

ABSTRACT

IRIZARRY ROSARIO, JULISSA I. Patch dynamics and Permeability of Fragmented Habitats in Southwestern Puerto Rico. (Under the direction of Jaime A. Collazo, Ph.D.).

Landscapes modified by human activities lead to habitat fragmentation, a process where habitat patches may become increasingly smaller, isolated and of lower quality. In Puerto Rico, urban growth has been the primary driver of habitat fragmentation in recent decades. The spatial arrangement and composition of resources in fragmented habitats have a strong influence on the dynamics and persistence of populations through their direct contribution (e.g., reproductive output), influence on patch colonization and extinction rates, and permeability. Increasing knowledge about the factors that mediate these demographic processes is of value to conservation planners. We estimated species richness and quantified patch dynamics of 8 resident and endemic avian species occurring within the Guánica and Susúa Forests, and the agricultural, urbanized and forested matrices that lie between forests in southwestern Puerto Rico in 2010 and 2011. We also experimentally translocated 28 Puerto Rican Bullfinch (*Loxigilla portoricensis*) within the Guánica State Forest and across the forest and the urbanized matrix that separates the forests to assess how the amount (forest cover) and resistance (time to return) of habitat influenced permeability to avian movement. Avian communities per matrix were comprised of a mix of resident and introduced (exotic) species, but similar in richness (42 to 46 species). The presence of forest specialists in human-modified habitats was not unusual for island species, adept at exploiting novel resources. Initial species occupancy was mediated by matrix type. Subsequent seasonal occupancy did not vary markedly because colonization and extinction rates were time-

invariant, suggesting that occupancy of focal species was not in transition during the study. Occupancy was higher in the Guánica and Susúa Forest reserves and the forested matrix than in the urban and agricultural matrices, a pattern consistent with the forest affinities of most of focal species (e.g., Antillean Euphonia, Puerto Rican Bullfinch, Vireo and Woodpecker). Factors affecting how a species colonizes a patch (isolation) and the quality of patches (e.g., fruit availability) were the strongest determinants of occupancy. Patch size did not exert a strong influence on extinction rates. Similarities in occupancy rates between the forested matrix and forest reserves highlighted the conservation value of the forested matrix, even in its current condition of low human density and other land uses. Habitat matrices were differentially permeable to the Puerto Rican Bullfinch. All birds translocated within the forest returned successfully to where they were captured, whereas 43% did so when birds were translocated across urban and forest habitat matrices or within the urbanized matrix. Distance between capture and release site negatively influenced return success. Successful returns occurred within 5 days after translocations, after which the probability of returning successfully was <50%. Bullfinches used patches with high forest cover as they traversed through the urban matrix, particularly those from Guánica Forest (70% cover). Our research supports the growing body of work that indicates that habitat matrices between forest reserves are not ecologically irrelevant, and may play an important role in the dynamics and persistence of populations in human-modified landscapes. Insights and conservation implications from this work are applicable to similar landscapes in Puerto Rico and the Caribbean.

© Copyright 2012 by Julissa I. Irizarry

All Rights Reserved

Patch dynamics and Permeability of Fragmented Habitats in Southwestern Puerto Rico

by
Julissa I. Irizarry

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

Zoology

Raleigh, North Carolina

2012

APPROVED BY:

Nick M. Haddad, Ph.D.

Theodore R. Simons, Ph.D.

Jaime A. Collazo, Ph.D.
Chair of Advisory Committee

DEDICATION

I would like to dedicate this thesis to three generations of amazing women in my family: my grandmother Rosa, my mother Ivelisse and my sisters Gabriela and María. The most difficult thing about completing this thesis has been the time spent away from you. Your support and encouragement through all this time has been invaluable. Thank you for everything you have done for me.

BIOGRAPHY

Julissa I. Irizarry is originally from Toa Alta, Puerto Rico. She graduated magna cum laude from the University of Puerto Rico at Mayagüez with a Bachelor of Science in Biology. While completing her undergraduate degree, courses in zoology and ecology caught her attention and led to further studies in ornithology and an interest in field research. Interest in the ecology of fragmented landscapes in Puerto Rico led to a research opportunity in North Carolina State University, which culminates in this thesis. Following the completion of her Master's degree, she plans to continue her career in ecological research, with an emphasis on conservation.

ACKNOWLEDGMENTS

This research project was supported by Puerto Rico's Department of Natural and Environmental Resources Federal Aid Program (W-31). The staff at Guánica State Forest was extremely helpful, in particular Menqui and Chago for providing helpful advice and access to the forest at all hours. This project would not have been a success if it weren't for the help of field technicians who risked life and limbs in order to contribute to our research: Chris Nytch, Noelia Baéz, Kim Romano, Alan Kniedel, Phillip Howard, Alcides Morales, José Vargas, Mariel Rivera, Michael Díaz, Isabel Monteverde, Loreli Sepúlveda, Amarilys Irizarry, Tanya Martinez, Mel Rivera, Sara Ocasio, Erica Badger and Kate Freeman. Landowners and stakeholders in Guánica, Yauco, Lajas and Sabana Grande provided vital access to survey points and telemetry release sites. Kennen Muñoz from Autoridad de Acueductos y Alcantarillados was an asset in granting us access to forest patches in Yauco. Walter Ramírez and Norma Acosta, our landlords in Puerto Rico always made sure our team was comfortable and taken care of. Krishna Pacifici and Jim Nichols were incredibly helpful with statistics advice, as was Steve Williams in providing GIS help. The administrative staff at the department of Biology, Wendy Moore and Meredith Henry in particular, was essential in ensuring that the project always ran smoothly and responsibly. I would like to recognize the members of my committee, Nick Haddad, Ted Simons and in particular, my advisor Jaime Collazo for their continued guidance, advice and support throughout the project. Finally, I thank my family for their support, encouragement and unflappable belief in me. I would not have made it this far if it weren't for them.

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	x
INTRODUCTION	1
LITERATURE CITED	5

Chapter 1: Patch dynamics of resident avian species in three habitat matrices that separate forest reserves in southwestern Puerto Rico	11
--	----

ABSTRACT	11
INTRODUCTION	12
STUDY AREA	17
METHODS	17
<i>Avian Survey Stations</i>	17
<i>Presence-Non-Presence (Absence) Surveys</i>	18
<i>Survey Station and Landscape Covariates</i>	19
DATA ANALYSIS	21
<i>Species Richness</i>	21
<i>Occupancy Models</i>	22
RESULTS	25
<i>Species Richness</i>	25
<i>Occupancy</i>	26
DISCUSSION	29
LITERATURE CITED	36
APPENDICES	84
Appendix A	85
Appendix B	89
Appendix C	92
Appendix D	95

Chapter 2: Permeability of an urban matrix to the movements of an endemic avian frugivore in the tropics	97
---	----

ABSTRACT	97
INTRODUCTION	98
STUDY AREA	102
METHODS	103
<i>Mist-netting, Translocations and Radio Tracking</i>	103
DATA ANALYSIS	105
RESULTS	107

DISCUSSION	108
LITERATURE CITED	114
APPENDICES	129
Appendix A	130
Appendix B	131
Appendix C	132
Appendix D	140

LIST OF TABLES

CHAPTER 1: APPENDIX

Table 1.1	List of species detected at survey stations in three habitat matrices and the Guánica and Susúa State Forests in Southwestern Puerto Rico.....	49
Table 1.2	Model selection for the Puerto Rican Spindalis' initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	51
Table 1.3	Model selection for the Puerto Rican Woodpecker's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	53
Table 1.4	Beta estimates for colonization and extinction probability based on multiseason occupancy models.....	55
Table 1.5	Model selection for the Antillean Euphonia's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	57

Table 1.6	Model selection for the Black-Faced Grassquit's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	59
-----------	---	----

Table 1.7	Model selection for the Shiny Cowbird's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models....	61
-----------	--	----

Table 1.8	Model selection for the Puerto Rican Bullfinch's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	62
-----------	--	----

Table 1.9	Model selection for the Puerto Rican Vireo's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	64
-----------	--	----

Table 1.10	Model selection for the Caribbean Elaenia's initial occupancy, colonization, extinction and detection probability based on multi-season occupancy models.....	66
------------	---	----

CHAPTER 2: APPENDIX

Table 2.1	Least squares means estimates for the forest cover percentage of sites used by translocated bullfinches that returned to their original capture locations....	128
-----------	---	-----

LIST OF FIGURES

CHAPTER 1: APPENDIX

Figure 1.1 Map of the study area showing three habitat matrices (agriculture, urban, forest) and the Guánica and Susúa State Forests in southwestern Puerto Rico.....68

Figure 1.2 Patch extinction probability for the Puerto Rican Spindalis as a function of the average fruit availability index at survey stations (patches) in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico..... 69

Figure 1.3 Patch extinction probability for the Puerto Rican Woodpecker as a function of the average fruit availability index at survey stations (patches) in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico..... 70

Forget 1.4 Patch colonization probability for the Black-Faced Grassquit as a function of matrix type: agriculture, urban, forest and forest reserves..... 71

Figure 1.5 Patch extinction probability for the Black-Faced Grassquit as a function of the sum of percent forest and herbaceous cover at survey stations (patches) in three

habitat matrices and forest edge of the Guánica and Susúa State Forests in southwestern Puerto Rico	72
---	----

Figure 1.6 Patch extinction probability for the Antillean Euphonia as a function of matrix type, namely, agriculture, urban, forest and forest reserves	73
---	----

Figure 1.7 Patch extinction probability for the Puerto Rican Vireo as a function of percent forest cover at survey stations (patches) in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	74
---	----

Figure 1.8 Patch extinction probability for the Puerto Rican Vireo as a function of percent forest cover at survey stations (patches) in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	75
---	----

Figure 1.9 Patch extinction probability for the Puerto Rican Bullfinch as a function of matrix type, namely, agriculture, urban, forest and forest reserves	76
---	----

Figure 1.10 Seasonal patch occupancy probability for the Antillean Euphonia in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	77
---	----

Figure 1.11	Seasonal patch occupancy probability for the Puerto Rican Bullfinch in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	78
Figure 1.12	Seasonal patch occupancy probability for the Caribbean Elaenia in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	79
Figure 1.13	Seasonal patch occupancy probability for the Puerto Rican Vireo in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico.	80
Figure 1.14	Seasonal patch occupancy probability for the Puerto Rican Woodpecker in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	81
Figure 1.15	Seasonal patch occupancy probability for the Puerto Rican Spindalis in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico.	82

Figure 1.16	Seasonal patch occupancy probability for the Shiny Cowbird in three habitat matrices and forest Guánica and Susúa State Forests in southwestern Puerto Rico	83
-------------	---	----

Figure 1.17	Seasonal patch occupancy probability for the Black-faced Grassquit in three habitat matrices and the Guánica and Susúa State Forests in southwestern Puerto Rico	84
-------------	--	----

CHAPTER 2: APPENDIX

Figure 2.1	Map of the study area in southwestern Puerto Rico showing the spatial configuration of the agricultural, urban and forested matrixes that separate the Guánica and Susúa state forests	134
------------	--	-----

Figure 2.2	Map of the urbanized matrix detailing land cover types, remaining forest cover and capture and release locations used in experimental translocations for Puerto Rican Bullfinches	135
------------	---	-----

Figure 2.3	Map of the Guánica State Forest detailing capture and release locations used in experimental translocations for Puerto Rican Bullfinches	136
------------	--	-----

Figure 2.4 Probability of successful return to the site of capture by Puerto Rican
Bullfinches in southwestern Puerto Rico, from March to September 2011 ... 137

Figure 2.5 Survival of translocated Puerto Rican Bullfinches within Guánica State
Forest and the urbanized matrix between the Guánica and Susúa Forest Reserves
between March and September 2011138

Figure 2.6 Average forest cover of sites used by translocated birds returning to
their capture site, grouped by type of translocation 139

INTRODUCTION

Habitat fragmentation is the process of subdividing a continuous habitat into smaller patches (Andrén 1994). It is primarily driven by deforestation, increasing urbanization and other changes in land use (Geist and Lambin 2002). The reduction in number and size of habitat patches in the landscape may hamper the dispersal of many species, exacerbating the isolation of habitat patches and creating unnatural metapopulation complexes (Noss and Cooperrider 1994; Matthysen et al. 1995; Fahrig 2003; Urbanová 2009). Species that avoid or are unable to cross the intervening land cover or non-habitat areas (referred to in this work as the matrix) will become increasingly isolated; populations occurring in small patches are likely to undergo a reduction in size and probability of persistence (Gascon et al. 1999; Fahrig 2003). In contrast, some species are relatively resistant to habitat fragmentation, these tend to be habitat generalists characterized by high dispersal abilities and reproductive rates (Urbanová 2009). The persistence and predominance of such species on a landscape could lead to biotic homogenization over time (McKinney and Lockwood 1999; Blair 2001).

The persistence of a species within a fragmented landscape will often depend on its ability to move through the intervening land covers that make up the matrix. Successful dispersal is dependent on the vagility of the species and the characteristics of the habitat within the matrix (Fahrig and Merriam 1994). Past research has dismissed the role of the matrix, labeling it inhospitable and homogeneous (McIntyre and Hobbs 1999; Rodewald 2003; Manning et al. 2004; Murphy and Lovett-Doust 2004; Kupfer et al. 2006). Upon closer examination, its role is far from irrelevant (Watling et al. 2011). For example, the matrix surrounding habitat patches may act as a source of perturbations (e.g., edge effects)

and exotic or invasive species (Keyser 2002; Rodewald and Yahner 2001; Hodgson et al. 2007). In other instances, the matrix may serve as an alternative or secondary habitat (Perfecto and Vandermeer 2002) or even facilitate dispersal through the use of corridors and stepping-stones (Baum et al. 2004).

The Caribbean is one of the world's most densely populated regions (Potter 1993) and as such, its agricultural and forested lands are under strong pressure from rapid population growth and a high rate of urbanization (López et al. 2001). This is exemplified by landscapes in Puerto Rico (López et al. 2001), whose forest cover has decreased and increased during the 20th century in response to socioeconomic changes. This is contrary to the general trend of deforestation in the tropics, which appears to be leading towards a consistent, irreversible loss of forest cover (Turner et al. 1990; DeFries et al. 2000; Watson et al. 2001; Grau et al. 2003). In Puerto Rico, forest cover has gone from about 6-10% in the late 1930s (when 90% of the island was in some form of agriculture; Dietz 1986; Birdsey and Weaver 1987), to about 57% in 2003 (Brandeis et al. 2007). This increase in forest cover was directly associated with the decrease in use of agricultural lands, many of which were abandoned and allowed to regenerate as new forests (Lugo and Helmer 2004). However, Puerto Rico's human population has increased more than threefold during the last century (U.S. Bureau of Census 1990-1994) and gains in forest cover are again under pressure, this time primarily from urban development and other non-agricultural anthropogenic land uses (Birdsey and Weaver 1987; Ramos-Gonzalez 2001; Lugo et al. 2012). As in the early 20th century, the loss of forested lands and increasingly patchy distribution of habitat remnants

may lead to the demographic vulnerability of avian species associated with forested landscapes (Brash 1987).

Research on connectivity among remaining habitat patches has been scarce on the island of Puerto Rico, although its functional importance has been implicitly recognized by the State's Department of Natural Resources and affirmed by legislation to foster corridors and linkages between forest reserves (Commonwealth of Puerto Rico Law #14; Green et al. 2001). Understanding factors that influence matrix quality for organisms as well as how species navigate human-dominated environments is necessary to guide conservation planning in fragmented landscapes (Prevedello and Vieira 2010). Birds, which are often forced to migrate through such matrixes, respond quickly to landscape changes and are easily monitored due to their conspicuousness and high mobility (Urbanová 2009). This makes them a suitable organism with which to study the effects of matrix types and fragmentation.

This project was designed to characterize the species composition, permeability, and patch dynamics of avian communities occurring in three habitat matrices that separate two forest reserves in southwestern Puerto Rico. This region is characterized by high avian species richness and is home to many endemic and endangered species (Gould et al. 2007). Two reserves in the region, the Guánica and Susúa State Forests, are separated by approximately 7 kilometers. The intervening habitat matrix between reserves is characterized by a gradation of land cover types, spanning from agriculture to the west of the reserves, to urban between reserves, and finally increasingly dominated by forested cover to the east of the reserves. This spatial configuration presented a unique opportunity to investigate avian species composition, seasonal occupancy and patch dynamics among the

predominant land cover types in the matrix. This study objective is addressed in Chapter 1. We also assessed how well an endemic frugivore and forest specialist, the Puerto Rican Bullfinch (*Loxigilla portoricensis*), moved through the urban matrix, as a measure of matrix permeability (Kennedy and Marra 2010; Gobeil and Villard 2002; Tremblay and St. Clair 2011). This study objective is addressed in Chapter 2. It is hoped that our work will help inform conservation planning by elucidating factors that influence the dynamics and permeability of human created habitat matrices and foster the creation of linkages that facilitate avian movement between forest reserves in Puerto Rico and the Caribbean.

LITERATURE CITED

- Andr  n, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. *Oikos* 71: 355-66.
- Baum K., Haynes K.J., Dilleuth F.P. and J. Cronin. 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85: 2671-2676.
- Birdsey R.A. and P.L. Weaver. 1987. *Forest area trends in Puerto Rico*. New Orleans, LA: US Department of agriculture forest service, Southern forest experiment station. Research note SO-331.
- Birdsey, R.A. and P.L. Weaver. 1987. Forest area trends in Puerto Rico. USDA Forest Service. Southern Forest Experiment Station SO-331.
- Blair, R.B. 2001. Creating a homogeneous avifauna. *Avian Ecology and Conservation in an urbanizing world*. Kluwer Academic Publishers. 459-486.
- Brandeix T.J., E.H. Helmer and S.N. Oswalt. 2007. *The Status of Puerto Rico's forests, 2003*. Asheville, NC: USDA Forest Service, Southern Research Station Resource Bulletin SRS-119.
- Brash, A.R. 1987. The history of avian extinction and forest conversion on Puerto Rico. *Biological Conservation* 39: 97-111.
- DeFries R., Hansen M., Townsend J.R.G., Janetos A.C. and T.R. Loveland. 2000. A new global 1km data set of percent tree cover derived from remote sensing. *Global Change Biology* 6: 247-254.
- Dietz, J.L. 1986. *Economic history of Puerto Rico*. Princeton, NJ: Princeton University Press.

- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*. 34(1): 487-515.
- Fahrig, L. and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8: 50-59.
- Gascon, C., Lovejoy T.E., Bierregaard R.O., Malcolm J.R., Stouffer P.C., Vasconcelos H.L., Laurance W.F., Zimmerman B, Torcher M. and Borges S. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91: 223-229.
- Geist, H. J. and E. F. Lambin. 2002. Proximate Causes and Underlying Driving Forces of Tropical Deforestation. *BioScience* 52: 143-150.
- Gould, W.A. 2008. Puerto Rico Gap Analysis Project. U.S. Department of Agriculture, Forest Service and International Institute of Tropical Forestry. Rio Piedras, PR. 159 pp. and 8 Appendices.
- Grau H.R., Aide T.M., Zimmerman J.K., Thomlinson J.R., Helmer E. and X. Zou. 2003. The ecological consequences of socioeconomic and land use changes in postagriculture Puerto Rico. *BioScience* 53 (12): 1159-1168.
- Green C., Kling M., Kuzsma R. and J. McAlary. 2001. Biological Corridors: Promoting and maintaining biodiversity in Puerto Rico. Report submitted to S. Vernon-Gerstenfeld and A. Gerstenfeld, Worcester Polytechnic Institute.
- Gobeil J.F. and M.A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98: 447-458.

- Helmer E.H., Ramos O.R., López T.M., Quiñones M. and W. Diaz. 2002. Mapping forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science* 38: 165-183.
- Hodgson P., French K. and R.E. Major. 2007. Avian movement across abrupt ecological edges: differential responses to housing density in an urban matrix. *Landscape and Urban Planning* 79: 266-272.
- Kennedy C.M. and P.P. Marra. 2010. Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. *Biological Conservation* 143: 2136-2145.
- Keyser A.J. 2002. Nest predation in fragmented forests: landscape matrix by distance from edge interactions. *The Wilson Bulletin* 114: 186-191.
- Kupfer J.A., Malanson G.P. and S.B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix based processes of forest fragmentation effects. *Global Ecology and Biogeography* 15: 8-20.
- López T.d.M., Aide T.M. and J.R. Thomlinson. 2001. Urban expansion and the loss of prime agricultural lands in Puerto Rico. *Ambio* 30 (1): 49-54.
- Lugo A.E. and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190: 145-161.
- Lugo, A. E., T. A. Carlo, and J. M. Wunderle, Jr. 2012. Natural mixing of species: novel plant-animal communities on Caribbean Islands. *Animal Conservation* 15:233-241.

- Manning A.D., Lindenmayer D.B. and H.A. Nix. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos* 104: 621-628.
- Matthysen E., F. Adriaensen, and A. A. Dhondt. 1995. Dispersal distances of nuthatches, *Sitta europea*, in a highly fragmented forest habitat. *Oikos* 72: 375-381.
- McIntyre S. and R.J. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13: 1282-1292.
- McKinney M.L. and J.L. Lockwood. 1999. Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology and Evolution* 14: 450-453.
- Murphy H.T. and J. Lovett-Doust. 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos* 105: 3-14.
- Noss R.F. and A.Y. Cooperrider. 1994. *Saving nature's legacy: protecting and restoring biodiversity*. Island Press, Washington D.C.
- Perfecto I. and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* 16: 174-182.
- Potter, R.B. 1993. Urbanization in the Caribbean and trends in of global convergence-divergence. *Geographical Journal* 159: 1-21.
- Prevedello J.A. and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* 19: 1205-1223.

- Ramos-González, O.M. 2001. Assessing vegetation and land cover changes in northeastern Puerto Rico: 1978-1995. *Caribbean Journal of Science* 37: 95-106.
- Rodewald A.D. and R.H. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82: 3493-3504.
- Rodewald, A.D. 2003. The importance of land uses within the landscape matrix. *Wildlife Society Bulletin* 31: 586-592.
- Thomlinson, J.R. and L.Y. Rivera. 2000. Suburban growth in Luquillo, Puerto Rico: Some consequences of development on natural and seminatural systems. *Landscape and Urban Planning* 49: 15-23.
- Tremblay M.A. and C.C. St. Clair. 2011. Permeability of a heterogeneous urban landscape to the movements of forest songbirds. 2011. *Journal of Applied Ecology* 48: 679-688.
- Turner B.L., Turner B.C., Clark R.W., Kates J.F., Richards J.T. and Meyer W.B. eds. *The Earth as transformed by human action*. Cambridge, U.K. Cambridge University Press.
- United States Bureau of Census. 1990-1994. *Data of population density, selected years: 1990-1994*. U.S. Department of Commerce. Washington D.C., U.S.A.
- Urbanová, T. 2009. How to support avian diversity in an urban landscape: a bibliography. *Journal of Planning Literature* 24(2): 123-136.
- Watling J.I., A.J. Nowakowski, M.A. Donnelly and J.L. Orrock. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography* 20: 209-217.

Watson R.T., Noble I.R., Bolin B., Ravindranath N.H., Verardo D.J. and D.J. Dokken. eds.
Land use, land use change, and forestry. Cambridge, U.K. Cambridge University Press.

Woodworth B. L, J. Faaborg, and W. J. Arendt. 1998. Breeding and Natal Dispersal in the Puerto Rican Vireo. *Journal of Field Ornithology* 69 (1): 1-7.

Chapter 1: Patch dynamics of resident avian species in three habitat matrices that separate forest reserves in southwestern Puerto Rico

ABSTRACT

Avian communities in human-modified landscapes exhibit varying patterns of patch colonization and extinction rates, determinants of species occurrence and persistence on a landscape. These rates will depend on the species' vagility and the characteristics of the modified habitat matrix. Understanding the dynamics of avian populations in these contexts is of interest because habitat patches tend to become smaller, isolated and of lower quality. The objectives of this work were to estimate species richness and quantify patch dynamics of 8 resident and endemic avian species occurring within the Guánica and Susúa Forests, and the agricultural, urbanized and forested matrices that lie between these forests in southwestern Puerto Rico in 2010 and 2011. Avian community composition per matrix was a mix of resident and introduced (exotic) species, but similar in richness (42 to 46 species). The presence of forest endemics in human-modified habitats was attributable to their ability to exploit novel resources, an attribute of island species. Initial species occupancy was mediated by matrix type. Subsequent seasonal occupancy did not vary markedly because colonization and extinction rates were time-invariant, suggesting that occupancy of focal species were not in transition during the study. Occupancy was higher in the forest reserves and forested matrix than in the urban and agricultural matrices, a pattern consistent with the forest affinities of most of focal species (e.g., Antillean Euphonia, Puerto Rican Bullfinch,

Vireo and Woodpecker). Factors affecting how a species colonize a patch (isolation) and the quality of patches (e.g., fruit availability) were the strongest determinants of occupancy. Patch size did not exert a strong influence on extinction rates. Similarities in species occupancy rates between the Guánica and Susúa Reserves and forest matrix highlighted the conservation value of the forest matrix, even in its current condition of low human density and other land uses. This work supported a growing body of work that suggests that habitat matrices are not ecologically irrelevant, and may play an important role in the dynamics and persistence of populations in human-modified landscapes. Insights and conservation implications from this work are applicable to similar landscapes in Puerto Rico and the Caribbean.

INTRODUCTION

Widespread levels of fragmentation turn landscapes into a patchwork of habitats of differing quality for fauna (Gascon et al. 1999; Grau et al. 2003; Lambin et al. 2003). Species in these habitat remnants are confronted with a modified environment of reduced area, increased isolation and novel ecological boundaries (Ewers and Didham 2006). These conditions may trigger large-scale reorganization of species assemblages and influence the persistence of resident species (Gustafson and Gardner 1996; Szacki 1999; Keitt and Stanley 1998; Brown et al. 2001). Changes in avian community composition, for example, may occur through a biological filtering effect, where species that lack the biological repertoire to bridge gaps of inhospitable matrices are unable to survive in the remaining fragments of native habitat (Saunders et al. 1991; Croci et al. 2008). Ultimately, species persistence could

be affected because isolation, size and quality of habitat remnants alter the colonization-extinction dynamics of metapopulations encompassed by the matrix (Hanski 1998; Brotons et al. 2003; Urbanová et al. 2009; Watling et al. 2011).

Habitat matrices contain features and attributes that can benefit or hinder key biological processes (e.g., colonization and extinction dynamics), which may vary by species. For example, urbanization promotes biotic homogenization, which increases avian biomass while reducing species richness (Blair 2001; Chace and Walsh 2006). Generally, urbanization tends to select for the presence of granivores, omnivores and cavity nesting species (Chace and Walsh 2006), although frugivores and nectarivores in the tropics might be more flexible (i.e., synanthropic; Lugo et al. 2012). Landscape changes also affect the permeability of the resulting habitat matrices. Permeability refers to the ease with which a species moves through a habitat matrix (Gobeil and Villard 2002). For example, avian species associated with forested habitats, including tropical species, take longer to complete movements between patches in fragmented landscapes, moving along forested routes and avoiding open areas (Awade and Metzger 2008; Boscolo et al. 2008; Gillies and St. Clair 2008; Moore et al. 2008; Hadley and Betts 2009; Kennedy and Marra 2010). Fragmented landscapes may also lead to higher rates of nest predation and brood parasitism (Andrén 1995; Robinson et al. 1995). This is believed to be a major determinant of the range expansion and increase in brood parasitism rates of the Shiny Cowbird (*Molothrus bonariensis*) in Puerto Rico. The cowbird parasitizes several native and endemic species, and is believed to be a major contributor of the population decline of the Puerto Rican Vireo

(*Vireo latimeri*) in southwestern Puerto Rico (Cruz et al. 1985; Faaborg et al. 1997; Woodworth et al. 1998).

Forested landscapes in Puerto Rico have undergone dramatic changes due to deforestation and agriculture expansion in the 20th century (Lugo and Helmer 2004). Demographic and socioeconomic factors have driven these transformations, leading to substantial changes in the spatial distribution of the human population and land use practices (Lopez et al. 2001; Grau et al. 2003). For example, 90% of Puerto Rico was in some form of agriculture by the late 1930s (Dietz 1986; Birdsey and Weaver 1987). A shift towards an industrial-based economy in the late 1950s prompted a transition in land cover, and by 1991, 42% of the island's land cover was forested (Helmer et al. 2002). However, Puerto Rico exhibits a high level of habitat fragmentation, with its few areas of continuous forest surrounded by urban or other land covers (Lugo and Helmer 2004). Anthropogenic influences on Puerto Rico's forests are intense and widespread. This is highlighted by the fact that the island has the highest road density of any Caribbean island (López et al. 2001) and that its human population has increased more than threefold in the last century (U.S. Bureau of Census 2011).

The dynamic processes that underlie avian responses to fragmented landscapes have been poorly studied, particularly in the tropics (Suarez-Rubio and Thomlinson 2009; Lugo et al. 2012). These processes have their theoretical basis in the theories of island biogeography and metapopulations (MacArthur and Wilson 1967; Hanski 1998). This body of work posits that the occurrence of species on a fragmented landscape will be the result of rates of colonization, mediated by the degree of isolation between habitat patches, and rates of

extinction, mediated by the size of habitat patches. In a recent study, Kennedy et al. (2011) reported that habitat matrices mediated the occupancy dynamics of 9 forest-dependent avian species in Jamaica. Patch isolation influenced colonization rates; however, patch quality, not patch size, had a stronger influence on extinction rates. The influence of patch quality (e.g., available food, shelter) on demographic parameters in fragmented landscapes had been previously reported. For example, avian abundance in fragmented landscapes responded positively when the quality of habitat patches was increased (Andrén 1997). In some cases, habitat matrices may provide resources that are not available in adjacent forested patches (Ries and Sisk 2004). This suggests that extinction rates in habitat remnants might be ameliorated by the presence of a hospitable matrix, resulting in unexpected occurrence patterns, at least temporarily (Watling et al. 2011).

In this study, we described the resident avian community and determined the species richness of the identifiable urban, agricultural and forested matrices that separate the Guánica and Susúa State Forest Reserves. We also surveyed the Susúa and Guánica Forest Reserves to obtain an estimate that served as a reference for comparison with estimates from the intervening habitats between forest reserves. Furthermore, we quantified local occupancy, extinction and colonization rates of surveyed stations, hereafter referred to as patches, for eight avian species across all matrices over 5 consecutive seasons (15 months) between 2010 and 2011. Estimates were obtained using a multi-season occupancy modeling framework, which adjusted parameter estimates by accounting for imperfect detection (MacKenzie et al. 2006; MacKenzie et al. 2009). We chose to focus on six forest-specialist species, as most native avian species in Puerto Rico are associated with forested land cover (Gould et al.

2007; Acevedo and Restrepo 2008). We selected three predominantly insectivore and frugivore species for our analysis, although some of the selected species may have a broader or more flexible diet (Lugo et al. 2012). The insectivores were the Puerto Rican Vireo (*Vireo latimeri*), the Puerto Rican Woodpecker (*Melanerpes portoricensis*) and the Caribbean Eleania (*Elaenia martinica*). The frugivores were the Puerto Rican Bullfinch (*Loxigilla portoricensis*), the Puerto Rican Spindalis (*Spindalis portoricensis*) and the Antillean Euphonia (*Euphonia musica*). To complement our analysis and provide a contrast for the forest-associated focal species, we included the Shiny Cowbird (*Molothrus bonarensis*) and the Black-Faced Grassquit (*Tiaris bicolor*). The Shiny Cowbird is an omnivorous brood parasite, often associated with disturbed habitats and agriculture and livestock (Cruz et al. 1985). The Black-faced Grassquit is a native granivore associated with open habitats that is likely adept at exploiting fragmented landscapes.

We expected matrix conditions to mediate occupancy dynamics in accord to the species primary habitat associations (Acevedo and Restrepo 2008; Vásquez-Plass and Wunderle 2011). We hypothesized that the forest reserves and the forested matrix would have similar levels of species richness and higher rates of occupancy of forest-specialists, providing a contrast with the urban and agricultural matrices. We also expected occupancy to vary with isolation, patch size and habitat quality, exerting a stronger influence on colonization and extinction rates of forest-specialists in the urban and agricultural matrices. Our reasoning assumed that human activities have modified the composition and spatial arrangements of resources to a greater extent. We discuss the conservation implications of

our results for species of avian forest specialists in southwestern Puerto Rico, elsewhere on the island and the rest of the Caribbean.

STUDY AREA

Our study area consisted of the municipalities of Guánica, Yauco, as well as parts of Lajas and Sábana Grande in southwestern Puerto Rico. Figure 1.1 shows the extent, spatial arrangement of the habitats, and land cover classes in the study area. The matrix that separates the Guánica and Susúa forests was divided into three identifiable matrices using ArcGIS (ESRI 2010; Gould et al. 2007). Boundaries among these matrices were identified visually by sharp transitions between urban and forest or urban and agricultural lands. From east to west, the matrix was classified as predominantly (or at least 70%) forested, urbanized and agricultural. The extent of each matrix was 7,066 ha (agriculture), 6,116 ha (urban), and 5,536 ha (forested). Appendix A provides a detailed breakdown of land cover classes per habitat matrix.

METHODS

Avian Survey Stations

A total of 128 survey stations were randomly established across the three matrices and the Guánica and Susúa Forests. These stations were used to conduct avian surveys as detailed below. There were 30 stations in each of the agricultural, urban and forested matrices, for a total of 90 stations. An additional 38 stations were established anywhere between 300 and 1500 m within the Guánica and Susúa Forest Reserves. Eighteen (18) of

these stations were established in the northern edges of the Guánica Forest and the remaining twenty (20) were established at the southern edges of the Susúa forest. Figure 1.1 depicts the location of the survey stations across the landscape. Survey stations within matrices were ≥ 500 m apart to minimize spatial autocorrelation, with those in the forested matrix and within the forest reserves > 1 km apart (Collazo and Noble 2008). Between matrices, the nearest two surveys stations were at 1.1 km (Urban – Forest matrices) and 2.9 km (Urban – Agricultural matrices) apart. Appendix A provides a more detailed depiction of the location of surveys stations per matrix.

Presence-Non-presence (absence) Surveys

Avian surveys were designed around a multi-season occupancy robust design framework with five seasons as the primary sampling periods, and three surveys per station as the secondary sampling occasions (Pollock 1982; MacKenzie et al. 2006, 2009). In this design, patches (survey stations) are closed to changes in occupancy within seasons, but open to changes between seasons, through the processes of local patch colonization and extinction. Surveys were conducted during two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). These periods were defined based on breeding chronology reported by Collazo and Groom (2000) and Wiewel (2011) for the Guánica State forest. Patterns of seasonal reproductive output and hypothesized post-breeding dispersal provided a reasonable temporal framework for sampling. Surveys were conducted from dawn until 1000 hrs. Surveys were not conducted during inclement weather (e.g., rainy days). All resident avian species

detected by sight or hearing during a 10-minute period were recorded within a 100 m radius. We expanded the sampling radius from the traditional 50 m radius (e.g., Alldredge et al. 2007) to 100 m because most survey stations were located in open habitat contexts. Appendix B lists all the avian species detected during the study.

Survey Station and Landscape level Covariates

We measured 7 covariates at each survey station. These were canopy height (m), canopy cover (%), understory cover (%), slope (degrees) and aspect (cardinal direction). Understory and canopy cover were coded as: 1 = 0-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%. Fruit availability was also recorded, but assessed within a 10 m radius from the center of the station and used as a fruit availability index (FAI). At each station we coded the number of fruiting tree species with available fruit as: 0 = none, 1 = 1-2 species, 2 = 3-4 species, 3 = 4-5 species, 4 = 6 or more species (Carlo et al. 2003). We also created a categorical expression of the fruit availability index. This index was defined as the average proportion of survey stations within a matrix that contained fruits preferred by the Puerto Rican Bullfinch and Puerto Rican Spindalis (Carlo et al. 2003; Carlo et al. 2004; Carlo et al. 2012). Appendix C lists all fruit tree species identified in patches, specifying those used to calculate the adjusted fruit availability index.

We further characterized the landscape using data layers from PR Gap Analysis and program ArcGIS (Gould et al. 2007; ESRI 2010), as well as aerial imagery obtained through Google Earth (Google Inc. 2011). We estimated distance to patch (DP), a measure of survey station (patch) isolation. This was defined as the straight line distance (m) between the

center of the station and the nearest forest patch or clump of trees using aerial photography from Google Earth. This measurement represented the nearest potential stepping-stone birds could use while traveling or seeking shelter and could consist of a substantial number of trees (clumps), hedgerows and remaining habitat patches in the landscape (e.g., agricultural matrix). We also included distance to forest patch cover (DF) as another measure of patch isolation. Within any given matrix, this distance was defined as the distance from the survey station to the nearest patch (200 m disk) that matched the average forest patch cover of survey stations in the forest matrix (61%, range: 24-88%). We justify the inclusion of this covariate because: (1) it represented the average cover in the least human-modified matrix between reserves, reflecting cover found in forested landscapes (forest reserves); and (2) its value was similar to the patch cover at sites used by birds returning to the site-of-capture during translocation experiments (70-80%; Chapter 2). We estimated forest and herbaceous cover (FCov, HCov) for each survey station as the percent of forest or herbaceous cover pixels within 200 m radius of the center of each survey station. The 200 m radius represented twice the size of the surveyed area to better capture the habitat context in which survey stations occurred. Finally, the patch size (PS), the size of the forested area containing the survey station was calculated using the 4 cardinal direction patch rule (ESRI 2011). In this rule, pixels (30 x 30 m) in a raster dataset were grouped provided a full side, not a corner, touched the adjacent pixel of the same cover class type (i.e., forest). The initial point of this process was the survey station location. Patch size (ha) was the sum of the area of all the pixels that met the criterion for the cardinal rule.

DATA ANALYSIS

Species Richness

We used a capture-recapture approach to estimate species richness. This approach was justified because avian communities in different habitat matrices may have different detection probabilities and the probability of detection is likely to vary strongly among species. We used the Chao (1988) estimator implemented in program MARK (White and Burnham 1999). This estimator assumes that there is heterogeneity in species detectability, and it is robust when encounter histories are made of < 5 visits. The method uses encounter histories of species detected and not detected on a series of sampling occasions of the same avian community. We used data collected during the breeding season (March-June) of 2010, during which 3 surveys were conducted at each survey station. We assumed that within one season the avian community was closed to immigration or emigration. The model requires the encounter histories of all species that were detected and the number of species detected per habitat matrix. Prior to running the models, we summarized our data by determining if a species (e.g., A or B) was detected in any of the survey stations within a habitat matrix (see methods section for details on number of stations per matrix). An example of this summary could be denoted as h_A101 and h_B110 . These encounter histories indicate that species A was detected on the first and third occasion, but not on the second sampling occasion. Species B was detected on the first two sampling occasions, but not on the third sampling occasion. Model output is an estimate ($\pm$ SE) of the number of species per habitat matrix after adjusting for detection probability.

Occupancy Models

We constructed multi-season occupancy models to estimate initial occupancy (ψ_1), local colonization (γ), and local extinction (ϵ) over 5 seasons from January 2010 to June 2011 for each focal species separately (MacKenzie et al. 2006). This framework builds on Pollock's Robust design (1982), where the model structure specifies primary sampling periods (i.e., seasons), and secondary sampling occasions within each season (i.e., surveys within season). Initial occupancy was defined as the probability that a surveyed station (patch) was occupied by a species in the initial season of the study ($\psi_{\text{pre-breeding 2010}}$). Local extinction probability (ϵ_t) is the probability that a patch occupied by that species at season t is no longer occupied by the species in season $t + 1$. Local colonization probability (γ_t) is the probability that a patch unoccupied by a species at season t becomes occupied at season $t + 1$. In this model, parameters are adjusted by detection probability or the probability that at least 1 individual of a species was detected in season t , provided the individual was available to be detected. Count data for every surveyed station were converted into an encounter history of presence (1) and non-presence (0). For example, an encounter history of 101, 111, 110 indicates that at least 1 individual of a species was detected on the first and third sampling occasion of the first season, but not on the second occasion. During the second season, at least one individual was detected on every occasion. During the final season, at least one individual was detected on the first and second surveys, but not on the third or last survey.

We developed a candidate model set of 8 basic parameterizations to test the effects of patch isolation, patch size, vegetation cover, fruit availability and matrix type on the aforementioned parameters of interest. We did not include elevation as a covariate because it

was not a significant influence for occupancy along an elevation gradient between the Guánica State Forest (<100 m) and Maricao State Forest (~800-900 m). We tested for the influence of elevation on occupancy for the Puerto Rican Bullfinch, Puerto Rican Spindalis, and the Puerto Rican Vireo (Collazo 2012). The basic parameterizations of the models were: (1) constant (.) and season-specific (S) detection probability; (2) constant (.) and season-specific (S) colonization and extinction probability and (3) initial occupancy (constrained by matrix type or not). We constrained these model parameterizations with covariates as follows. First, we modeled the detection process to determine if survey-station characteristics influenced the ability of observers to detect the presence of individuals (Anthony et al. 2004; Kennedy et al. 2011). Covariates for this process were canopy height (CAHT), canopy cover (CACOV), understory cover (UC), slope and aspect. We adopted the model with the lowest AIC obtained in this initial process to then assess support in the data for either constant or season-specific colonization and extinction rates. We then determined if constraining initial occupancy by matrix type was better supported by the data than a model without it. The resultant parameter model structure of these three steps was then constrained by patch size, isolation, habitat quality and matrix type. Initial occupancy was constrained by matrix type because we hypothesized that initial occupancy would be influenced by where the birds occurred at the onset of the study (Andrén 1994). We hypothesized that patch colonization would be negatively influenced by the degree of isolation of the survey station or patch (DP or DF), and that patch extinction would be negatively influenced by the size of the forest patch containing the survey station and its quality. Patch quality was represented by percent forest or herbaceous cover (FCov, HCov)

and the availability of food resources at the time surveys were conducted (FAI or FAIadj). We used an average estimate of FAI per station as a patch covariate rather than as a sampling or seasonal covariate because using the later overparameterized models. The FAIadj was defined as the average proportion of survey stations within a matrix that contained fruits preferred by the Puerto Rican Bullfinch and Puerto Rican Spindalis. Data permitting, we also modeled both colonization and extinction by matrix type (Kennedy et al. 2011). In the case of the bullfinch and spindalis, we could only model colonization and extinction as a function of the forested areas (forest reserves and forested matrix); modeling all matrices overparameterized the model. We modeled all covariates as additive factors. We did not consider interaction terms because there was no spatial replication in our study design. A random effects term would have also overparameterized models. Before running models, all continuous covariates were normalized in program PRESENCE. Appendix D lists covariates, definitions and codes used to model parameters in this study.

We used Akaike's information criterion (AIC) to select the most parsimonious model (Anderson and Burnham 2002). Models were ranked by AIC, and the model with the lowest AIC value had the most support in the data. The difference in AIC values (ΔAIC) between the best-supported model and other models was used to calculate model weights (AIC wgt), which indicate the relative likelihood of the model given the data and the model set (Burnham and Anderson 2002). Models with $\Delta AIC \leq 2$ were considered models with highest support, provided that such models were not more complex versions of a simpler and better-supported model (Burnham and Anderson 2002). The relationship between the probability of occupancy and covariates was established using a logistic model (logit link) in program

PRESENCE (Hines 2006). We considered an effect (i.e., covariate beta coefficient) to be strongly supported if the 95% confidence intervals did not overlap zero. Parameter estimates are reported $\pm$ SE.

Careful consideration of model assumptions is important for interpreting results. Multi-season occupancy models assume that: (1) occupancy state at each survey site does not change over surveys within a season; (2) the species was not falsely detected; (3) species detections and detection histories at each survey site were independent; and (4) rate parameters (e.g., occupancy, extinction, colonization or detection) are constant across sites at any given time. The first two assumptions were likely met given that surveys within every season were conducted at 2 week intervals and by qualified bird observers. We addressed the third assumption by establishing survey sites at ≥ 500 m within matrices, many exceeding 1 km apart. Between matrices, the two closest survey stations were at 1.1 km (urban-forest) and 2.9 km (agriculture – urban). We also assumed that both the grain (i.e., 30 x 30 m pixels) and the thematic resolution (habitat classes) of the Puerto Rico Gap Analysis landcover data were reasonable for developing avian species-habitat models, that is, an adequate representation of the available habitat on the ground.

RESULTS

Species Richness

Species richness estimates for the agriculture, urban, forested matrices and forest reserves were similar (95% confidence intervals overlapped). The estimated number of species for the agriculture matrix was 47 ± 6.90 (95% CI: 42 – 73). For the urban matrix, the

estimated species richness was 46 ± 3.057 (95% CI: 44 – 58) and for the forested matrix the estimate was 44 ± 6.08 (95% CI: 40 – 69). Finally, the estimated species richness for the forest reserves was 45 ± 1.46 (95% CI: 45 – 52).

Although estimates of species richness were similar, there were some differences in species composition among matrices (Table 1.1). For example, the Great Egret (*Ardea alba*), Indian Silverbill (*Euodice malabarica*) and Ruddy Quail Dove (*Geotrygon montana*) were not detected in the urban matrix in any of the 5 seasons of this study. Similarly, the Bronze Mannikin (*Spermestes cucullatus*), Cave Swallow (*Petrochelidon fulva*), Grasshopper Sparrow (*Ammodramus savannarum*), Indian Silverbill (*Euodice malabarica*), Mangrove Cuckoo (*Coccyzus minor*), Nutmeg Mannikin (*Lonchura punctulata*), Orange Bishop (*Euplectes franciscanus*) and Rock Pigeon (*Columba livia*) were never detected in the forest matrix. The only species not detected in the forest reserves was the Indian Silverbill (*Euodice malabarica*). In contrast, every one of the 50 species detected during the study was detected at least once in the agricultural matrix.

Occupancy

Most of the variation in the data for the Puerto Rican Spindalis and Puerto Rican Woodpecker was captured by the top model ($AIC_{\text{wgt}} > 0.65$; Tables 1.2 and 1.3). Some variation was captured by alternative models, but these did not receive strong support ($\Delta AIC > 2$). Detection probability for these species varied seasonally and was influenced by slope (spindalis) and canopy cover (woodpecker). Patch colonization and extinction probabilities were constant over the study. Distance to patch and the fruit availability index influenced

both rate parameters (Tables 1.2, 1.3). However, only fruit availability had a strong and negative influence on extinction probabilities for both species (95% CI for the Beta estimates did not overlap zero; Table 1.4, Figures 1.2 and 1.3).

Model selection for the Antillean Euphonia, Black-faced Grassquit, and Shiny Cowbird featured 1 or 2 competing models with strong support ($\Delta AIC < 2$; Tables 1.5, 1.6, 1.7). Detection probability for these species varied seasonally and was influenced by slope (euphonia) and canopy cover (grassquit, cowbird). Patch colonization rates for the grassquit were constant over the study period, and strongly and negatively influenced by the forest matrix (Table 1.4, Figure 1.4), whereas extinction rates were strongly and positively influenced by the combined forest and ground cover (Table 1.4, Figure 1.5). Patch extinction rates for the euphonia were constant over the study period, and strongly and negatively influenced by the adjusted fruit availability index (Table 1.4, Figure 1.6). Only horizontal cover converged in the Shiny Cowbird's models, but it did not have a strong influence on patch extinction rates. No other covariate had an influence on colonization or extinction probability (Table 1.4).

There was greater uncertainty among models for the Puerto Rican Bullfinch, Puerto Rican Vireo and Caribbean Elaenia. Model support (AIC_{wgt}) for top models ranged from 0.23 to 0.37 (Tables 1.8, 1.9 and 1.10). Detection probability for all species varied seasonally and was influenced by understory cover. For the Puerto Rican Vireo, competing models featured distance to nearest patch (DP) or distance to large forest patches (DF) as factors influencing patch colonization probabilities, albeit both having a weak effect (Table 1.4). Patch extinction probabilities were consistently influenced by percent forest cover, and

strongly and negatively in the model with highest support ($AIC_{\text{wgt}} = 0.37$, Table 1.4, Figure 1.7). Patch colonization rates for the Puerto Rican Bullfinch were matrix-mediated and consistently influenced by distance to large forest patches (DF). Indeed, the influence of DF was strong and positive for the model with highest support ($AIC_{\text{wgt}} = 0.37$, Table 1.4, Figure 1.8). Patch extinction probability was also matrix-mediated, strongly and negatively influenced in the forested matrix and forest reserves (Table 1.4, Figure 1.9). Model uncertainty was most prevalent for the Caribbean Elaenia. Six models were considered plausible alternatives ($\Delta AIC < 2$). Patch colonization probability was weakly influenced by either distance to the nearest patch (DP) or distance to large forest patches (DF; Table 1.4). There was also weak support for the influence of patch size (PS) and forest cover on extinction rates.

Generally, initial and subsequent seasonal occupancy probabilities highlighted differences between agriculture and urban matrices as compared to forested matrix and the forest reserves. This was the case for the Antillean Euphonia, Puerto Rican Bullfinch, Caribbean Elaenia, and Puerto Rican Vireo (Figures 1.10 to 1.13). In contrast, occupancy estimates for the Puerto Rican Woodpecker, Puerto Rican Spindalis, Shiny Cowbird and Black-faced Grassquit overlapped substantially (95% CIs), indicating that patterns by matrices were not distinct (Figures 1.14 to 1.17). For some species occupancy appeared to increase or decrease throughout the study (e.g., Puerto Rican Spindalis, Puerto Rican Vireo, Shiny-Headed Cowbird). However, the 95% CI of the initial and last estimate occupancy estimates overlapped, suggesting that there was no support for a statistical trend.

DISCUSSION

We documented an avian community comprised of native, endemic and introduced or naturalized species within the Guánica and Susúa State Forest Reserves and the agricultural, urbanized and forested habitat matrices that lie between them in southwestern Puerto Rico. Estimates of species richness were similar among matrices, ranging from 42 to 46 species. Differences in species composition were most noticeable in the forested matrix, where several introduced or naturalized species (e.g., seed-eating finches and doves) were not detected. These species are typically associated with open habitats (Raffaele 1998). Conversely, we did not detect the Rudy Quail Dove in the urban matrix, possibly because it is known to have a strong affinity to forested habitats. Highly mixed species communities in Puerto Rico are commonplace, in large part because species are capable of enduring landscape changes and disturbances, and exploiting novel resources (Lugo et al. 2012). These traits characterize island birds (Ricklefs and Cox 1978), some of which have evolved through the process of ecological release (Terborg and Faaborg 1973) and adaptive responses to disturbances such as hurricanes (Wiley and Wunderle 1993; Ricklefs and Bermingham 2008). Urbanized landscapes and other such novel habitats may provide resources that are otherwise unavailable in habitat remnants (Ries and Sisk 2004). Moreover, many resident and endemic species are synanthropic, benefitting from novel foraging resources associated with human presence on landscapes (Lugo et al. 2012). These include ornamental plant species and fruiting trees used for human consumption, such as those documented in our fruit availability index (FAI). This phenomenon has been documented for other taxa (Leidner and Haddad 2010).

In this study, we also quantified colonization, extinction and occupancy rates in three habitat matrices between two forest reserves in southwestern Puerto Rico, and within both forest reserves (300 m to 1.5 km meters inside the boundary facing the intervening habitats between reserves). These parameters have direct bearing on the probability of a species occurring and persisting on the landscape. In landscapes modified by anthropogenic activities (e.g., urbanization, agriculture), variation may stem from the tendency of habitat patches to become increasingly smaller, isolated and of lower quality (Ewers and Didham 2006; Suarez-Rubio and Thomlinson 2009; Lugo et al. 2012). We focused on avian forest-specialists because Puerto Rico has been historically dominated by forested landscapes (Acevedo and Restrepo 2008). We found that initial species occupancy was mediated by matrix type. Subsequent, seasonal occupancy did not vary markedly from the initial estimate. This was consistent with the poor support in the data for models with season-specific local colonization and extinction rates. This suggests that the focal species in this study were not in transition or experiencing major changes in occupancy due to changes in land use or urban growth during our fifteen month study period (McKenzie et al. 2006; Nichols et al. 2011). Similar findings were reported by Kennedy et al. (2011) in a multi-year project in Jamaica. Model support was stronger for rates that were constant over the study period or constant but mediated by matrix type. We suggest that studies aimed at assessing the possibility of transient dynamics in human-modified landscapes should be conducted on multi-annual scales, a temporal scale corresponding with that of urban growth and other land use changes. Because our study was conducted over short period of time (15 months), we cannot assert that the avian community was at equilibrium or close to reaching it. The

apparent magnitude and relative rapidity of landscape changes in Puerto Rico would make reaching that state unlikely (Lugo et al. 2012).

Our findings indicated that occupancy was consistently higher in the forest reserves and forested matrix than in the urban and agricultural matrices. This pattern was also consistent with the forest affinities of most of our focal species (e.g., Antillean Euphonia, Puerto Rican Bullfinch, Puerto Rican Vireo, Puerto Rican Woodpecker). We interpret the lower occupancy rates in urban and agricultural matrices of these species as an indicator of species' sensitivity to human-modified landscapes. This provides a stark contrast to the Black-faced Grassquit, which is adept at using open habitats (Raffaele et al. 1998). The grassquit's occupancy rates were high across all matrices. Occupancy of Shiny Cowbirds, a brood parasite, did not exhibit a strong tendency towards in any particular matrix type. We were only able to incorporate one habitat quality covariate into our models, but it did not have a strong influence on extinction rates. We speculate that these results may reflect the species' life history trait of searching and tracking potential hosts (Cruz et al. 1985), rather than engaging in habitat selection. Moreover, the cowbird is adept at exploiting human modified landscapes (e.g., pastures, edges, fragmented forests; Cruz et al. 1985; Lugo et al. 2012).

Our results highlighted the importance of patch isolation and its influence on colonization rates. Isolation had a significant influence on the colonization rates of the Puerto Rican Bullfinch. Contrary to expectations, extinction rates were strongly influenced by covariates that served as proxies or indicators of patch quality, not patch size. Long-term experimental work in the Amazon has shown that patch size has a strong influence on avian

occupancy (Ferraz et al. 2007). In our results, patch size was featured among competing models ($\Delta AIC \leq 2$) for the Puerto Rican Bullfinch and Caribbean Eleania; but support in the data for its influence on patch extinction was weak (95% confidence intervals overlapped zero). Two other studies have reported findings similar to ours. Kennedy et al. (2011) found that patch size had a strong influence on two of nine avian species in Jamaica, but argued that within-patch quality (e.g., cover) and context (matrix type) were stronger determinants of patch extinction. Watling and Donnelly (2008) reported that patch isolation, not size was a better predictor of species richness and composition of amphibians in Bolivia. In this case it was not clear why species richness would increase with forest island area because amphibians were generalists and there was no evidence of habitat quality variation as a function of forest island area. In light of the weak support for patch size in our models, we inferred that factors affecting how species colonize a patch (isolation) and the quality of those patches were stronger determinants of occupancy in the landscape under study. We acknowledge that our sampling scheme was not appropriate for testing the relationship between extinction and patch size in the urban and agricultural matrices. Fifty-nine of the sixty survey stations randomly allocated in these matrices did not fall within a forested location. However, this was not the case for the forested matrix and forest reserves, where we sampled a wide range of patch sizes (0.25 to 5,420 ha). In these contexts, the influence of patch size may have been obscured by the proximity of patches to the forest reserves. We also note that our occupancy estimates ignored processes that could be more sensitive to patch size. For example, it is possible that an occupied site was also used for reproduction. This possibility could be incorporated into future studies by adopting multi-state models, a

framework that estimates the probability of detecting reproductive activities, given that a patch is occupied (Nichols et al. 2007; Rogers 2011).

Our findings could help guide conservation efforts in southwestern Puerto Rico, particularly those aimed at conserving and facilitating movements of forest-specialist species between the Guánica and Susúa Forest Reserves. Occupancy rates in the forested matrix were similar to those estimated for the forest reserves, which represented forested habitat within a 300-1,500 m band along the perimeter of the forest reserves. The similarities hint at the conservation value of the forest matrix for forest-associated species, even in its current condition of low human density and other land uses (Gould et al. 2007). The specific covariates influencing colonization and extinction rates are also valuable for conservation planning. Patch isolation influenced the colonization rates of Puerto Rican Bullfinches, specifically, the distance to the nearest forest patch with a cover value similar to the average cover value of patches in the forested matrix (DF). The highest patch colonization probabilities were documented when these patches were < 0.5 km away from the survey station. Experimentally translocated Puerto Rican Bullfinches used patches with similar cover while traveling through the urbanized matrix to return to their original capture locations (Chapter 2). This example helped visualize how remaining habitat patches may serve two functions: (1) facilitate patch colonization, enhancing the persistence of avian species within the matrix and (2) permit the passage of species through the matrix, providing vital permeability and enhancing the connectivity of the landscape.

The negative relationship between the fruit availability index and patch extinction rates for species such as the Antillean Euphonia, Puerto Rican Spindalis and Puerto Rican

Woodpecker was also of value for informing conservation planning. Extinction rates decreased as the average number of tree species bearing fruits increased. In sampled patches, three or more trees bearing fruits per season fostered the lowest patch extinction rates. Increasing forest cover also contributed to lower patch extinction rates for species such as the Puerto Rican Vireo. We speculate that a higher percentage of forest cover or tree foliage increased patch quality by providing greater foraging resources (e.g., arthropods), cover from predators and potential nesting substrates. While our discussion has so far targeted forest-specialist species, our approach could be aimed at species with other habitat requirements. For example, we found that increasing values of understory and forest cover led to an increase in extinction rates for the Black-faced Grassquit. The lowest patch extinction rates were documented patches with less than 20% forest cover. The influence of cover should not be surprising, as the grassquit is a native granivore associated with open habitats (Lugo et al. 2012).

Occupancy estimates among matrices also suggested that some species might be “adapters” or adept at exploiting urban landscapes (e.g., Puerto Rican Spindalis; Croci et al. 2008). This possibility has also been reported in studies by Vázquez-Plass and Wunderle (2012) and Suarez-Rubio and Thomlinson (2009), who documented higher abundance of Puerto Rican Spindalis in urbanized landscapes when compared to species like the Puerto Rican Bullfinch. In accord with Kennedy et al. (2011) and Watling et al. (2011), we demonstrated that matrix type and other characteristics of habitat matrices (e.g., quality, isolation) mediate avian community occupancy and dynamics for many avian species in southwestern Puerto Rico. These same factors are believed to be important in making

matrices permeable to species movements and enhancing connectivity between large forest patches (Watling et al. 2011). Gaining a better understanding of matrix dynamics and how it could be used to enhance connectivity between Guánica and Susúa Forests was the main objective of this study. With this in mind, we recommend that landowners be encouraged to voluntarily or through incentives (e.g., NRCS) preserve and restore most of the forest cover contained in the forested matrix. Planting trees would be particularly effective in the urban matrix, providing as many “stepping-stones” as possible. This will facilitate the movements of avian species through the landscape and reduce patch isolation. Plantings should target fruiting tree species preferred by frugivores and nectarivores as a means to improve patch quality, and foster occupancy (Pérez-Rivera 1994; Carlo et al. 2003; Carlo et al. 2004; Carlo et al. 2011). We recognize that our work was not spatially replicated, but believe it sheds light on how habitat context (matrix type), patch size, isolation and habitat quality might influence population dynamics of resident and endemic avian species. Our work provides a benchmark and insights to further explore the dynamics and potential demographic contributions to persistence of avian species in human-modified landscapes elsewhere in Puerto Rico and the Caribbean (Watling et al. 2011; Lugo et al. 2012).

LITERATURE CITED

- Acevedo M.A. and C. Restrepo. 2008. Land-cover and land-use changes and its contribution to the large-scale organization of Puerto Rico's bird assemblages. *Diversity and Distributions* 14: 114-122.
- Allredge M.W., K.H. Pollock, T.R. Simons, J.A. Collazo and S.A. Shriner. 2007. Time-of-detection method for estimating abundance from point count surveys. *The Auk* 124(2): 653-664.
- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Andrén, H. 1995. Effects of landscape composition in predation rates at habitat edges. In: L. Hansson, L. Fahrig and G. Merriam (Eds.), *Mosaic landscapes and ecological processes*. Chapman and Hall, New York. pp 225-255.
- Andrén, H. 1997. Population response to landscape changes depends on specialization to different landscape patterns. *Oikos* 84: 306-308.
- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. Gutierrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid and S. G. Soeven. 2006. Status and trends in demography of northern spotted owls, 1985-2003. *Wildlife Monographs* 163:1-48.
- Ås, S. 1999. Invasion of matrix species in small habitat patches. *Conservation Ecology* 3: 1.

- Awade M. and J.P. Metzger. 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology* 33: 863-871.
- Bélisle M. and C.C. St. Clair. 2001. Cumulative effects of barriers on the movements of forest birds. *Conservation Ecology* 5(2): 9. [online] URL: <http://www.consecol.org/vol15/iss2/art9/>
- Birdsey R.A. and P.L. Weaver. 1987. Forest area trends in Puerto Rico. New Orleans (LA): US Department of Agriculture Forest Service. Southern forest experiment station. Research note SO-331.
- Blair, R.B. 2001. Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna? In: Lockwood J.L., McKinney M.L. (Eds.), *Biotic Homogenization: The loss of diversity through invasion and extinction*. Kluwer Academic Publishers, Boston MA. pp 33-56.
- Boscolo D., Candia-Gallardo C., Awade M. and J.P. Metzger. 2008. Importance of interhabitat gaps and stepping-stones for Lesser woodcreepers (*Xiphorhynchus fuscus*) in the Atlantic forest, Brazil. *Biotropica* 40: 273-276.
- Brotons L., Monkkonen M. and J.L. Martin. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *American Naturalist* 162: 343-357.
- Brown J.H., Ernest S.K.M., Parody J.M. and J.P. Haskell. 2001. Regulation of diversity: maintenance of species richness in changing environments. *Oecologia* 126: 321-332.

- Burnham K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer Science and Business Media. Fort Collins, Colorado USA.
- Burnham K.P. and W.S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60: 927-936.
- Carlo T.A., R.A. Pérez-Rivera and J.M. Gelditsch. 2012. Folivory by a tropical tanager: species of plants used and the relationship between leaf consumption and fruit abundance. *Journal of Field Ornithology* 83(1): 11-16.
- Carlo, T.A., J.A. Collazo and M.J. Groom. 2003. Avian fruit preferences across a Puerto Rican forest landscape: pattern consistency and implications for seed removal. *Oecologia* 134: 119-131.
- Carlo, T.A., J.A. Collazo and M.J. Groom. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. *Biotropica* 36(4): 602-614.
- Chace J.F. and J.J. Walsh. 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74: 46-69.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265-270.
- Collazo, J.A. 2012. Annual Report, Segment 3, Puerto Rico Department of Natural and Environmental Resources. San Juan, Puerto Rico.

- Collazo, J.A. and M.J. Groom. 2000. Avian conservation in north central forested habitats in Puerto Rico. Final report to the Puerto Rican Department of Natural Resources. San Juan, PR. 375pp.
- Collazo, J.A. and R. Noble. 2008. Avian conservation in karstic forests in Puerto Rico. Final report, Puerto Rico Department of Natural Resources. San Juan, PR. 470pp.
- Cook W.M., Lane K.T., Foster B.L., and R.D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters* 5: 619-623.
- Croci S., Butet A. and P. Clergeau. 2008. Does urbanization filter birds on the basis of their biological traits? *The Condor* 110: 223-240.
- Cruz A., T. Manolis and J. W. Wiley. 1985. The shiny cowbird: a brood parasite expanding its range in the Caribbean region. *Ornithological Monographs* 36: 607-620.
- Dietz, J.L. 1986. Economic history of Puerto Rico. Princeton (NJ): Princeton University Press.
- ESRI (Environmental Systems Research Institute Inc.). 2010. ArcGIS Desktop (Version 10) [Software].
- Ewers R.M. and R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81: 117-142.
- Faaborg J., K.M. Dugger, W.J. Arendt, B.L. Woodworth and M.E. Baltz. 1997. Population declines of the Puerto Rican Vireo in Guánica Forest. *The Wilson Bulletin* 109(2): 195-202.

- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*. 34(1): 487-515.
- Ferraz G., J.D. Nichols, J.E. Hines, P.C. Stouffer, R.O. Bierregaard Jr. and T.E. Lovejoy. 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* 315: 238-241.
- Gascon C., Lovejoy T.E., Bierregaard R.O., Malcolm J.R., Stouffer P.C., Vasconcelos H.L., Laurance W.F., Zimmerman B., Tocher M. and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91: 223-229.
- Gilles, C. S. and C. C. St. Clair. 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences USA* 105:19774-19779.
- Gobeil, J. F. and Villard M. A. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98:447-458.
- Google Inc. 2011. Google Earth (Version 6.0.3.2197) [Software]. Available from <http://www.google.com/earth/index.html>.
- Gould, W., C. Alarcón, B. Fevold, M. E. Jiménez, S. Martinuzzi, G. Potts, M. Solórzano, and E. Ventosa. 2007. Puerto Rico Gap Analysis Project – Final Report. USGS, Moscow, ID and USDA Forest Service International Institute of Tropical Forestry, Rio Piedras, PR. 159 pp. and 8 Appendices.

- Grau H.R., Aide T. M., Zimmerman J.K., Thomlinson J.R., Helmer E. and X. Zou. 2003. The ecological consequences of socioeconomic and land-use changes in postagriculture Puerto Rico. *BioScience* 53(12): 1159-1168.
- Gustafson E.J. and R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77: 94-107.
- Hadley A.S. and M.G. Betts. 2009. Tropical deforestation alters hummingbird movement patterns. *Biology Letters* 5: 207-210.
- Hanski, I. 1998. Metapopulation Dynamics. *Nature* 396: 41-49.
- Helmer E.H., Ramos O.R., López T.M., Quiñones M. and W. Diaz. 2002. Mapping forest type and land cover of Puerto Rico, a component of the Caribbean biodiversity hotspot. *Caribbean Journal of Science* 38: 98-114.
- Hines J.E., T. Boulinier, J.D. Nichols, J.R. Sauer and K. Pollock. 1999. COMDYN: software to study the dynamics of animal communities using a capture-recapture approach. *Bird Study* 46: S209-S217.
- Hines, J.E. 2006. PRESENCE2 – Software to estimate patch occupancy and related parameters. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence.html>
- Hodgson P., French K. and R. E. Major. 2007. Avian movement across abrupt ecological edges: Differential responses to housing density in an urban matrix. *Landscape and urban planning* 79:266-272.
- Ibarra-Macias A., Robinson W.D. and M.S. Gaines. 2011. Forest corridors facilitate movement of tropical forest birds after experimental translocations in a

- fragmented Neotropical landscape in Mexico. *Journal of Tropical Ecology* 27: 547-556.
- Keitt T.H. and H.E. Stanley. 1998. Dynamics of North American breeding bird populations. *Nature* 393: 257-260.
- Kennedy C.M. and P.P. Marra. 2010. Matrix mediates avian movements in tropical forested landscapes: inference from experimental translocations. *Biological Conservation* 143: 2136-2145.
- Kennedy C.M., E.H. Campbell Grant, M.C. Neel, W.F. Fagan and P.P. Marra. 2011. Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores. *Ecological Applications* 21(5): 1837-1850.
- Lambin E.F., Geist H.J. and E. Lepers. 2003. Dynamics of land use and land-cover change in tropical regions. *Annual Review of Environmental Research* 28: 205-241.
- Leider A. K. and N. M. Haddad. 2010. Natural, not urban, barriers define population structure for a coastal endemic butterfly. *Conservation Genetics* 11: 2311-2320.
- López T.d.M., Aide T.M. and J.R. Thomlinson. 2001. Urban expansion and the loss of prime agricultural lands in Puerto Rico. *Ambio* 30: 49-54.
- Lugo A.E. and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190: 145-161.
- Lugo A.E., Molina S., Scatena F., Vélez L.L. 1996. A fifty-three year record of land use change in the Guánica forest biosphere reserve and its vicinity. Río Piedras, Puerto Rico. International institute of tropical forestry.

- Lugo A.E., T.A. Carlo and J.M. Wunderle Jr. 2012. Natural mixing of species: novel plant-animal communities on Caribbean islands. *Animal Conservation* 15: 233-241.
- Lugo, A. E., T. A. Carlo, and J. M. Wunderle, Jr. 2012. Natural mixing of species: novel plant-animal communities on Caribbean Islands. *Animal Conservation* 15:233-241.
- MacArthur R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press. Princeton, New Jersey, USA.
- MacKenzie D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey and J.E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press. Burlington, Massachusetts, USA.
- MacKenzie D.I., J.D. Nichols, M.E. Seamans and R.J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90(3): 823-835.
- McKay, W.D. 1980. The influence of agriculture on avian communities near Villavicencio, Colombia. *Wilson Bulletin* 92(3): 381-389.
- Moore R.P., Robinson W.D., Lovette I.J. and T.R. Robinson. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11: 960-968.
- Nichols J.D., M.D. Koneff, P.J. Heglund, M.G. Knutson, M.E. Seamans, J.E. Lyons, J.M. Morton, M.T. Jones, G.S. Boomer and B.K. Williams. 2011. Climate change, uncertainty, and natural resource management. *Journal of Wildlife Management* 75(1): 6-18.

- Pérez-Rivera, R.A. 1986. Parasitism by the Shiny Cowbird in the interior parts of Puerto Rico. *Journal of Field Ornithology* 57: 99-104.
- Pérez-Rivera, R.A. 1994. Feeding ecology of the Puerto Rican Bullfinch (*Loxigilla portoricensis*) in the Carite and Guánica Forests. *Caribbean Journal of Science* 30 (3-4): 242-249.
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of wildlife management* 46: 757-760.
- Post W., T.K. Nakamura and A. Cruz. 1990. Patterns of Shiny Cowbird parasitism in St. Lucia and southwestern Puerto Rico. *The Condor* 92: 461-469.
- Prevedello, J.A. and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* 19: 1205-1223.
- Raffaele H.A. et al. 1998. A guide to the birds of the West Indies. Princeton University Press. New Jersey, USA.
- Ricklefs R. and E. Bermingham. 2008. The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactionss of the Royal Society B: Biological Sciences* 363 (1502): 2393-2413.
- Ricklefs R.E. and G.W. Cox. 1978. Stage of taxon cycle, habitat distribution and population density in the avifauna of the West Indies. *American Naturalist* 112: 875-895.
- Ries L. and T.D. Sisk. 2004. A predictive model of edge effects. *Ecology* 85: 2917-2926.

- Robertson O.J. and J.Q. Radford. 2009. Gap-crossing decisions of forest birds in a fragmented landscape. *Austral Ecology* 34: 435-446.
- Robinson S.K., Thompson III F.R., Donovan T.M., Whitehead D.R. and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987-1990.
- Saunders D.A., Hobbs R.J. and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18-32.
- Scott, T.A. 1993. Initial effects of housing construction on woodland birds along the wildland urban interface. In: Keeley J.E. (Ed.), *Interface between ecology and land development in California*. Southern California Academy of Sciences, Los Angeles. pp. 181-187.
- Suarez-Rubio M. and J.R. Thomlinson. Landscape and patch-level factors influence bird communities in an urbanized tropical island. *Biological Conservation* 142: 1311-1321.
- Sued M. 2003. Plan estratégico para la protección de comunidades y sistemas naturales de Caguana y Santa Rosa, Utuado. Master's thesis. School of Planning, University of Puerto Rico, Río Piedras.
- Szacki, J. 1999. Spatially structured populations: How much do they match the classic metapopulation concept? *Landscape Ecology* 14: 369-379.
- Terborgh J. and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. *The Auk* 90: 759-779.

- U.S. Bureau of Census. Data of population density from the United States Bureau of Census, selected years: 1900 to 1994. U.S. Department of Commerce, Washington D.C. USA.
- Urbanová, T. 2009. How to support avian diversity in an urban landscape: A bibliography. *Journal of Planning Literature* 24(2): 123-136.
- Vázquez-Plass E.O. and J.M. Wunderle Jr. 2012. Avian distribution along a gradient of urbanization in northeastern Puerto Rico. *Ecological Bulletins* 54: *In press*.
- Watling J.I. and M.A. Donnelly. 2007. Multivariate correlates of extinction proneness in a naturally fragmented landscape. *Diversity and Distributions* 13: 372-378.
- Watling J.I., A.J. Nowakowski, M.A. Donnelly and J.L. Orrock. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography* 20: 209-217.
- White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation for populations of marked animals. *Bird Study Supplement* 46:120-138.
- Wiewel, A.N. 2011. Breeding-season biology of the Puerto Rican Bullfinch (*Loxigilla portoricensis*). Master's Thesis. Iowa State University.
- Wiley J. and J.M. Wunderle Jr. 1993. The effects of hurricanes on birds, with special reference to the Caribbean islands. *Bird Conservation* 3: 319-349.
- Wiley, J. 1985. Shiny Cowbird parasitism in two avian communities in Puerto Rico. *The Condor* 87: 165-176.
- Woodworth, B. L, J. Faaborg, and W. J. Arendt. (1998). Breeding and Natal Dispersal in the Puerto Rican Vireo. *Journal of Field Ornithology* 69: 1, 1-7.

Woodworth, B.L. 1997. Brood parasitism, nest predation and season-long reproductive success of a tropical island endemic. *The Condor* 99: 605-621.

Table 1.1: List of species detected at survey stations in three habitat matrices and a 300-1500 m band within the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). “x” represents at least one detection during any of the 5 seasons of the study.

Species Name	Agriculture	Urban	Forest	Reserve
Adelaide's Warbler	x	x	x	x
African Collared Dove	x	x	x	x
American Kestrel	x	x	x	x
Antillean Euphonia	x	x	x	x
Antillean Mango	x	x	x	x
Bananaquit	x	x	x	x
Black-Faced Grassquit	x	x	x	x
Bronze Mannikin	x	x		x
Black-Whiskered Vireo	x	x	x	x
Cattle Egret	x	x	x	x
Caribbean Elaenia	x	x	x	x
Cave Swallow	x	x		x
Common Ground Dove	x	x	x	x
Greater Antillean Grackle	x	x	x	x
Gray Kingbird	x	x	x	x
Great Egret	x		x	x
Grasshopper Sparrow	x	x		x
House Sparrow	x	x	x	x
Indian Silverbill	x			
Key West Quail-Dove	x	x	x	x
Lesser Antillean Peewee	x	x		x
Loggerhead Kingbird	x	x	x	x
Mangrove Cuckoo	x	x		x
Mourning Dove	x	x	x	x

Table 1.1: (Continued)

Species Name	Agriculture	Urban	Forest	Reserve
Northern Mockingbird	x	x	x	x
Nutmeg Mannikin	x	x		x
Orange-Cheeked Waxbill	x	x	x	x
Orange Bishop	x	x		x
Pearly-Eyed Thrasher	x	x	x	x
Puerto Rican Emerald	x	x	x	x
Orange Bishop	x	x		x
Pearly-Eyed Thrasher	x	x	x	x
Puerto Rican Emerald	x	x	x	x
Puerto Rican Flycatcher	x	x	x	x
Puerto Rican Lizard Cuckoo	x	x	x	x
Puerto Rican Oriole	x	x	x	x
Puerto Rican Spindalis	x	x	x	x
Puerto Rican Tody	x	x	x	x
Puerto Rican Vireo	x	x	x	x
Puerto Rican Woodpecker	x	x	x	x
Pin-Tailed Whydah	x	x	x	x
Puerto Rican Bullfinch	x	x	x	x
Red-Legged Thrush	x	x	x	x
Rock Pigeon	x	x		x
Red-Tailed Hawk	x	x	x	x
Ruddy Quail-Dove	x		x	x
Smooth-Billed Ani	x	x	x	x
Shiny-Headed Cowbird	x	x	x	x
Scaly-Naped Pigeon	x	x	x	x
Troupial	x	x	x	x
White-Winged Dove	x	x	x	x
Yellow-Faced Grassquit	x	x	x	x
Zenaida Dove	x	x	x	x

Table 1.2: Model selection for Puerto Rican *Spindalis* initial occupancy ($\psi_{\text{hat}}\psi$), colonization ($\gamma_{\text{hat}}\gamma$), extinction ($\varepsilon_{\text{hat}}\varepsilon$) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time $t+1$, given that it was absent at t . ε represents the probability of a species being absent at time $t+1$, given that it was present at t . p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F + E), γ (DP), ε (FAI*), p (S + Slope)	1142.31	0	0.6979	1	13	1116.31
ψ (F + E), γ (F + E), ε (FAI), p (S + Slope)	1144.97	2.66	0.1846	0.2645	14	1116.97
ψ (F + E), γ (DP), ε (Fcov), p (S + Slope)	1148.37	6.06	0.0337	0.0483	13	1122.37
ψ (F + E), γ (.), ε (FAI), p (S + Slope)	1148.77	6.46	0.0276	0.0396	12	1124.77
ψ (F + E), γ (DP), ε (.), p (S + Slope)	1149.49	7.18	0.0193	0.0276	12	1125.49
ψ (F + E), γ (F + S), ε (FAIadj), p (S + Slope)	1150.04	7.73	0.0146	0.021	14	1122.04
ψ (F + E), γ (F + S), ε (Fcov), p (S + Slope)	1151.03	8.72	0.0089	0.0128	14	1123.03
ψ (F + E), γ (DP), ε (PS), p (S + Slope)	1151.43	9.12	0.0073	0.0105	13	1125.43
ψ (F + E), γ (F + S), ε (.), p (S + Slope)	1153.35	11.04	0.0028	0.004	13	1127.35
ψ (F + E), γ (F + S), ε (PS), p (S + Slope)	1155.25	12.94	0.0011	0.0015	14	1127.25
ψ (F + E), γ (.), ε (FAIad), p (S+Slope)	1155.82	13.51	0.0008	0.0012	12	1131.82

Table 1.2: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F + E), γ (.), ε (.), p (S + Slope)	1156.73	14.42	0.0005	0.0007	11	1134.73
ψ (F + E), γ (.), ε (Fcov), p (S + Slope)	1157.48	15.17	0.0004	0.0005	12	1133.48
ψ (F + E), γ (DF), ε (.), p (S + Slope)	1158.28	15.97	0.0002	0.0003	12	1134.28
ψ (F + E), γ (.), ε (PS), p (S + Slope)	1158.62	16.31	0.0002	0.0003	12	1134.62
ψ , γ (.), ε (.), p (S + Slope)	1161.5	19.19	0	0.0001	9	1143.5
ψ , γ (.), ε (.), p (S)	1168.27	25.96	0	0	8	1152.27
ψ , γ (.), ε (.), p (S + CAHT)	1169.38	27.07	0	0	9	1151.38
ψ , γ (.), ε (.), p (S + CACOV)	1169.96	27.65	0	0	9	1151.96
ψ , γ (.), ε (.), p (S + UC)	1170.07	27.76	0	0	9	1152.07
ψ , γ (t), ε (t), p (S + Slope)	1170.76	28.45	0	0	15	1140.76
ψ , γ (t), ε (t), p (S)	1176.38	34.07	0	0	14	1148.38
ψ , γ (.), ε (.), p (.)	1178.26	35.95	0	0	4	1170.26

Table 1.3: Model selection for Puerto Rican Woodpecker initial occupancy ($\psi_{\text{hat}}\psi$), colonization ($\gamma_{\text{hat}}\gamma$), extinction ($\varepsilon_{\text{hat}}\varepsilon$) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time $t+1$, given that it was absent at t . ε represents the probability of a species being absent at time $t+1$, given that it was present at t . p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+A+U), γ (DP), ε (FAI*), p (S+CACOV)	1286.93	0	0.6517	1	14	1258.93
ψ (F+A+U), γ (.), ε (FAI), p (S+CACOV)	1290.2	3.27	0.127	0.195	13	1264.2
ψ (F+A+U), γ (t+DP), ε (FAI), p (S+CACOV)	1292.22	5.29	0.0463	0.071	17	1258.22
ψ (F+A+U), γ (DP), ε (t+FAI), p (S+CACOV)	1292.47	5.54	0.0408	0.0627	17	1258.47
ψ (F+A+U), γ (DP), ε (Fcov), p (S+CACOV)	1293.32	6.39	0.0267	0.041	14	1265.32
ψ (F+A+U), γ (DP), ε (F+A+U), p (S+CACOV)	1293.89	6.96	0.0201	0.0308	16	1261.89
ψ (F+A+U), γ (DP), ε (F+A+U+PS), p (S+CACOV)	1294.16	7.23	0.0175	0.0269	17	1260.16
ψ (F+A+U), γ (.), ε (F+A+U), p (S+CACOV)	1294.6	7.67	0.0141	0.0216	15	1264.6
ψ (F+A+U), γ (.), ε (F+A+U+PS), p (S+CACOV)	1294.86	7.93	0.0124	0.019	16	1262.86

Table 1.3: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F + A + U), γ (DP), ε (F + A + U + Fcov), p (S + CACOV)	1295.09	8.16	0.011	0.0169	17	1261.09
ψ (F + A + U), γ (.), ε (Fcov), p (S + CACOV)	1295.42	8.49	0.0093	0.0143	13	1269.42
ψ (F + A + U), γ (.), ε (F + A + U + Fcov), p (S + CACOV)	1295.67	8.74	0.0082	0.0127	16	1263.67
ψ (F + A + U), γ (DP), ε (PS), p (S + CACOV)	1296.17	9.24	0.0064	0.0099	14	1268.17
ψ (F + A + U), γ (DP), ε (.), p (S + CACOV)	1296.6	9.67	0.0052	0.0079	13	1270.6
ψ (F + A + U), γ (.), ε (PS), p (S + CACOV)	1299.04	12.11	0.0015	0.0023	13	1273.04
ψ (F + A + U), γ (.), ε (.), p (S + CACOV)	1299.51	12.58	0.0012	0.0019	12	1275.51
ψ (F + A + U), γ (DF), ε (.), p (S + CACOV)	1301.5	14.57	0.0004	0.0007	13	1275.5
ψ , γ (.), ε (.), p (S + CACOV)	1344.68	57.75	0	0	9	1326.68
ψ , γ (.), ε (.), p (S + CAHT)	1355.16	68.23	0	0	9	1337.16
ψ , γ (t), ε (t), p (S + CACOV)	1355.43	68.5	0	0	15	1325.43
ψ , γ (.), ε (.), p (S + Slope)	1360.55	73.62	0	0	9	1342.55
ψ , γ (.), ε (.), p (S)	1371.02	84.09	0	0	8	1355.02
ψ , γ (.), ε (.), p (S + UC)	1372.63	85.7	0	0	9	1354.63
ψ , γ (.), ε (.), p (.)	1380.31	93.38	0	0	4	1372.31
ψ , γ (t), ε (t), p (S)	1382.23	95.3	0	0	14	1354.23

Table 1.4: Beta (SE) estimates for colonization (γ) and extinction (ϵ) probability based on multi-season occupancy models and avian surveys conducted in three habitat matrices and within a 300-1500 m band within of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The influence of covariates (strong or weak) is indicated. Strong influence means that 95% CIs for Beta estimates did not overlap zero. Model covariates are defined in the text and Appendix D.

Species	Colonization	Extinction	Beta Estimate	Std. Error	Lower CI	Upper CI	Influence
Antillean Euphonia	DP	-	-0.94	0.56	-2.04	0.17	Weak
	-	FAI Adj.	-2	0.64	-3.25	-0.76	Strong
Puerto Rican Spindalis	DP	-	-1.97	1.43	-4.77	0.82	Weak
	-	FAI	-1.07	0.45	-1.94	-0.19	Strong
Puerto Rican Bullfinch	For	-	-1.07	1.01	-3.04	0.9	Weak
	Reserves	-	-0.81	1.8	-4.33	2.71	Weak
	DF	-	-1.19	0.53	-2.22	-0.15	Strong
	-	For	-1.56	0.66	-2.85	-0.26	Strong
	-	Reserves	-3.58	0.9	-5.34	-1.82	Strong
	-	-	-	-	-	-	-
Black-Faced Grassquit	For	-	-2.41	0.83	-4.04	-0.79	Strong
	Ag	-	-1.61	0.83	-3.24	0.02	Weak
	Urb	-	-1.4	1	-3.35	0.56	Weak
	-	For + Herb Cov	0.82	0.22	0.39	1.26	Strong
Caribbean Elaenia	DP	-	-1.84	2.47	-6.69	3	Weak
	-	Constant	N/A	N/A	N/A	N/A	N/A

Table 1.4: (Continued)

Species	Colonization	Extinction	Beta Estimate	Std. Error	Lower CI	Upper CI	Influence
Puerto Rican Vireo	DF	-	-0.85	0.56	-1.94	0.24	Weak
	-	Fcov	-1.18	0.41	-1.98	-0.39	Strong
Puerto Rican Woodpecker	DP	-	-1.15	0.79	-2.7	0.4	Weak
	-	FAI	-1.3	0.47	-2.21	-0.38	Strong
Shiny Cowbird	Constant	-	N/A	N/A	N/A	N/A	N/A
	-	Constant	N/A	N/A	N/A	N/A	N/A

Table 1.5: Model selection for Antillean Euphonia initial occupancy (ψ_{hat}), colonization (γ_{hat}), extinction (ε_{hat}) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time $t+1$, given that it was absent at t . ε represents the probability of a species being absent at time $t+1$, given that it was present at t . p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+A+U), γ (DP), ε (FAIad*), p (S+Slope)	961.08	0	0.4512	1	14	933.08
ψ (F+A+U), γ (F+A+U), ε (FAIad), p (S+Slope)	962.17	1.09	0.2616	0.5798	16	930.17
ψ (F+A+U), γ (F+A+U+DP), ε (FAIad), p (S+Slope)	963.38	2.3	0.1429	0.3166	17	929.38
ψ (F+A+U), γ (.), ε (FAIad), p (S+Slope)	964.15	3.07	0.0972	0.2155	13	938.15
ψ (F+A+U), γ (.), ε (FAI), p (S+Slope)	967.86	6.78	0.0152	0.0337	13	941.86
ψ (F+A+U), γ (F+A+U+DP), ε (.), p (S+Slope)	968.22	7.14	0.0127	0.0282	16	936.22
ψ (F+A+U), γ (.), ε (FCov), p (S+Slope)	969.07	7.99	0.0083	0.0184	13	943.07
ψ (F+A+U), γ (DP), ε (.), p (S+Slope)	969.95	8.87	0.0053	0.0119	13	943.95
ψ (F+A+U), γ (DP), ε (PS), p (S+Slope)	971.54	10.46	0.0024	0.0054	14	943.54
ψ (F+A+U), γ (DF), ε (.), p (S+Slope)	972.34	11.26	0.0016	0.0036	13	946.34
ψ (F+A+U), γ (.), ε (.), p (S+Slope)	973.1	12.02	0.0011	0.0025	12	949.1

ψ (F+A+U), γ (.), ε (PS), p (S+Slope) 974.86 13.78 0.0005 0.001 13 948.86

Table 1.5: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ, γ (.), ε (.), p (S+Slope)	1009.65	48.57	0	0	9	991.65
ψ, γ (t), ε (t), p (S+Slope)	1014.64	53.56	0	0	15	984.64
ψ, γ (.), ε (.), p (S+CAHT)	1014.67	53.59	0	0	9	996.67
ψ, γ (.), ε (.), p (S+CACOV)	1014.99	53.91	0	0	9	996.99
ψ, γ (.), ε (.), p (S)	1020.85	59.77	0	0	8	1004.85
ψ, γ (.), ε (.), p (S+UC)	1022.39	61.31	0	0	9	1004.39
ψ, γ (t), ε (t), p (S)	1025.63	64.55	0	0	14	997.63
ψ, γ (.), ε (.), p (.)	1030.27	69.19	0	0	4	1022.27

Table 1.6: Model selection for Black-faced Grassquit initial occupancy (ψ_{hat}), colonization (γ_{hat}), extinction (ε_{hat}) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time t+1, given that it was absent at t. ε represents the probability of a species being absent at time t+1, given that it was present at t. p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+A+U), γ (F*+A+U), ε (Fcov+HCov*), p (S+CACOV)	2184.48	0	0.5551	1	16	2152.48
ψ (F+A+U), γ (F+A+U+DP), ε (FH), p (S+CACOV)	2185.54	1.06	0.3268	0.5886	17	2151.54
ψ (F+A+U), γ (.), ε (FH), p (S+CACOV)	2188.25	3.77	0.0843	0.1518	13	2162.25
ψ (F+A+U), γ (DP), ε (FH), p (S+CACOV)	2190.09	5.61	0.0336	0.0605	14	2162.09
ψ , γ (.), ε (.), p (S+CACOV)	2200.67	16.19	0.0002	0.0003	9	2182.67
ψ , γ (t), ε (t), p (S+CACOV)	2203.7	19.22	0	0.0001	15	2173.7
ψ (F+A+U), γ (.), ε (PS), p (S+CACOV)	2205.51	21.03	0	0	13	2179.51
ψ (F+A+U), γ (DP), ε (.), p (S+CACOV)	2205.6	21.12	0	0	13	2179.6
ψ (F+A+U), γ (DP), ε (PS), p (S+CACOV)	2207.47	22.99	0	0	14	2179.47
ψ , γ (t), ε (t), p (S+CAHT)	2226.79	42.31	0	0	15	2196.79
ψ , γ (t), ε (t), p (S+Slope)	2234.4	49.92	0	0	15	2204.4
ψ , γ (t), ε (t), p (S+UC)	2238.66	54.18	0	0	15	2208.66

Table 1.6: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
$\psi, \gamma(t), \varepsilon(t), p(S)$	2238.68	54.2	0	0	14	2210.68
$\psi, \gamma(\cdot), \varepsilon(\cdot), p(S)$	2241.28	56.8	0	0	8	2225.28
$\psi, \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	2272.27	87.79	0	0	4	2264.27

Table 1.7: Model selection for Shiny Cowbird initial occupancy (ψ_{hat}), colonization (γ_{hat}), extinction (ε_{hat}) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time t+1, given that it was absent at t. ε represents the probability of a species being absent at time t+1, given that it was present at t. p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+A+U), γ (.), ε (.), p (S+CACOV)	733.59	0	0.6331	1	12	709.59
ψ (F+A+U), γ (.), ε (Hcov), p (S+CACOV)	734.69	1.1	0.3653	0.5769	13	708.69
ψ , γ (.), ε (.), p (S+CACOV)	745.93	12.34	0.0013	0.0021	9	727.93
ψ , γ (.), ε (.), p (S+CAHT)	750.18	16.59	0.0002	0.0002	9	732.18
ψ , γ (.), ε (.), p (S+Slope)	751.37	17.78	0.0001	0.0001	9	733.37
ψ , γ (.), ε (.), p (S)	753.5	19.91	0	0	8	737.5
ψ , γ (S), ε (S), p (S+CACOV)	754.14	20.55	0	0	15	724.14
ψ , γ (.), ε (.), p (S+UC)	755.5	21.91	0	0	9	737.5
ψ , γ (S), ε (S), p (S)	760.02	26.43	0	0	14	732.02
ψ , γ (S), ε (S), p (.)	769.87	36.28	0	0	10	749.87
ψ , γ (.), ε (.), p (.)	769.92	36.33	0	0	4	761.92

Table 1.8: Model selection for Puerto Rican Bullfinch initial occupancy (ψ_{hat}), colonization (γ_{hat}), extinction (ε_{hat}) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time t+1, given that it was absent at t. ε represents the probability of a species being absent at time t+1, given that it was present at t. p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+R), γ (F+R+DF*), ε (F*+ R*), p (S+AVGUC)	1248.16	0	0.3754	1	16	1216.16
ψ (F+R), γ (F+R+DF), ε (F+R+FAI), p (S+AVGUC)	1249.1	0.94	0.2346	0.625	17	1215.1
ψ (F+R), γ (F+R+DF), ε (F+R+PS), p (S+AVGUC)	1250.05	1.89	0.1459	0.3887	17	1216.05
ψ (F+R), γ (F+R+DF), ε (F+R+FCov), p (S+AVGUC)	1250.07	1.91	0.1445	0.3848	17	1216.07
ψ (F+R), γ (F+R), ε (F+R+FAI), p (S+AVGUC)	1253.42	5.26	0.0271	0.0721	16	1221.42
ψ (F+R), γ (F+R+DP), ε (F+R), p (S+AVGUC)	1254.41	6.25	0.0165	0.0439	16	1222.41
ψ (F+R), γ (F+R), ε (F+R+FCov), p (S+AVGUC)	1254.49	6.33	0.0158	0.0422	16	1222.49
ψ (F+R), γ (F+R), ε (F+R+PS), p (S+AVGUC)	1254.64	6.48	0.0147	0.0392	16	1222.64
ψ (F+R), γ (F+R+DP), ε (F+R+FAI), p (S+AVGUC)	1255.1	6.94	0.0117	0.0311	17	1221.1
ψ (F+R), γ (F+R+DP), ε (F+R+Fcov), p (S+AVGUC)	1256.19	8.03	0.0068	0.018	17	1222.19
ψ (F+R), γ (F+R+DP), ε (F+R+PS), p (S+AVGUC)	1256.33	8.17	0.0063	0.0168	17	1222.33
ψ (F+R), γ (.), ε (FAIad), p (S+AVGUC)	1262.35	14.19	0.0003	0.0008	12	1238.35

Table 1.8: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+R), γ (DP), ε (FAIad), p (S+AVGUC)	1263.56	15.4	0.0002	0.0005	13	1237.56
ψ (F+R), γ (DF), ε (.), p (S+AVGUC)	1265.5	17.34	0.0001	0.0002	12	1241.5
ψ (F+R), γ (F+R+DP), ε (FAIad), p (S+AVGUC)	1266.18	18.02	0	0.0001	15	1236.18
ψ (F+R), γ (.), ε (FCov), p (S+AVGUC)	1266.95	18.79	0	0.0001	12	1242.95
ψ (F+R), γ (.), ε (PS), p (S+AVGUC)	1267.11	18.95	0	0.0001	12	1243.11
ψ (F+R), γ (DP), ε (FCov), p (S+AVGUC)	1267.84	19.68	0	0.0001	13	1241.84
ψ (F+R), γ (DP), ε (PS), p (S+AVGUC)	1268.13	19.97	0	0	13	1242.13
ψ (F+R), γ (.), ε (FAI), p (S+AVGUC)	1270.18	22.02	0	0	12	1246.18
ψ (F+R), γ (.), ε (.), p (S+AVGUC)	1271.9	23.74	0	0	11	1249.9
ψ (F+R), γ (DP), ε (.), p (S+AVGUC)	1272.97	24.81	0	0	12	1248.97
ψ (F+R), γ (t), ε (t), p (S+AVGUC)	1275.52	27.36	0	0	17	1241.52
ψ , γ (.), ε (.), p (S+AVGUC)	1356	107.84	0	0	9	1338
ψ , γ (t), ε (t), p (S+AVGUC)	1359.84	111.68	0	0	15	1329.84
ψ , γ (.), ε (.), p (S+CAHT)	1371.92	123.76	0	0	9	1353.92
ψ , γ (.), ε (.), p (S+Slope)	1372.57	124.41	0	0	9	1354.57
ψ , γ (.), ε (.), p (S)	1373.46	125.3	0	0	8	1357.46
ψ , γ (.), ε (.), p (S+CACOV)	1374.5	126.34	0	0	9	1356.5
ψ , γ (t), ε (t), p (S)	1378.31	130.15	0	0	14	1350.31
ψ , γ (.), ε (.), p (.)	1438.09	189.93	0	0	4	1430.09

Table 1.9: Model selection for Puerto Rican Vireo initial occupancy (ψ_{hat}), colonization (γ_{hat}), extinction (ϵ_{hat}) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time $t+1$, given that it was absent at t . ϵ represents the probability of a species being absent at time $t+1$, given that it was present at t . p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+A+U), γ (DF), ϵ (Fcov*), p (S+UC)	822.11	0	0.3741	1	14	794.11
ψ (F+A+U), γ (.), ϵ (Fcov), p (S+UC)	822.78	0.67	0.2676	0.7153	13	796.78
ψ (F+A+U), γ (DP), ϵ (Fcov), p (S+UC)	823.35	1.24	0.2012	0.5379	14	795.35
ψ (F+A+U), γ (F+A+U+DF), ϵ (Fcov), p (S+UC)	825.77	3.66	0.06	0.1604	17	791.77
ψ (F+A+U), γ (F+A+U), ϵ (Fcov), p (S+UC)	826.14	4.03	0.0499	0.1333	16	794.14
ψ (F+A+U), γ (F+A+U+DP), ϵ (Fcov), p (S+UC)	826.65	4.54	0.0386	0.1033	17	792.65
ψ (F+A+U), γ (DF), ϵ (.), p (S+UC)	831.29	9.18	0.0038	0.0102	13	805.29
ψ (F+A+U), γ (DF), ϵ (PS), p (S+UC)	832.72	10.61	0.0019	0.005	14	804.72
ψ (F+A+U), γ (.), ϵ (.), p (S+UC)	833.87	11.76	0.001	0.0028	12	809.87
ψ (F+A+U), γ (DP), ϵ (.), p (S+UC)	834.3	12.19	0.0008	0.0023	13	808.3

Table 1.9: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F+A+U), γ (.), ε (PS), p (S+UC)	835.18	13.07	0.0005	0.0015	13	809.18
ψ (F+A+U), γ (DP), ε (PS), p (S+UC)	835.71	13.6	0.0004	0.0011	14	807.71
ψ , γ (.), ε (.), p (S+UC)	871.4	49.29	0	0	9	853.4
ψ , γ (t), ε (t), p (S+UC)	874.54	52.43	0	0	15	844.54
ψ , γ (.), ε (.), p (S+CACOV)	877.35	55.24	0	0	9	859.35
ψ , γ (.), ε (.), p (S+CAHT)	879.6	57.49	0	0	9	861.6
ψ , γ (.), ε (.), p (S)	880.22	58.11	0	0	8	864.22
ψ , γ (.), ε (.), p (S+Slope)	881.91	59.8	0	0	9	863.91
ψ , γ (.), ε (.), p (.)	882.84	60.73	0	0	4	874.84
ψ , γ (t), ε (t), p (S)	887.94	65.83	0	0	14	859.94

Table 1.10: Model selection for Caribbean Elaenia initial occupancy (ψ_{hat}), colonization (γ_{hat}), extinction (ϵ_{hat}) and detection (p_{hat}) probabilities based on multi-season occupancy models and avian surveys conducted in three habitat matrices and a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted every season. ψ represents the probability of a site being occupied, given that the species was available for detection. γ represents the probability of a species being present at time $t+1$, given that it was absent at t . ϵ represents the probability of a species being absent at time $t+1$, given that it was present at t . p represents the probability of a species being detected. Model terms and covariates are defined in Appendix D. Models are ranked according to their associated AIC values. Competitive models are those with a $\Delta\text{AIC} \leq 2$. Top model parameters that are strongly influenced by a covariate (95% CIs for Beta estimates did not overlap zero) are identified with an asterisk (*).

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
ψ (F + A + U), γ (DP), ϵ (.), p (UC)	681.75	0	0.2304	1	9	663.75
ψ (F + A + U), γ (.), ϵ (.), p (UC)	681.88	0.13	0.2159	0.9371	8	665.88
ψ (F + A + U), γ (DP), ϵ (PS), p (UC)	683.21	1.46	0.111	0.4819	10	663.21
ψ (F + A + U), γ (DF), ϵ (.), p (UC)	683.37	1.62	0.1025	0.4449	9	665.37
ψ (F + A + U), γ (.), ϵ (PS), p (UC)	683.43	1.68	0.0995	0.4317	9	665.43
ψ (F + A + U), γ (.), ϵ (Fcov), p (UC)	683.66	1.91	0.0887	0.3848	9	665.66
ψ (F + A + U), γ (DP), ϵ (Fcov), p (UC)	683.66	1.91	0.0887	0.3848	10	663.66
ψ (F + A + U), γ (F + A + U + DP), ϵ (.), p (UC)	685.65	3.9	0.0328	0.1423	12	661.65
ψ (F + A + U), γ (F + A + U), ϵ (.), p (UC)	685.79	4.04	0.0306	0.1327	11	663.79
ψ , γ (.), ϵ (.), p (UC)	710.34	28.59	0	0	5	700.34
ψ , γ (.), ϵ (.), p (CAHT)	716.96	35.21	0	0	5	706.96

Table 1.10: (Continued)

Model	AIC	ΔAIC	AIC wgt	Model Likelihood	Parameters	-2*LogLike
$\psi, \gamma(t), \varepsilon(t), p(UC)$	719.11	37.36	0	0	11	697.11
$\psi, \gamma(\cdot), \varepsilon(\cdot), p(\cdot)$	722.1	40.35	0	0	4	714.1
$\psi, \gamma(\cdot), \varepsilon(\cdot), p(\text{Slope})$	723.13	41.38	0	0	5	713.13
$\psi, \gamma(\cdot), \varepsilon(\cdot), p(CACOV)$	724.1	42.35	0	0	5	714.1
$\psi, \gamma(\cdot), \varepsilon(\cdot), p(S)$	729.51	47.76	0	0	8	713.51
$\psi, \gamma(t), \varepsilon(t), p(\cdot)$	733.48	51.73	0	0	10	713.48

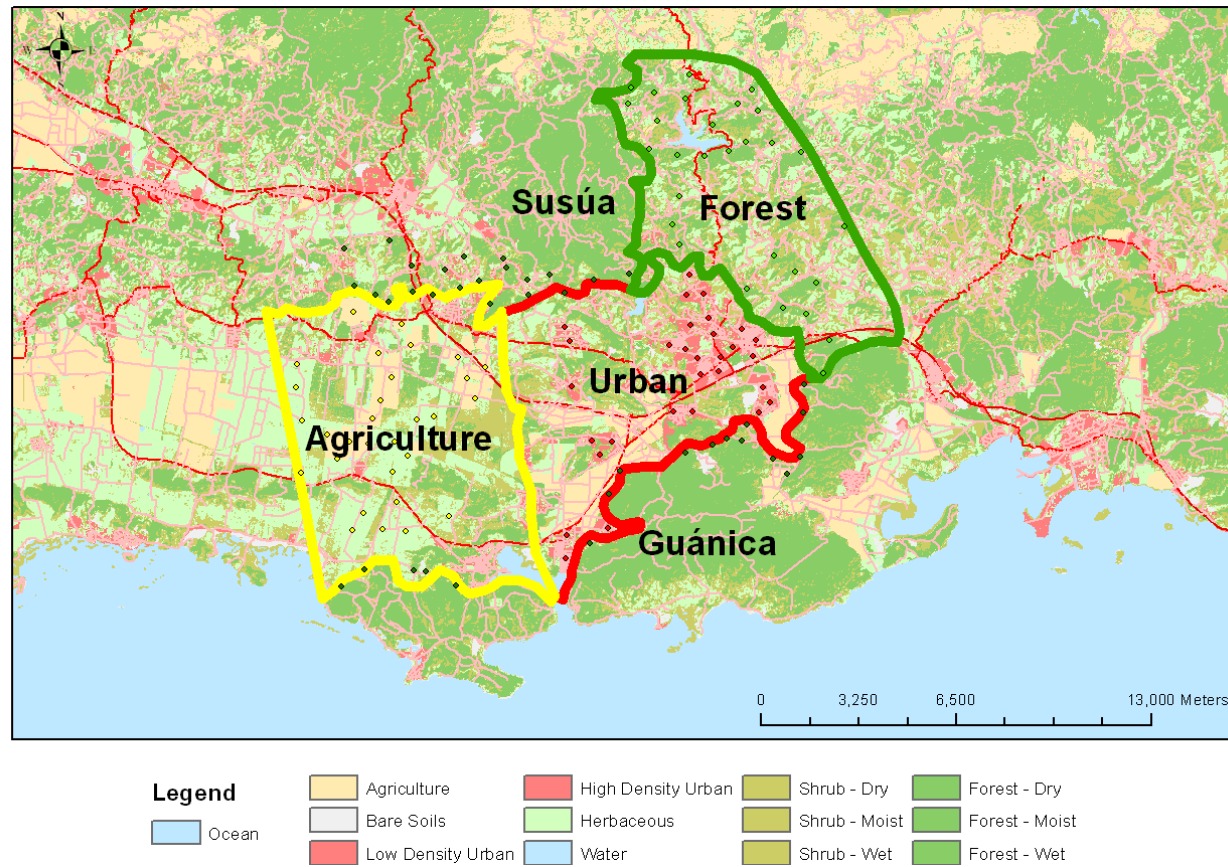


Figure 1.1: Map of the study area showing three habitat matrices (agriculture, urban, forest) and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. The agricultural matrix is delimited in yellow, the urban in red and the forest in green. The map also depicts land cover classes and the location of avian survey stations per matrix.

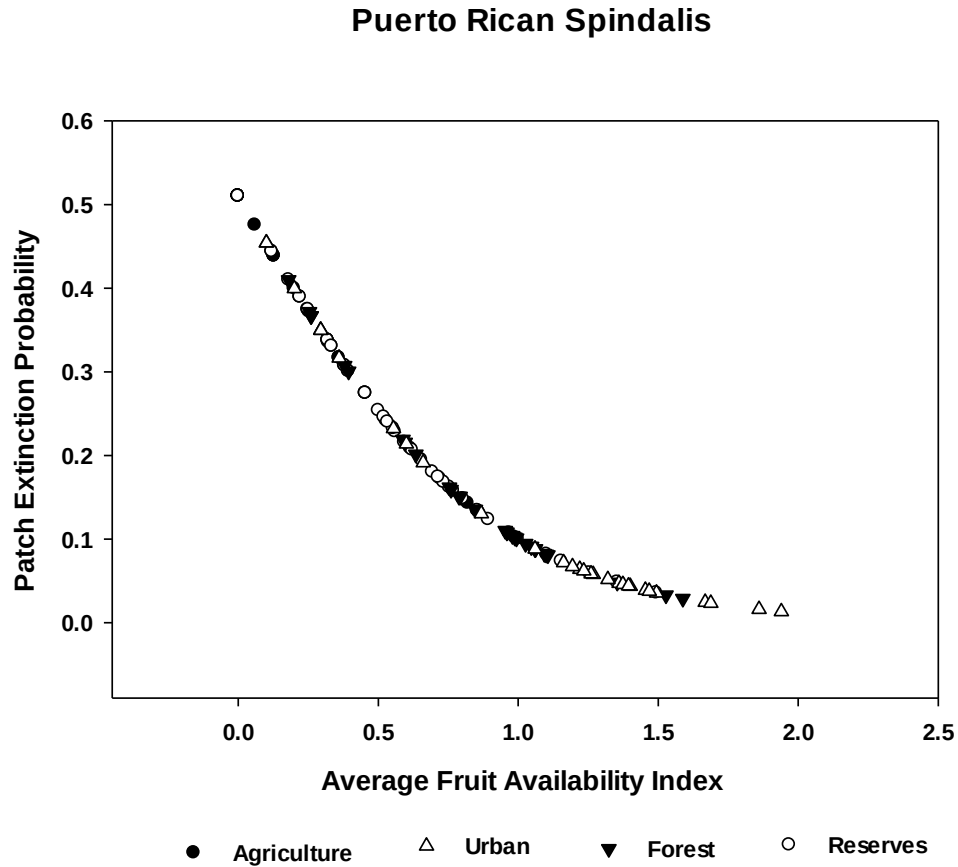


Figure 1.2: Patch extinction probability for the Puerto Rican Spindalis as a function of the average fruit availability index at survey stations (patches) in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

Puerto Rican Woodpecker

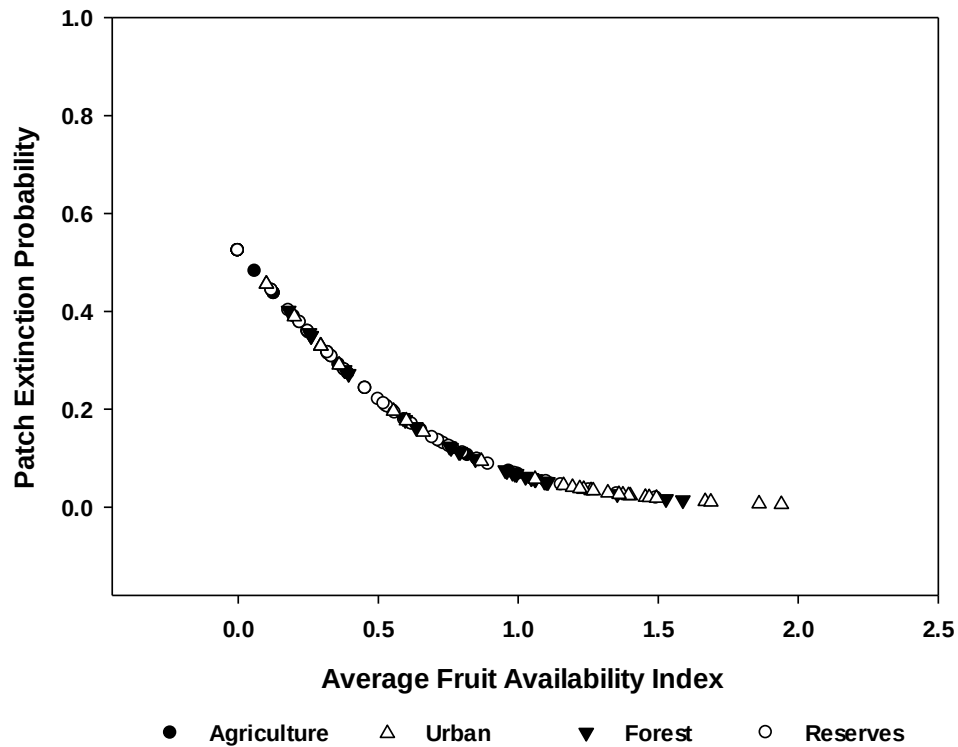


Figure 1.3: Patch extinction probability for the Puerto Rican Woodpecker as a function of the average fruit availability index at survey stations (patches) in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

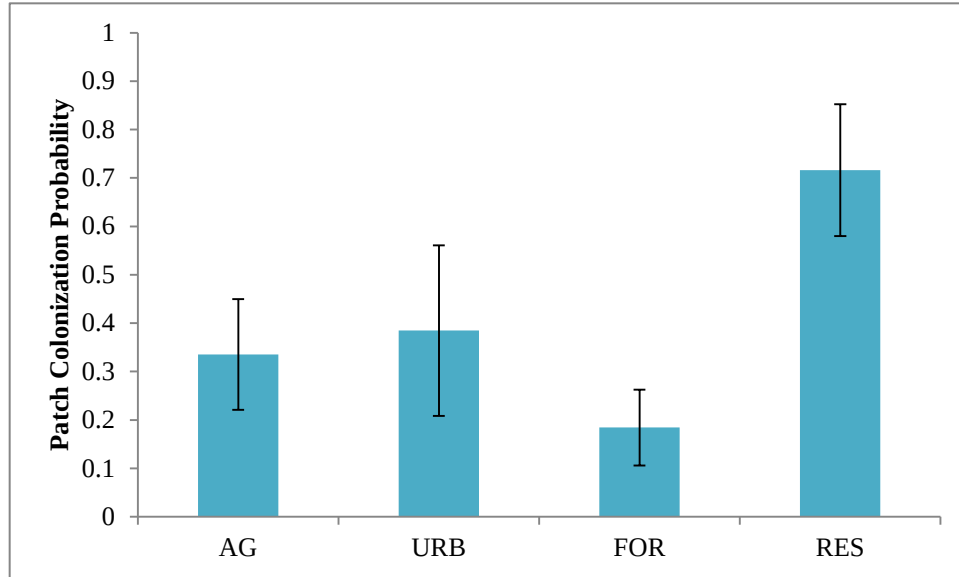


Figure 1.4: Patch colonization probability (SE) for the Black-Faced Grassquit as a function of matrix type, namely, agriculture (AG), urban (URB), forest (FOR) and forest reserves (RES). Matrices were located between the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

Black-faced Grassquit

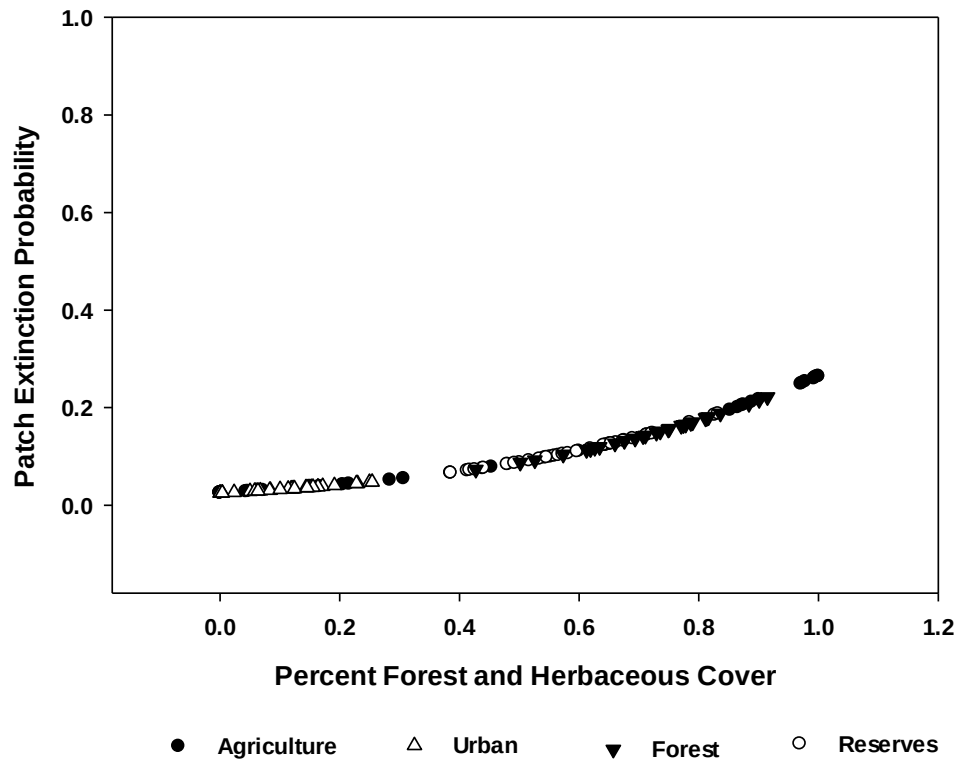


Figure 1.5: Patch extinction probability for the Black-Faced Grassquit as a function of the sum of percent forest and herbaceous cover at survey stations (patches) in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

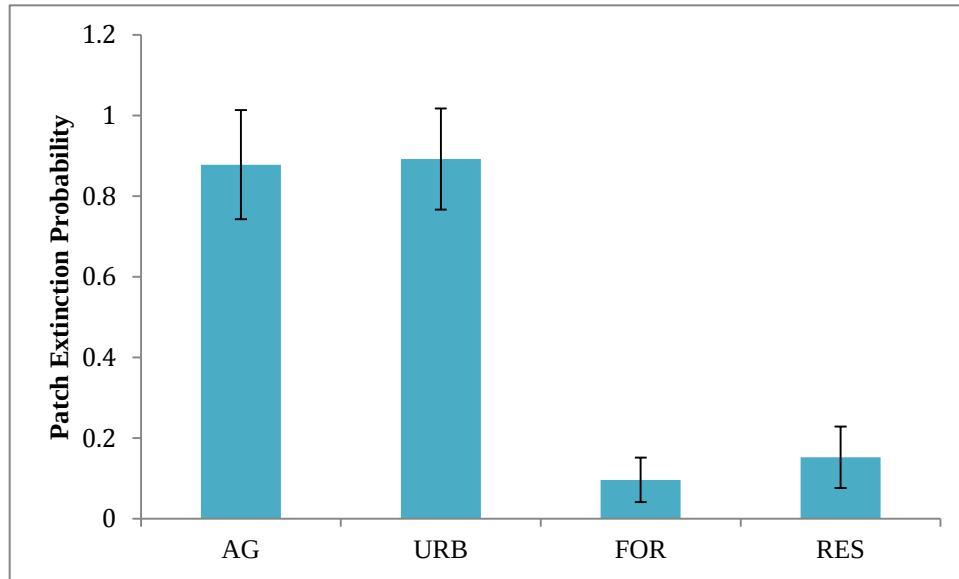


Figure 1.6: Patch extinction probability (SE) for the Antillean Euphonia as a function of matrix type, namely, agriculture (AG), urban (URB), forest (FOR) and forest reserves (RES). Matrices and forest reserves (300-1500 band) were located between Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

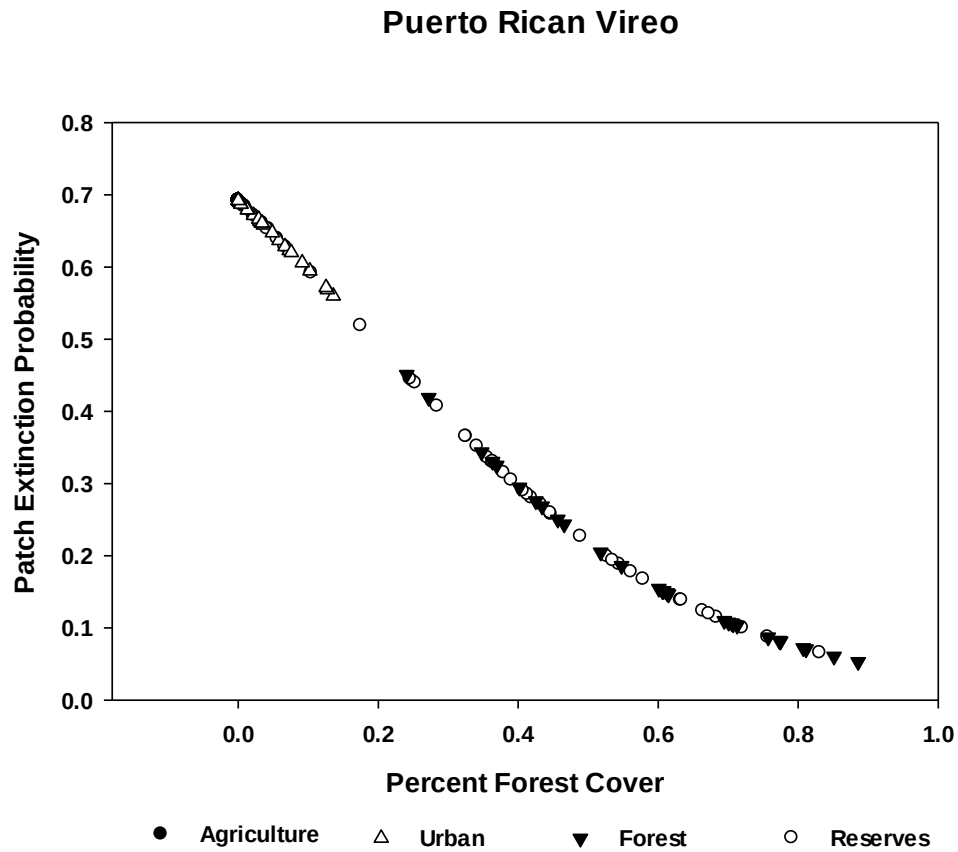


Figure 1.7: Patch extinction probability for the Puerto Rican Vireo as a function of percent forest cover at survey stations (patches) in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

Puerto Rican Bullfinch

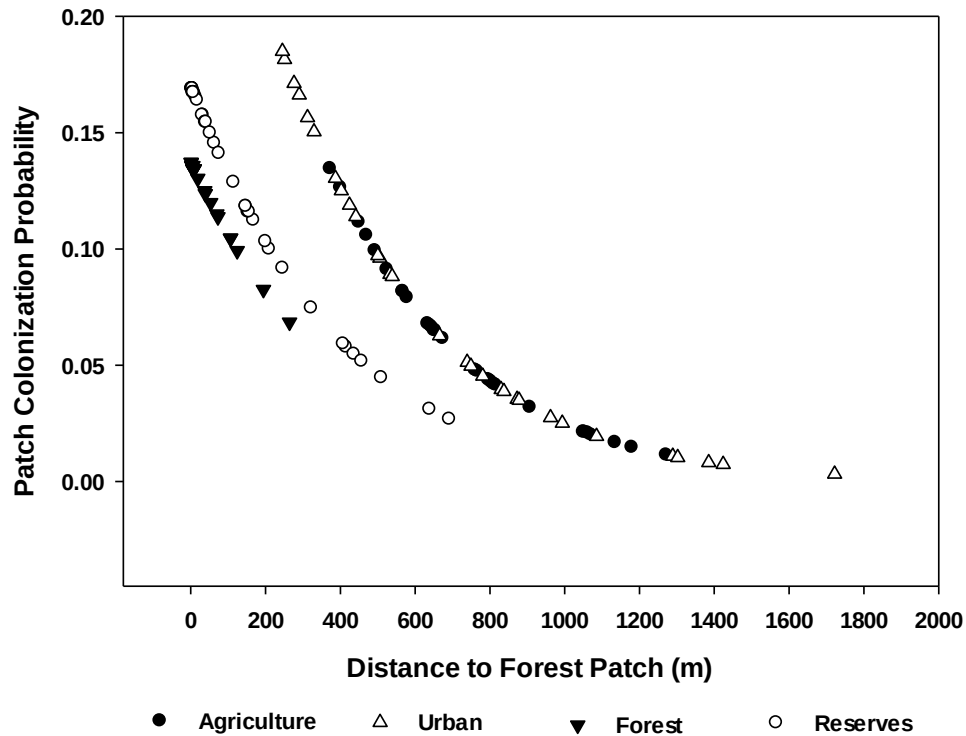


Figure 1.8: Patch colonization probability for the Puerto Rican Bullfinch as a function of percent forest cover at survey stations (patches) in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

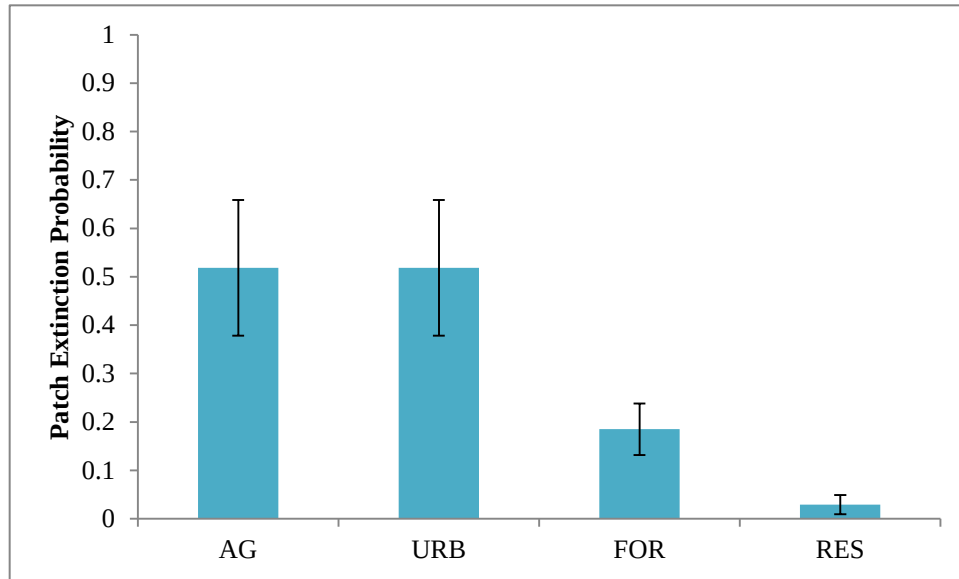


Figure 1.9: Patch extinction probability (SE) for the Puerto Rican Bullfinch as a function of matrix type, namely, agriculture (AG), urban (URB), forest (FOR) and forest reserves (RES). Matrices and forest edge (300-1500 band) were located between Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season.

Antillean Euphonia

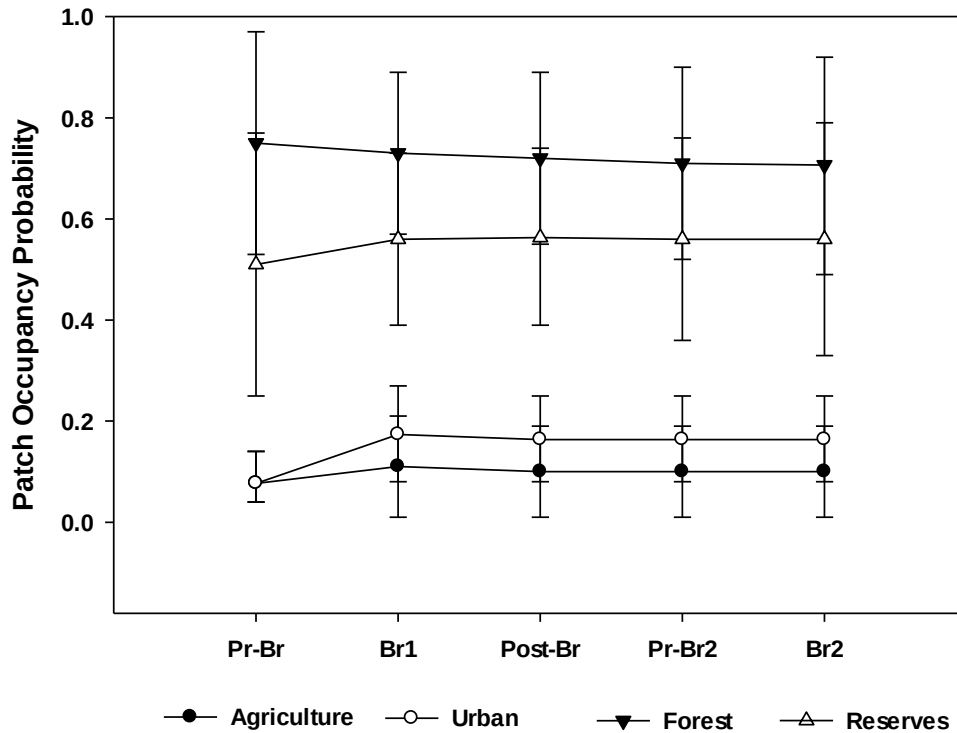


Figure 1.10: Seasonal patch occupancy probability for the Antillean Euphonia in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Puerto Rican Bullfinch

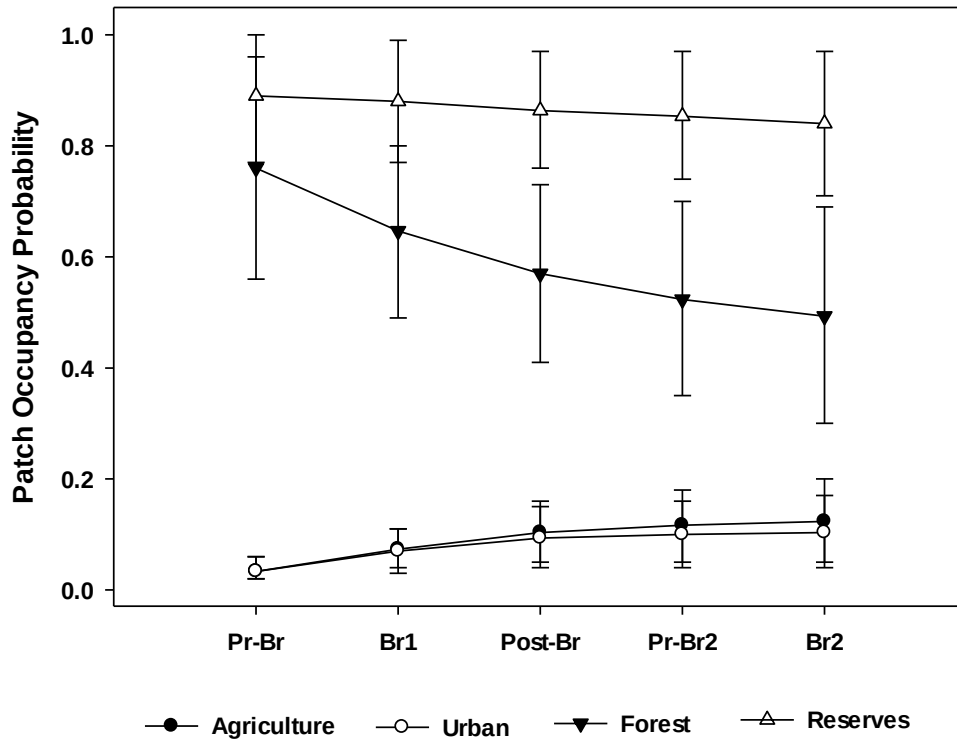


Figure 1.11: Seasonal patch occupancy probability for the Puerto Rican Bullfinch in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Caribbean Elaenia

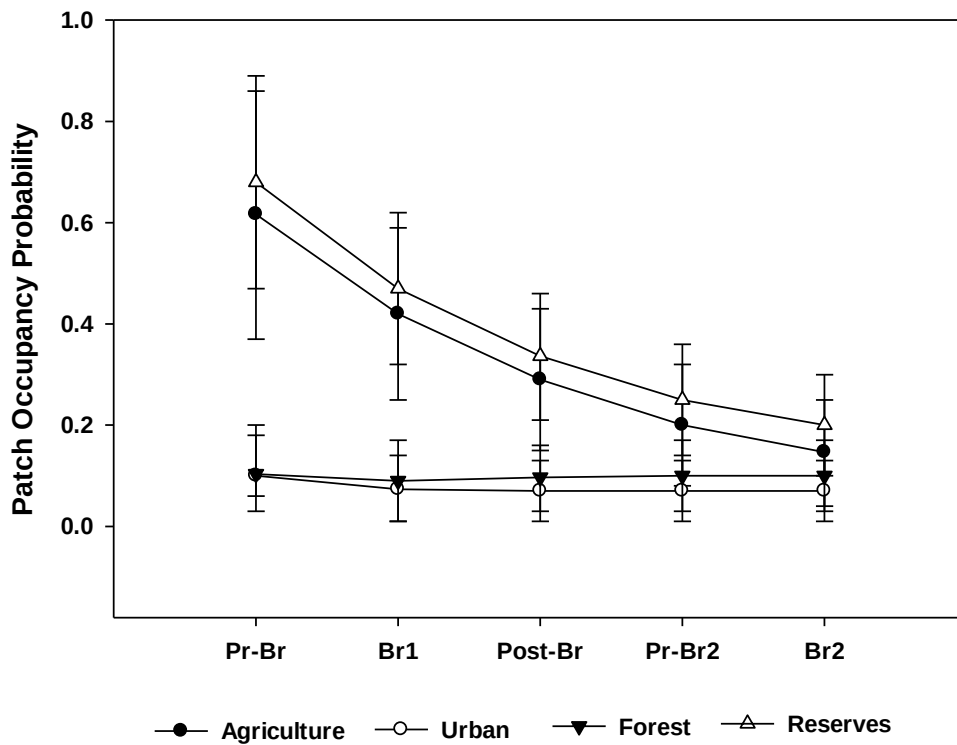


Figure 1.12: Seasonal patch occupancy probability for the Caribbean Elaenia in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Puerto Rican Vireo

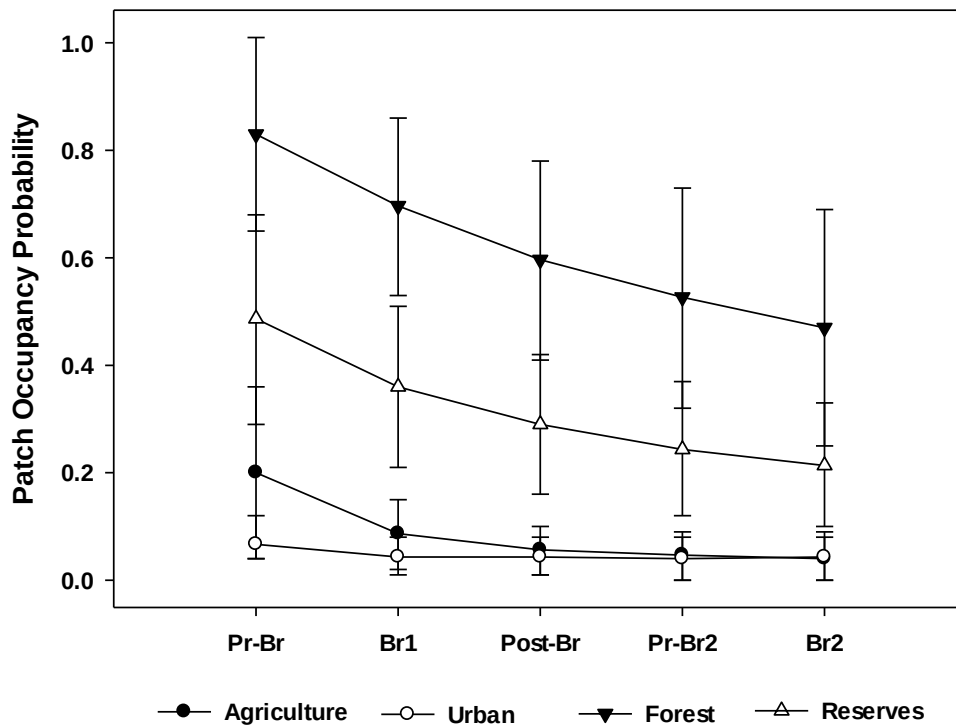


Figure 1.13: Seasonal patch occupancy probability for the Puerto Rican Vireo in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Puerto Rican Woodpecker

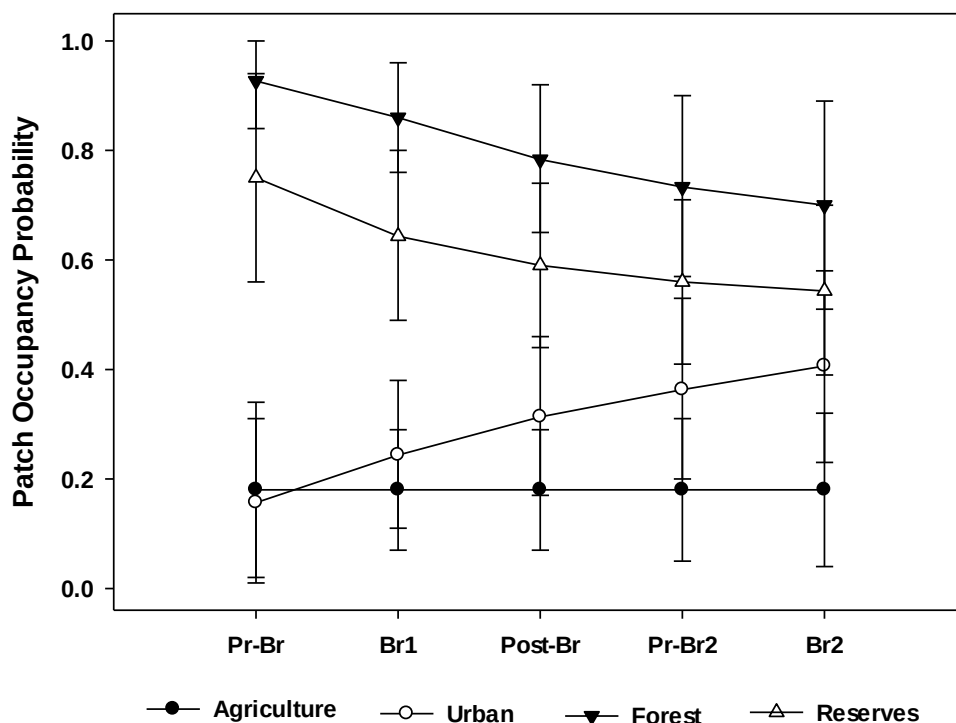


Figure 1.14: Seasonal patch occupancy probability for the Puerto Rican Woodpecker in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Puerto Rican Spindalis

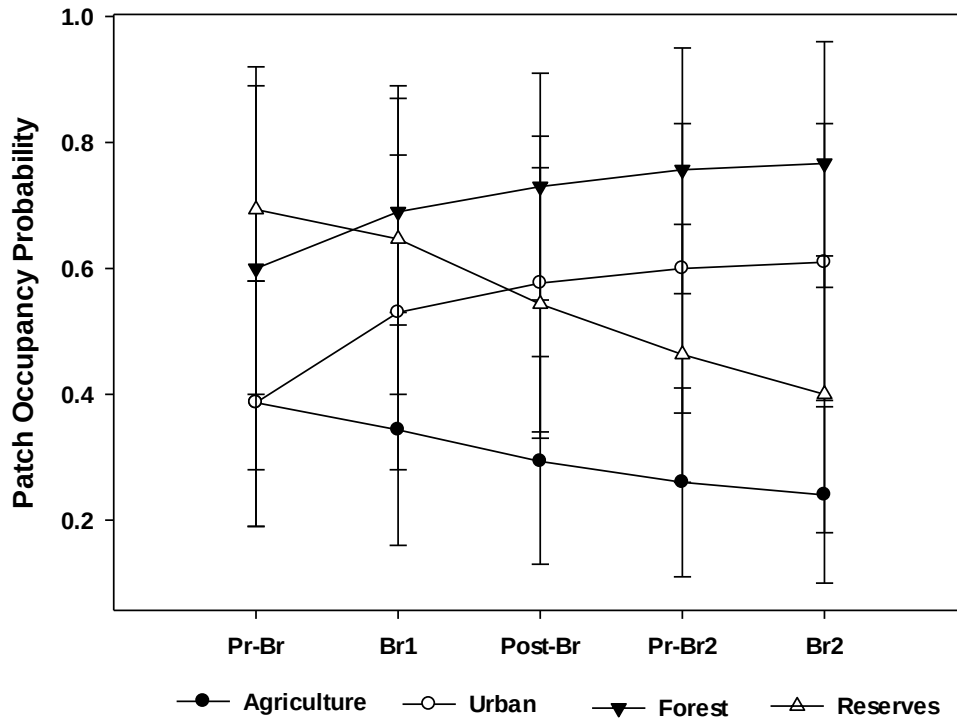


Figure 1.15: Seasonal patch occupancy probability for the Puerto Rican Spindalis in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Shiny Cowbird

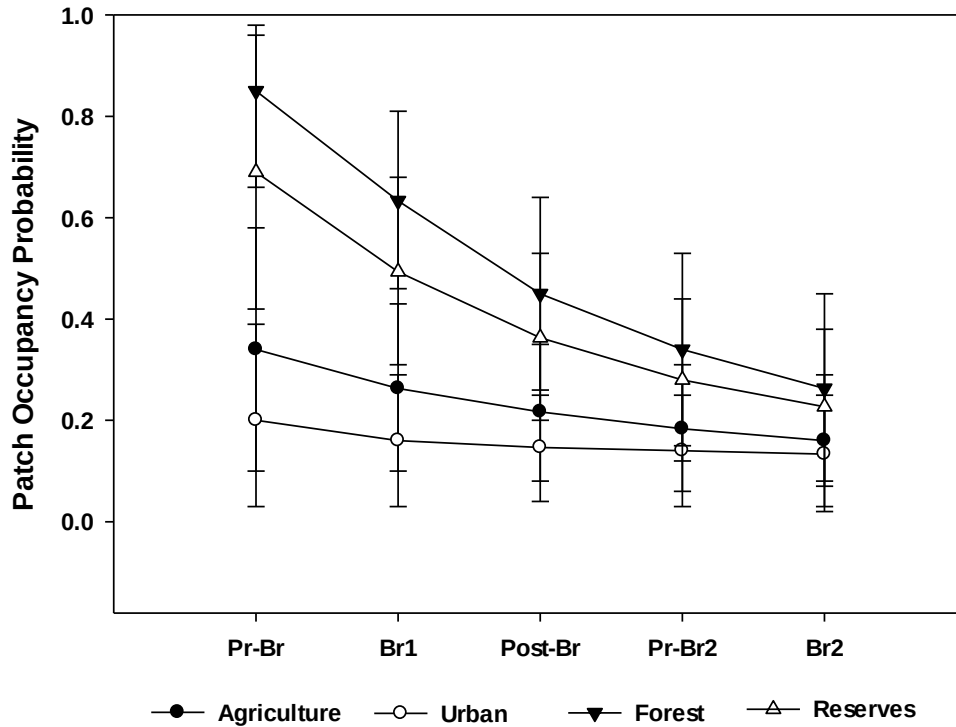


Figure 1.16: Seasonal patch occupancy probability for the Shiny Cowbird in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

Black-faced Grassquit

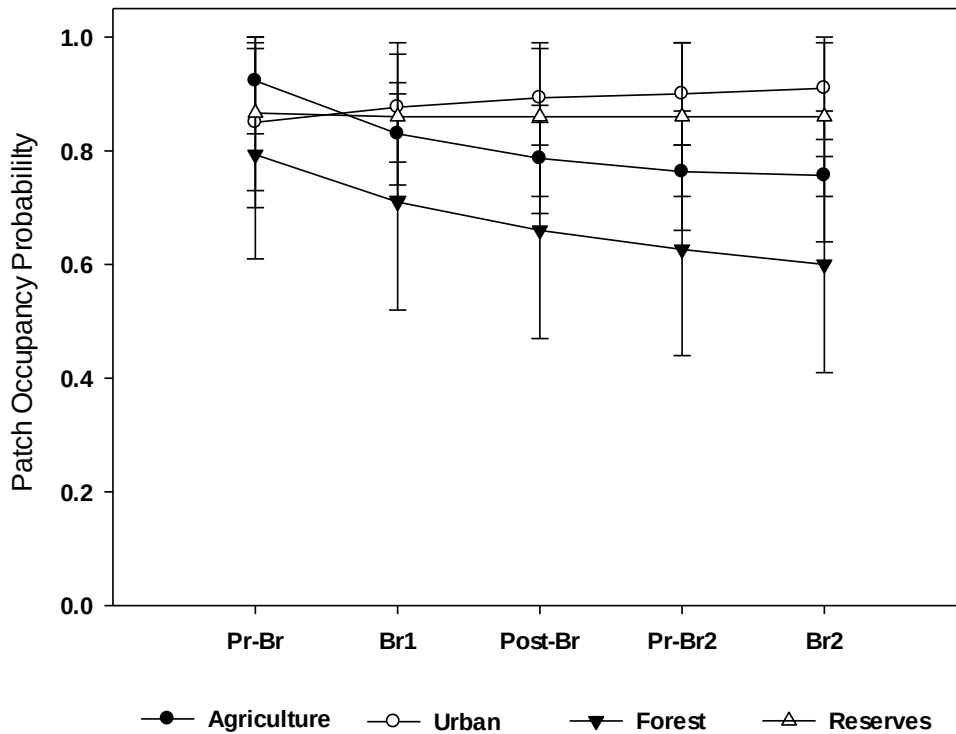


Figure 1.17: Seasonal patch occupancy probability for the Black-faced Grassquit in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Estimates were obtained using a multi-season occupancy model and avian surveys conducted during 5 primary sampling periods: two pre-breeding seasons (Pr-Br and Pr-Br2; January-February 2010 and 2011), two breeding seasons (Br1 and Br 2; March-June 2010 and 2011) and a post-breeding season (Post-Br; July-August 2010). Three surveys (secondary sampling occasions) were conducted in every season. The 95% confidence intervals for each seasonal estimate are depicted.

APPENDICES

Appendix A. Maps of the landscape between the Guánica and Susúa State Forests in southwestern Puerto Rico, depicting land cover classes and location of avian survey stations. There are three habitat matrices between forests reserves. A yellow line delineates the agricultural matrix, a red line delineates the urban matrix and a green line delineates the forest matrix.

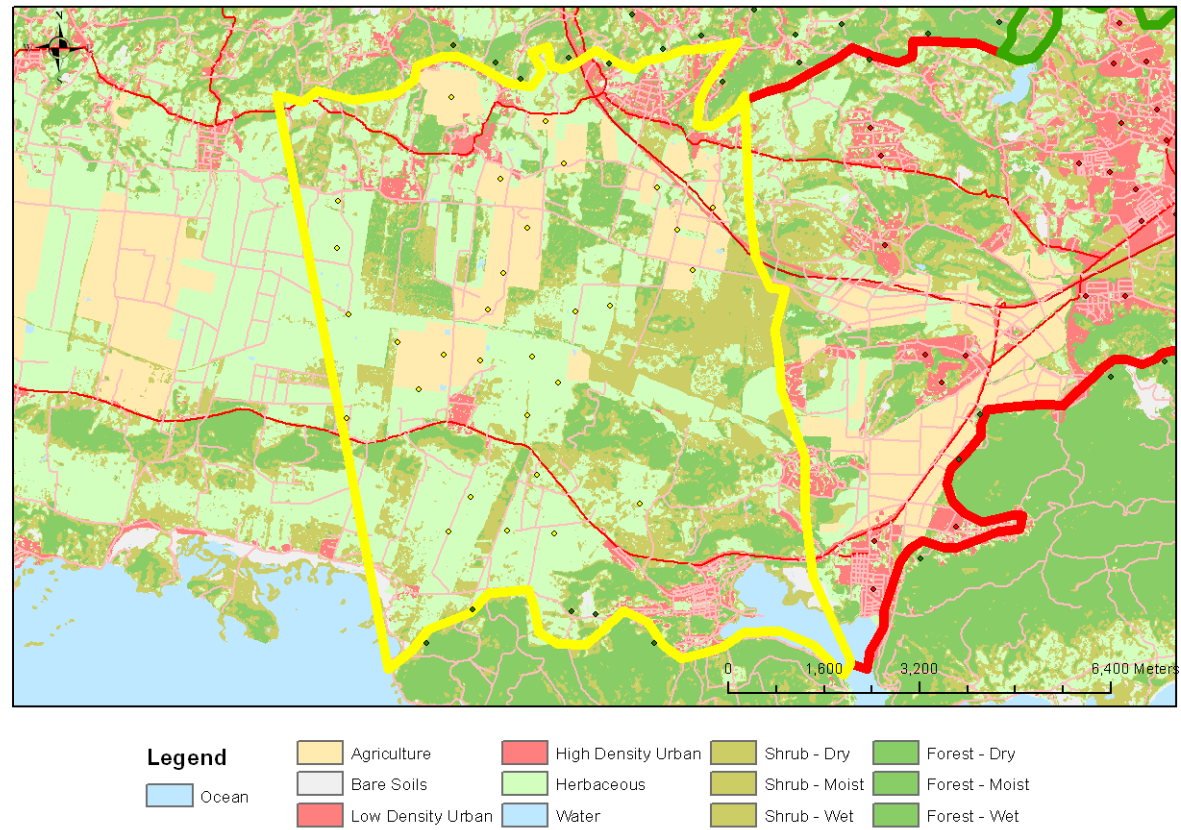


Figure A.1: The agricultural matrix located to the west of the Guánica and Susúa reserves. The locations of survey patches are represented on the map by yellow points.

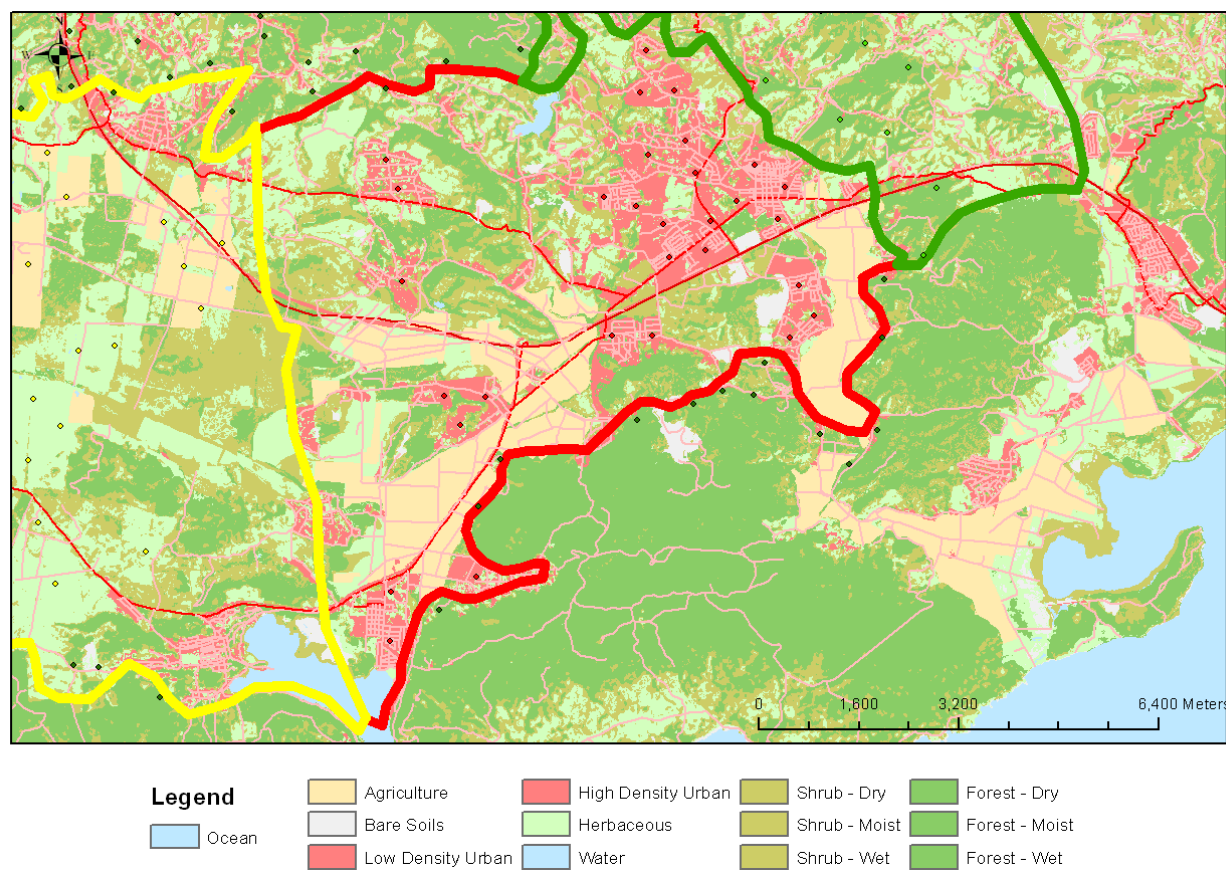


Figure A.2: The urban matrix located between the of the Guánica and Susúa reserves. The locations of survey patches are represented on the map by red points.

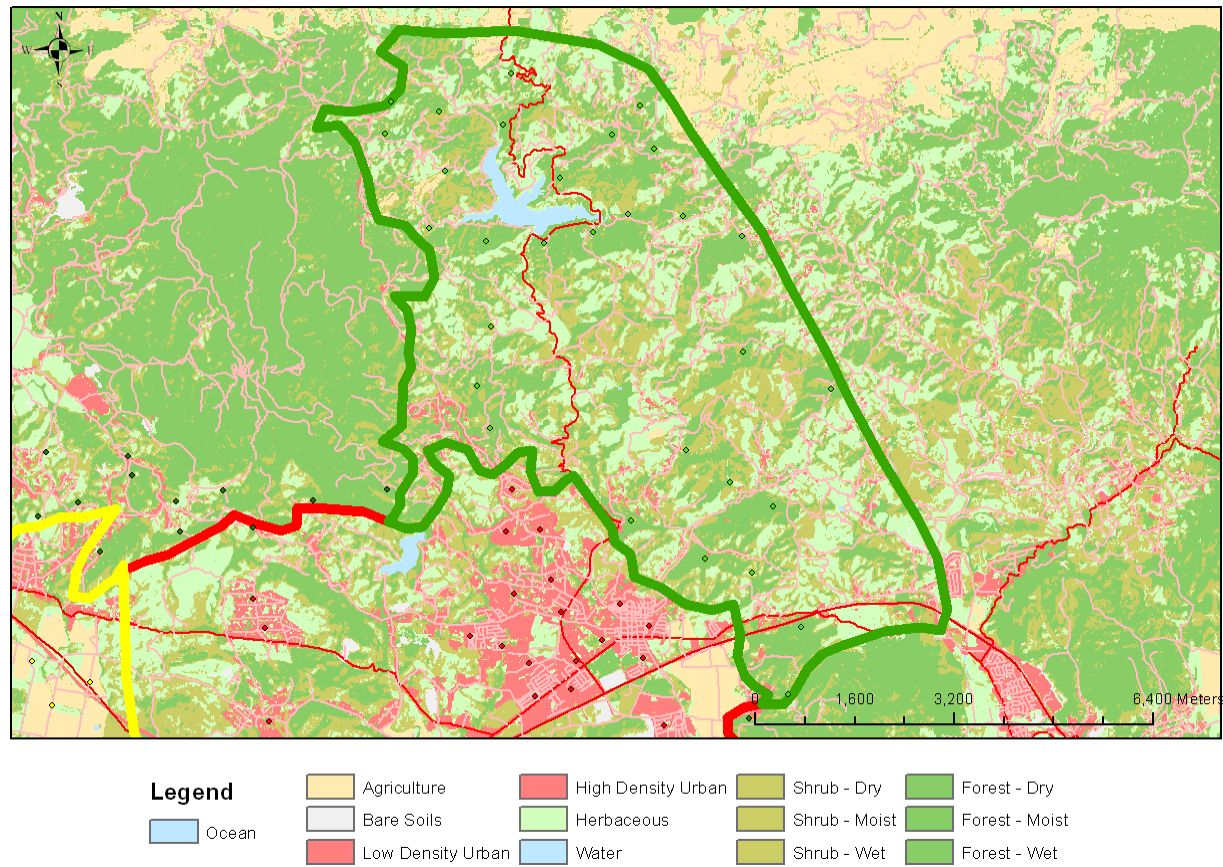


Figure A.3: The forested matrix located to the east of the Guánica and Susúa reserves. The locations of survey patches are represented on the map by a green points.

Appendix B: List of resident avian species detected in survey stations in three habitat matrices and within a 300-1500 m band of the e Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Species are also classified by foraging guild.

Common Name	AOU Species Code	Scientific Name	Status	Guild
American Kestrel	AMKE	<i>Falco sparverius</i>	Resident	Carnivore
Puerto Rican Lizard Cuckoo	PRLC	<i>Coccyzus vieilloti</i>	Endemic	Carnivore
Red-Tailed Hawk	RTHA	<i>Buteo jamaicensis</i>	Resident	Carnivore
Antillean Euphonia	ANEU	<i>Euphonia musica</i>	Resident	Frugivore
Puerto Rican Bullfinch	PUEB	<i>Loxigilla portoricensis</i>	Endemic	Frugivore
Puerto Rican Spindalis	PRSP	<i>Spindalis portoricensis</i>	Endemic	Frugivore
Red-Legged Thrush	RLTH	<i>Turdus plumbeus</i>	Resident	Frugivore
Scaly-Naped Pigeon	SNPI	<i>Patagioenas squamosa</i>	Resident	Frugivore
African Collared Dove	AFCD	<i>Streptopelia roseogrisea</i>	Resident	Granivore
Black Faced Grassquit	BFGR	<i>Tiaris bicolor</i>	Resident	Granivore
Bronze Mannikin	BRMA	<i>Lonchura cucullata</i>	Introduced	Granivore
Common Ground Dove	COGD	<i>Columbina passerina</i>	Resident	Granivore
House Sparrow	HOSP	<i>Passer domesticus</i>	Introduced	Granivore
Indian Silverbill	INSI	<i>Euodice malabarica</i>	Introduced	Granivore
Key West Quail-Dove	KWQD	<i>Geotrygon chrysia</i>	Resident	Granivore
Nutmeg Mannikin	NUMA	<i>Lonchura punctulata</i>	Introduced	Granivore
Orange Bishop	ORBI	<i>Euplectes franciscanus</i>	Introduced	Granivore

Appendix B: (Continued)

Common Name	AOU Species Code	Scientific Name	Status	Guild
Orange Cheeked Waxbill	ORAW	<i>Estrilda melpoda</i>	Introduced	Granivore
Pin-Tailed Whydah	PTWH	<i>Vidua macrocura</i>	Introduced	Granivore
Ruddy Quail-Dove	RUQD	<i>Geotrygon montana</i>	Resident	Granivore
White-Winged Dove	WWDO	<i>Zenaida asiatica</i>	Resident	Granivore
Yellow-Faced Grassquit	YFGR	<i>Tiaris olivaceus</i>	Resident	Granivore
Zenaida Dove	ZEND	<i>Zenaida aurita</i>	Resident	Granivore
Adelaide's Warbler	ADWA	<i>Dendroica adelaidae</i>	Endemic	Insectivore
Black-Whiskered Vireo	BWVI	<i>Vireo altiloquus</i>	Resident	Insectivore
Caribbean Elaenia	CAEL	<i>Elaenia martinica</i>	Resident	Insectivore
Cattle Egret	CAEG	<i>Bulbulcus ibis</i>	Resident	Insectivore
Cave Swallow	CASW	<i>Petrochelidon fulva</i>	Resident	Insectivore
Gray Kingbird	GRAK	<i>Tyrannus dominicensis</i>	Resident	Insectivore
Lesser Antillean Peewee	LAPE	<i>Contopus latirostris</i>	Resident	Insectivore
Loggerhead Kingbird	LOKI	<i>Tyrannus caudifasciatus</i>	Resident	Insectivore
Mourning Dove	MODO	<i>Zenaida macrocura</i>	Resident	Insectivore
Puerto Rican Flycatcher	PRFL	<i>Myiarchus antillarum</i>	Endemic	Insectivore
Puerto Rican Oriole	PROR	<i>Icterus dominicensis</i>	Endemic	Insectivore
Puerto Rican Tody	PRTO	<i>Todus mexicanus</i>	Endemic	Insectivore
Puerto Rican Vireo	PRVI	<i>Vireo latimeri</i>	Endemic	Insectivore
Puerto Rican Woodpecker	PRWO	<i>Melanerpes portoricensis</i>	Endemic	Insectivore

Appendix B: (Continued)

Common Name	AOU Species Code	Scientific Name	Status	Guild
Antillean Mango	ANMA	<i>Anthracothorax dominicus</i>	Resident	Nectarivore
Bananaquit	BANA	<i>Coereba flaveola</i>	Resident	Nectarivore
Puerto Rican Emerald	PREM	<i>Chlorostilbon maugaeus</i>	Endemic	Nectarivore
Grasshopper Sparrow	GRSP	<i>Ammodramus savannarum</i>	Resident	Omnivore
Great Egret	GREG	<i>Ardea alba</i>	Resident	Omnivore
Greater Antillean Grackle	GAGR	<i>Quiscalus niger</i>	Resident	Omnivore
Mangrove Cuckoo	MACU	<i>Coccyzus minor</i>	Resident	Omnivore
Northern Mockingbird	NOMO	<i>Mimus polyglottos</i>	Resident	Omnivore
Pearly-Eyed Thrasher	PETH	<i>Margarops fuscatus</i>	Resident	Omnivore
Rock Pigeon	ROPI	<i>Columba livia</i>	Introduced	Omnivore
Shiny Cowbird	SHCO	<i>Molothrus bonariensis</i>	Introduced	Omnivore
Smooth-Billed Ani	SBAN	<i>Crotophaga ani</i>	Resident	Omnivore
Troupial	TROU	<i>Icterus icterus</i>	Introduced	Omnivore

Appendix C: List of tree species with available fruit encountered in survey stations in three habitat matrices and within a 300-1500 m band of the Guánica and Susúa State Forests in southwestern Puerto Rico. Surveys were conducted during two pre-breeding seasons (January-February 2010 and 2011), two breeding seasons (March-June 2010 and 2011) and a post-breeding season (July-August 2010). Preferred fruit tree species by the Puerto Rican Bullfinch and Puerto Rican Spindalis were used to calculate the adjusted fruit availability index (FAI adj.) and are identified with a superscript by the scientific name. Sources of information were: (1) Carlo et al. 2003, (2) Carlo et al. 2004, (3) Carlo et al. 2011, (4) Wiewel 2011 and (5) Pérez-Rivera 1994.

Common Name	Spanish Name	Scientific Name
Adonidia Palm	Palma Adonidia	<i>Adonidia merrillii</i>
African tuliptree	Tulipán Africano	<i>Spatodea campanulata</i>
Almond	Almendro	<i>Prunus dulcis</i>
American Muskwood	Guaraguao	<i>Guarea guidonia</i> ^{1,2}
Avocado	Aguacate	<i>Persea americana</i>
Balsam Apple / Balsam		
Pear	Cundeamor	<i>Momordica balsamina</i>
Balsampear	n/a	<i>Momordica charantia</i>
Banana	Guineo / Banano	<i>Musa sp.</i>
Bastard Cedar	Guácima	<i>Guazuma ulmifolia</i>
Bayahonda	Bayahonda Blanca	<i>Prosopis juliflora</i>
Blackrodwood	Pitangueira	<i>Eugenia biflora</i> ¹
Bodywood	Palo de Vaca	<i>Bourreria succulenta</i> ⁴
Boxleaf Stopper	n/a	<i>Eugenia foetida</i>
Breadfruit	Pana	<i>Artocarpus altilis</i>
Broomstick	Conejo Colorado	<i>Trichilia hirta</i>
Cabbagebark Tree	Moca	<i>Andira inermis</i>
Copperwood	Almácigo	<i>Bursera simaruba</i> ⁵
Custard apple	Corazón	<i>Annona reticulata</i>
Day Jessamine	Dama de Día	<i>Cestrum diurnum</i>
Fig Tree	Ficus	<i>Ficus sp.</i> ^{2,5}
Florida Bitterbush	n/a	<i>Picramnia pentandra</i>
Genipap	Jagua	<i>Genipa americana</i>
Grapefruit	Toronja	<i>Citrus sp.</i> ⁵
Gregorywood	Úcar	<i>Bucida buceras</i> ^{1,2}

Appendix C: (Continued)

Common Name	Spanish Name	Scientific Name
Guadeloupe Marlberry	Mameyuelo	<i>Ardisia obovata</i>
Guava	Guayaba	<i>Psidium sp.</i>
Guyanese Wild Coffee	Palo de la Cruz	<i>Casearia guianensis</i> ¹
Hammock Velvetseed	n/a	<i>Guettarda elliptica</i>
Hog Plum	Jobo	<i>Spondias mombin</i>
Jack in the Bush	Santa María	<i>Chromolaena odorata</i>
Jasmine	Jazmín Falso	<i>Jasminum fluminense</i>
Lantana	Lantana	<i>Lantana camara</i>
Lime	Lima	<i>Citrus sp.</i>
Madras Thorn	Guamá americano	<i>Pithecellobium dulce</i>
Mahoe	Hibisco	<i>Hibiscus sp.</i>
Maidenberry	Pico de paloma	<i>Crossopetalum rhacoma</i>
Mandarin Orange	China Mandarina	<i>Citrus reticulata</i>
Mango	Mango	<i>Mangifera indica</i>
Manjack	Bocote	<i>Cordia sp.</i> ^{2, 5}
Marbletree	n/a	<i>Cassine xylocarpa</i>
Milkberry	Bejuco de berac	<i>Chiococca sp.</i>
Monkey's hand	Baquiña	<i>Lepianthes peltatum</i>
n/a	Bayahonda Blanca	<i>Prosopis juliflora</i>
n/a	Camasey	<i>Miconia sp.</i> ^{1, 2, 5}
n/a	Cupey de Monte	<i>Clusia minor</i> ¹
n/a	Gia Verde	<i>Casearia arborea</i> ⁵
n/a	Maga	<i>Thespesia grandiflora</i>
n/a	Mameyuelo	<i>Mouriri helleri</i>
n/a	Mata Gallina	<i>Dioscorea polygonoides</i>
n/a	n/a	<i>Duranta sp.</i>
n/a	Palo de Vaca	<i>Dendropanax laurifolius</i>
n/a	pata de gallina	<i>Teliostachya alopecuroidea</i>
n/a	Rabo de Ratón	<i>Gonzalagunia spicata</i>
Nettle Tree	n/a	<i>Trema sp.</i>
Noni	Noni	<i>Morinda citrifolia</i>
Orange	China	<i>Citrus sp.</i>
Palo de Vaca	Palo de Vaca	<i>Dendropanax laurifolius</i> ²
Papaya	Papaya	<i>Carica papaya</i>
Passionfruit	Parcha	<i>Passiflora edulis</i>
Pepper plant	n/a	<i>Piper sp.</i> ^{2, 5}
Plantain	Plátano	<i>Musa sp.</i>

Appendix C: (Continued)

Common Name	Spanish Name	Scientific Name
Poison Ash	Chicharrón	<i>Comocladia dodonaea</i>
Prickly Palm	Palma de Corozo	<i>Acrocomia media</i>
Prickly Pear	Tuna	<i>Opuntia sp.</i>
Princess Vine	Bejuco de Caro	<i>Cissus sicyoides</i>
	Palma Real de Puerto Rico	
Puerto Rican Royal Palm	Rico	<i>Roystonea borinquena</i> ¹
Red Pepper	Ají Caballero	<i>Capsicum frutescens</i>
Royen's tree cactus	Cactus Dildo	<i>Pilosocereus royenii</i>
Santa Maria	María	<i>Calophyllum sp.</i>
Sapodilla	Nispero	<i>Manilkara sp.</i>
Sea Grape	Uva Playera	<i>Coccoloba uvifera</i>
Sea Torchwood	Teilla	<i>Amyris elemifera</i>
Season Vine	Bejuco de Caro	<i>Cissus verticillata</i>
Sebucan	Sebucán	<i>Leptocereus quadricostatus</i>
Soldierwood	Mabí	<i>Colubrina elliptica</i>
Sorrelvine	n/a	<i>Cissus trifoliata</i>
Soursop	Guanábana	<i>Annona muricata</i>
Spanish Lime / Honeyberry	Quenepa / Limoncillo	<i>Melicoccus bijugatus</i>
Star Apple	Caimito	<i>Chrysophyllum cainito</i>
Starfruit	Carambola	<i>Averrhoa carambola</i>
Strawberrytree	Capulín	<i>Muntingia calabura</i>
Tamarind	Tamarindo	<i>Tamarindus indica</i>
Turkey Berry	Berenjena Cimarrona	<i>Solanum sp.</i> ³
West Indian Jasmine	Jazmín	<i>Ixora sp.</i>
West Indian Sour Cherry	Acerola	<i>Malpighia emarginata</i>
White Indigoberry	Tintillo	<i>Randia aculeata</i>
		<i>Zanthoxylum martinicense</i> ^{1, 5}
White Prickle	Espino Rubial	
Whiteroot	Bejuco Indio	<i>Gouania lupuloides</i>
Whitewood	n/a	<i>Coccoloba krugii</i>
Wild ackee	Guara	<i>Cupania americana</i> ¹
Wild Coffee	Jaboncillo	<i>Colubrina arborescens</i>
Wild Sage	Carriacillo Santa María	<i>Lantana involucrata</i>
Yagrumo	Yagrumo	<i>Cecropia schreberiana</i> ^{1, 2}
Yellow Mombin	Jobillo	<i>Spondias mombin</i>
Yellow Prickle	Espino Blanco	<i>Zanthoxylum monophyllum</i>

Appendix D: List of covariates, definitions, codes and parameters used to model occupancy (psi), colonization (gamma), extinction (eps), and detection (p) probabilities in three habitat matrices and Guánica and Susúa State Forests in southwestern Puerto Rico. Data were collected from January 2010 to June 2011.

Symbol	Covariate	Influence	Definition
A	Agricultural Matrix	psi, gamma, eps	Refers to survey points located in the Agricultural matrix.
U	Urban Matrix	psi, gamma, eps	Refers to survey points located in the Urban matrix.
F	Forested Matrix	psi, gamma, eps	Refers to survey points located in the Forested matrix.
E	Edge Matrix	psi, gamma, eps	Refers to survey points located in the Edges of forest reserves.
t	Seasonal Effect	gamma, eps	Introduces a seasonal effect - covariates will vary by season.
DP	Distance to Patch	gamma	Distance in meters to the nearest forest patch or visible clump of trees.
DF	Distance to Forest	gamma	Distance in meters to the nearest to the nearest patch with at least the average forest cover percentage of the matrix (?) in which the survey point is located.
PS	Patch Size	eps	Area of the nearest forest patch, measured in hectares.
Fcov	Forest Cover	eps	Percentage of forest cover of the 200 meter radius surrounding survey point.
Hcov	Herbaceous Cover	eps	Percentage of herbaceous cover of the 200 meter radius surrounding survey point.
F+Hcov	Forest + Herbaceous Cover	eps	Sum of forest and herbaceous cover measurements from the 200 meter radius surrounding the survey point. Used as a measure of open areas.

Appendix D: (Continued)

Symbol	Covariate	Influence	Definition
FAI	Fruit Availability Index	eps	Measures all available fruit species within the 10 meter radius surrounding the survey point.
Avg FAI	Average Fruit Availability Index	eps	All available fruit species within the 10 meter radius surrounding the survey point, averaged by sampling season.
FAIadj	Adjusted Fruit Availability Index	eps	Measure of available fruit species within the 10 meter radius surrounding the survey point, adjusted for fruits preferred by the Puerto Rican Bullfinch (<i>Loxia portoricensis</i>) and Puerto Rican Spindalis (<i>Spindalis portoricensis</i>).
S	Seasonal Effect	p	Introduces a seasonal effect - detection will vary by season.
SLOPE	Slope	p	Slope of the survey point.
CAHT	Canopy Height	p	Height of the forest canopy (when available), measured in meters.
CACOV	Canopy Cover	p	Percentage of cover in the forest canopy (when available) above the survey point.
UC	Understory Cover	p	Percentage of understory cover in the 10 meter radius surrounding the survey point.
Avg UC	Average Understory Cover	p	Percentage of understory cover in the 10 meter radius surrounding the survey point averaged by season.

Chapter 2: Permeability of an urban matrix to the movements of an endemic avian frugivore in the tropics

ABSTRACT

Urban growth has been the primary driver of habitat fragmentation in Puerto Rico in recent decades. Fragmented habitats may limit dispersal of avian forest specialists and reduce their probability of persistence. Factors influencing movements through human-modified landscapes have been poorly studied in the tropics. Available information suggests that forest specialists prefer to move along forested routes or “stepping stones” patches, avoiding open areas. Conservation planners are interested in understanding how permeable human-modified landscapes are to movements of wildlife, and what actions might improve their permeability. We quantified how the amount and resistance of habitat influenced permeability to movements of the Puerto Rican Bullfinch (*Loxigilla portoricensis*) in spring and summer 2011, an endemic frugivore that is not common in urbanized landscapes. We experimentally translocated 28 radio-tagged bullfinches within the Guánica State Forest and between the forest and urbanized matrix that separates the Guánica and Susúa state forests in southwestern Puerto Rico. Habitat types were differentially permeable. All birds translocated within the forest returned successfully to where they were captured, whereas 43% did so when birds were translocated across urban and forest habitat matrices or within the urbanized matrix. Distance between capture and release site negatively influenced return success. Successful returns were made within 5 days after translocations, after which the

probability of returning successfully was < 50%. Bullfinches used patches with high forest cover as they traversed through the urban matrix, particularly those from Guanica Forest (70% cover). Our work provides guidelines for “softening” or lowering the contrast between the urban matrix and forested landscapes by increasing structural similarity and quality of habitat patches. These actions should enhance the permeability of the urban matrix separating the Guanica and Susua Forests, and therefore, the persistence of avian forest specialists on the landscape.

INTRODUCTION

Little is known about the effects of urbanization on avifauna in the tropics, despite the fact that its rich biota is under pressure from a rapidly increasing human population (Marzluff et al. 2001; Ramos-González 2001; Acevedo and Restrepo 2008). Urban matrices may filter birds out on the basis of their biological traits (Crocini et al. 2008). For example, forest specialists or members of guilds such as frugivores might be more sensitive to urbanized landscapes than species adept at exploiting open habitats or belonging to a different foraging guild (e.g., the Black-faced Grassquit, *Tiaris bicolor*, a granivore; Vázquez Plass and Wunderle 2012). Previous work has also shown that forest specialists prefer to move along forested routes, using small forest fragments within urban matrices as “stepping stones” while avoiding crossing open areas (Awade and Metzger 2008; Boscolo et al. 2008; Gilles and St. Clair 2008; Hadley and Betts 2009; Kennedy and Marra 2010; Tremblay and St. Clair 2011). Translocation studies have also shown that birds require more time and are less

successful in returning to their capture site when moving through non-forested landscapes (Castellon and Sieving 2006; Kennedy and Marra 2010; Ibarra-Macias et al. 2011).

Disruptions of movement among habitat patches have focused attention on the value of strategies that promote habitat connectivity (Haddad 1999a; Leidner and Haddad 2010). Connectivity is defined as the degree to which landscape structure facilitates movements of organisms among patches (Taylor et al. 1993) and can be separated into two components. Structural connectivity refers to the degree of physical connection that exists among habitat patches measured in the landscape, regardless of the requirements of particular organisms (Gobeil and Villard 2002). The second component is functional connectivity, which is defined as a species-specific behavioral response to landscape structure (Tischendorf and Fahrig 2001). In the context of fragmentation, some species might have difficulties or be completely averse to moving between habitat patches if the intervening habitat (or matrix) is compositionally different (Ricketts 2001; Bender and Fahrig 2005; Revilla et al. 2004; Hodgson et al. 2007; Leider and Haddad 2011). It follows that knowledge about factors that influence these processes could be useful for guiding conservation design (Ricketts 2001; Vandermeer and Carvajal 2001).

In Puerto Rico, urban development is currently the primary driver for landscape change (Martinuzzi et al. 2007). Fragmented landscapes, including those dominated by urbanized and impervious surfaces, could lead to altered metapopulation complexes by hampering a species' dispersal capabilities and consequently undermining its persistence (Templeton et al. 1990; Noss and Cooperrider 1994; Hanski 1998; Fahrig 2003; Leider and Haddad 2011). Persistence is undermined because patch colonization or "rescue" processes

are reduced or severed. In southwestern Puerto Rico, for example, the Guánica State Forest is considered one of the best examples of a subtropical dry forest in the Caribbean and the World (Ewel and Whitmore 1973; Lugo et al. 1996), but the reserve has become increasingly isolated as a result of nearby urban sprawl. The closest forest reserve is the Susúa State Forest, located approximately 7 kilometers northwest. Determining the degree of permeability of the intervening urban matrix between forest reserves represented a research priority by the Puerto Rico Department of Natural and Environmental Resources, a component of a comprehensive initiative aimed at understanding and creating linkages to facilitate avian movement between forest reserves (Green et al. 2001). Permeability refers to the combined effects that the amount, configuration and resistance of habitats impose on bird movements (Gobeil and Villard 2002).

In this study, we focused on two elements characterizing permeability, namely, habitat amount and resistance to avian movement. We translocated radio-tagged Puerto Rican Bullfinches (*Loxigilla portoricensis*) to quantify how this species moved through the urbanized matrix that separates Guánica and Susúa forests. Our objectives were to: (1) determine whether the type of translocation (within or across matrices) influenced the likelihood of birds returning successfully to the capture site, (2) determine the time it took birds to return to the capture site, and (3) determine the structure (measured as vegetation cover) of habitat patches used when birds returned to the capture site. We hypothesized that return success would be higher for birds moving within the same habitat or matrix type (e.g., forest to forest or urban to urban) as compared to birds moving between habitat types (e.g., urban to forest or forest to urban) because birds moving within a matrix that is

compositionally similar poses fewer transitions or movements over different habitat types. For this same reason, we also expected that birds moving within a compositionally similar forested landscape (our control group) would take less time to return to the capture site than birds moving across different habitat types (e.g., forest to urban).

We chose the bullfinch because it is a frugivorous species, its distribution is associated with forested landscapes, and is considered uncommon in urban landscapes (Chapter 1; Acevedo and Restrepo 2008; Vázquez Plass and Wunderle 2012). These attributes make it a suitable biological model to gain insights about how other frugivores and forest-specialists might respond to urbanized landscapes. Fifty-one percent of the resident avifauna in the island could be categorized as forest specialists, with forest cover classes as their primary predictor of distribution (Raffaele 1998; Gould et al. 2007; Lugo et al. 2012). Our approach was mechanistic because we did not have spatial replicates. We quantified the response of multiple individuals under the assumption that individuals elsewhere on the island would respond similarly if confronted with similar landscapes. We believe that the insights gained from this work will be relevant to other landscapes because the patterns of human population growth and socio-economic changes found in the study area were representative of patterns found elsewhere on the island of Puerto Rico (Ramos 2001). We discuss the implications of our results, placing them in the context of permeability in urbanized landscapes and the conservation of avifauna in Puerto Rico and elsewhere in the Caribbean.

STUDY AREA

This study was conducted in the Guánica State Forest, which served as a control site, and the intervening urban matrix that separates the Guánica and Susúa State Forests (Figure 2.1). The urban matrix is approximately 6,116 ha in size, whereas the Guánica Forest is approximately 4,000 ha. The shortest linear distance between reserves is 6.6 km. The urban matrix encompassed the towns of Yauco and outskirts of Guánica. Overall, 23% of the matrix is urbanized, 15% is forested, while the rest is comprised of bare soils (2%), agriculture (17%), herbaceous (19%), shrub (23%), and water (1%) (Gould et al. 2007). Land use to the west of the urban matrix is dominated by 11% agriculture, with 42% herbaceous (pasture) land cover. Land use to the east of the urban matrix is dominated by forest cover (34%) in a lower human density context (Gould et al. 2007).

METHODS

Mist-netting, Translocations and Radio Tracking

We captured 28 adult Puerto Rican Bullfinches using mist-nets (12 m in length, 30 mm mesh) opportunistically placed in trails within the Guánica State Forest and on selected habitat patches in the urban matrix of varying forest cover and distance to the Guánica Forest (Figures 2.2, 2.3, Appendix A). Net lines ranged from three to ten nets per site, depending on available space. Birds were captured between March and September 2011. Net lines were opened from dawn to approximately 1100 hrs, weather (no rain or heavy winds) and temperature permitting. Net lines were operated for no more than three consecutive days in the same site and then moved to another location because birds avoided nets after a few days

of sampling (Kornegay 2011). We used Puerto Rican Bullfinch song playbacks to aid in attracting birds to the nets.

A major challenge in assessing permeability is that movement is influenced by an individual's state and motivation. These factors dictate the choice of destination and the amount of risk and energetic cost individuals are willing to incur (Belisle 2005). We standardized both the motivation and destination of birds by translocating breeders or adult bullfinches defending a territory. We assumed that birds with these attributes would exhibit strong site fidelity (e.g., Kennedy and Marra 2010; Tremblay and St. Clair 2011).

Captured birds were marked with size 1A USGS aluminum bands and tagged with radio telemetry transmitters. The transmitters (model BD-2N from Holohil Systems Ltd., weighing 0.53 g) were attached with a Rappole-Tipton backpack-style harness (Rappole and Tipton 1991). Puerto Rican Bullfinches average 17 - 19 centimeters in length and weigh 32 - 33 grams (Oberle 2006), therefore the weight of transmitters was only 1.6% of their body mass, well below the standard 3% specified by the USGS Bird Banding Laboratory. Radio-tagged birds were transported by car to their release location. Exposure to excessive noise, extreme temperatures and other external stressors was avoided during transport by keeping the bird in a cotton bag suspended by drawstrings. On average, birds were handled for approximately 20 to 25 minutes before release. Only alert, healthy birds were used for translocations. This work was conducted under Institutional Animal Care and Use Committee permit number 09-0404-O. Appendices B and C detail the locations and forest cover of capture and release sites.

We performed four types of translocations in two habitat types: (1) captured and released in forest (6 birds), (2) captured in forest and released in urban (9 birds), (3) captured in urban and released in forest (4 birds) and (4) captured and released in urban (9 birds). Capture and release sites were randomized among these translocation types to avoid correlative patterns in bird responses (Kennedy and Marra 2010). Exceptions to this protocol occurred when traffic and other conditions affected travel time to a release location. In such cases, we opted to release birds at the nearest feasible release site to avoid undue stress (this occurred 4 times; 3 when alert birds began to show signs of stress during transport and 1 when traffic conditions caused a detour). Distance between capture and release sites within the Guánica State Forest ranged between 1 and 4 km. Translocations outside the forest ranged mostly between 2 and 4 km. Distances for urban to forest translocations ranged between 2 and 4 km; for urban to urban translocations distances ranged between 2.5 and 3.75 km. For forest to urban translocations distances ranged between 3.5 and 6.7 km. The longer distances reflected the fact that trapping occurred in trails well within the Guánica State Forest. However, the average distance (measured as a straight line) between release sites and the boundary of the Guánica Forest was 3.0 km. We note that most distances were between 1.14 and 5.68 km. These distances represent the bullfinch median and 95% natal dispersal distance (i.e., only 5% are expected to disperse beyond 5.68 km; Sutherland et al. 2000). Radio tracking began immediately after releasing a bullfinch. Teams of 2-3 technicians scanned for radio signals at 20-30 min intervals in the mornings and afternoons, ensuring that several location estimates were obtained daily. Signals were tracked using Advanced Telemetry Systems R410 scanning receivers with three element Yagi antennas. Observers

wrote down paired azimuths and location coordinates for each signal measured. All birds were tracked until (1) the transmitter was recovered, (2) transmitter battery life ended (approximately 25 to 30 days), or (3) birds could not be found. Appendix D summarizes the tracking history of the 28 translocations.

DATA ANALYSIS

We estimated the location for each tracked bird using a maximum likelihood estimation option in program LOAS (Ecological Software Solutions LLC 2010). Intersecting bearings beyond 2 kilometers were excluded because they were outside the recommended range of the transmitters. We plotted the estimated locations of each tracked bird on maps characterizing the landscape (Gould et al. 2007; Appendix A). Percent forest cover of estimated locations was calculated based on a 200 m radius using ArcGIS (ESRI 2010). This radius was adopted because it encompassed the area sampled during bird surveys (100 m radius) and an additional 100 m to better capture the land cover context surrounding survey plots (see Chapter 1). It was also a means to account for the possibility of location errors. The estimated home range of Puerto Rican Bullfinches in Guánica State Forest was 9.00 ha (95% CI: 8.03 to 10.15; Kornegay 2011). Our estimate of cover encompassed 12.6 ha, thus, it is likely that this area included the true location of bullfinches. We also reported the forest cover of 30 randomly established plots (200 m radius) within the urban matrix. We used these estimates to help us interpret results from sites used by birds returning to their

site of capture (e.g., used versus average available patch cover).

We tested whether the probability of returning successfully to capture sites differed among the 4 types of translocations using logistic regression (JMP Pro 9, SAS Institute Inc. 2010). We used type of translocation and distance between capture and release sites as covariates. We used a Cox regression to compare return time (days) by translocation type (Kennedy and Marra 2010; Ibarra-Macias et al. 2011). The Cox regression compares survival curves; with survival being equal to time elapsed before occurrence of a terminal event (Cox 1972). In this study, a successful return to the capture site was treated as the terminal event. Individuals were censored if there was evidence that their transmitter had failed or fallen off, or if their fate could not be ascertained (i.e., failed to detect a signal after release). We modeled return time using only data from birds that successfully returned to the capture site to prevent confounding movement with other mechanisms (philopatry and mortality; Kennedy and Marra 2010). Due to low sample sizes, we modeled return times as a function of distance and three translocation types. The translocation types were birds captured and released within Guánica State Forest (control) and birds released in an urban matrix (i.e., forest to urban and urban to urban). Finally, we determined if the percent cover of patches used during a bird's movement differed by type of translocation using a repeated measures ANOVA (PROC MIXED, SAS Institute Inc. 2011). Model terms were: percent cover (response variable); type of translocation (4 types) and days of observation (days) were main effects; individual bird was a random effect; repeated measures were made on the individual bird*type of translocation. Correlations between estimates of forest cover taken over time were modeled using a first-order autoregressive covariance structure (AR1).

Before running the analysis, percent cover was log-transformed to meet homogeneity of variance assumption (Levene's Test, $P > 0.05$). Differences in percent cover (lsmeans) by type of relocation were assessed using orthogonal contrasts. Unless indicated, we reported untransformed means ($\pm$ SE). Test significance was set as $\alpha = 0.05$.

RESULTS

Twenty-eight birds were radio-tagged during the study. Two radios were lost (1 recovered near the release site in Guánica Forest; 1 stopped signaling immediately after release in an urban-to-urban translocation). On average, bullfinches were monitored for 9.89 days ($SD = 5.77$; $N = 28$). We know the fates of 26 birds. Of these, the 5 birds captured and released within Guánica State Forest returned successfully to the capture site (100%). Similarly, all birds translocated from urban to forest returned successfully. Only 22% (2/9) and 37.5% (3/8) of birds returned successfully when the translocation type was forest to urban and urban to urban, respectively.

The probability of a bullfinch returning to the capture site was influenced by translocation type and distance ($\chi^2 = 23.39$, $df = 4$, $P < 0.001$). Successful returns were influenced by type of translocation (L-R $\chi^2 = 12.33$, $df = 3$, $P = 0.006$) and decreased significantly with distance (L-R $\chi^2 = 11.14$, $df = 1$, $P < 0.001$). For the same distance interval (2-4 km), the probability of returning decreased more sharply when movement involved urban-to-urban translocations than in forest-to-urban translocations (Figure 2.4). Birds released in the urban matrix took, on average, a day longer to return to the capture site (5.7 ± 1.72 SE vs. 4.5 ± 2.28 SE). Return time was not influenced by type of translocation or

distance ($\chi^2 = 3.53$, $df = 2$, $P = 0.17$), although distance was the most influential of the two factors (L-R $\chi^2 = 3.29$, $df = 1$, $P = 0.06$). The likelihood of a bird returning successfully to its capture site was $< 50\%$ after the 4th day (Figure 2.5).

Forest cover percentage characterizing the estimated locations used by bullfinches while moving between released and capture sites differed by type of translocation ($F = 4.78$, $df = 3$, 75 ; $P = 0.004$). Birds involved in forest to urban translocations used locations that had significantly higher percent cover than locations used by birds in the urban to forest or urban to urban translocations (Table 2.4; Figure 2.6). Forest cover for locations used by birds in forest-to-urban and forest-to-forest (control group) translocations did not differ ($P > 0.05$). The percent of forest cover at locations used by birds in all types of translocations was higher than the percent forest cover of randomly selected points representative of the overall urban matrix ($4\% \pm 0.04$ SD).

DISCUSSION

We assessed the permeability of a forested and urbanized landscape in southwestern Puerto Rico by tracking the movements of radio-tagged Puerto Rican Bullfinches. We focused on two of the elements of permeability, namely, the influence of the amount (e.g., percent forest cover) and resistance (e.g., time) of habitats on bird movements (Gobeil and Villard 2002). We found that all the birds in our control group, the birds translocated within the Guánica State Forest, returned to the capture site. In contrast, only 43% of all other translocations were successful (i.e., forest to urban, urban to forest and urban to urban). While success differed among translocation types, the time it took to return to the capture site

did not. The majority of successful returns in this study occurred within 5 days, with exceptions associated with longer distances between release and capture sites. For those exceptions, it is possible that homing was mediated by distance, which negatively influenced the probability of successfully returning. The negative effect distance had on successful returns was consistent with other studies in the tropics (Castellón and Sieving 2006; Kennedy and Marra 2010; Ibarra-Macias et al. 2001). Birds may become risk averse with increasing distance, adding time to their journey or settling in new areas to avoid traveling across unfamiliar habitats (Gillies 2008). Lack of differences in return time could have also been an artifact of small sample sizes. Evidence indicating that forest specialists take longer time to return to capture sites when moving across non-forested habitat matrices is strong, both in tropical and temperate environments (Castellón and Sieving 2006; Kennedy and Marra 2010; Ibarra-Macias et al. 2001; Tremblay and St. Clair 2011).

The scale at which dispersal occurs is difficult to estimate, particularly for avian species in the tropics. Kennedy and Marra (2010) derived distance thresholds to make inferences about successful returns and their conservation implications. In the absence of prior data on bullfinches, we estimated natal dispersal distances (Sutherland et al. 2000) as a means to help us interpret results. The estimated median dispersal distance was 1.14 km (median) with only an estimated 5% of birds dispersing beyond 5.68 km. Successful returns in this study were mostly in the 1-4 km range, which were within the range of estimated natal dispersal distances. We view these distances as an appropriate scale with which to design conservation design strategies such as the creation of habitat stepping-stones, but suggest that emphasis should be given to the lower values of that range. This is because distances ≤ 1 km

encompass both the median natal dispersal distance of bullfinches and yield the highest patch colonization rates (Chapter 1). Stepping stones are a series of habitat patches that promote connectivity by reducing habitat gaps in fragmented landscapes (Saunders et al. 1991; Vandermeer and Carvajal 2001; Tremblay and St. Clair 2011).

We measured the percent forest cover at locations used by birds returning to capture sites. Birds moving within the Guánica Forest used sites with higher cover (84.5%) than those captured in the urban matrix (18.5%). These differences largely reflect the context within which birds were captured. The percent cover at the capture sites within the Guánica State forest was 78%, compared to 36% in the urban sites. We speculate that bullfinches captured within urban matrix were more tolerant to lower forest cover, giving them greater behavioral flexibility to move through the matrix. Regardless of where birds were captured, translocated birds used locations of higher forest cover than in randomly selected locations throughout the urban matrix (4%). These findings suggest that bullfinches were selective of habitat as they traveled, which may influence functional connectivity (Tischendorf and Fahrig 2001). In other words, decisions to move across fragmented landscapes could be influenced by differences in habitat structure between the source patches (or nature reserves) and the intervening habitat (Baum et al. 2004; Kennedy and Marra 2010; Leidner and Haddad 2010).

Knowledge of dispersal distances and the habitat structure used during dispersal movements could be used to “soften” an urbanized matrix (Baum et al. 2004). A “softer” matrix leads to a higher probability of a species successfully crossing patch edges by lowering the degree of contrast between the source patch and the matrix (Stamps et al. 1987;

Collinge and Palmer 2002; Baum et al. 2004; Ewers and Didham 2006). Forest cover serves as a proxy to an undetermined number of habitat quality attributes that species seek as they move through the landscape. At the very least forested patches provide a place to rest and shelter from threats (e.g., avian predators). Management actions could also target fruiting trees consumed by resident frugivores as a means to improve the quality of habitat patches (Carlo et al. 2003, 2005; Saracco et al. 2004). Fruiting trees known to be used by bullfinches were virtually absent in the urbanized landscape matrix, but resident endemic species are also known to use novel resources in human-dominated landscapes (Lugo et al. 2012).

The urban matrix between the Guánica and Susúa Forest in southwestern Puerto Rico was permeable to movements of Puerto Rican Bullfinches. However, there was evidence of some resistance to movements when birds were translocated within the urban matrix or from the Guánica State Forest to the urban matrix. This resistance may explain why occupancy or abundance of bullfinches in the urban matrix was lower than in the forest reserves and forested matrix (Chapter 1; Vázquez Plass and Wunderle 2012). We gained insights on how this forest specialist selected habitats while moving through forested and urban matrices, and we hope that they will be applicable to other frugivores of similar size (e.g., the endemic Puerto Rican Spindalis, *Spindalis portoricensis*). Extending the insights of this work is facilitated by the fact that the urban matrix between Guánica and Susúa Forest was representative of patterns of urban sprawl found elsewhere on the island (Ramos 2001). Nonetheless, we recommend that translocations with other species are conducted in future studies. This could allow managers to “fine-tune” or tailor conservation plans and strategies. Knowledge about a broader suite of species might be useful because species responses may

vary due to differences in vagility and adaptability to urban conditions (Ewers and Didham 2006; Tremblay and St. Clair 2011). The conservation of the Guánica and Susúa reserves should be placed firmly within the context of the surrounding landscape (Saunders et al. 1991). Forest cover in the urban matrix was approximately 15%, whereas the less densely populated region in the east of Yauco contained 34%. The latter region has a lower contrast between forest reserves and the intervening habitat and may facilitate greater avian movement (Taylor et al. 1993; Tischendorf and Farhig 2001; Gustafson and Gardner 1996; Ewers and Didham 2006; Haddad 1999b). Creating a linkage between the Guánica and Susúa Forest reserves is a strategic planning priority for the Puerto Rico Department of Natural and Environmental Resources (PR Law # 14, 1999; Green et al. 2001), this region represents a suitable focal area for such aims. Our work provides criteria to develop a complementary conservation strategy focused on facilitating avian movement across the adjacent urban matrix between reserves.

This study adds to the growing body of evidence that demonstrates that habitat matrices are not ecologically irrelevant as previously thought (Prevedello and Vieira 2010; Watling et al. 2011). While the establishment of habitat corridors and stepping-stones remains the primary conservation strategy to enhance the safe passage of species through non-habitat matrices, it has been shown that their effectiveness is dependent on the quality of the surrounding habitat (Baum et al. 2004). Our results support recommendations often found in the literature--lowering the contrast of the matrix by increasing its structural similarity to remaining habitat patches will help prevent habitat boundaries from functioning as dispersal barriers to organisms (Hodgson et al. 2007; Prevedello and Vieira 2010). Along

with more careful urban planning to control sprawl, “softening” the matrix may be a viable management option in landscapes that are facing rapid urbanization pressures with limited resources. Building or restoring, and maintaining entire habitat corridors may not be a realistic strategy for many landscapes with limited resources. However, focusing on the quality of the matrix may prove to be a useful start, as it will allow planners to work within their local constraints and available resources (Arendt 2004).

LITERATURE CITED

- Acevedo M.A. and C. Restrepo. 2008. Land-cover and land-use changes and its contribution to the large-scale organization of Puerto Rico's bird assemblages. *Diversity and Distributions* 14: 114-122.
- Andr n, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355-366.
- Arendt, R. 2004. Linked landscapes – Creating greenway corridors through conservation subdivision design strategies in the northeastern and central United States. *Landscape and Urban Planning* 68:241-269.
- Awade, M. and J. P. Metzger. 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology* 33: 863-871.
- Baum K. A., Haynes K. J., Dilleuth F. P. and J. T. Cronin. 2004. The matrix enhances the effectiveness of corridors and stepping-stones. *Ecology* 85:2671-2676.
- Belisle M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86: 1988-1995.

- Bender, D. J. and L. Fahrig. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86:1023-1033.
- Boscolo, D., Candia-Gallardo, C., Awade, M. and J.P. Metzger. 2008. Importance of interhabitat gaps and stepping-stones for Lesser woodcreepers (*Xiphorhynchus fuscus*) in Atlantic forest, Brazil. *Biotropica* 40: 273-276.
- Brooker L., Brooker M. and P. Cale. 1999. Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use and dispersal mortality. *Conservation Ecology* [Online] 3(1): 4 <http://www.consecol.org/vol3/iss1/art4/>
- Carlo T. A., Collazo J. A. and M. J. Groom. 2003. Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia* 134:119-131.
- Carlo T.A., Collazo J.A. and M.J. Groom. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. *Biotropica* 36(4): 602-614.
- Castellón T.D. and K.E. Sieving. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* 20(1): 133-145.

- Collinge S. K. and T. M. Palmer. 2002. The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. *Landscape Ecology* 17: 647-656.
- Cox, D.R. 1972. Regression models and life tables. *Journal of the Royal Statistical Society Series B-Statistical Methodology* 34: 187-220.
- Croci S., Butet A., Clergeau P. 2008. Does urbanization filter birds on the basis of their biological traits? *The Condor* 110: 223-240.
- Cronin, J. T. 2003. Matrix heterogeneity and host-parasitoid interactions in space. *Ecology* 84:1506-1516.
- Desrochers, A. and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* 11:1204-1210.
- Ecological Software Solutions LLC. 2010. LOAS (Location of a Signal) (Version 4.0.3.8) [Software]. Available from <http://www.ecostats.com/software/loas/loas.htm>.
- ESRI (Environmental Systems Research Institute Inc.). 2010. ArcGIS Desktop (Version 10) [Software].

- Ewel J.J. and J.L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service, Institute of Tropical Forestry. Research paper ITF-18. Río Piedras, Puerto Rico.
- Ewers R. M. and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81:117-142.
- Faaborg, J. 1982. Avian Population Fluctuations During Drought Conditions in Puerto Rico. *Wilson Bulletin* 94:20-30.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*. 34(1): 487-515.
- Fischer J. and D. B. Lindenmayer. 2002. The conservation value of paddock trees for birds a variegated landscape in southern New South Wales. Paddock trees as stepping stones. *Biodiversity and Conservation* 11:833-849.
- Gilles, C. S. and C. C. St. Clair. 2008. Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences USA* 105:19774-19779.

- Gillies C. S. 2008. Corridor use, habitat selection and route choice by forest birds in the fragmented tropical dry forests of Costa Rica. PhD thesis. University of Alberta, Edmonton, Canada.
- Gilpin M. E. 1980. The role of stepping-stone islands. *Theoretical population biology* 17: 247-253.
- Gobeil, J. F. and Villard M. A. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* 98:447-458.
- Google Inc. 2011. Google Earth (Version 6.0.3.2197) [Software]. Available from: <http://www.google.com/earth/index.html>.
- Gould, W., C. Alarcón, B. Fevold, M. E. Jiménez, S. Martinuzzi, G. Potts, M. Solórzano, and E. Ventosa. 2007. Puerto Rico Gap Analysis Project – Final Report. USGS, Moscow, ID and USDA Forest Service International Institute of Tropical Forestry, Rio Piedras, PR. 159 pp. and 8 Appendices.
- Green C., Kling M., Kuzsma R. and J. McAlary. 2001. Biological Corridors: Promoting and maintaining biodiversity in Puerto Rico. Report submitted to S. Vernon-Gerstenfeld and A. Gerstenfeld, Worcester Polytechnic Institute.

- Grimm N. B., Grove J. M., Pickett S. T. A. and C. L. Redman. 2000. Integrated approaches to long-term studies of urban ecological systems. *BioScience* 50:571-584.
- Gustafson, E. J. and Gardner, R. H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* 77, 94-107.
- Haddad, N.M. 1999a. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. *Ecological Applications* 9(2): 612-622.
- Haddad, N.M. 1999b. Corridor use predicted from behaviors at habitat boundaries. *The American Naturalist* 153(2): 215-227.
- Haddad, N. M. 2000. Corridor length and patch colonization by a butterfly, *Junonia coenia*. *Conservation Biology* 14:738-745.
- Hadley A. S. and M. G. Betts. 2009. Tropical deforestation alters hummingbird movement patterns. *Biology Letters* 5:207-210.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396: 41-49.
- Haynes K. J. and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* 84:2856-2866.

Helmer, E. H. 2000. The landscape ecology of secondary forest in montane Costa Rica. *Ecosystems* 3:98-114.

Hodgson P., French K. and R. E. Major. 2007. Avian movement across abrupt ecological edges: Differential responses to housing density in an urban matrix. *Landscape and urban planning* 79:266-272.

Holmes R. T., Marra P. P. and T. W. Sherry. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65:183-195.

Holohil Systems Ltd. 2012. Transmitters. <http://holohil.com/transmitters.htm>

Ibarra-Macias A., Robinson W.D. and M.S. Gaines. 2011. Forest corridors facilitate movement of tropical forest birds after experimental translocations in a fragmented neotropical landscape in Mexico. *Journal of Tropical Ecology* 27: 547-556.

Jackson, H. B. and L. Fahrig. 2012. What size is a biologically relevant landscape? *Landscape Ecology* 27(7): 929-941.

- Kennedy, C. M. and P. P. Marra. 2010. Matrix mediates avian movements in tropical forested landscapes: inference from experimental translocations. *Biological Conservation* 143:2136-2145.
- Kornegay M.E. 2011. Abundance and breeding productivity of resident avian species in Guánica State Forest. M.S. Thesis. North Carolina State University. Raleigh, North Carolina, USA.
- Leidner, A. K. and N. M. Haddad. 2010. Natural, not urban, barriers define population structure for a coastal endemic butterfly. *Conservation Genetics* 11:2311-2320.
- López T. d. M., A. T. Mitchell and J. R. Thomlinson. 2001. Urban expansion and the loss of prime agricultural lands in Puerto Rico. *Ambio* 30: 49-54.
- Lugo, A. E., O. Ramos, S. Molina, F. N. Scatena, and L. L. Velez-Rodríguez. 1996. A fifty-three year record of land use change in the Guánica Forest Biosphere Reserve and its vicinity. USDA, Forest Service. International Institute of Tropical Forestry, Río Piedras, Puerto Rico, USA.
- Lugo A. E. and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190:145-161.

- Lugo, A.E., T.A. Carlo, and J.M. Wunderle, Jr. 2012. Natural mixing of species: novel plant-animal communities on Caribbean Islands. *Animal Conservation* 15: 233-241.
- Machtans C. S., Villard, M. A. and S. J. Hannon. 1996. Use of riparian buffer strips as movement corridors by forest birds. *Conservation Biology* 10:1366-1379.
- Martinuzzi S., Gould W. A. and O.M. Ramos Gonzalez. Land development, land use and in Puerto Rico: integrating remote sensing and population census data. 2007. *Landscape and Urban Planning* 79 (3-4): 288-297.
- Marzluff, J. M., Bowman, R. and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms and approaches in *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston. pp 1-17.
- Moilanen, A. and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* 79:2503-2515.
- Murphy H. T. and J. Lovett-Doust. 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? *Oikos* 105: 3-14.
- Noss R.F. and A.Y. Cooperrider. 1994. *Saving nature's legacy: protecting and restoring biodiversity*. Island Press, Washington D.C.

- Oberle, M. 2006. *Puerto Rico's Birds in Photographs*. Second Edition. Editorial Humanitas. Seattle. 132pp.
- Prevedello, J.A. and M.V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation* 19: 1205-1223.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.
- Raffaele H.A. 1998. A guide to the birds of the West Indies. Princeton University Press. Princeton N.J., USA. 511 pp.
- Rail J. F., Darveau, M., Desrochers, A. and J. Huot. 1997. Territorial responses of boreal forest birds to habitat gaps. *The Condor* 99: 976-980.
- Ramos-González, O.M. 2001. Assessing vegetation and land cover changes in northeastern Puerto Rico: 1978-1995. *Caribbean Journal of Science* 37: 95-106.
- Rappole J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of field ornithology* Vol. 62 No. 3: 335-337.

- Revilla E., Wiegand, T., Palomares, F., Ferreras, P. and M. Delibes. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. *American Naturalist* 164: E130-E-153.
- Ricketts, T.H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist* 158:87-99.
- Ries, L. and Sisk, T.D. 2004. A predictive model of edge effects. *Ecology* 85: 2917-2926.
- Roland J., Keyghobadi N. and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* 81: 1642-1653.
- Saracco J.F., Collazo J.A. and M.J. Groom. 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139(2): 235-245.
- SAS Institute Inc. 2011. SAS (Version 9.3) [Software]. Available from <http://www.sas.com/>.
- SAS Institute Inc. 2010. JMP Pro 9 (Version 9.0.2, 64-bit edition) [Software]. Available from <http://www.jmp.com/>.

- Saunders D. A., Hobbs R. J. and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5(1): 18-32.
- Schultz, C. B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* 12: 284-292.
- Simberloff D., J.A. Farr, J. Cox and D.W. Mehlman. 1992. Movement corridors: conservation bargains or poor investments? *Conservation Biology* 6: 493-504.
- St. Clair C.C., M. Bélisle, A. Desrochers and S. Hannon. 1998. Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology* [Online] 2(2): 13 <http://www.consecol.org/vol2/iss2/art13/>.
- Stamps J.A., M. Buechner M. and V.V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* 129: 533-552.
- Stouffer, P.C. and R.O. Bierregard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76: 2429-2445.

- Suarez-Rubio, M. and J.R. Thomlinson. 2009. Landscape and patch-level factors influence bird communities in an urbanized tropical island. *Biological Conservation* 142: 1311-1321.
- Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of Natal Dispersal in Terrestrial Birds and Mammals. *Conservation Ecology* 4:16. [online] URL: <http://www.consecol.org/vol4/iss1/art16>
- Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.
- Templeton A.R., Shaw K, Routman E. and S.K. Davis. 1990. The genetic consequences of habitat fragmentation. *Annals of the Missouri Botanical Garden* 77: 13-27.
- Tischendorf, L. and L. Fahrig. 2001. On the usage and measurement of landscape of landscape connectivity. *Oikos* 68: 571-573.
- Tremblay M.A. and C.C. St. Clair. 2011. Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *Journal of applied ecology* 48: 679-688.
- U.S. Bureau of Census. 2010. Puerto Rico 2010 demographic profile [online]. URL: <http://www.census.gov/popfinder/?fl=72>

USGS Bird Banding Laboratory. 1999. Memorandum to all banders [online]. URL:
<http://www.pwrc.usgs.gov/bbl/resources/MTAB/mtab83111999.htm>

Vandermeer J. and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. *The American Naturalist* 158: 211-220.

Vazquez Plass E. O. and J.M. Wunderle, Jr. 2012. Avian distribution along a gradient of urbanization in northeastern Puerto Rico. *Ecological Bulletins* 54: *In press*.

Watling J.I., A.J. Nowakowski, M.A. Donnelly and J.L. Orrock. 2011. Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography* 20: 209-217.

Wiens J.A. 1997. Metapopulation dynamics and landscape ecology. In: *Metapopulation Biology: ecology, genetics, and evolution*. Hanski A. and E. Gilpin, eds. Academic Press, San Diego, California USA. pp 43-62.

Table 2.1: Least squares (LS) means of log-transformed estimates of forest cover (%) of sites used by translocated bullfinches that returned to their original capture locations. Least squares means were obtained with a repeated measures analysis. Percent cover was the response variable; type of translocation and days of observations as main effects. Repeated measures were made on bird (individual)*type of translocation. Translocation types were: F-F = forest to forest, F-U = forest to urban patch, U-F = urban patch to forest and U-U = urban patch to urban patch. Untransformed estimates (SE) of forest cover for the same sites used by bullfinches are also reported.

Translocation Type	LS Means Estimate	Standard Error	Untransformed Estimate	Standard Error
F-F	0.2918	0.04114	0.829323	0.04685
F-U	0.3095	0.04994	0.713106	0.05153
U-F	0.144	0.04498	0.287248	0.06209
U-U	0.1112	0.05842	0.153604	0.0661

APPENDICES

Appendix A: Estimated area and percent forest cover of capture and release sites during translocation experiments in the urbanized matrix between the Guánica and Susúa Forest Reserves in southwestern Puerto Rico, March – September 2011. Percent cover was estimated within 200 m radius of the estimated location of each site.

Site name	Percent forested	Forested area (sqM)
FL 1	60	71.550
FL 2	51	60.750
FS 1	2	2.475
FS 2	21	25.425
NL 1	46	54.900
NL 2	36	43.425
NS 1	3	3.600
NS 2	17	19.800

Appendix B: Coordinates, site names and type of matrix for sites of capture and release for Puerto Rican Bullfinches during translocation experiments in the urbanized matrix between the Guanica and Susua Forest Reserves in southwestern Puerto Rico, March – September 2011.

Site name	Type	Location (UTM)
FL 1	Urban Patch	19 Q 727447 1994852
FL 2	Urban Patch	19 Q 723109 1994538
FS 1	Urban Patch	19 Q 728340 1993364
FS 2	Urban Patch	19 Q 725382 1994579
Forest 5	Source Forest	19 Q 725058 1989444
Forest 4	Source Forest	19 Q 727772 1986506
Forest 6	Source Forest	19 Q 725990 1988348
Forest 7	Source Forest	19 Q 724365 1987678
Forest 8	Source Forest	19 Q 726137 1988784
Forest 2	Source Forest	19 Q 726944 1988605
Forest 3	Source Forest	19 Q 724392 1989224
Forest 1	Source Forest	19 Q 724507 1988534
NL 1	Urban Patch	19 Q 721996 1991472
NL 2	Urban Patch	19 Q 726658 1992455
NS 1	Urban Patch	19 Q 720599 1991692
NS 2	Urban Patch	19 Q 722042 1988603

Appendix C: Summary of experimental translocations conducted in the urbanized matrix between the Guánica and Susúa Forest Reserves, and within Guánica Forest Reserve in southwestern Puerto Rico, March – September 2011. Forest = Guánica State Forest; NS, NS, FL, FS were sites embedded in the urbanized matrix.

Bird ID	Frequency	Capture Date	Capture Location	Release Location	Distance Translocated (km)	Return Success	Return Time (Days)
PUEB 1	150.087	10/3/2011	Forest 1	Forest 2	2.5	Yes	3
PUEB 2	150.108	14/3/11	Forest 2	Forest 1	2.5	Yes	3
PUEB 3	150.128	16/3/11	Forest 2	Forest 3	0.7	Yes	3
PUEB 4	150.147	21/3/11	Forest 1	Forest 4	3.85	N/A	-
PUEB 5	150.167	21/3/11	Forest 1	Forest 4	3.85	Yes	9
PUEB 6	150.187	28/3/11	Forest 1	Forest 4	4	N/A	-
PUEB 7	150.207	18/4/11	Forest 1	NS Site 2	2.47	N/A	-
PUEB 8	150.227	19/4/11	Forest 8	NS Site 1	6.3	N/A	-
PUEB 9	150.375	19/4/11	Forest 1	FL Site 2	6.2	No	-
PUEB 10	150.417	19/4/11	Forest 1	FL Site 2	6.2	No	-

Appendix C: (Continued)

Bird ID	Frequency	Capture Date	Capture Location	Release Location	Distance Translocated (km)	Return Success	Return Time (Days)
PUEB 11	150.248	20/4/11	Forest 1	NL Site 2	4.45	N/A	-
PUEB 12	150.48	3/5/2011	Forest 6	FL Site 1	6.71	N/A	-
PUEB 13	150.518	4/5/2011	Forest 6	FS Site 2	6.25	N/A	-
PUEB 14	150.537	11/5/2011	Forest 6	FS Site 1	5.54	N/A	-
PUEB 15	151.028	1/6/2011	NL Site 2	Forest 5	3.55	Yes	3
PUEB 16	151.066	1/6/2011	NL Site 2	Forest 5	3.55	Yes	3
PUEB 17	151.047	6/6/2011	NL Site 2	Forest 5	3.55	Yes	3
PUEB 18	151.11	22/6/11	NS Site 1	Forest 5	4.89	No	-
PUEB 19	151.225	28/6/11	NS Site 1	FL Site 2	3.75	N/A	-
PUEB 20	151.329	27/7/11	FL Site 2	NS Site 1	3.75	N/A	-
PUEB 21	151.378	27/8/11	FL Site 2	NS Site 1	3.75	No	-
PUEB 22	151.267	29/8/11	NL Site 2	FS Site 2	2.34	Yes	-
PUEB 23	151.147	29/8/11	NL Site 2	FS Site 1	1.89	Yes	4
PUEB 24	151.288	20/8/11	NL Site 2	FL Site 2	4	No	-
PUEB 25	151.328	15/9/11	Forest 7	NS Site 2	2.5	Yes	1
PUEB 26	151.309	21/9/11	NL Site 2	FL Site 1	2.5	N/A	16
PUEB 27	151.227	29/9/11	NL Site 2	FL Site 1	2.5	N/A	-
PUEB 28	151.268	30/9/11	NL Site 2	FL Site 1	2.5	Yes	8

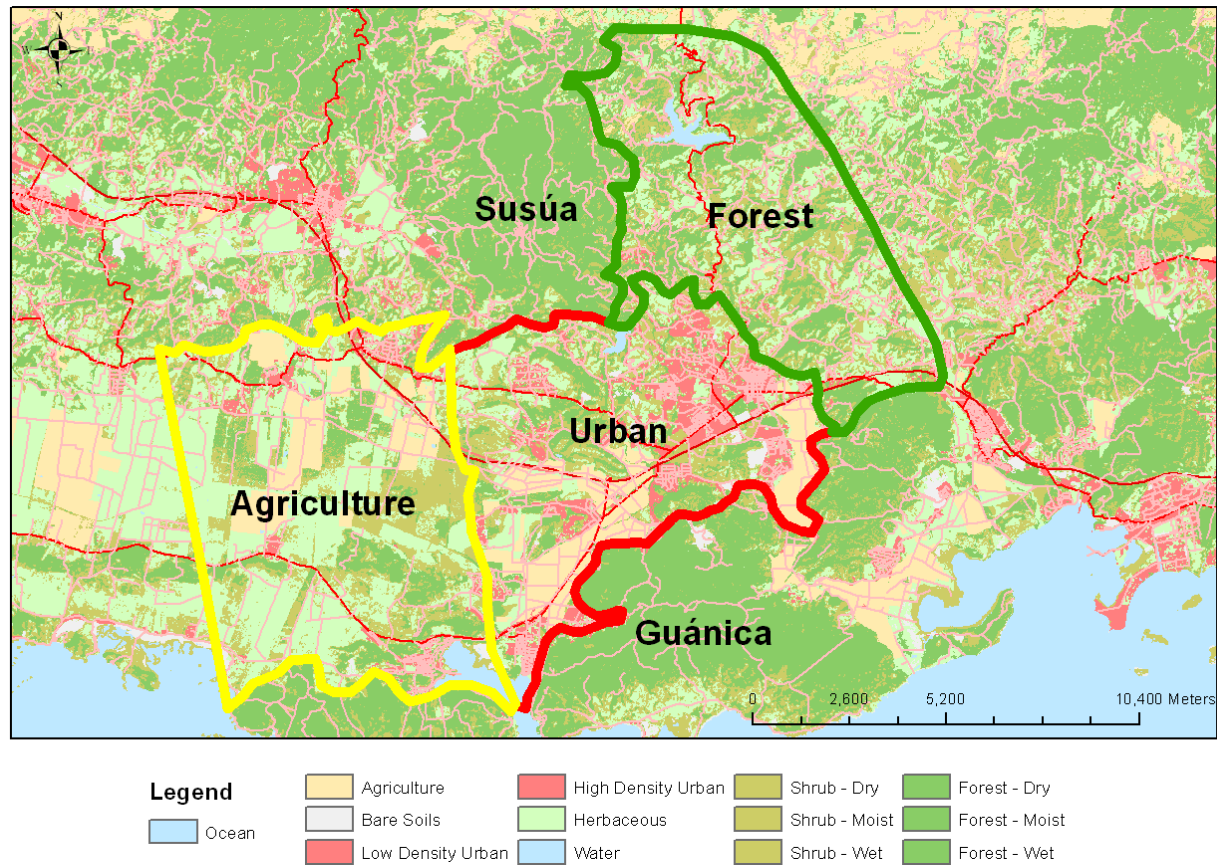


Figure 2.1: Map of the study area in southwestern Puerto Rico showing the spatial configuration of the agricultural, urban and forested matrixes that separate the Guánica and Susúa state forests. Translocation experiments were conducted in the Guánica State Forest and in the urban matrix.

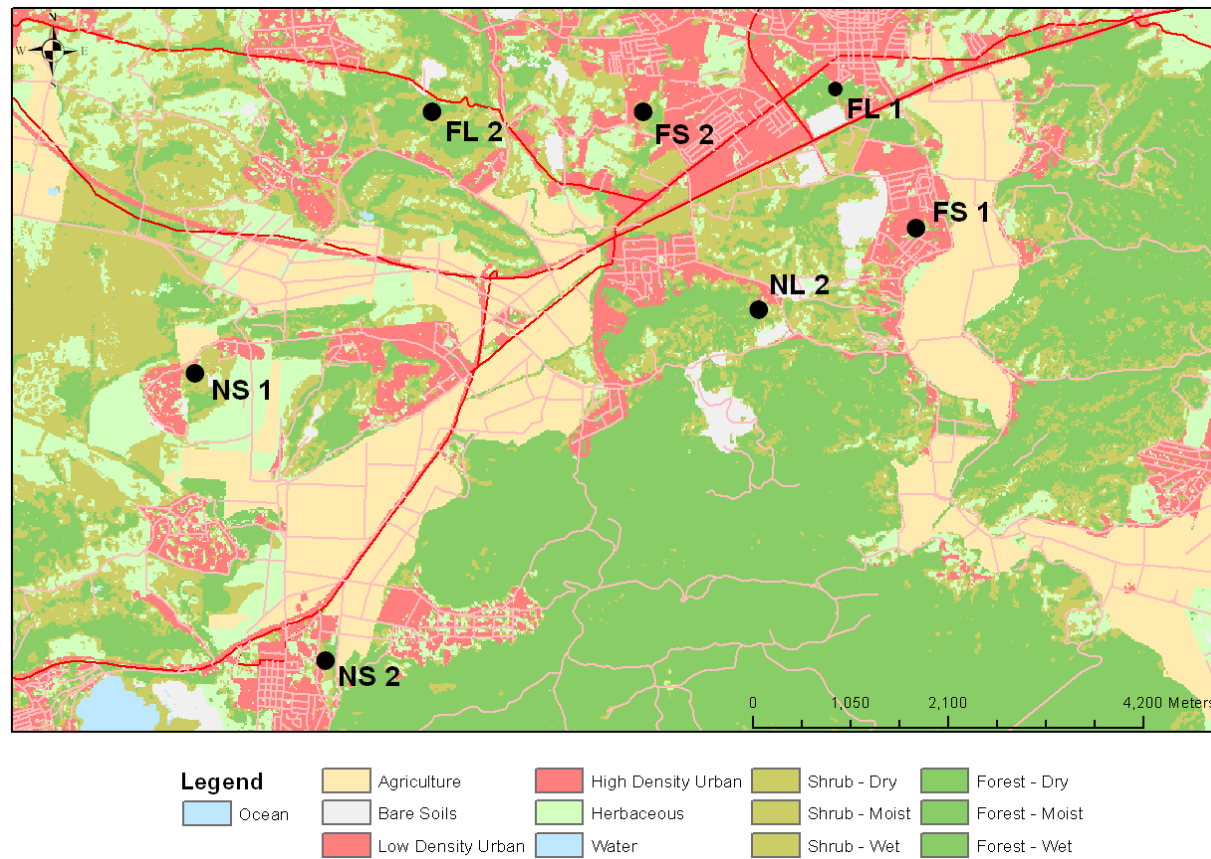


Figure 2.2: Map of the urbanized matrix detailing land cover types and remaining forest cover (in green). Capture and release locations for Puerto Rican Bullfinches are identified by large black dots. These represent patch access points where birds were released or trails within forest patches where mist net lines were established for capturing birds.

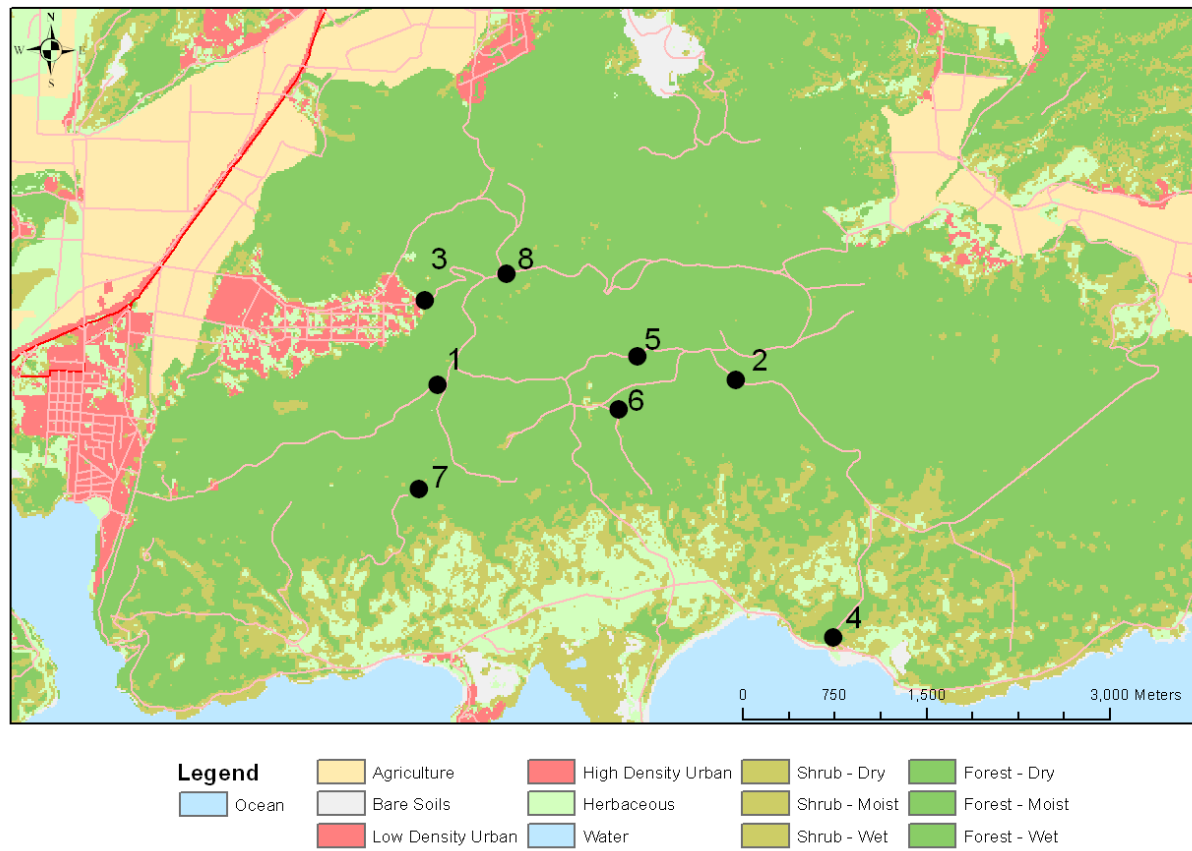


Figure 2.3: Map of the Guánica State Forest detailing capture and release locations for Puerto Rican Bullfinches. Each location is identified by a black dot and represents trails within the forest where mist-net lines were established for capturing birds.

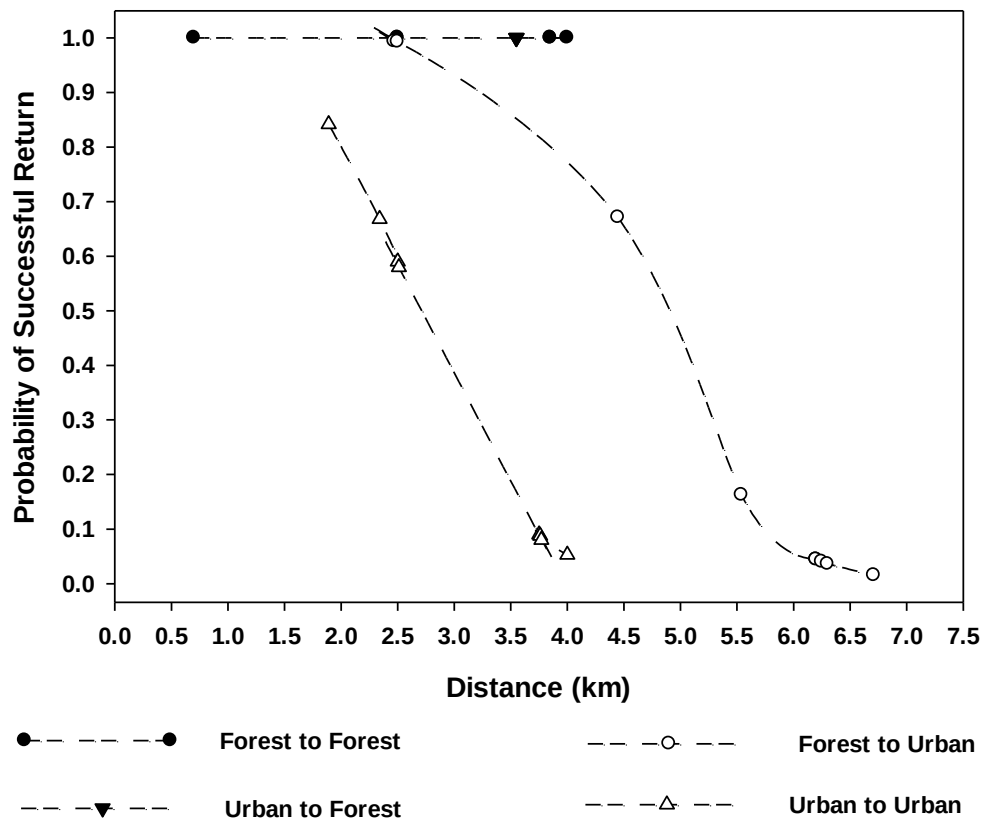


Figure 2.4: Probability of successful return to the site of capture by Puerto Rican Bullfinches in southwestern Puerto Rico, from March to September 2011. Probability of successful return was estimated by the type of translocation: forest to forest matrix, forest to urban matrix, urban to forest matrix, and urban to urban matrix. The probability of return was 1.0 for birds translocated within the forest or forest-to-forest (Guánica State Forest) and forest-to-urban matrices. The probability of return decreased sharply when translocations were conducted within the urban matrix (urban-to-urban).

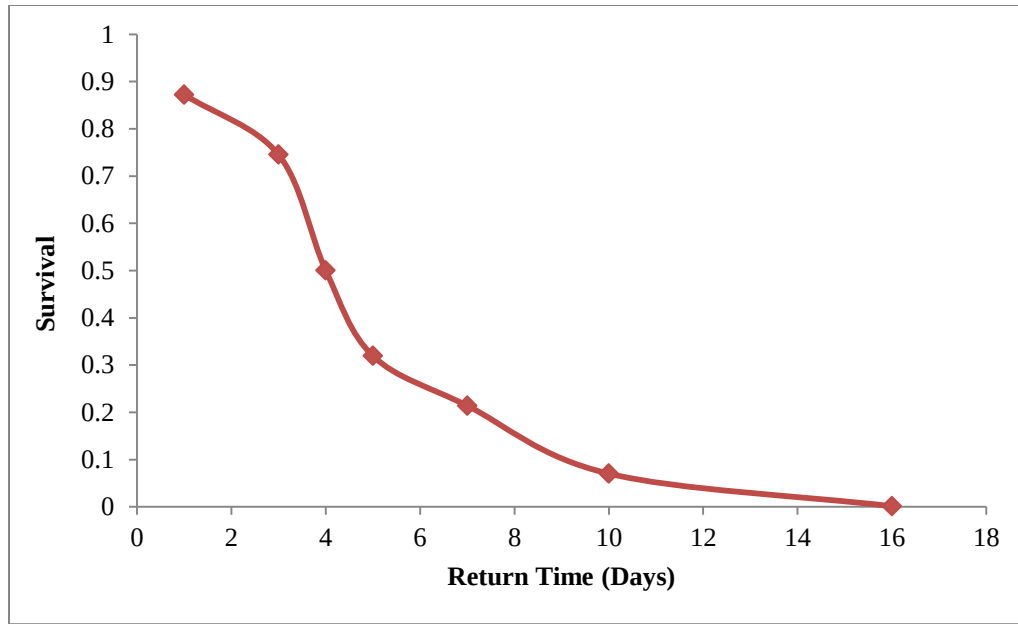


Figure 2.5: Survival of translocated Puerto Rican Bullfinches within Guánica State Forest and the urbanized matrix between the Guánica and Susúa Forest Reserves between March and September 2011. Survival is interpreted as the probability of successfully returning to the capture site as function of days elapsed since release. The probability of successful return was less than 50% after the 4th day. Estimates were obtained using Cox's proportion hazard regression model, which examined the effect of translocation type and distance between capture and release sites on survival times.

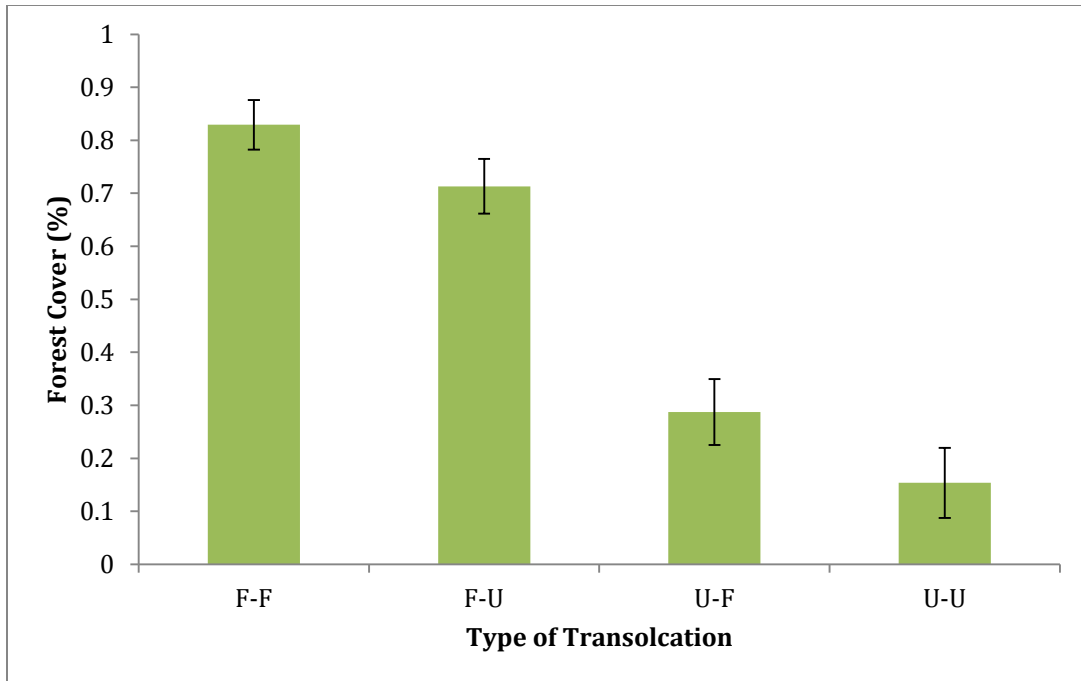


Figure 2.6: Average forest cover (SE) of sites used by translocated birds returning to their capture site. Averages are grouped by type of translocation: (F-F = forest to forest, F-U = Forest to Urban, U-F = Urban to Forest, U-U = Urban to Urban). Forest cover was estimated as the percent cover within 200 meter radius of the estimated location of birds based on triangulation.

Appendix D: Maps delineating the estimated locations and routes used by translocated birds in this study. Location estimates are numbered in chronological order to depict sequential movement, assumed to be directed towards the capture site. Capture and release locations are shown.

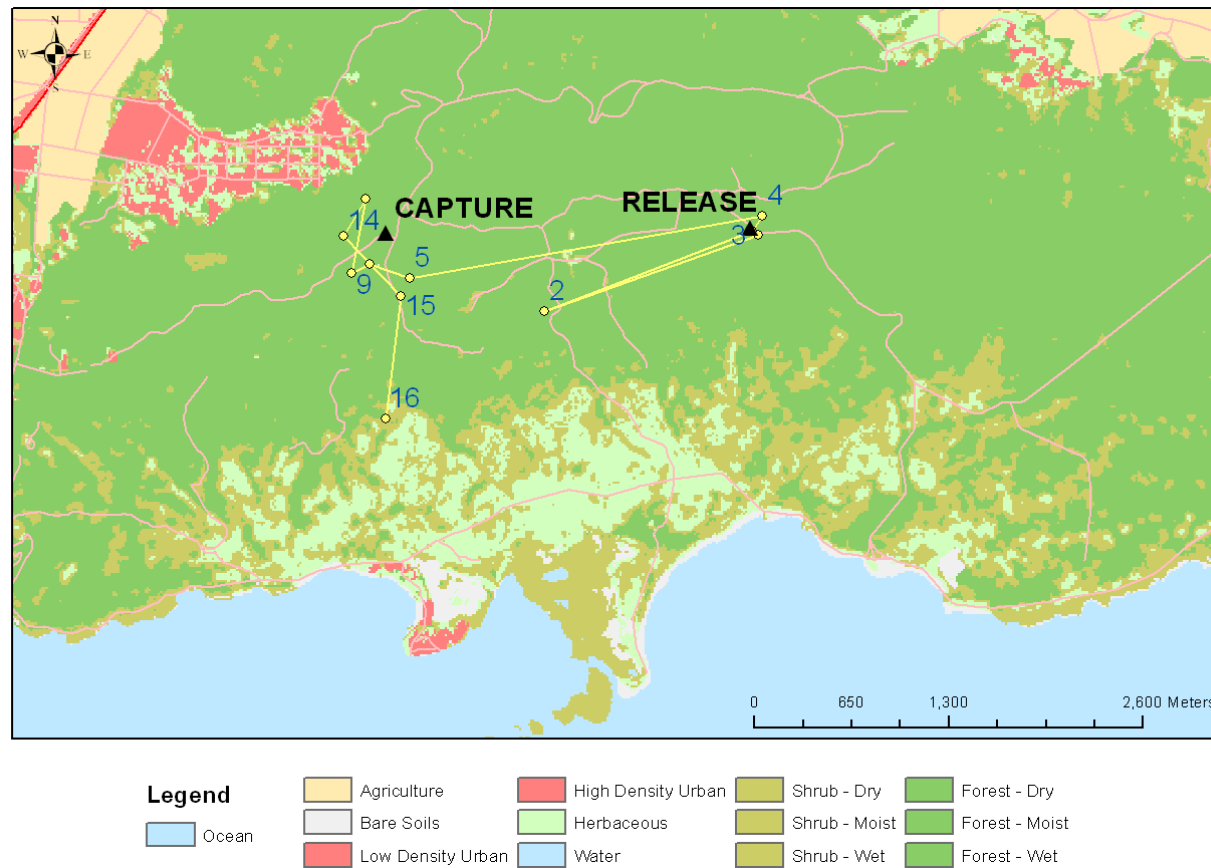


Figure D.1: Estimated locations and travel route for PUEB 1, captured and released within the Guánica State Forest.

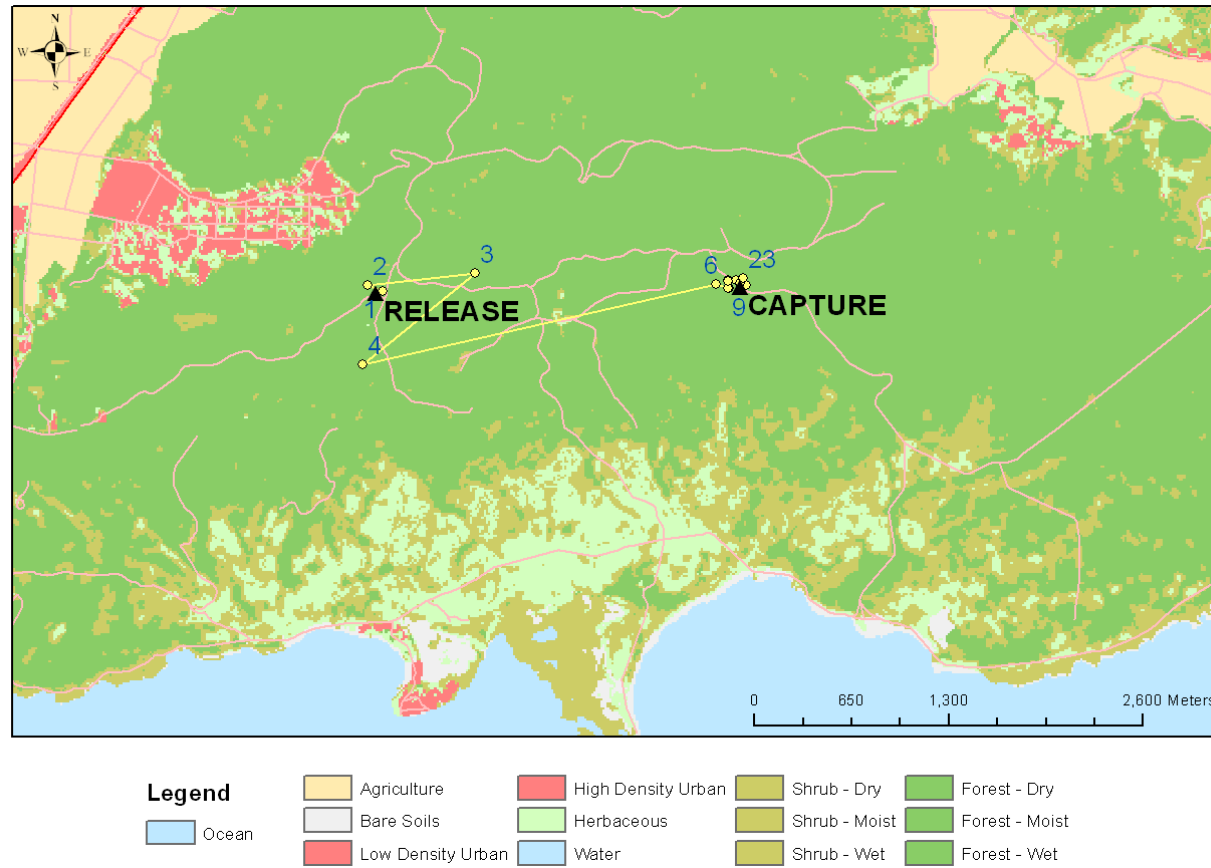


Figure D.2: Estimated locations and travel route for PUEB 2, captured and released within the Guánica State Forest.

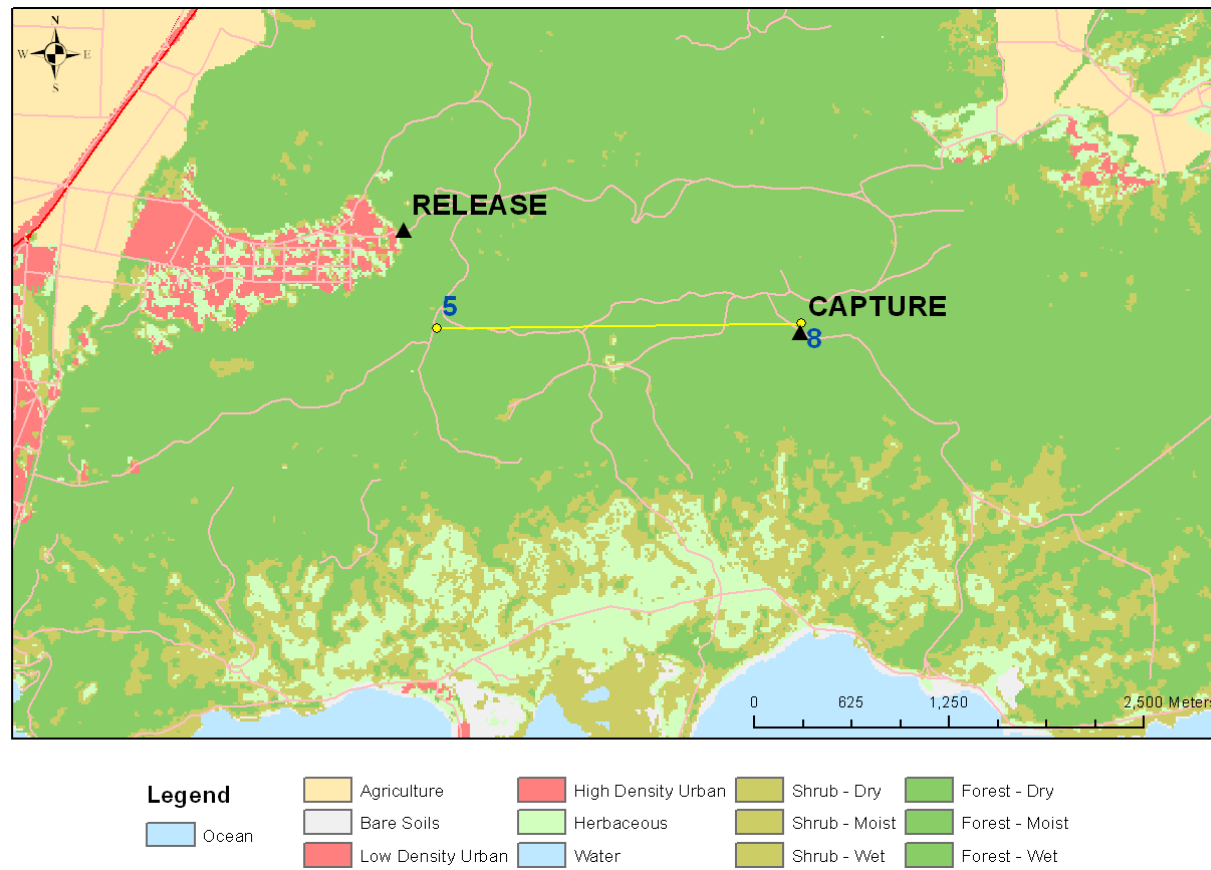


Figure D.3: Estimated locations and travel route for PUEB 3, captured and released within the Guánica State Forest.

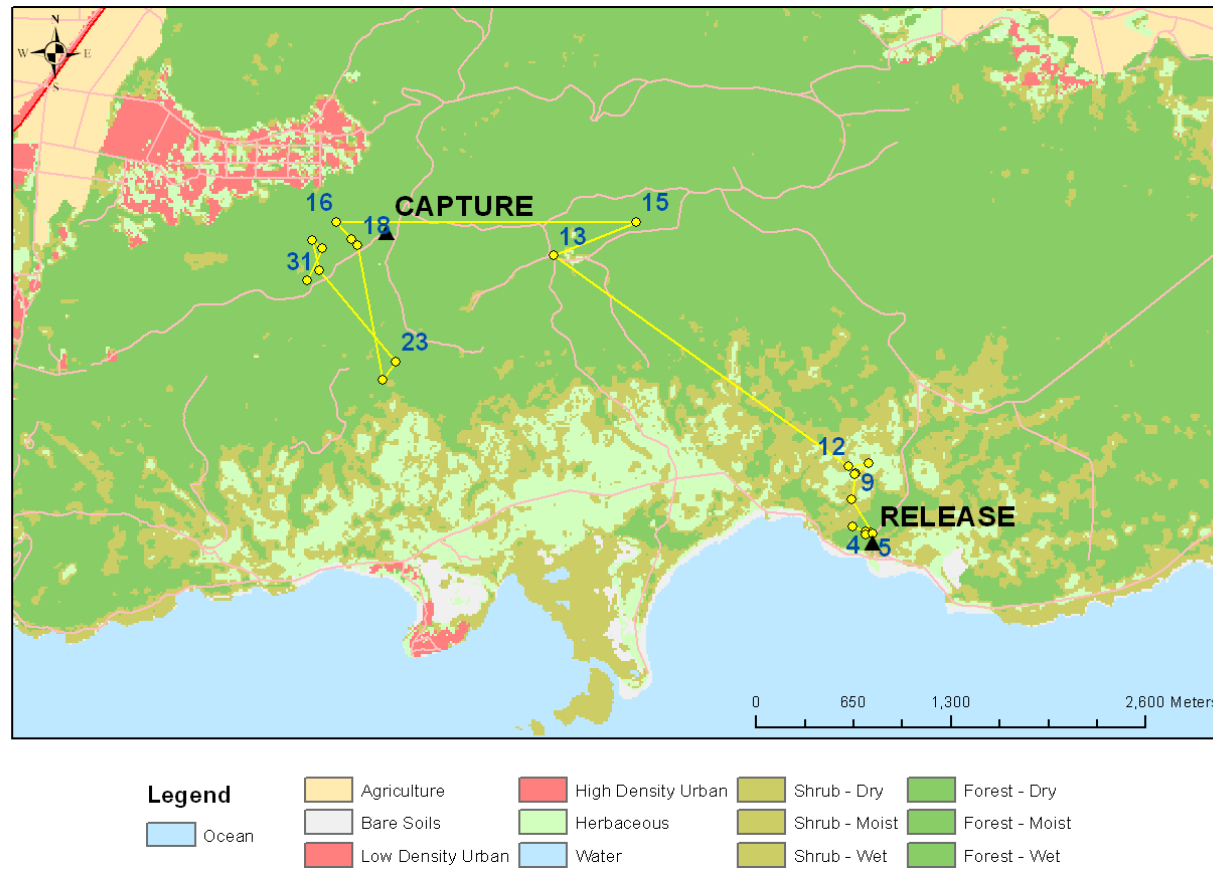


Figure D.4: Estimated locations and travel route for PUEB 5, captured and released within the Guánica State Forest.

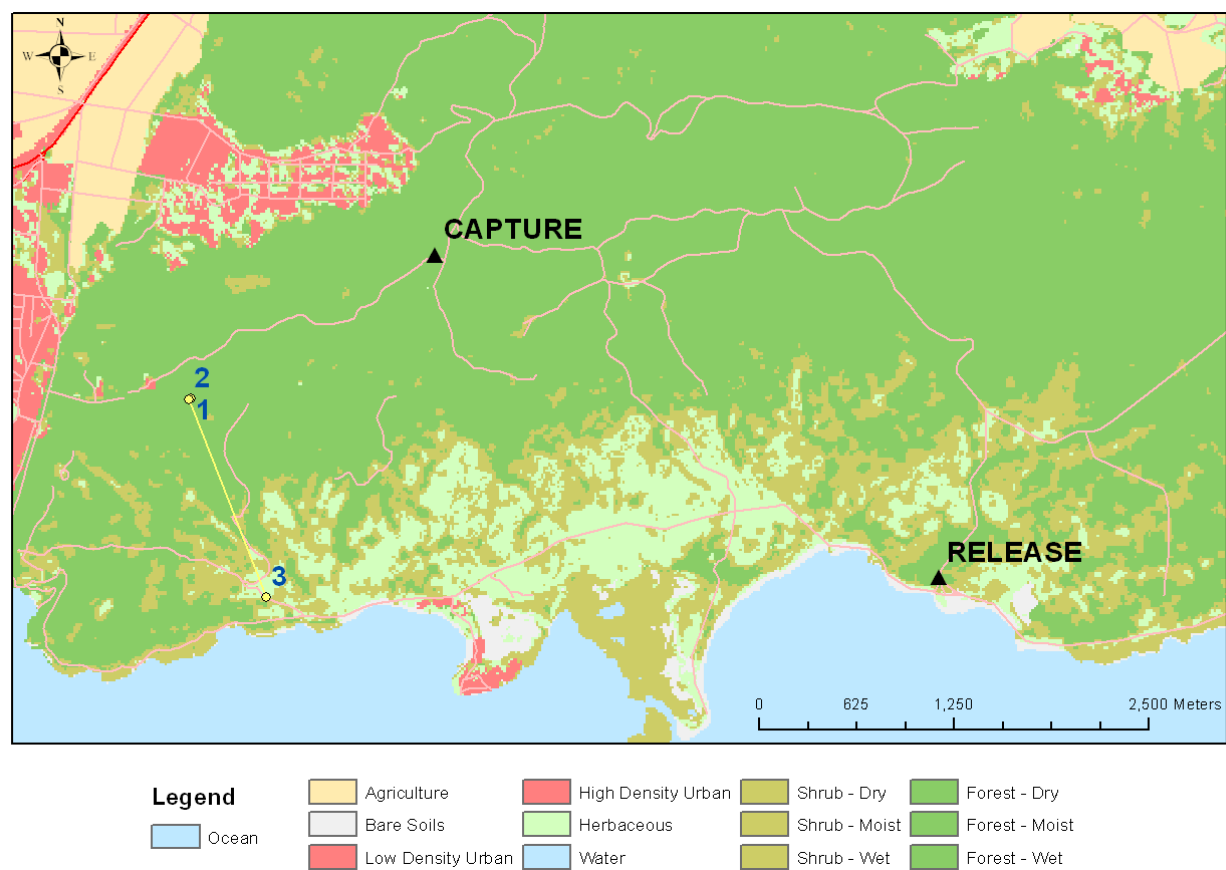


Figure D.5: Estimated locations and travel route for PUEB 6, captured and released within the Guánica State Forest.

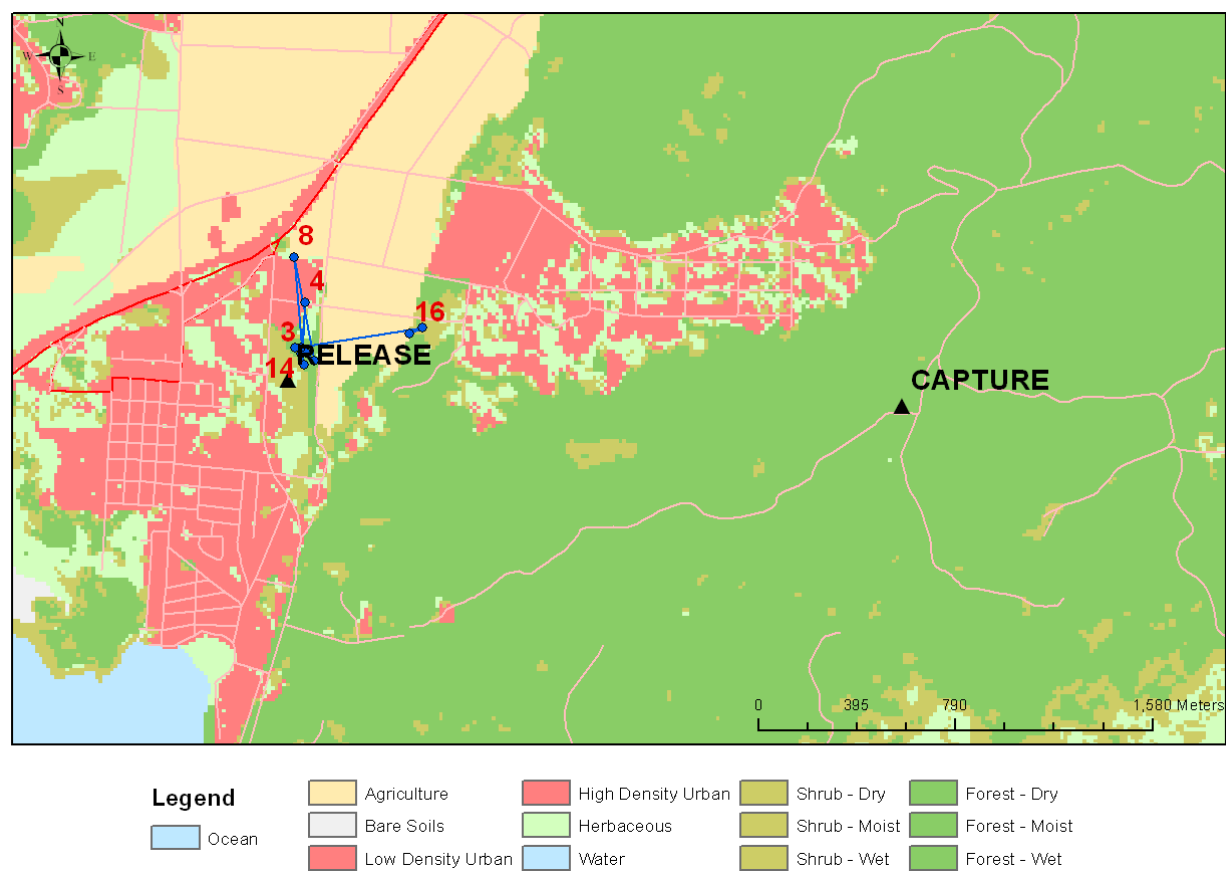


Figure D.6: Estimated locations and travel route for PUEB 7, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

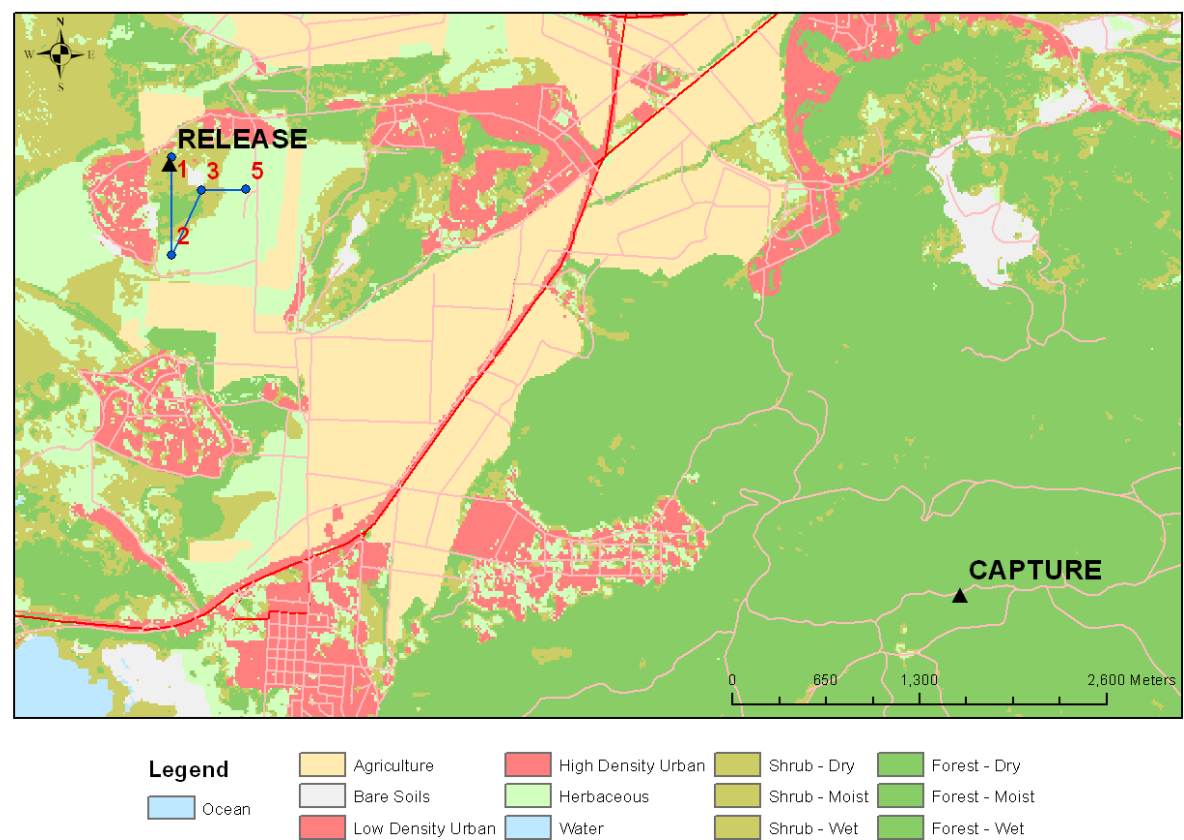


Figure D.7: Estimated locations and travel route for PUEB 8, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

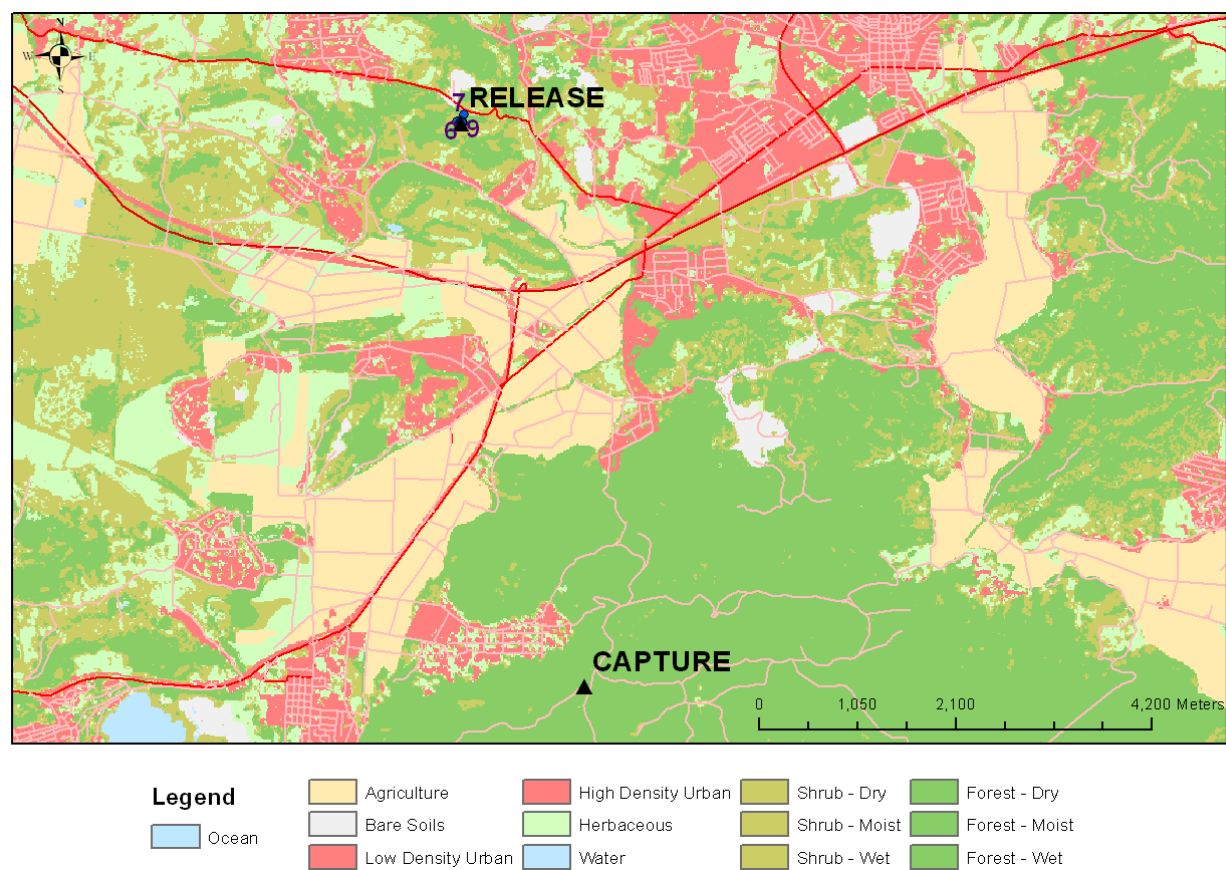


Figure D.8: Estimated locations and travel route for PUEB 9, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

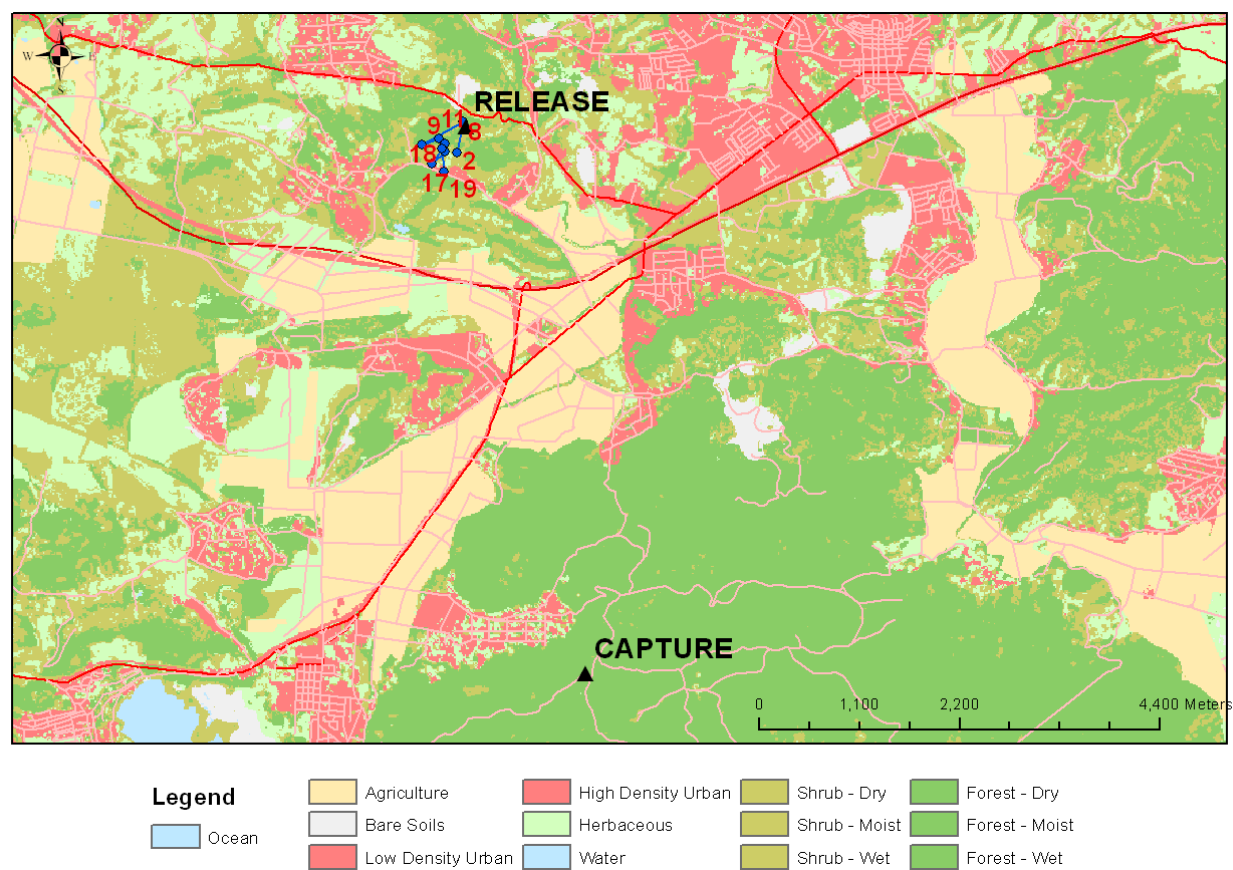


Figure D.9: Estimated locations and travel route for PUEB 10, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

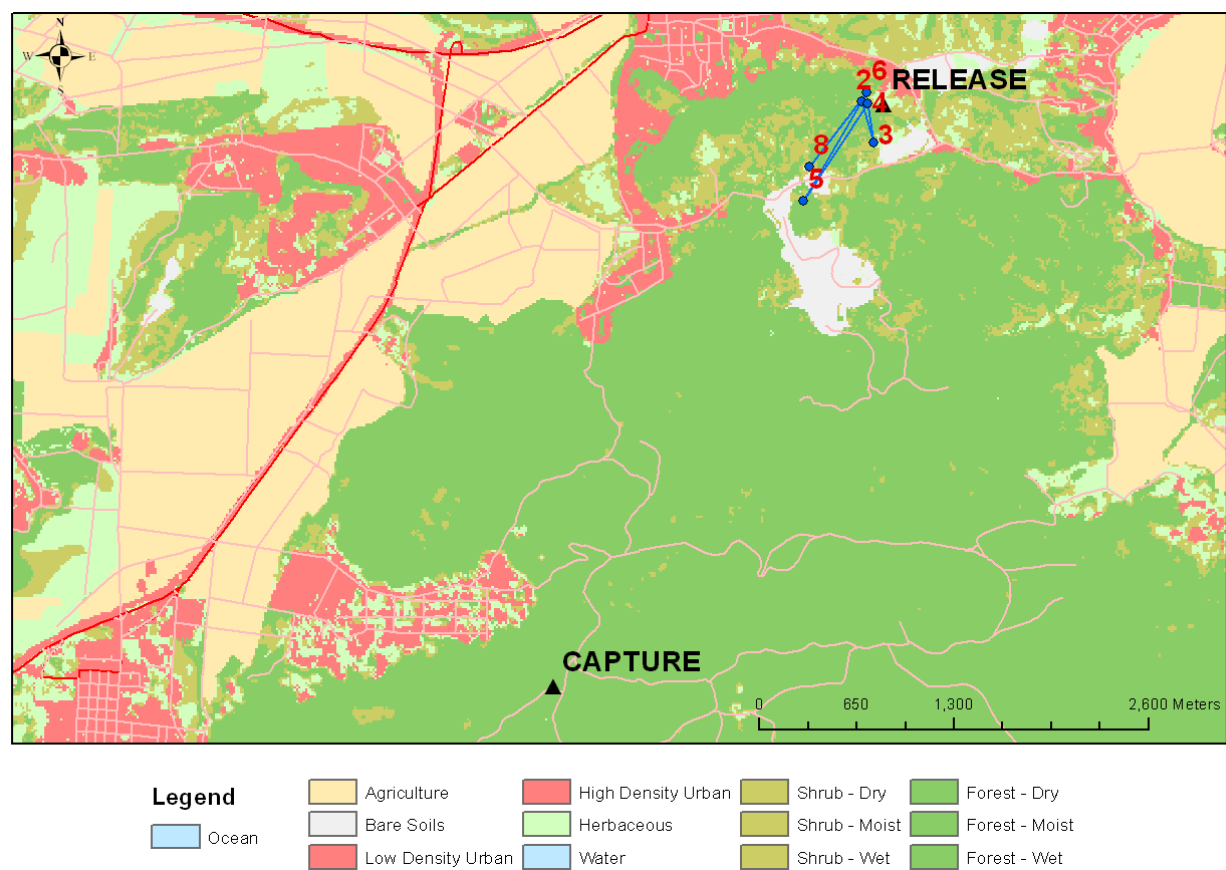


Figure D.10: Estimated locations and travel route for PUEB 11, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

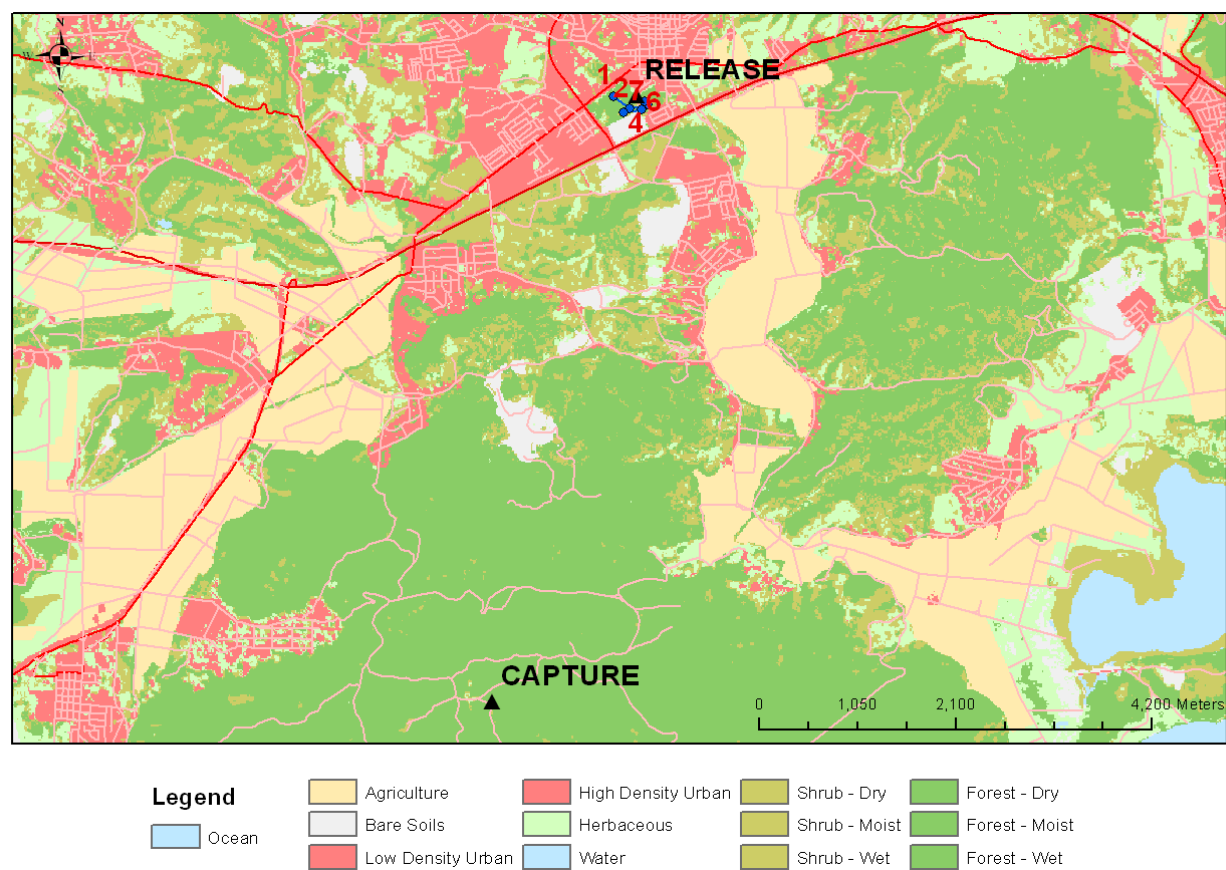


Figure D.11: Estimated locations and travel route for PUEB 12, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

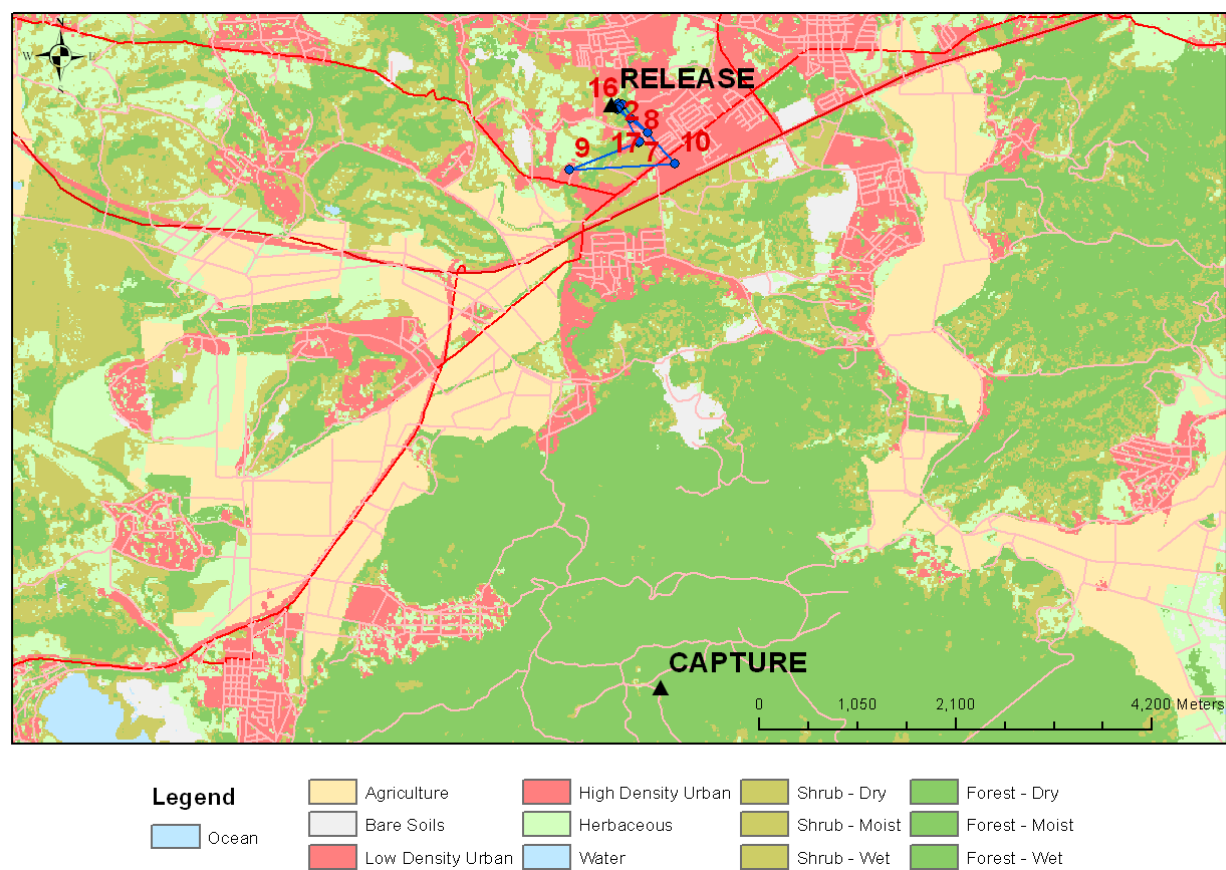


Figure D.12: Estimated locations and travel route for PUEB 13, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

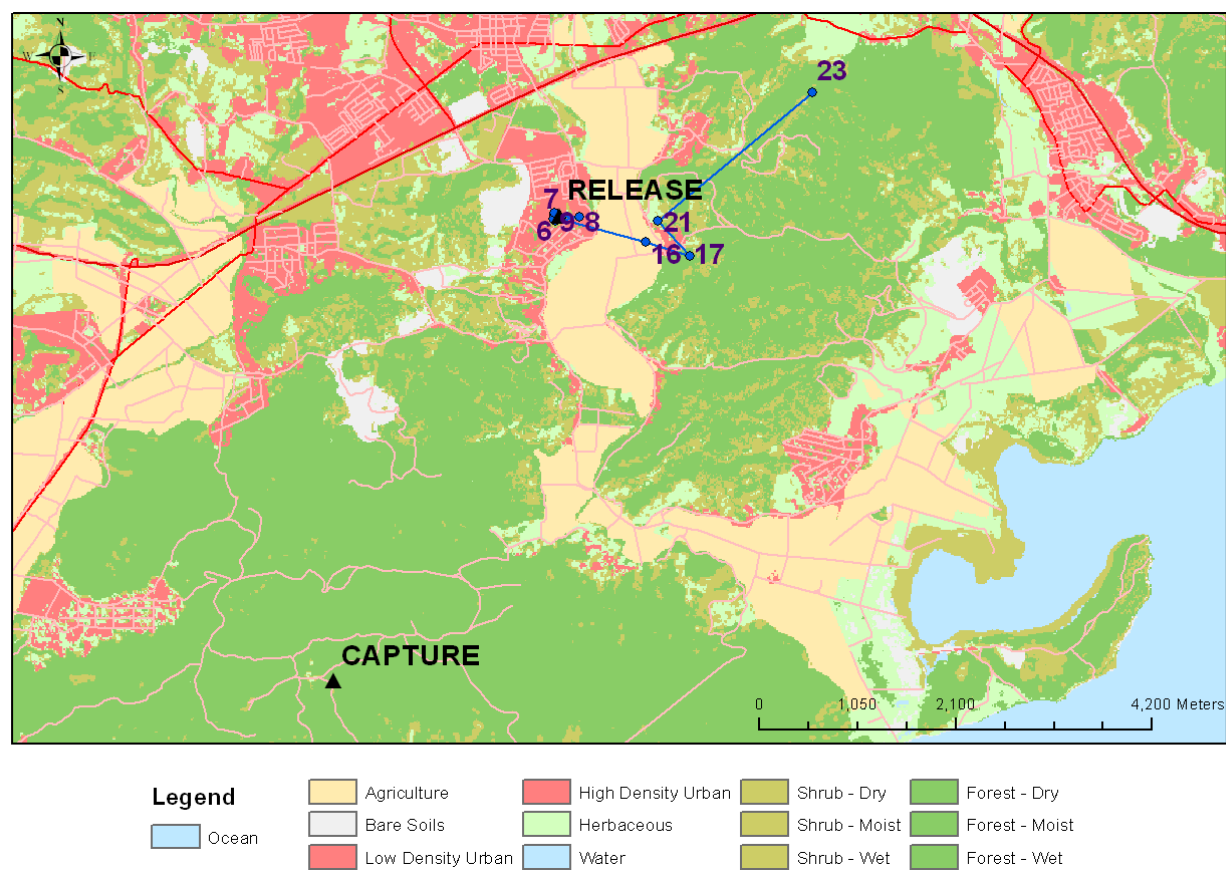


Figure D.13: Estimated locations and travel route for PUEB 14, captured within the Guánica State Forest and released in a forest patch embedded in the urban matrix.

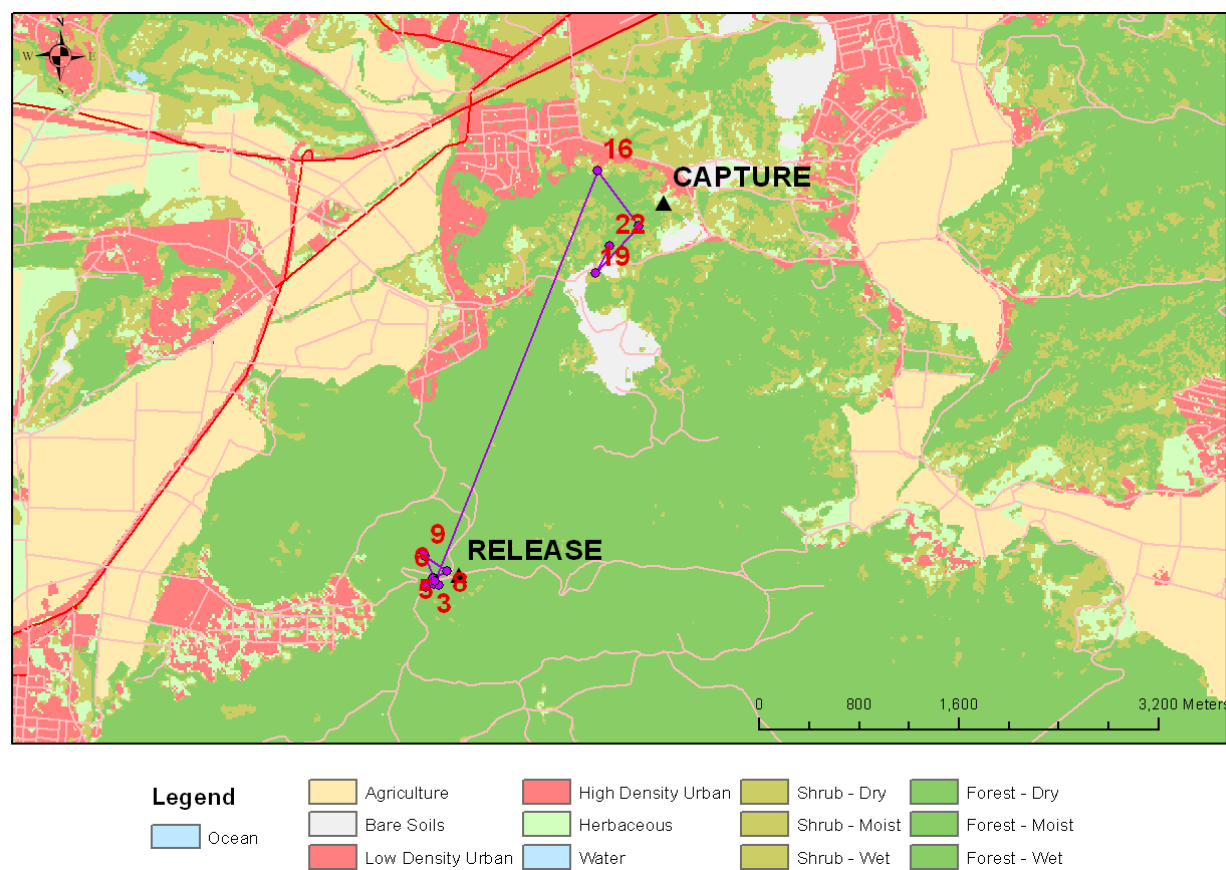


Figure D.14: Estimated locations and travel route for PUEB 15, captured in a forest patch embedded in the urban matrix and released within Guánica State Forest.

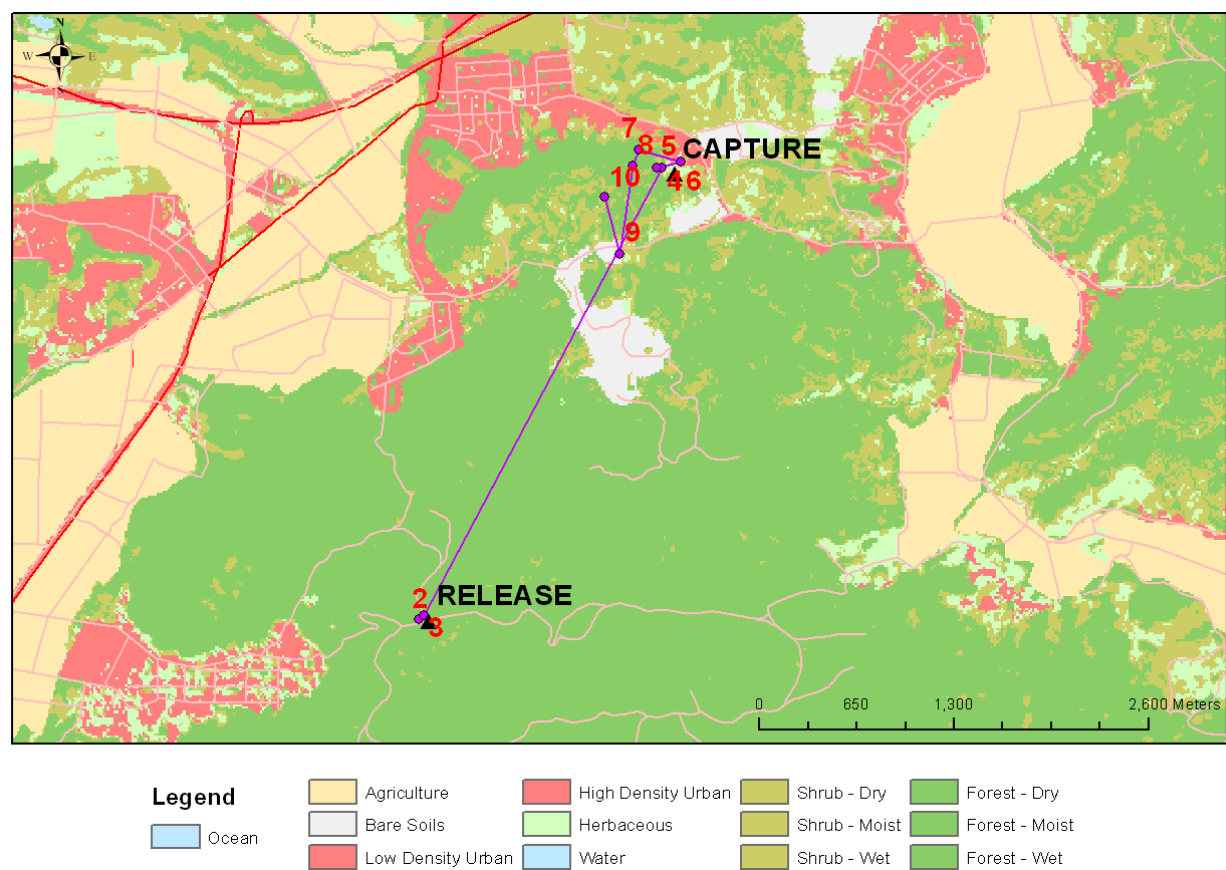


Figure D.15: Estimated locations and travel route for PUEB 16, captured in a forest patch embedded in the urban matrix and released within Guánica State Forest.

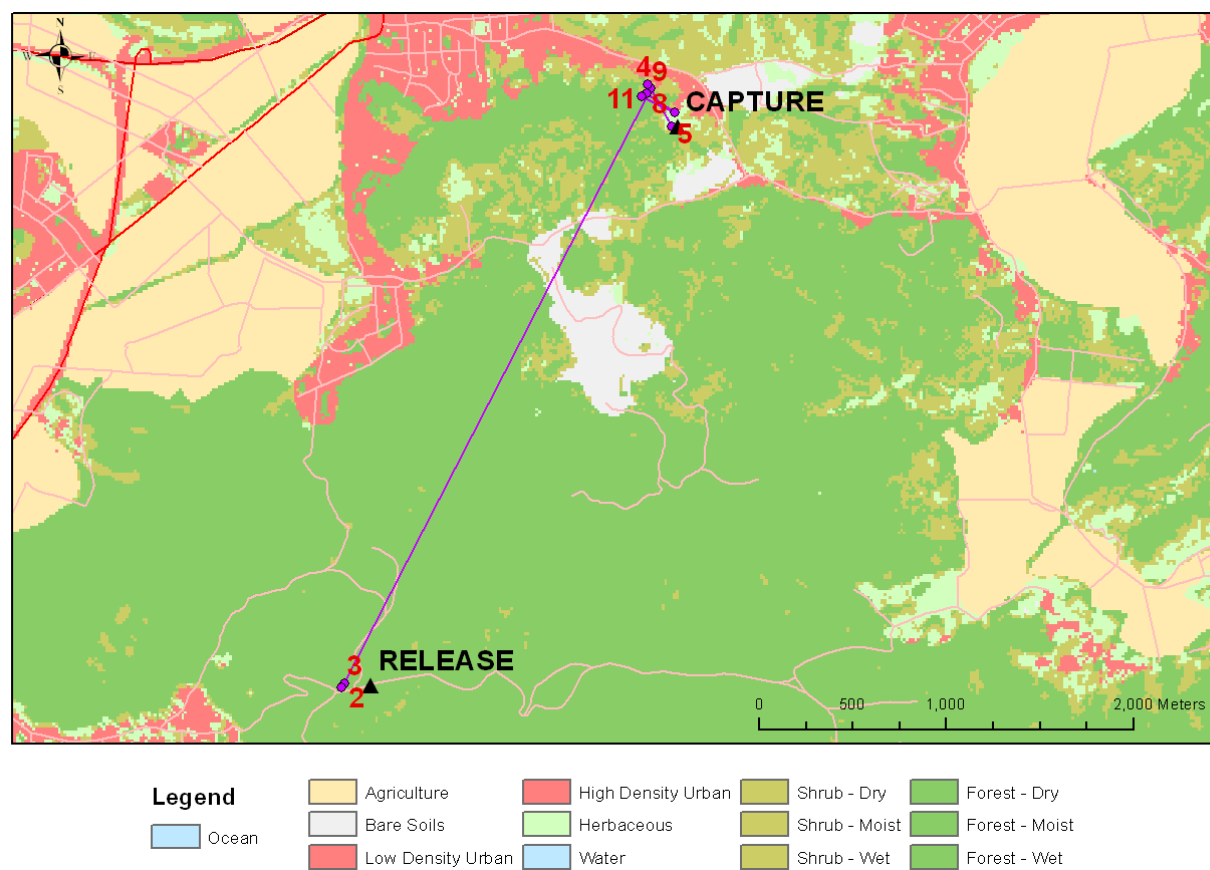


Figure D.16: Estimated locations and travel route for PUEB 17, captured in a forest patch embedded in the urban matrix and released within Guánica State Forest.

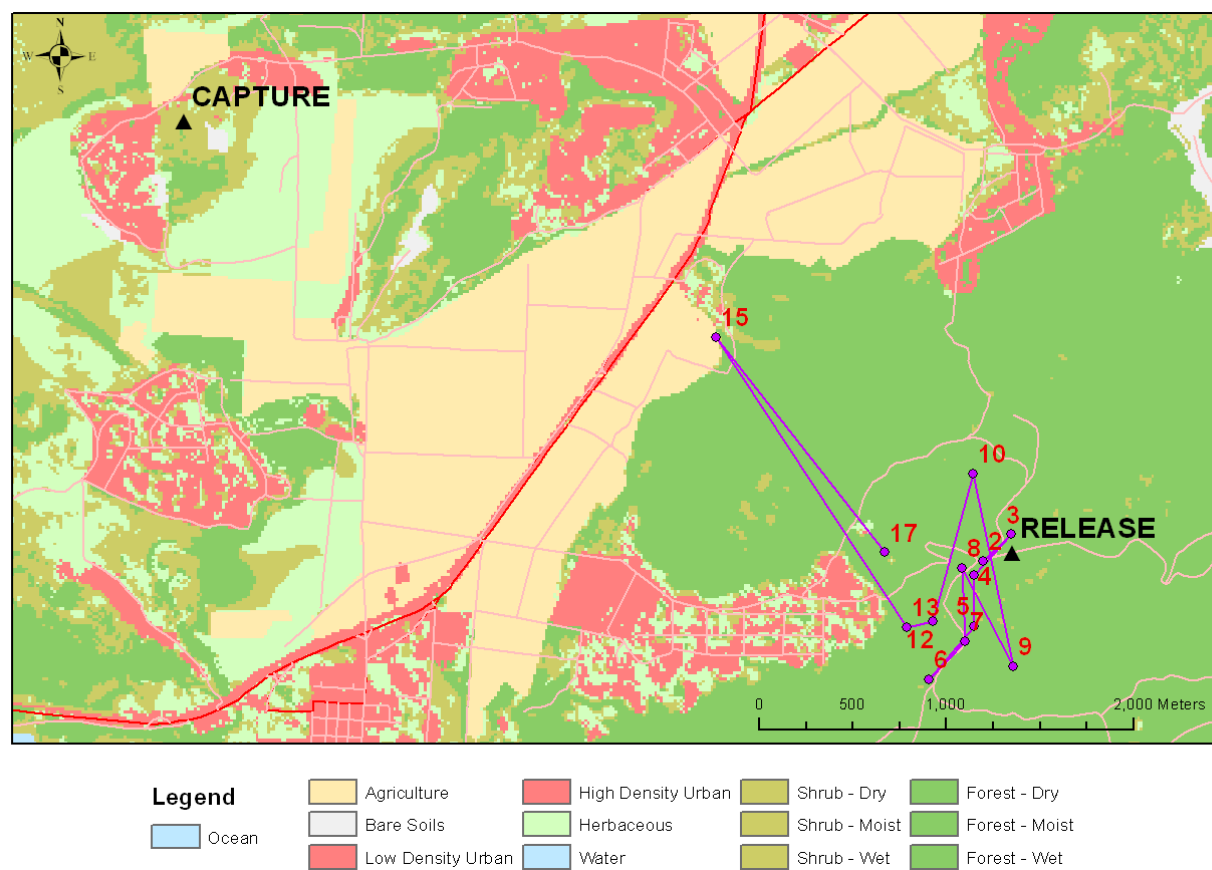


Figure D.17: Estimated locations and travel route for PUEB 18, captured in a forest patch embedded in the urban matrix and released within Guánica State Forest.

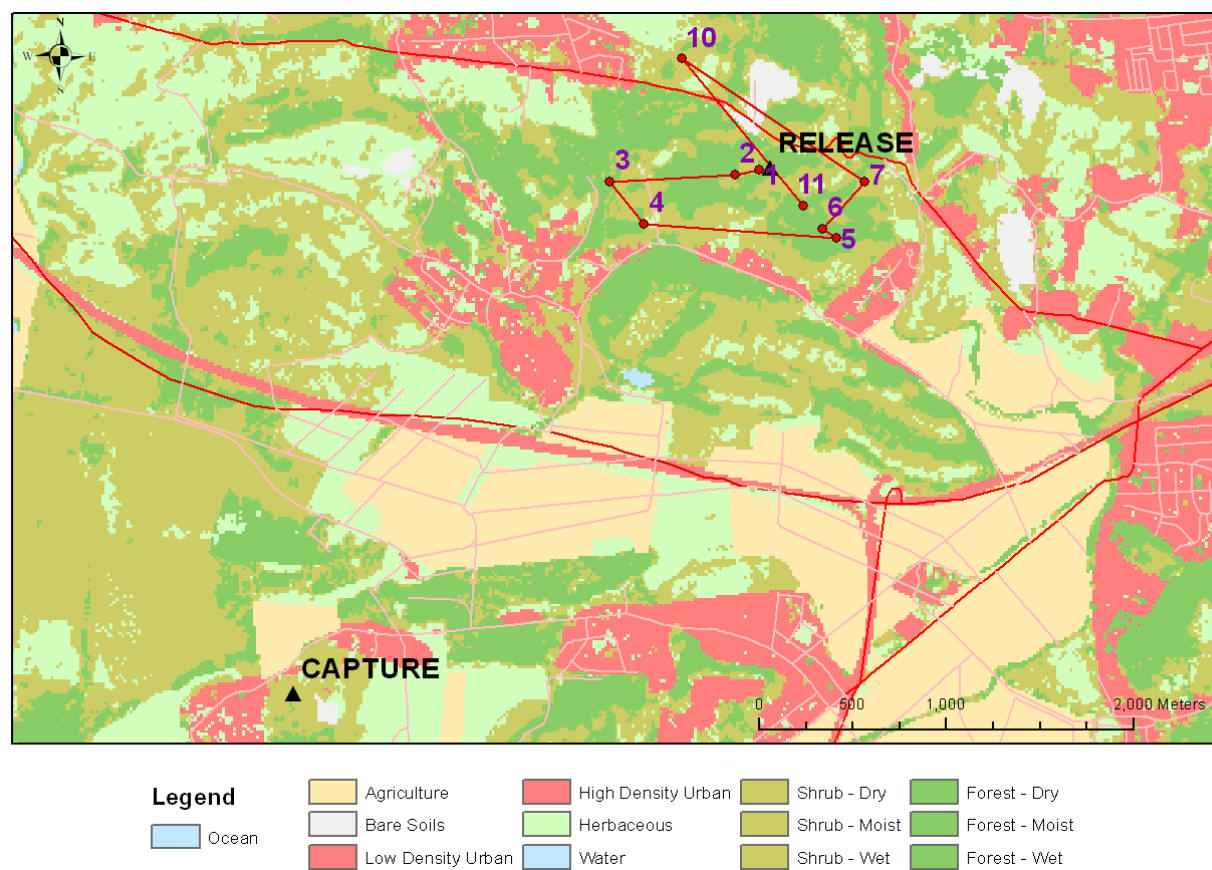


Figure D.18: Estimated locations and travel route for PUEB 19, captured and released within forest patches embedded in the urban matrix.

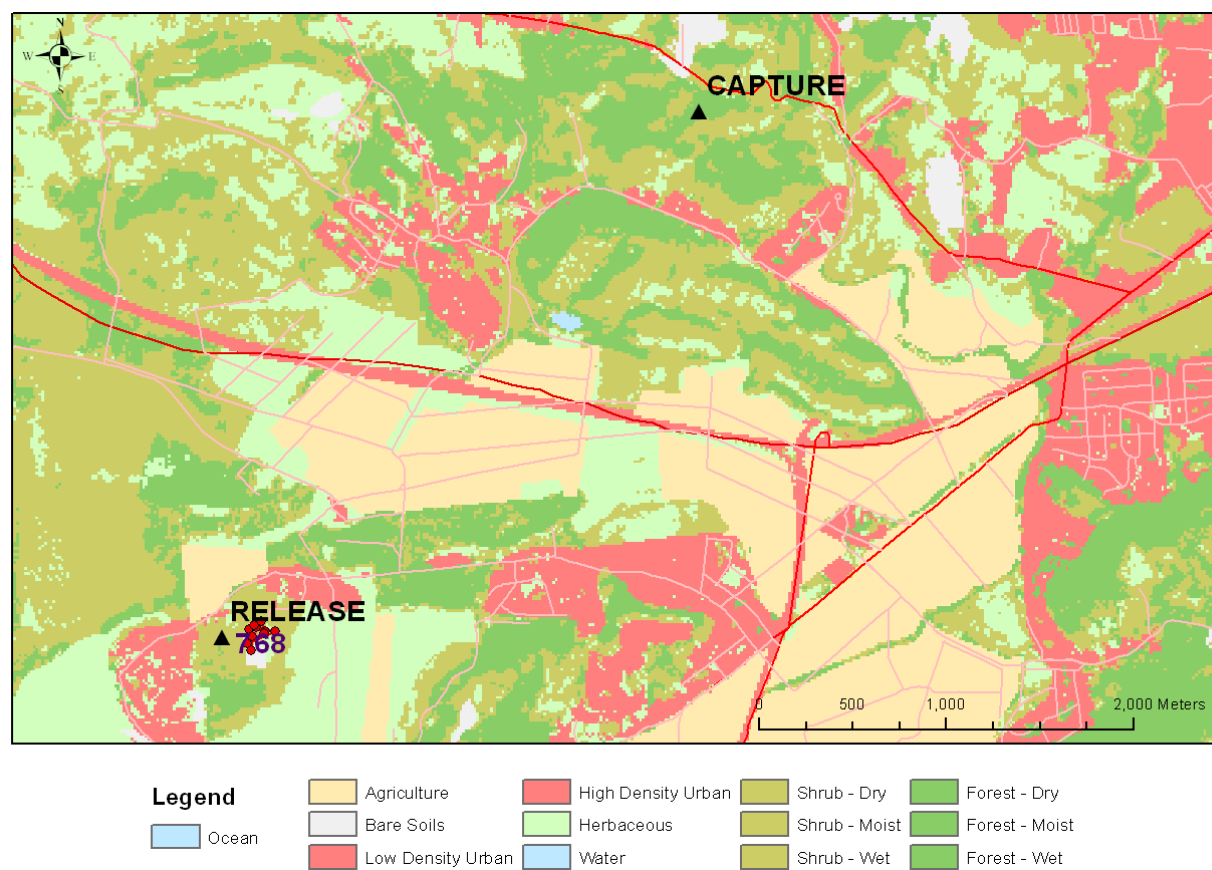


Figure D.19: Estimated locations and travel route for PUEB 20, captured and released within forest patches embedded in the urban matrix.

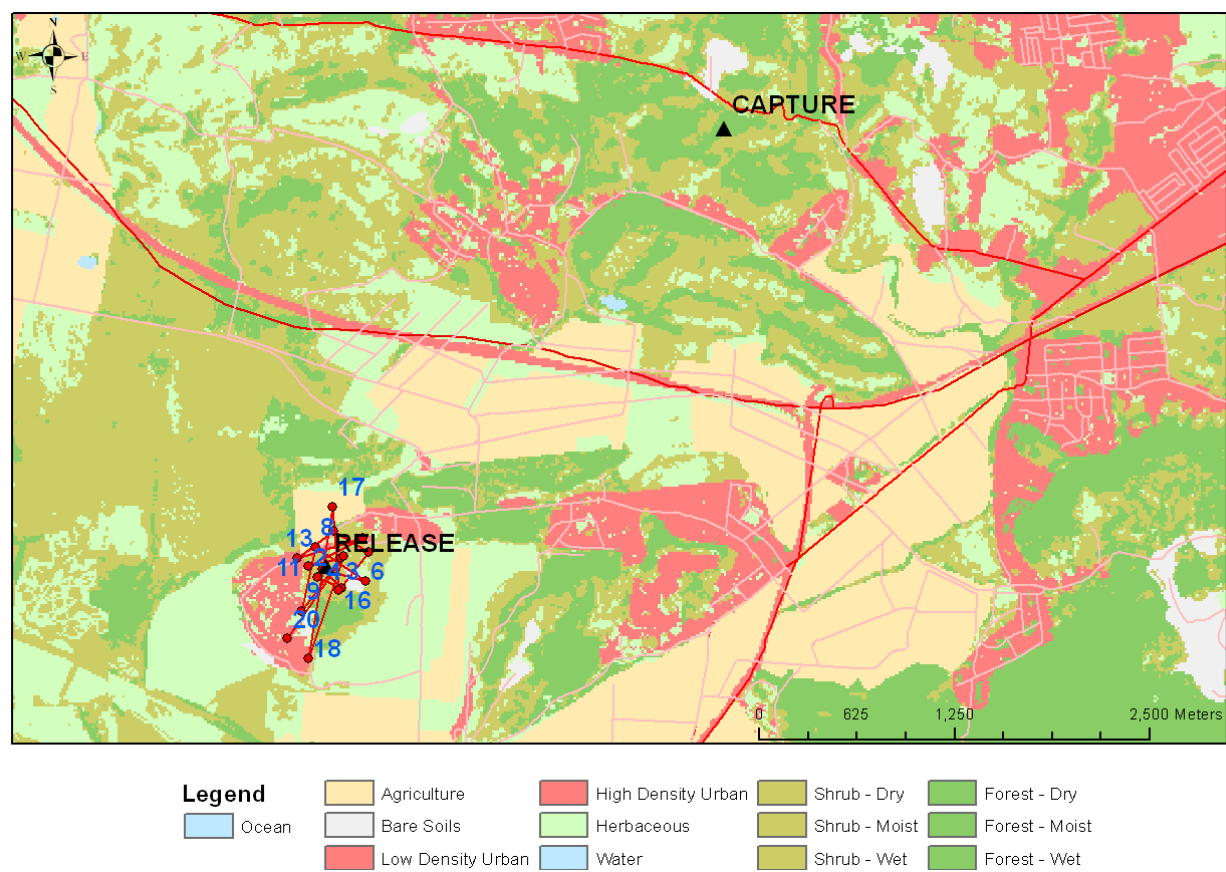


Figure D.20: Estimated locations and travel route for PUEB 21, captured and released within forest patches embedded in the urban matrix.

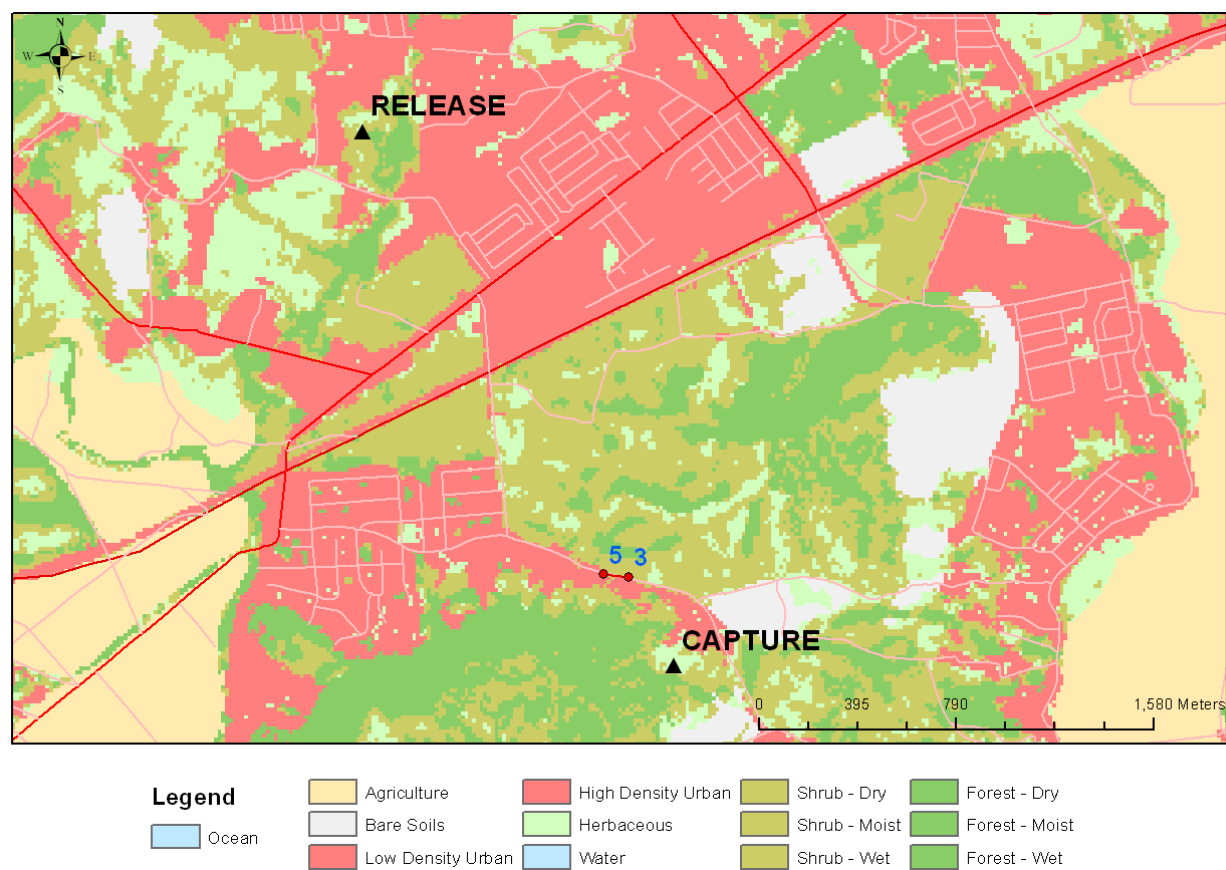


Figure D.21: Estimated locations and travel route for PUEB 22, captured and released within forest patches embedded in the urban matrix.

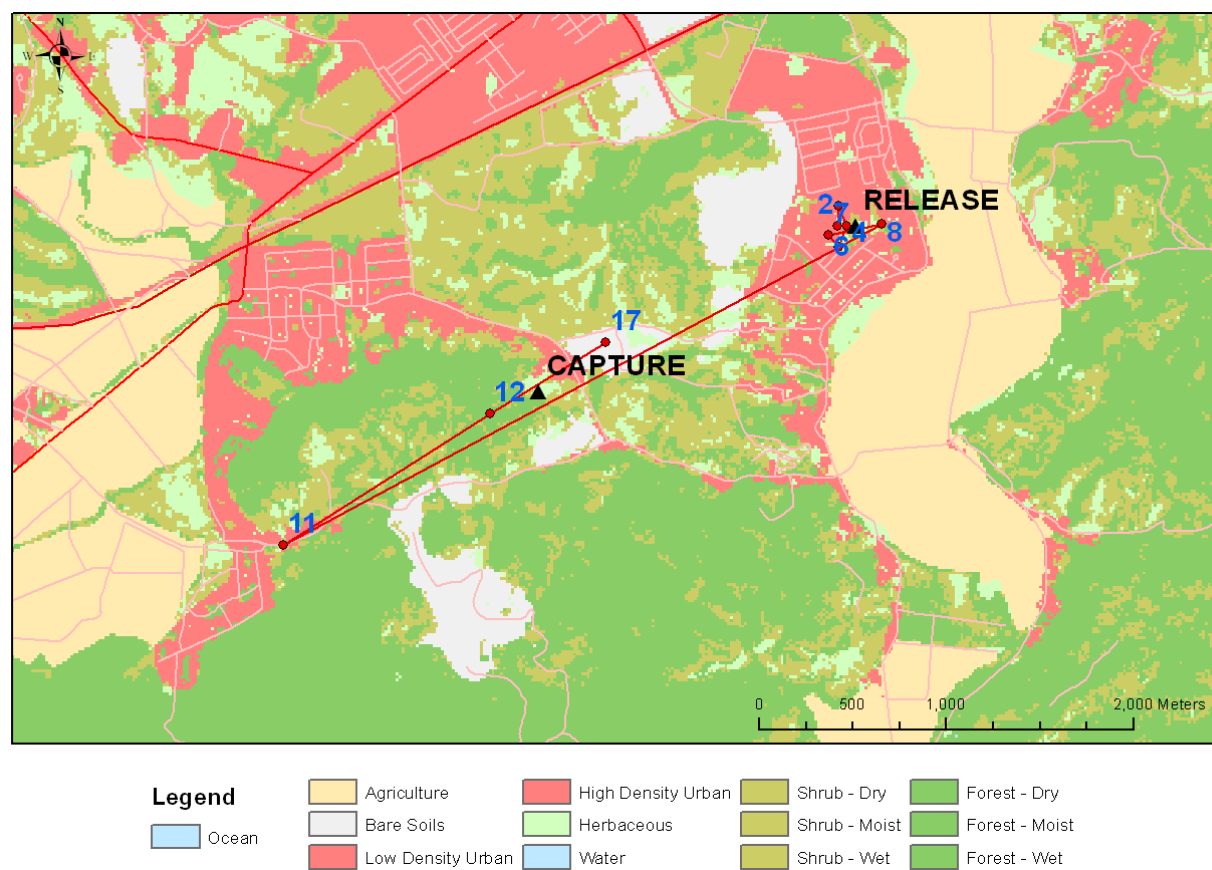


Figure D.22: Estimated locations and travel route for PUEB 23, captured and released within forest patches embedded in the urban matrix.

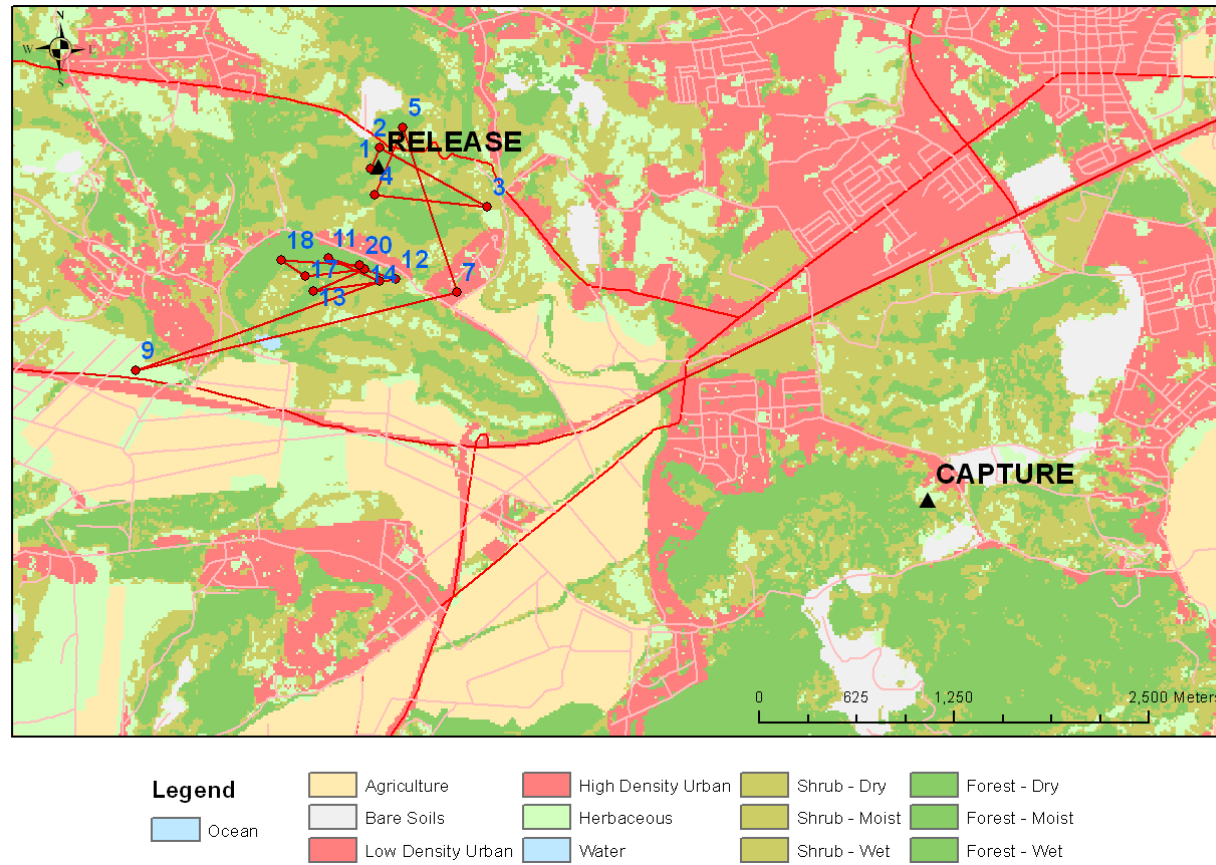


Figure D.23: Estimated locations and travel route for PUEB 24, captured and released within forest patches embedded in the urban matrix.

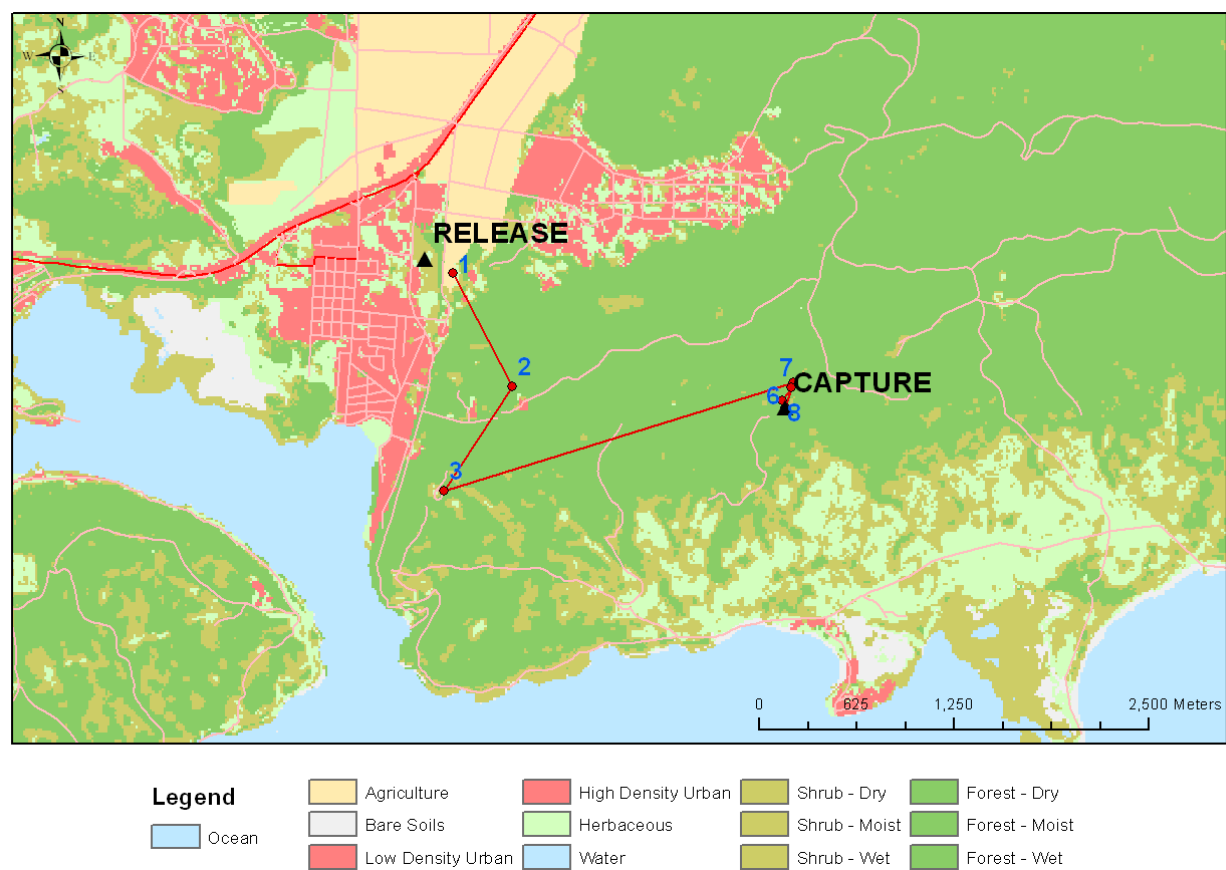


Figure D.24: Estimated locations and travel route for PUEB 25, captured in a forest patch embedded in the urban matrix and released within Guánica State Forest.

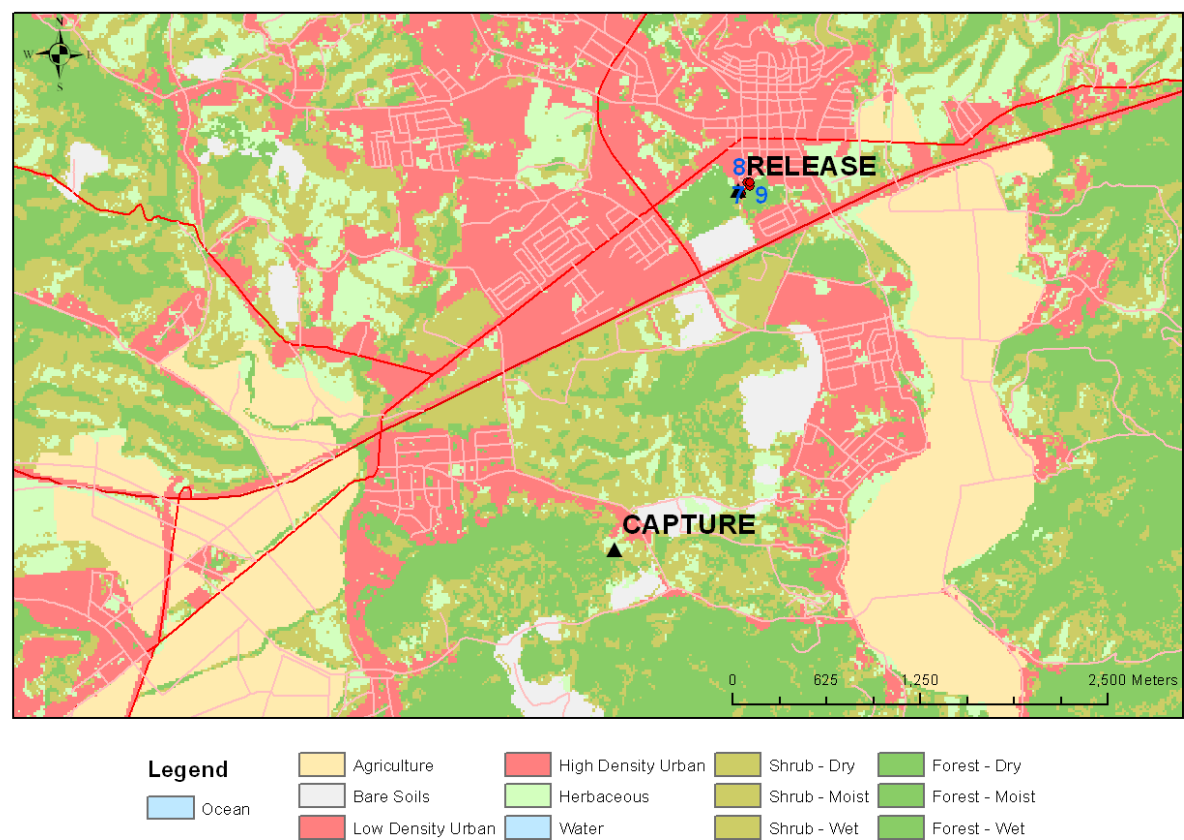


Figure D.25: Estimated locations and travel route for PUEB 26, captured and released within forest patches embedded in the urban matrix.

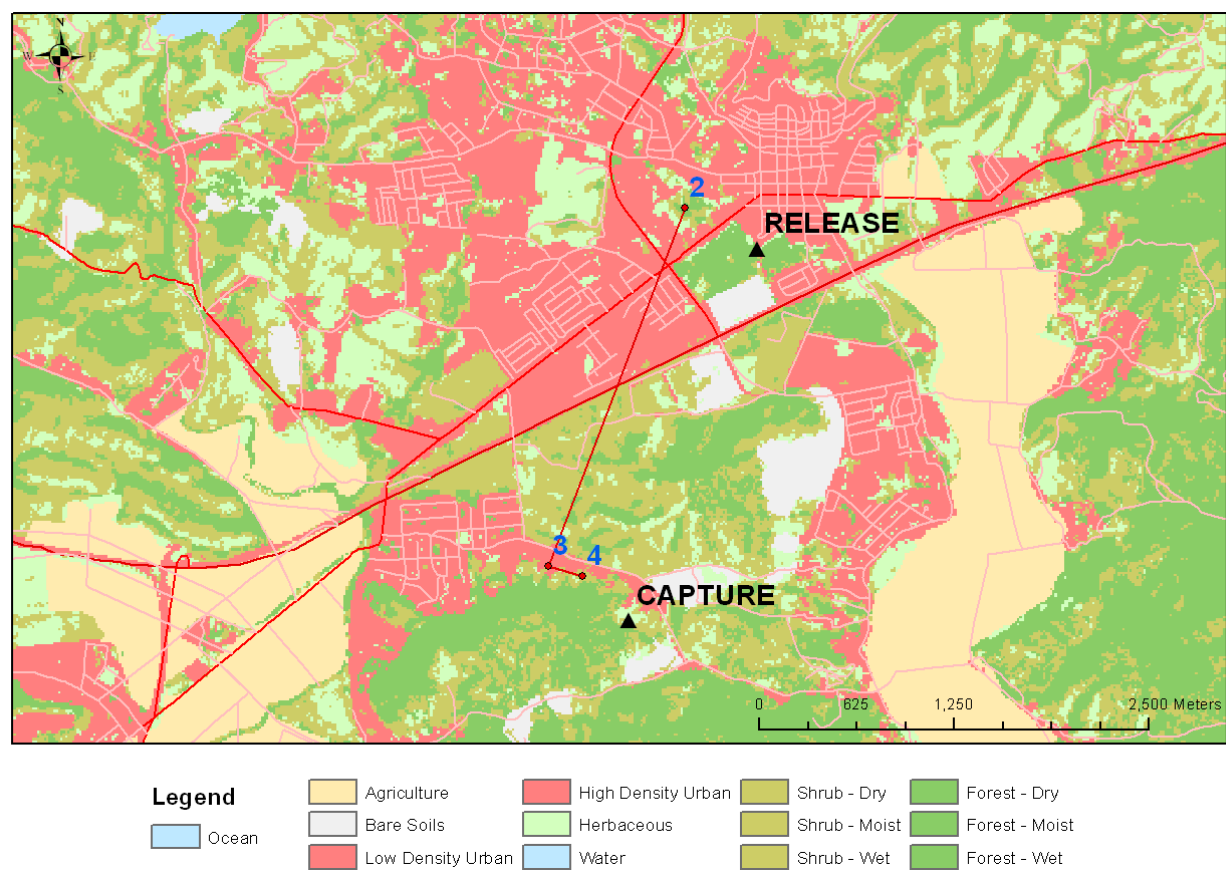


Figure D.26: Estimated locations and travel route for PUEB 28, captured and released within forest patches embedded in the urban matrix.