todies and 15 redstarts). We captured birds in 69 unique locations and released them in 75 different sites (≥ 100 m in distance). On nine occasions (three times per treatment) individuals had the same capture and release locations, due to logistical constraints. Repeated use of sites was required because of a scarcity of locations in treatments accessible by roads and/or trails.

Translocation protocol

We translocated todies from mid February to early May and redstarts from late February to early April in 2007 (median date: 29 March 2007). Individuals were targeted for translocation after three to six visits, during which we confirmed territorial status based on repeated presence of redstarts and the interaction of a pair of todies, territorial displays (e.g., agonistic displays, fighting, and chasing behavior), and/or tody courtship or nesting behavior. We used the same protocol for pre- and post-translocation surveys (see below) to estimate detection probabilities. Redstarts and todies were detected with probabilities of 0.76 (± 0.06) and 0.72 (± 0.04) in forested landscapes, 0.70 (± 0.07) and 0.78 (± 0.04) in peri-urban landscapes, and 0.75 (± 0.04) and 0.74 (± 0.05) in bauxite landscapes, respectively; probabilities not differing by landscape type ($\chi^2_{\text{redstart}} = 1.004$, $\chi^2_{\text{tody}} = 1.003$, df = 2, $P = 0.606$, based on likelihood ratio tests of occupancy models fit in PRESENCE with and without matrix type as a covariate on detection) (Hines and MacKenzie 2008). Given high detection rates and a lack of bias among treatments, we were confident in the reliability of our return estimates for inference. Moreover, we have no reason to expect systematic bias in bird behavior as a function of landscape type even if detectability decreased in response to capture.

Individuals were caught between 0615 to 1220 hrs (mean: 0838 hrs) by attracting them into mist-nets via conspecific bird decoys and species-specific vocalizations to increase the capture probability of territory-holders rather than floaters that may fail to exhibit strong site fidelity. Individuals of both species consistently responded to playbacks during the entire capture period, suggesting similar territoriality and return propensity during the experiment. After catching each bird, we measured body mass and length of tarsus, culmen, and unflattened wing chord, and we banded it with a unique color combination. We targeted male redstarts but translocated the few females caught, given their known defense of winter territories. We were unable to standardize for sex among todies due to a lack of external dimorphism (i.e., monomorphic plumage, lack of detectable cloacal protuberances, brood patch development by both sexes) (Merola-Zwartjes and Ligon 2000; Pyle et al. 2004) (C. M. Kennedy, *unpublished data*). We standardized age based on plumage characteristics when feasible. Translocated individuals of both species were after-hatch-year birds. We were able to distinguish second-year from after-second-year redstarts based on plumage characteristics (Pyle et al. 1987); > 82% of redstarts were after-second-years. Hatch-year todies were easily distinguishable by their red throat patch heavily fringed with white, the brownish tinge in juvenile plumage, and unpneumaticized skull areas (S. E. Koenig, *unpublished data*). However, we could not definitively age todies beyond hatch-year (Pyle et al. 2004). In total, we translocated 51 redstarts (43 males and 8 females) and 91 todies (67 males and 24 female).

Immediately upon capture, birds were placed in an opaque cloth bag and transported by vehicle to release sites. Total capture-release time averaged 60.90 ± 1.45 min. Handling time was higher in forested landscapes (69.22 ± 2.66 min) than peri-urban (56.54 ± 2.46 min) or bauxite landscapes (57.26 ± 2.03 min) due to greater road inaccessiblity (ANOVA, $F_{2,139} = 8.795$, $P < 0.001$), but did not vary by species ($F_{1,140} = 1.269$, $P = 0.262$). Individuals were translocated > 560 m to 4 km (1.741 ± 0.06 km) from the site of their capture. Redstarts were translocated on average 2.34 (± 0.08) km, which was significantly farther than the distance todies were translocated (1.407 ± 0.06 km) (ANOVA, $F_{1,140} = 102.72$, $P < 0.001$). We selected these distances to be sufficiently large to reduce bias due to prior landscape knowledge from daily bird movements but small enough to reduce bias due to navigation ability during migration events (Bélisle et al. 2001; Bélisle and Clair 2002; Gobeil and Villard 2002). On wintering grounds, redstarts are rarely observed beyond their territory boundaries (C. E. Studds, *personal communication*, P. P. Marra, *unpublished data*) that are generally ≤ 0.25 ha in size

(Holmes et al. 1989). The size of the Jamaican Tody's home range is unknown, but territories of the congener *T. mexicanus* are an average 0.70 ha with daily movements expanding only ~ 60 m beyond these boundaries (Kepler 1977); we suspect territories may be even smaller for *T. todus* based on our observations (C. M. Kennedy, *unpublished data*). Translocation distance of todies did not vary by landscape treatment ($F_{2,88}$ = 0.048, *P* = 0.953) (forest: 1.47 ± 0.14 km; peri-urban: 1.39 ± 0.07 km; bauxite: 1.36 ± 0.09 km); but redstarts were translocated farther in bauxite relative to forested landscapes (forest: 2.10 ± 0.12 km; peri-urban: 2.16 ± 0.13 km; bauxite: 2.56 ± 0.12 km) ($F_{2,48}$ = 4.977, *P* = 0.011). To account for these differences, we included translocation distance as a covariate in our models.

Upon release of each bird, one to two observers remained at the site in a concealed location to ensure that each bird exhibited normal flight capability. An additional observer returned to the capture site and monitored for the potential return of the color-banded individual at the vicinity of its territory and surrounding areas (> 1 ha). If individuals were not detected on the first day, an observer returned to the capture site every day for the first five days, followed by day 7, day 10, day 14, with visits thereafter at weekly intervals for up to three months or until the target individual was observed. During each visit, we patrolled the territory grounds for at least one hour, searching passively for the first 30 minutes followed by broadcasting playbacks at 5-minute intervals for the final 30 minutes.

Covariates on return success and time

Besides our primary interest in landscape type, we considered four variables that we predicted would most influence species return patterns: sex, body condition, territory habitat quality, and translocation distance. We determined sex of redstarts based on plumage characteristics (Pyle et al. 1987). We determined sex of todies sex based on DNA extraction from blood samples drawn from a toenail clipping for 73 of 91 translocated individuals, using restriction fragment length differences in the ATP synthase gene (Carmichael et al. 2000) and sequence differences in spindlin genes (de Kloet and de Kloet 2005) between the Z and W chromosomes. Twenty todies were sexed as female and 53 as male based on DNA analyses. We determined sex of the remaining 18 todies by comparing their tarsus, culmen, and wing chord lengths to those of individuals of known sex, using discriminant function analysis (30.14% misclassification rate, Wilk's Lambda = 0.79, $F_{4,68} = 4.586$, $P < 0.002$, mass considered but excluded from final model), which resulted in all but four individuals being classified as male.

To account for variation in body condition of translocated birds, we estimated body mass corrected for the structural size of each bird by first reducing data on wing chord, tarsus, and tail length, using principal components analysis (PC) for each species separately. We then regressed body mass on PC axis 1 and axis 2 scores and used the model residuals as an index of body condition. The extent to which the predicted values deviated from expected mass given structural body size (i.e., residuals) indicated whether the bird was in good (i.e., positive residuals) or poor (i.e., negative residuals) body condition (Marra et al. 1998).

To quantify territory habitat quality, we measured 12 vegetation variables in a 10-m radius plot centered at each capture location: tree diameter, basal area, canopy height, leaf area index, leaf litter depth, abundance of woody and herbaceous vines, and percent herbaceous cover (0-0.5-m height class), low shrub (0.5-2 m), tall shrub (2-6 m), trees (>

6 m), and open canopy. We conducted a principal component analysis (PC) on these variables, and used the PC axis 1 score as a proxy for vegetation structure. This metric is expected to indicate territory habitat quality, given it has been identified as an important determinant of extinction rates for todies in the region (Chapter 2), with similar measures linked to habitat quality for redstarts on their wintering grounds (Parrish and Sherry 1994; Marra and Holmes 2001).

Translocation distance was determined based on the Euclidean distance between capture and release locations for each bird based on measurements taken in the field with a hand-held global positioning system (Garmin GPS 72) (≤ 10-m accuracy). Landscape treatment was defined categorically as to whether birds were translocated in a forested, peri-urban, or bauxite mining matrix, and served as a surrogate for matrix composition and structure, given the extent of forest fragmentation was similar between peri-urban and bauxite mining landscapes.

Modeling of return success and return time

We determined whether return success and return time differed by species over the entire observation period based on univariate models with species as the only covariate. We tested whether return success was influenced by all variables (as listed above), and return time by all variables except territory habitat quality. Given that the relative importance of environmental factors might vary between species, we fit models separately for redstarts and todies. We also considered the interaction between translocation distance and landscape type for redstarts. We analyzed return success (i.e., return versus no return) at a three-day threshold for redstarts and a thirty-five day threshold for todies, because the majority of returns for each species (84% of redstarts and 80% of todies) fell within these time frames. Additionally, we analyzed return success when closest to 50% (after Bélisle et al. 2001), which was at one-day and two-week time frames for redstarts and todies, respectively. Results for both the majority and the 50% thresholds were consistent; thus, final models are presented for the 3-day and 35-day post-translocation time periods only.

To assess the influence of covariates on return success and return time, we used generalized linear models with a binomial error distribution (logit link function) and Cox proportional hazards regression models, respectively. We analyzed return time (i.e., days since translocation) using survival analysis, which compares time-to-failure curves, where "failure" represented the detected return of a bird to its territory. We excluded birds that did not return to their territories in Cox regressions to prevent confounding movement with other potential mechanisms (i.e., philopatry and mortality). Model fitting was conducted using forward step-wise likelihood ratio estimation (Harrell 2001), in which variables were added that produced the most significant change in the model chi-square ($P < 0.10$), with variables considered statistically significant at $\alpha = 0.05$ in final models. Variables significant at $\alpha = 0.10$ were not included in final models, but we discuss associated covariates because they may indicate ecologically important trends. Final model significance was determined via the likelihood ratio test and the significance of coefficients via the Wald statistic with posthoc comparisons among groups based on Tukey's multiple comparison procedure. To ensure our conclusions were not dependent on our model building procedure, we investigated backward-stepwise selection, which produced similar final models. Each translocation was treated as an independent event in models, given that each individual bird was translocated only once and that > 90% of birds were captured in and released at different locations. To investigate the potential for spatial dependence, we conducted preliminary analyses in which we modeled capture and release patches as the only covariate on return success and time. For both species, patch identity failed to be a strong predictor for either return success ($P > 0.50$) or return time ($P > 0.10$).

Statistical analyses were performed in the *R* statistical system (R Development Core Team 2008) using the 'stats' package for univariate tests, generalized linear models, and principal components analysis, the 'MASS' package (v 7.2-44) (Venables 2002) for discriminant analysis, the 'survival' package (v 2.34-1) (Therneau and Lumley 2008) for Cox regressions, and the 'multcomp' package (Hothorn et al. 2008) for multiple comparisons. We assessed model fit based on plots of residuals versus fitted values, and model assumptions were met (e.g., constant error variance, approximately normal errors, and proportional hazards for Cox regression). Untransformed means ± 1 SE are reported.

Results

Return success

Return success was higher for the American Redstart (96% of 51 individuals) than the Jamaican Tody (62% of 91 individuals) (Figure 3.3, $\chi^2 = 24.78$, df = 1, $P < 0.001$). The most important determinant of redstart return success was the distance of translocation, with birds translocated farther having lower return probability ($\chi^2 = 8.26$, df = 1, $P = 0.004$) (Table 3.1). Body condition, territory vegetation structure, and sex did not influence redstart return probabilities at $P > 0.10$. Sex was the only significant predictor of tody return success, with males more likely to return than females ($\chi^2 = 5.50$, df = 1, *P* = 0.019). Sixty-nine percent of male todies versus 42% of female todies were found to return to their territories by the end of the three-month observation period. Translocation distance, body condition, and territory vegetation structure did not influence the return probability for the resident species (*P* > 0.10). Although not significant at *P* < 0.05, there was a trend of lower return success by redstarts and todies released in the bauxite matrix relative to peri-urban development and forested treatments (redstarts: χ^2 = 5.72, df = 2, *P* = 0.057; todies: χ^2 = 4.15, df = 2, *P* = 0.126; Figure 3.4).

Return time

Mean time for todies to return to territories was 20.6 (± 2.79) days, which was significantly longer than that for redstarts (2.6 ± 0.49 days) (χ^2 = 50.00, df = 1, *P* < 0.001). The return time of redstarts was influenced by the additive effects of landscape treatment and translocation distance (χ^2 = 16.40, df = 3, *P* < 0.001), whereas landscape treatment was the only significant factor influencing the return time for todies (χ^2 = 8.46, df = 2, *P* < 0.001). For both species, individuals returned faster in forested than in bauxite mining landscapes; return times were intermediate in peri-urban landscapes (Table 3.1, Figure 3.5). Redstarts that were translocated farther from their territories had slightly longer return times (*P* < 0.05), but translocation distance did not affect return time for todies (*P* > 0.10). Sex and body condition were not important predictors for the return time for either species (*P* > 0.10).

Discussion

Species traits mediate bird movement

The American Redstart returned with greater success across all landscape types than the Jamaican Tody, with almost 1.5 times as many redstarts found to return to territories. The lower return probability of todies may be explained in part by a greater proportion of female todies (26.4%) translocated than female redstarts (15.7%), which may have been less site-faithful. The age of individuals and their pairing status (Greenwood and Harvey 1982; Holmes et al. 1996) may also underlie the reason why fewer todies returned if we translocated juveniles and/or siblings that were acting as helpers on territories (this type of communal breeding has been documented for the congener *T. mexicanus*; Raffaele et al. 1998). The ultimate reason(s) todies failed to return to capture sites within the three months surveyed is thus unknown – whether due to mortality during dispersal (i.e., predation), behavioral decisions to settle in new locations, and/or an inability to orient successfully to original territories after displacement. The landscape matrix may also have played a role, given fewer returns of both redstarts and todies in bauxite landscapes, but this factor was not found to be significant, perhaps due to insufficient sample size.

An even more striking result was that of individuals that returned, redstarts were eight times faster than todies. With an average return time > 20 days, the tody displayed relatively poor dispersal capabilities when considering that temperate (e.g., Bélisle et al. 2001; Bélisle and Clair 2002; Gobeil and Villard 2002) and other tropical bird insectivores (Gillies and Clair 2008) have been reported to return to territories within 2 to 3 days using similar translocation experiments. Such low vagility was surprising, given todies are more abundant in disturbed and fragmented forests in Jamaica than are many other forest-dwelling insectivorous birds (Chapter 1, Lack 1976). Enhanced dispersal by redstarts may be due to their greater willingness to cross open spaces and to navigate in a wide variety of non-native habitats. This assertion is based on the fact that redstarts commonly use diverse habitats on their wintering grounds (e.g., Greenberg 1992; Wunderle and Waide 1993; Confer and Holmes 1995); thus, they may be less behaviorally inhibited in fragmented landscapes (e.g., Greenberg 1983). Given they are long-distance migrants, redstarts may have also evolved greater cognitive abilities (e.g., memory and processing of environmental information) that enhance their exploratory and navigational abilities (e.g., Mettke-Hofmann and Gwinner 2004).

Landscape matrix mediates bird movement

Although it is widely recognized that land cover surrounding primary habitat can affect bird mobility, this is the first study of which we are aware to test this hypothesis among different types of human-modified landscapes that are similar in structural habitat fragmentation (i.e., amount and configuration of forest cover) and in continuous forest. We found no significant difference in return success among landscape treatments in contrast to our predictions, perhaps due to low sample size, but a weak trend was detected of fewer returns of birds released in the bauxite matrix. The speed of return, however, did significantly differ in accordance with our predictions, with both species returning significantly more quickly in a forested matrix than in a bauxite matrix. Movement rates through peri-urban landscapes were more similar to intact forest relative to mining landscapes. This differential permeability is due to differential movement and not to differential mortality, because the pattern is based only on birds that successfully returned. Moreover, energetic inefficiencies from potential lower quality habitats and/or exposure to more stressful environmental conditions (ecto-, endo-parasite loads) in certain landscape types are likely not involved, given that territory habitat structure and body condition failed to be important predictors of return time.

Differential landscape permeability is most parsimoniously explained by the behavioral inhibitions to movement. Bauxite landscapes typically have little vegetation cover in matrix areas (Appendix B). Birds are thus subject to expansive open spaces and are forced to cross wide gaps (often hundreds of meters) when navigating between forest fragments. Previous experiments using song playbacks indicate that many forest species demonstrate a strong reluctance to cross even small habitat gaps (e.g., < 25-50 m) despite their presumed physical capabilities (e.g., Harris and Reed 2002). Gap-crossing and recent translocation experiments reveal that birds may avoid venturing into open areas and instead preferentially move through landscape features most similar to their optimal habitat at an energetic cost of greater travel time (e.g., Desrochers and Hannon 1997; Gillies and Clair 2008). This reluctance to cross gaps may be a response to avoid predators (e.g., Lima and Dill 1990), the result of a limited perceptual range that inhibits navigation to certain landscape elements (Lima and Zollner 1996; Zollner and Lima 2005), or the result of a lack of motivation (e.g., few suitable resources in the matrix; Bélisle and Desrochers 2002). Thus, birds in bauxite landscapes may have remained longer in release patches (e.g., Castellon and Sieving 2006), searched a longer time for suitable cover, or taken more circuitous routes back to territories (e.g., Gillies and Clair 2008; Hadley and Betts 2009). Given the size of target species (tody: 6.7 ± 0.05 g; redstart: 7.1 ± 0.08 g), we were unable to use radio transmitters to track behavioral decisions and detailed movement patterns by birds on their return paths. Thus, although the dispersal trends detected by this experiment provide essential insight into the differential permeability of common Caribbean landscapes, the specific landscape features that either facilitated or impeded movement remain unknown because we could not document bird dispersal trajectories and differential use of matrix features. Recent advances in miniaturized tracking technology, however, are making feasible the more precise tracking of smaller animals (e.g., Hadley and Betts 2009), which will enhance future research on bird movement behavior.

Conservation implications

Treating anthropogenically modified lands as a single cover type (i.e., non-habitat) and categorizing landscapes into "matrix" versus "habitat" components in fragmentation research and conservation planning has the potential to lead to erroneous decision-making. Based on our experiments, both the migrant American Redstart and the resident Jamaican Tody display differential dispersal abilities contingent upon whether once-continuous forest was converted to peri-urban or bauxite mining development. We hypothesize that similarity in permeability of peri-urban landscapes and continuous forest was due to trees in the peri-urban matrix acting as stepping stones. Residential landscapes have greater tree cover between forested hilltops as a result of ornamental gardens in lawns, abandoned woodlots, and treelined roadsides (Appendix B). Maintaining matrix vegetation cover, even if composed of non-native species and in isolated clusters of trees, seemingly facilitates bird movement between otherwise isolated forest patches. Similarly, Castellón and Sieving (2006) found that the Chucao Tapaculo (*Scelorchilus rubecula*) dispersed as readily in matrix habitat composed of shrubby vegetation as they did in wooded corridors, with vegetation cover the likely dominant cue over species composition. Their study and our data support the utility of restoring and/or maintaining matrix vegetation cover to serve as potential stepping stones for bird movement. Encouraging private land owners to restore tree cover either via native forest regeneration or ornamental planting of trees may be a more feasible, alternative management strategy to the creation of corridors, which has been the primary focus of conservation planning and may be more costly in terms of required restoration efforts and land acquisition.

The persistence of populations in fragmented landscapes may hinge upon the ability of individuals to disperse successfully through different matrix types to (re)colonize habitat patches and rescue populations from local extirpation (e.g., Revilla et al. 2004; Wiegand et al. 2005). Lack of vegetation structure in bauxite landscapes may be imposing great constraints on bird movement. After mining is complete, these landscapes are typically converted to pasture for cattle, which also lacks tree cover. These mined landscapes present an opportunity to test experimentally the importance of tree cover to the maintenance of functional connectivity for forest-dependent birds in an adaptive management framework. Planting trees in specific spatial arrangements and floristic assemblages would help to ascertain the relative effect(s) of matrix vegetation configuration, structure, and composition on movement success of birds and to identify threshold gap distances (*sensu* Harris and Reed 2002), above which the probability of movements become dramatically reduced.

Experimental studies designed to elucidate the relative impact of matrix lands on species dispersal abilities are thus needed for further comparison. Given the seemingly idiosyncratic responses by species to fragmentation, experimental movement studies may prove useful in predicting which species and/or guilds are most threatened by habitat conversion (e.g., Lees and Peres 2009). Our findings build upon emerging empirical evidence that supports long-standing hypotheses that particular groups of species may be more susceptible to extirpation in fragmented systems due to dispersal limitation. In particular, specialists appear more at risk than generalists (Haddad 1999; Gobeil and Villard 2002; Lees and Peres 2009), tropical species appear more at risk than temperate species (Moore et al. 2008), and resident species appear more at risk than migrants (Paradis et al. 1998; Bélisle and Clair 2002, this study).

Table 3.1. Variables that significantly influenced the return success and the return time (at $P < 0.05$) of the American Redstart and the Jamaican Tody when translocated ~ 550 m to 4 km from their territories in three landscape treatments (peri-urban development, bauxite mining, and forested matrix) in central Jamaica. Return success was modeled via generalized linear models (with binomial errors) and return time via Cox regression models.

	Variable	Coefficient	SE	*P*-value
Return success				
American Redstart	Constant	5.8825	1.81	0.001
(N = 51)	Translocation distance (m)	-0.0018	0.00	0.008
Jamaican Tody	Constant	-0.8873	0.45	0.048
(N = 91)	Sex-male	1.1576	0.51	0.024

	Variable	Hazard ratio	Coefficient	SE	*P*-value
Return time					
American Redstart	Translocation distance (m)	1.00	-0.0006	0.00	0.034
(N = 49)	Landscape-Forest	2.73	1.0029	0.39	0.010
	Landscape-Peri-urban	1.28	0.2431	0.43	0.570
Jamaican Tody	Landscape-Forest	2.92	1.0700	0.39	0.006
(N = 56)	Landscape-Peri-urban	2.09	0.7380	0.37	0.046

The reference category is female for "Sex" and bauxite for "Landscape" variable.

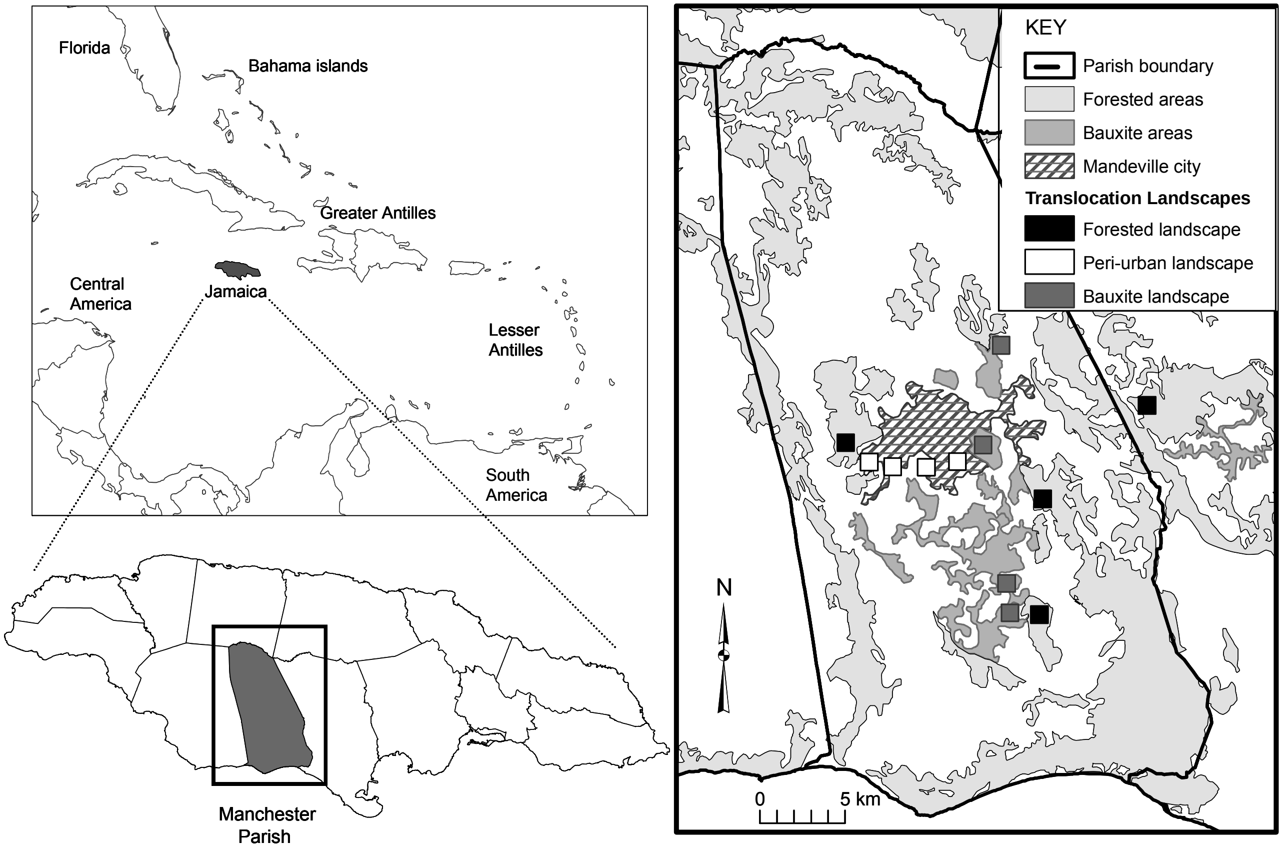


Figure 3.1. Locations of the 12 landscapes where experimental translocations were performed as shown in the context of the West Indies (latitude: 17 56'44"-18 05'36" N; longitude: 77 23'19"- 77 34'18" W). Landscapes are delineated by 1-km^2 areas centered around capture sites for geographic reference

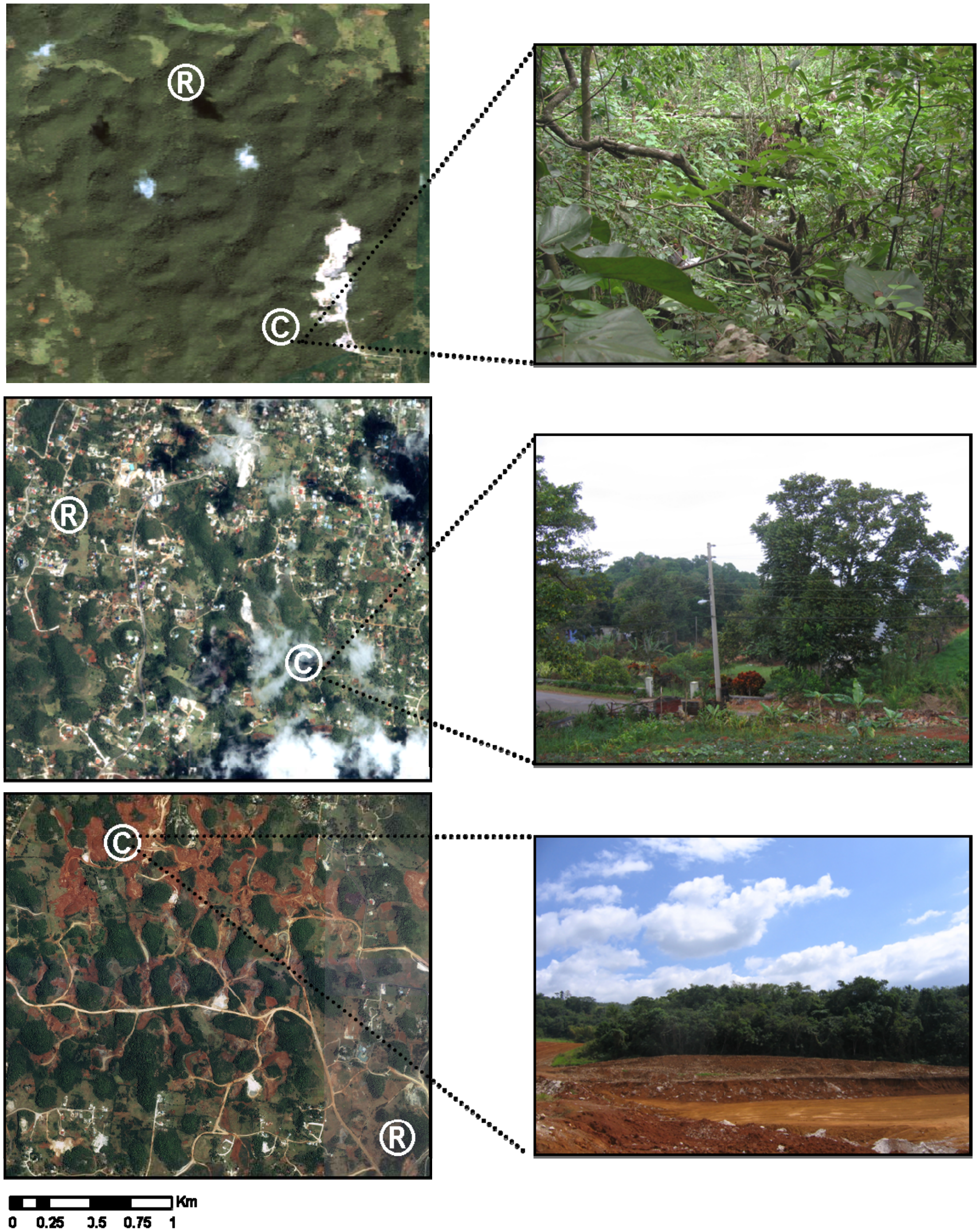


Figure 3.2. Three landscape treatments where birds were translocated: (1) landscapes comprising continuous forest (top), (2) landscapes fragmented by peri-urban development (middle), and (3) landscapes fragmented by bauxite mining (bottom). Capture (©) and release (®) locations of one example translocation is overlaid on 2001-2002 IKONOS imagery (left panel), juxtaposed with photographs taken in the field near capture patches (right panel). All birds were capture and released in limestone forest patches. Forest cover appears in dark green, surrounded by lawns, ornamental gardens, roadside vegetation, roads, and houses in peri-urban landscapes, and exposed bauxitic soil (as shown in red) and early growth of ferns and *Acacia* stands in bauxite mining landscapes.

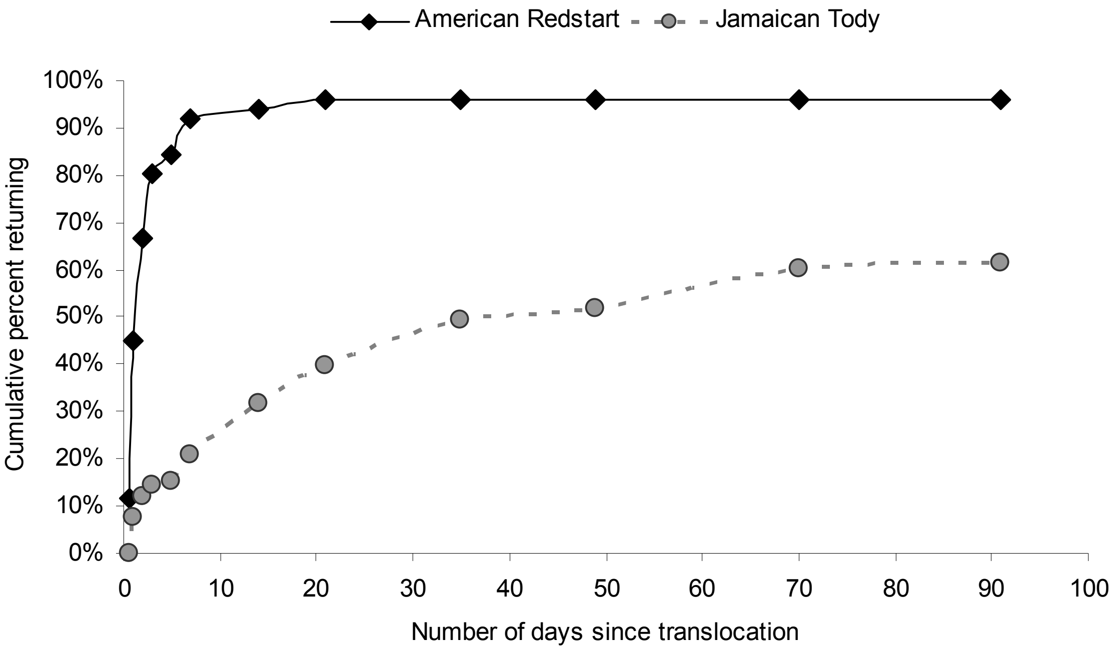


Figure 3.3. Cumulative proportion of the number of American Redstarts (N = 51) and Jamaican Todies (N = 91) detected to return to their territories as a function of the number of days since translocation.

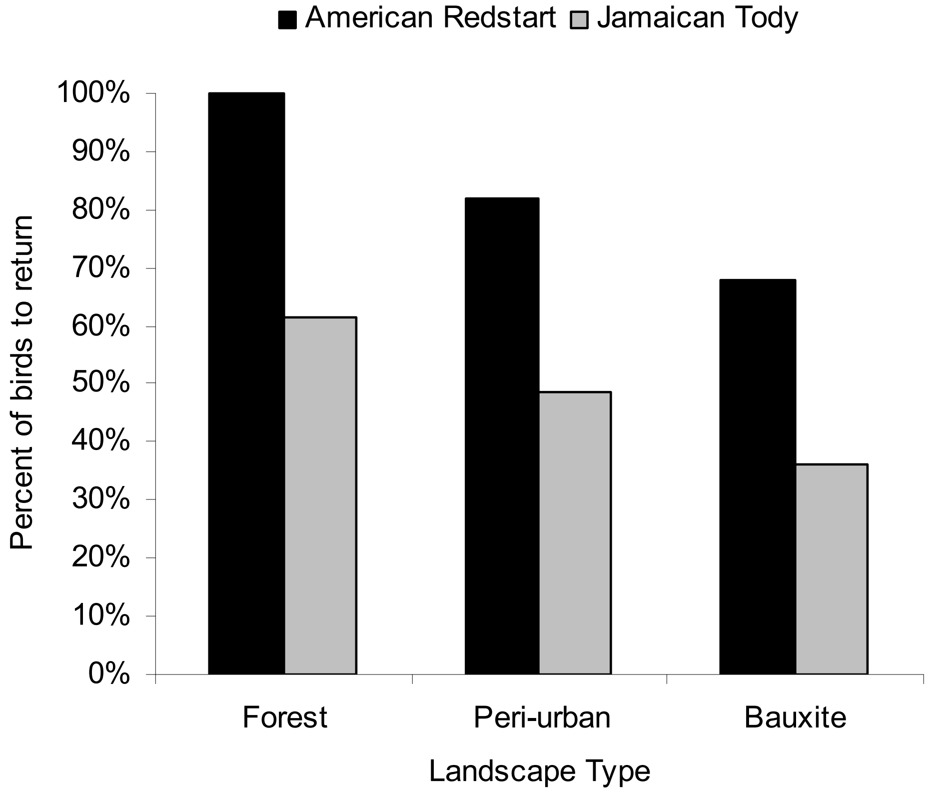


Figure 3.4. Return success 3-days after translocation (American Redstart) and 35-days after translocation (Jamaican Tody) in three landscape treatments (forest: N = 46, 15 redstarts and 31 todies; peri-urban development: N = 46, 11 redstarts and 35 todies; and bauxite mining: N = 50: 25 redstarts and 25 todies). Return thresholds (3-day and 35-day) were chosen to provide comparable percentages of returning birds for the two species. Return success did not differ by landscape treatment at $P < 0.05$ for either species, but differed at $P = 0.057$ for the American Redstart and $P = 0.126$ for the Jamaican Tody.

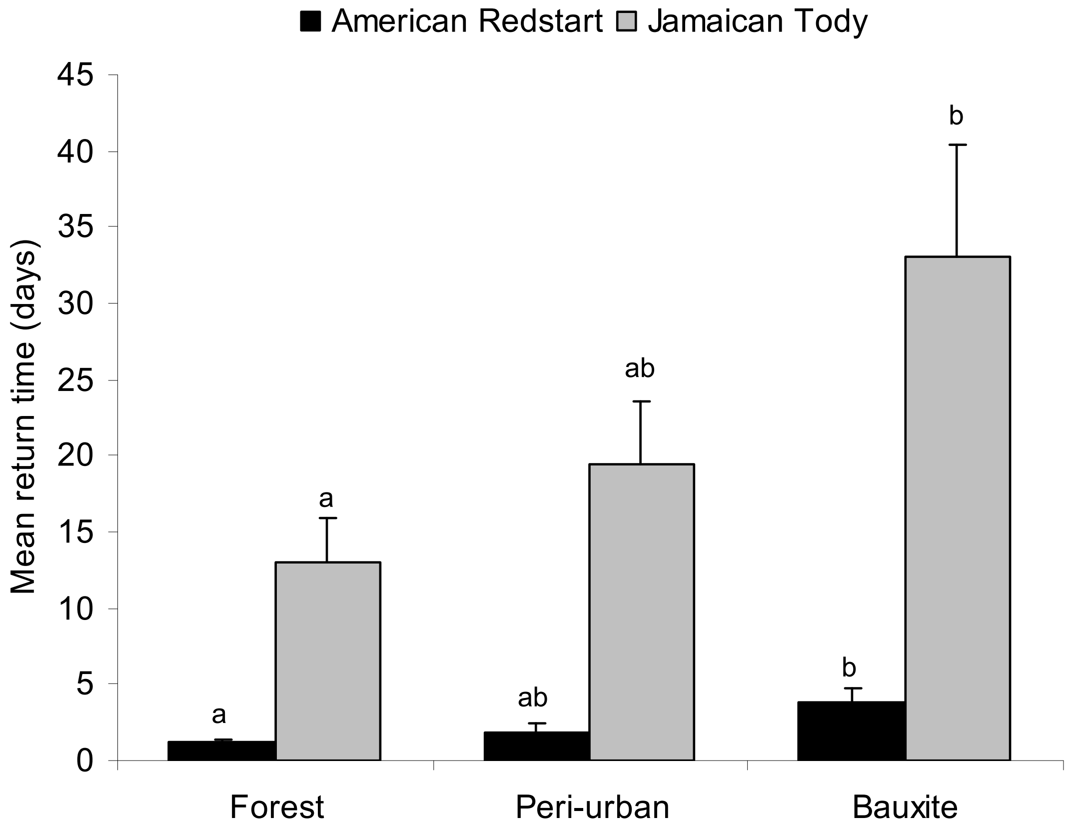


Figure 3.5. Mean return time (± 1 SE) by the American Redstart and the Jamaican Tody after translocation in three landscape treatments (forest: N = 35, 15 redstarts and 20 todies; peri-urban development: N = 32, 10 redstarts and 22 todies; and bauxite mining: N = 38: 24 redstarts and 14 todies). Shared letters indicate no significant difference ($P < 0.05$) among treatments based on Cox regression models and post-hoc Tukey's HSD tests. Return time of todies differed at $P < 0.10$ between peri-urban and bauxite treatments.

Appendices

Appendix A. Habitat fragmentation pattern among landscape types

Methods

To characterize the nature of forest fragmentation among anthropogenic landscapes (Figure A1), we derived landscape-level metrics based on a map of the study region in which we digitized forest cover from 2001-2002 IKONOS imagery (1-m resolution, Space Imaging 2002) and 2007 ground-truthing surveys using ArcGIS 9.3 (ESRI 2008) (LCC, WGS 84 projection). Forest habitat was categorized by a closed canopy and visual dominance of native broadleaf trees; producer's and user's accuracy for this cover type were estimated at 92% and 84%, respectively. We calculated 'class-level' metrics based on total forest cover per landscape using FRAGSTATS 3.3 (using 4-m raster cell size, an eight-neighbor rule for patch delineation, and 250-m search radius for patch connectance) (McGarigal et al. 2002). We derived the following metrics for each 1-km^2 agricultural, peri-urban, and bauxite mining landscape: percent forest cover (PLAND), number of forest patches (NP), mean patch area (AREA_AM), patch shape complexity (PAFRAC), mean patch isolation (ENN_AM), number of patch connections (CONNECT) and spatial aggregation of forest patches (CLUMPY) (Table A1). These metrics were selected because they have been found useful in quantifying the amount and configuration of habitat in landscapes (Neel et al. 2004), and have been shown to be associated with the effects of forest fragmentation on birds (e.g., Donovan and Flather 2002). These metrics were not highly inter-correlated (i.e., Pearson's correlation coefficient $r < 0.6$) (McGarigal et al. 2000); thus, they captured different aspects of landscape structure. Sampled forest remnants were located within the 1-km^2 landscapes; thus, landscape-level metrics captured the patch-level characteristics of sampled sites. For further comparison, we estimated the size of sampled patches, as well as their distances to the nearest forest fragment greater than 0.5 ha, 5 ha, or ≥ 100 ha. These threshold sizes were selected because they provided an estimate of the distance a bird would travel to reach the nearest forest patch of any size or greater than the average patch size (≥ 5 ha) within landscapes, as well as to a potential source population (≥ 100 ha).

Statistical analyses

Based on the seven landscape-level metrics, we tested for differences in the amount and spatial structure of primary habitat within agricultural, peri-urban, and bauxite mining landscapes using multi-response permutation procedure (MRPP) (based on mean standardized variables, Euclidean distance measure, and 1000 permutations) (Mielke and Berry 2001; McCune and Grace 2002) in the *R* 'vegan' package (v 1.13-1) (Oksanen et al. 2008). We tested for differences in the size and isolation of sampled forest patches using one-way ANOVAs in the *R* 'stats' package (v 2.8.1) (R Development Core Team 2008). For parametric tests, all variables were tested for normality and homogeneity of variances, and transformations were performed where necessary. Untransformed means ± 1 standard error are reported.

Results

Sampled plots within continuous forest ranged from 1.2 to 25 ha, and sampled patches within fragmented landscapes ranged from 0.6 to 19.6 ha in agricultural, 1.0 to 8.3 ha in peri-urban, and 0.6 to 13.3 ha in bauxite landscapes. The average plot size within forested landscapes was 4.29 (± 0.9 SE) ha, and the average fragment size was 4.9

(± 1.2) ha, 3.46 (± 0.5) ha, and 3.39 (± 0.6) ha in agricultural, peri-urban, and bauxite landscapes, respectively. Overall, study sites within the four matrix treatments did not differ in forest area (ANOVA, $F_{3,95} = 0.389$, $P = 0.7612$) (Table A2). Pooled across all anthropogenic landscapes, sample patches were 33.58 (± 3.48) m on average from the closest edge of another forest fragment of any size, 160.80 (± 19.79) m from a fragment at least 5 ha, and 2381.75 (± 147.07) m from a large forest tract at least 100 ha. Patch isolation distances did not differ among the three anthropogenic landscape types (ENN_0.5ha: $F_{2,65} = 2.834$, $P = 0.0661$; ENN_5ha: $F_{2,65} = 2.364$, $P = 0.1020$; ENN_100ha: $F_{2,65} = 1.435$, $P = 0.2456$).

In addition to sampled patches being similar in size and isolation, they were also embedded in landscapes with a similar proportion and spatial configuration of forest cover. Agricultural, peri-urban, and bauxite landscapes contained 34.2% (± 1.6) to 38.8% (± 3.5) of forest cover and an average of 18 (± 1.5) to 23 (± 4.0) forest fragments with area-weighted means ranging from 3.8 (± 0.4) to 5.8 (± 1.3) ha (Table A3). Shape complexity of forest fragments was similar, based on equivalent PAFRAC estimates, which measure how patch perimeter increases per unit increase in area. This suggests a potential similarity in the amount of edge-influenced habitat within landscapes. The extent of isolation or the proximity among all forest fragments in sampled landscapes was similar. The average area-weighted inter-patch distance among fragments within replicate landscapes was 19.8 (± 2.3) m, 24.3 (± 3.8) m, and 28.9 (± 4.0) m for peri-urban, agricultural, and bauxite landscapes, respectively. The number of possible connections among patches within a 250-m radius was consistent, with approximately 34% connected. This pattern remained consistent under varying search distances (i.e., 50, 100, and 500 m). Forest aggregation was also consistent among replicate landscapes based on average CLUMPY indices of 0.92 to 0.94. Simultaneously taking into account these seven landscape-level metrics, we found no difference in the amount and extent of forest fragmentation among the three anthropogenic landscape types (MRPP, A = 0.0247, $P = 0.2488$).

Table A1. Description and units of patch-level metrics derived for sampled forest patches and landscape-level metrics derived for forest cover within 1-km^2 agricultural, peri-urban, and bauxite mining landscapes used to characterize habitat amount and fragmentation (as described by McGarigal et al. 2002).

Metric	Description	Unit
Patch-level		
AREA	area of a forest patch	ha
ENN_0.5ha	nearest neighbor distance between target patch and another forest patch at least 0.5 ha in size based on shortest edge-to-edge euclidean distance	m
ENN_5ha	nearest neighbor distance between target patch and another forest patch at least 5 ha in size based on shortest edge-to-edge euclidean distance	m
ENN_100ha	nearest neighbor distance between target forest patch and forest tract at least 100 ha in size based on shortest edge-to-edge euclidean distance	m
Landscape-level		
PLAND	proportion of forest cover	percent
NP	number of forest patches	none
AREA_AM	area-weighted mean patch area of forest patches	ha
PAFRAC	perimeter-area fractal dimension: a measure of convolution of forest patch boundaries	none
ENN_AM	area-weighted mean nearest neighbor distance among forest patches based on shortest edge-to-edge euclidean distance	m
CONNECT	connectance index: a measure of the maximal number of joinings among forest patches within 250 m (distance based on unpublished mist-net data; Koenig, *pers. comm*.)	percent
CLUMPY	clumpiness index: a measure of spatial aggregation of forest land as determined by the frequency of adjacent forest cells as compared to a random distribution	none

Table A2. Means (± 1 SE) of four metrics measuring the size of sampled sites within continuous forest (N = 31), and the area and isolation of sampled forest patches in agriculture (N = 22), peri-urban (N = 27), or bauxite mining (N = 19) landscapes. *P*-values from one-way ANOVAs are provided.

	Forest†		Agriculture		Peri-urban		Bauxite		
Patch Metric	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P*-value
AREA	4.29	0.85	4.86	1.12	3.46	0.50	3.39	0.59	0.7612*
ENN_0.5ha	NA	NA	23.67	5.10	33.16	7.01	41.95	5.65	0.0661**
ENN_5ha	NA	NA	124.00	31.65	140.80	35.75	204.85	33.63	0.1020**
ENN_100ha	NA	NA	2362.34	222.76	2794.84	346.69	2106.87	204.05	0.2456**

† Area of sites within forested landscapes are based on size of sampled plots, and distance measures are not provided because plots were embedded within continuous forest

* Based on log transformation of response variable

** Based on square root transformation of response variable

Table A3. Means (± 1 SE) of seven metrics measuring the amount and spatial configuration of forest cover in 1-km^2 replicate landscapes fragmented by agriculture (N = 5), peri-urban development (N = 4), or bauxite mining (N = 5) in central Jamaica.

	Agriculture		Peri-urban		Bauxite	
Landscape Metric	Mean	SE	Mean	SE	Mean	SE
PLAND	38.77	3.52	34.20	1.59	34.21	2.40
NP	18.00	1.52	23.00	4.02	19.80	1.56
AREA_AM	5.78	1.32	6.63	2.93	3.77	0.43
PAFRAC	1.29	0.07	1.39	0.08	1.34	0.06
ENN_AM	24.33	3.79	19.80	2.79	28.86	3.93
CONNECT*	34.30	3.48	33.17	2.22	33.82	2.27
CLUMPY	0.94	0.00	0.92	0.01	0.94	0.01

* Metric based on 250 m distance, but results similar at 50, 100, and 500 m distances

Figure A1. Aerial view of representative landscapes fragmented by agriculture (left), peri-urban development (middle), and bauxite mining (right), based on 2001-2002 IKONOS imagery. Forest cover appears in dark green largely surrounded by linear hedgerows, tree stands, and pasture in agricultural landscapes; by houses, roads, ornamental lawns and gardens, and roadside vegetation in peri-urban landscapes; and exposed bauxitic (terra rossas) soil (as shown in red) and early growth of ferns and *Acacia* stands in bauxite mining landscapes.

Appendix B. Habitat structure within anthropogenic matrices

Methods

To determine the amount of resources available for birds outside of forest patches that may provide foraging or nesting substrates or aid movement in fragmented landscapes, we quantified land-cover composition and foliage structure in agricultural, peri-uban, and bauxite matrices. On four randomly placed transects located in matrix areas, we established 10-m radius plots at 100-m intervals and measured percent foliage cover in four height classes (0-0.5 m, > 0.5-2 m, > 2-6 m, > 6 m) based on visual estimation. For each survey we categorized matrix habitats into four cover types: (1) Herbaceous cover: areas dominated by herbaceous growth (usually < 0.5 m) – including pasture; ornamental lawns; cultivated bamboo (*Bambusa vulgaris)* or kinggrass (*Pennisetum purpureum*); recent growth of grass, ferns, and saplings in abandoned mining areas (i.e., bauxite regrowth); or herbaceous gardens dominated by non-woody crops (e.g., corn, pumpkin, cassava, sweet potatoes). (2) Shrubland: areas dominated by low stature shrubs (< 4 m) – including *Acacia* stands and ornamental shrubbery. (3) Linear vegetation: rows of trees (often 15-30 m wide) planted along property boundaries (i.e., live fences) or roadsides. (4) Scattered trees: widely-spaced trees dominated by cultivated species that were > 4 m in height and commonly lacking understory vegetation. Three subcategories of scattered trees were recognized, including tree stands, tree gardens, and mixed woodlands. Tree stands were defined as clusters of ornamental trees (< 0.25 ha) often maintained in isolation in pasture or development. Tree gardens were subsistence gardens dominated by fruit or nut trees (e.g., coffee, citrus, papaya, banana or breadfruit). Mixed woodlands were areas dominated by ornamental tree species but with

≥ 25% natural secondary growth. We delineated these land-cover features because they captured the structural variation in vegetation among the three anthropogenic matrix types. Areas lacking vegetation, including houses, roads, or active mining pits, were not surveyed due to lack of bird use. Remnant native forest was also not included as a cover type because it was not considered a matrix feature and was sampled at bird stations. We conducted ~ 55 matrix samples per landscape, for a total of 713 surveys (225 surveys in 4 agricultural landscapes, 218 surveys in 4 peri-urban landscapes, and 270 surveys in 5 bauxite landscapes). One agricultural landscape was not sampled due to fire destruction in 2005. Samples were proportional to the occurrence of each matrix cover type per landscape and were taken by three observers from May 21 to June 17, 2007.

Statistical analyses

To characterize differences in land-cover composition and foliage structure among matrix types, we averaged surveys per replicate landscape and conducted multivariate tests based on multi-response permutation procedure (MRPP) (with Euclidean distance measure and 1000 permutations) (Mielke and Berry 2001; McCune and Grace 2002) using the *R* 'vegan' package (v 1.13-1) (Oksanen et al. 2008), and one-way ANOVAs using the *R* 'stats' package (v 2.8.1) (R Development Core Team 2008). All variables were tested for normality and homogeneity of variances for parametric tests, and transformations were performed where necessary. Familywise error was controlled at $\alpha = 0.05$ for pairwise comparisons using the Bonferroni method (Sokal and Rohlf 1995). Tukey's multiple comparison procedure was used to separate treatment means (Westfall and Young 1993) via the *R* 'multcomp' package (Hothorn et al. 2008). Untransformed means ± 1 standard error are reported.

Results

Land-cover composition within matrix areas differed substantially among agricultural, peri-urban development, and bauxite mining landscapes (MRPP, A = 0.4522, $P < 0.0010$). Agricultural landscapes were dominated by pasture and herbaceous gardens (58.63% herbaceous cover), with interspersed fencerows, isolated tree stands, and shrubbery (41.37% combined) (Table B1). The percentage of linear vegetation was significantly greater in agricultural than in either peri-urban or bauxite matrices (ANOVA, $F_{2,10} = 11.37$, $P = 0.0027$). Peri-urban landscapes had fewer herbaceous cover types ($F_{2,10} = 14.93$, $P = 0.0010$) but greater scattered tree classes than either agricultural or bauxite landscapes due to the presence of subsistence tree gardens, ornamental tree stands, and mixed woodlands ($F_{2,10} = 36.65$, $P = < 0.001$). Over 70% of peri-urban matrix areas was tree or shrub cover types. Bauxite matrices were comparatively devoid of trees, but were dominated by herbaceous growth of ferns and/or grass in abandoned mining areas (77.79%) with some shrubs due to secondary growth of *Acacia* stands (19.29%).

Differences in land-cover composition translated into differences in foliage structure by matrix type (MRPP, A = 0.3243, $P = 0.0020$). Peri-urban matrices had greater tall shrub cover (2-6 m) than either agricultural or bauxite matrices (Table C1). Percent herbaceous (< 0.5 m), low shrub (0.5-2 m), and tree (> 6 m) cover were similar in agricultural and peri-urban matrices. Bauxite landscapes had less foliage cover overall – with less herbaceous cover (0-0.5 m) than agricultural or peri-urban landscapes ($F_{2,10} = 13.92$, $P = 0.0013$); less tall shrub cover (2-6 m) and less tree cover (> 6 m) than peri-urban landscapes ($F_{2,10} = 10.68$, $P = 0.0033$; $F_{2,10} = 7.34$, $P = 0.0109$, respectively); and strong trends toward less cover of low shrubs (0.5-2 m) ($F_{2,10} = 3.47$; $P = 0.0717$). These results confirm that anthropogenic landscapes differed substantially in composition and foliage structure of matrix habitats, with peri-urban and agricultural matrices containing greater foliage stratification than bauxite matrices, largely due to the presence of ornamental tree gardens, tree stands, and fencerows.

Table B1. Means (± 1 SE) of eight variables measuring matrix land-cover composition and foliage structure in landscapes fragmented by agriculture (N = 4), peri-urban development (N = 4), or bauxite mining (N = 5) in central Jamaica. *P*-values from one-way ANOVAs are provided (values in bold significant at familywise $\alpha = 0.05$ and * at $\alpha = 0.10$). Letters indicate pairwise comparisons based on posthoc Tukey's HSD tests ($P < 0.05$).

	Agriculture		Peri-urban		Bauxite		
Matrix Measures	Mean	SE	Mean	SE	Mean	SE	*P*-value
Percent Land Type							
Herbaceous Cover	58.63^{a}	0.08	28.49^{b}	0.06	77.79^{a}	0.05	**0.0010**
Bauxite regrowth	0.00	0.00	0.00	0.00	31.47	0.06	
Pasture	41.35	0.11	8.35	0.02	32.86	0.06	
Herbaceous garden	15.43	0.08	9.32	0.03	7.67	0.02	
Ornamental lawn	0.93	0.01	10.34	0.02	0.78	0.00	
Bamboo/kinggrass	0.93	0.01	0.48	0.00	5.01	0.04	
Shrubland	10.43	0.02	18.53	0.03	19.29	0.05	0.3055
Natural shrubs	10.03	0.02	9.72	0.02	19.29	0.05	
Ornamental shrubs	0.40	0.00	8.81	0.02	0.00	0.00	
Linear Vegetation	17.83^{a}	0.05	3.08^{b}	0.01	1.53^{b}	0.00	**0.0027**
Scattered Trees	13.12^{a}	0.03	49.90^{b}	0.08	1.39^{c}	0.01	**<0.0001****
Tree stand	8.77	0.04	12.33	0.01	0.70	0.00	
Tree garden	1.32	0.01	26.38	0.04	0.00	0.00	
Mixed woodland	3.03	0.02	11.19	0.05	0.70	0.00	
Percent Vegetation Cover							
Herbaceous layer***	90.84^{a}	3.19	82.50^{a}	1.84	68.16^{b}	3.65	**0.0013**
Low shrub layer†	21.19	3.80	26.55	2.07	16.38	2.31	0.0718
Tall shrub layer‡	13.78^{b}	2.86	23.86^{a}	2.19	8.82^{b}	2.05	**0.0033**
Tree layer•	13.58^{ab}	3.91	24.23^{a}	5.81	3.72^{b}	1.56	0.01091*

Landscapes with similar superscript letters did not differ ($P > 0.05$) in vegetation variable (ANOVA, Tukey's HSD)

** Based on square root transformation of response variable

*** Estimated percent foliage cover of herbaceous growth < 0.5 m in height

† Estimated percent foliage cover of shrubs 0.5 - 2 m in height

‡ Estimated percent foliage cover of shrubs or trees 2 - 6 m in height

• Estimated percent foliage cover of trees > 6 m in height

Appendix C. Habitat structure within forest patches

Methods

To capture habitat complexity of forest patches in the four landscape types (forested, agricultural, peri-urban development, and bauxite mining), we measured 12 variables: tree diameter, basal area, canopy height, leaf area index, leaf litter depth, abundance of woody and herbaceous vines, and percent herbaceous cover (0-0.5-m height class), low shrub (0.5-2 m), tall shrub (2-6 m), trees (> 6 m), and open canopy. Surveys were conducted at each bird station (with the exception of two bauxite patches due to logistical reasons), totaling 283 vegetation surveys (87 in forest, 77 in agricultural, 49 in peri-urban, and 70 in bauxite landscapes). We established 10-m radius plots centered at each station, divided into four equal quadrats based on 10-m transects in each cardinal direction. We measured tree basal area using a 10-factor prism at each plot center. Within each quadrat, we measured diameter breast height and canopy height of the largest tree, and we estimated the abundance of herbaceous and woody vines based on a categorical scale (0 = absent, 1 = solitary, 2 = few, scattered individuals, 3 = common, 4 = abundant). At 2-m intervals along each transect, we measured leaf litter depth and foliage structure. Foliage structure was scored based on foliage touches along a pole at four height classes (0-0.5 m, 0.5-2 m, 2-6 m, > 6 m), with percent cover calculated as the percent of all points at a given height interval with ≥ 1 touch (after Schemske and Brokaw 1981). Percent canopy openness and effective leaf area were estimated based on hemispherical canopy photographs taken at 5-m intervals in two randomly selected transects with a Nikon Coolpix 950 Camera and FC-E8 Nikon Fisheye lens. Percent canopy openness and effective leaf area (Leaf Area Index Ring 4) (Stenberg et al. 1994) were calculated using the Gap Light Analyzer (GLA) program (v 2.0) (Frazer et al. 1999). Sampling was conducted April 27 to July 2, 2005, with all measurements calibrated between two observers. We determined patch-level vegetation by averaging repeat measurements across quadrats, transects, and plots within a patch (N = 97).

Statistical analyses

Due to violations of multivariate normality, differences in overall forest structure by matrix type were determined based on multi-response permutation procedure (MRPP) (with mean standardized variables, Euclidean distance measure, and 1000 permutations) (Mielke and Berry 2001; McCune and Grace 2002) in the *R* 'vegan' package (v 1.13-1) (Oksanen et al. 2008). We conducted MRPP on 10 of the 12 vegetation variables, excluding leaf area index and tree diameter due to high inter-correlation ($r > 0.6$) with percent open canopy and tree height, respectively.

We tested for differences in individual vegetation variables using one-way ANOVAs in the *R* 'stats' package (v 2.8.1) (R Development Core Team 2008). All variables were tested for normality and homogeneity of variances. Familywise error was controlled at $\alpha = 0.05$ for pairwise comparisons in both MRPP and one-way ANOVAs using the Bonferroni method (Sokal and Rohlf 1995). Tukey's multiple comparison procedure was used to separate treatment means (Westfall and Young 1993) via the *R* 'multcomp' package (Hothorn et al. 2008). Untransformed means ± 1 standard error are reported.

Results

Forest structure of patches differed by landscape type (MRPP, $A = 0.0538$, $P < 0.0001$). Based on pairwise comparisons, fragments embedded in an agricultural matrix differed significantly in forest structure from the other landscape types (forest: A = 0.0505, *P* < 0.0001; peri-urban: A = 0.0399, *P* = 0.0004; bauxite: A = 0.0713, *P* < 0.0001). Vegetation structure of sites within forested landscapes differed from forest patches in a bauxite matrix (A = 0.0338, *P* = 0.0003), and marginally from those in a peri-urban matrix (A = 0.0127, *P* = 0.043). Forest structure of peri-urban and bauxite patches did not differ (A = 0.0072, *P* = 0.1348).

Five vegetation variables significantly differed among matrix types: tree basal area, tree diameter, canopy height, percent tree layer, and percent herbaceous layer (based on familywise $\alpha = 0.05$) (Table C1). Tree basal area was significantly higher in patches in an agricultural matrix as compared to patches in forested and bauxite matrices, but did not differ from patches in peri-urban landscapes (ANOVA, $F_{3,93} = 4.84$, $P = 0.0036$). Tree diameter was greater in agricultural patches as compared to all other matrix types ($F_{3,93} = 8.49$, $P < 0.0001$). Canopy height did not differ between patches in agricultural and forested landscapes, but was higher in agricultural patches relative to peri-urban or bauxite patches ($F_{3,93} = 8.13$, $P < 0.0001$). Forest in agricultural landscapes had a greater proportion of trees (> 6 m) relative to bauxite landscapes, with no significant difference among patches in forested, agricultural, and peri-urban landscapes ($F_{3,93} = 9.03$, $P < 0.0031$). Percent herbaceous cover was higher in forest patches in bauxite matrices as compared to those in agricultural and forested matrices, but did not differ from patches in peri-urban landscapes ($F_{3,93} = 9.93$, $P < 0.0001$).

Leaf area index, percent open canopy, and percent low shrub and tall shrub layers marginally varied among landscape types at $P < 0.05$, whereas leaf litter depth and abundance of herbaceous and woody vines did not. Forested landscapes had greater leaf area index ($F_{3,93} = 3.15$, $P < 0.0286$), more tall shrubs ($F_{3,93} = 3.76$, $P < 0.0144$), and less open canopy ($F_{3,93} = 3.8772$, $P < 0.0286$). Forest in bauxite landscapes, and to a lesser extent in peri-urban landscapes, had more low shrubs ($F_{3,93} = 4.03$, $P < 0.0096$).

Overall, forest patches in agricultural landscapes, and to a lesser extent sites within continuous forest, had greater stand basal area, leaf area index, tree diameter, tree canopy height, and tree cover than patches in peri-urban and bauxite landscapes. In contrast, forest in bauxite and peri-urban landscapes had more open canopy and greater proportion of herbaceous cover and low shrubs, indicating these sites may be in earlier successional stages and/or have undergone greater disturbance.

Table C1. Means (± 1 SE) of 12 variables measuring vegetation structure of forest patches in landscapes fragmented by agriculture (N = 22), peri-urban development (N = 19), or bauxite mining (N = 25) or of sites within continuous forest (N = 31) in central Jamaica. *P*-values from one-way ANOVAs are provided (with values significant at familywise α = 0.05 in bold). Letters indicate pairwise comparisons based on posthoc Tukey’s HSD tests ($P < 0.05$).

	Forest		Agriculture		Peri-urban		Bauxite		
Vegetation Variable	Mean	SE	Mean	SE	Mean	SE	Mean	SE	*P*- value
Leaf Area Index	2.90^{a}	0.06	2.72^{ab}	0.06	2.62^{b}	0.09	2.65^{ab}	0.09	0.0286
Basal Area (m^{2}/ha)	21.57^{b}	1.16	28.37^{a}	1.69	23.03^{ab}	1.61	22.20^{b}	1.24	**0.0036**
Tree Diameter (cm)	17.45^{b}	1.31	26.64^{a}	1.86	20.37^{b}	1.98	16.67^{b}	1.12	**<0.0001**
Canopy Height (m)	12.79^{ab}	0.66	15.05^{a}	0.63	11.81^{b}	0.82	10.62^{b}	0.42	**<0.0001**
Percent Cover (%)									
Open canopy	9.26^{b}	0.37	10.54^{ab}	0.50	11.52^{ab}	0.67	11.73^{a}	0.85	0.0096
Herbaceous layer	39.77^{b}	3.51	37.44^{b}	3.65	50.07^{ab}	3.84	61.35^{a}	2.98	**<0.0001**
Low shrub layer	63.46^{ab}	3.07	56.07^{b}	2.76	67.86^{ab}	3.63	70.62^{a}	2.69	0.0096
Tall shrub layer	85.32^{a}	1.78	74.21^{b}	1.96	78.96^{ab}	4.16	81.07^{ab}	2.21	0.0144
Tree layer	48.85^{ab}	5.46	57.89^{a}	2.83	40.33^{ab}	4.29	34.05^{b}	3.95	**0.0031**
Abundance**									
Herbaceous vines	2.18	0.15	2.65	0.15	2.53	0.13	2.53	0.13	0.0913
Woody vines	2.28	0.13	2.38	0.14	2.20	0.11	2.47	0.10	0.4667
Litter Depth (cm)	5.01^{a}	0.24	5.7^{a}	0.22	4.97^{a}	0.20	5.72^{a}	0.20	0.0218

Landscapes with similar superscript letters did not differ ($P > 0.05$) in vegetation variable (ANOVA, Tukey's HSD)

** Based on scale: 0 = absent, 1 = solitary, 2 = few, scattered individuals, 3 = common, 4 = abundant

Appendix D. Sampling effort across landscapes in 2005–2007

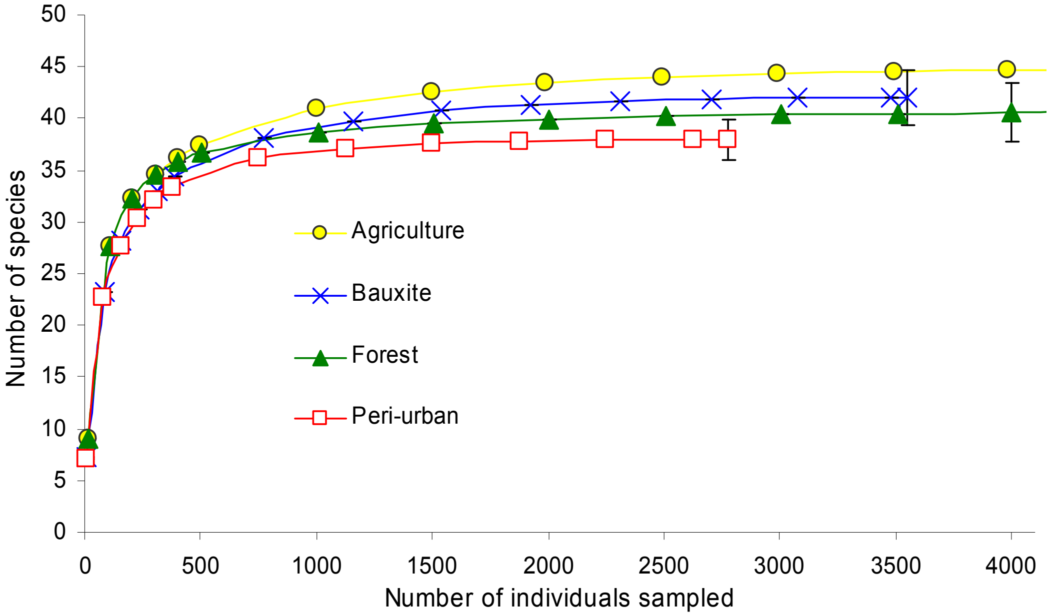


Figure D1. Mean number of native resident bird species detected in central Jamaica based on cumulative number of point counts in forested, agricultural, peri-urban development, and bauxite mining landscapes pooled across three years (2005-2007). Species accumulation curves were calculated using the sample-based rarefaction index (Mao Tau), rescaled in terms of numbers of individuals (as shown in x-axis, up to 4000 individuals) and computed in *EstimateS* 8.0 (Gotelli and Colwell 2001). Error bars denote ± 95% CI and were calculated using a general binomial mixture model with 100 randomizations (via replacement sampling) (Colwell et al. 2004). Curves quickly approached an asymptote, indicating sampling effort was sufficient in capturing species richness per landscape treatment during the duration of the study. Based on overlapping confidence intervals, species accumulation patterns did not significantly vary among landscape types (at a 0.05 level). For graphical illustration, only a subset of point count samples is displayed.

Appendix E. Traits of resident Jamaican birds

Table E1. Definitions, codes and data sources used to categorize species traits. Sources are listed in order of reliance.

Trait	Definition and Categories	Code	Source(s)*
Taxonomy	Taxonomic order		1
	Apodiformes, Ciconiiformes, Columbiformes, Coraciiformes, Cuculiformes, Passeriformes, Piciformes, Psittaciformes		
Body mass	Estimated body mass (g), averaged across male, female, and unknown sexes		5, 6, 3
Clutch size	Average number of eggs laid during single nesting period		1, 2, 4
Rarity	Mean density within continuous forest (i.e., forested landscapes) for forest-restricted and generalist species; mean density within matrix habitats for open-associated species		10
Geographic range	Worldwide distribution of a species		1
	Jamaica: endemic species confined to Jamaica	(J)	
	Caribbean: species whose range includes Greater and Lesser Antilles, and may include Gulf of Mexico (i.e., South Florida, Yucatan Peninsula, or the islands of Mexico)	(C)	
	Neotropical: species whose range includes Caribbean islands and New World tropics, including Central and South America	(N)	
	Temperate-tropical: species whose range includes both nearctic (North America) and neotropical regions (Caribbean islands, Central and South America)	(TT)	
Altitudinal range	Altitudinal distribution of a species on the island of Jamaica		3
	Low-Mid-elevation: found in lowland (0-300 m) up to mid-elevation areas (300-1200 m)	(L-M)	
	Mid-High elevation: found in mid-elevation (300-1200 m) up to montane forests (600-2000m)	(M-H)	
	Low-Mid-High: found in lowland, mid-elevation, and montane forest (0-2000 m)	(L-M-H)	
Diet guild	Dominant food source		3, 7, 9, 1, 2
	Frugivore: feeds primarily on fruits	(F)	
	Nectarivore: feeds primarily on nectar	(N)	
	Insectivore: feeds primarily on insects	(I)	
	Omnivore: feeds on both animals (e.g., insects, lizards) and plant substances (e.g., fruits, seeds)	(O)	
	Granivore: feeds primarily on seeds or nuts	(G)	
	Carnivore: preys primarily on vertebrate animals (lizards, mice, birds)	(C)	

Foraging strata	Dominant height zone where a species forages		7, 8, 1, 11
	Ground: forages predominately on the ground (< 0.5 m)	(G)	
	Understory: forages predominately in lower to mid forest or shrub layer (0.5 to < 5 m)	(U)	
	Canopy: forages predominately in upper forest canopies (> 5 m)	(C)	
	Multiple: forages commonly among more than one height zone (i.e., undergrowth up to canopy)	(M)	
Nest height	Dominant height zone where a species is found to nest		1, 2, 4, 11
	Ground: nests predominately on the ground (< 0.5 m)	(G)	
	Understory: nests predominately in lower to mid forest or shrub layer (0.5 to < 5 m)	(U)	
	Canopy: nests predominately in upper forest canopies (> 5 m)	(C)	
	Multiple: nests commonly among more than one height zone	(M)	
	Unknown: nesting height is unknown	(NA)	
Nest type	Type of nest typically constructed by the species (see Ehrlich 1988 for definitions)		1, 2, 12
	open: nest types with large openings, including cup, saucer, and platform nests	(O)	
	closed: partially closed nest types, including cavity, burrow, sphere, and pendant nests	(C)	
Habitat association	Habitat preference based on relative species' densities within forest as compared to non-forest habitats (i.e., matrix)		10, 1, 2
	Forest-restricted: birds with densities three times greater in continuous forest than matrix habitats	(FR)	
	Generalist: birds with densities that did not differ by three fold in either forest or matrix habitats	(G)	
	Open-associated: birds with densities three times greater in open/matrix habitats than intact forest	(OA)	

*Data sources: 1. Raffaele et al. 1998; 2. Downer and Sutton 1995; 3. Lack 1976; 4. Bond 1993; 5. Windsor Research Centre 2009; 6. Dunning 2003; 7. Cruz 1974; 8. Cruz 1980; 9. Cruz 1981; 10. Kennedy unpublished data; 11. Consultation with local ornithologists (P.P. Marra, A.M. Haynes-Sutton, H.A. Davis); 12. Ehrlich et al. 1998

Table E2. Traits of the 41 resident bird species detected in the study region, and included in richness and community analyses. * indicates species excluded from Poisson mixed model regressions and decision tree analyses due to insufficient detections.

Order: Family & Species	Body mass	Clutch size	Rarity	Geographic range	Altitudinal range	Diet guild	Foraging strata	Nest height	Nest type	Habitat association
Apodiformes: Trochilidae										
Jamaican Mango (*Anthracothorax mango*)	7.9	2.0	0.05	J	L-M	N	U	C	O	OA
Red-billed Streamertail (*Trochilus polytmus*)	5.2	2.0	0.68	J	L-M-H	N	M	U	O	G
Vervain Hummingbird (*Mellisuga minima*)	2.3	2.0	0.09	C	L-M-H	N	U	U	O	G
Ciconiiformes: Falconidae										
American Kestrel (*Falco sparverius*)*	115.5	4.5	0.08	TT	L-M-H	C	M	C	C	OA
Ciconiiformes: Accipitridae										
Red-tailed Hawk (*Buteo jamaicensis*)*	1126.0	2.5	0.00	TT	L-M-H	C	M	C	O	G†
Columbiformes: Columbidae										
Common Ground-Dove (*Columbina passerina*)	33.4	2.0	0.06	N	L-M	G	G	U	O	G
Ruddy Quail Dove (*Geotrygon montana*)	116.6	2.0	0.11	N	M-H	G	G	G	O	FR
White-Bellied Dove (*Leptotila jamaicensis*)	164.1	2.0	0.07	C	L-M	G	G	G	O	G
White-crowned Pigeon (*Columba leucocephala*)	242.5	2.0	0.39	N	L-M	F	C	M	O	FR
White-winged Dove (*Zenaida asiatica*)	153.0	2.0	0.11	N	L-M	G	G	U	O	OA
Zenaida Dove (*Zenaida aurita*)	159.0	2.0	0.16	N	L-M	G	G	M	O	OA
Coraciiformes: Todidae										
Jamaican Tody (*Todus todus*)	6.8	2.5	0.38	J	L-M-H	I	M	G	C	FR
Cuculiformes: Cuculidae										
Chestnut-bellied Cuckoo (*Hyetornis pluvialis*)	178.5	3.0	0.05	J	M-H	C	M	M	O	G
Jamaican Lizard-Cuckoo (*Saurothera vetula*)	74.5	3.5	0.04	J	L-M	C	U	U	O	FR
Mangrove Cuckoo (*Coccyzus minor*)	66.3	2.5	0.04	N	L-M	C	U	U	O	FR
Smooth-billed Ani (*Crotophaga ani*)	98.3	5.0	0.37	N	L-M	O	G	M	O	OA
Passeriformes: Corvidae										
Jamaican Crow (*Corvus jamaicensis*)*	277.0	3.0	0.00	J	M-H	O	C	C	O	FR†
Passeriformes: Cotingidae										
Jamaican Becard (*Pachyramphus niger*)	38.6	3.0	0.14	J	M-H	I	C	C	C	FR

Passeriformes: Emberizidae										
Bananaquit (*Coereba flaveola*)	8.5	3.0	0.99	N	L-M-H	N	M	M	C	G
Black-faced Grassquit (*Tiaris bicolor*)	11.3	3.0	0.24	N	L-M-H	G	G	U	C	OA
Greater Antillean Bullfinch (*Loxigilla violacea*)	28.0	3.5	0.46	C	L-M-H	F	U	M	C	FR
Jamaican Euphonia (*Euphonia jamaica*)	15.1	3.5	0.31	J	L-M-H	F	C	M	C	G
Jamaican Spindalis (*Spindalis nigricephala*)‡	42.3	3.0	0.31	J	L-M-H	F	C	U	O	G
Orangequit (Euneornis campestris)	15.7	3.0	1.15	J	L-M-H	N	M	NA	O	FR
Yellow-faced Grassquit (*Tiaris olivacea*)	9.3	3.0	0.68	N	L-M	G	G	G	C	OA
Yellow-shouldered Grassquit (*Loxipasser anoxanthus*)	10.7	3.5	0.20	J	L-M-H	F	U	U	C	G
Passeriformes: Icteridae										
Jamaican Oriole (*Icterus leucopteryx*)	44.2	4.0	0.25	C	L-M-H	I	M	U	C	G
Passeriformes: Mimidae										
Northern Mockingbird (*Mimus polyglottos*)	48.6	4.0	0.58	TT	L-M	O	G	M	O	OA
Passeriformes: Muscicapidae										
Rufous-throated Solitaire (*Myadestes genibarbis*)*	25.0	2.0	0.01	C	M-H	F	U	NA	C	FR†
White-chinned Thrush (*Turdus aurantius*)	77.6	2.5	0.42	J	L-M-H	O	G	M	O	G
White-eyed Thrush (*Turdus jamaicensis*)	59.6	2.0	0.15	J	M-H	O	M	M	O	FR
Passeriformes: Parulidae										
Arrow-headed Warbler (*Dendroica pharetra*)	10.3	2.0	0.26	J	M-H	I	M	U	O	FR
Passeriformes: Tyrannidae										
Jamaican Elaenia (*Myiopagis cotta*)	12.8	3.0	0.16	J	L-M-H	I	C	C	O	FR
Jamaican Pewee (*Contopus pallidus*)	9.9	3.0	0.21	J	M-H	I	U	C	O	FR
Loggerhead Kingbird (*Tyrannus caudifasciatus*)	38.2	3.0	0.25	C	L-M-H	O	M	M	O	OA
Rufous-tailed Flycatcher (*Myiarchus validus*)	41.4	4.0	0.16	J	M-H	I	C	C	C	FR
Sad Flycatcher (*Myiarchus barbirostris*)	13.4	3.5	0.13	J	L-M-H	I	U	U	C	G
Stolid Flycatcher (*Myiarchus stolidus*)*	22.9	3.5	0.03	C	L-M	I	U	NA	C	FR†
Passeriformes: Vireonidae										
Jamaican Vireo (*Vireo modestus*)	10.5	2.5	0.71	J	L-M-H	I	U	U	O	FR
Piciformes: Picidae										
Jamaican Woodpecker (*Melanerpes radiolatus*)	99.8	4.0	0.28	J	L-M-H	I	M	C	C	G
Psittaciformes: Psittacidae										
Olive-throated Parakeet (*Aratinga nana*)	85.1	4.0	0.17	N	L-M	F	M	C	C	G

‡ Previously named Jamaican Stripe-headed Tanager (*Spindalis nigricephalus*) (Banks et al. 2000)

† Habitat association determined from published natural history information because species were detected in fewer than 15 percent of sites

Appendix F. Candidate model set

Four parameters were estimated based on multi-season patch-occupancy models: initial occupancy (ψ), and the probabilities of local colonization (γ), local extinction (ε), and species detection (*p*). Initial occupancy (ψ_1) is the probability that a sampled patch is occupied by the species in the initial year (i.e., t = 2005). Local extinction probability (ε_t) is the probability that a patch occupied by the species at year *t* is no longer occupied by the species at year *t+1* (i.e., the patch goes locally extinct). Local colonization probability (γ_t) is the probability that a patch unoccupied by the species at year *t* becomes occupied at year *t+1*. Lastly, detection probability (p_t) is the probability that at least one individual of a species is detected in year *t*. This modeling framework includes detection probability as a variable that is simultaneously estimated with local extinction and colonization probabilities via likelihood maximization (MacKenzie et al. 2003; MacKenzie et al. 2006).

We developed a candidate model set including 28 models specifying different covariate relationships for colonization and extinction probabilities (Table F1). Detection probability was modeled as a constant or as a function of survey order and sampling effort (Table F2). Survey order indicated whether a survey was the first, second, or third point count conducted within a season. Surveys were conducted from early February to mid-June, and detectability may have varied during this period due to changes in bird activity or behavior (e.g., singing frequency) related to breeding cycles or weather (e.g., rainfall patterns) (Best 1981; Ralph 1981). In addition, survey order included variability related to observer learning within a season; this indirectly accounted for potential observer bias, because observers were rotated among each survey round. Because sampling was proportional to forest area, small patches had fewer samples than larger patches (as described above). A direct correlation between effort and detectability is widely recognized (e.g., Williams et al. 2002). To account for this potential source of variability, we also modeled *p* based on the number of points surveyed per patch. Other covariates, such as observer and time of day, might influence species detection (Ralph and Scott 1981), but their effects were diminished by our rotating observers and the temporal order of sampling. Thus, within a season each patch was sampled at least once by each observer and at rotating time periods. We also considered the potential effect of matrix type on detection probability. Variation in noise, vegetation structure, and bird abundances in different landscape contexts could influence species detection. Initial modeling of matrix type on *p* for over half of the species, however, gave systematic model convergence and parameter identifiability problems, suggesting a lack of a detectable relationship (J. E. Hines, *personal communication*). We therefore could not include matrix type as a detection covariate, and were confident that survey order and sampling effort covariates captured the essential components of detection variability in our study. The best covariate structure on detection was determined separately for each species and was based on the most general model structure for occupancy (i.e., global model, including all covariates on γ and ε). The most supported detection covariates were then applied when modeling occupancy and related rate parameters to investigate the covariate relationships with the rate parameters, which was of primary interest in our study.

For all models, initial occupancy was modeled without any covariates to focus investigation on rate parameters (after Ferraz et al. 2007). We modeled γ as a function of patch isolation and matrix type and ε as a function of patch area, local vegetation structure, and matrix type. For a subset of models, colonization was modeled as constant through space and time, because previous research indicated that differential responses by birds to fragmentation in Jamaica were due to potential resource limitation (i.e., extinction processes) rather than to movement inhibition (i.e., colonization processes) (Chapter 1). Only additive relationships were modeled for all covariates, given that our data set (N = 99 sites) would not support additional modeling complexity involving several interaction parameters in a multi-season occupancy modeling framework.

Table F1. Candidate model structures of occupancy (ψ), local colonization probability (γ), and local extinction probability (ε). “Isolation” is the nearest-neighbor distance from each sampled patch to a forest fragment ≥ 100 ha. “Area” is the size of a forest patch in hectares. “Vegetation” is a composite index of 12 vegetation variables measuring canopy cover, canopy height, tree basal area, vertical stratification, and leaf litter depth of sampled patches (see Appendix G). “Matrix type” is a categorical variable that identifies whether a patch was embedded in agriculture, peri-urban development, bauxite mining, or intact forest.

Colonization (γ)		**Extinction (ε)**			
Isolation	Matrix Type	Area	Vegetation	Matrix Type	Model Function
		√			ψ (.), γ (.), ε (area)
			√		ψ (.), γ (.), ε (veg)
				√	ψ (.), γ (.), ε (matrix)
		√	√		ψ (.), γ (.), ε (area+veg)
		√		√	ψ (.), γ (.), ε (area+matrix)
			√	√	ψ (.), γ (.), ε (veg+matrix)
		√	√	√	ψ (.), γ (.), ε (area+veg+matrix)
√		√			ψ (.), γ (isol), ε (area)
√			√		ψ (.), γ (isol), ε (veg)
√				√	ψ (.), γ (isol), ε (matrix)
√		√	√		ψ (.), γ (isol), ε (area+veg)
√		√		√	ψ (.), γ (isol), ε (area+matrix)
√			√	√	ψ (.), γ (isol), ε (veg+matrix)
√		√	√	√	ψ (.), γ (isol), ε (area+veg+matrix)
	√	√			ψ (.), γ (matrix), ε (area)
	√		√		ψ (.), γ (matrix), ε (veg)
	√			√	ψ (.), γ (matrix), ε (matrix)
	√	√	√		ψ (.), γ (matrix), ε (area+veg)
	√	√		√	ψ (.), γ (matrix), ε (area+matrix)
	√		√	√	ψ (.), γ (matrix), ε (veg+matrix)
	√	√	√	√	ψ (.), γ (matrix), ε (area+veg+matrix)
√	√	√			ψ (.), γ (isol+matrix), ε (area)
√	√		√		ψ (.), γ (isol+matrix), ε (veg)
√	√			√	ψ (.), γ (isol+matrix), ε (matrix)
√	√	√	√		ψ (.), γ (isol+matrix), ε (area+veg)
√	√	√		√	ψ (.), γ (isol+matrix), ε (area+matrix)
√	√		√	√	ψ (.), γ (isol+matrix), ε (veg+matrix)
√	√	√	√	√	ψ (.), γ (isol+matrix), ε (area+veg+matrix)

Table F2. Candidate model structures of species detection probability (*p*). "Survey order" refers to whether a survey was the first, second, or third survey conducted within a season and is correlated with survey month. "Sampling effort" is the number of points surveyed per patch.

Detectability (*p*)		
survey order	sampling effort	Model Function
		p (.)
√		*p* (survey)
	√	*p* (effort)
√	√	*p* (survey+effort)

Appendix G. Vegetation structure based on PC analyses

Table G1. Factor loadings from a principal component analysis of plot-level vegetation variables for each sampled forest patch. The first principal component axis (PC1) explained 32.17% of variance in plot-level vegetation structure. All variables were significantly correlated with PC1 scores based on Pearson correlation coefficients at familywise $\alpha = 0.05$ (indicated in bold).

Vegetation Variable	PC1
Leaf Area Index	**-0.3324**
Basal Area (m^2/ha)	**-0.3228**
Tree Diameter (cm)	**-0.3182**
Canopy Height (m)	**-0.3817**
Percent Cover (%)	
Open Canopy	**0.3489**
Herbaceous Layer	**0.2959**
Low Shrub Layer	**0.2410**
Tall Shrub Layer	**-0.1312**
Tree Layer	**-0.4101**
Abundance (scale 0:4)	
Herbaceous Vines	**0.2308**
Woody Vines	**0.1115**
Litter Depth (cm)	**-0.1408**

Appendix H. Model selection results

Table H1. Summary of model selection statistics for the top 95% confidence set ($\Sigma\ w = 0.95$) for the nine avian insectivores detected in central Jamaica from 2005-2007. K is the number of parameters included in the model; -2LL is twice the negative log-likelihood value, where *L* is the maximized value of the likelihood function for the estimated model; AIC is Akaike's Information Criterion, which judges a model by how close its fitted values are to true values and can be interpreted as the weight of evidence in favor of model *i* being the best model for the data with respect to the entire model set; ΔAIC is the difference in AIC value for model *i* when compared with the top ranked model; w_i is the Akaike weight of model *i*, which is interpreted as the probability that model *i* is the best model. The model set provided are those whose weights sum to 0.95 based on entire candidate model set; weights were then adjusted to sum to one for model averaging. Models in bold are within 2 ΔAIC units of the top model, and considered equally supported. The global model was ψ(.), γ(isolation + matrix), ε (area + veg + matrix).

	95% Confidence Model Set Per Species	K	-2LL	AIC	ΔAIC	*w*	∑*w*
Arrow-headed Warbler (*Dendroica pharetra*)							
1	**ψ (.), γ (matrix), ε (area+veg), p (effort)**	**10**	**546.53**	**566.53**	**0.00**	**0.25**	**0.25**
2	**ψ (.), γ (isol), ε (area+veg), p (effort)**	**8**	**550.72**	**566.72**	**0.19**	**0.22**	**0.47**
3	**ψ (.), γ (.), ε (area+veg), p (effort)**	**7**	**552.81**	**566.81**	**0.29**	**0.21**	**0.69**
4	**ψ (.), γ (isol+matrix), ε (area+veg), p (effort)**	**11**	**546.38**	**568.38**	**1.85**	**0.10**	**0.78**
5	ψ (.), γ (matrix), ε (area+veg+matrix), p (effort)	13	542.75	568.75	2.22	0.08	0.86
6	ψ (.), γ (isol+matrix), ε (area+veg+matrix), p (effort)	14	542.43	570.43	3.90	0.04	0.90
7	ψ (.), γ (.), ε (area+veg+matrix), p (effort)	10	550.53	570.53	4.00	0.03	0.93
8	ψ (.), γ (isol), ε (area+veg+matrix), p (effort)	11	548.95	570.95	4.42	0.03	0.96
Jamaican Becard (*Pachyramphus niger*)							
1	**ψ (.), γ (matrix), ε (veg+matrix), p (effort+srvy)**	**14**	**356.60**	**384.60**	**0.00**	**0.80**	**0.80**
2	ψ (.), γ (.), ε (veg+matrix), p (effort+srvy)	11	366.65	388.65	4.06	0.10	0.90
3	ψ (.), γ (matrix), ε (matrix), p (effort+srvy)	13	363.61	389.61	5.02	0.06	0.97

Jamaican Elaenia (*Myiopagis cotta*)							
1	**ψ (.), γ (matrix), ε (veg+matrix), p (effort+srvy)**	**14**	**434.97**	**462.97**	**0.00**	**0.86**	**0.86**
2	ψ (.), γ (matrix), ε (area+matrix), p (effort+srvy)	14	439.24	467.24	4.27	0.10	0.97
Jamaican Pewee (*Contopus pallidus*)							
1	**ψ (.), γ (matrix), ε (veg+matrix), p (effort)**	**12**	**395.69**	**371.69**	**0.00**	**1.00**	**1.00**
Jamaican Tody (*Todus todus*)							
1	**ψ (.), γ (.), ε (matrix), p (effort+srvy)**	**10**	**578.93**	**598.93**	**0.00**	**0.30**	**0.30**
2	**ψ (.), γ (.), ε (area+matrix), p (effort+srvy)**	**11**	**577.98**	**599.98**	**1.05**	**0.18**	**0.48**
3	**ψ (.), γ (.), ε (veg+matrix), p (effort+srvy)**	**11**	**578.32**	**600.32**	**1.40**	**0.15**	**0.64**
4	ψ (.), γ (.), ε (area+veg+matrix), p (effort+srvy)	12	577.33	601.33	2.40	0.09	0.73
5	ψ (.), γ (matrix), ε (matrix), p (effort+srvy)	13	576.51	602.51	3.59	0.05	0.78
6	ψ (.), γ (isol), ε (area+matrix), p (effort+srvy)	12	579.18	603.18	4.26	0.04	0.81
7	ψ (.), γ (isol+matrix), ε (matrix), p (effort+srvy)	14	575.42	603.42	4.49	0.03	0.85
8	ψ (.), γ (matrix), ε (area+matrix), p (effort+srvy)	14	575.79	603.79	4.86	0.03	0.87
9	ψ (.), γ (matrix), ε (veg+matrix), p (effort+srvy)	14	575.80	603.80	4.87	0.03	0.90
10	ψ (.), γ (isol+matrix), ε (area+matrix), p (effort+srvy)	15	574.41	604.41	5.48	0.02	0.92
11	ψ (.), γ (isol+matrix), ε (veg+matrix), p (effort+srvy)	15	574.84	604.84	5.92	0.02	0.94
12	ψ (.), γ (.), ε (veg), p (effort+srvy)	8	588.94	604.94	6.02	0.02	0.95
Jamaican Vireo (*Vireo modestus*)							
1	**ψ (.), γ (.), ε (veg+matrix), p (effort+srvy)**	**11**	**565.28**	**587.28**	**0.00**	**0.24**	**0.24**
2	**ψ (.), γ (.), ε (matrix), p (effort+srvy)**	**10**	**568.45**	**588.45**	**1.17**	**0.13**	**0.38**
3	**ψ (.), γ (isol), ε (veg+matrix), p (effort+srvy)**	**12**	**564.81**	**588.81**	**1.54**	**0.11**	**0.49**
4	**ψ (.), γ (.), ε (area+veg+matrix), p (effort+srvy)**	**12**	**565.26**	**589.26**	**1.99**	**0.09**	**0.58**
5	ψ (.), γ (isol), ε (matrix), p (effort+srvy)	11	567.95	589.95	2.68	0.06	0.64
6	ψ (.), γ (.), ε (area+matrix), p (effort+srvy)	11	568.14	590.14	2.86	0.06	0.70
7	ψ (.), γ (.), ε (area), p (effort+srvy)	8	574.51	590.51	3.23	0.05	0.75

8	ψ (.), γ (.), ε (veg), p (effort+srvy)	8	574.76	590.76	3.48	0.04	0.79
9	ψ (.), γ (isol), ε (area+veg+matrix), p (effort+srvy)	13	564.77	590.77	3.49	0.04	0.83
10	ψ (.), γ (isol), ε (area+matrix), p (effort+srvy)	12	567.57	591.57	4.29	0.03	0.86
11	ψ (.), γ (isol), ε (area), p (effort+srvy)	9	574.06	592.06	4.79	0.02	0.88
12	ψ (.), γ (matrix), ε (veg+matrix), p (effort+srvy)	14	564.22	592.22	4.94	0.02	0.90
13	ψ (.), γ (isol), ε (veg), p (effort+srvy)	9	574.30	592.30	5.02	0.02	0.92
14	ψ (.), γ (.), ε (area+veg), p (effort+srvy)	9	574.51	592.51	5.23	0.02	0.94
15	ψ (.), γ (matrix), ε (matrix), p (effort+srvy)	13	567.26	593.26	5.99	0.01	0.95

Jamaican Woodpecker (*Melanerpes radiolatus*)

1	**ψ (.), γ (matrix), ε (area+veg), p (effort)**	**10**	**633.84**	**653.84**	**0.00**	**0.19**	**0.19**
2	**ψ (.), γ (isol+matrix), ε (area+veg), p (effort)**	**11**	**632.45**	**654.45**	**0.61**	**0.14**	**0.32**
3	**ψ (.), γ (matrix), ε (veg+matrix), p (effort)**	**12**	**630.50**	**654.50**	**0.67**	**0.13**	**0.46**
4	**ψ (.), γ (.), ε (veg+matrix), p (effort)**	**9**	**637.20**	**655.20**	**1.37**	**0.09**	**0.55**
5	**ψ (.), γ (isol+matrix), ε (veg+matrix), p (effort)**	**13**	**629.67**	**655.67**	**1.83**	**0.07**	**0.62**
6	ψ (.), γ (matrix), ε (area+veg+matrix), p (effort)	13	630.37	656.37	2.53	0.05	0.68
7	ψ (.), γ (.), ε (matrix), p (effort)	8	640.58	656.58	2.74	0.05	0.72
8	ψ (.), γ (isol), ε (veg+matrix), p (effort)	10	636.74	656.74	2.91	0.04	0.77
9	ψ (.), γ (matrix), ε (matrix), p (effort)	11	634.91	656.91	3.07	0.04	0.81
10	ψ (.), γ (.), ε (area+veg+matrix), p (effort)	10	637.06	657.06	3.23	0.04	0.84
11	ψ (.), γ (isol+matrix), ε (area+veg+matrix), p (effort)	14	629.51	657.51	3.67	0.03	0.87
12	ψ (.), γ (.), ε (area+matrix), p (effort)	9	640.42	658.42	4.59	0.02	0.89
13	ψ (.), γ (isol), ε (matrix), p (effort)	9	640.47	658.47	4.64	0.02	0.91
14	ψ (.), γ (isol), ε (area+veg+matrix), p (effort)	11	636.62	658.62	4.79	0.02	0.93
15	ψ (.), γ (isol+matrix), ε (matrix), p (effort)	12	634.65	658.65	4.82	0.02	0.94
16	ψ (.), γ (matrix), ε (area+matrix), p (effort)	12	634.82	658.82	4.99	0.02	0.96

Rufous-tailed Flycatcher (*Myiarchus validus*)

1	**ψ (.), γ (isol+matrix), ε (veg+matrix), p (effort+srvy)**	**15**	**442.24**	**472.24**	**0.00**	**0.31**	**0.31**

2	**ψ (.), γ (matrix), ε (veg+matrix), p (effort+srvy)**	**14**	**445.27**	**473.27**	**1.03**	**0.19**	**0.49**
3	**ψ (.), γ (.), ε (veg+matrix), p (effort+srvy)**	**11**	**452.08**	**474.08**	**1.84**	**0.12**	**0.62**
4	ψ (.), γ (.), ε (matrix), p (effort+srvy)	10	454.64	474.64	2.40	0.09	0.71
5	ψ (.), γ (isol+matrix), ε (matrix), p (effort+srvy)	14	446.77	474.77	2.53	0.09	0.80
6	ψ (.), γ (isol), ε (veg+matrix), p (effort+srvy)	12	451.14	475.14	2.90	0.07	0.87
7	ψ (.), γ (matrix), ε (matrix), p (effort+srvy)	13	449.70	475.70	3.47	0.05	0.92
8	ψ (.), γ (isol), ε (matrix), p (effort+srvy)	11	454.63	476.63	4.39	0.03	0.96
Sad Flycatcher (*Myiarchus barbirostris*)							
1	**ψ (.), γ (.), ε (matrix), p (effort)**	**8**	**503.85**	**519.85**	**0.00**	**0.21**	**0.21**
2	**ψ (.), γ (isol), ε (matrix), p (effort)**	**9**	**503.00**	**521.00**	**1.15**	**0.12**	**0.33**
3	**ψ (.), γ (.), ε (veg), p (effort)**	**6**	**509.13**	**521.13**	**1.29**	**0.11**	**0.45**
4	**ψ (.), γ (.), ε (veg+matrix), p (effort)**	**9**	**503.84**	**521.84**	**1.99**	**0.08**	**0.52**
5	**ψ (.), γ (.), ε (area+matrix), p (effort)**	**9**	**503.84**	**521.84**	**2.00**	**0.08**	**0.60**
6	ψ (.), γ (.), ε (area), p (effort)	6	510.09	522.09	2.24	0.07	0.67
7	ψ (.), γ (isol), ε (veg), p (effort)	7	508.33	522.33	2.48	0.06	0.73
8	ψ (.), γ (isol), ε (area+matrix), p (effort)	10	502.75	522.75	2.91	0.05	0.78
9	ψ (.), γ (.), ε (area+veg), p (effort)	7	508.78	522.78	2.93	0.05	0.83
10	ψ (.), γ (isol), ε (veg+matrix), p (effort)	10	502.95	522.95	3.11	0.05	0.88
11	ψ (.), γ (.), ε (area+veg+matrix), p (effort)	10	503.84	523.84	3.99	0.03	0.91
12	ψ (.), γ (isol), ε (area+veg), p (effort)	8	508.13	524.13	4.29	0.03	0.93
13	ψ (.), γ (isol), ε (area+veg+matrix), p (effort)	11	502.68	524.68	4.83	0.02	0.95

(ψ) initial occupancy probability; (γ) local colonization probability; (ε) local extinction probability; (*p*) detection probability.
Covariates defined as: (isol) nearest-neighbor distance from patch to forest fragment ≥100 ha; (area) patch size in hectares; (veg) patch-level vegetation structure; (matrix) whether a patch was in an agricultural, peri-urban, bauxite mining, or forested matrix; (effort) number of points surveyed per patch; (srvy) related to survey order and whether a survey was the first, second, or third survey conducted in a season.
Best covariate structure on *p* was determined based on global model. When >1 covariate structure was supported (i.e., ΔAIC < 2), we reran entire model set with all supported structures. In all cases, model outcomes were similar; so we present the *p* covariate structure based on the lowest AIC.

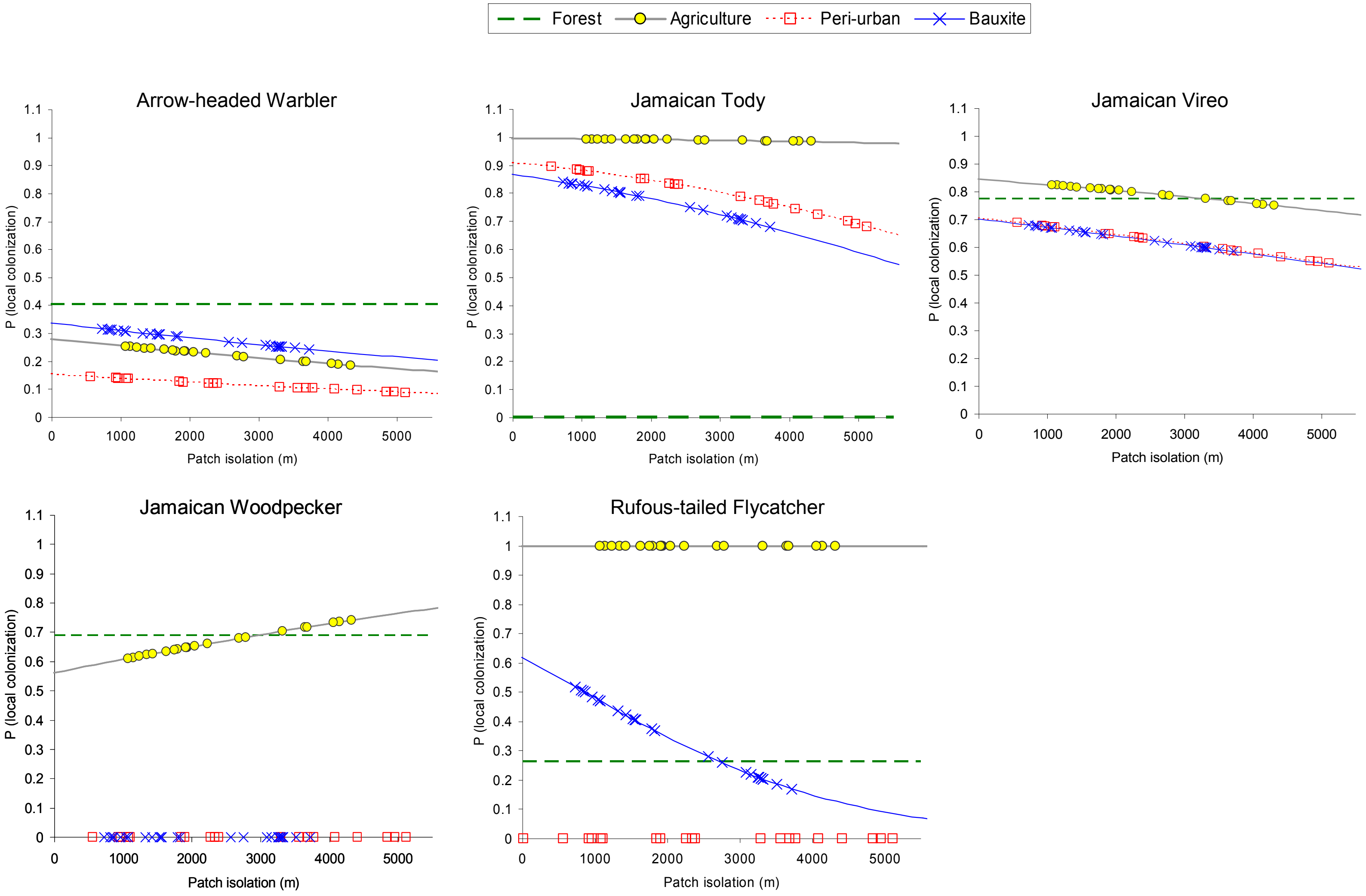
Table H2. Estimated probabilities of initial occupancy and detection for each species, based on top models (see Table H1 for model structures). Probability of occupancy was based on constant occupancy across all landscape matrix types. Probability of detection was based on the first survey and on the average number of point counts conducted per patch (N = 4).

	Occupancy		Detection	
Species	$\hat{\psi}$	SE	$\hat{\rho}$	SE
Arrow-headed Warbler	0.63	0.07	0.54	0.04
Jamaican Becard	0.42	0.08	0.31	0.05
Jamaican Elaenia*	0.50	0.08	0.39	0.05
Jamaican Pewee	0.39	0.06	0.67	0.05
Jamaican Tody	1.00	–	0.90	0.02
Jamaican Vireo	0.85	0.05	0.85	0.03
Jamaican Woodpecker	0.80	0.06	0.57	0.03
Rufous-tailed Flycatcher	0.52	0.08	0.42	0.05
Sad Flycatcher	0.91	0.11	0.38	0.05
Average	0.67	0.08	0.56	0.07

*Estimates based on second best model due to variance-covariance error associated with top model.

(–) variance could not be estimated due to estimation of Beta at boundary (i.e., 0 or 1).

Figure H1. Relationships between local colonization probabilities and patch isolation by matrix type based on model-averaged estimates. Species not presented for which there was no detected effect of patch isolation (i.e., Jamaican Becard, Jamaican Elaenia, Jamaican Pewee, and Sad Flycatcher). (Refer to Table 2.4, 2.5 for unconditional standard errors).



Arrow-headed Warbler

Jamaican Tody

Jamaican Vireo

Jamaican Woodpecker

Rufous-tailed Flycatcher

Figure H2. Relationships between local extinction probabilities and patch area by matrix type based on model-averaged estimates. Species not presented for which there was no detected effect of patch isolation (i.e., Jamaican Becard, Jamaican Elaenia, Jamaican Pewee, and Rufous-tailed Flycatcher). (Refer to Table 2.4, 2.5 for unconditional standard errors).

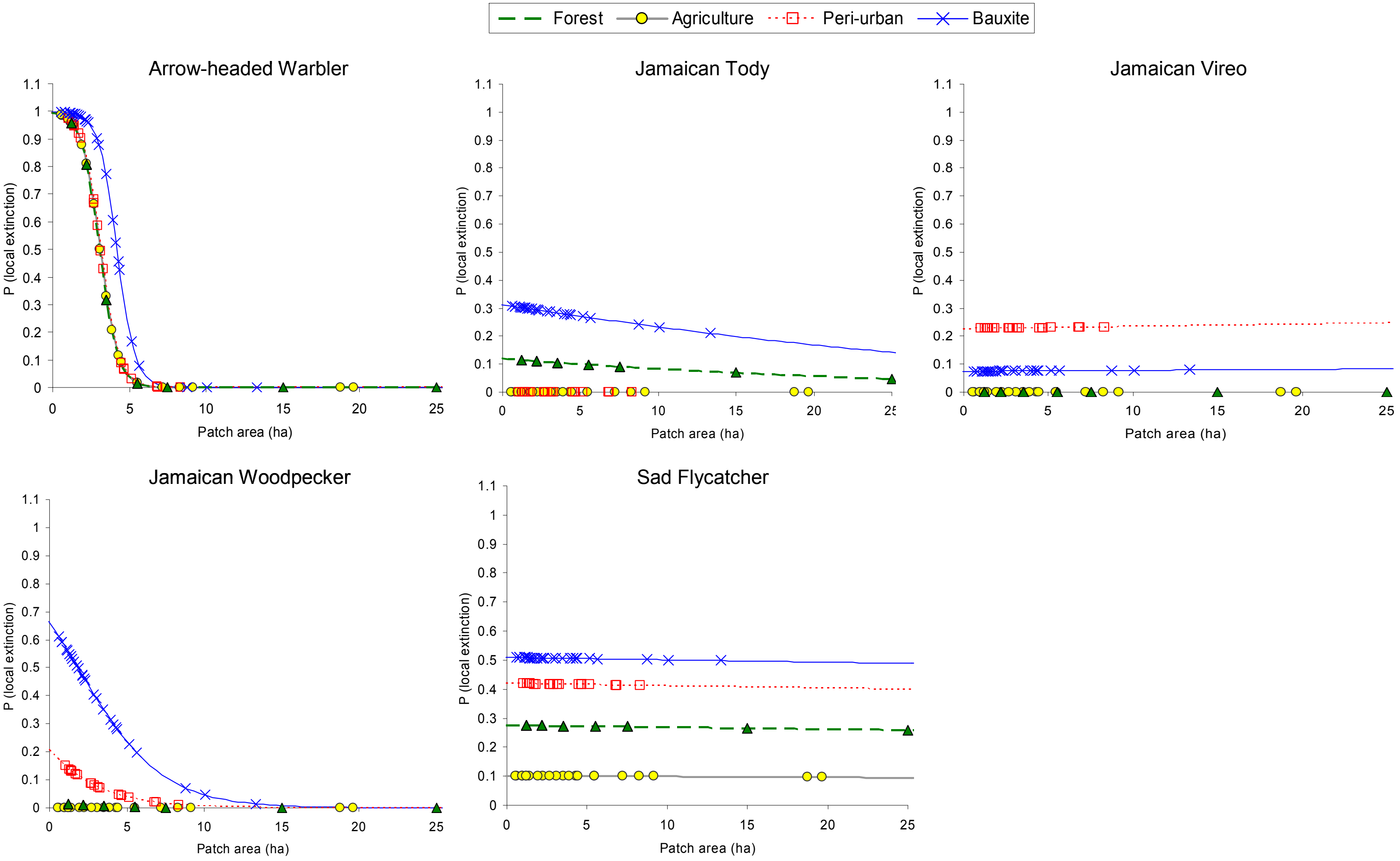
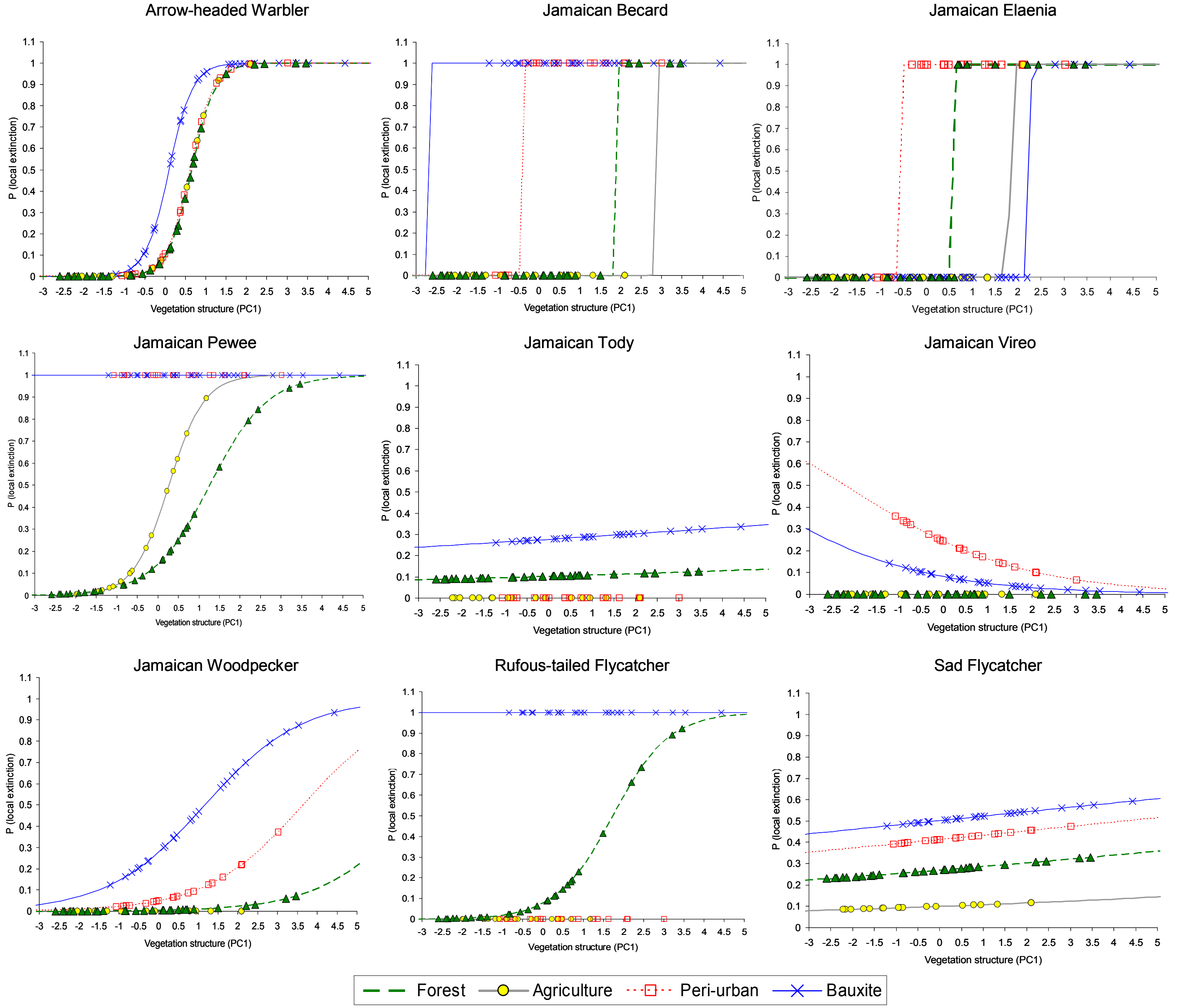


Figure H3. Relationships between local extinction probabilities and patch-level vegetation structure by matrix type based on model-averaged estimates. (Refer to Table 2.4, 2.5 for unconditional standard errors).



Appendix I. Object-based classification of land cover in central Jamaica using high-resolution IKONOS imagery

Introduction

Study area

This study was conducted in central Jamaica in the Manchester Parish and bordering Parishes (latitude: 17 56'24"-18 11'6" N; longitude: 77 23'13"- 77 37'5" W). This region was selected for investigation because it supports an extensive native bird community, yet is unprotected and experiencing increasing human development pressure. Wet limestone forest (Asprey and Robbins 1953) (also referred to as Evergreen Seasonal Forest formation (Beard 1944; Beard 1955)) once dominated the region but is now largely restricted to hilltop remnants on limestone outcrops that are often < 10 ha. Surrounding valleys are typically cleared for agriculture (i.e., primarily cattle pasture), residential development, and mining for bauxite (Evelyn and Camirand 2003). Agricultural areas in the valley floors consist of pasture for livestock grazing with treelined fence/hedgerows, paddock trees, fallow fields, and herbaceous garden plots. In residential areas (termed peri-urban landscapes), valleys are dominated by housing development and native/exotic vegetation that includes grass lawns, ornamental plantings, gardens of fruiting trees, abandoned woodlots, and secondary tree growth along roadsides. Bauxite mining areas are typically former agricultural lands, where bauxite is being extracted largely in the valley floors. Bauxite landscapes comprise relictual hilltop forests surrounded by exposed bauxitic soils, with some recent growth of ferns, *Acacia* trees, or planted grassland.

Given the karst limestone topography (Porter 1990) in combination with the increasing spatial proximity among native forest, non-native vegetation, and developed areas, detailed land-cover mapping is essential to delineate potential wildlife habitat in this region. Previously developed land-cover maps for Jamaica were produced using moderate resolution satellite imagery, including Landsat Multispectral Scanner (MSS) (80-m resolution) (Tole 2002) and Landsat Thematic Mapper (TM) (30-m resolution) data (Grossman et al. 1992; Forestry Department 1999). Existing land cover products failed to capture important landscape features, because they were limited in their spatial resolution and/or by the interpretation applied to the data. Small remnant forests, less than < 5 ha in size, have been found to support extensive native bird assemblages in the region. Vegetation cover common in human-modified landscapes may also influence species movement or usage patterns. For example, certain bird species have been found to frequently utilize urban gardens (e.g., Bland et al. 2004; Cannon et al. 2005; French et al. 2005), as well as fencerows and solitary trees in agricultural landscapes for foraging resources and movement conduits (e.g., Haas 1995; Estrada et al. 2000; Sykes and Hannon 2001). A visual comparison of high-resolution multispectral pan-sharpened IKONOS imagery (1-m resolution, Space Imaging 2002) clearly shows that small land-cover features have not been captured in a previous land-cover map developed by Jamaica's Forestry Department (Forestry Department 1999) (Figure I1). Thus, our objective was to develop more detailed land-cover maps for the study region, based on IKONOS imagery, to capture both small forest fragments and surrounding vegetation features in human-modified landscapes.

Land-cover classes

It was necessary to identify and map five main land-cover types based on expected bird usage and movement in the study region:

(1) **Development** – Built-up areas, including commercial and industrial buildings, residential housing, and road infrastructure.

(2) **Cleared land** (referred to as clearings) – Areas consisting of predominantly exposed soil, including recently excavated bauxite mining areas, fallow fields, and forest clearings.

(3) **Low-stature vegetation** (referred to as fields) – Areas dominated by herbaceous growth, including pasture, ornamental lawns, or herbaceous gardens (i.e., non-woody crops, such as corn, pumpkin, cassava, and sweet potatoes). This cover type also includes low-stature shrubs (< 4 m), in particular recent secondary growth of *Acacia* in agricultural and bauxite mining areas.

(4) **Scattered trees** – Widely-spaced trees, often dominated by cultivated species > 4 m in height and lacking understory vegetation, typical of tree stands, ornamental tree gardens, and rows of trees found along property boundaries of roadsides (termed linear vegetation). Tree stands typically include clusters of ornamental trees (< 0.25 ha) often maintained in isolation in pasture or development. Ornamental tree gardens are largely found within residential areas and comprise cultivated fruit or nut trees (e.g., coffee, citrus, pawpaw, banana, or breadfruit) and secondary tree growth. Linear vegetation is rows of trees (often 15-30 m wide) found along property boundaries (i.e., fencerows) or roadsides.

(5) **Forest** – Native broadleaf forest with overlapping canopy trees and understory vegetation. Non-native species may be included in this class, such as late-stage exotic pine plantations and bamboo (*Bambusa vulgaris)* embedded in forest.

Less common land-cover types were not considered for classification because their inclusion would have negatively impacted the training of major land-cover classes (e.g., exotic bamboo stands, pine plantations, scrub vegetation, small water bodies).

Methods

Data acquisition and image pre-processing

Ten IKONOS imagery scenes (11.3 km x 11.3 km per scene) from the south central region of Jamaica were needed to capture the study area (scenes: 9F-G, 15A-G and 21B). Scenes were acquired by the Jamaica Foresty Department and were collected between December and April 2001-2002. Multispectral pan-sharpened imagery was orthorectified by Space Imaging, LLC. (Reference-level product, false color image, 11.8 m horizontal accuracy, 1-m resolution) (Space Imaging 2002; Dial et al. 2003). Cloud-cover areas were digitized in GIS and converted to a mask prior to classification so as to preclude them from being involved in the statistics. We used a 3-band combination for all classifications performed, using spectral wavelength regions 0.52-0.60 µm (green, band 2), 0.63-0.69 µm (red, band 3), and 0.76-0.90 µm (near-infrared, band 4). Region 0.45-0.52 µm (blue, band 1) was not used, because it is most affected by atmospheric water vapor. Because the images were acquired on different dates, the digital number (DN) values varied per scene, reflecting differences in scene phenology, atmospheric conditions, and sensor view angles. To avoid potential errors caused by these variations, we performed separate classifications on each IKONOS scene. Post-classification, the images were mosaicked together and accuracy was assessed on the land-cover map for the entire study region. Data were projected using Lambert Conformal Conic WGS 1984.

Pixel-based classification

Prior to object-based classification, we conducted pixel-based classifications on one scene (15B) using a standard unsupervised classifier the Iterative Self-Organizing Data Analysis Technique (ISODATA) (using a range of classes, iterations and thresholds), as well as a supervised classifier the Maximum Likelihood algorithm with 5 classes and 0.95 convergence threshold (Jensen 1996) on the three-band imagery using ENVI v 4.5 (ITT Visual Information Solutions, 2008; http://www.ittvis.com). The results were visually compared to determine which classification method best represented land-cover classes targeted for delineation (Figure I2). Due to the high spatial resolution of the imagery, pixel-based classifications were found to be inferior when compared to the object-based classification. Based on visual inspection, target land-cover classes were poorly delineated with frequent misclassifications among fields, development, and cleared land, and between scattered trees and forest. Pixel-based classifications produced maps lacking spatial cohesiveness of class types and with spurious pixel effects, which led us to pursue an object-based classification. The object-oriented software algorithm classifies objects based on a combination of spectral, spatial, and textural components, which improves the differentiation of classes often similar in spectral reflectance. Several studies comparing spectral and object-based classification techniques support the use of object-based classification for high-resolution imagery rather than standard spectral-based approaches (Willhauck 2000; Repaka et al. 2004; Cleve et al. 2008).

Object-based classification

We performed the object-based classification, using ENVI Feature Extraction (FX) (v 4.5), which is an add-on module used through the ENVI Zoom interface. The first step in the object-based classification is image “segmentation,” which creates objects into meaningful entities (e.g., houses or forest patches) by grouping adjacent pixels with similar characteristics based on the computation of over 25 spatial, textural, and spectral attributes (ITT Visual Information Solutions 2008). We conducted image segmentation, then trained the algorithm, using a supervised classification approach by selecting representative features (i.e., segmented objects) to discern common landscape features (termed “select by example” by the FX software). This method is similar to performing a supervised classification using traditional methods, but rather than training by selecting individual pixels, segmented objects are selected and attributed specified land-cover classes (e.g., forest, field, development). We selected an average of 3435 objects per scene to serve as training examples, based on visual interpretation of the IKONOS imagery as informed by our extensive field experience in the study region. The number of training objects for a class was proportional to the prevalence of the class within a scene. We selected an average of 1500 training points for common land-cover types (i.e., forest), 1000 training points for those that were moderately common (i.e., scattered trees), and 200-400 points for less common features (i.e., clearings, fields, and development). Segmented images were classified using the K Nearest Neighbor method, which is similar to, but more robust than, the traditional nearest neighbor classifier (ITT Visual Information Solutions 2008).

The supervised classification algorithm in ENVI FX employs an edge-based approach, which has been shown to be expedient in speed and efficient in its stepwise approach as compared to other segmenting software (Neubert and Herold 2008). The FX algorithm requires only one user-defined parameter, the scale level, which controls the size of the image-object or the level of segmentation. The higher the scale level, the larger the image objects (i.e., fewer defined segments), and the lower the scale level, the smaller the image objects (i.e., more defined segments). The optimum segmentation parameter depends on the scale and the nature of the features to be detected, and is maximized when segments resemble polygons that would be created during manual interpretation (Kim et al. 2009). We devoted much time and effort to developing the best scale level, given that the quality of segmentation influences the accuracy of image classification (e.g., Dorren et al. 2003; Addink et al. 2007). Based on systematic trial and error and validation by visual inspection of output object topology, we selected a scale level between 45 and 50. This level best delineated the smaller features of interest (e.g., houses) without fragmenting larger features (e.g., forest cover) (Figure I3).

Following segmentation, we performed a “merge” step, which groups similarly classified adjacent segments by reassembling over-segmented or highly textured results. This proved beneficial for forested regions to better ensure that forest patches remained relatively intact and homogenous. Based on systematic trial and error, we selected a 90-95 merge level, which employs the Full Lambda-Schedule algorithm (Robinson et al. 2002). To remove the mixed pixel effect (Myung et al. 2001) and better extract the scattered tree class, we performed the sieving function in ENVI, and reclassified forest stands < 0.10 ha as scattered trees. Finally, we performed majority filtering, which convolves smaller classes into the dominant surrounding land-cover class (Kim 1996; Canty 2007). In our classification, the smaller class was any “scattered tree” segment that was surrounded by a “forest” class. To conduct this filtering in a relational manner (i.e., one class based solely on one other class), we performed majority filtering in ArcGIS 9.3 (ESRI 2008) to remove the scattered tree segments embedded completely within forest (Figure I4).

Accuracy assessment

Classification accuracy was measured using a standard error matrix that compares the classes predicted by the object-oriented classifier to those observed in the field (i.e., reference points) (Stehman and Czaplewski 1998). Accuracy was based on 1,985 reference points collected across our study region that were taken with a hand-held global positioning system (Garmin GPS 72) (≤ 5 m accuracy); ~ 10% of the points were used in the training of the classification algorithm. The ratio of reference to training points ranged from the 3% to 20% for each land-cover class (Table I1), which was well-above the recommended 1% (Congalton 1991). The assessment was based on the 10 IKONOS scenes mosaicked together to smooth out different distributions of reference points collected per scene. Descriptive statistics (user’s accuracy, producer’s accuracy, and overall accuracy) as well as kappa statistics (K) were computed (Congalton 1991).

Results

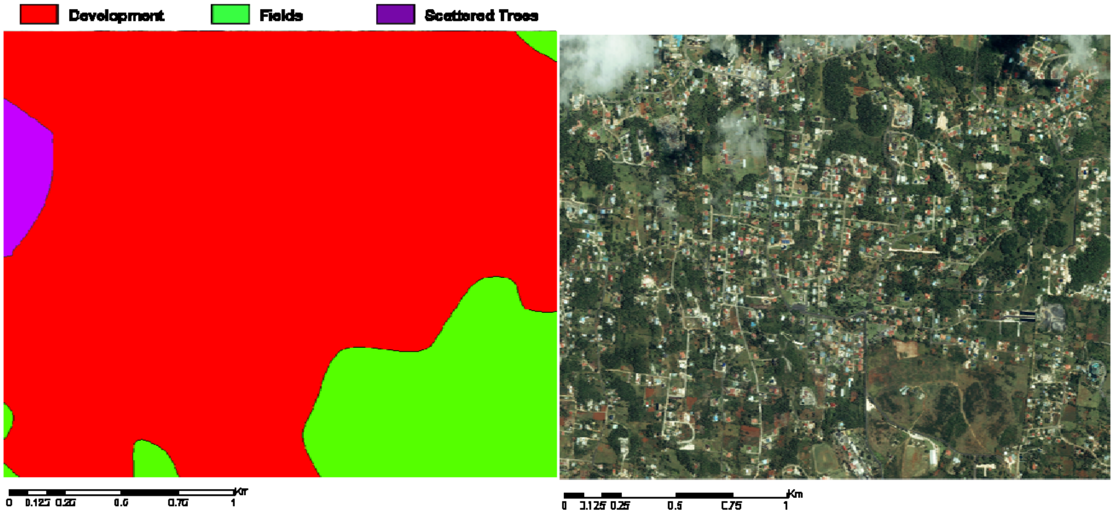
The greatest number of pixels were classified as forest cover (45%, 38,262,915 m^2), followed by fields (22%, 18,873,033 m^2), scattered trees (20%, 16,813,856 m^2), cleared land (9%, 7,829,838 m^2) and lastly development (4%, 3,073,998 m^2) (see Figure I5 for example classifications per landscape type). The forest class was most accurately delineated (94.2% producer's accuracy), with the greatest confusion with scattered trees (7.5%) (Table I2). Cleared land had the second-highest accuracy (93.4%), with similar accuracy for the dominant subclasses of bauxite mining areas and fallow fields. Clearings were most often confused with development (8.7%) due to the similarity in spectral reflectance between exposed bauxitic soil/rock and impervious surfaces in developed areas (e.g., houses and roads). Low-stature vegetation (i.e., fields) was classified with ~ 90% accuracy, with accuracy of subclasses ranging from 86.7% for manicured lawns, 88.6% for herbaceous gardens, and 91.4% for agricultural pasture. The class most confused with fields was scattered trees (9.7%) due to secondary growth of *Acacia* stands in pasture. Developed areas were classified with 87.7% accuracy, with housing/commercial development more accurately classified than road infrastructure (89.0 and 83.6%, respectively). The class delineated most poorly was scattered trees (80.7% accuracy), which was predominantly confused with fields (5.8%) and forest (4.5%). Within this class, tree stands were classified most accurately (87.6%), followed by linear vegetation (83.8%), and lastly ornamental tree gardens (76.0%). The overall accuracy of the classification was 88.84%, which is on average higher than for other object-oriented classifications (e.g., Repaka et al. 2004; Mathieu et al. 2007; Cleve et al. 2008; Kim et al. 2009).

Table I1. Number of reference points collected in the field in relation to the number of training points used in the object-based classifier for the development of the land-cover map for central Jamaica.

Land-cover class	Total Reference Pts	Total Training Pts	Reference:Training Ratio
Development	310	3753	8%
Clearings	230	2529	9%
Fields	415	2069	20%
Scattered Trees	494	9873	5%
Forest	536	16060	3%

Table I2. Error matrix of the object-based classification of 5 land-cover classes and their representative subclasses. The rows define the classes in the reference data, and the columns define the classes in the classified data being evaluated for accuracy. Results in the cell matrix are in percentage of producer's accuracy, with user's accuracy specified separately for major land classes. The overall accuracy is the percentage of correct classifications based on the entire matrix. The Kappa statistic measures the accuracy considering the actual agreement in relation to chance agreement, and indicates whether the classification is better than random.

	Classified					
Reference	Development	Clearings	Fields	Scattered Trees	Forest	User's Accuracy
Development	**87.7**	3.5	1	0.6	0.4	94.12
Housing/Built areas	**89**	9.7	0	1.4	0	
Roads	**83.6**	1.5	3	10.5	1.5	
Clearings	8.7	**93.4**	1.5	1.2	0	84.52
Bauxite	4.1	**93.2**	2.1	0.7	0	
Fallow fields	2.4	**93.9**	2.4	1.2	0	
Fields	2.6	2.2	**89.9**	9.7	0.9	84.93
Herbaceous garden	0	2.3	**88.6**	4.6	4.6	
Lawn	4.9	7.9	**86.7**	0	0.6	
Pasture	0.7	1.3	**91.4**	5	1.7	
Scattered Trees	0.7	0.9	5.8	**80.7**	4.5	88.44
Tree gardens	9.8	1.6	0	**76**	12.2	
Tree stands	2.9	1	5.7	**87.6**	2.9	
Linear vegetation	0	0.7	12.7	**83.8**	2.8	
Forest	0.3	0	1.9	7.5	**94.2**	91.65
					Overall	**88.84**
					Kappa	**85.78**



FD Classification (1999)

IKONOS Imagery

Figure I1. Comparison of Forestry Department (FD) land cover developed based on TM imagery (left panel) (FD, 1999) and 2001-2002 IKONOS imagery (right panel) for a peri-urban landscape in central Jamaica.

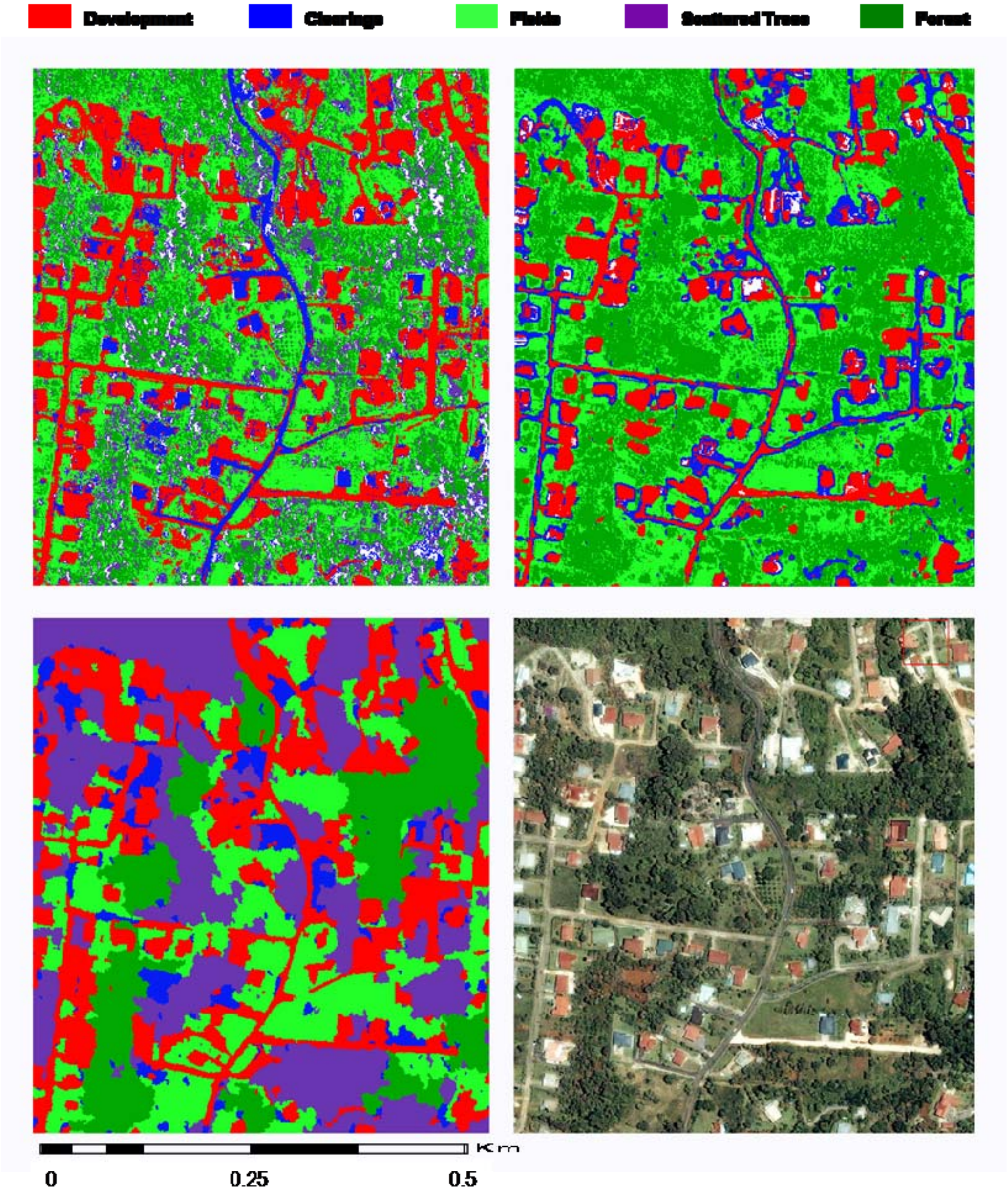


Figure I2. Comparison of a pixel-based unsupervised (ISODATA) (top left) and supervised classification (Maximum Likelihood) (top right) versus the object-based classification (bottom left) in reference to the true color imagery (bottom right).

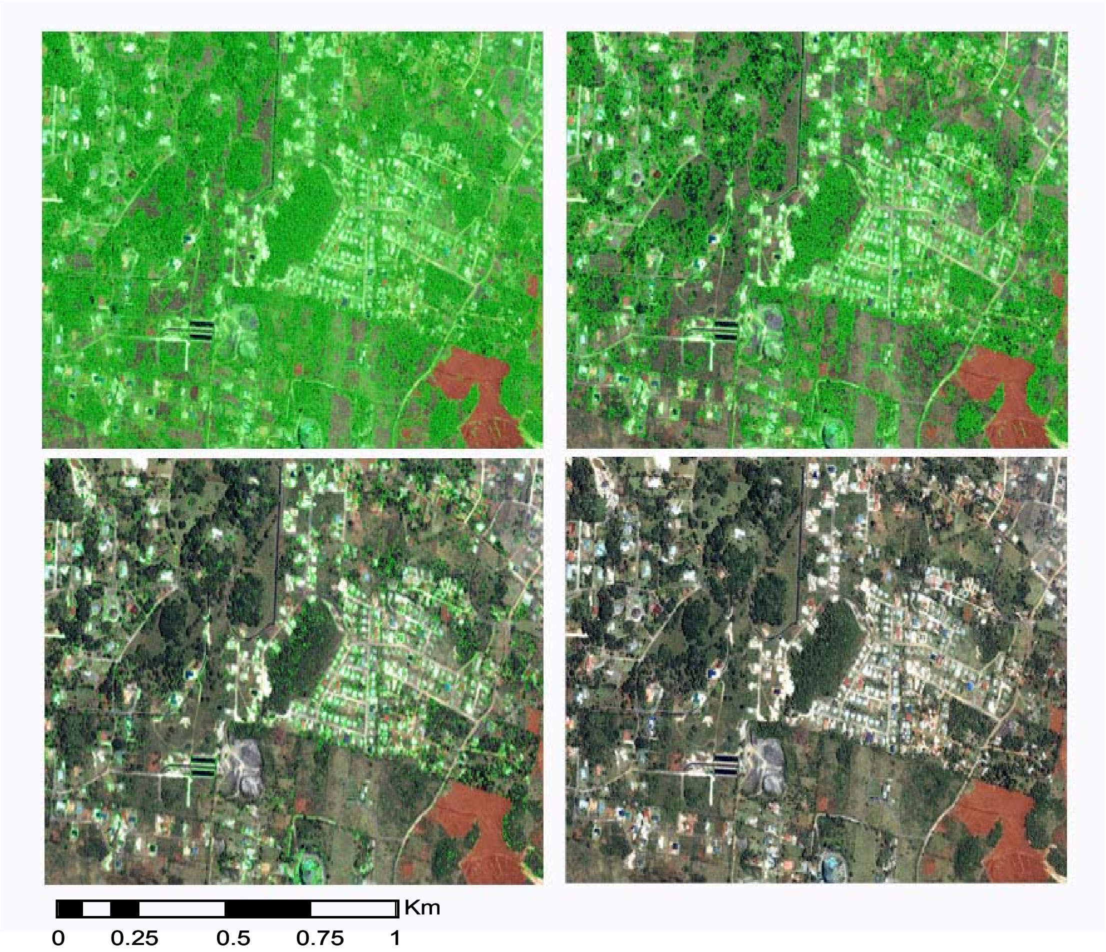


Figure I3. Segmentation of the IKONOS image at the scale of 20 (upper left), 50 (upper right), and 80 (lower left) of a true color image of a subset of our study area (lower right). The green lines delineate the image objects.

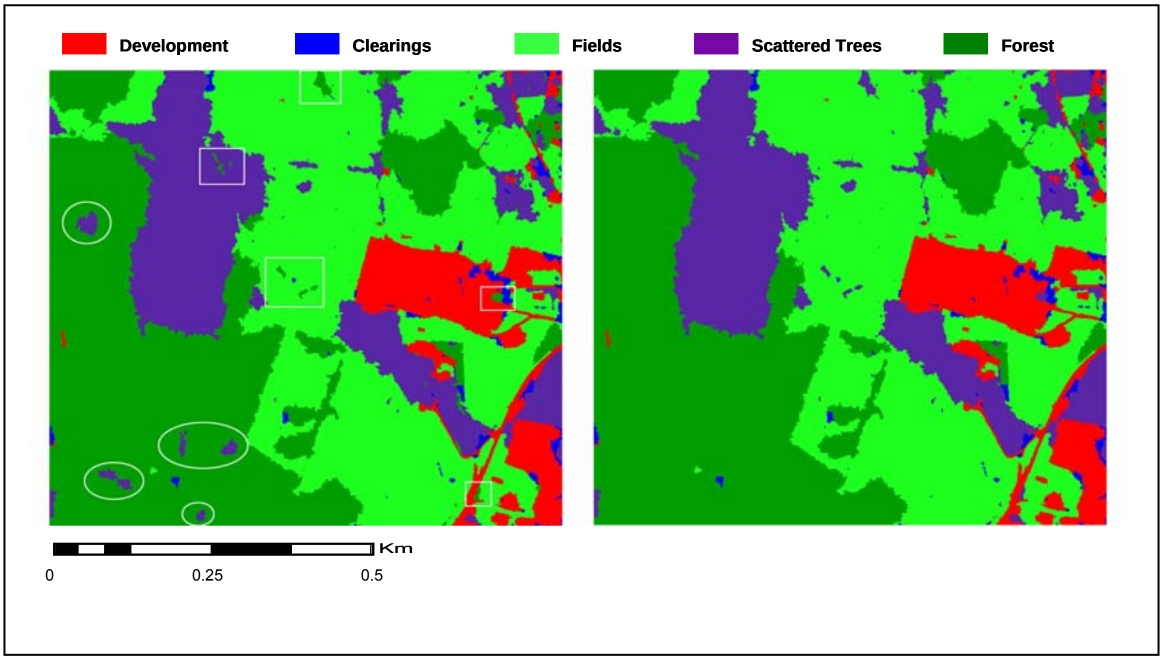


Figure I4. Classification before post-processing (left) compared to after post-processing (right). Circles indicate features removed during the sieving process and squares indicate those removed during majority filtering.

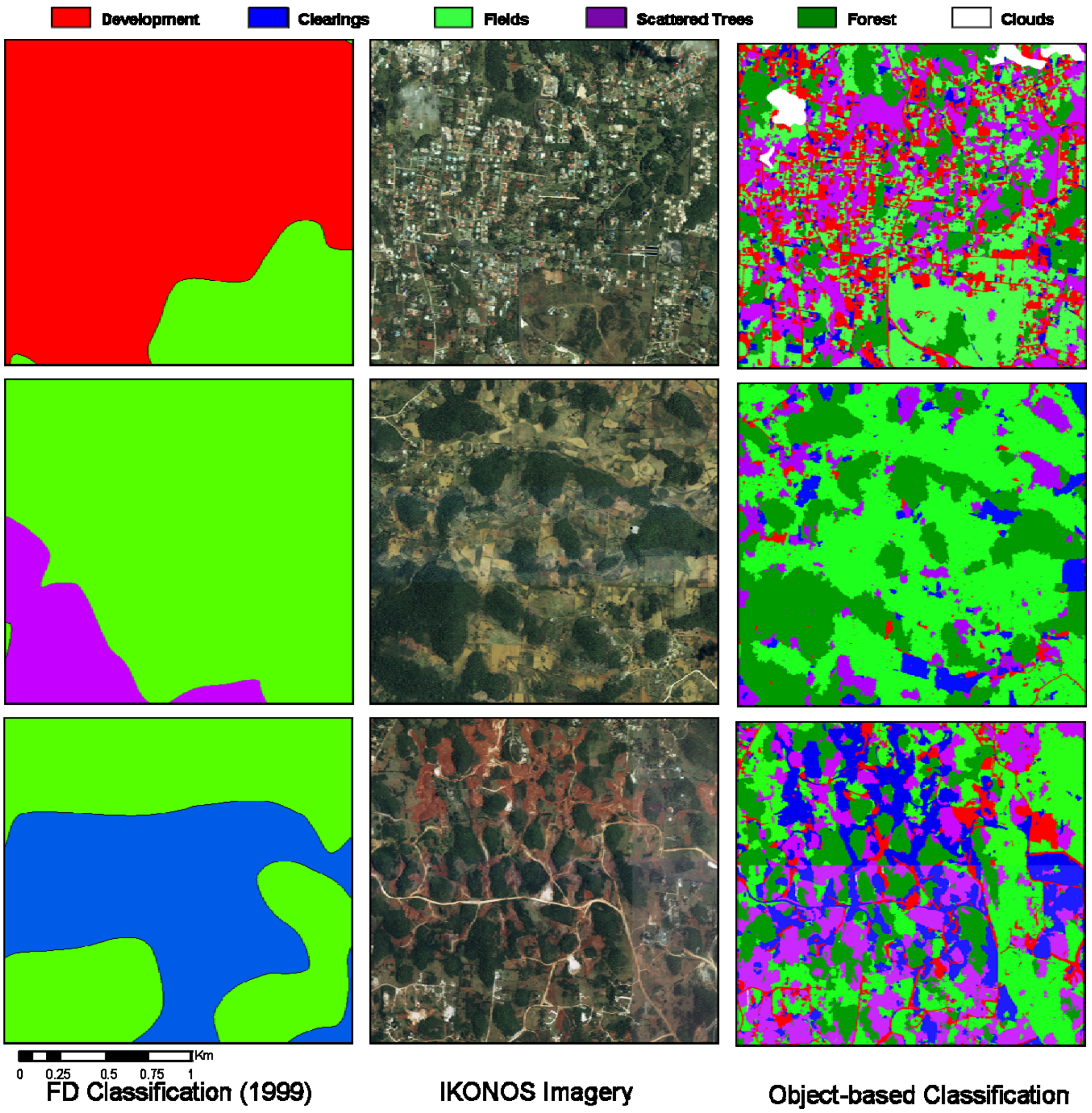


Figure I5. Comparison of Forestry Department land cover (FD, 1999) (left panel), IKONOS imagery (middle panel), and the object-based land-cover classification (right panel). The top row displays a representative example of a peri-urban landscape, the middle row an agricultural landscape, and the bottom row a bauxite mining landscape found within the study region in central Jamaica.

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