OF PALMS, PARASITES, AND PEOPLE:
INTERSPECIES ENTANGLEMENTS AND IMPLICATIONS FOR CHAGAS DISEASE TRANSMISSION IN CENTRAL PANAMA

by

CAITLIN E. MERTZLUFFT

(Under the Direction of Marguerite Madden)

ABSTRACT

Zoonotic diseases, transmissible between humans and other animal species, represent a growing global health concern, comprising a majority of newly discovered or newly evolved emerging infectious diseases. Drawing from socionatural and assemblage literatures, I approach zoonotic disease research through a focus on interrelated human and nonhuman networks of actors. Using a mixed methods approach, I examine the spaces of interaction where species meet, and assess the socioeconomic and ecological drivers that dictate multispecies individuals' interactions. This dissertation examines the impact of anthropogenic landscape change on human-environmental interaction associated with the transmission of Chagas disease, or American Trypanosomiasis. Specifically, I focus on human interaction with, and influence on, the distribution of the royal palm species *Attalea butyracea.* This palm species is the preferred habitat of the primary insect carrier of Chagas disease in Panama. Human-*A. butyracea* interaction and co-influence is well documented. Human communities throughout Central and South America, and the Caribbean, utilize this palm species for a number of goods and services.

Additionally, increased *A. butyracea* propagation is associated with landscape disturbance linked to anthropogenic agricultural practices. Rather than a linear approach to disease transmission, wherein a human population becomes ill due to novel exposure to pathogens through their disruption of a "natural” environment, this research suggests that zoonotic disease is co-produced through a complex and iterative interaction of human and non-human agents.

INDEX WORDS: Panama, zoonoses, palms, One Health, neglected tropical diseases, remote sensing, *Attalea butyracea*, Chagas disease, medical geography, species distribution models

OF PALMS, PARASITES, AND PEOPLE:
INTERSPECIES ENTANGLEMENTS AND IMPLICATIONS FOR CHAGAS DISEASE TRANSMISSION IN CENTRAL PANAMA

by

CAITLIN E. MERTZLUFFT
BS, University of Georgia, 2008
MPH, Emory University, 2011

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2020

OF PALMS, PARASITES, AND PEOPLE:

INTERSPECIES ENTANGLEMENTS AND IMPLICATIONS FOR CHAGAS DISEASE TRANSMISSION IN CENTRAL PANAMA

by

CAITLIN E. MERTZLUFFT

Major Professor:	Marguerite Madden
Committee:	Nicole L. Gottdenker Jennifer L. Rice Julie Velásquez Runk Xiaobai A. Yao

Electronic Version Approved:

Ron Walcott
Interim Dean of the Graduate School
The University of Georgia
May 2020

DEDICATION

To my mother, my first and most enthusiastic cheerleader, who knew many years before I did that I would pursue a PhD one day. You always were right. I wish you could be here to see it.

ACKNOWLEDGEMENTS

This research was funded through a UGA-CDC Seed Funding for Collaborative Research grant (as one part of a much larger project); a Tinker Foundation grant through UGA’s Latin American and Caribbean Studies Institute (LACSI); and an Innovated and Interdisciplinary Research Grant from the UGA grad school. I am grateful for this support.

I am also grateful for my Panamanian colleagues and the opportunity to collaborate with such a fantastic group of people, especially: Dr. Jose Calzada, Dr. Azael Saldaña, Tamara Anderson, Milixa Perea, and Chystrie Rigg.

I am indebted to my committee members and other UGA geography and/or ICON faculty who have provided me advice and encouragement along this journey, and for the time, knowledge and energy they devote to these graduate programs. In particular, I wish to acknowledge Dr. Peter Brosius, founder of ICON, who I stumbled into working for nearly fifteen years ago as an undergrad looking for some GIS experience. Thanks for taking me on then, and thank you for all the work you’ve done for ICON.

It’s been a busy several years, and it is not an exaggeration to say that I would not have made it through this program without the unflagging support of my Athens and Atlanta communities. In Athens I’ve been so fortunate to have an established network of old friends and extended family plus a heap of new friends I’ve collected on this venture. Thank you for my continued sanity, especially: Mollie and Steve Armor, for the weekly dinner routine, the O’Toole’s, my forever second family, and the Smilie’s, Megan Westbrook, Molly Williams,

Kishana Taylor, Jennifer Bloodgood, Walker DePuy, Dean Hardy, Danielle Haskett, Gretchen Sneegas and Jonathan Hallemeier, among many others.

In Atlanta, thank you to my Atlanta-based Emory friends, Zach and Kira Barbre, and Jessie and Koo Chung, for all the dinners, board games, and lively conversation. Thank you to my CDC colleagues and GRASP family, who make the commute worthwhile, and to my boss, Andy Dent, for his continued support of this work. Most especially, thank you to the most fantastic group of CDC geography colleagues, who have been my unwavering support system, confidantes, cheerleaders, mentors and friends for several years: Shannon Graham, Stephanie Foster, Kim Elmore, Ginny Lee, Melissa Smith, Janet Heitgard, and Linda Scheib. I don't know where I'd be without all of you, but it wouldn't be pretty. Thank you especially to Kim and Ginny, for my homes away from home!

Last but not least, to my husband Cord, who is unequivocally my favorite thing I've gotten out of this program. Here's to many more adventures together, but maybe fewer at the same time.

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS v

LIST OF TABLES ix

LIST OF FIGURES xi

CHAPTERS

1 INTRODUCTION AND LITERATURE REVIEW 1

- Theoretical Framework 3
- Research Overview 5
- Background 9
- References 20

2 MAXIMUM ENTROPY MODELING OF *ATTALEA BUTYRACEA* PALMS AS AN INDICATOR OF CHAGAS DISEASE RISK IN CENTRAL PANAMA 25

- Abstract 26
- Introduction 27
- Methods 30
- Results 38
- Discussion 40
- Conclusion 45
- References 57

3 LANDSCAPE DISTURBANCE IMPACTS ON *ATTALEA BUTYRACEA* PALM DISTRIBUTION IN CENTRAL PANAMA: IMPLICATIONS FOR CHAGAS DISEASE TRANSMISSION.....63
  Abstract.....64
  Introduction.....65
  Background: Chagas disease in Panama.....67
  Methods.....70
  Results.....80
  Discussion.....86
  Conclusion.....94
  References.....107
4 A QUANTITATIVE ASSESSMENT OF PALM USE AMONG SIX RURAL COMMUNITIES IN CENTRAL PANAMA.....113
  Abstract.....114
  Introduction.....114
  Materials and Methods.....116
  Results.....119
  Discussion.....120
  Conclusion.....125
  References.....129
5 Conclusion.....132
  Summary.....132
  Key Findings.....137

References 142
APPENDIX A. Palm sample distribution by predictive variable for the models considered (Chapter 2) 143
APPENDIX B. Survey questions analyzed for human-palm interaction study (Chapter 4) 145

LIST OF TABLES

Page

Table 2.1: Classification Scheme of the Two Variables Derived from Panama’s Official Land Cover Dataset 46

Table 2.2: Environmental Variables Considered for *A. butyracea* Niche Model 47

Table 2.3: Model Comparison by Palm Observation Type, Complexity, and Regularization Multiplier 48

Table 2.4: Relative Variable Contribution to Final Models 48

Table 3.1: 2012 Panama Land Cover Categories....96

Table 3.2: Field Assessment of Remotely Collected Palm Data 97

Table 3.3: Palm and Palm Cluster Distribution and Density by Land Disturbance Gradient 98

Table 3.4: Average *A. butyracea* Crown Diameter by Disturbance Gradient 98

Table 3.5: Cluster Area by Land Disturbance Gradient 99

Table 3.6: Distance from Probable Households to Palms (m)....99

Table 3.7: Average Distance (m) of Palms and Clusters to Objects of Interest 100

Table 4.1: Independent Variables Considered in the Analysis....126

Table 4.2: Self-reported Palm Use Among Survey Respondents....126

Table 4.3. Self-Reported Use-Type of Palm Materials by Province and Land Cover among Survey Respondents who Use Palms (n=97)....127

Table 4.4: Reported Palm Use by Species....127

Table 4.5: Table 4.5. Logistic Regression Model: Survey Respondents who Report Palm Use for Construction vs. Other Means 127

LIST OF FIGURES

Page

Figure 1.1: Zoonotic disease transmission as a socionatural assemblage....................................18

Figure 1.2: Map of dissertation study sites..19

Figure 2.1: Study area in central Panama...49

Figure 2.2: Ground and satellite image of *A. butyracea* palm...50

Figure 2.3: Systematic sample for data collection...51

Figure 2.4: Jackknife tests provide an estimate of variable contribution to each model..............52

Figure 2.5: Maximum entropy model response curves...53

Figure 2.6: Relative habitat suitability maps of *Attalea butyracea* palms..................................54

Figure 2.7: A comparison of populated areas, based on the 2010 census, with estimated moderate to high *Attalea butyracea* habitat suitability between models..55

Figure 2.8: A comparison of modeled habitat suitability with field-collected palm data.............56

Figure 3.1: Picture of *A. butyracea*..101

Figure 3.2: Study area...102

Figure 3.3: Satellite depiction of *A. butyracea*..103

Figure 3.4: Palm sample and testing sites overlaid on the masked disturbance gradient...........104

Figure 3.5: *A. butyracea* palm wrapped in another tree species...105

Figure 3.6: Proximity of palms and palm clusters to features of interest: buildings, rivers, and other palms/clusters...106

Figure 4.1: Communities surveyed regarding palm use..128

Figure 4.2: Ranch with palm thatch roof 128

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

There are nearly 1,500 unique infectious organisms known to cause disease in humans (Taylor, Latham and Woolhouse 2001). Of these, a majority are zoonotic disease, transmissible between humans and other animal species (Taylor et al. 2001). Zoonoses represent a growing global health concern, comprising a majority of newly discovered or newly evolved emerging infectious diseases, which are occurring at an increased rate (Han, Kramer and Drake 2016, Jones et al. 2008). Outbreaks of Zika virus, Ebola hemorrhagic fever, and the novel coronavirus, SARS-CoV-2, are notable recent examples of zoonotic epidemics and pandemics that have captured global attention just within the span of time it has taken to produce this body of work.

Although many zoonotic diseases pass readily among humans, all originate in human populations via direct interspecies contact. To better understand the context in which interspecies disease transmission occurs, and so to anticipate and prevent disease outbreaks (primarily among human populations), the fields of public health, human medicine, and veterinary medicine have championed an interdisciplinary approach to zoonotic disease. Termed “One Health,” this movement recognizes the existence and inherent interconnection of separate human, animal, and environmental healths, and calls for an interdisciplinary engagement to address threats to these healths in a holistic manner (Atlas and Maloy 2014, King 2008). Since its inception at the turn of the millennium, the reach and popularity of the One Health movement has fomented a surge of integrative research and training programs across academic, governmental, and non-government organizational spheres (Baum et al. 2017, Conrad et al. 2009, Gibbs 2014, King 2008, Rabinowitz et al. 2017).

However, in recent years the One Health framework has been criticized as reductionist and oversimplified. Although zoonotic disease emergence and transmission is linked with behavioral and socio-economic risk factors (Jones et al. 2008), critics suggest the One Health framework neglects to examine the influence of social processes on the spread of disease (Giles-Vernick et al. 2015, King 2010), ignoring or overlooking questions of power, vulnerability, and positionality (Hinchliffe 2015, Paige et al. 2015, Rock and Degeling 2015, Smith, Taylor and Kingsley 2015, Tirado, Gómez and Rocamora 2015, Wallace et al. 2015, Yates-Doerr 2015). Further critiques suggest a lack of disciplinary and epistemological diversity within One Health scholarship (Craddock and Hinchliffe 2015, Zinsstag et al. 2011). The overwhelming majority of One Health research is conducted by disease ecologists, human- and veterinary-health experts, who predominantly consider disease transmission in purely biological terms (Giles-Vernick et al. 2015, King 2008). This disciplinary bias has prioritized human and animal health, undermining a clear definition or equal focus on what is meant by the health of “the environment” or “nature” within the One Health triad (Antoine-Moussiaux et al. 2019, Essack 2018).

This dissertation examines a more complex and critically-driven zoonotic disease model that incorporates social processes and questions the framings of “the environment” in public health framing of disease transmission. Using a mixed methods approach, I assess the socioeconomic and ecological drivers that dictate key human and nonhuman (inter)actions and distributions through space at community, regional, and provincial scales (defined here as spatial extent) as related to the transmission of Chagas disease, or American Trypanosomiasis, in the context of landscape change in central Panama. I focus this research on the *Attalea butyracea* palm species as simultaneously “the environment” for sylvatic transmission cycles of Chagas disease and an active and dynamic agent in the co-production of Chagas disease in this region. This approach to zoonotic disease research identifies multi-species assemblages that result in the co-production of disease and examine how these assemblages fluctuate at different levels of analysis. Rather than a linear approach to disease transmission, wherein a human population becomes ill due to novel exposure to pathogens through their disruption of a “natural” environment, I examine zoonotic disease as a co-production of complex and iterative interactions of human and non-human networks of actors, which vary across space and time but are inherently influenced by social processes.

Theoretical Framework

Even the relatively straightforward human-to-human transmission of disease is a complex process when examined closely. Disease transmission becomes vastly more complicated when additional species are added to the mix. To characterize the interactions of the many individuals across many species that collectively are involved in the continuous cycle of Chagas disease transmission, and to begin to account for the social and ecological forces that cause these species to interact with each other across a range of spatial extents, some kind of organizational framework is required. To avoid the technocratic and reductionist approach of the One Health framework, this research pulls its organizational framing on interspecies disease transmission from socionatural and assemblage literature.

This research is grounded in the understanding that nature, or the “natural world” is inherently social. This socionatural worldview sees the conceptualization of “nature” and “society” as falsely separate entities, because (1) humans cannot know nature apart from ourselves, and must intrinsically understand it, define it and describe it from a human perspective, and (2) because humanity has always repurposed or redefined our surroundings to serve (typically dominant) social demands (Castree 2001). By dissolving the false nature-society dualism, we can move away from the knee-jerk and negative reaction that anthropogenic changes are inherently “unnatural,” while recognizing the innate inequality in their cause and effects (Castree 2001). A socionatural approach asks us to view humans as *part of* rather than *acting on* nature, which allows us to investigate the nuances of the drivers and consequences of interspecies interactions, which are heterogeneously realized across different species, across power and social inequalities, and at different scales (Castree 2001, Robbins 2011).

This interwoven socionature does not imply that our surroundings and fellow life forms are necessarily only passive and reactionary objects, however; we are influenced and changed by our environment even as we recreate it to serve our purposes. The co-production of Chagas disease is one outcome of one example of multi-species engagement within a dynamic and multi-scalar socionature influenced by specific social, political, economic and ecological drivers. Assemblage theory provides a framework to characterize both the *structure* and *process* by which socionatures are remade, by organizing this complex interaction and it’s driving forces as an interconnected and dynamic network of actors (Figure 1.1). I draw from assemblage scholarship to investigate the “contact zones” where the multiple species necessarily involved in vector borne Chagas disease transmission meet (Haraway 2013). This research follows the style and strategy of what Robbins and Marks call “intimate” assemblages, which stress the way interspecies individuals are mutually remade through close interaction with each other (Robbins and Marks 2010).

Research Overview

The research described in this dissertation is a subset of a larger interdisciplinary research project funded through a 2014 Seed Funding in Support of Collaborative Research grant offered jointly through the University of Georgia (UGA) and the U.S. Centers for Disease Control and Prevention (CDC), titled “Integrating Anthropology, Ecoepidemiology, and Veterinary Science to Define Drivers of Vector-Borne Zoonotic Disease Transmission in Changing Landscapes” (hereafter: UGA-CDC Seed Funding Project). This funding enabled a collaboration between members of the Geospatial Research, Analysis, and Services Program (GRASP) of the U.S. Agency for Toxic Substances and Disease Registry (ATSDR); multiple UGA departments and faculty (Susan Tanner and Julie Velasquez Runk, Anthropology; Nicole Gottdenker, Veterinary Pathology); and partners from the Gorgas Memorial Institute for Health Studies (ICGES) in Panama City, Panama (Dyer et al. 2016). The goals of the UGA-CDC Seed Funding Project were to identify socioeconomic and ecological variables driving Chagas disease and acute cutaneous leishmaniasis transmission across a range of spatial (household, community, regional) and temporal (time since deforestation) scales (Dyer et al. 2016).

The research that comprises the work of this document was not directly included in the UGA-CDC Seed Funding Project proposal, but was purposefully designed to complement and accompany the Chagas disease research defined in the broader project in collaboration with its PIs, through my focus on human-palm interaction, and follows the same spatial and temporal breakdown (Dyer et al. 2016). My dissertation research benefited greatly from the planning, logistics, data collection and sharing agreements, permits, and professional network of this broader project and its collaborators, all of whom appear as co-authors or are acknowledged due to their significant contribution to or facilitation of this research. A majority of the data analyzed and described in following chapters were collected under the permits of the CDC-UGA Seed Funding Project (including UGA IRB:STUDY00001786, and field permits issued by the Panamanian Ministry of the Environment through the facilitation of the Smithsonian Tropical Research Institute) or through the collaborative relationships this project facilitated. These data include field-collected palm data, both that I was able to personally collect and palm locations provided by ICGES colleagues, Panama spatial datasets (census data and 2012 landcover data), satellite imagery, and household survey data. My in-field palm data collection in 2015 and 2016 occurred while I supported the CDC-UGA Seed Funding Project as part of field team collecting observational data and household survey data. I was able to design and contribute a series of palm-use questions to the household survey designed for this larger project, and able to include certain observation and demographic variables in my analysis (Chapter 4) through a data usage agreement. I extended my field work with the CDC-UGA Seed Funding Project to collect additional data through funding from a UGA Innovative and Interdisciplinary Research Grant and a graduate Field Research Award from the Tinker Foundation and UGA's Latin and Caribbean Studies Institute. My 2017 field work was conducted under a second permit awarded through the Panama Ministry of the Environment, which I applied for in collaboration with ICGES colleague Azael Saldaña, through the facilitation of the Smithsonian Tropical Research Institute, where one of our UGA collaborators is a fellow (JVR).

In this dissertation, I use a mixed methods approach to investigate the overall question of how social and ecological drivers influence *A. butyracea* distribution and human-*A. butyracea* interaction across different spatial extents in the context of Chagas disease transmission. I focus on the *A. butyracea* palm as the preferred habitat of triatomine bug species *Rhodnius pallescens*, the primary vector of Chagas disease in central Panama (Romaña et al. 1999). *R. pallescens* are evolutionarily linked with palms and cannot propagate outside of the microclimate of a palm crown, which is most commonly *A. butyracea* (Abad-Franch et al. 2015). Furthermore, the *A. butyracea* palm has a well-documented relationship with human distribution: this species thrives in disturbed landscapes associated with human settlement and agriculture (Henderson, Galeano and Bernal 2019, Wright and Duber 2001), and is sometimes purposefully kept by human communities in otherwise cleared landscapes due to its usefulness for a number of household goods and services (Bernal et al. 2010, Smith 2015). However, close proximity of households to *A. butyracea* palms is linked to increased risk of Chagas disease transmission in some human populations, due to increased likelihood of contact between humans and the infectious bugs that often reside in the palm's crown (Abad-Franch et al. 2015, Vasquez et al. 2004). Each chapter in this research focuses on interspecies dynamics between humans, palms, and vectors at one of three decreasing administrative extents: province-level, a sub-province regional area, and at the household and community level.

Chapter 2 focuses on evaluating *A. butyracea* habitat suitability across two Panamanian provinces and quantifying potential risk of Chagas disease transmission to the inhabitants of this region. We focus our study on Panama and Panama Oeste Provinces, in south central Panama. This region covers an area of approximately 11,200 square kilometers (7,000 square miles) and contains both Panama City, the nation's capital, and most of the Panama Canal. It is also home to a majority of the nation's populace, over half of whom live in the capital alone (Sigler 2014). This paper introduces known climatic and ecological drivers of palm distribution in the neotropics, and further considers anthropogenically-linked landscape variables to address the question: **What social and ecological variables are significantly associated with *A. butyracea* distribution across the Panama and Panama Oeste Provinces of Panama?** This chapter relies on a maximum entropy ecological niche model to hypothesize suitable palm habitat in this region by extrapolating the observed relationship between (satellite-derived) palm locations and social and ecological explanatory variables. We find that anthropogenically-linked land cover and landscape disturbance are some of the highest predictors of *A. butyracea* habitat suitability, in addition to ecological variables soil type and bioclimatic measure, Holdridge life zones. These findings suggest human activity and influence on landscape have a significant influence on Chagas disease transmission at this scale. We find evidence to support that consideration of *A. butyracea*-associated social and ecological drivers may refine existing distribution models of Chagas vector, *R. pallescens*, by accounting for previously unincorporated variables associated with its preferred palm habitat. Furthermore, we find that a majority of the human population in this highly populated region lives in areas of moderate to high *A. butyracea* habitat suitability.

Chapter 3 further examines the relationship between anthropogenic landscape change and *A. butyracea* distribution to address the question: **How is *A. butyracea* distribution, density, and proximity to human settlements influenced by an anthropogenically altered landscape within the Panamá Province of Panama?** We focus on a sub-regional, 300-km^2 heterogenous tropical landscape in the Panama Oeste Province that encompasses a variety of landcover and anthropogenically-linked landscape disturbance, but little to no variation in the ecological variables associated with *A. butyracea* distribution. Using satellite-imagery and a field-verified sample of locations of *A. butyracea* palms, we remotely conducted a complete census of over 50,000 *A. butyracea* palms in this study area. Using spatial analysis (a local Getis-Ord Gi*) we identified stands of closely growing palms as palm “clusters”. Statistical analyses were used to test the relationship between landscape disturbance and (1) the distribution and density of both individual palms and palm clusters (Chi-square tests for Homogeneity and z-tests for proportions), and (2) palm age and proximity to human populations or vector movement corridors (Kruskal-Wallace non-parametric analysis of variance). We found a statistically significant increase in *A. butyracea* palm populations in secondary forest and a significant decrease in pasture and agricultural landscapes. A large number of palms were found near peoples' homes. Our findings indicate probable anthropogenic thinning of palms in agricultural, but not residential, settings. Furthermore, we see evidence in this region that mature *A. butyracea* palms remain in land that has recently otherwise been cleared.

Given this evidence of retained mature palms in cleared landscapes, and given support in the literature that *A. butyracea* palms are sometimes purposefully maintained for their useful properties, Chapter 4 explores human-palm interaction at the household level. We ask: **What socioeconomic and ecological factors influence self-reported use and interactions with palms in Panama?** Using statistical analyses (Chi-square test for Independence) and a generalized linear mixed methods logistic model, we analyzed the relationship between self-reported palm use trends and demographic, environmental, and behavioral characteristics in six communities. Three communities each were selected from Panama Oeste and Panama provinces. Each set of three communities contained one community each positioned in a heavily-forested, semi-forested, and predominately pastoral setting. Our findings indicate that a majority of households utilize palms, and that palm use for construction and as a supplemental food source are the most frequently reported use categories. Four species of palms were reported, including *A. butyracea*. Palm use trends did not vary by province or landscape disturbance category. We were not able to compare households that use palms to households that do not, due to an insufficient sample size in the latter category, but trends among frequent use categories were predominately linked with behavioral, rather than socioeconomic, characteristics. Our findings differ from specific socioeconomic drivers of household palm use found in other case studies, which supports research suggesting that drivers of palm use are hyperlocal. It’s important to recognize that palm use is widely reported across many locations in this region, and that the reasons for this may vary from other communities both within and outside of Panama.

Study Location

This dissertation employs a multiscalar approach, examining interspecies relationships at a decreasing extent from province- to household-level in central Panama (Figure 1.2). The Republic of Panama is known for its connectivity. Situated between Colombia, to the east, and Costa Rica, to the west, this narrow isthmus is the link between the northern and southern halves of the American continent, and through its canal, the connection between Pacific and Atlantic Oceans. This country is a key juxtaposition of naturally and anthropogenically formed passageways.

Panama is located between 7-10º N latitude and 77-83º W longitude, situating it firmly in the tropics of the Western hemisphere. It covers an extent of approximately 77,400 km^2, which is similar in size to the United States' state of South Carolina (Palka 2005). It is home to approximately 3.5 million people as of the 2010 census (INEC 2019), and it has one of the fastest growing economies in Central America (Bakari and Mabrouki 2017). It is bounded by oceans on two sides. The interior of the country is dominated by a discontinuous range of mountains, which extend beyond Panama's borders throughout Central America. Belying its small size and tropical context, which generally results in uniform rain and temperature patterns, Panama's combination of coastal region and varied topography result in highly variable temperature and precipitation patterns throughout the country (Holdridge 1967, Palka 2005).

Background

Overview: Chagas disease

Chagas disease is a major cause of death and disability due to heart disease endemic throughout Central and South America, affecting an estimated 6-8 million individuals (Miranda-Schaeubinger et al. 2019). Although this disease occurs throughout Latin America, risk factors for human infection vary spatially, due to differences in insect carrier and reservoir species' preferred habitats, as well as variability in human lifestyles (Rassi Jr, Rassi and Marin-Neto 2010). Chagas disease specifically refers to infection by the protozoan parasite, *Trypanosoma cruzi*, which is transmitted from mammalian reservoirs to humans through any of several species of triatomine insect (Lent and Wygodzinsky 1979). These insects, also called kissing bugs or assassin bugs, are true bugs, and are blood-sucking species that feed primarily on small mammals (Lent and Wygodzinsky 1979, Vasquez et al. 2004). Vectorborne transmission occurs when the parasite is deposited on the host via infected triatomine feces (after a blood-meal) and enters a break in the potential host's skin (such as the feeding site) or mucosal membrane (Rassi Jr et al. 2010). Some studies suggest that almost all triatomine species maintain enzootic (maintained within animal populations only) cycles of *T. cruzi* among wildlife in both terrestrial and arboreal ecotypes (Noireau, Diosque and Jansen 2009). However, only a handful of these species are known to feed upon human hosts or synanthropic animals, thereby posing a risk of Chagas transmission; these are the vectors that are of primary human and veterinary medicine concern (Rassi Jr et al. 2010).

This research is focused on interspecies assemblages that co-produce vector borne instances of Chagas disease, but it is important to note that other routes of infection are possible, including human-to-human transmission. These infection pathways each have their own socionatural assemblages, which may occur both within or alongside of the networks described in this dissertation, or in different geospatial locales or extents altogether. The *T. cruzi* parasite may be transmitted congenitally (mother to child, through pregnancy), iatrogenically (via blood transfusion or organ transplant), through ingestion (of food or liquid contaminated with triatomine feces, or through consumption of an infected triatomine—considered a likely route of transmission to some domestic animals, such as dogs) (Rassi Jr et al. 2010). Rarely, transmission may also occur via exposure to infected insects or medical equipment in laboratory settings (Rassi Jr et al. 2010, Abad-Franch et al. 2015).

Chagas disease typically presents initially as a short-term febrile illness, which may go unnoticed or untreated due to similarities with many other tropical fevers (Prata 2001). Acute infection is followed by a latent period that may last for several years as the parasite migrates from the host's blood stream and into many different cells (e.g. heart, intestines), where it multiplies (Prata 2001). In a subset of patients, swelling or malfunction of the affected hollow organ occurs, with corresponding high rates of morbidity or mortality (Rassi Jr et al. 2010). Currently, no vaccine exists for Chagas disease, and treatment, where available, is costly and poorly tolerated; in endemic countries, prevention of initial infection by deterring vectors' access to susceptible human hosts is the best-recommended strategy for reducing morbidity and mortality related to this disease (Moncayo and Silveira 2017, Rabinovich et al. 2011, Rodriguez and Loaiza 2017). In non-endemic countries, *T. cruzi* infection is most likely to occur via congenital transmission or through blood transfusion or organ transplant (Coura and Viñas 2010, Schmunis 2007).

Chagas disease in Panama and association with Attalea butyracea *palms*

Ten species of triatominae are found in Panama; however, only two are of primary concern for Chagas transmission: *Triatoma dimidiata* and *Rhodnius pallescens* (Vasquez et al. 2004). Both species are occasionally found in households within Panama, particularly those with palm-thatched roofs; specimens that are found in roofs are more likely to have fed on humans, and are thus more likely to transmit the *T. cruzi* parasite (Calzada et al. 2010, Calzada et al. 2006, Saldaña et al. 2015). The specimens that have been found within households are generally adults, rather than nymphal stages, which implies that domestication of this species has not occurred in Panama (Calzada et al. 2006). Due to the narrow temperature and relative humidity ranges tolerated by these insects, previous research suggests that households do not maintain the microenvironment that these insects require to thrive and propagate (Arboleda et al. 2009, Parra-Henao, Suarez-Escudero and Gonzalez-Caro 2016, Zeledón et al. 2006, Saldaña et al. 2015).

R. pallescens is the dominant of the two Chagas vectors in Panama, and the primary focus of this body of work (Saldaña et al. 2015). Prevalence of the *T. cruzi* parasite within *R. pallescens* is thought to be extremely high, with studies reporting 74.3%-85.4% of sampled bugs infected in tested areas (Gottdenker et al. 2011, Vasquez et al. 2004). Sloths and opossums are the preferred targets of these bugs, however domesticated animals (notably dogs) and humans are also targeted (Calzada et al. 2006, Saldaña et al. 2015, Vasquez et al. 2004). Within Panama, Chagas disease prevention is targeted by the Ministry of Health with active vector control measures as well as recent intra-governmental collaborative measures to streamline and standardize approaches to Chagas prevention and screening (Vasquez et al. 2004). Despite the high prevalence of this parasite found in captured insect vectors, however, the prevalence of disease among human populations in Panama appears quite low at this time: in tested human communities, prevalence ranges from < 1-5.9 % of the population (Calzada et al. 2010, Saldaña et al. 2012). However, due to the habitat preference of the insect species that transmits Chagas in Panama, this disease is likely to be an ongoing risk to humans, and due to human-environmental trends in Panama, may be a larger public health threat in some “hot spot” areas of the country (Calzada et al. 2006, Noireau et al. 2009).

The low prevalence of human infection with Chagas disease in Panama is likely due to the preferred habitat of its main insect vector. In contrast to other Latin American countries where the primary insect vectors of Chagas reside in or near peoples’ houses, the *R. pallescens* bugs in Panama almost exclusively inhabit palm trees (Romaña et al. 1999). In particular, *R. pallescens* bugs are strongly associated with *A. butyracea* palms, which boast large crowns dense with organic material that is well suited to supporting the microclimate these bugs require, and attractive to the mammalian reservoirs on which *R. pallescens* preferentially feed (Abad-Franch et al. 2015, Condit, Pérez and Daguerre 2010, Romaña et al. 1999), although they are occasionally found in other palm species (Rodrigues et al. 2018). Thus, the Chagas-causing *T. cruzi* parasite in Panama is typically confined to sylvatic transmission cycles within palm crowns, absent humans and constrained to insect vectors and arboreal mammal reservoirs (Vasquez et al. 2004). However, while sylvatic transmission cycles are a lesser threat to human populations than the “domiciliary” (household) transmission cycles, sylvatic transmission also makes the disease more difficult to eradicate completely—separating humans from insects that typically live in trees but periodically wander indoors is more difficult on a large scale than say, organizing spraying campaigns to target insects that prefer to live in peoples’ houses. Keeping human populations completely removed from *R. pallescens* in Panama is additionally difficult, because 1) the insects’ preferred habitat of *A. butyracea* palms flourish in anthropogenically disturbed landscapes (Henderson et al. 2019, Wright and Duber 2001, Wright et al. 2000), 2) people use this tree and sometimes purposefully keep it around (Bernal et al. 2010, Olivares and Galeano 2013), and 3) *A. butyracea* palms in otherwise deforested areas, like those found near human communities, are more likely to be inhabited with *R. pallescens* bugs than palms located in contiguous forest (Gottdenker et al. 2011).

It is hypothesized that close proximity of households to *A. butyracea* palms may heighten risk of transition from a sylvatic Chagas transmission cycle to a household cycle; for this reason, human proximity to and engagement with *A. butyracea* is hypothesized to increase risk for contracting Chagas disease in human populations in Panama (Romaña et al. 1999, Vasquez et al. 2004). While presence of *A. butyracea* does not guarantee corresponding presence of *R. pallescens* bugs, because of its affinity for this palm species, a better understanding of the distribution and density of *A. butyracea* may facilitate targeting populations of this key Chagas disease vector. Findings of these analyses will contribute to a better understanding of the complex interactions between social and ecological processes, especially as related to infectious disease transmission, and may help target risk zones of Chagas disease transmission in central Panama.

A brief overview of landscape change in Panama

Because this dissertation draws heavily on landscape change as a social process, it is useful to have context for much of the landscape change that is mentioned in passing in upcoming chapters. Anthropogenic landscape change is not inherently negative, particularly in a socionatural framing. However, it is important to realize that changing landscapes in Panama are neither a new occurrence nor an apolitical one, and has through most of the last several centuries occurred as a result of exogenous political and economic forces.

Panama has undergone centuries of anthropogenic landscape alteration via indigenous and colonialist populations. Prehistoric records place the beginning of human activity on the isthmus to over 11,000 years ago (Cooke 2005, Palka 2005). Vegetation that is today considered not only indigenous to the region, but key staples, including maize and manioc, has been shown to have originated in other areas of the Americas; these were introduced with the arrival and settlement of early humans (Cooke 2005). These populations, originally hunters and gathers, and eventually farmers, are known to have begun altering the landscape in this area through swidden agricultural practices as early as 9,000 years ago; populations were large enough, and this occurred on such scales, that some archaeologists consider the land to have been "considerably modified" (Cooke 2005).

Deforestation trends in Panama in the last five centuries reflect the changing goals and initiatives of global trade and numerous international powers. Cattle have arguably played a key role in the formation of Panama as it exists today, affecting both its cultural and physical development since the 1500s. The locations where Spanish colonialists originally settled, chosen because the rainfall was best suited to cattle ranching, has had direct effects on areas that presently remain forested within the country, which are concentrated in areas where colonial agriculture did not take place (Herrera 2001, Wright and Samaniego 2008).

The United States held significant power in Panama during the 20th century due to its role in the Canal construction and maintenance, and its role in securing Panama’s independence from Colombia. From the early 20th century until 1999 when it was turned over to the Panamanian government, the United States occupied and controlled the former “Canal Zone,” a tract of land that borders the canal and bisected the entirety of Panama, and oversaw its land use. Through intergovernmental treaties, during construction of the canal, the United States was able to appropriate lands “as needed,” which resulted in both the immense alteration of land and water to construct the Panama Canal and the displacement of significant numbers of people (Lasso 2019).

Within the last century, increased deforestation in Panama is attributed to expanded cattle ranching and increased development of land by rural campesino farmers (Heckadon Moreno 1984). In contrast, areas of afforestation are attributed to government maintenance of protected areas and incentives to increase tree cover, and to some extent through conversion of abandoned ranch land to secondary forest, as people move into cities (Wright and Samaniego 2008).

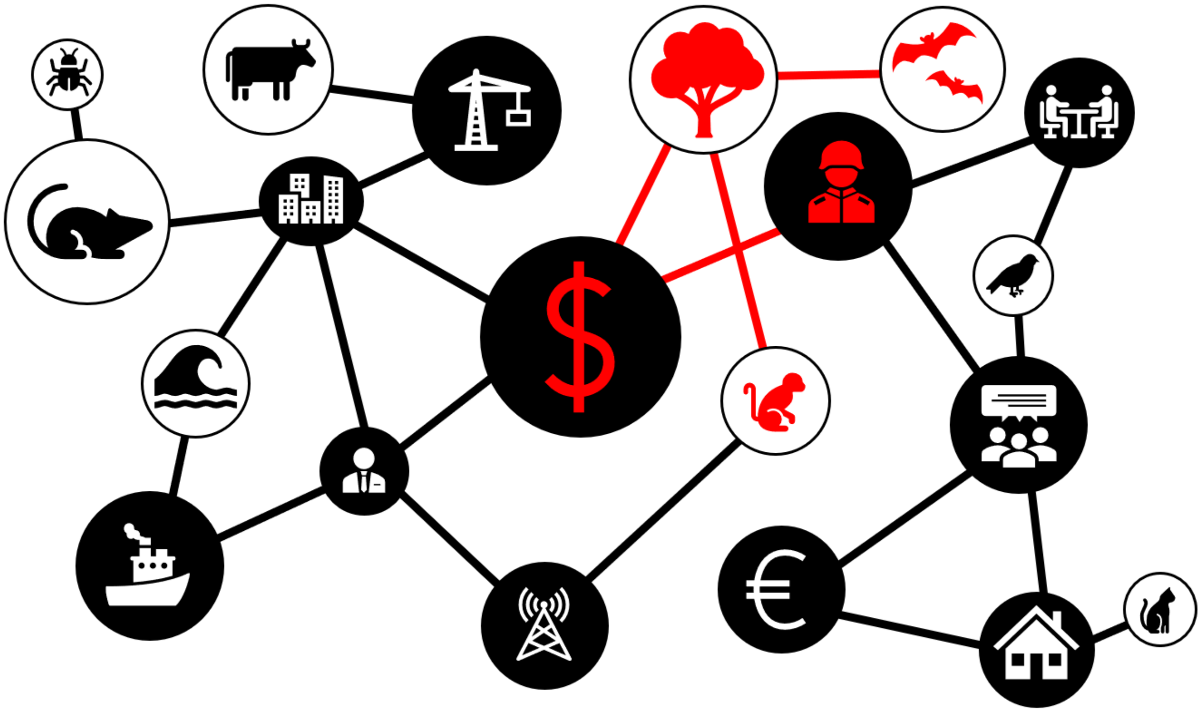

Figure 1.1 Zoonotic disease transmission as a socionatural assemblage: Assemblage theory provides a framework to characterize both the *structure* and *process* by which socionatures are remade, by organizing this complex interaction and it's driving forces as an interconnected and dynamic network of actors. Scale and framing matter in these investigations, as a focus on only one element or extent of a transmission scenario may overlook broader, but connected, social and ecological drivers (shown in red).

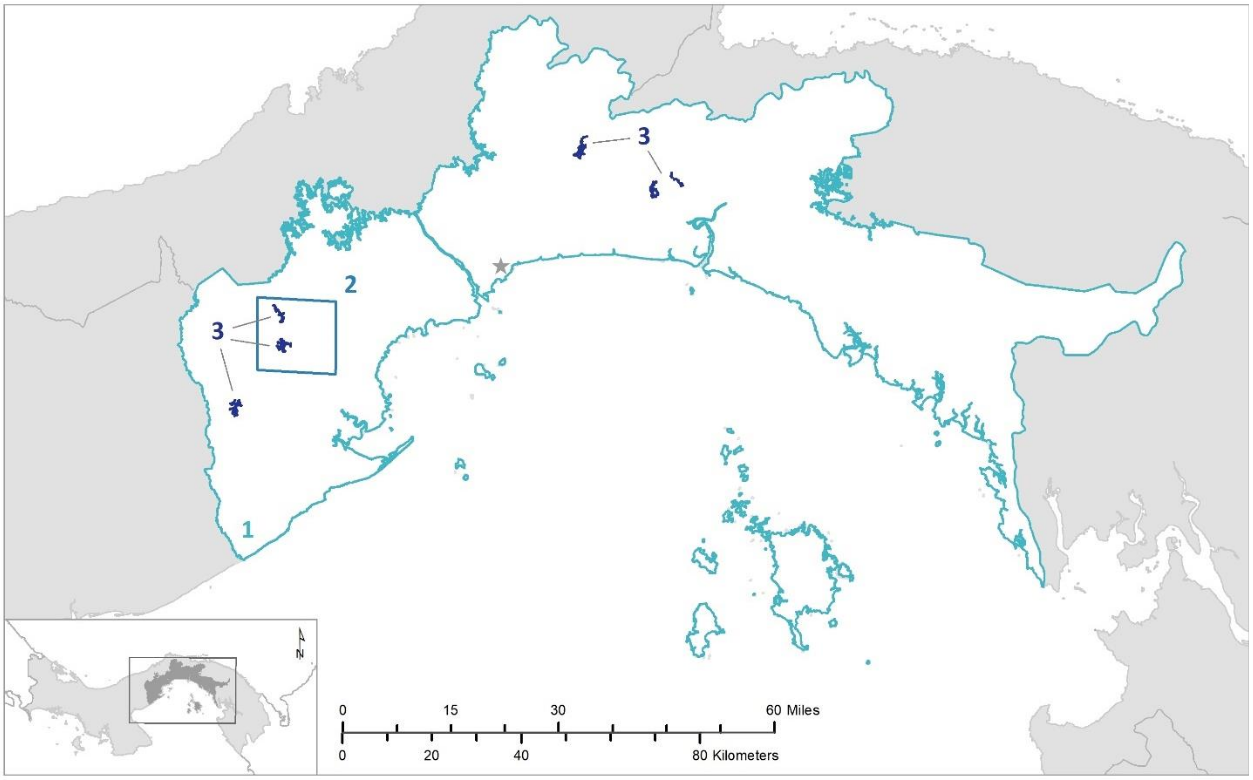

Figure 1.2 Map of dissertation study sites: Chapter 2 focuses on the entire extent of Panama and Panama Oeste Provinces (1); Chapter 3 focuses on a 300km^2 region within the Panama Oeste Province (2); and Chapter 4 focuses on six communities within the Panama and Panama Oeste Provinces (3).

REFERENCES

Abad-Franch, F., M. M. Lima, O. Sarquis, R. Gurgel-Goncalves, M. Sanchez-Martin, J. Calzada, A. Saldana, F. A. Monteiro, F. S. Palomeque, W. S. Santos, V. M. Angulo, L. Esteban, F. B. Dias, L. Diotaiuti, M. E. Bar & N. L. Gottdenker (2015) On palms, bugs, and Chagas disease in the Americas. *Acta Tropica,* 151**,** 126-41.

Antoine-Moussiaux, N., L. J. de Bisthoven, S. Leyens, T. Assmuth, H. Keune, Z. Jakob, J. Huge & M. P. Vanhove (2019) The good, the bad and the ugly: framing debates on nature in a One Health community. *Sustainability Science,* 14**,** 1729-1738.

Arboleda, S., D. E. Gorla, X. Porcasi, A. Saldana, J. Calzada & O. N. Jaramillo (2009) Development of a geographical distribution model of *Rhodnius pallescens* Barber, 1932 using environmental data recorded by remote sensing. *Infect Genet Evol,* 9**,** 441-8.

Atlas, R. M. & S. Maloy. 2014. *One Health: people, animals, and the environment*. ASM Press.

Bakari, S. & M. Mabrouki (2017) Impact of exports and imports on economic growth: new evidence from Panama. *Journal of Smart Economic Growth,* 2**,** 67-79.

Baum, S. E., C. Machalaba, P. Daszak, R. H. Salerno & W. B. Karesh (2017) Evaluating one health: Are we demonstrating effectiveness? *One Health,* 3**,** 5-10.

Bernal, R., G. Galeano, N. García, I. L. Olivares & C. Cocomá (2010) Uses and commercial prospects for the wine palm, *Attalea butyracea,* in Colombia. *Ethnobotany Research and Applications,* 8**,** 255-268.

Calzada, J. E., V. Pineda, J. D. Garisto, F. Samudio, A. M. Santamaria & A. Saldaña (2010) Human trypanosomiasis in the eastern region of the Panama Province: new endemic areas for Chagas disease. *Am J Trop Med Hyg,* 82**,** 580-582.

Calzada, J. E., V. Pineda, E. Montalvo, D. Alvarez, A. M. Santamaria, F. Samudio, V. Bayard, L. Caceres & A. Saldana (2006) Human trypanosome infection and the presence of intradomicile *Rhodnius pallescens* in the western border of the Panama Canal, Panama. *Am J Trop Med Hyg,* 74**,** 762-765.

Castree, N. 2001. Socializing Nature: Theory, Practice, and Politics. In *Social Nature: Theory, Practice, and Politics,* eds. N. Castree & B. Braun. Malden, MA: Blackwell Publishing.

Condit, R., R. Pérez & N. Daguerre. 2010. *Trees of Panama and Costa Rica*. Princeton University Press.

Conrad, P. A., J. A. Mazet, D. Clifford, C. Scott & M. Wilkes (2009) Evolution of a transdisciplinary "One Medicine–One Health" approach to global health education at the University of California, Davis. *Preventive Veterinary Medicine,* 92**,** 268-274.

Cooke, R. (2005) Prehistory of native Americans on the Central American land bridge: Colonization, dispersal, and divergence. *Journal of Archaeological Research,* 13**,** 129-187.

Coura, J. R. & P. A. Viñas (2010) Chagas disease: a new worldwide challenge. *Nature,* 465**,** S6-S7.

Craddock, S. & S. Hinchliffe (2015) One World One Health? Social science engagements with the one medicine agenda. *Social Science and Medicine,* 129**,** 1-4.

Dyer, J. L., S. Tanner, J. Velasquez Runk, C. Mertzlufft, N. Gottdenker (2016) Deforestation, Dogs, and Zoonotic Disease. *Anthropology News*, e92-e95.

Essack, S. Y. (2018) Environment: the neglected component of the one health triad. *The Lancet Planetary Health,* 2**,** e238-e239.

Gibbs, E. P. (2014) The evolution of One Health: a decade of progress and challenges for the future. *Veterinary Record,* 174**,** 85-91.

Giles-Vernick, T., J. Owona-Ntsama, J. Landier & S. Eyangoh (2015) The puzzle of Buruli ulcer transmission, ethno-ecological history and the end of "love" in the Akonolinga district, Cameroon. *Social Science and Medicine,* 129**,** 20-27.

Gottdenker, N. L., J. E. Calzada, A. Saldaña & C. R. Carroll (2011) Association of anthropogenic land use change and increased abundance of the Chagas disease vector *Rhodnius pallescens* in a rural landscape of Panama. *Am J Trop Med Hyg,* 84**,** 70-77.

Han, B. A., A. M. Kramer & J. M. Drake (2016) Global patterns of zoonotic disease in mammals. *Trends Parasitol,* 32**,** 565-577.

Haraway, D. J. 2013. *When species meet*. U of Minnesota Press.

Heckadon Moreno, S. 1984. Panama's expanding cattle front: the Santeno campesinos and the colonization of the forests. University of Essex (RU).

Henderson, A., G. Galeano & R. Bernal. 2019. *Field guide to the palms of the Americas*. Princeton University Press.

Herrera, G. C. (2001) On cattle and ships: Culture, history and sustainable development in Panama. *Environment and History***,** 201-217.

Hinchliffe, S. (2015) More than one world, more than one health: re-configuring interspecies health. *Social Science and Medicine,* 129**,** 28-35.

Holdridge, L. 1967. *Life zone ecology*. San Jose, Costa Rica: Tropical Science Center.

INEC. 2019. Cuadro 10: Población de la República, por Provincia y Comarca indígena: Censos de 1911 a 2010. Instituto Nacional de Estadística y Censo - Panamá.

Jones, K. E., N. G. Patel, M. A. Levy, A. Storeygard, D. Balk, J. L. Gittleman & P. Daszak (2008) Global trends in emerging infectious diseases. *Nature,* 451**,** 990-993.

King, B. (2010) Political ecologies of health. *Progress in Human Geography,* 34**,** 38-55.

King, L. 2008. One world, one health. In *Proceedings of the 2008 World Veterinary Congress*, 1-9.

Lasso, M. 2019. *Erased: The Untold Story of the Panama Canal*. Harvard University Press.

Lent, H. & P. Wygodzinsky (1979) Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. *Bulletin of the American museum of Natural History,* 163**,** 123-520.

Miranda-Schaeubinger, M., I. Chakravarti, K. C. F. Lidani, Z. Omidian, & R. H. Gilman (2019) Systematic Review of the Epidemiology of Chagas Disease in the Americas: a Call for Standardized Reporting of Chagas Disease Prevalence. *Current Tropical Medicine Reports,* 6, 23-34

Moncayo, Á. & A. C. Silveira. 2017. Current epidemiological trends of Chagas disease in Latin America and future challenges: Epidemiology, surveillance, and health policies. In *American Trypanosomiasis, Chagas Disease: One Hundred Years of Research,* eds. J. Telleria & M. Tibayrenc, 59-88. Amsterdam, Netherlands: Elsevier.

Noireau, F., P. Diosque & A. M. Jansen (2009) Trypanosoma cruzi: adaptation to its vectors and its hosts. *Veterinary Research,* 40**,** 1-23.

Olivares, I. & G. Galeano (2013) Leaf and inflorescence production of the wine palm (*Attalea butyracea*) in the dry Magdalena River Valley, Colombia. *Caldasia,* 35**,** 37-48.

Paige, S. B., C. Malavé, E. Mbabazi, J. Mayer & T. L. Goldberg (2015) Uncovering zoonoses awareness in an emerging disease 'hotspot'. *Social Science and Medicine,* 129**,** 78-86.

Palka, E. J. 2005. A geographic overview of Panama. In *The Río Chagres, Panama,* 3-18. Dordrecht: Springer.

Parra-Henao, G., L. C. Suarez-Escudero & S. Gonzalez-Caro (2016) Potential Distribution of Chagas Disease Vectors (Hemiptera, Reduviidae, Triatominae) in Colombia, Based on Ecological Niche Modeling. *J Trop Med,* 2016**,** 1439090.

Prata, A. (2001) Clinical and epidemiological aspects of Chagas disease. *The Lancet infectious diseases,* 1**,** 92-100.

Rabinovich, J. E., U. D. Kitron, Y. Obed, M. Yoshioka, N. Gottdenker & L. F. Chaves (2011) Ecological patterns of blood-feeding by kissing-bugs (Hemiptera: Reduviidae: Triatominae). *Memorias do Instituto Oswaldo Cruz,* 106**,** 479-494.

Rabinowitz, P. M., B. J. Natterson-Horowitz, L. H. Kahn, R. Kock & M. Pappaioanou (2017) Incorporating one health into medical education. *BMC Medical Education,* 17**,** 45.

Rassi Jr, A., A. Rassi & J. A. Marin-Neto (2010) Chagas disease. *The Lancet,* 375**,** 1388-1402.

Robbins, P. 2011. *Political ecology: A critical introduction*. John Wiley & Sons.

Robbins, P. & B. Marks. 2010. Assemblage geographies. In *Sage Handbook of Social Geographies,* eds. S. Smith, R. Pain, S. Marston & J. Jones III, 176-194. London, UK: Sage.

Rock, M. J. & C. Degeling (2015) Public health ethics and more-than-human solidarity. *Social Science and Medicine,* 129**,** 61-67.

Rodriguez, I. G. & J. R. Loaiza (2017) American trypanosomiasis, or Chagas disease, in Panama: a chronological synopsis of ecological and epidemiological research. *Parasit Vectors,* 10**,** 459.

Rodriquez, I. G., A. Saldaña, K. González, V. Pineda, M. Perea, A. M. Santamaria, C. de Junca, L. F. Chavez, & J Calzada (2018) *Trypanosoma cruzi* infection in *Rhodnius pallescens* (Heteroptera: Reduviidae) infesting coyol palms in the dry arch of Panamá. *Journal of Medical Entomology,* 55, 691-700.

Romaña, C., J. Pizarro, E. Rodas & E. Guilbert (1999) Palm trees as ecological indicators of risk areas for Chagas disease. *Trans R Soc Trop Med Hyg,* 93**,** 594-595.

Saldaña, A., J. E. Calzada, V. Pineda, M. Perea, C. Rigg, K. González, A. M. Santamaria, N. L. Gottdenker & L. F. Chaves (2015) Risk factors associated with *Trypanosoma cruzi* exposure in domestic dogs from a rural community in Panama. *Memórias do Instituto Oswaldo Cruz,* 110**,** 936-944.

Saldaña, A., V. Pineda, I. Martinez, G. Santamaria, A. M. Santamaria, A. Miranda & J. E. Calzada (2012) A new endemic focus of Chagas disease in the northern region of Veraguas Province, Western Half Panama, Central America. *PLoS One,* 7**,** e34657.

Schmunis, G. A. (2007) Epidemiology of Chagas disease in non endemic countries: the role of international migration. *Memórias do Instituto Oswaldo Cruz,* 102**,** 75-86.

Sigler, T. J. (2014) Monaco with bananas, a tropical Manhattan, or a Singapore for Central America? Explaining rapid urban growth in Panama City, Panama. *Journal of Tropical Geography,* 35**,** 261-278.

Smith, J., E. M. Taylor & P. Kingsley (2015) One World-One Health and neglected zoonotic disease: Elimination, emergence and emergency in Uganda. *Social Science and Medicine,* 129**,** 12-19.

Smith, N. 2015. *Attalea butyracea*. In *Palms and People in the Amazon*, 83-89. Switzerland: Springer.

Taylor, L. H., S. M. Latham & M. E. Woolhouse (2001) Risk factors for human disease emergence. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 356**,** 983-989.

Tirado, F., A. Gómez & V. Rocamora (2015) The global condition of epidemics: Panoramas in A (H1N1) influenza and their consequences for One World One Health programme. *Social Science and Medicine*, 129**,** 113-122.

Vasquez, A. M. d., F. E. Samudio, A. Saldaña, H. M. Paz & J. E. Calzada (2004) Eco-epidemiological aspects of *Trypanosoma cruzi*, *Trypanosoma rangeli* and their vector (*Rhodnius pallescens*) in Panama. *Revista do Instituto de Medicina Tropical de São Paulo,* 46**,** 217-222.

Wallace, R. G., L. Bergmann, R. Kock, M. Gilbert, L. Hogerwerf, R. Wallace & M. Holmberg (2015) The dawn of structural one health: a new science tracking disease emergence along circuits of capital. *Social Science and Medicine,* 129**,** 68-77.

Wright, S. J. & H. C. Duber (2001) Poachers and Forest Fragmentation Alter Seed Dispersal, Seed Survival, and Seedling Recruitment in the Palm *Attalea butyraceae,* with Implications for Tropical Tree Diversity. *Biotropica,* 33**,** 583-595.

Wright, S. J. & M. J. Samaniego (2008) Historical, demographic, and economic correlates of land-use change in the Republic of Panama. *Ecology and Society,* 13.

Wright, S. J., H. Zeballos, I. Domínguez, M. M. Gallardo, M. C. Moreno & R. Ibáñez (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology,* 14**,** 227-239.

Yates-Doerr, E. (2015) The world in a box? Food security, edible insects, and "One World, One Health" collaboration. *Social Science and Medicine,* 129**,** 106-112.

Zeledón, R., F. Marín, N. Calvo, E. Lugo & S. Valle (2006) Distribution and ecological aspects of *Rhodnius pallescens* in Costa Rica and Nicaragua and their epidemiological implications. *Memórias do Instituto Oswaldo Cruz,* 101**,** 75-79.

Zinsstag, J., E. Schelling, D. Waltner-Toews & M. Tanner (2011) From "one medicine" to "one health" and systemic approaches to health and well-being. *Preventive Veterinary Medicine,* 101**,** 148-156.

CHAPTER 2

MAXIMUM ENTROPY MODELING OF *ATTALEA BUTYRACEA* PALMS AS AN INDICATOR OF CHAGAS DISEASE RISK IN CENTRAL PANAMA[1]

---

[1] Mertzlufft, C., M. Madden, N. Gottdenker, X. Yao, J. Velasquez Runk, J. Calzada, A. Saldaña. To be submitted to: *PLoS Neglected Tropical Diseases*

Abstract

The palm species *Attalea butyracea* is the preferred habitat of the triatomine bug species, *Rhodnius pallescens,* the primary vector of the protozoan parasite, *Trypanosoma cruzi*, that causes Chagas disease in Panama. This palm species thrives in disturbed landscapes associated with human settlement and agriculture; however, close proximity of households to *A. butyracea* palms is linked to increased risk of Chagas disease in some human populations. This study assesses the influence of biotic and abiotic drivers on the distribution of *A. butyracea* in central Panama and hypothesizes locations of elevated transmission risk of Chagas disease in this region. Utilizing over 400 records of *A. butyracea* collected in central Panama in 2015-2017, we characterize the environmental niche associated with *A. butyracea* distribution using maximum entropy modeling as an enhancement to existing distribution models of Panama's primary vector species, *R. pallescens*. We observe that all of the environmental drivers currently associated with *R. pallescens*' distribution also influence *A. butyracea*'s environmental niche, but additional biotic and abiotic drivers significantly influence *A. butyracea*'s habitat suitability, notably soil, habitat disturbance, and land cover. This suggests that further refinement to vector distribution is possible by accounting for drivers of this species preferred habitat. While presence of *A. butyracea* does not guarantee corresponding presence of *R. pallescens* bugs, because of its affinity for this palm species, a better understanding of the ecological niche of *A. butyracea* may facilitate targeting populations of this key Chagas disease vector. Findings of these analyses will contribute to a better understanding of the complex interactions between social and ecological processes, especially as related to infectious disease transmission, and may help target risk zones for Chagas disease in central Panama.

Introduction

Chagas disease, or American trypanosomiasis, is a vector-borne zoonotic infectious disease caused by the kinetoplastid protozoan parasite, *Trypanosoma cruzi* (Lent and Wygodzinsky 1979, Noireau, Diosque and Jansen 2009). Currently no vaccine exists to prevent Chagas disease, and an estimated 6-7 million individuals are affected worldwide (Beaumier et al. 2016, Malik, Singh and Amsterdam 2015). Although non-vector-borne transmission does occur, typically congenitally or through blood or organ donation, triatomine bug vectors of *T. cruzi* are the most common infection source of this disease (Rassi Jr, Rassi and Marin-Neto 2010). Vector-borne transmission is endemic to Latin America, where the parasite is transferred to human hosts through the feces of blood-sucking triatomine bugs, typically via infection of mucosal membranes (Rassi Jr et al. 2010). Ingestion of triatomine vectors is thought to be a key transmission route to other mammalian species (Barrett 1991) and ingestion of triatomine feces, as through contaminated foodstuffs, has been linked to acute and severe infections in humans (Pereira et al. 2009, de Noya and González 2015).

Prevention of initial infection is currently the best-recommended strategy for reducing disease burden. Left untreated, 30-40% of infected individuals eventually develop cardiovascular or intestinal complications resulting in high morbidity and mortality (Rassi Jr et al. 2010). Given the important role of vectors in the transmission of this disease, primary Chagas prevention strategies have hinged on reducing contact between susceptible populations and triatomine bugs (Abad-Franch et al. 2015, Rabinovich et al. 2011), which has necessitated a better understanding of vector spatial distribution. Although most triatomine species are capable hosts of the *T. cruzi* parasite, only a relative few are significant vectors to human populations (Noireau et al. 2009), and variations among these key vectors' ranges and preferred habitats result in risk factors and prevalence of Chagas disease varying spatially throughout Latin America (Rassi Jr et al. 2010).

Ecological Niche Modeling (ENM) has been widely applied in the field of ecology to better understand species distributions. ENMs compare known species occurrence data to spatially corresponding biotic and abiotic variables in order to provide insight to environmental drivers and tolerances, or to predict spatial or temporal distributions in changing landscapes (Elith and Leathwick 2009). As triatominae are sensitive to small changes in relative humidity and temperature(Parra-Henao et al. 2016a), disease ecologists are increasingly applying this method to Chagas vectors. Triatominae ENMs throughout Latin America specify existing vector ranges and environmental tolerances (Arboleda et al. 2009, Batista and Gurgel-Gonçalves 2009, Costa, Peterson and Beard 2002, de la Vega and Schilman 2018, Gurgel-Gonçalves and Cuba 2009, Gurgel-Goncalves et al. 2012, Gurgel-Goncalves and Silva 2009, López-Cárdenas et al. 2005, Parra-Henao et al. 2016a, Parra-Henao, Suarez-Escudero and Gonzalez-Caro 2016b, Peterson et al. 2002, Sandoval-Ruiz, Zumaquero-Rios and Rojas-Soto 2014), and anticipate future distributional impacts of climate change (Carmona-Castro, Moo-Llanes and Ramsey 2018, Medone et al. 2015). However, existing ENMs of Chagas vectors do not always consider the confounding effects of certain species-specific ecotopes. Several vectors are closely associated with a specific host or habitat, suggesting that host- or habitat-dependent vector models may be improved by controlling for variables associated with host habitat, or fine-tuned through comparison of spatial models that directly assess host or habitat species' distributions (Galvão and Justi 2015).

Considered true palm specialists, *R. pallescens* require sylvatic ecotopes to thrive (Abad-Franch et al. 2015) and are primarily associated with *A. butyracea* palms (Romaña et al. 1999).

However, existing distribution studies of *R. pallescens* do not account for environmental drivers of palm habitat in their models, although these vectors rarely propagate outside of their palm crown habitats (Arboleda et al. 2009, Parra-Henao et al. 2016a). In this paper, we describe an ENM of the *Attalea butyracea* palm in the Panama and Panama Oeste Provinces, Panama as an enhancement to existing models of Panama's primary vector species, *Rhodnius pallescens* (Saldaña et al. 2015).

The objectives of this paper are two-fold. First, we aim to characterize the biotic and abiotic environmental factors associated with *A. butyracea* palm distribution in central Panama in order to identify key palm-specific variables that may enhance existing and future ENMs geared towards *R. pallescens* or other palm-dependent triatominae. Second, we seek to identify areas of elevated transmission risk of Chagas disease in this region, defined as residential settings located in areas of moderate to high *A. butyracea* habitat suitability. Close proximity of *A. butyracea* palms to residential settings is considered a risk factor for Chagas disease transmission, due to enhanced likelihood of cross-over from a sylvatic to domestic disease transmission cycle (Abad-Franch et al. 2015, Erazo and Cordovez 2016, Feliciangeli et al. 2004, Sanchez-Martin et al. 2006, Teixeira et al. 2001, Vasquez et al. 2004). Although *A. butyracea* palm presence does not guarantee corresponding vector presence; as *R. pallescens'* preferred habitat, a better understanding of this palm species' ecological niche and distribution is crucial to understanding potential vector distribution in Panama and the associated risk of Chagas disease transmission.

Methods

Study area

This research focuses on *A. butyracea* palm distribution within the Panama Oeste and Panama Provinces in central Panama (Figure 2.1). This region covers an area of approximately 11,200 square kilometers (7,000 square miles) and contains both Panama City, the nation's capital, and most of the Panama Canal. It is also home to a majority of the nation's populace, over half of whom live in the capital alone (Sigler 2014). Panama is located in the tropics of the western hemisphere, between latitudes 7-10° N and longitudes 77-83° W. Its combination of coastal regions and varied topography result in highly variable temperature and precipitation patterns throughout the country. The Panama Oeste and Panama Provinces' topography is characterized on its northern border by the discontinuous mountain chain that runs through central Panama, reaching elevations of 1,100 meters in the far northern, western, and eastern parts of these provinces. The landscape descends to a lowland corridor that transitions to the southern coast. Due to the mid-continental mountain ridge in Panama, this region comprising these provinces is drier than the northern half of the country and receives approximately half as much rainfall as the Caribbean coast at around 1,650 mm, although it experiences a more pronounced rainy season from May-November (Palka 2005).

Palm occurrence data

A. butyracea is a large, densely-crowned palm in the subtribe, *Attaleinae* (Henderson, Galeano and Bernal 2019, Smith 2015). Colloquially called "palma real" (royal palm) in Panama, this species ranges from Mexico through northern South America, reaching as far as western Amazonia (Smith 2015). Reaching heights up to 30 meters over a lifespan of over 200 years, this palm is characterized in its mature form by its large crown: individual palm fronds may reach up to 10 meters in length, and the base of the crown is packed with dead organic matter (De Steven et al. 1987, Jansen et al. 2014, Smith 2015).

A. butyracea occurrence locations were obtained through a combination of field surveys and remote sensing via satellite imagery. A field survey of 175 occurrence points was collected via convenience sample (close proximity to roads) in Panama and Panama Oeste Provinces between 2015 and 2017 using a Garmin Oregon 550T handheld global positioning device. This field sample was supplemented with an additional 75 *A. butyracea* occurrence records collected in this region by colleagues from the Gorgas Memorial Institute for Health Studies (ICGES). Panama's Ministry of the Environment (MiAmbiente) authorized this fieldwork, which was undertaken as part of a larger cross-disciplinary and multiagency zoonotic disease research collaboration (Dyer et al. 2016).

Because our field data exhibited significant spatial bias and clustering, we used high-resolution satellite imagery to remotely conduct a systematic sample of the complete extent of *A. butyracea* occurrences in Panama and Panama Oeste provinces, which resulted in an additional sample of 155 palm locations. Mature *A. butyracea* crowns are highly visible on high-resolution imagery (Figure 2.2), making this species an ideal candidate for remote data collection. A systematic sampling scheme ensures an even sampling effort across the region of interest by designating sample locations at fixed intervals across the extent of the study area based on a randomly generated starting point. To select our remote survey locations, we created a 5 km-by-5 km grid overlaying our study area using hollow square tessellation in ArcMap (v 10.5.1, ESRI, Redlands, California, USA). We defined a survey area as a 250-m buffer zone generated around the center point ("centroid") of each grid cell. Each survey area was carefully analyzed for presence of mature *A. butyracea* crowns using both panchromatic (< 1-m spatial-resolution) and multispectral (1.46-m spatial resolution) WorldView2 and WorldView3 satellite imagery collected between 2015-2018 (Digital Globe Inc, Westminster, Colorado, USA) (Figure 2.3).

Systematic sampling is a preferred data collection method for reducing spatial bias of occurrence records in ecological niche modeling (Hirzel and Guisan 2002). At a fixed interval of 5 km, our smallest environmental gradients were sampled at least once, while larger environments were sampled proportionally. Among the 368 locations visually surveyed for palm presence, 42% (n=155) contained one or more probable *A. butyracea* palms based on crown signature. In occupied survey locations, the coordinates of the palm closest to the centroid of the survey area was added to our occurrence dataset. A 2017 field validation of our *A. butyracea* identification via satellite imagery suggests that we correctly identify *A. butyracea* palms with high accuracy, or low commission error (positive predictive value = 0.8), but that many true *A. butyracea* are overlooked, particularly in dense canopy (negative predictive value = 0.6; high omission error) (Chapter 3). For this reason, we substituted confirmed, field-collected *A. butyracea* occurrence data over remotely sensed occurrence data in 18 locations where our remote survey locations overlapped with the field-collected convenience sample.

Our complete palm occurrence dataset consisting of convenience sample, supplemental and remotely sensed palm records totaled 405 records.

Environmental data

We tested a range of biotic and abiotic variables known to influence neotropical palms broadly (Eiserhardt et al. 2011, Montúfar et al. 2011, Pyke et al. 2001, Salm et al. 2007, Vormisto, Tuomisto and Oksanen 2004) and *A. butyracea* specifically (Garzon-Lopez et al.

2013, Henderson et al. 2019, Normand et al. 2006, Wright and Duber 2001). Panama land cover data at a spatial resolution of 5-m was obtained directly from Panama's Ministry of the Environment (MiAmbiente). Derived from a mosaic of 5-m spatial resolution RapidEye satellite sensor data between January 1, 2011 and April 30, 2012, this land cover dataset is the most recent and highest resolution official Panamanian landscape data currently available (Castillo, Samaniego and Kindgard 2015). To facilitate land cover interpretation and reduce variable load within our model, we consolidated the 21 land cover classes identified within our study area to eight generalized categories. In addition, to account for *A. butyracea*'s known tendency to thrive in anthropogenically-altered habitats, we assigned each of the original land cover classes an alteration rating (lowest to highest: 0-3) to form a disturbance index. The generalized land cover category and disturbance classification assigned to each original land cover class is shown in Table 2.1.

Four climate variables were obtained from the WorldClim database (Version 2, www.worldclim.org) at a spatial resolution of 30-arc seconds: annual precipitation, precipitation seasonality (Coefficient of variation), mean temperature, and temperature seasonality (standard deviation x 100) (Fick and Hijmans 2017). WorldClim variables reflect a variety of monthly temperature and precipitation data collected and interpolated from regional weather stations between 1970-2000 (Fick and Hijmans 2017). A digital elevation model (DEM) (30-meter spatial resolution; NASA Shuttle Radar Topology Mission) of Panama was obtained through the Smithsonian Tropical Research Institute's (STRI) GIS OpenData Portal. In addition to elevation, this DEM was used to derive slope and two aspect variables (easting and northing) via the ArcGIS spatial analyst toolbox (ESRI, Redlands, California, USA). Holdridge life zone data, a global bioclimate measure of landscape classification based on axes of potential evapotranspiration, annual precipitation, and humidity (Holdridge 1967), were also obtained through the STRI GIS OpenData Portal. Soil data for our region was obtained from the Soil and Terrain Digital Database for Latin America and the Caribbean (SOTERLAC) (Dijkshoorn, Huting and Tempel 2005). Both soil and Holdridge life zone data were obtained as vector shapefiles and converted to raster datasets. All raster data were resampled to match the 5-m land cover data.

The full set of environmental variables were tested for high correlation (Pearson's r $\geq$ |0.75|) using the Band Collection Statistics Tools in ArcMap (v 10.5.1, ESRI, Redlands, CA). To avoid multicollinearity, highly correlated variables were reduced to the single variable most likely to directly influence palm growth over time. Additionally, we removed variables with consistently low contribution to the model (< 3% permutation importance or percent contribution) as these reductions resulted in improved model performance. The full and reduced independent variable list is shown in Table 2.2.

Environmental niche modeling

We employed maximum entropy modeling to identify suitable habitat of *A. butyracea* palms in our study region using Maxent 3.4.1 software (Phillips, Dudík and Schapire 2004). We chose a presence-only modeling strategy given the high potential for omission error among recorded absence locations within our remotely-derived palm occurrence dataset. Maxent compares occurrence records to environmental parameters via (~10,000) randomly selected background points, termed "pseudo-absences". The model determines a range of possible species distributions wherein the average background environmental data reflects the empirical average of the supplied occurrence records (Phillips and Dudík 2008). The broadest, or least constrained, of these possible distributions is the one with the maximum entropy.

Two primary settings in Maxent heavily influence model output by adjusting the constraints the software uses to match potential distributions to occurrence points: features and a regularization multiplier (Phillips and Dudík 2008). Features control the type of functions used to transform continuous environmental predictors, which alters the complexity of species-environment relationships (Phillips and Dudík 2008, Merow et al. 2014). At a sample size greater than 100 records, Maxent defaults to linear (L), quadratic (Q), product (P), and hinge (H) features (Phillips and Dudík 2008). Hinge features transform continuous data to piecewise linear functions (Elith et al. 2011). The other three features constrain environmental data by mean, variance, and co-variance, respectively (Merow, Smith and Silander 2013). The regularization multiplier (β) is a smoothing variable to correct overfitting, which defines how closely the projected habitats must empirically match occurrence data (Merow et al. 2013). Although Maxent software presents default feature and β settings, species-specific parameter tuning is highly recommended to maximize model performance and increase the accuracy and reliability of results (Anderson and Gonzalez 2011, Merow et al. 2013, Morales, Fernandez and Baca-Gonzalez 2017, Radosavljevic and Anderson 2014, Warren and Seifert 2011). Therefore, we tested 48 possible combinations of features, βs, and occurrence record subsets to construct the optimal model for this dataset. To test optimal model fit and complexity, we tested a range of eight βs (0.001, 1*, 1.5, 2, 4, 6, 8, 16) and two feature settings (LQ, LQPH*) (*default). Our restricted model allowed for only linear and quadratic transformations. Although species responses to their environment are often non-linear (Austin 2002), overly complex models risk ascribing too much importance to noise and face a loss of interpretability (Merow et al. 2014).

In addition to feature and βs settings, we compared three occurrence record subsets for model performance: population 1 (POP1) contained only the systematic sample (n=160); population 2 included POP1 and field-collected occurrence records spatially filtered to constrain the nearest distance between palms to either 1km (POP2_1km, n=194) or 2 km (POP2_2km, n=174). Our field-collected sample data exhibit extreme spatial bias and clustering, but represent true *A. butyracea* locations at all points. However, spatially biased occurrence records may lead to spurious conclusions about a species' ecological niche due to over- or under-sampled regions (Phillips et al. 2009, Kramer-Schadt et al. 2013). In contrast, our systematic sample data (remotely sensed with field-collected supplements) are spatially neutral, but may contain false-positive occurrence records. Spatial filtering was applied to our palm data to minimize spatial bias and maximize data confidence (Kramer-Schadt et al. 2013, Radosavljevic and Anderson 2014); these spatial filter distances were chosen to maximize the number of retained occurrence points on a similar scale (km) as the systematic sample spacing. Spatial filtering lessens, but does not completely rectify, spatially biased data.

This combination of model settings resulted in 16 possible models for POP1 and 32 possible models for POP2. Given the limitations within each dataset, we present and compare the best model from each population in this paper. We evaluated model performance using sample size corrected Akaike Information Criteria (AIC_c), calculated via ENMTools 1.4.4 software (Warren and Seifert 2011). Optimally complex models are associated with the lowest AICc score. This method has been shown to be a more objective measure of selecting appropriately complex Maxent models than the commonly reported maximum area under the receiver operating curve (AUC), especially at lower sample sizes (~100) (Warren and Seifert 2011, Lobo, Jiménez-Valverde and Real 2008). Our top models were run through a 10-fold cross validation to test for generality at 1,500 iterations; resulting model metrics were averaged across these ten models (Merow et al. 2013).

Identifying potential transmission zones of Chagas disease

For the purpose of this paper, we define regions at risk of Chagas disease transmission as the coexistence of human and vector populations in the same geographic space. Although human susceptibility and vector infection will vary among individuals even in highly prone regions, vector and human population distributions must overlap for even the chance of direct vector-borne transmission to occur. To identify potential hotspots of elevated Chagas transmission risk in our study area, we compared residential data taken from the 2010 Panama Census to areas of probable *A. butyracea* presence. Administrative boundaries of Panamanian communities (*lugares poblados*) were obtained through Panama's GEORED Platform, a geospatial data platform hosted by Panama's National Authority of Land Administration (ANATI) (geored.maps.arcgis.com). We derived probability of *A. butyracea* presence by post-processing the raw Maxent output (relative habitat suitability) of our top two models as described by Guillera-Arroita et al. (Guillera-Arroita et al. 2014). Although default Maxent settings automatically provide species probability estimates, the accuracy of this estimate requires users to input a measure of species rarity (*s*), or the probability of species presence within suitable habitat, which is otherwise arbitrarily set at $s = 0.5$ (Elith et al. 2011, Guillera-Arroita et al. 2014). This probability is not the same as species prevalence, which does not take habitat suitability into account, and is difficult to measure when suitable habitat is not already known. In contrast, Guillera-Arroita et al.'s estimate of species probability transforms raw output through a multiplier of species prevalence and the number of background points used by the model

(Guillera-Arroita et al. 2014). The estimate of *A. butyracea* prevalence ($\psi = n$ occurrence records/ total n sample sites) was derived from our systematic sample and adjusted based on the 2017 field validation efforts: field-derived positive predictive and negative predictive values were applied to summed presence and absence data, respectively, to account for false positive (FP) and false negative (FN) occupation estimates. The adjusted prevalence (ψ_{adj}) calculation, then, is:

$$\psi_{\mathrm{adj}} = \frac{\text{remotely sensed occurrence records} - \widehat{\mathrm{FP}} + \widehat{\mathrm{FN}}}{\text{total number sampled sites}}$$

We applied ψ_{adj} to scale the raw Maxent output into an estimate of probability of presence given the environmental variables (z) and number of background points applied by the model (n):

$$\Pr(y = 1|z) = raw * n * \psi_{\mathrm{adj}}$$

An *A. butyracea* probability of presence $\geq$ to 0.5 was used as the cutoff to create a binary map of potential species distribution. At this probability threshold, predicted *A. butyracea* distribution aligns with moderate to high relative habitat suitability indicated by our top models.

Results

Based on lowest AICc scores, the optimal complexities of the top two models were identical, at $\beta = 4$ and constrained to simple features (LQ). The AICc score of the best model fitted only with systematic survey data (POP1) was lower than the best spatially filtered occurrence record model (POP2_2k), suggesting a better model fit (Table 2.3). However, the best POP2 model reflected a higher mean $\mathrm{AUC}_{\mathrm{test}}$ score across the 10 cross-fold replicates at 0.65 than the best POP1 model ($\mathrm{AUC}_{\mathrm{test}}$=0.62), suggesting it is slightly better able to distinguish between known *A. butyracea* occurrence records and background. Overall, POP1 models had much lower AICc scores than POP2, regardless of filtering, complexity, or β-multiplier (Table

2.3). Simple models (LQ) generally outperformed those with more complex features (LQPT), and among POP2, a spatial filter of 2 km slightly outperformed 1km; however, both findings were mediated somewhat by very high β multipliers. Optimal βs varied, but were generally higher than Maxent's default (β=1), which is consistent with past single-species studies (Anderson and Gonzalez 2011, Radosavljevic and Anderson 2014, Morales et al. 2017).

After predictor reduction to account for variable correlation and low permutation importance, six predictor variables contributed to model fit (Table 2.4). Average temperature had the highest permutation importance in both top models. Jackknife tests, which provide an alternative assessment of variable importance, also showed similar trends between both models (Figure 2.4). Holdridge life zones and soil type contribute the most information in both models, as single variables; annual precipitation contributes the least. In contrast, average temperature contains the most information not contributed by other predictors.

Response curves depict the relationship between each predictor variable and relative *A. butyracea* habitat suitability (Figure 2.5). In both POP1 and POP2 models, relative *A. butyracea* habitat suitability increases as average temperature, average precipitation and landscape disturbance increases. Among categorical variables, high relative habitat suitability is linked to tropical moist forest and nitisol soils. Secondary forest is also linked with elevated habitat suitability, but the strength of this association varies between models. Low relative habitat suitability is associated with premontane moist forest and premontane rainforest, as well as planted landscapes (crops and timber). Relative habitat suitability of categorical variables is influenced by the observed versus expected distribution of occurrence records by variable category. For this reason, although wetlands, surface water, and non-permeable surfaces are ecologically unsuited to supporting *A. butyracea* palms, as reflected in our occurrence record data, this distinction is not picked up in the model because of the relatively small percentage of study area associated with each category (Appendix A).

The spatial distribution of relative habitat suitability is consistent between models (Figure 2.6). Although general distribution of habitat suitability is nearly identical, the POP1 model output is smoother and predicts higher relative suitability in the far western and central regions of our study area. Figure 2.7 depicts potential *A. butyracea* palm species distribution compared to the distribution of human populated communities (*lugares poblados*) in the study area. We observe that over 60% of the study area is favorable for *A. butyracea* distribution by one or both models, with more than 90% agreement between models. Over 75% of the 1509 communities in these two provinces completely composed of suitable *A. butyracea* habitat, and an additional 5% of communities have some area of suitable habitat within their administrative boundary. These findings suggest that, as of the 2010 census, nearly half a million people reside in areas suitable for Chagas disease vector habitat and may already or potentially live in close proximity to *A. butyracea* palms.

Discussion

Although some variation exists between models, there is significant agreement in the distribution of suitable habitat for this species within this region. Suitable *A. butyracea* habitat is predicted throughout much of the Panama Oeste Province west of the Panama Canal, along a central corridor stretching through the middle and northeast of the Panama Province, and on the Isla del Rey in the Gulf of Panama. Chagas disease prevalence is passively recorded in this region, and known cases are assumed to be underreported (Rodriguez and Loaiza 2017). However, our prediction map supports the locations of previously reported Chagas disease cases in both human populations (Calzada et al. 2006, Calzada et al. 2010) as well as in domestic canine populations (Pineda et al. 2011, Saldaña et al. 2015), which are considered sentinels of human infection risk (Castillo et al. 2015). The predicted distribution also aligns closely with our field observations of this species' distribution in both provinces, even in the model driven by systematic sampling that did not incorporate existing field samples (Figure 2.8). We take these findings to be a positive confirmation of our models' utility.

A. butyracea palms are abundant in suitable habitat, especially secondary forest and pasture settings, which account for a high proportion of our study area. This ubiquity may explain the low AUC values reported in our models (POP1, AUC=0.62; POP2, AUC=0.65). The AUC is a measure of model discrimination commonly used in ecological niche modeling that ranges from 0-1, where 1 is perfect discrimination and 0.5 is comparable to chance. Although high AUC values are often falsely conflated with high model performance, this measure does not reflect model accuracy, but rather the ability of the model to distinguish between occurrence points and background data (presence-only models), which includes both presence and absence information (Merow et al. 2013). Stated another way, it is the ability of the model to distinguish between known palm locations and everything else, even though the rest of the study area also includes unknown number of additional palm occurrence points. Therefore, when the species is widespread, as we observe in this study region, AUC scores are low even with highly accurate models (Lobo et al. 2008).

Although our models indicate moderate to high habitat suitability in a majority of Panama Oeste and Panama provinces, *A. butyracea* are not expected to be present in all suitable locations. Regional species predictions do not account for the effects of biodiversity and species composition that influence the distribution and abundance of species at local scales (Eiserhardt et al. 2011, Pyke et al. 2001). However, the environmental niche described here may help rule out unsuitable habitat, and refine existing vector distribution models by allowing for control of the ecological factors driving habitat suitability. The existing ecological niche models of *R. pallescens* vectors vary in methodology, geographic scale, and specific environmental variables, but are consistent in their findings: *R. pallescens* require high relative humidity in their habitat, and do not tolerate extreme fluctuations in humidity, temperature, or precipitation (Arboleda et al. 2009, Parra-Henao et al. 2016a, Zeledón et al. 2006). *R. pallescens'* associated life zones range from tropical rainforest to tropical very dry forests (Pizarro Novoa and Romaña 1998, Parra-Henao et al. 2016a); survival in drier regions and dry seasons is associated with the protective microclimate found in palm crowns (Zeledón et al. 2006, Parra-Henao et al. 2016a). We observe that all of the environmental drivers currently associated with *R. pallescens*' distribution also influence *A. butyracea*'s environmental niche. This suggests that further refinement to vector distribution is possible through the additional biotic and abiotic drivers found to influence *A. butyracea*'s habitat suitability, notably soil, habitat disturbance, and land cover.

Six variables contributed to *A. butyracea*'s environmental niche at regional scales, four abiotic (average temperature, average precipitation, Holdridge life zones, soil type) and two biotic (land cover, landscape disturbance). As with vector distribution, high and stable temperature and precipitation were the strongest predictors of habitat suitability in both of our final models, which is typical of most palm species. Arecaceae are strongly associated with high temperatures and precipitation and do not tolerate extreme shifts in climate (Salm et al. 2007). Temperature is considered the primary limiting factor of palm distribution at a global scale, while moisture typically accounts for regional variations (Salm et al. 2007, Eiserhardt et al.

2011). *A. butyracea* are rarely found at elevations greater than 300 m, a trend we observe and link directly to average temperature patterns in this region (Henderson et al. 2019). Panama has highly variable topography, which indirectly restricts palm distribution due through a direct influence of elevation on temperature and precipitation patterns, and slope and aspect on drainage and soil weathering (Vormisto et al. 2004). Some studies have also linked *R. pallescens* vectors to low altitudes (< 400 m) (Galindez et al. 1996, Zeledón et al. 2006), which may be directly related to palm habitat. Although low temperature seasonality (the difference between warmest and coldest periods of the year) has been linked to palm suitability in other studies (Salm et al. 2007), and is also linked with vector suitability (Arboleda et al. 2009), it was not a significant indicator in either of our models, likely due to minimal variation across our regional study area.

A. butyracea palms prefer moist habitats (Normand et al. 2006), which is reflected in the models in the high average precipitation, nitisol soils, and tropical moist forest life zones preferred by this species. *A. butyracea* palms also thrive in disturbed habitats, whether natural or anthropogenic (Henderson et al. 2019). Their close association with nitisol soils are therefore concerning, as these soils are sought after for agriculture due to their high productivity (Stocking and University of East Anglia 1988), which may lead directly to habitat disturbance in areas especially suited to *A. butyracea* growth. Vegetation disturbance is also linked to higher abundance of some triatomine species, including *R. pallescens* (Parra-Henao et al. 2016a). In Panama, palms in perturbed vegetation were more like to host *R. pallescens* populations than palms in contiguous forest (Gottdenker et al. 2011). Our models suggest that *A. butyracea* habitat suitability is positively associated with anthropogenic landscape disturbance until the point that disturbance renders landscape unsuitable to vegetation (e.g. impervious surfaces, mining).

Consistent with previous research, our models detect elevated habitat suitability in secondary forest and decreased suitability in pastoral settings (Chapter 3). *A. butyracea* are particularly associated with secondary forest, and are an indication of past forest upheaval in some regions. Panamanian forest disturbed by poachers was linked to high seedling survival rates, although limited seed dispersal, due to associated reductions in mammalian populations associated with seed dispersal and seed predation (Dittel et al. 2015, Wright and Duber 2001). However, fewer than expected pastoral palms have been recorded in this area in other studies, which is linked to anthropogenic thinning, either purposeful or indirectly as a result of cattle ranching, rather than ecological unsuitability (Chapter 3).

We observe that a majority of residential communities in Panama and Panama Oeste provinces overlap with areas of moderate-to-high *A. butyracea* habitat suitability, particularly in the western third of our study area and along the lowland central corridor along and south of the Pan-American Highway. Households in close proximity to *A. butyracea* palms are linked to elevated risk of Chagas disease transmission (Abad-Franch et al. 2015, Erazo and Cordovez 2016, Feliciangeli et al. 2004, Sanchez-Martin et al. 2006, Teixeira et al. 2001, Vasquez et al. 2004). Other studies in central Panama indicate a high level of *R. pallescens* infestation among *A. butyracea* palms, particularly in deforested peridomestic habitats (Gottdenker et al. 2011), as well as a significant number of households within *R. pallescens* flight distance (702 m) (Castro et al. 2014) of an *A. butyracea* palm (Chapter 3). However, it is important to note that individual risk of contracting Chagas disease will vary even in highly prone regions, due to variations in residential construction and household behavioral characteristics. Although the prevalence of *T. cruzi* among vector populations in Panama is high, prevalence in human populations is low, estimated at 0.52% for the entire country, with incidence of 1 in 100,000 inhabitants (Peterson et al. 2019b). In general, sylvatic vectors are linked to far fewer Chagas disease cases than domestic species, which are inherently more likely to encounter human hosts due to their co-habitation. However, domesticated vectors are effectively controlled through the application of household pesticides, while sylvatic vectors are not; application of pesticides to combat sylvatic vectors is neither an ecologically sound nor a cost-effective solution (Peterson et al. 2019a, Brito et al. 2017, Rodriguez and Loaiza 2017).

Conclusion

In Panama and in other regions of Latin America where sylvatic species pose a secondary re-infestation hazard, Chagas disease transmission is considered a low but constant threat. The identification of regions with elevated transmission risk, defined here as likely vector presence in close proximity to susceptible human populations, can help target vector control strategies and direct limited resources to further reduce disease burden in these areas. The findings of this paper suggest that further refinement to distribution models of Panama's primary Chagas disease vector, *Rhodnius pallescens,* is possible through accounting for drivers of its preferred habitat, notably soil, habitat disturbance, and land cover.

Table 2.1 Classification scheme of the two variables derived from Panama's official land cover dataset

Original Land Cover Classification	**Disturbance Level**†	**Consolidated Land Cover**
Aquaculture Ponds	3	Surface Water
Beach and Natural Sand	0	No Vegetation
Conifer Planted Forest	2	Planted Crops/Timber
Corn	2	Planted Crops/Timber
Hardwood Planted Forest	2	Planted Crops/Timber
Infrastructure	3	No Vegetation
Mangrove Forest	0	Wetlands
Mining	3	No Vegetation
Mixed Agriculture	2	Planted Crops/Timber
Mixed Mature Broadleaf Forest	0	Mature Forest
Mixed Secondary Broadleaf Forest	1	Secondary Forest
Natural meadows	0	Grassland
Other Annual Crop	2	Planted Crops/Timber
Pasture	2	Grassland
Pineapple	2	Planted Crops/Timber
Populated Area	3	Built Environment
Rice	2	Planted Crops/Timber
Rock Outcrop and Bare Earth	0	No Vegetation
Surface Water	0	Surface Water
Swamp	0	Wetlands
Vegetation Regrowth and Bushes	2	Secondary Forest

Table 2.2 Environmental variables considered for *A. butyracea* niche model

Avg. Precipitation *(mm)*[†]
Avg. Temperature *(°C)*[†]
Consolidated Land Cover[†]
Easting
Elevation
Holdridge Life Zones[†]
Landscape Disturbance[†]
Northing
Precipitation Seasonality (coefficient of variation)
Slope
Soil Type[†]
Temperature Seasonality (standard deviation x 100)

[†] Variable retained in model after testing for collinearity (Pearson's $r > |0.75|$) and low model contribution (< 3% permutation importance)

Table 2.3. Model comparison by palm observation type, complexity, and regularization multiplier

Model	Complexity[†]	β-multiplier[‡]	AICc score
POP1	LQPH	2	6290.15
	LQPH	4	6280.27
	LQPH	6	6280.79
	LQPH	8	6279.71
	LQ	2	6281.02
	LQ	**4**	**6277.46**
	LQ	6	6279.89
	LQ	8	6278.84
POP2_1k	LQPH	2	7581.43
	LQPH	4	7573.82
	LQPH	6	7562.79
	LQPH	8	7561.54
	LQ	2	7549.59
	LQ	4	7550.50
	LQ	6	7551.63
	LQ	8	7557.29
POP2_2k	LQPH	2	6784.34
	LQPH	4	6781.24
	LQPH	6	6781.76
	LQPH	8	6782.21
	LQ	2	6781.02
	LQ	**4**	**6777.88**
	LQ	6	6777.98
	LQ	8	6778.74

[†] Functions: linear (L), quadratic (Q), product (P), and hinge (H)

[‡] For table clarity, we display only a subset of all models run for model comparison

Table 2.4. Relative variable contribution to final models

	POP1		**POP2_2km**	
Variable	*PC*	*PI*	*PC*	*PI*
Soil Type	38.4	17.8	44.5	14.9
Holdridge Life Zones	13.2	7	11.1	16.2
Consolidated Land Cover	7.7	6	4.2	2
Landscape Disturbance	10.4	12.8	14.8	14.7
Avg. Temperature *(°C)*	21.1	40.6	17.4	27.3
Avg. Precipitation *(mm)*	9.2	15.9	7.9	24.9

PC = percent contribution; PI = permutation importance

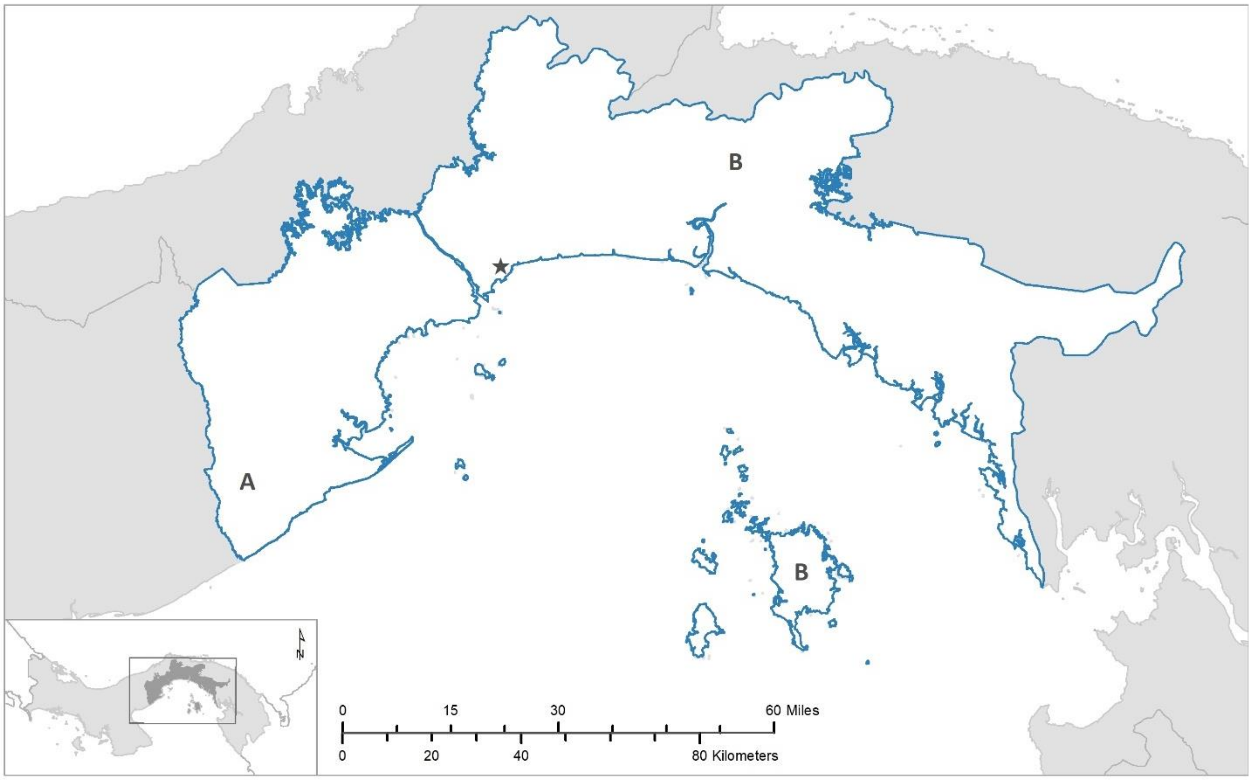

Figure 2.1 Study area in central Panama. Figure shows Panama Oeste Province (A) and Panama Provence (B).

Figure 2.2. Ground and satellite image of *A. butyracea* palm. Mature *A. butyracea*’s distinctive crowns (top) are highly visible on high-resolution satellite imagery (bottom).

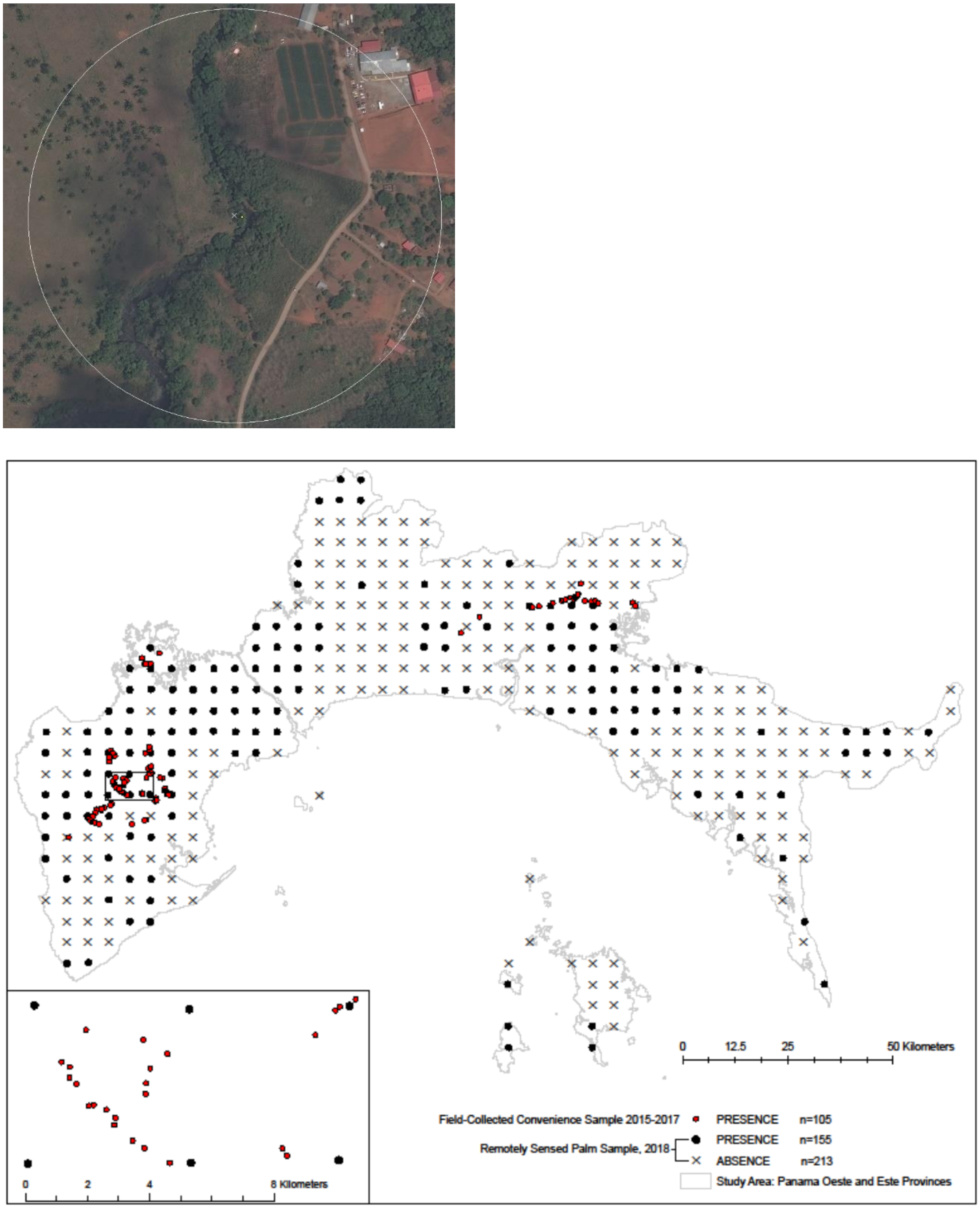

Figure 2.3 Systematic sample for data collection. The map on the bottom depicts the 5km survey points that were sampled across the study area. The image on the top shows an example of the satellite imagery wher the closest palm sample to the centroid is recorded. This is an image from the Panama Oeste region, where palms are clearly abundant.

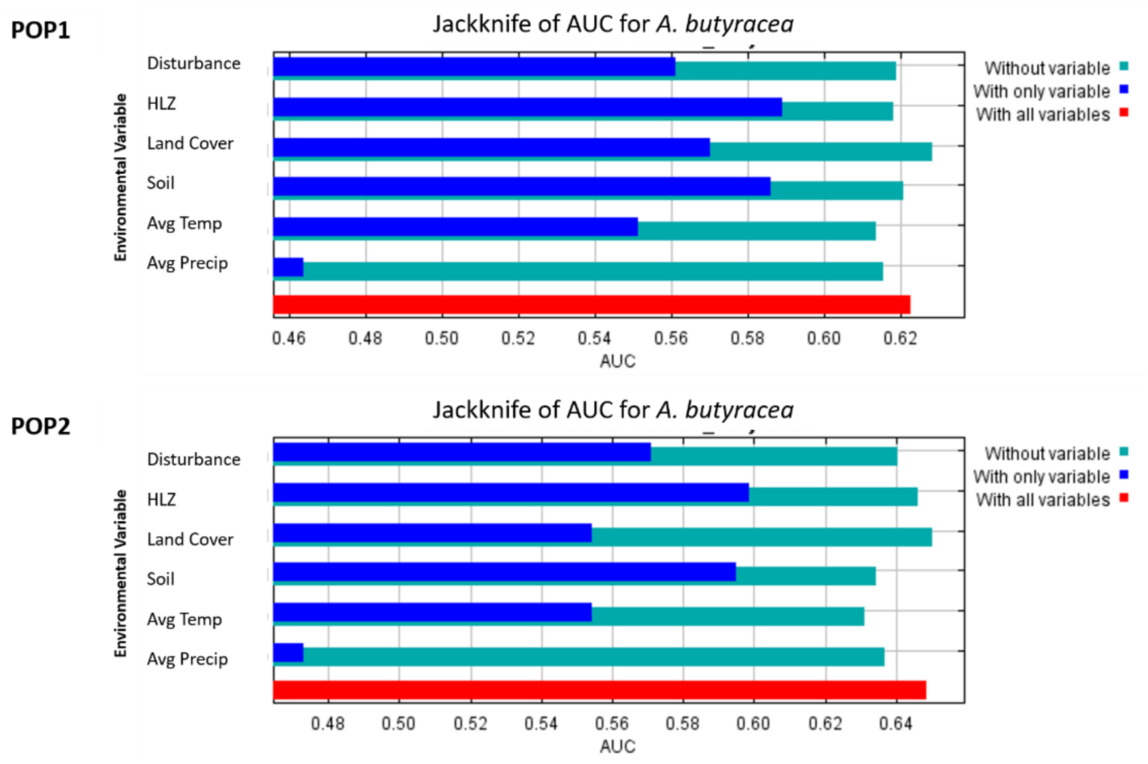

Figure 2.4 Jackknife tests provide an estimate of variable contribution to each model.

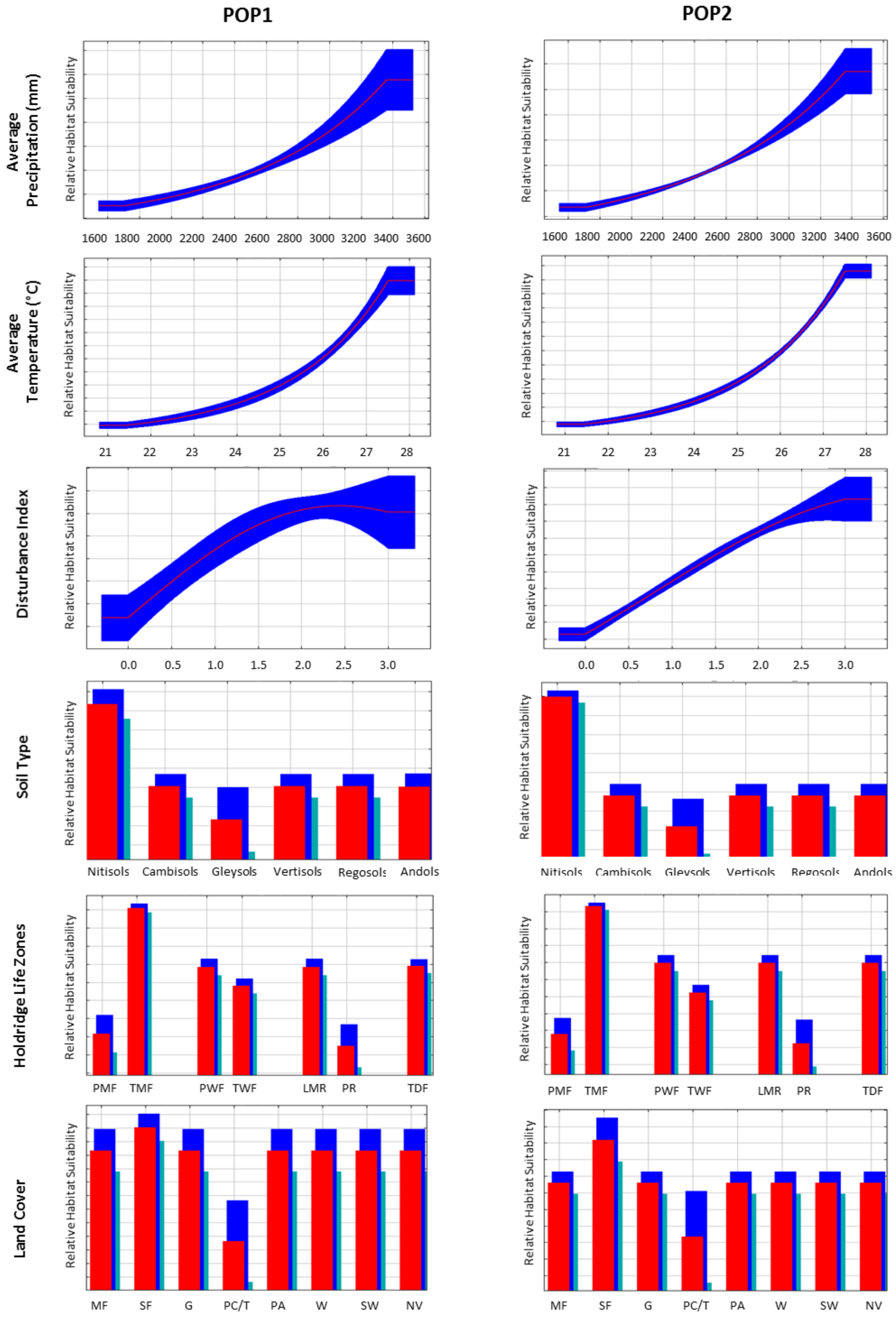

Figure 2.5 Maximum entropy model response curves. Response curves depict the relationship between each predictor variable and relative *A. butyracea* habitat suitability.

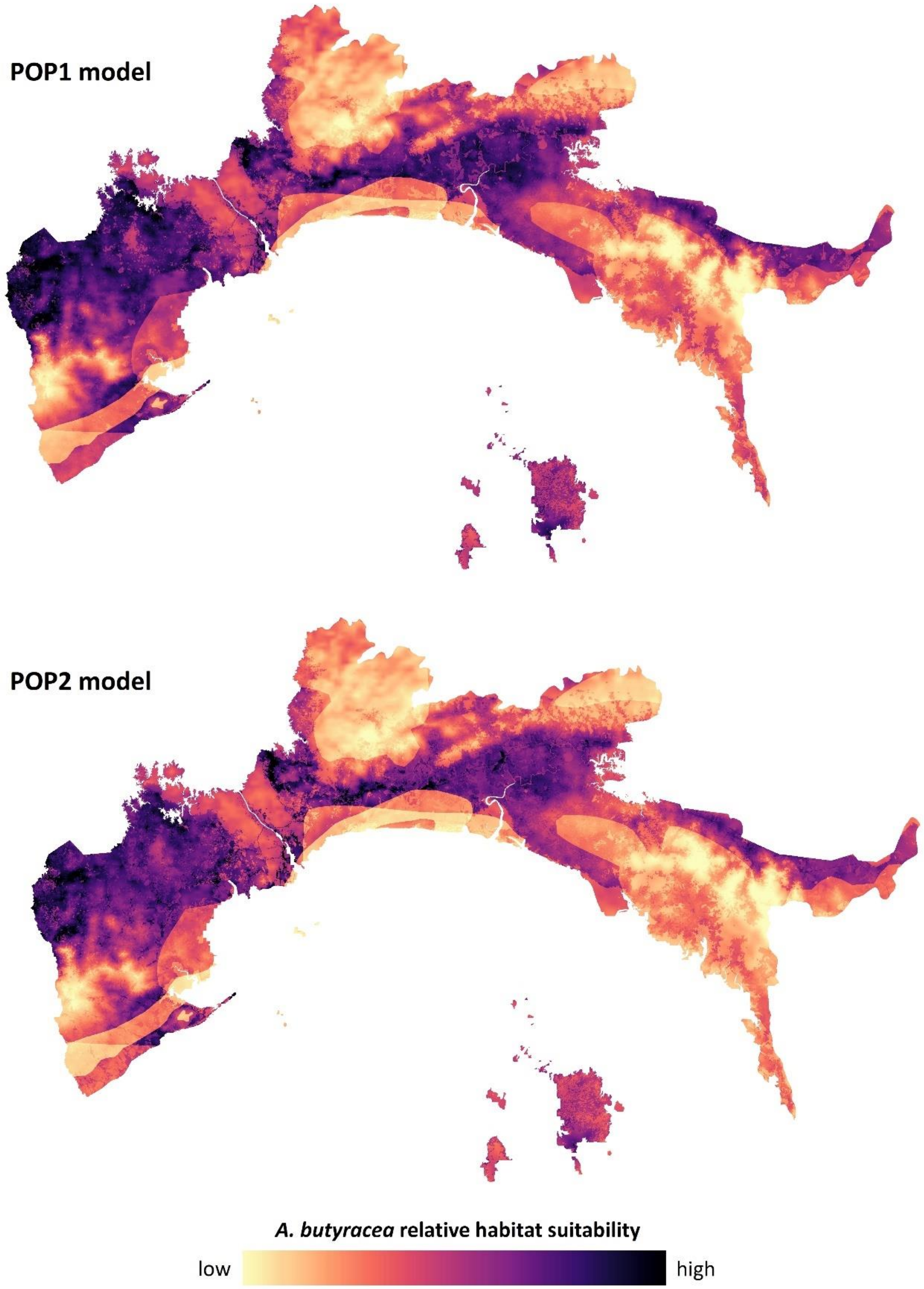

Figure 2.6 Relative habitat suitability maps of *Attalea butyracea* palms. This figure compares suitable habitat predicted from the best POP1 model (A) and best POP2 model (B).

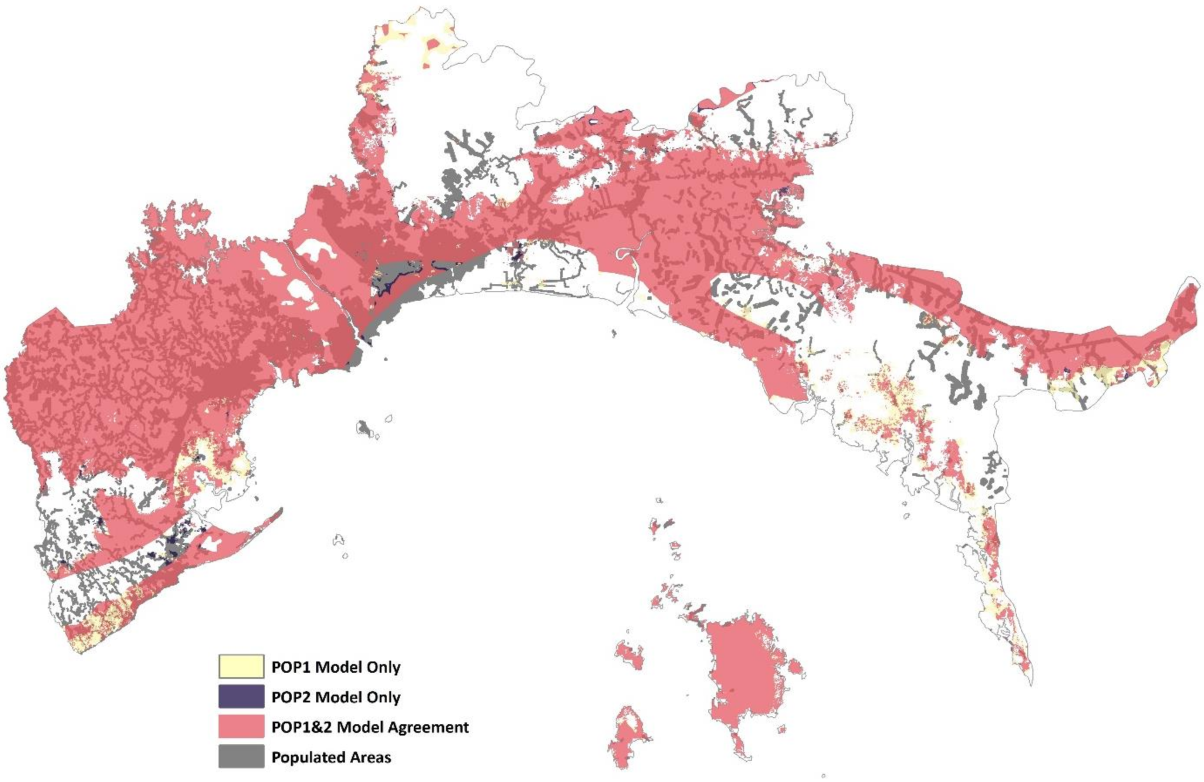

Figure 2.7 A comparison of populated areas, based on the 2010 census, with estimated moderate to high *Attalea butyracea* habitat suitability between models.

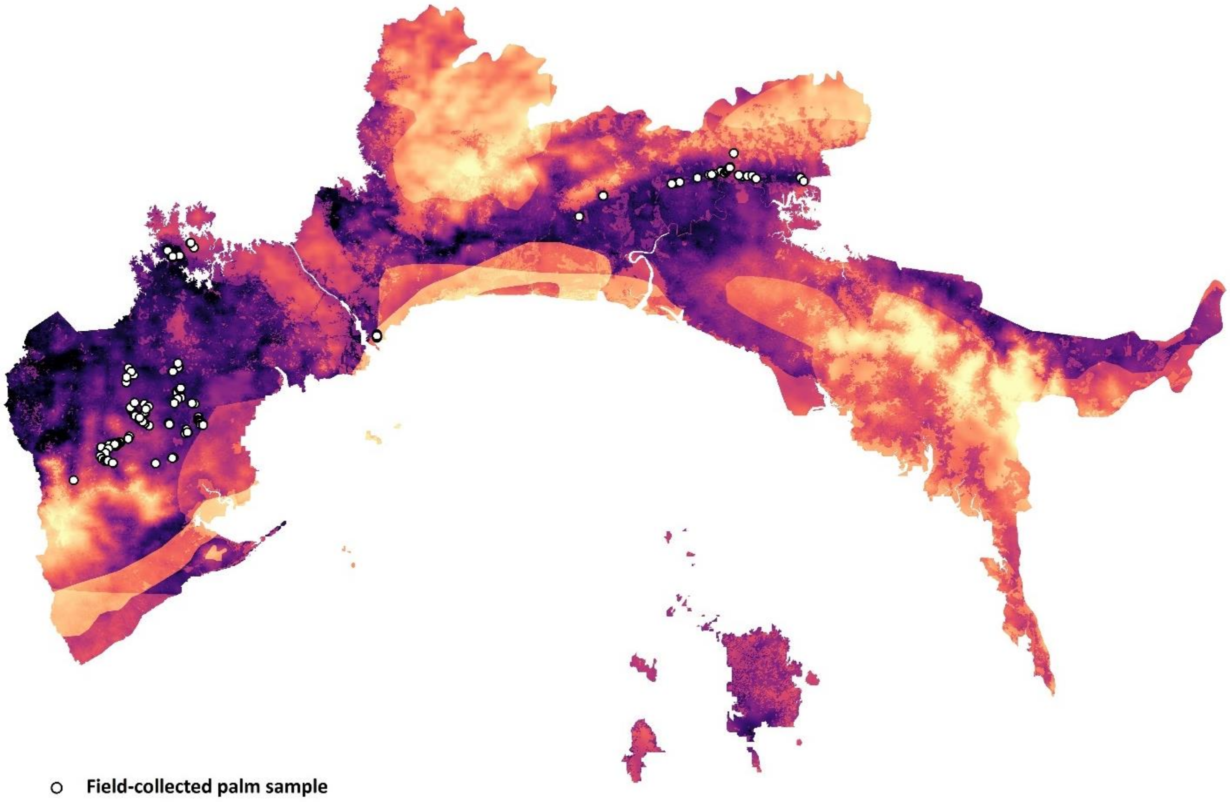

Figure 2.8 A comparison of modeled habitat suitability with field-collected palm data. The observed palm sample aligns closely with the distribution of proposed suitable habitat, even for the model based soley on remote, systematic sampling of palms. This is a good indication of the models' efficacy.

REFERENCES

Abad-Franch, F., M. M. Lima, O. Sarquis, R. Gurgel-Goncalves, M. Sanchez-Martin, J. Calzada, A. Saldana, F. A. Monteiro, F. S. Palomeque, W. S. Santos, V. M. Angulo, L. Esteban, F. B. Dias, L. Diotaiuti, M. E. Bar & N. L. Gottdenker (2015) On palms, bugs, and Chagas disease in the Americas. *Acta Tropica,* 151**,** 126-41.

Anderson, R. P. & I. Gonzalez (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling,* 222**,** 2796-2811.

Arboleda, S., D. E. Gorla, X. Porcasi, A. Saldana, J. Calzada & O. N. Jaramillo (2009) Development of a geographical distribution model of *Rhodnius pallescens* Barber, 1932 using environmental data recorded by remote sensing. *Infect Genet Evol,* 9**,** 441-8.

Austin, M. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling,* 157**,** 101-118.

Barrett, T. V. 1991. Advances in triatomine bug ecology in relation to Chagas' disease. In *Advances in Disease Vector Research*, 143-176. Springer.

Batista, T. A. & R. Gurgel-Gonçalves (2009) Ecological niche modelling and differentiation between *Rhodnius neglectus* Lent, 1954 and *Rhodnius nasutus* Stål, 1859 (Hemiptera: Reduviidae: Triatominae) in Brazil. *Memórias do Instituto Oswaldo Cruz,* 104**,** 1165-1170.

Beaumier, C. M., P. M. Gillespie, U. Strych, T. Hayward, P. J. Hotez & M. E. Bottazzi (2016) Status of vaccine research and development of vaccines for Chagas disease. *Vaccine,* 34**,** 2996-3000.

Brito, R. N., D. E. Gorla, L. Diotaiuti, A. C. F. Gomes, R. C. M. Souza & F. Abad-Franch (2017) Drivers of house invasion by sylvatic Chagas disease vectors in the Amazon-Cerrado transition: A multi-year, state-wide assessment of municipality-aggregated surveillance data. *PLoS Negl Trop Dis,* 11**,** e0006035.

Calzada, J. E., V. Pineda, J. D. Garisto, F. Samudio, A. M. Santamaria & A. Saldaña (2010) Human trypanosomiasis in the eastern region of the Panama Province: new endemic areas for Chagas disease. *Am J Trop Med Hyg,* 82**,** 580-582.

Calzada, J. E., V. Pineda, E. Montalvo, D. Alvarez, A. M. Santamaria, F. Samudio, V. Bayard, L. Caceres & A. Saldana (2006) Human trypanosome infection and the presence of intradomicile *Rhodnius pallescens* in the western border of the Panama Canal, Panama. *Am J Trop Med Hyg,* 74**,** 762-765.

Carmona-Castro, O., D. A. Moo-Llanes & J. M. Ramsey (2018) Impact of climate change on vector transmission of *Trypanosoma cruzi* (Chagas, 1909) in North America. *Med Vet Entomol,* 32**,** 84-101.

Castillo, M., R. Samaniego & A. Kindgard. 2015. Mapa de Cobertura y Uso de la Tierra 2012. ed. M. d. Ambiente. Panamá.

Castro, L. A., J. K. Peterson, A. Saldana, M. Y. Perea, J. E. Calzada, V. Pineda, A. P. Dobson & N. L. Gottdenker (2014) Flight behavior and performance of *Rhodnius pallescens* (Hemiptera: Reduviidae) on a tethered flight mill. *J Med Entomol,* 51**,** 1010-8.

Costa, J., A. T. Peterson & C. B. Beard (2002) Ecologic niche modeling and differentiation of populations of *Triatoma brasiliensis* Neiva, 1911, the most important Chagas' disease vector in northeastern Brazil (Hemiptera, Reduviidae, Triatominae). *Am J Trop Med Hyg,* 67**,** 516-520.

de la Vega, G. J. & P. E. Schilman (2018) Ecological and physiological thermal niches to understand distribution of Chagas disease vectors in Latin America. *Medical and Veterinary Entomology,* 32**,** 1-13.

de Noya, B. A. & O. N. González (2015) An ecological overview on the factors that drives to *Trypanosoma cruzi* oral transmission. *Acta Tropica,* 151**,** 94-102.

De Steven, D., D. M. Windsor, F. E. Putz & B. de Leon (1987) Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica***,** 342-356.

Dittel, J.W., T. D. Lambert, G. H. Alder (2015) Seed dispersal by rodents in a lowland forest in central Panama. *J Trop Ecol,* 31, 403-412.

Dijkshoorn, K., J. Huting & P. Tempel (2005) Update of the 1: 5 million soil and terrain database for Latin America and the Caribbean (SOTERLAC). *ISRIC Rep,* 1**,** 25.

Dyer, J. L., S. Tanner, J. Velasquez Runk, C. Mertzlufft, N. Gottdenker (2016) Deforestation, Dogs, and Zoonotic Disease. *Anthropology News,* e92-e95.

Eiserhardt, W. L., J. C. Svenning, W. D. Kissling & H. Balslev (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann Bot,* 108**,** 1391-416.

Elith, J. & J. R. Leathwick (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics,* 40**,** 677-697.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee & C. J. Yates (2011) A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions,* 17**,** 43-57.

Erazo, D. & J. Cordovez (2016) Modeling the effects of palm-house proximity on the theoretical risk of Chagas disease transmission in a rural locality of the Orinoco basin, Colombia. *Parasit Vectors,* 9**,** 592.

Feliciangeli, M. D., H. Carrasco, J. S. Patterson, B. Suarez, C. Martinez & M. Medina (2004) Mixed domestic infestation by *Rhodnius prolixus* Stäl, 1859 and *Panstrongylus geniculatus* Latreille, 1811, vector incrimination, and seroprevalence for *Trypanosoma cruzi* among inhabitants in El Guamito, Lara State, Venezuela. *Am J Trop Med Hyg,* 71**,** 501-505.

Fick, S. E. & R. J. Hijmans (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology,* 37**,** 4302-4315.

Galindez, I., S. Curto de Casas, R. Carcavallo, J. Jurberg & C. Mena Segura (1996) Geographical distribution and alti-latitudinal dispersion of the tribe Rhodniini (Hemiptera, Reduviidae, Triatominae). *Entomol Vect,* 3**,** 3-20.

Galvão, C. & S. A. Justi (2015) An overview on the ecology of Triatominae (Hemiptera:Reduviidae). *Acta Tropica,* 151**,** 116-125.

Garzon-Lopez, C. X., S. A. Bohlman, H. Olff & P. A. Jansen (2013) Mapping tropical forest trees using high-resolution aerial digital photographs. *Biotropica,* 45**,** 308-316.

Gottdenker, N. L., J. E. Calzada, A. Saldaña & C. R. Carroll (2011) Association of anthropogenic land use change and increased abundance of the Chagas disease vector *Rhodnius pallescens* in a rural landscape of Panama. *Am J Trop Med Hyg,* 84**,** 70-77.

Guillera-Arroita, G., J. J. Lahoz-Monfort, J. Elith & R. B. O'Hara (2014) Maxent is not a presence-absence method: a comment on Thibaud et al. *Methods in Ecology and Evolution,* 5**,** 1192-1197.

Gurgel-Gonçalves, R. & C. A. C. Cuba (2009) Predicting the potential geographical distribution of *Rhodnius neglectus* (Hemiptera, Reduviidae) based on ecological niche modeling. *J Med Entomol,* 46**,** 952-960.

Gurgel-Goncalves, R., C. Galvao, J. Costa & A. T. Peterson (2012) Geographic distribution of chagas disease vectors in Brazil based on ecological niche modeling. *J Trop Med,* 2012**,** 705326.

Gurgel-Goncalves, R. & R. B. Silva (2009) Analysis of the geographical distribution of *Psammolestes bergroth* (Hemiptera: Heteroptera: Reduviidae: Triatominae) in South America, with new records of *Psammolestes tertius* Lent & Jurberg. *Zootaxa,* 2033**,** 41-48.

Henderson, A., G. Galeano & R. Bernal. 2019. *Field guide to the palms of the Americas*. Princeton University Press.

Hirzel, A. & A. Guisan (2002) Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling,* 157**,** 331-341.

Holdridge, L. 1967. *Life zone ecology*. San Jose, Costa Rica: Tropical Science Center.

Jansen, P. A., M. D. Visser, S. Joseph Wright, G. Rutten & H. C. Muller-Landau (2014) Negative density dependence of seed dispersal and seedling recruitment in a neotropical palm. *Ecol Lett,* 17**,** 1111-20.

Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, M. Stillfried, I. Heckmann, A. K. Scharf, D. M. Augeri, S. M. Cheyne, A. J. Hearn, J. Ross, D. W. Macdonald, J. Mathai, J. Eaton, A. J. Marshall, G. Semiadi, R. Rustam, H. Bernard, R. Alfred, H. Samejima, J. W. Duckworth, C. Breitenmoser-Wuersten, J. L. Belant, H. Hofer, A. Wilting & M. Robertson (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions,* 19**,** 1366-1379.

Lent, H. & P. Wygodzinsky (1979) Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. *Bulletin of the American museum of Natural History,* 163**,** 123-520.

Lobo, J. M., A. Jiménez-Valverde & R. Real (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography,* 17**,** 145-151.

López-Cárdenas, J., F. E. G. Bravo, P. M. S. Schettino, J. C. G. Solorzano, E. R. Barba, J. M. Mendez, V. Sánchez-Cordero, A. T. Peterson & J. M. Ramsey (2005) Fine-scale predictions of distributions of Chagas disease vectors in the state of Guanajuato, Mexico. *J Med Entomol,* 42**,** 1068-1081.

Malik, L. H., G. D. Singh & E. A. Amsterdam (2015) Chagas Heart Disease: An Update. *Am J Med,* 128**,** 1251 e7-9.

Medone, P., S. Ceccarelli, P. E. Parham, A. Figuera & J. E. Rabinovich (2015) The impact of climate change on the geographical distribution of two vectors of Chagas disease: implications for the force of infection. *Philos Trans R Soc Lond B Biol Sci,* 370.

Merow, C., M. J. Smith, T. C. Edwards, A. Guisan, S. M. McMahon, S. Normand, W. Thuiller, R. O. Wüest, N. E. Zimmermann & J. Elith (2014) What do we gain from simplicity versus complexity in species distribution models? *Ecography,* 37**,** 1267-1281.

Merow, C., M. J. Smith & J. A. Silander (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography,* 36**,** 1058-1069.

Montúfar, R., F. Anthelme, J.-C. Pintaud & H. Balslev (2011) Disturbance and resilience in tropical American palm populations and communities. *The Botanical Review,* 77**,** 426-461.

Morales, N. S., I. C. Fernandez & V. Baca-Gonzalez (2017) MaxEnt's parameter configuration and small samples: are we paying attention to recommendations? A systematic review. *PeerJ,* 5**,** e3093.

Noireau, F., P. Diosque & A. M. Jansen (2009) Trypanosoma cruzi: adaptation to its vectors and its hosts. *Veterinary Research,* 40**,** 1-23.

Normand, S., J. Vormisto, J.-C. Svenning, C. Grández & H. Balslev (2006) Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecology,* 186**,** 161-176.

Palka, E. J. 2005. A geographic overview of Panama. In *The Río Chagres, Panama,* 3-18. Dordrecht: Springer.

Parra-Henao, G., O. Quiros-Gomez, O. N. Jaramillo & A. S. Cardona (2016a) Environmental Determinants of the Distribution of Chagas Disease Vector *Triatoma dimidiata* in Colombia. *Am J Trop Med Hyg,* 94**,** 767-74.

Parra-Henao, G., L. C. Suarez-Escudero & S. Gonzalez-Caro (2016b) Potential Distribution of Chagas Disease Vectors (Hemiptera, Reduviidae, Triatominae) in Colombia, Based on Ecological Niche Modeling. *J Trop Med,* 2016**,** 1439090.

Pereira, K. S., F. L. Schmidt, A. M. Guaraldo, R. M. Franco, V. L. Dias & L. A. Passos (2009) Chagas' disease as a foodborne illness. *Journal of Food Protection,* 72**,** 441-446.

Peterson, A. T., V. Sánchez-Cordero, C. B. Beard & J. M. Ramsey (2002) Ecologic niche modeling and potential reservoirs for Chagas disease, Mexico. *Emerging Infectious Diseases,* 8**,** 662.

Peterson, J. K., K. Hashimoto, K. Yoshioka, P. L. Dorn, N. L. Gottdenker, A. Caranci, L. Stevens, C. Zuniga, A. Saldaña & S. Rodriguez (2019a) Chagas Disease in Central America: Recent Findings and Current Challenges in Vector Ecology and Control. *Current Tropical Medicine Reports,* 6**,** 76-91.

Peterson, J. K., K. Yoshioka, K. Hashimoto, A. Caranci, N. Gottdenker, C. Monroy, A. Saldaña, S. Rodriguez, P. Dorn & C. Zúniga (2019b) Chagas disease epidemiology in Central America: an update. *Current Tropical Medicine Reports,* 6**,** 92-105.

Phillips, S. J. & M. Dudík (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography,* 31**,** 161-175.

Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick & S. Ferrier (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications,* 19**,** 181-197.

Phillips, S. J., M. Dudík & R. E. Schapire. 2004. A maximum entropy approach to species distribution modeling. In *Proceedings of the twenty-first international conference on Machine learning,* 83. ACM.

Pineda, V., A. Saldana, I. Monfante, A. Santamaria, N. L. Gottdenker, M. J. Yabsley, G. Rapoport & J. E. Calzada (2011) Prevalence of trypanosome infections in dogs from Chagas disease endemic regions in Panama, Central America. *Vet Parasitol,* 178**,** 360-3.

Pizarro Novoa, J. C. & C. Romaña (1998) Variacion estacional de una población silvestre de *Rhodnius pallescens* Barber 1932 (*Heteroptera: triatominae*) en la costa caribe colombiana. *Bulletin de l'Institut Français d'Études Andines,* 27**,** 309-325.

Pyke, C. R., R. Condit, S. Aguilar & S. Lao (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science,* 12**,** 553-566.

Rabinovich, J. E., U. D. Kitron, Y. Obed, M. Yoshioka, N. Gottdenker & L. F. Chaves (2011) Ecological patterns of blood-feeding by kissing-bugs (Hemiptera: Reduviidae: Triatominae). *Memorias do Instituto Oswaldo Cruz,* 106**,** 479-494.

Radosavljevic, A. & R. P. Anderson (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography,* 41**,** 629-643.

Rassi Jr, A., A. Rassi & J. A. Marin-Neto (2010) Chagas disease. *The Lancet,* 375**,** 1388-1402.

Rodriguez, I. G. & J. R. Loaiza (2017) American trypanosomiasis, or Chagas disease, in Panama: a chronological synopsis of ecological and epidemiological research. *Parasit Vectors,* 10**,** 459.

Romaña, C., J. Pizarro, E. Rodas & E. Guilbert (1999) Palm trees as ecological indicators of risk areas for Chagas disease. *Trans R Soc Trop Med Hyg,* 93**,** 594-595.

Saldaña, A., J. E. Calzada, V. Pineda, M. Perea, C. Rigg, K. González, A. M. Santamaria, N. L. Gottdenker & L. F. Chaves (2015) Risk factors associated with *Trypanosoma cruzi* exposure in domestic dogs from a rural community in Panama. *Memórias do Instituto Oswaldo Cruz,* 110**,** 936-944.

Salm, R., N. V. d. Salles, W. J. Alonso & C. Schuck-Paim (2007) Cross-scale determinants of palm species distribution. *Acta amazónica,* 37**,** 17-25.

Sanchez-Martin, M. J., M. D. Feliciangeli, D. Campbell-Lendrum & C. R. Davies (2006) Could the Chagas disease elimination programme in Venezuela be compromised by reinvasion of houses by sylvatic *Rhodnius prolixus* bug populations? *Tropical Medicine and International Health,* 11**,** 1585-1593.

Sandoval-Ruiz, C., J. Zumaquero-Rios & O. Rojas-Soto (2014) Predicting geographic and ecological distributions of triatomine species in the southern Mexican state of Puebla using ecological niche modeling. *J Med Entomol,* 45**,** 540-546.

Sigler, T. J. (2014) Monaco with bananas, a tropical Manhattan, or a Singapore for Central America? Explaining rapid urban growth in Panama City, Panama. *Journal of Tropical Geography,* 35**,** 261-278.

Smith, N. 2015. *Attalea butyracea*. In *Palms and People in the Amazon*, 83-89. Switzerland: Springer.

Stocking, M. & N. S. o. D. S. University of East Anglia. 1988. Tropical red soils: Fertility management and degradation. In *The Red Soils of East and Southern Africa: Proceedings of an International Symposium, Harare, Zimbabwe, 24-27 February, 1986*, 24. International Development Research Centre.

Teixeira, A., P. S. Monteiro, J. M. Rebelo, E. R. Argañaraz, D. Vieira, L. Lauria-Pires, R. Nascimento, C. A. Vexenat, A. R. Silva & S. K. Ault (2001) Emerging Chagas disease: trophic network and cycle of transmission of *Trypanosoma cruzi* from palm trees in the Amazon. *Emerging Infectious Diseases,* 7**,** 100.

Vasquez, A. M. d., F. E. Samudio, A. Saldaña, H. M. Paz & J. E. Calzada (2004) Eco-epidemiological aspects of *Trypanosoma cruzi*, *Trypanosoma rangeli* and their vector (*Rhodnius pallescens*) in Panama. *Revista do Instituto de Medicina Tropical de São Paulo,* 46**,** 217-222.

Vormisto, J., H. Tuomisto & J. Oksanen (2004) Palm distribution patterns in Amazonian rainforests: What is the role of topographic variation? *Journal of Vegetation Science,* 15**,** 485-494.

Warren, D. L. & S. N. Seifert (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications,* 21**,** 335-342.

Wright, S. J. & H. C. Duber (2001) Poachers and Forest Fragmentation Alter Seed Dispersal, Seed Survival, and Seedling Recruitment in the Palm *Attalea butyraceae,* with Implications for Tropical Tree Diversity. *Biotropica,* 33**,** 583-595.

Zeledón, R., F. Marín, N. Calvo, E. Lugo & S. Valle (2006) Distribution and ecological aspects of *Rhodnius pallescens* in Costa Rica and Nicaragua and their epidemiological implications. *Memórias do Instituto Oswaldo Cruz,* 101**,** 75-79.

CHAPTER 3

LANDSCAPE DISTURBANCE IMPACTS ON *ATTALEA BUTYRACEA* PALM DISTRIBUTION IN CENTRAL PANAMA: IMPLICATIONS FOR CHAGAS DISEASE TRANSMISSION[2]

---

[2] Mertzlufft, C., M. Madden, N. Gottdenker, J. Velasquez Runk, A. Saldaña, S. Tanner, J. Calzada, X. Yao. To be submitted to: *The International Journal of Health Geographics*

Abstract

Background: Chagas disease is a vector-borne zoonotic disease endemic to Latin America. In Panama, *Attalea butyracea* palm trees are the preferred habitat of the region's primary Chagas disease vector (*Rhodnius pallescens)*. Close proximity of these palms to human dwellings is linked to increased risk of Chagas disease transmission. However, these palms thrive in disturbed habitats associated with human settlement and agriculture. This study examines the relationship between landscape disturbance and mature *A. butyracea* spatial distribution, density, and proximity to susceptible populations and vector movement corridors in a heterogeneous tropical region in central Panama. Presence of *A. butyracea* does not guarantee corresponding presence of *R. pallescens*, but as the vectors' preferred habitat, quantifying *A. butyracea* response to disturbance may provide new insight into Chagas transmission risks in changing landscapes.

Methods: We remotely identified the locations of over 50,000 mature *A. butyracea* palms using high-resolution WorldView2 satellite imagery. A local Getis-Ord Gi* spatial analysis identified significant clusters of aggregated palms. Associations between palm and cluster abundance and a landscape disturbance gradient, derived from official Panama landcover data, were tested using Chi-square tests for Homogeneity and Z-test for proportions. Kruskall-Wallace non-parametric analysis of variance tests were run to assess whether palm cluster area varied by disturbance level, or whether disturbance influenced average proximity of palms and palm clusters to susceptible populations or vector movement corridors.

Results: Our findings indicate a regional relationship between landscape disturbance and *A. butyracea* occurrence. We observe a significant increase in both individual and clustered *A. butyracea* in secondary forest, but a reduction in palms in agricultural settings. Notably, we do not detect evidence of any thinning in abundance of palms in residential settings. All but one household in our study area is within vector flight distance of potential vector habitat in palm crowns.

Conclusions: We observe probable anthropogenic thinning of *A. butyracea* palms in agricultural, but not residential, settings. Even in heavily deforested regions, significant concentrations of mature palms remain in close proximity to human establishments. The potential of *A. butyracea* palms as a source of infectious Chagas disease vectors in this region warrants further study.

Introduction

Landscape disturbance, ranging from local (e.g., deforestation, mining) to global scales (e.g., climate change), is associated with altering the pattern and distribution of several zoonotic diseases (Daszak, Cunningham and Hyatt 2001, Daszak, Cunningham and Hyatt 2000, Dobson et al. 2006, Foley et al. 2005, Gottdenker et al. 2014). The primary vector of Chagas disease in Panama, the triatomine bug (Hemiptera: Reduviidae), *Rhodnius pallescens*, preferentially inhabits royal palm trees (*Attalea butyracea)*, which thrive in disturbed habitats (Henderson, Galeano and Bernal 2019, Rassi Jr, Rassi and Marin-Neto 2010). *A. butyracea* palms in secondary growth regions are more likely to be infested with Chagas vectors (Gottdenker et al. 2011), and, when initial deforestation occurs as a result of human settlement and agriculture, inherently more likely to exist in close proximity to human establishments (Smith 2015, Wright et al. 2000). This close proximity of households to *Attalea spp* palms has been linked to increased risk of Chagas disease transmission in humans (Abad-Franch et al. 2015, Erazo and Cordovez 2016, Feliciangeli et al. 2004, Sanchez-Martin et al. 2006, Teixeira et al. 2001, Vasquez et al. 2004) and domestic dogs (Saldaña et al. 2015).

Increased *A. butyracea* propagation in response to landscape disturbance has been recorded in individual palm studies in Panama (Wright and Duber 2001, Wright et al. 2000). This study tests this association at a regional scale. Using high-resolution WorldView2 satellite imagery, we have identified a comprehensive subset of over 50,000 mature *A. butyracea* palms within a 300-km^2 heterogeneous tropical landscape in central Panama. We explore the spatial distribution of this palm sample across a gradient of landscape disturbance, which ranges from areas with limited natural or anthropogenic alteration to areas highly and regularly impacted by human activities: mature forest, secondary and planted forest, pasture, planted food crops, and the built environment. Controlling for other environmental factors known to influence palm distribution, (i.e. elevation, precipitation, soil type, average temperature and temperature seasonality) we ask the following questions:

1. Is there a relationship between landscape disturbance and the distribution or density of individual *A. butyracea* palms?
2. Is there a relationship between landscape disturbance and the distribution, density, or area of monospecific stands of *A. butyracea* palms?
3. Is there a relationship between landscape disturbance and the proximity of palms or palm stands to either susceptible human hosts or movement corridors for Chagas vectors and sylvatic hosts (e.g., riparian zones or nearby habitat)?

Although presence of *A. butyracea* does not guarantee corresponding presence of Chagas vectors or the offending pathogen, because of the vector's affinity for this palm species, quantifying *A. butyracea* response to landscape disturbance may provide new insight into Chagas transmission risks in changing landscapes. Assessing how vector habitat responds to landscape change may help target vector and at-risk human populations, and aid strategic distribution of financial and personnel resources for both current and future Chagas prevention and mitigation strategies.

Background: Chagas Disease in Panama

Chagas disease, or American trypanosomiasis, is a vector-borne zoonotic infectious disease endemic to Latin America that is caused by infection with kinetoplastid protozoan parasite, *Tyrpanosoma cruzi* (Lent and Wygodzinsky 1979). The *T. cruzi* parasite is most often transmitted to human hosts through direct contact with the fecal matter of certain triatomine species (Rassi Jr et al. 2010). Currently, no vaccine exists for Chagas disease, and treatment, where available, is often costly and poorly tolerated; prevention of initial infection by deterring vectors' access to susceptible human hosts is the best-recommended strategy for reducing morbidity and mortality related to this disease (Rabinovich et al. 2011, Rodriguez and Loaiza 2017, Moncayo and Silveira 2017).

In Panama, there are 10 triatomine bug species that are *T. cruzi* vectors. However, only two species, *Triatoma dimidiata* and *Rhodnius pallescens,* are associated with Chagas disease transmission to human populations in this region; of these, *R. pallescens* is Panama's dominant vector (Saldaña et al. 2015, Vasquez et al. 2004). *R. pallescens'* preferred habitat, the *A. butyracea* palm (Figure 3.1), is a dense-crowned species in the subtribe *Attaleinae* that ranges from Mexico to western Amazonia (Henderson et al. 2019, Smith 2015). This palm is characterized by a large crown (individual fronds may reach up to 10 meters in length), which contains dense organic material. The dense crown is well suited to supporting the microclimate

R. pallescens bugs require, as well as habitat for the arboreal mammals on which they preferentially feed (Abad-Franch et al. 2015, Condit, Pérez and Daguerre 2010, De Steven et al. 1987, Romaña et al. 1999, Smith 2015, Jansen et al. 2014).

R. pallescens vectors often inhabit palm crown ecotopes, and *T. cruzi* parasite transmission in Panama is typically confined to sylvatic transmission cycles within palm crowns (Calzada et al. 2006, Whitlaw Jr and Chaniotis 1978). *R. pallescens* vectors do not reproduce in human dwellings (Pineda et al. 2008). The sylvatic habitat of these insects likely contributes to the relatively low prevalence of human infection in this country, as compared historically to other Latin American countries with predominantly domiciliated vectors. The prevalence of Chagas disease among tested Panamanian communities ranges from < 1 - 5.9% (Calzada et al. 2010, Saldaña et al. 2012). In contrast, the reported prevalence of *T. cruzi* infection among captured *R. pallescens* vectors in similar regions ranges from 73.4 - 85.4% (Gottdenker et al. 2012, Vasquez et al. 2004).

Although prevalence is low among human populations, Chagas disease transmission remains a low but constant risk in Panama due to potential crossover from sylvatic to domestic transmission cycles (Abad-Franch et al. 2015, Calzada et al. 2006). *A. butyracea* palms are key sources of triatomine colonies in Panama, particularly peridomestic palms (Gottdenker et al. 2011). However, adult bugs in palms near households occasionally invade homes, either in search of potential food sources due to overcrowding of palm canopies (Coura et al. 2002, Teixeira et al. 2001), or through attraction to electric lights (Castro et al. 2010, Zeledón et al. 2006). Therefore, living, working, or otherwise engaging with nearby *A. butyracea* is considered a risk factor for contracting this disease (Romaña et al. 1999, Vasquez et al. 2004). However, although intradomiciliary *R. pallescens* are more likely to have fed on humans than their palm-based counterparts (Calzada et al. 2006, Pineda et al. 2008), household environments lack the microclimate *R. pallescens* require to thrive and reproduce, and indoor specimen are typically adults that have made their way inside, not immature nymphs or eggs produced indoors (Pineda et al. 2008).

The spatial and temporal randomness of triatomine entry renders indoor insecticide spraying an economically inefficient barrier in this region. Triatomine bug populations are also difficult to control in their native environment without additional harmful ecological effects (Abad-Franch et al. 2015). Interwoven social and ecological processes complicate the deceptively straightforward solution of spatially distancing *A. butyracea* palms and human populations. The fractured landscapes associated with human settlement and agriculture decrease biodiversity, which is shown to decrease predation on *A. butyracea* seeds within Panama. Decreased predation results in increased propagation of *A. butyracea* in disturbed habitats, and enhances the formation of monospecific stands of palms (Wright and Duber 2001, Wright et al. 2000). Concurrently, mature *A. butyracea* palms are socially valued regionally for a number of goods and services, including household thatch, palm wine, medicine, and shade for livestock (Olivares and Galeano 2013). These useful properties lead some people to purposefully maintain *A. butyracea* in pasture or nearby residential or commercial areas, even, occasionally, in otherwise clear-cut environments (Bernal et al. 2010). All of these factors increase the risk of interaction between susceptible human populations and infectious vectors in this region.

Methods

Study Area

The study area is located in the Panamá Oeste Province in central Panama, straddling La Chorrera and Capira districts and covering all or part of seventeen *corregimientos* (sub-districts) (Figure 3.2). Guided by satellite imagery and the expert regional knowledge of members of our team, we selected this location due to its known history of Chagas disease transmission, abundance of *A. butyracea* palms, and adequate representation of each category of our disturbance gradient. Because landscape disturbance is by no means the only variable associated with *A. butyracea* prevalence, we chose an area with minor variation in other environmental variables known to influence palm distribution: elevation, precipitation, soil type and temperature (Eiserhardt et al. 2011, Garzon-Lopez et al. 2013, Henderson et al. 2019, Normand et al. 2006).

Data Collection and Pre-processing

1. Satellite Imagery

To conduct our remote identification of *A. butyracea* palm locations, we obtained a high-resolution WorldView2 (WV2) satellite image in both multispectral and panchromatic format covering 300.1 km^2 of our region of interest (bounding coordinates NW: -80.013, 8.94; NE: -79.854, 8.93; SE: -79.855, 8.785; SW: -80.013, 9.793) (DigitalGlobe, Inc., 2017). Our imagery was collected February 1, 2013 at an off-nadir angle of 16.19°, producing a spatial resolution of 2.03 m for multispectral bands and 0.51 m panchromatic. To remove distortions due to image tilt and region topography, the imagery was orthorectified with a NASA Shuttle Radar Topography

Mission (SRTM) 30-m digital elevation model of Panama, obtained through the Smithsonian Tropical Research Institute's (STRI) GIS OpenData Portal.

2. Palm Collection and Validation

The palm data used in this study were obtained through a combination of manual field sampling in our study area in 2016 and 2017 and remote palm coordinate collection via visual interpretation of the WV2 satellite imagery. Our fieldwork was authorized by the Panama Ministry of the Environment (MiAmbiente), the Gorgas Memorial Institute for Health Studies (ICGES), and STRI.

We recorded the field locations of an initial convenience sample of 131 *A. butyracea* palms in our study region in July 2016. This palm dataset consisted primarily of easily accessible roadside palms, comprising both freestanding individuals and those located within a contiguous forest. We collected coordinate points of each palm with a Garmin Oregon 550T handheld GPS unit and photos of each palm crown as a record of species identification; coordinates and photos were linked with a unique identifier. We converted the palm coordinates to a point shapefile and overlaid these on our WV2 image, where each point was manually assessed to confirm visibility of a corresponding palm crown within the satellite image. We randomly selected 30% (n=39) of our palm sample to reserve as a validation subset; the remaining 70% (n=92) of the sample was used for training to manually digitize *A. butyracea* crowns across the remainder of the WV2 image.

For the methodological remote detection of *A. butyracea* palm crowns in our study area, we created a grid across the imagery's extent, consisting of 535 0.75-km-by-0.75-km cells, which was generated by hollow square tessellation in ArcMap 10.5.1 software (ESRI, Redlands, California). Each one of these 0.56 km^2 cells was carefully analyzed for palm presence using both panchromatic and pan-sharpened (i.e., a fused 2-m multispectral and 0.5-m panchromatic image having both high spatial resolution and four color bands) WV2 imagery. Mature palm crowns are readily distinguished on remotely sensed imagery, due to their distinctive starburst shape (Figure 3.3). However, to increase palm visibility, each color band of the pan-sharpened image was enhanced with high contrast settings and brightened. The pansharpened imagery was set to a true color display for visualization of palm crowns, which was useful for palm species differentiation, along with scale and texture, (Figure 3.3a). Texture showed more clearly on the panchromatic imagery, which was especially useful in recognizing palm crowns in dense, contiguous canopy (Figure 3.3b). Beginning with our training dataset and then moving systematically through the grid cells, a trained analyst identified all large-crowned (7-12 m diameter) palms either fully or partially visible that matched the *A. butyracea* training set's shading and crown shape/texture characteristics. Palm locations were delineated as points centered on the palm crown and recorded in a point shapefile. Our final dataset totaled 50,955 possible mature *A. butyracea* palms.

We tested the accuracy of this large dataset both against the reserved validation sample of known *A. butyracea* palm locations and against an additional field sample of 86 *A. butyracea* and non-*A. butyracea* palms collected expressly for this purpose in our study region in late 2017. To ensure an adequately sized and novel sample for the 2017 palm validation dataset, we randomly selected three of our grid cells for in-field data collection after excluding those with fewer than 30 identified palms and those that contained any of the 2016 convenience palm locations (Figure 3.4). The grid cells in our resulting validation pool subset (n=439) were assigned unique numerical IDs. We randomly chose three using an online random number generator. In each of the three 0.56 km^2 grid cells, we field-collected locational coordinates and photos of approximately 30 large-crowned palms, comprising both *A. butyracea* and non-*A. butyracea* palm species. Though our field sites were randomly selected, the palms we sampled within them were not. Logistical (e.g., natural and manmade terrain barriers, inability to locate some landowners to request permission to access property) and time constraints made either a truly random sample or a full census of palms in these regions infeasible. Instead, led by the remotely identified palm dataset, we prioritized data collection in accessible areas that contained a combination of pasture and contiguous canopy and were removed from major roadways.

From our 2017 field validation sample, we calculated positive and negative predictive values, as well as sensitivity (true positive rate) and specificity (true negative rate), in order to quantify our ability to remotely detect and properly identify palm species, and to assess likelihood of Type 1 (false positive) and Type II (false negative) errors. We further compared the accuracy of our *A. butyracea* identification stratified by contiguous canopy forest and open pasture. Accurately identified *A. butyracea* (true positives) were palms identified remotely via WV2 imagery that were field-verified as *A. butyracea*. Accurately identified non-*A. butyracea* (true negatives) were field-verified non-*A. butyracea* palms that were ignored in our remote sensing effort as “other” species.

3. Disturbance Gradient

We derived our natural and anthropogenic landscape disturbance gradient using spatial data from two official Panamanian government datasets: 2012 land cover data and 2010 census data. Both datasets were obtained directly from the ministries responsible for their creation. The 2012 Panama land cover data were generated by Panama’s Ministry of the Environment

(MiAmbiente; formerly ANAM) in collaboration with the Food and Agricultural Organization of the United Nations (FAO) (Castillo, Samaniego and Kindgard 2015). These data were compiled using 5-m spatial-resolution satellite images collected by the RapidEye sensor between January 1, 2011 and April 30, 2012 to form a seamless, 5-m resolution land cover dataset for the entire extent of Panama (ANAM 2003, Castillo et al. 2015). Panamanian census data are collected on a decadal basis by the National Institute of Statistics and Census (INEC). The census spatial data used in this study includes administrative boundaries of La Chorrera and Capira districts and sub-districts, as well as the locations of buildings, rivers and streams within this region.

The 2012 land cover dataset contains 24 land cover classifications, 11 of which comprise our study region: mixed mature broadleaf forest, mixed mature secondary broadleaf forest, conifer planted forest, hardwood planted forest, new growth/bushes, corn, pineapple, pasture, surface water, populated areas, and infrastructure. We extracted land cover data within the boundaries of our satellite image extent and consolidated similar land cover types to form a 5-category disturbance gradient (Table 3.1). From least- to most-altered, this disturbance gradient consists of mature forest, secondary and planted forest, pasture, planted food crops, and the built environment. The built environment is a term that encompasses anthropogenic structures and their supporting infrastructure (e.g. roads), to support human activity spaces for living, working, and recreation (Lawrence and Low 1990).

A comparison of the 2012 land cover data and our 2013 satellite imagery indicated high consistency between the two datasets. However, we observed poor representation in the land cover data of considerable contiguous tree cover associated with the riparian zones of minor streams and rivers, which may serve as important wildlife and vector movement corridors. To spatially define these riparian zones for inclusion in our disturbance database, we applied buffers to the river and stream locations contained in the 2010 census data, which were more complete than the surface water estimates within the 2012 land cover dataset. We applied a 25-m buffer to all rivers and streams within our study area, based on an average of riparian area widths measured in the satellite image. The land cover within this 50-m wide area was reclassified "riparian zone" and included in the secondary forest category of our disturbance gradient.

Due to the heterogeneity of land cover classes that comprise the secondary and planted forest classification, for some analyses we further stratified this category into riparian zone, recent growth ($\leq$ 5 years), and established forest (> 5 years). Recent growth corresponds to the official Panama land cover classification of "rastrojo", which refers to the initial stages of secondary forest at five years of age or less (ANAM 2003). Established secondary and planted forest is a combination of mixed secondary broadleaf forest, and both coniferous and deciduous planted forests.

Due to cloud cover and cloud shadow, which covered approximately 6% of our satellite image surface, certain regions of the imagery were obscured to remote palm extraction. To accurately calculate the density of our palm sample stratified by our disturbance gradient, it was necessary to mask the land cover data to replicate the visible satellite surface. We first generated a shapefile of the obscuring cloud cover/cloud-shadow using object-based image analysis (OBIA) software, eCognition Developer 8.1 (Trimble Inc., Sunnydale, CA). OBIA is an image classification method that transforms high-resolution pixels into meaningful objects, based on user-defined combinations of size, shape, and band metrics; pixels are first grouped, then joined, into desired categories through user manipulation (Blaschke 2010). This shapefile was used to remove obscured regions in our study area for both the original 2012 land cover data and consolidated disturbance dataset, resulting in two masked subsets that exactly matched the visible satellite imagery extent (see Figure 3.4). Using z-tests for proportion comparisons, we assessed whether the masked datasets were representative samples of the total study region for each dataset. For each classification scheme, we found no significant difference in land cover distribution between the original dataset and its corresponding masked subset. We conclude that the masked region used for palm extraction and density analyses is representative of the entire study area; no significant bias was introduced to the analysis by disregarding the approximately 6% of the satellite image obscured by clouds or shadow.

Spatial Analysis of Palm Data

Natural and anthropogenic landscape disturbance is linked with increased *A. butyracea* propagation at local scales (Henderson et al. 2019). To assess the relationship between landscape disturbance and palm propagation at a regional scale, we compared palm distribution, density, and proximity to key features across the disturbance gradient within our 300-km^2 study area. Because landscape disturbance is also associated with increased likelihood of *A. butyracea* forming monospecific stands (Jansen et al. 2014, Wright and Duber 2001, Wright et al. 2000), we assessed the spatial relationship of both individual palms and statistically significant clusters of mature palms, a proxy for monospecific stands, for all spatial analyses. All geospatial analyses were conducted using ArcGIS 10.5.1 software (ESRI, Redlands, California) and all statistical analyses were conducted using SAS 9.4 software (SAS Institute Inc., Cary, NC).

1. Palm Clustering

We assessed our *A. butyracea* palm dataset for spatially clustered groupings of points that may indicate a monospecific stand, or cluster, of this palm species. Our palm data consisted only of x,y coordinate information, and the very large sample size and narrow distance increment of interest for clusters (~30-m) made traditional point pattern analysis of clustering (e.g. Ripley's K analysis) prohibitively computationally intensive. Instead, we aggregated palm points to the cells of a 50x50-m grid vector shapefile overlaid on our study region, which provides a uniform and comparable measure of palm density across our sample area. We tested grid overlays at spatial resolutions of 5-m (an exact replicate of the underlying landscape raster), 30-m, 50-m, and 100-m; however, the 50-m spatial resolution best characterized palm distribution without including too much "empty" space (100m & 250m), or creating too many "islands" of non-contiguous occupied cells (30m). Additionally, *A. butyracea* propagation literature suggests an average of <10-m seed migration (by predators who feed on the surrounding fleshy mesocarp) from the parent tree, with occasional migration up to 30 meters (Dittel, Lambert and Adler 2015, Lambert et al. 2014). We anticipate a cell size of 50-m spatial resolution is large enough to pick up clusters of related palms within a single cell, or among neighboring cells. We filtered unoccupied grid cells from the dataset to limit our assessment of palm clustering solely within the observed palm distribution area.

We assessed overall presence or absence of palm clustering in our study area using a global Moran's I spatial analysis. To reduce the bias of edge effects in our Moran's I analysis, we row-standardized the spatial weighting scheme, which proportionally controls the weighting of cells with unequal numbers of neighbors (Tiefelsdorf, Griffith and Boots 1999). Specific clusters of occupied cells were identified using the local Getis-Ord Gi* analysis, or commonly called hotspot analysis, with an inverse-distance weighting scheme. Local Getis-Ord Gi* is a popular type of Local Indicator of Spatial Autocorrelation (LISA). Given our large sample size, we applied a false discovery rate (FDR) correction to the hotspot analysis, which applies a more conservative threshold to cluster significance in order to reduce Type-1 errors associated with multiple testing and spatial dependency (Caldas de Castro and Singer 2006).

2. Palm Distribution

Palms and significant palm clusters were assigned a disturbance gradient category based on their location and surrounding land cover. To adjust for any minor spatial disagreement between our land cover data and satellite imagery due to limitations of positional error of the two data sets, which might introduce error when overlaying the palm coordinate data with level of disturbance, we assigned palms a corresponding gradient based on the disturbance category that comprised a majority of area within a 10-m buffer zone surrounding each palm point. Palm clusters were assigned the disturbance category that comprised the majority of their area. We used a Pearson's chi-squared test of homogeneity to analyze whether our observed palm point and cluster distributions statistically deviated from an expected distribution. Because *A. butyracea* palms are ubiquitous across central Panama and our study area controls for known drivers of *A. butyracea* palm distribution (i.e. soil, temperature, precipitation), we expect our palm and cluster distribution to be generally evenly distributed across the disturbance gradient categories if no relationship exists between landscape disturbance and palm presence at a regional scale. We employed pairwise z-tests for proportions to identify the disturbance category or categories driving statistically significant variances from this expected distribution, where applicable.

We also assessed a random, stratified sample of 150 palm trees (thirty palms from each of our five disturbance gradient categories) to test whether average crown diameter, a proxy of palm age, differed significantly across the disturbance gradient. We used an analysis of variance (ANOVA) test to assess whether average palm diameter differed significantly by disturbance type.

3. Palm Density

Using the disturbance gradient assigned to each palm and palm cluster, we assessed average density of palms and clusters stratified by disturbance gradient. Palm density was measured as number of palms per square kilometer disturbance gradient. Cluster density was measured as average cluster hectare per square kilometer disturbance gradient.

4. Palm Proximity to Key Features

We assessed the distance of each palm and palm cluster to the nearest feature of interest in each of three categories: buildings, rivers, and other palms/clusters. Palm distance was measured from the center point of each crown. Cluster proximity was calculated between the feature of interest and the cluster's boundary. Proximity to buildings is used as a proxy of Chagas risk to human populations, given concerns of crossover between sylvatic and domestic transmission cycles. Distance to riparian areas and other palms/clusters were considered as potential pathways of either vector or reservoir species' movement (De Lima and Gascon 1999, Laurance and Laurance 1999).

We considered palm proximity to all buildings within our study region, as well as a household subset. The Panama census building database does not specify residential buildings, but does specify *fincas* or occupied ranches, as well as many commercial, administrative and agricultural building types (e.g., schools, supermarkets, henhouses). Through process of elimination, we considered *fincas* and all buildings not otherwise labeled to be households. To further exclude buildings improbably large or small for residences, we further refined this potential household dataset to structures between 50-275 m^2 in size which we derived spatially from the building's footprint.

All distances were stratified by the originating palm/cluster's corresponding disturbance gradient and averaged. To statistically compare stratified average proximity of palms and clusters to our key features of interest, we employed Kruskall-Wallace analysis of variance by ranks tests (Kruskal and Wallis 1952). Palms and clusters tended to be quite close to features of interest, with a minority of longer-distanced outliers. This skewed distribution violates assumptions associated with the more common statistical test to compare averages, the Analysis of Variance (ANOVA); the Kruskal-Wallace test is the non-parametric equivalent. Where necessary, we followed this test with a pairwise Dunn's test for non-parametric post-hoc analysis, using a SAS macro developed by Elliott and Hynan (Elliott and Hynan 2011).

Results

Accuracy of remote A. butyracea identification

Of the 30% (n=39) known *A. butyracea* locations withheld from our 2016 convenience sample for validation testing, we accurately identified 95% (n=37) as *A. butyracea* palms. The two overlooked palms were both partially obscured by non-*Attalea* contiguous canopy. In one instance, only a partial shadow indicated the palm's presence. However, we found that canopy cover was not a general barrier to *A. butyracea* identification within this subset; we correctly located and digitized all six additional palms partially or mostly obscured by canopy. The validation subset was added to the total palm dataset used for this analysis, and their identifying characteristics studied for further palm extraction.

In our 2017 field survey used to validate a random subset of our final remotely collected palm sample, we collected coordinate and photographic records for 86 mature, large-crowned palms. Of this validation sample, 64% (n=55) were *A. butyracea*, while the remainder were non-*A. butyracea* controls. The *A. butyracea* sample was evenly divided between pasture palms (n=28, defined as solitary individuals with minimal undergrowth and no surrounding contiguous canopy) and canopy palms (n=27, defined as individuals in the understory or part of contiguous canopy). A majority of the non-*A. butyracea* control palms (n=26, 84%) were solitary pasture palms. Coconut palms (*Cocus nucifera*) comprised most of the control subset; the remainder comprised a variety of large-crowned pinnate palm species.

Overall, this field sample suggests high success in correctly identifying *A. butyracea* remotely via satellite imagery, with an overall positive predictive value of 80% (Table 3.2). However, we observed an underestimation of true *A. butyracea* palm presence in our study area, particularly in areas of contiguous canopy: we identified via remote sensing nearly all of the pasture *A. butyracea* palms collected in our field sample (89%), but missed 45% of those collected in canopy areas. Palms obscured from overhead by tree cover were almost always overlooked via satellite imagery. While the majority of the obscured palms were located in contiguous canopy, we observed multiple instances of otherwise solitary pasture *A. butyracea* that were nearly completely encased in other tree species, altering their characteristic crown shape (Figure 3.5). We also noted several instances of closely clustered *A. butyracea* palms, particularly along forest edge boundaries, incorrectly marked as a single palm via remote sensing.

Landscape disturbance

Our landscape disturbance gradient suggests that 99.77% of our study area has experienced significant natural or anthropogenic alteration; less than one quarter of one percent of this region is composed of the least disturbed mature forest (Table 3.3). However, over a third of the study region comprises secondary forest, which is second lowest on the disturbance index. Nearly six percent of the secondary forest and just over two percent of the entire study area is recent forest growth, aged five years or less as of 2012. A majority of the study area (55.45%) is pasture, which is typically reserved for cattle. Food crops and infrastructure combined comprise just over five percent of the region.

Both pastoral and secondary forested gradients comprise large spaces of contiguous coverage in our study area, but the secondary forest also comprises substantial amounts of forest fragments (Figure 3.4). Mature forest is primarily confined to small islands of forest surrounded by large contiguous regions of secondary growth, although in two instances it directly abuts pasture. We see the most forest cover in the more elevated southwest region of our study area.

Is there a relationship between the distribution and density of individual A. butyracea palms and landscape disturbance?

Given uniform palm distribution across the landscape, we expect the frequency of palm occurrence to match the proportional breakdown of our landscape disturbance gradient.

However, we observe significant divergence in expected distribution of palms in secondary forest, pasture and food crop settings (see Table 3.3).

Nearly half of the palms (49.72%) in our study area are found in secondary and planted forest, which is significantly higher ($p < 0.01$) than the approximately 40% of the region's area covered by this gradient type. When secondary forest is further stratified by subtype, we observe that established secondary forest (> 5 years) drives the significance of this category, comprising over 60% of individual secondary forest palms. Palm distribution in secondary forest associated with riparian zones and new growth (≤ 5 years) does not deviate from expected.

In contrast, we observe fewer palms than expected in agricultural settings ($p < 0.05$). Palms in pastoral and food agriculture zones comprise 47.43% and 0.59% of our total sample, respectively, although these regions account for 55.45% and 1.66% of our study area. This may be indicative of purposeful thinning of palms associated with agricultural environments. However, given the sheer number and density of palms that remain in pastoral settings, at nearly 200 palms/km^2, thinning of *A. butyracea* in these regions appears gradual. We observe the highest palm density in the secondary and planted forested regions, particularly within new growth (≤ 5 years) forest, at 289 palms/km^2. Palm density is lowest in cropland (76.47 palms/km^2).

Of particular relevance for Chagas disease transmission, thinning of palm trees appears confined to agricultural, and not residential, settings. We do not observe any statistically significant reduction in *A. butyracea* presence associated with the built environment, resulting in ample potential vector habitat located near human households. At a density of 125 palms/km^2, we find over 1000 *A. butyracea* palms within the 8-km^2 area classified as the built environment, over 95% of which is populated residential and commercial areas.

Additionally, our observations do not support a relationship between landscape disturbance and the average age of palms in this region, as measured through the proxy of palm crown size (Table 3.4). Our random sample of palm crowns ranged from 4.26-15.97 meters in diameter, but their stratified averages did not meaningfully deviate across disturbance categories. However, this finding may also reflect a bias towards the remote detection of larger, mature palms, which our field validation indicated were more likely to be detected in satellite imagery.

Is there a relationship between distribution, density, or area of monospecific stands of A. butyracea palms and landscape disturbance?

The Global Moran's I analysis revealed highly significant (p-value < 0.0001) spatial clustering of mature palms within the broader area of observed palm distribution in our study area. The Getis-Ord Gi* analysis with FPR correction identified 342 statistically significant distinct palm clusters, indicative of monospecific stands of mature palms (Table 3.3). Given the much smaller sample size, cluster density is far lower than individual palm density throughout the region. We observe the highest density of clusters in established secondary and planted forest (2.24 clusters/km^2), and lowest densities in areas with planted food crops (0.26 clusters/km^2) and the built environment (0.37 clusters/km^2).

The distribution pattern of clustered palms generally mirrors that of individual palm trees. As with individual palms, we observe a statistically significant increase in palm clusters in secondary and planted forest (p-value < 0.01), which is also driven by significance in established growth (Table 3.3). However, in contrast to individual palms, we find no association with pasture or food agriculture, but do observe significantly fewer clusters than expected in the built environment (p-value < 0.05).

Most palm clusters observed in our study region are less than a hectare in area. The average area of the palm stands remotely identified in this region is 0.42 ha, although the largest single contiguous area with a high density of palms reaches 4.5 ha (Table 3.5). We find no evidence to support that the average size of palm clusters differs by landscape disturbance level.

Is there a relationship between landscape disturbance and the proximity of A. butyracea palms or palm stands to susceptible populations or movement corridors?

Overall, palm and palm clusters are heavily skewed toward close proximity to features of interest (Figure 3.6). Individual palms were closest in proximity to other palms on average, and farthest from buildings. Palm clusters, in contrast, were furthest from other clusters by a large margin, and closest in proximity to rivers. However, the observed average proximity in all categories is well within the recorded average flight distance of *R. pallescens* vectors (702 m) (Castro et al. 2014). A majority (71%, n=1849) of houses were within 21-100 m of our *A. butyracea* palm sample (Table 3.6). Just over five percent (n=145) of households were within 10 m of an identified palm.

When stratified by disturbance gradient, we observe no significant difference in proximity of palms or clusters to other palms/clusters, but significant variations in average distance to buildings and riparian corridors (Table 3.7). Clusters are spaced much farther apart than individual palms, at more than 300 meters in all areas but the built environment (average spacing 168.75 m) compared to only slightly over 20 m separation of individual palms on average. Individual palms and palm clusters within the built environment are closest to households, at less than 60 m each on average, while those in a mature forest setting are farthest away, at over 8000 m each on average. There is no clear relationship between palm and palm cluster proximity to rivers in association with our disturbance gradient, except those in riparian zones are inherently closest.

Discussion

Remote sensing of A. butyracea palms

Understanding the locations of *A. butyracea* palms is critical for locating potential Chagas vector populations. However, manually censusing the locations of palm trees in the field is a labor-intensive task, particularly over large or remote areas. Where palm location, count, or crown-size are the key variables of interest, many studies have turned to remote data acquisition from satellite or aerial sensors to facilitate palm identification. Our identification of *A. butyracea* palm crowns using high spatial-resolution WV2 satellite imagery is consistent with the challenges and findings of previous tropical studies of remote tree crown extraction. Our field validation survey suggests overall high accuracy (80%) in assigning the correct species to visible *A. butyracea* crowns (low commission error), but frequent underestimation (58%) of true numbers of our target species (high omission error). Inability to observe understory *A. butyracea* crowns obscured by forest canopy or to distinguish closely-spaced individual *A. butyracea* contributed to underreporting via remote sensing. Through field validation, we discovered multiple instances of two or more close-growing *A. butyracea* palms in a location where one large *A. butyracea* crown was identified via satellite imagery. It is possible that other very large "single" crowns elsewhere in our study area actually depict closely packed palm clusters.

However, our commission and omission errors are consistent with manual remote tree crown assessments for both palm (Garzon-Lopez et al. 2013, Jansen et al. 2008) and non-palm tropical tree species (Trichon 2001, Trichon and Julien 2006). Notably, despite high omission errors, these previous studies found that remotely detected palm crowns reliably tracked overall spatial patterning of their study species, including clustering, based on full censuses of field-verified palm distribution (Garzon-Lopez et al. 2013, Jansen et al. 2008). Due to the heterogeneous land cover in our study area, we are able to further build upon these studies by comparing remote palm crown identification accuracy in deforested as well as forested settings. Unsurprisingly, given increased visibility of single palm crowns growing in open pastures, we observe increased accuracy in both detecting (decreased omission error) and identifying (decreased commission error) *A. butyracea* crowns in pastoral settings due to less crowding and canopy overlap.

Also consistent with previous studies, we detect a bias in our dataset toward mature palms (dos Santos et al. 2017). We also observed that many of the palms missed in our remote inspection, both canopy and pasture palms, were individuals with relatively sparse crowns—an indication of either young age or heavy harvesting of palm fronds, such as in the use of thatching. Without exception, juvenile palms (palms without mature stalks) were missed altogether, despite our < 0.2 m spatial-resolution imagery. Palm crowns at immature growth stages are generally difficult to visualize even on high spatial-resolution imagery, based on smaller crown size and indistinct morphological characteristics (dos Santos et al. 2017). The bias in our dataset toward large-crowned palms in deforested regions is still useful for locating potential Chagas vector populations, however. There is evidence that *R. pallescens* preferentially inhabit larger, mature *A. butyracea* (Urbano, Poveda and Molina 2015), especially in peridomestic settings (Gottdenker et al. 2012). Larger palm crowns contain more organic material to support the microclimate and sylvatic host species *R. pallescens* require to thrive

(Abad-Franch et al. 2015, Condit et al. 2010, Romaña et al. 1999, Whitlaw Jr and Chaniotis 1978).

Landscape disturbance and A. butyracea *palms*

Our findings indicate a regional relationship between landscape disturbance and both individual *A. butyracea* palm and monospecific palm cluster distribution and density, but little evidence to support a direct relationship between landscape disturbance and proximity of palms or clusters to key features of interest. Although we observe statistically significant variation between palms and palm clusters and proximity to both buildings and rivers, these observations are more likely a result of direct relationships between the location of these features and anthropogenic landscape change. For example, we see a general trend of increasingly closer proximity of palms and palm clusters to human establishments as landscape disturbance increases, which is almost certainly due to a positive correlation between landscape disturbance and human population density. In contrast, although palms and clusters are both skewed towards close proximity to rivers, the absence of a clear pattern of river proximity when stratified by disturbance is likely more indicative of no strong relationship between river location and landscape disturbance.

Among both individual palms and palm clusters, we find that even given a probable underestimation of *A. butyracea* presence in forested regions, based on our field validation findings, we observe a much greater abundance of palms and clusters in established secondary forest than we would expect given the landscape distribution. This finding is consistent with *A. butyracea*'s known propensity to thrive in deforested and fragmented regions (Henderson et al. 2019, Scariot 1999) and supports at a regional scale localized studies that link increased likelihood of monospecific stands *A. butyracea* to anthropogenic landscape disturbance and fragmentation (Wright and Duber 2001, Wright et al. 2000). However, our study suggests the relationship between habitat disturbance and *A. butyracea* clustering may be parabolic rather than linear. As expected, we observe minimal clustering of palms in mature forest (Table 3.3), which is linked to interspecific competition, reduced available sunlight, and increased seed dispersal patterns associated with higher biodiversity in undisturbed landscapes (Wright and Duber 2001). However, we also observe significantly fewer palm clusters than expected in our most disturbed habitat, the built environment. Palm cluster abundance is concentrated in established secondary forest and pasture settings, which are both landscapes that have experienced prior disturbance, but experience little to no day-to-day anthropogenic maintenance.

We also link anthropogenic influence to the significantly fewer individual palms observed in pastoral and agricultural settings. We observe a gradual thinning of palms in pastoral settings, and a sharp decrease in the number of palms associated with planted cropland. This may be due to competing incentives to produce the best agricultural product: although grasses are inherently the dominate vegetation of pastures, solitary palms and small stands of trees are a common feature in pastoral settings in this region, where they provide shade for cattle and other livestock. In contrast, the two predominate crops in our study area, corn and pineapple, both require full sun to flourish.

Critically, notable thinning of individual *A. butyracea* does *not* extend to residential and commercial areas within our study region. Even in heavily built up environments, we find significant numbers of mature *A. butyracea* in close proximity to commercial and residential structures. We do not have sufficient evidence to determine whether this observation corresponds with purposeful maintenance of these palms for their goods and services, as has been recorded elsewhere in this species' range (Bernal et al. 2010, Smith 2015). However, *A. butyracea* is a long-lived species that matures slowly (De Steven et al. 1987, Jansen et al. 2014, Smith 2015), and the identification of substantial individual palms (n=1593) and nine clusters of mature *A. butyracea* in new forest growth suggest that palms are retained or otherwise survive forest clearing in at least some areas (Table 3.3). Further research is needed to regionally assess why mature *A. butyracea* palms in otherwise deforested areas remain in pastures and in close proximity to households, and to assess whether this occurrence is accidental or purposeful. In our fieldwork, we observed several instances of these palms used for household thatch and other services, but a more comprehensive study to understand the social context of this palm in Panama is warranted.

Implications for Chagas disease transmission

Actual risk of Chagas disease transmission almost certainly varies within our study region: variations among housing structure, human interaction with palms, and vector infestation of palms will all influence individual risk of contracting Chagas disease. However, as informed solely by close proximity to an *A. butyracea* palm, our analyses suggest that nearly all of the commercial and residential establishments within our study area are at increased risk of Chagas transmission, assuming that other microclimatic conditions in palms in our study locations are suitable vector habitat. *A. butyracea* palms are common throughout the populated regions of this study area, at a density of 125 palms/km^2 within the built environment (Table 3.3). We observe that all but one household is within median observed vector flight distance (307 m) of a palm, and all are well within the average flight distance (702 m) (Castro et al. 2014), which reflects findings seen elsewhere in central Panama (Vasquez et al. 2004). We also find that it is likely well within the ability of any vectors in this region to move between sylvatic and riparian movement corridors as needed. The observed palm-to-palm or palm-to-riparian area routes of travel occur at even shorter distances from palms than buildings, which may provide movement corridors for both vectors and their preferred blood meal species (De Lima and Gascon 1999, Laurance and Laurance 1999). However, more research is required to determine whether movement corridors are protective (by deflecting vectors to preferred hosts) or increase transmission risk for certain human populations.

Our observations provide evidence that palm abundance is thinned in agricultural settings, but not meaningfully reduced or expanded in residential regions. However, *A. butyracea* palms in otherwise deforested peridomestic environments often harbor larger vector populations than their forested counterparts (Gottdenker et al. 2011). Additionally, these peridomestic vector populations may be more prone to fly in search of new hosts as their preferred sylvatic host species decrease due to habitat loss, which has been implicated in increased domestic presence of sylvatic vectors in other Latin American countries (Reyes-Lugo and Rodríguez-Acosta 2000, Wolff and Castillo 2002). Therefore, increased propagation of *A. butyracea* in disturbed environments may pose a threat of increased Chagas transmission risk due to a greater abundance of vector habitat, but this is likely a long-term and low-risk threat given this species' slow growth to maturity. In contrast, mature palms retained during forest clearing arguably pose a more immediate threat of Chagas disease transmission to human populations.

In Chagas-endemic regions, infection prevention strategies hinge on deterring vectors' access to susceptible human hosts (Rabinovich et al. 2011). Peridomestic and sylvatic, or "intrusive", vectors are both a lesser threat to humans than domiciliated vectors, due to their intrinsic separation from human residences, and a greater challenge to deter (Waleckx, Gourbière and Dumonteil 2015b). Vectors that are well suited to co-habiting with humans are typically well-managed with residual insecticide spraying (Abad-Franch et al. 2015, Dias, Silveira and Schofield 2002), although regular spraying has led to insecticide-resistance among vectors in some regions (Lardeux et al. 2010, Picollo et al. 2005). Insecticide spraying is an inefficient way to control sylvatic and peridomestic species, however, and re-infestation or house invasion of even chemically-treated homes is common where no structural barriers to entry exist (Abad-Franch et al. 2015, Feliciangeli et al. 2007). Intrusive vectors are typically repelled by use of window screens or insecticide-treated bed nets or curtains (Barbu, Dumonteil and Gourbiere 2009, Barbu, Dumonteil and Gourbiere 2011, Ferral et al. 2010, Herber and Kroeger 2003), but are attracted to light sources in anthropogenic environments, particularly street lights (Pacheco-Tucuch et al. 2012). Peridomicile ecosystem management, to remove vector havens or attractants such as woodpiles, is also recommended for certain triatomine species, but has shown ineffective for sylvatic vectors (Barbu et al. 2011).

Effective vector control strategies, however, must also take into account social contexts in target regions, not just vector ecology. Social and ecological drivers influence not just the risk of Chagas transmission, but also the success of preventative vector control. Poor prevention outcomes have been observed, for Chagas disease and other vectorborne diseases more broadly, where planners have failed to understand, for example, the role and burden of women in vector control (Gunn et al. 2018, Winch et al. 1994), or cultural barriers to successfully engage indigenous communities (Dell’Arciprete et al. 2014). Calls have been made for socially and culturally sensitive transdisciplinary approaches to integratively assess and respond to the social and ecological drivers of vectorborne disease (Spiegel et al. 2005, Wilcox and Colwell 2005). Some recent vector control plans for Chagas prevention are taking a two-pronged approach to address both factors (Magana-Valladares et al. 2018, Rojas-de-Arias 2001, Waleckx et al. 2015a). The development of adequate and sustainable triatomine vector control is critical, as this study supports claims that Chagas disease may be a continuous, if low-intensity, risk to populations in this region (Abad-Franch et al. 2015).

Limitations

Although we observe a relationship between *A. butyracea* distribution and density and landscape disturbance, we have limited information on the age of our palm sample or on the disturbance timeline within our study area; we are assessing a “snap-shot” in a dynamic process of landscape alteration and vegetation (re)growth. Although additional official Panamanian land cover datasets exist for years 1992 and 2000, they were derived from 30-m spatial resolution Landsat imagery, and are not directly comparable to the 2012 data due to their coarser resolution (ANAM 2003). The 1992 and 2000 datasets, which *are* directly comparable, indicate significant deforestation in the Capira District and slight reforestation in the La Chorrera District during this eight-year period; both regions were described as less than 6% forested in 2000 (ANAM 2003). A brief comparison of the 1992 land cover to our palm data suggests presence of mature palms in recently (< 20 years) deforested regions, which may further indicate survival or purposeful maintenance of mature palms in otherwise cleared landscapes. Because of their large size and slow growth, mature palms are presumed to be > 20 years of age, therefore predating the 1992 data (Wright et al. 2000). However, with the scale discrepancy between the datasets, it is impossible to verify whether this observation is a true occurrence or an artifact of the lower-resolution imagery.

Any suggestion of purposeful maintenance of palms, however, is an indication that a better understanding of the social context of *A. butyracea* palms is critical to fully understanding the risk of Chagas disease transmission in this region. Further research is needed to comprehensively assess whether social practices in Panama, as in other areas, influence the retention of this species in otherwise deforested peridomestic environments, and whether these practices vary spatially. The high density of *A. butyracea* palms observed in our study area is not consistent throughout all parts of the country. A better understanding of the interwoven social and ecological factors that influence palm prevalence and distribution will facilitate identification of hotspots of current and potential vector habitat. This will aid the production of more targeted Chagas prevention and mitigation strategies in this region.

Conclusion

Our findings support previous studies linking *A. butyracea* abundance to landscape disturbance and fragmentation, as well as those that advise the use of high-resolution satellite imagery as a method of palm detection. It is clear from the distribution, density, and proximity of these palms to both human settlements and natural movement corridors that the potential of *A. butyracea* as a source of infectious Chagas disease vectors is widespread in rural settings. We observe a relationship between landscape disturbance and *A. butyracea* palm prevalence, particularly in secondary forest and agricultural environments. Critically, we observe probable anthropogenic thinning of *A. butyracea* palms in agricultural, but not residential, settings. Even in heavily deforested regions, significant concentrations of mature palms remain in close proximity to human establishments. Given *A. butyracea*'s slow growth to maturity, increased propagation of *A. butyracea* due to anthropogenic or natural landscape disturbance may have a long-term impact on vector habitat abundance. However, landscape disturbance that results in closer proximity of human establishments to mature palms may heighten both short- and long-term risk of Chagas transmission to susceptible human populations.

Table 3.1 2012 Panama Land Cover Categories

Original Assigned Category[*] **2012**		*Disturbance Gradient*	*Total Area* *km²*	*%*	*Masked Area*[†] *km²*	*%*	*Palms* *#*	*%*
Bosque latifoliado mixto maduro	Mixed Mature Broadleaf Forest	Mature Forest	0.67	0.22	0.53	0.23	125	0.25
Bosque latifoliado mixto secundario	Mixed Secondary Broadleaf Forest	Secondary/Planted Forest (established)	78.72	26.18	59.50	25.30	16521	32.42
Bosque plantado de coníferas	Conifer Planted Forest	Secondary/Planted Forest (established)	0.03	0.01	0.02	0.01	3	0.01
Bosque plantado de latifoliadas	Hardwood Planted Forest	Secondary/Planted Forest (established)	1.04	0.35	0.70	0.30	94	0.18
Rastrojo y vegetación arbustiva	Vegetation Regrowth and Bushes	Secondary/Planted Forest (new growth)	6.52	2.17	5.51	2.34	1593	3.13
Maíz	Corn	Food Crops	0.12	0.04	0.12	0.05	1	0.00
Piña	Pineapple	Food Crops	6.31	2.10	3.79	1.61	298	0.58
Pasto	Pasture	Pasture	164.02	54.56	130.42	55.45	24169	47.43
Superficie del agua	Surface Water	Secondary/Planted Forest (riparian)	33.45	11.13	26.43	11.24	7126	13.98
Área poblada	Populated Area	Built Environment	9.39	3.12	7.86	3.34	1016	1.99
Infraestructura	Infrastructure	Built Environment	0.37	0.12	0.34	0.14	9	0.02
		Total:	300.65		235.22		50955	

[*] Landcover categories assigned by the Panamanian Ministry of the Environment (MiAmbiente), formerly La Autoridad Nacional de Ambiente de Panama (ANAM)

[†] There was no significant difference between masked area and total area in any category

Table 3.2 Field Assessment of Remotely Collected Palm Data

Total Field Sample *(n=86)*

		Remotely Sensed *A. butyracea*						
		YES	NO		*Sensitivity:*	0.73	[*]*PPV:*	0.80
Field-verified	YES	**40**	**15**	55				
A. butyracea	NO	**10**	**21**	31	*Specificity:*	0.68	[**]*NPV:*	0.58
		50	36	86				

Pasture Sample *(n=54)*

		Remotely Sensed *A. butyracea*						
		YES	NO		*Sensitivity:*	0.89	*PPV:*	0.74
Field-verified	YES	**25**	**3**	28				
A. butyracea	NO	**9**	**17**	26	*Specificity:*	0.65	*NPV:*	0.85
		34	20	54				

Canopy Sample *(n=32)*

		Remotely Sensed *A. butyracea*						
		YES	NO		*Sensitivity:*	0.56	*PPV:*	0.94
Field-verified	YES	**15**	**12**	27				
A. butyracea	NO	**1**	**4**	5	*Specificity:*	0.8	*NPV:*	0.25
		16	16	32				

[*] Positive Predictive Value

[**] Negative Predictive Value

Table 3.3 Palm and Palm Cluster Distribution and Density by Land Disturbance Gradient

	Land Cover		*Palms*			*Palm Clusters*		
			Distribution		*Density*	*Distribution*		*Density*
	km^2	*%*	*N*	*%*	*N/km^2*	*N*	*%*	*N/km^2*
Mature Forest	0.53	0.23	125	0.25	235.85	1	0.29	1.89
Secondary/Planted Forest	92.16	39.18	25337	49.72‡	274.92	173	50.58‡	1.88
New growth (≤ 5 years)	*5.51*	*2.34*	*1593*	*3.13*	*289.11*	*9*	2.63	1.63
Established (> 5 years)	*60.22*	*25.60*	*16618*	*32.61*†	*275.95*	*135*	39.47‡	2.24
Riparian Zone	*26.43*	*11.24*	*7126*	*13.98*	*269.62*	*29*	8.48	1.10
Pasture	130.42	55.45	24169	47.43†	185.32	164	47.95	1.26
Food Crops	3.91	1.66	299	0.59†	76.47	1	0.29	0.26
Built Environment	8.20	3.49	1025	2.01	125.00	3	0.88†	0.37
Total:	235.22		50955			342		

†P-value < 0.05 based on z-test for proportion compared to associated land cover (bold)
‡p-value < 0.01 based on z-test for proportion compared to associated land cover (bold)

Table 3.4 Average *A. butyracea* Crown Diameter by Disturbance Gradient

		Crown Diameter *(m)*			
	N	*Min*	*Max*	$\bar{x}$†	*sd*
Overall	**150**	**4.26**	**15.97**	**9.03**	**2.36**
Mature Forest	30	5.41	15.97	9.49	2.67
Secondary/Planted Forest	30	5.65	14.28	9.27	2.29
Pasture	30	5.16	15.00	9.40	2.56
Food Crops	30	5.5	12.76	8.09	1.6
Built Environment	30	4.26	14.74	8.89	2.25

†There is no evidence of statistical difference among average crown size, given by a one-way analysis of variance (ANOVA)

Table 3.5 Cluster Area by Land Disturbance Gradient

	Cluster Area *(ha)*				
	Total	*Min*	*Max*	$\bar{x}$[†]	*sd*
Mature Forest	0.25	0.25	0.25	0.25	0
Secondary/Planted Forest	70.50	0.25	4.50	0.41	0.5
New growth (≤ 5 years)	*7.25*	*0.25*	*4.50*	*0.81*	*1.32*
Established (> 5 years)	*55*	*0.25*	*3.75*	*0.41*	*0.44*
Riparian Zone	*8.25*	*0.25*	*0.50*	*0.28*	*0.09*
Pasture	69.75	0.25	3.00	0.43	0.43
Food Crops	0.25	0.25	0.25	0.25	0
Built Environment	1.25	0.25	0.75	0.42	0.24
Overall	142.00	0.25	4.50	0.42	0.47

[†] There is no evidence of statistical difference among average cluster size by disturbance gradient, given by Kruskal-Wallis non-parametric analysis of variance by ranks test

Table 3.6 Distance from Probable Households to Palms (m)

Distance to Nearest Palm	Households (*n=2591*)	
≤ 10 m	145	5.6 %
11 - 20 m	265	10.23 %
21 - 100 m	1849	71.36 %
≤ 300 m	2590	99.96 %

Table 3.7 Average Distance (m) of Palms and Clusters to Objects of Interest

	Buildings		Rivers		Other Palm/Cluster	
	Palm	*Cluster*	*Palm*	*Cluster*	*Palm*	*Cluster*
Mature Forest	833.27[†]	1047.6[‡]	166.64	0[‡]	23.53	403.21
Secondary/Planted Forest	380.17[†]	322.15	141.79[†]	119.38	22.16	520.75
New growth (≤ 5 years)	*358.42*	*358.87*	*181.27*	*180.23*	*19.83*	*335.59*
Established (> 5 years)	*404.53*	*327.73*	*193.87*	*140.94*	*21.32*	*550.42*
Riparian Zone	*328.23*	*284.82*	*11.51*	*0.11*	*24.62*	*440.10*
Pasture	352.34[†]	292.36	182.01[‡]	124.03	23.66	438.89
Food Crops	263.37[†]	340.62	159.47	130.9[‡]	25.96	403.20
Built Environment	57.12[†]	31.63[‡]	136.77[‡]	95.77	27.08	168.75

Comparisons run using Dunn's Multiple Comparison Test for non-parametric post-hoc pairwise analysis, alpha=0.05.
[†] Average distance is significantly different from all other disturbance categories in proximity to the object of interest.
[‡] Shared categories are only significantly different from each other.

Figure 3.1 Picture of *A. butyracea*. These palms are characterized by their large, dense canopies, are the preferred habitat of key Panamanian Chagas vector *R. pallescens*.

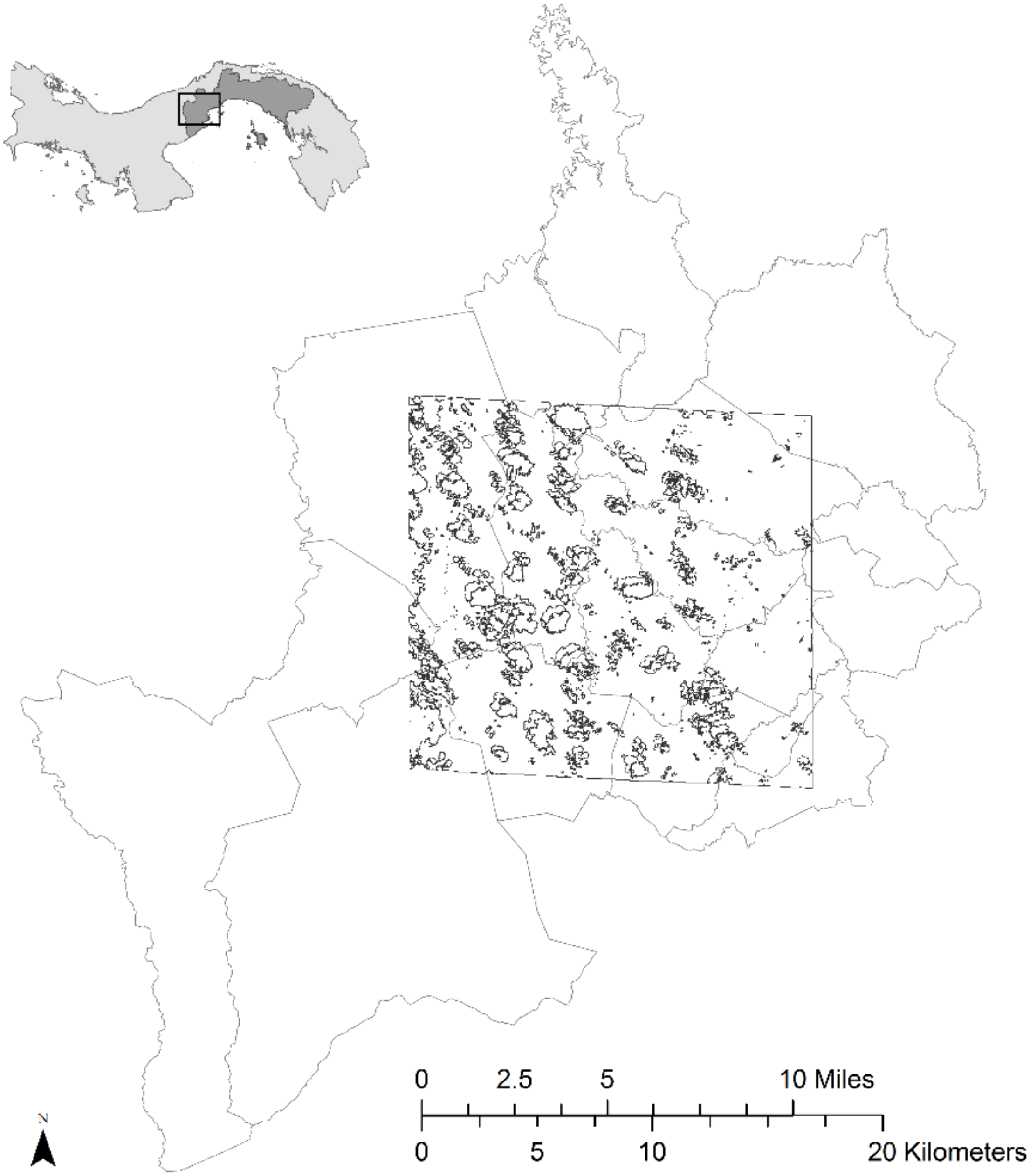

Figure 3.2. Study area. This image shows the WorldView2 satellite image footprint, with clouds and shadows masked, includes all or part of 17 corregimientos in the central Panama Oeste district.

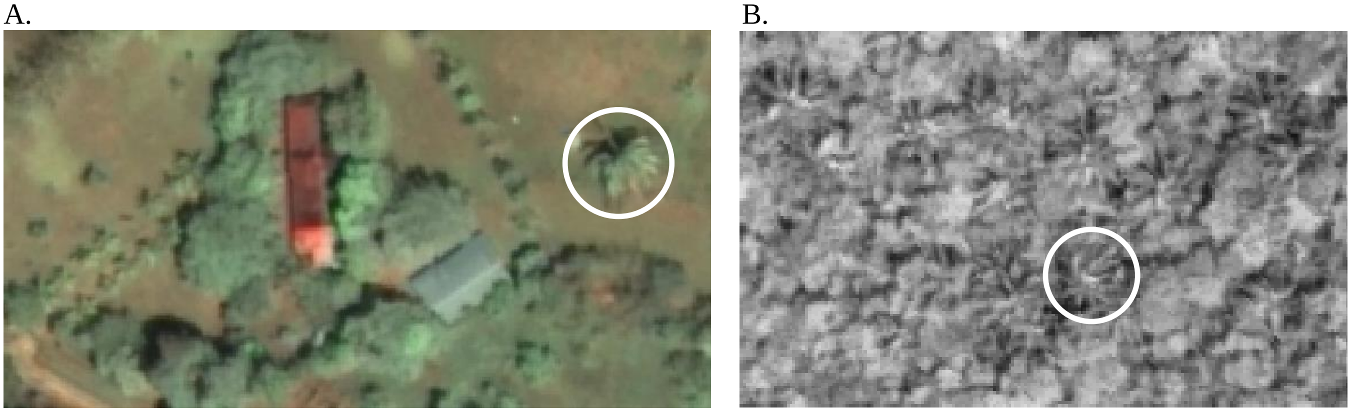

Figure 3.3 Satellite depiction of *A. butyracea* palms. (A) Aerial view of palm crowns in pansharpened true-color WorldView2 satellite imagery. The suspected *A. butyracea* palm (circled) is distinguished from the palms lining the entry-way (left) by size, texture, and color. These palms are readily visible due to their size despite the graininess of the zoomed-in image. (B) *A. butyracea* palm crowns are clearly visible by their texture and star-shaped crown in dense canopy in the 0.5m spatial resolution panchromatic WorldView2 imagery. (one of several circled)

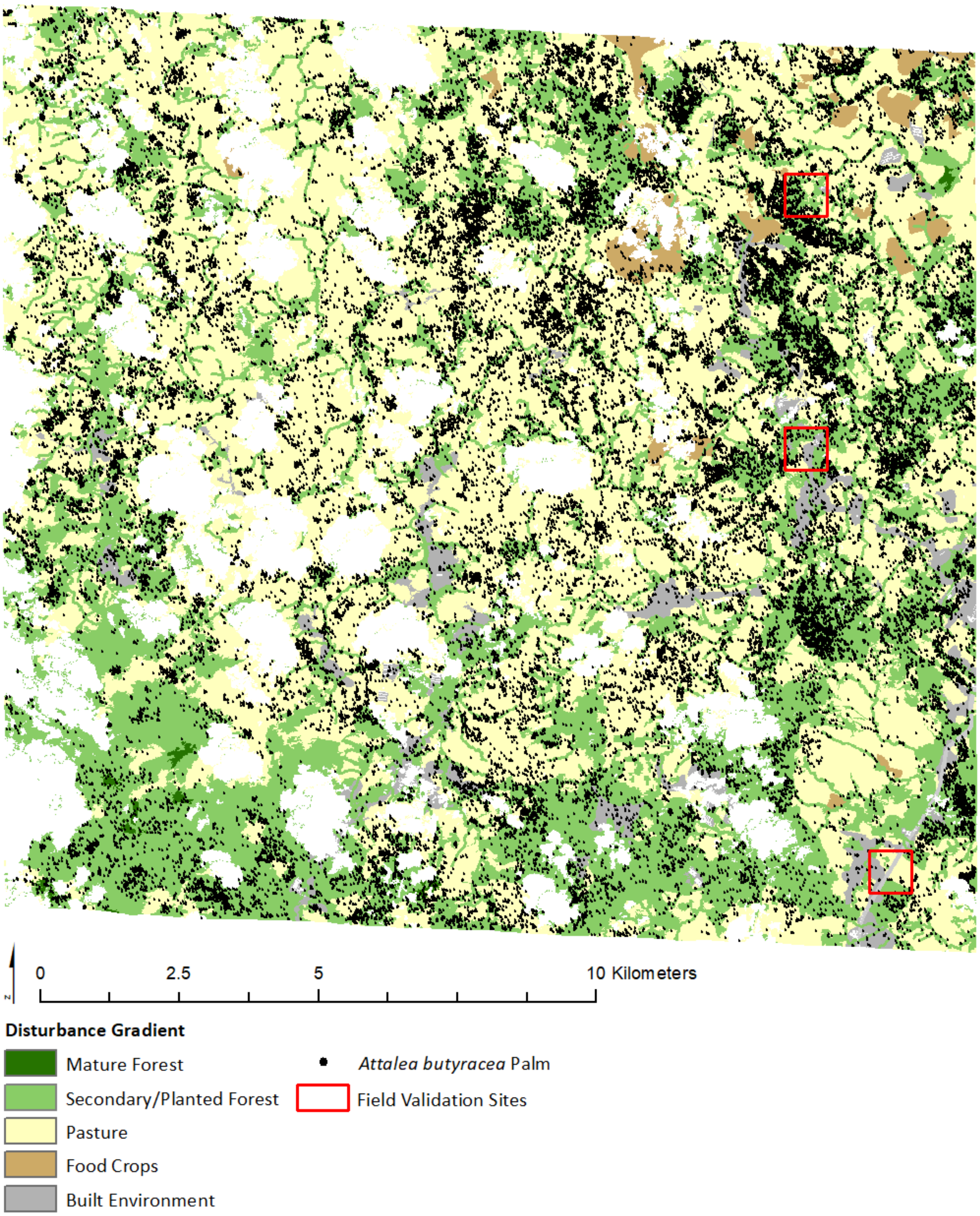

Figure 3.4 Palm sample and testing sites overlaid on the masked disturbance gradient. Disturbance categories are derived from 2012 official Panama land cover data.

Figure 3.5 *A. butyracea* palm wrapped in another tree species. Although a solitary pasture palm, this individual’s crown was obscured from satellite imagery by the crown of its encasing tree.

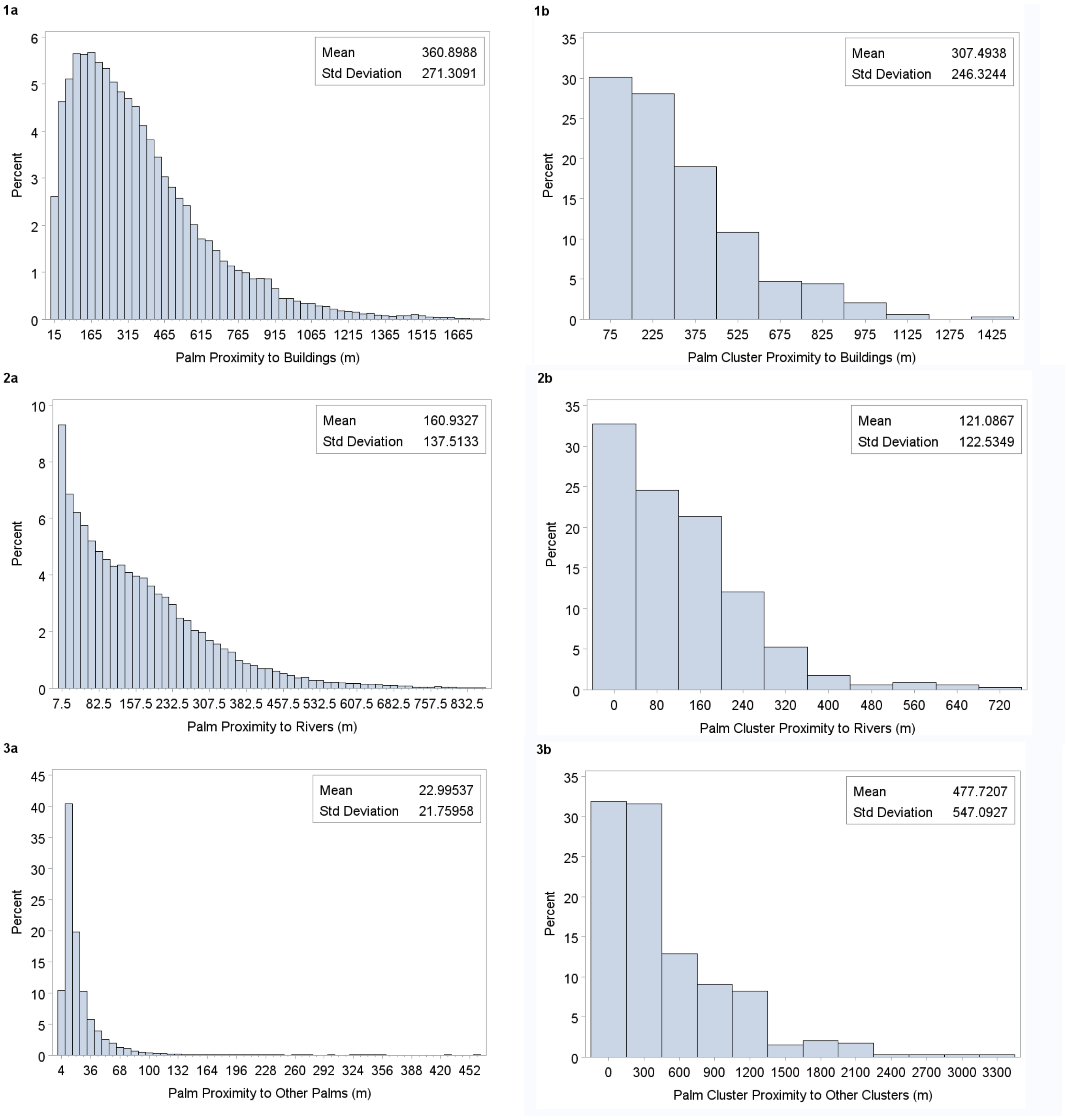

Figure 3.6 Proximity of palms and palm clusters to features of interest: buildings, rivers, and other palms/clusters.

REFERENCES

Abad-Franch, F., M. M. Lima, O. Sarquis, R. Gurgel-Goncalves, M. Sanchez-Martin, J. Calzada, A. Saldana, F. A. Monteiro, F. S. Palomeque, W. S. Santos, V. M. Angulo, L. Esteban, F. B. Dias, L. Diotaiuti, M. E. Bar & N. L. Gottdenker (2015) On palms, bugs, and Chagas disease in the Americas. *Acta Tropica,* 151**,** 126-41.

ANAM. 2003. Informe Final de Resultados de la Cobertura Boscosa y Uso de Suelo de la República de Panamá 1992-2000. Panamá.

Barbu, C., E. Dumonteil & S. Gourbiere (2009) Optimization of control strategies for non-domiciliated *Triatoma dimidiata*, Chagas disease vector in the Yucatan Peninsula, Mexico. *PLoS Negl Trop Dis,* 3**,** e416.

--- (2011) Evaluation of spatially targeted strategies to control non-domiciliated *Triatoma dimidiata* vector of Chagas disease. *PLoS Negl Trop Dis,* 5**,** e1045.

Bernal, R., G. Galeano, N. García, I. L. Olivares & C. Cocomá (2010) Uses and commercial prospects for the wine palm, *Attalea butyracea*, in Colombia. *Ethnobotany Research and Applications,* 8**,** 255-268.

Blaschke, T. (2010) Object based image analysis for remote sensing. *ISPRS Journal of Photogrammetry and Remote Sensing,* 65**,** 2-16.

Caldas de Castro, M. & B. H. Singer (2006) Controlling the false discovery rate: a new application to account for multiple and dependent tests in local statistics of spatial association. *Geographical Analysis,* 38**,** 180-208.

Calzada, J. E., V. Pineda, J. D. Garisto, F. Samudio, A. M. Santamaria & A. Saldaña (2010) Human trypanosomiasis in the eastern region of the Panama Province: new endemic areas for Chagas disease. *Am J Trop Med Hyg,* 82**,** 580-582.

Calzada, J. E., V. Pineda, E. Montalvo, D. Alvarez, A. M. Santamaria, F. Samudio, V. Bayard, L. Caceres & A. Saldana (2006) Human trypanosome infection and the presence of intradomicile *Rhodnius pallescens* in the western border of the Panama Canal, Panama. *Am J Trop Med Hyg,* 74**,** 762-765.

Castillo, M., R. Samaniego & A. Kindgard. 2015. Mapa de Cobertura y Uso de la Tierra 2012. ed. M. d. Ambiente. Panamá.

Castro, L. A., J. K. Peterson, A. Saldana, M. Y. Perea, J. E. Calzada, V. Pineda, A. P. Dobson & N. L. Gottdenker (2014) Flight behavior and performance of *Rhodnius pallescens* (Hemiptera: Reduviidae) on a tethered flight mill. *J Med Entomol,* 51**,** 1010-8.

Castro, M., T. V. Barrett, W. S. Santos, F. Abad-Franch & J. A. Rafael (2010) Attraction of Chagas disease vectors (Triatominae) to artificial light sources in the canopy of primary Amazon rainforest. *Memórias do Instituto Oswaldo Cruz,* 105**,** 1061-1064.

Condit, R., R. Pérez & N. Daguerre. 2010. *Trees of Panama and Costa Rica*. Princeton University Press.

Coura, J. R., A. C. Junqueira, O. Fernandes, S. A. Valente & M. A. Miles (2002) Emerging Chagas disease in Amazonian Brazil. *Trends Parasitol,* 18**,** 171-176.

Daszak, P., A. A. Cunningham & A. D. Hyatt (2000) Emerging infectious diseases of wildlife--threats to biodiversity and human health. *Science,* 287**,** 443-449.

--- (2001) Anthropogenic environmental change and the emergence of infectious diseases in wildlife. *Acta Tropica,* 78**,** 103-116.

De Lima, M. G. & C. Gascon (1999) The conservation value of linear forest remnants in central Amazonia. *Biological Conservation,* 91**,** 241-247.

De Steven, D., D. M. Windsor, F. E. Putz & B. de Leon (1987) Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica***,** 342-356.

Dell'Arciprete, A., J. Braunstein, C. Touris, G. Dinardi, I. Llovet & S. Sosa-Estani (2014) Cultural barriers to effective communication between Indigenous communities and health care providers in Northern Argentina: an anthropological contribution to Chagas disease prevention and control. *International Journal for Equity in Health,* 13**,** 6.

Dias, J. C. P., A. C. Silveira & C. J. Schofield (2002) The impact of Chagas disease control in Latin America: a review. *Memórias do Instituto Oswaldo Cruz,* 97**,** 603-612.

Dittel, J. W., T. D. Lambert & G. H. Adler (2015) Seed dispersal by rodents in a lowland forest in central Panama. *Journal of Tropical Ecology,* 31**,** 403-412.

Dobson, A., I. Cattadori, R. D. Holt, R. S. Ostfeld, F. Keesing, K. Krichbaum, J. R. Rohr, S. E. Perkins & P. J. Hudson (2006) Sacred cows and sympathetic squirrels: the importance of biological diversity to human health. *PLoS Medicine,* 3**,** e231.

dos Santos, A. M., D. Mitja, E. Delaître, L. Demagistri, I. de Souza Miranda, T. Libourel & M. Petit (2017) Estimating babassu palm density using automatic palm tree detection with very high spatial resolution satellite images. *Journal of Environmental Management,* 193**,** 40-51.

Eiserhardt, W. L., J. C. Svenning, W. D. Kissling & H. Balslev (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Ann Bot,* 108**,** 1391-416.

Elliott, A. C. & L. S. Hynan (2011) A SAS((R)) macro implementation of a multiple comparison post hoc test for a Kruskal-Wallis analysis. *Comput Methods Programs Biomed,* 102**,** 75-80.

Erazo, D. & J. Cordovez (2016) Modeling the effects of palm-house proximity on the theoretical risk of Chagas disease transmission in a rural locality of the Orinoco basin, Colombia. *Parasit Vectors,* 9**,** 592.

Feliciangeli, M. D., H. Carrasco, J. S. Patterson, B. Suarez, C. Martinez & M. Medina (2004) Mixed domestic infestation by *Rhodnius prolixus* Stäl, 1859 and *Panstrongylus geniculatus* Latreille, 1811, vector incrimination, and seroprevalence for *Trypanosoma cruzi* among inhabitants in El Guamito, Lara State, Venezuela. *Am J Trop Med Hyg,* 71**,** 501-505.

Feliciangeli, M. D., M. Sanchez-Martin, R. Marrero, C. Davies & J. P. Dujardin (2007) Morphometric evidence for a possible role of *Rhodnius prolixus* from palm trees in house re-infestation in the State of Barinas (Venezuela). *Acta Tropica,* 101**,** 169-77.

Ferral, J., L. Chavez-Nunez, M. Euan-Garcia, M. J. Ramirez-Sierra, M. R. Najera-Vazquez & E. Dumonteil (2010) Comparative field trial of alternative vector control strategies for non-domiciliated Triatoma dimidiata. *Am J Trop Med Hyg,* 82**,** 60-6.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily & H. K. Gibbs (2005) Global consequences of land use. *Science,* 309**,** 570-574.

Garzon-Lopez, C. X., S. A. Bohlman, H. Olff & P. A. Jansen (2013) Mapping tropical forest trees using high-resolution aerial digital photographs. *Biotropica,* 45**,** 308-316.

Gottdenker, N. L., J. E. Calzada, A. Saldaña & C. R. Carroll (2011) Association of anthropogenic land use change and increased abundance of the Chagas disease vector *Rhodnius pallescens* in a rural landscape of Panama. *Am J Trop Med Hyg,* 84**,** 70-77.

Gottdenker, N. L., L. F. Chaves, J. E. Calzada, A. Saldaña & C. R. Carroll (2012) Host life history strategy, species diversity, and habitat influence *Trypanosoma cruzi* vector infection in changing landscapes. *PLoS Negl Trop Dis,* 6**,** e1884.

Gottdenker, N. L., D. G. Streicker, C. L. Faust & C. Carroll (2014) Anthropogenic land use change and infectious diseases: a review of the evidence. *EcoHealth,* 11**,** 619-632.

Gunn, J. K. L., K. C. Ernst, K. E. Center, K. Bischoff, A. V. Nunez, M. Huynh, A. Okello & M. H. Hayden (2018) Current strategies and successes in engaging women in vector control: a systematic review. *BMJ Glob Health,* 3**,** e000366.

Henderson, A., G. Galeano & R. Bernal. 2019. *Field guide to the palms of the Americas*. Princeton University Press.

Herber, O. & A. Kroeger (2003) Pyrethroid-impregnated curtains for Chagas' disease control in Venezuela. *Acta Tropica,* 88**,** 33-38.

Jansen, P. A., S. A. Bohlman, C. X. Garzon-Lopez, H. Olff, H. C. Muller-Landau & S. J. Wright (2008) Large-scale spatial variation in palm fruit abundance across a tropical moist forest estimated from high-resolution aerial photographs. *Ecography,* 31**,** 33-42.

Jansen, P. A., M. D. Visser, S. Joseph Wright, G. Rutten & H. C. Muller-Landau (2014) Negative density dependence of seed dispersal and seedling recruitment in a neotropical palm. *Ecol Lett,* 17**,** 1111-20.

Kruskal, W. H. & W. A. Wallis (1952) Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association,* 47**,** 583-621.

Lambert, T. D., K. L. Sumpter, J. W. Dittel, S. Dupre, K. Casanova, A. Winker & G. H. Adler (2014) Roads as barriers to seed dispersal by small mammals in a neotropical forest. *Tropical Ecology,* 55**,** 263-269.

Lardeux, F., S. Depickère, S. Duchon & T. Chavez (2010) Insecticide resistance of *Triatoma infestans* (Hemiptera, Reduviidae) vector of Chagas disease in Bolivia. *Tropical Medicine and International Health,* 15**,** 1037-1048.

Laurance, S. G. & W. F. Laurance (1999) Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. *Biological Conservation,* 91**,** 231-239.

Lawrence, D. L. & S. M. Low (1990) The built environment and spatial form. *Annual Review of Anthrolopology,* 19**,** 453-505.

Lent, H. & P. Wygodzinsky (1979) Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. *Bulletin of the American museum of Natural History,* 163**,** 123-520.

Magana-Valladares, L., M. H. Rodriguez, A. F. Betanzos-Reyes, H. Riojas-Rodriguez, M. L. Quezada-Jimenez, J. E. Suarez-Conejero & H. Lamadrid-Figueroa (2018) Design and efficacy of an Ecohealth competency-based course on the prevention and control of vector diseases in Latin America. *Salud Publica Mex,* 60**,** 86-96.

Moncayo, Á. & A. C. Silveira. 2017. Current epidemiological trends of Chagas disease in Latin America and future challenges: Epidemiology, surveillance, and health policies. In *American Trypanosomiasis, Chagas Disease: One Hundred Years of Research,* eds. J. Telleria & M. Tibayrenc, 59-88. Amsterdam, Netherlands: Elsevier.

Normand, S., J. Vormisto, J.-C. Svenning, C. Grández & H. Balslev (2006) Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. *Plant Ecology,* 186**,** 161-176.

Olivares, I. & G. Galeano (2013) Leaf and inflorescence production of the wine palm (*Attalea butyracea*) in the dry Magdalena River Valley, Colombia. *Caldasia,* 35**,** 37-48.

Pacheco-Tucuch, F. S., M. J. Ramirez-Sierra, S. Gourbière & E. Dumonteil (2012) Public street lights increase house infestation by the Chagas disease vector *Triatoma dimidiata*. *PLoS One,* 7**,** e36207.

Picollo, M. I., C. Vassena, P. S. Orihuela, S. Barrios, M. Zaidemberg & E. Zerba (2005) High resistance to pyrethroid insecticides associated with ineffective field treatments in *Triatoma infestans* (Hemiptera: Reduviidae) from Northern Argentina. *Journal of Medical Entomology,* 42**,** 637-642.

Pineda, V., E. Montalvo, D. Alvarez, A. M. Santamaría, J. E. Calzada & A. Saldaña (2008) Feeding sources and trypanosome infection index of *Rhodnius pallescens* in a Chagas disease endemic area of Amador County, Panama. *Revista do Instituto de Medicina Tropical de São Paulo,* 50**,** 113-116.

Rabinovich, J. E., U. D. Kitron, Y. Obed, M. Yoshioka, N. Gottdenker & L. F. Chaves (2011) Ecological patterns of blood-feeding by kissing-bugs (Hemiptera: Reduviidae: Triatominae). *Memorias do Instituto Oswaldo Cruz,* 106**,** 479-494.

Rassi Jr, A., A. Rassi & J. A. Marin-Neto (2010) Chagas disease. *The Lancet,* 375**,** 1388-1402.

Reyes-Lugo, M. & A. Rodríguez-Acosta (2000) Domiciliation of the sylvatic Chagas disease vector *Panstrongylus geniculatus* Latreille, 1811 (Triatominae: Reduviidae) in Venezuela. *Transactions of the Royal Society of Tropical Medicine and Hygiene,* 94.

Rodriguez, I. G. & J. R. Loaiza (2017) American trypanosomiasis, or Chagas disease, in Panama: a chronological synopsis of ecological and epidemiological research. *Parasit Vectors,* 10**,** 459.

Rojas-de-Arias, A. (2001) Chagas disease prevention through improved housing using an ecosystem approach to health. *Cadernos de Saúde Pública,* 17**,** S89-S97.

Romaña, C., J. Pizarro, E. Rodas & E. Guilbert (1999) Palm trees as ecological indicators of risk areas for Chagas disease. *Trans R Soc Trop Med Hyg,* 93**,** 594-595.

Saldaña, A., J. E. Calzada, V. Pineda, M. Perea, C. Rigg, K. González, A. M. Santamaria, N. L. Gottdenker & L. F. Chaves (2015) Risk factors associated with *Trypanosoma cruzi* exposure in domestic dogs from a rural community in Panama. *Memórias do Instituto Oswaldo Cruz,* 110**,** 936-944.

Saldaña, A., V. Pineda, I. Martinez, G. Santamaria, A. M. Santamaria, A. Miranda & J. E. Calzada (2012) A new endemic focus of Chagas disease in the northern region of Veraguas Province, Western Half Panama, Central America. *PLoS One,* 7**,** e34657.

Sanchez-Martin, M. J., M. D. Feliciangeli, D. Campbell-Lendrum & C. R. Davies (2006) Could the Chagas disease elimination programme in Venezuela be compromised by reinvasion of houses by sylvatic *Rhodnius prolixus* bug populations? *Tropical Medicine and International Health,* 11**,** 1585-1593.

Scariot, A. (1999) Forest fragmentation effects on palm diversity in central Amazonia. *Journal of Ecology,* 87**,** 66-76.

Smith, N. 2015. *Attalea butyracea*. In *Palms and People in the Amazon*, 83-89. Switzerland: Springer.

Spiegel, J., S. Bennett, L. Hattersley, M. H. Hayden, P. Kittayapong, S. Nalim, D. N. C. Wang, E. Zielinski-Gutiérrez & D. Gubler (2005) Barriers and Bridges to Prevention and Control of Dengue: The Need for a Social–Ecological Approach. *EcoHealth,* 2**,** 273-290.

Teixeira, A., P. S. Monteiro, J. M. Rebelo, E. R. Argañaraz, D. Vieira, L. Lauria-Pires, R. Nascimento, C. A. Vexenat, A. R. Silva & S. K. Ault (2001) Emerging Chagas disease: trophic network and cycle of transmission of *Trypanosoma cruzi* from palm trees in the Amazon. *Emerging Infectious Diseases,* 7**,** 100.

Tiefelsdorf, M., D. A. Griffith & B. Boots (1999) A variance-stabilizing coding scheme for spatial link matrices. *Environment and Planning A,* 31**,** 165-180.

Trichon, V. 2001. Crown typology and the identification of rain forest trees on large-scale aerial photographs. In *Tropical Forest Canopies: Ecology and Management*, 301-312. Springer.

Trichon, V. & M.-P. Julien (2006) Tree species identification on large-scale aerial photographs in a tropical rain forest, French Guiana—application for management and conservation. *Forest ecology and management,* 225**,** 51-61.

Urbano, P., C. Poveda & J. Molina (2015) Effect of the physiognomy of *Attalea butyracea* (Arecoideae) on population density and age distribution of *Rhodnius prolixus* (Triatominae). *Parasit Vectors,* 8**,** 199.

Vasquez, A. M. d., F. E. Samudio, A. Saldaña, H. M. Paz & J. E. Calzada (2004) Eco-epidemiological aspects of *Trypanosoma cruzi*, *Trypanosoma rangeli* and their vector (*Rhodnius pallescens*) in Panama. *Revista do Instituto de Medicina Tropical de São Paulo,* 46**,** 217-222.

Waleckx, E., J. Camara-Mejia, M. J. Ramirez-Sierra, V. Cruz-Chan, M. Rosado-Vallado, S. Vazquez-Narvaez, R. Najera-Vazquez, S. Gourbiere & E. Dumonteil (2015a) An innovative ecohealth intervention for Chagas disease vector control in Yucatan, Mexico. *Trans R Soc Trop Med Hyg,* 109**,** 143-9.

Waleckx, E., S. Gourbière & E. Dumonteil (2015b) Intrusive versus domiciliated triatomines and the challenge of adapting vector control practices against Chagas disease. *Memórias do Instituto Oswaldo Cruz,* 110**,** 324-338.

Whitlaw Jr, J. T. & B. N. Chaniotis (1978) Palm trees and Chagas' disease in Panama. *The American Journal of Tropical Medicine and Hygiene,* 27**,** 873-881.

Wilcox, B. A. & R. R. Colwell (2005) Emerging and reemerging infectious diseases: biocomplexity as an interdisciplinary paradigm. *EcoHealth,* 2**,** 244.

Winch, P. J., L. S. Lloyd, L. Hoemeke & E. Leontsini (1994) Vector control at the household level: an analysis of its impact on women. *Acta Tropica,* 56**,** 327-339.

Wolff, M. & D. Castillo (2002) Domiciliation trend of *Panstrongylus rufotuberculatus* in Colombia. *Memórias do Instituto Oswaldo Cruz,* 97**,** 297-300.

Wright, S. J. & H. C. Duber (2001) Poachers and Forest Fragmentation Alter Seed Dispersal, Seed Survival, and Seedling Recruitment in the Palm *Attalea butyraceae,* with Implications for Tropical Tree Diversity. *Biotropica,* 33**,** 583-595.

Wright, S. J., H. Zeballos, I. Domínguez, M. M. Gallardo, M. C. Moreno & R. Ibáñez (2000) Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conservation Biology,* 14**,** 227-239.

Zeledón, R., F. Marín, N. Calvo, E. Lugo & S. Valle (2006) Distribution and ecological aspects of *Rhodnius pallescens* in Costa Rica and Nicaragua and their epidemiological implications. *Memórias do Instituto Oswaldo Cruz,* 101**,** 75-79.

CHAPTER 4

A QUANTITATIVE ASSESSMENT OF PALM USE IN SIX RURAL COMMUNITIES IN CENTRAL PANAMA[3]

---

[3] Mertzlufft, C., S. Tanner*†, J. Velasquez Runk*‡, M. Perea*†, C. Rigg*†, N. Gottdenker*‡, J. Calzada*†, S. Saldaña*†. (*Denotes anticipated co-authors who have provided significant contributions to study design, data collection, and data access but who have not had an opportunity to revise the current draft† or whose revisions and edits have not been completely addressed at this stage‡. Chapter to be considered a manuscript in progress that will likely deviate from final published form.) To be submitted to: *Journal of Ethnobiology*

Abstract

We describe trends in palm tree usage in six non-indigenous rural communities in the Panama and Panama Oeste provinces, Panama. Palm use related to the royal palm, *Attalea butyracea*, was particularly considered, given this palm's association with the leading vector of Chagas disease in Panama. Using generalized linear mixed models, we tested the association between palm use and demographic, environmental, and behavioral characteristics at the household level. Chi-squared tests for Independence were used to test for difference in overall palm use trends by province and forest cover. We find that palm use is ubiquitous in this region, and that behavioral characteristics are linked with the most frequently reported use categories: construction and human food consumption. *A. butyracea* palms were reported for use as thatch and palm wine. This study supports findings that household indicators of palm use are highly localized, and suggests this heterogeneity also applies to palm-derived behavioral risk factors linked to elevated risk of Chagas disease.

Introduction

Palm use is ubiquitous in tropical latitudes, ranging from fine-scale individual usage to widespread agribusiness cultivation. The Food and Drug Administration of the United Nations (FAO) has characterized palms as the third most versatile plant in human history, following grasses and legumes, due to the array of products and services palms provide (Johnson, the Pacific and Nations 1998). Archaeological evidence suggests human-palm interaction has occurred for thousands of years (Wake 2006, Dickau 2010).

Nearly every part of the plant is useful, although specific use-types vary regionally, culturally, and by palm species. In the Americas, palms have been recorded as sources of medicine, food, textiles and goods among numerous indigenous and non-indigenous communities (Balick 1984, Bernal et al. 2010, Dalle et al. 2002, Duke 1975, Haynes and McLaughlin 2000, Paniagua-Zambrana et al. 2014, Runk 2001, Sosnowska, Balslev and Ethnomedicine 2009, Sosnowska and Balslev 2008). However, despite calls for broader diversity, the majority of established studies remain qualitative in nature (Galeano 2000). Furthermore, with rare exception (Paniagua-Zambrana et al. 2014, Runk 2001), ethnobotanical palm studies detail the species and use-type of palms without describing the individuals within communities who most frequently interact with them. This presents us with a body of literature characterizing where and how palm species are used, but rarely by whom, except in the general sense of community name or indigenous group.

This paper quantitatively compares household palm use in six non-indigenous communities in central Panama to assess the association between use patterns and regional, demographic, and behavioral characteristics. Of particular interest is the use of the royal palm, *Attalea butyracea* (colloquially *palma real*), a widespread palm with known frequency of use in neighboring South American countries (Bernal et al. 2010, Smith 2015) that is also the preferred habitat of the primary insect vector of Chagas disease in this region (Gottdenker et al. 2012, Saldaña et al. 2015). Residing near this palm and use of its fronds as thatch are both linked with increased risk of Chagas disease transmission (Abad-Franch et al. 2015, Calzada et al. 2006). In addition to contributing to the ethnobotanic body of knowledge for this region, a better characterization of palm use trends may help inform Chagas mitigation and prevention strategies by identifying characteristics that place households at increased risk of contracting this disease.

Materials and Methods

Study Location and Data Collection

Household demographic and palm use characteristics were collected via household survey from January-July 2016 in six rural communities in the Panama and Panama Oeste Provinces in central Panama: Pueblo Nuevo (PN), Cañazas (CA), Bajo Bonito (BB), Tierra Prometida (TP), Altos de Pacora (AP), and Superación Campesino (SC) (Figure 1). These data were recorded as part of a broader survey assessing the ecoepidemiology of Chagas disease and cutaneous leishmaniasis in association with deforestation trends in this region (University of Georgia and US Centers for Disease Control and Prevention); study community locations were, therefore, selected due to known or probable history of these diseases. Six study communities were chosen so that we could compare palms use by province (Panama: PN, BB, CA; Panama Oeste: AP, TP, SC) and across a gradient of forest cover (heavily forested: AP, BB; semi-forested: CA, TP; predominately pasture: PN, SC). Forest cover was assessed through a comparison of community administrative boundary data from the 2010 Census and high-resolution land cover data (ANAM 2003, Magallys Castillo 2015), which were obtained directly from Panama's National Institute of Statistics and Census (INEC) and the Ministry of the Environment (MiAmbiente), respectively.

Survey-collected demographic variables used in this study consist of number of household occupants and maximum level of education completed by any resident. Palm-use characteristics include overall use of palms (yes/no), ways in which palms are used, and behavioral characteristics of forest interaction. To assess likelihood of interaction with palms, survey respondents were first asked whether they found utility in palm trees or materials derived from palms ("*¿Son útiles las palmas o los materiales de las palmas para usted*?"). Respondents who affirmed palm usefulness were asked to specify the ways in which palms are useful to themselves or their family ("*¿De qué manera son útiles las palmas para usted or su familia*?"), as drawn from broad categories of known royal palm (*A. butyracea*) use recorded in Latin America and the Caribbean. The eight use categories listed were: food (person), feed (animals/livestock), building materials, technology (e.g. brooms, hats), medicinal, cosmetic, cultural, or ornamental (Bernal et al. 2010). Although the species of palm(s) utilized for each use-type was not explicitly requested, this information was recorded if volunteered by the survey respondent, along with any other volunteered commentary on palm use or examples of use cases. Behavioral characteristics related to forest interaction were obtained with the question, "Why do you go to the forest?" ("¿Por qué va al monte?"), which included possible responses of gathering/harvesting plants, hunting, clearing forest for pasture or agriculture, traveling from one place to another, or a non-listed reason (other). Observational data on palm presence or absence was also recorded, including presence of thatch as roofing material for households or detached structures (e.g. outdoor kitchens, verandas) or presence of key palm species (royal palm, *A. butyracea*; coconut palm, *Cocus nuficera*) on the property.

Study participation was voluntary and oral informed consent was obtained from all respondents. Study design and survey vehicle were approved by the University of Georgia Institutional Review Board (STUDY00001786) and the Bioethics Committee of the Gorgas Memorial Institute for Health Studies (ICGES), Panama. Field permits for this study were obtained by the Panama Ministry of the Environment (MiAmbiente) as part of a larger collaborative research project studying Chagas disease and acute cutaneous leishmaniasis in Panama (Dyer et al. 2016).

Statistical Analysis

Self-reported palm use by survey respondents was assessed by region, demographics, forest cover and use-type using SAS 9.4 software (SAS Institute Inc, Cary, NC). Chi-square tests for independence were used to assess variation in reported palm use (overall and by use-type) by region and forest cover. Where low frequency reported use-types caused insufficient numbers for stratified comparison, use-types were aggregated to meet minimum count requirements (McHugh 2013).

To test whether any demographic, environmental, or behavioral characteristics were significantly associated with either of the two most frequently reported palm use-types, we employed generalized linear mixed logit models (SAS PROC GLIMMIX). This model type allows for the inclusion of random factors, which is necessary to account for the selection of our six study communities out of a pool of many possible communities within the Panama and Panama Oeste Provinces. These models were constructed to assess differences among households who reported either of the two most frequent palm use-types compared to those who did not. Palm use was understood to be a function of need or desire to use palms/palm materials and availability of suitable materials. Therefore, models were designed to account for all behavioral and observational variables that could reasonably serve as proxies for palm presence, while controlling for demographic and regional descriptors (Table 1). Several candidate models were tested, accounting for all possible combinations of independent variables after correcting for collinearity. The final model for each use-type was selected as the candidate model with the lowest Akaike information criterion (AIC) score.

Results

Among the 112 survey respondents, most households (n=97, 87%) reported using palms or palm materials in some way. A majority of those who reported palm use described only one use-type employed by their household (n=59); however, 38 respondents reported using palms in multiple ways (Table 2). Among the 97 palm users, use of palm materials for construction and as a supplemental food source were most frequently reported, at 57% (n=55) and 51% (n=49), respectively. No households reported use of palms for cosmetic purposes. Fewer than five percent of households among all survey respondents reported using palms for medicinal or cultural use.

A subset of survey respondents (n=26) reported preference of palm species for their chosen use type(s) (Table 3). Four palms were consistently reported as useful throughout our study area: *A. butyracea*, *Welfia regia*, *Bactris gasipaes*, and *Cocos nucifera*. These palms were most frequently indicated as sources of food (fruit) and/or construction materials (thatch), but were also cited for their cultural (palm wine), technological (brooms), and medicinal qualities.

Although we observe a general increase in households utilizing palm materials in forested communities and within the Panama Oeste province, there is no evidence to support statistically significant differences among overall palm-use trends between households in Panama and Panama Oeste provinces (chi-square= 3.1174, p-value= .5384), or between communities that vary by forest cover (chi-square= 2.8996, p-value= .9405) (Table 4). However, when controlling for community and forest cover, certain independent variables were significantly associated with both construction and food use of palms (Table 5). We found evidence to support an enhanced likelihood of palm use for construction among larger households and households who report felling and harvesting trees in surrounding forest, compared to household who use palms, but do not report construction as a use-type. When comparing households who report use of palms for supplemental food compared to those who did not report this use type, we find evidence to suggest that households who report palms as food sources are significantly less likely to harvest trees in nearby forest.

Discussion

Arecaceae are among the most frequently used plants globally (Haynes and McLaughlin 2000), and Panama is among the highest regions of palm diversity and species richness in the world (Bjorholm et al. 2005, Sosnowska and Balslev 2008). It is no great surprise, therefore, that we find palm utility to be so ubiquitously reported in our study region. This finding is consistent among several studies that have found high levels of traditional knowledge of palm usage among mestizo populations in Central and South America (Cámara-Leret et al. 2014, Fadiman 2008, Paniagua-Zambrana et al. 2014). We sought to characterize palm use trends in six non-indigenous rural communities in Panama and assess whether reported use was associated with regional, environmental, demographic, or behavioral characteristics within this population. We found evidence to support our finding that behavioral characteristics influence likelihood of households using palms for both construction and thatch. The demographic and behavioral characteristics that we find to be associated with palm use for construction and food differ from similar analyses in other regions, but this is not entirely unexpected given that past studies have shown the influence of socioeconomic factors on palm use are highly localized (Paniagua-Zambrana et al. 2014). However, our finding that family size is positively associated with palm use for construction has been similarly linked to traditional knowledge of palms at the household level (Byg, Balslev and Conservation 2001). The positive association of behavioral trends of felling or harvesting trees from nearby forest and construction are clearly linked, but the negative association between this behavior and use of palms for food is less clear. As self-reported tendencies to obtain food from the forest is not significantly associated with palm use as a food source, it may be that any local tree materials harvested for food are from non-palm sources (e.g. mango).

We found no difference in palm-use trends by region or by environment. However, this finding may be due to the relatively low sample size of our survey and relative clustering of communities, as it is unlikely that individuals in discrete communities will always use palms in the same way. Only construction and food use-types had enough responses to test differences in use when stratified, at a sample size of 55 and 49, respectively; trends among rarer palm use types may require a larger sample size to be seen, even at the regional level. We tested differences in forest cover to account for multiple palm habitats, and because previous studies have found associations between palm use and forest cover (Byg et al. 2001). However, given the high density of palms in Central Panama, it may be that suitable palms are available in any environment, even though the range and habitat of specific species will vary.

Our findings that the most commonly reported uses of palms are for construction and human consumption are consistent with many other studies of neotropical palm use (Sosnowska and Balslev 2008, Cámara-Leret et al. 2016, Galeano 2000, Moraes et al. 2015). The popularity of palms for both categories is attributed to the broad number of species that are suitable for each use-type, and the multitude of products that can be derived from a single plant. Both trunks and palm leaves are harvested for construction, for example, as poles, planks, or fencing (trunks), or as thatch for roofs (fronds) (Galeano 2000). In contrast, nearly every part of a palm is edible, from root to seed, when considering the family as a whole; however, the harvested palm product(s) and derived use(s) vary by species, region, and culture (Haynes and McLaughlin 2000). When construction was indicated, survey respondents most frequently cited palm fronds as use in thatch, or *penca*, particularly for *rancho* construction. Ranchos in this context are free-standing, open structures of varying sizes that are regularly roofed with thatch and are common fixtures in both Panama and Panama Oeste provinces (Figure 2). For food consumption, use of palm fruits (e.g. *pifa*, *B. gasipaes*) or seeds (e.g. coconut meat or water, *C. nucifera)* were most commonly reported.

The other six use categories recorded entail known uses of palms common throughout Latin America, among both indigenous and non-indigenous communities (Bernal et al. 2010, Moraes et al. 2015, Cámara-Leret et al. 2016). Medicinal use of palms was linked to treatment for asthma and diarrhea, and technological use to the making of brooms with palm fronds, which have been reported elsewhere in Latin America (López-Sáez and Pérez-Soto 2010, Moraes et al. 2015). Also reported was the use of palm material for weaving (end product not specified by survey respondents) and for the making palm wine (fruit, *A. butyracea*), which were self-reported as cultural use. *A. butyracea* is known in some regions as “wine palm,” due to the beverage than can be made from its fermented sap; in some studies, this use is characterized as a food product (Bernal et al. 2010). Where specified, the most common “other” use category reported for palms was shade. No household reported use of palms for cosmetic purposes, although this has been described in neighboring Colombia (*A. butyracea* palm oil for hair care) (Bernal et al. 2010). Although these use categories applied to fewer than ten percent of surveyed households, the low frequency of uses reported here does not necessarily reflect a lack of use of local plants these goods or services in the region. It may be that non-palm species are more preferred for these use types. For example, two surveys of medicinal plant use among non-indigenous communities neighboring our study area found abundant use of local plant life for this purpose, but only one palm species, *Oenocarpus mapora*, was among the over sixty species listed (Bermúdez and Chue 2014, Torres et al. 2016).

The four palm species consistently specified as the preferred use species in our study are well represented in the ethnobotanic record. *C. nucifera*, the coconut palm, is the only species of the four that is not native to Latin America (Zambrana et al. 2014). However, it is firmly established throughout the tropics and subtropics of the Americas, where it is valued for its well-known fruit (actually the seed of the palm), which serves as a supplemental food source and has numerous established medicinal properties (Haynes and McLaughlin 2000, Karadi et al. 2011, López-Sáez and Pérez-Soto 2010, Torres et al. 2016). In our survey and elsewhere it has also been reported as a source of thatch (Zambrana et al. 2014). *B. gasipaes*, colloquially *pifa* or *palma de pixbae*, is enjoyed in central Panama primarily for its starchy fruit, but it is also cultivated throughout Latin America for its heart of palm and for construction (Zambrana et al. 2014, Sylvester, AVALOS and CHÁVEZ FERNÁNDEZ 2012, Haynes and McLaughlin 2000). *A. butyracea* and *W. regia*, colloquially *palma real* and *conga*, respectively, are similarly large and large-crowned palms both reported for construction use (thatch) in our study. *A. butyracea* are widespread in the Panama Oeste province, and throughout a central lowland corridor that connects both provinces, while *R. welfia* are a more common fixture along the northern Caribbean coast in the Panama province (Condit, Pérez and Daguerre 2010). However, their ranges do overlap in certain parts of our study area; survey respondents in BB, in Panama Oeste province, report a preference for *R. welfia* thatch over *A. butyracea*, citing higher durability.

Evidence of use of *A butyracea* for thatch is notable given this species is the preferred habitat of the primary vector of Chagas disease in Panama, the triatomine bug, *Rhodnius* *pallescens* (Romaña et al. 1999). Chagas disease is a zoonotic vector borne disease endemic to Latin America that has no vaccine and no cure, and is best reduced through preventative avoidance of the triatomine vector (Rassi Jr, Rassi and Marin-Neto 2010). Harvesting *A. butyracea* fronds for thatch may put individuals in direct contact with this insect, which lives almost exclusively in the dense organic matter that collects at the base of this palm's crown (Abad-Franch et al. 2015). Furthermore, thatched roofs in general are known risk factors for this disease in this region. Although the insect vector is predominately sylvatic (i.e. confined to palm crowns) and cannot reproduce in thatched environments, the adult specimen that are sometimes found in thatched roofs are much more likely to feed on human occupants due to increased proximity (Calzada et al. 2006).

Despite these risk factors, realized elevation in transmission risk to individual households will vary and is difficult to quantify. Thatched roofs on free-standing *ranchos* may have a different risk factor than thatched roofs in residences, which are more likely to be occupied at night when the vector is most active (Lazzari and Lorenzo 2009). However, some studies suggest these bugs are attracted to electric light, so it may be that any attractive habitat in proximity of households might elevate risk of disease transmission. Additionally, despite the high percentage of households that report palm use for construction, few surveyed households had visible evidence of palm thatch or wood-based construction: among households who reported use of palms for construction, 11% had partially thatched roofs, and 44% contained any wood-based (origin non-specified) materials. Other studies have found similar discrepancies between reported and realized use, and have suggested that more precise language is likely needed in the assessment of palm use (Byg et al. 2001, Cámara-Leret et al. 2016). It may be that some survey respondents in our study reported traditional knowledge of hypothetical palm use, rather than active use of palm materials. Further evaluation is warranted, given the risk of thatch as a known transmission factor of Chagas disease in this region.

Conclusion

We find that palm use is ubiquitous in this region, and that behavioral characteristics are linked with the most frequently reported use categories: construction and human food consumption. We find no evidence to suggest that either region or forest cover influences the way palms are used from this survey sample. However, the characteristics found to drive palm-use among this population differ from drivers of palm-use trends in other parts of Central and South America. In that way, this study supports past findings that household indicators of palm use are highly localized. Furthermore, given the potential ties between Chagas disease transmission and *A. butyracea* palm use, we suggest this heterogeneity of palm use presents similarly localized behavioral risk factors that may lead to elevated risk of Chagas disease.

Table 4.1 Independent Variables Considered in the Analysis

Independent Variable	Variable Type	Levels
Provence (ref Panama Oeste)	Nominal	(1) Panama Oeste; (0) Panama
Forest cover	Ordinal	(1) mostly pasture; (2) semi-forested; (3) forested
Maximum household education	Ordinal	(0) none; (1) incomplete primary; (2) completed primary; (3) middle school; (4) secondary school; (5) university
Total number of people in household	Continuous	Between 2 and 9
Total number of children (age < 16) in household	Continuous	Between 0 and 6
Fells/harvests trees in forest	Nominal	(0) no; (1) yes
Thatched roof on property	Nominal	(0) no; (1) yes
Reported or observed presence of *A. butyracea*	Nominal	(0) no; (1) yes
Reported or observed presence of *C. nucifera*	Nominal	(0) no; (1) yes
Obtains food (fruit, insects, plants) from forest	Nominal	(0) no; (1) yes

Table 4.2 Self-reported Palm Use Among Survey Respondents (n=112)

Use Type	N	%
Any Use Type	97	86.61
Two or more use types	38	33.93
Construction	55	49.11
Food (human)	49	43.75
Ornamental	13	11.61
Technology	6	5.36
Feed (animal)	6	5.36
Culture	5	4.46
Medicine	3	2.68
Cosmetics	0	0.00
Other	10	8.93

Table 4.3 Self-Reported Use-Type of Palm Materials[†] by Province and Land Cover among Survey Respondents who Use Palms (n=97)

	Province		Land Cover		
	Panama	Panama Oeste	Forest	Semi-Forest	Pasture
Any Use-Type	41	56	35	33	29
Two or more Use-Types	16	22	18	10	10
Construction	19	36	24	16	15
Food (human)	23	26	18	15	16
All Other Types[‡]	22	21	16	16	11

[†] No statistically significant difference was indicated by a Chi-square test for independence.

[‡] Due to low response frequency, all other use-types were combined to meet minimum value assumptions

Table 4.4 Reported Palm Use by Species[†]

Species	Colloquial Name	Community	Associated Use-Type
Attalea butyracea	palma real	AP, CA, PN	construction, palm wine
Welfia regia	conga	BB	construction
Bactris gasipaes	pifa, palma de pixbae	AP, BB, TP	food (human), technology
Cocos nucifera	coco, pipa	BB, PN, SC, TP	food (human), construction, medicine

[†]Does not reflect all survey respondents, only subset (n=24) who reported this information

Table 4.5 Logistic Regression Model: Survey Respondents who Report Palm Use for Construction vs. Other Means

	Construction	Food
	β	β
Provence (ref Panama Oeste)	-0.5320	0.0456
Forest cover	0.2957	-0.1168
Maximum household education	-0.3976	0.2331
Total number of people in household	0.3520[†]	-0.1448
Fells/harvests trees in forest	2.3984[†]	-2.7698[†]
Thatched roof on property	1.5974	ne
Reported presence of *A. butyracea*	-0.0454	ne
Reported presence of *C. nucifera*	ne	-0.1503
Obtains food (fruit, insects, plants) from forest	ne	0.0641

[†]Significant at $p < 0.5$; ne = not evaluated

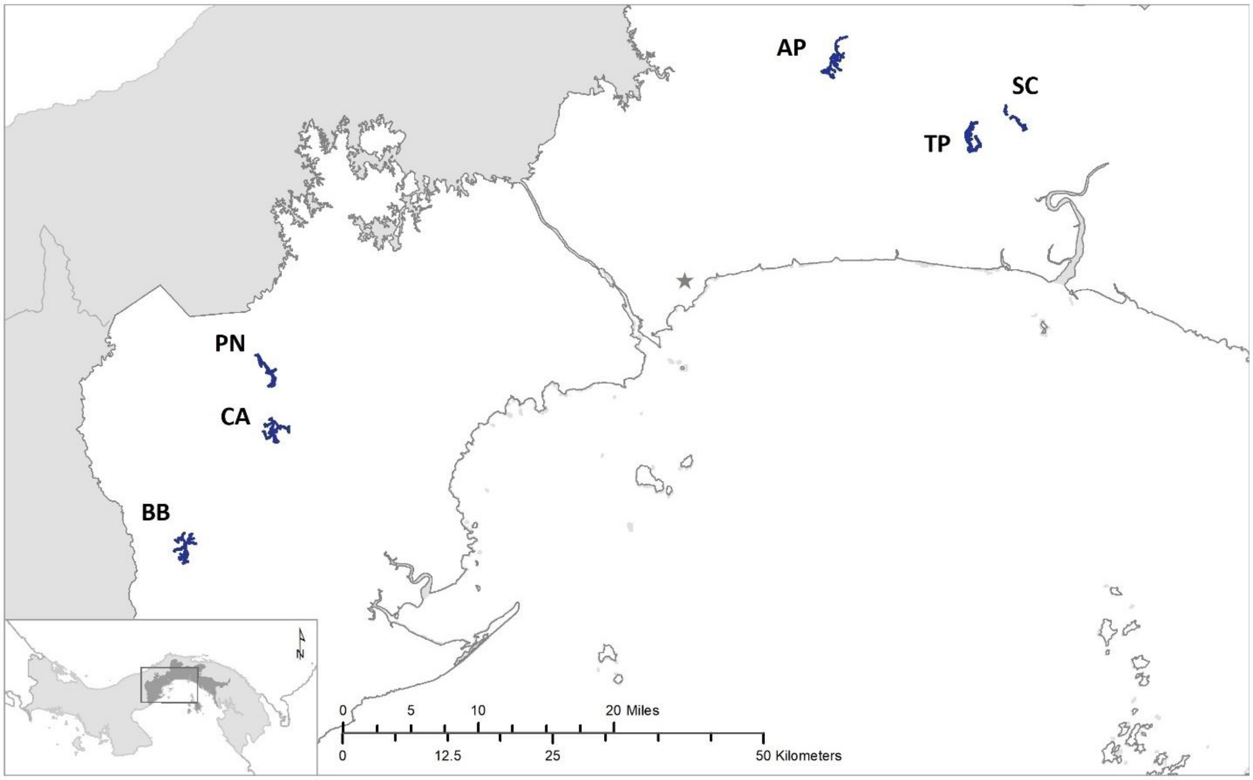

Figure 4.1 Chapter 4 study communities. We surveyed households in six rural communities, three each in Panama Oeste Province (PN: Pueblo Nuevo, CA: Cañazas, BB: Bajo Bonito) and Panama Province (AP: Altos de Pacora, SC: Superación Campesino, TP: Tierra Prometida).

Figure 4.2 Rancho with palm thatch roof (Photo: C. Mertzlufft)

REFERENCES

Abad-Franch, F., M. M. Lima, O. Sarquis, R. Gurgel-Goncalves, M. Sanchez-Martin, J. Calzada, A. Saldana, F. A. Monteiro, F. S. Palomeque, W. S. Santos, V. M. Angulo, L. Esteban, F. B. Dias, L. Diotaiuti, M. E. Bar & N. L. Gottdenker (2015) On palms, bugs, and Chagas disease in the Americas. *Acta Tropica,* 151**,** 126-41.

ANAM. 2003. Informe Final de Resultados de la Cobertura Boscosa y Uso de Suelo de la República de Panamá 1992-2000. Panamá.

Balick, M. J. (1984) Ethnobotany of palms in the Neotropics. *Advances in Economic Botany,* 1**,** 9-23.

Bermúdez, I. & J. R. Chue (2014) Etnobotánica en El Cacao, Capira, Panamá: Identificación y usos de plantas medicinales. *Revista Prisma Tecnológico,* 5**,** 48-52.

Bernal, R., G. Galeano, N. García, I. L. Olivares & C. Cocomá (2010) Uses and commercial prospects for the wine palm, *Attalea butyracea*, in Colombia. *Ethnobotany Research and Applications,* 8**,** 255-268.

Bjorholm, S., J.-C. Svenning, F. Skov & H. Balslev (2005) Environmental and spatial controls of palm (Arecaceae) species richness across the Americas. *Global Ecology and Biogeography,* 14**,** 423-429.

Byg, A. & H. Balslev (2001) Diversity and use of palms in Zahamena, eastern Madagascar. *Biodiversity and Conservation,* 10**,** 951-970.

Calzada, J. E., V. Pineda, E. Montalvo, D. Alvarez, A. M. Santamaria, F. Samudio, V. Bayard, L. Caceres & A. Saldana (2006) Human trypanosome infection and the presence of intradomicile *Rhodnius pallescens* in the western border of the Panama Canal, Panama. *Am J Trop Med Hyg,* 74**,** 762-765.

Cámara-Leret, R., J. C. Copete, H. Balslev, M. S. Gomez & M. J. Macía (2016) Amerindian and Afro-American perceptions of their traditional knowledge in the Chocó biodiversity hotspot. *Economic Botany,* 70**,** 160-175.

Cámara-Leret, R., N. Paniagua-Zambrana, H. Balslev & M. J. Macía (2014) Ethnobotanical knowledge is vastly under-documented in northwestern South America. *PLoS One,* 9.

Castillo, M., R. Samaniego & A. Kindgard. 2015. Mapa de Cobertura y Uso de la Tierra 2012. ed. M. d. Ambiente. Panamá.

Condit, R., R. Pérez & N. Daguerre. 2010. *Trees of Panama and Costa Rica*. Princeton University Press.

Dalle, S. P., H. López, D. Diaz, P. Legendre & C. Potvin (2002) Spatial distribution and habitats of useful plants: an initial assessment for conservation on an indigenous territory, Panama. *Biodiversity and Conservation,* 11**,** 637-667.

Dickau, R. 2010. Microbotanical and Macrobotanical Evidence of Plant Use and the Transition to Agriculture in Panama. In *Integrating Zooarchaeology and Paleoethnobotany*, 99-134.

Duke, J. A. (1975) Ethnobotanical observations on the Cuna Indians. *Economic Botany,* 29**,** 278-293.

Dyer, J. L., S. Tanner, J. Velasquez Runk, C. Mertzlufft, N. Gottdenker (2016) Deforestation, Dogs, and Zoonotic Disease. *Anthropology News*, e92-e95.

Fadiman, M. G. (2008) Use of Mocora, Astrocaryum standleyanum (Arecaceae), by three ethnic groups in Ecuador: differences, similarities and market potential. *Journal of Ethnobiology,* 28**,** 92-109.

Galeano, G. (2000) Forest use at the Pacific Coast of Chocó, Colômbia: a quantitative approach. *Economic Botany,* 54**,** 358-376.

Gottdenker, N. L., L. F. Chaves, J. E. Calzada, A. Saldaña & C. R. Carroll (2012) Host life history strategy, species diversity, and habitat influence *Trypanosoma cruzi* vector infection in changing landscapes. *PLoS Negl Trop Dis,* 6**,** e1884.

Haynes, J. & J. McLaughlin. 2000. *Edible palms and their uses*. University of Florida Gainesville.

Johnson, D. 1998. Tropical Palms. Rome: Food and Agriculture Organization of the United Nations.

Karadi, R., A. Shah, P. Parekh & P. Azmi (2011) Antimicrobial activities of *Musa paradisiaca* and *Cocos nucifera*. *International Journal of Research in Pharmaceutical and Biomedical Sciences,* 2**,** 264-267.

Lazzari, C. R. & M. G. Lorenzo (2009) Exploiting triatomine behaviour: alternative perspectives for their control. *Memórias do Instituto Oswaldo Cruz,* 104**,** 65-70.

López-Sáez, J. A. & J. Pérez-Soto (2010) Etnobotánica medicinal y parasitosis intestinales en la isla de Ometepe, Nicaragua. *Polibotánica***,** 137-161.

McHugh, M. L. (2013) The chi-square test of independence. *Biochemia medica,* 23**,** 143-149.

Moraes, M., N. Paniagua-Zambrana, R. Cámara-Leret, H. Balslev & M. Macia. 2015. Palmas útiles de Bolivia, Colombia, Ecuador y Perú. In *Cosecha De Palmas En El Noroeste De Sudamérica–Las Bases Científicas Para Su Manejo Y Conservación,* ed. H. Balslev, Macia, M., Navarrete, H., 87-102. Pontificia Universidad Católica del Ecuador.

Paniagua-Zambrana, N. Y., R. Camara-Lerét, R. W. Bussmann & M. J. Macía (2014) The influence of socioeconomic factors on traditional knowledge: a cross scale comparison of palm use in northwestern South America. *Ecology and Society,* 19.

Rassi Jr, A., A. Rassi & J. A. Marin-Neto (2010) Chagas disease. *The Lancet,* 375**,** 1388-1402.

Romaña, C., J. Pizarro, E. Rodas & E. Guilbert (1999) Palm trees as ecological indicators of risk areas for Chagas disease. *Trans R Soc Trop Med Hyg,* 93**,** 594-595.

Runk, J. V. (2001) Wounaan and Emberá use and management of the fiber palmAstrocaryum standleyanum (Arecaceae) for basketry in eastern Panamá. *Economic Botany,* 55**,** 72-82.

Saldaña, A., J. E. Calzada, V. Pineda, M. Perea, C. Rigg, K. González, A. M. Santamaria, N. L. Gottdenker & L. F. Chaves (2015) Risk factors associated with *Trypanosoma cruzi* exposure in domestic dogs from a rural community in Panama. *Memórias do Instituto Oswaldo Cruz,* 110**,** 936-944.

Smith, N. 2015. *Attalea butyracea*. In *Palms and People in the Amazon*, 83-89. Switzerland: Springer.

Sosnowska, J. & H. Balslev (2008) American palms used for medicine, in the ethnobotanical and pharmacological publications. *Revista Peruana de Biología,* 15**,** 143-146.

--- (2009) American palm ethnomedicine: A meta-analysis. *Journal of Ethnobiology and Ethnomedicine,* 5**,** 43.

Sylvester, O., G. Avalos & N. Chavez Fernandez (2012) Notes on the Ethnobotany of Costa Rica's Palms. *Palms,* 56.

Torres, N. L., J. L. Martínez, C. Laurido & A. Zapata (2016) Plantas medicinales de Panamá 1: Etnobotánica de la Reserva Forestal el Montuoso. *Boletín Latinoamericano y del Caribe de Plantas Medicinales y Aromáticas,* 15**,** 407-421.

Wake, T. A. (2006) Prehistoric Exploitation of the Swamp Palm (Raphia taedigera: Arecaceae) at Sitio Drago, Isla Colon, Bocas del Toro Province Panama. *Carribean Journal of Science,* 42**,** 11.

Zambrana, N. Y. P., R. W. Bussmann, C. Vega, C. Téllez, M. J. Macía, C. de Aviación & L. Wayku (2014) Nuestro Conocimiento y Uso de las Palmeras: Una herencia para nuestros hijos. Comunidades Llaquash, San Martín, Peru. *Ethnobotany Research and Applications,* 13**,** 001-105.

CHAPTER 5

CONCLUSION

Summary

The studies included in this dissertation were developed to address multiple facets of Chagas disease transmission in Panama in order to unravel a portion of the multi-scalar assemblage of interactions that result in the spread of disease in this region. Chapter 2 indicates that anthropogenic alteration of landscapes is one of the leading indicators of suitable palm habitat. In both of the final models examined in this paper, anthropogenic influence ranks higher in habitat suitability than general landcover type (which includes human-associated built environment and infrastructure, as well as purely ecologically-based categories that are defined by their primary vegetation or surface feature) or temperature and precipitation variables, which are generally considered the limiting factors of palm distribution at a regional scale (Eisenhardt et al. 2011). Much of this area is inhabited by humans and undergoes regular change to support human needs, such that palms might be expected throughout the region. We find that unsuitable soil type and lower temperatures due to elevation gain are the primary limiting factors of *A. butyracea* palm distribution in this area.

A. butyracea palms are known to propagate in disturbed habitats at both the individual-tree level (Wright and Duber 2001) and across entire landscapes (Chapter 2). However, neither of these scales is appropriate to tease out the *specific human actions* that directly or indirectly benefit palm distribution in the context of increased risk for Chagas transmission. For example, from a purely ecological standpoint, individual palm studies show that reductions in biodiversity linked to human-inhabited regions benefit the survival of *A. butyracea* seedlings through a reduction in predator populations (Wright and Duber 2001); however, this scale cannot say whether or not human activity influences the ability of these seedlings to reach maturity, at which point they become suitable habitat for vectors and increase Chagas risk. In contrast, studies that cover large extents aggregate, generalize, or mask individual- or household-level human activity to such a degree that meaningful interventions are difficult or impossible to establish—it is unrealistic to the point of absurdity to suggest halting Chagas transmission by no longer changing the landscape. Chapters 3 and 4 focus solely on human activities at household and inter-community scales to better understand anthropogenic drivers or restrictions to palm distribution.

Chapter 3 indicates that the increased propagation of *A. butyracea* seedlings in disturbed landscapes (as proposed by individual-palm studies) *do* grow to maturity to form the monospecific stands of palms anticipated by ecologists, but *only* in landscapes with a history of disturbance that are no longer heavily occupied by humans—namely, mature secondary forest (Chapter 3, Table 3.3). We observe increases in both individual palms and palm clusters in secondary forest, which we would expect from ecological studies, but find reductions in expected palm numbers in agricultural, but *not residential* settings. This suggests that there is some active thinning of palm growth by humans in pasture and croplands, either directly (removal of mature palms or palm seedlings, expected especially among crops) or indirectly (possible negative influence by cattle or ranching practices). This does not mean all of the palms have been removed, however; particularly in pasture settings, there are still massive quantities of palms, just statistically fewer than expected.

In residential areas we see no increase or decrease of palms, and still count over 1,000 palms in areas in very close proximity to households (all household within this study area were within known flight distance of the *R. pallescens* vector) (Chapter 3, Tables 3.3 and 3.6). In Chapter 2, the models predict that landscape disturbance increases habitat suitability of palms until disturbance is very high (e.g. within dense cities). We find in Chapter 3, however, that even the most built up areas within this study region still contain hundreds of palms. We find no evidence of purposeful thinning of palms in residential settings, which may have implications for Chagas transmission. Moreover, we worked with the local Control de Vectores (vector control) office of the Panamanian Ministry of Health in this region during our field work, and these individuals have door-to-door awareness campaigns about Chagas transmission. As mentioned in the conclusion of Chapter 3, the actual risk for any one person or household in this area is going to depend on many more factors than proximity to palms (e.g. behavioral practices, household construction, etc.). However, from a look at palm distribution alone, we cannot see an impact in the vector control measures (e.g. a reduction in palms near households). I stress that this does not mean that a protective impact is not occurring due to the Ministry's efforts, only that it cannot be measured at this scale and by this metric.

In Chapter 4 we sought to understand who is directly interacting with *A. butyracea* palms. This study evolved into an understanding of palms in general, not *A. butyracea* specifically, due to an unintentionally ambiguous key palm question in the household survey portion of our data collection that I did not catch until halfway through our survey was conducted: rather than asking respondents what palm they prefer to use as a follow-up to the question, we asked them what palms they preferred (Appendix B). This was frequently interpreted as "What is your favorite palm?" Given that this survey comprised questions from a number of different researchers as part of a broader collaboration (Dyer et al. 2016), and the palm questions were my contribution, no one else was in a position to catch this error, and I was not directly involved in the survey field testing or initial data collection. Therefore, I was only able to connect the use of palms with specific palm species when this information was voluntarily and explicitly mentioned by survey respondents, which was only a quarter of our survey pool.

The most interesting and unexpected (to me) finding was that nearly everyone we spoke to reported using palms in one or more ways. Most frequently, palms were used for construction or human consumption. Given the ubiquity of palm use and that there was no discernable (statistically) change in palm-use trends by region or across socioeconomic range in our study sample, it is difficult to say whether social practices of palms *influence the retention* of palms (i.e. people plant or do not clear palms because they are useful) or if these communities are just taking advantage of the useful properties of plants that grow in abundance near their households. For the purposes of Chagas risk, given the findings from Chapter 3, a more pertinent series of questions regarding individuals' interactions with palms might have been, "When do you purposefully remove palms, and why? When do you purposefully leave palms standing when other areas are removed, and why?" The retention of mature palms in otherwise cleared landscape has been attributed to both the social use of palms and practical logistics of palm clearing: they are hard to chop down, and sometimes they are fire resistant (Balslev and Blicher-Mathiesen 1991). For the social use of *A. butyracea* palms in the spread and mitigation of Chagas disease in this region, it may be worth pursuing why mature palms remain in cleared landscapes in more detail, as this is likely to post a more immediate elevated Chagas risk to existing communities than abundant palm seedlings, given both the slow growth to maturity (i.e.

suitable vector habitat) of this species and the likelihood that these seedlings are situated in secondary forest and not community settings.

This research was not conducted solo or in a vacuum (Dyer et al. 2016) and its goals are both to advance the understanding of *A. butyracea* palm distribution and to assist Panamanian colleagues in any way possible in their mission to protect the health of Panamanian communities. At a provincial scale, the findings of Chapter 2 suggest areas of anticipated suitable palm habitat, which in conjunction with health records of Chagas disease cases or heart disease, may highlight areas of past and potentially still active Chagas disease transmission for the direction of Ministry of Health Vector Control personnel outreach. These maps may also assist our colleagues at ICGES plan new regional locations of vector collection and field testing for Chagas disease presence. Suitable palm habitat does not guarantee presence of *A. butyracea* palms, which do not guarantee presence of vectors, which do not guarantee presence of the *T. cruzi* parasite. Our colleagues at ICGES are able to quantify these measures for the benefit of local communities and the understanding of Chagas risk in central Panama.

The findings of Chapters 3 and 4 inform community and household interactions with *A. butyracea* palm trees. These findings may aid the direction of communication and outreach already practiced by the Ministry of Health Vector Control offices in this region, who actively work with communities in vector identification and awareness. As previously mentioned, the risk to any individual household or person will vary on many more social, behavioral, and ecological factors than just the presence of even infected palm trees, but more knowledge on where palms are and why we see an abundance or reduction of palms in certain areas can inform one part of the dynamic network of zoonotic disease transmission. This information may be useful particularly in conjunction with the findings of the UGA-CDC Seed Funding Project, which may provide insight into addition social and economic drivers of Chagas disease transmission, as this research tested for Chagas disease presence, not just risk factors.

Key findings

This dissertation sought to identify the multi-species assemblages that result in the co-production of vector-borne Chagas disease transmission in Panama and examine how these assemblages fluctuate at different spatial extents. To supplement biomedical and ecological understandings of Chagas disease transmission, this research focuses heavily on the (re)actions and influence of humans on the distribution of the *Attalea butyracea* palm. By empirically documenting the impact of human activity on palm distribution and communities' self-reported interactions with palms, we can begin to infer the role of social processes in fomenting the interspecies interactions that result in Chagas disease transmission. This research is not to say that physical movement and interaction between humans and *R. pallescens* is not a direct cause of Chagas disease transmission to humans in Panama—only that this scenario is the purely biomedical framing, which is the default framing of disease transmission among most people actually paid to prevent disease transmission, and only *one of many* arguable causes of Chagas disease transmission (Wade and Halligan 2004). By focusing only on the biomedically-framed mode of transmission and its geospatial setting du jour, we lose the opportunity to understand and address the (often social, often political) root causes and effects of transmission.

In the biomedical framing, "the environment" is the space in which interactions that make people sick—between pathogens and susceptible host—occur. This research focuses particularly on the *A. butyracea* palm, which is simultaneously the habitat and context of sylvatic (non-human) transmission cycles of Chagas disease ("the environment") *and* a dynamic actor in domestic (human) transmission in this region. A central tenant of a socionatural framing is that the ways we describe, measure, and define our surroundings are inherently social constructs (Castree 2001). A socionatural assemblage theory as a theoretical framing for disease transmission removes the problem of the social construct of certain framings of the environment because it allows us to think *outside* of space. This way of thinking refocuses the transmission away from the physical movement of multispecies activity within an area by focusing instead on the *structure* (who or what is involved in the outcome, here: Chagas disease) and *process* (why is this happening: especially, what external processes are forcing these outcomes? Who controls or benefits from these processes?). This allows us to expand our understanding of Chagas transmission beyond the biomedical model of a few actors and to look at the driving forces of all the actors involved.

None of the studies in this dissertation focuses explicitly on the social processes driving any of these interactions, but, when considering the body of work as a whole, clear pictures begin to develop. As I have considered these three papers in the context of a socionatural assemblage framing, couched in what I know of the ecoepidemiology of Chagas disease and the history of landscape change in Panama, three main conclusions emerge:

Conclusion 1: *The view and understanding of socionatural assemblages change depending on both the extent and the timespan under which they are considered. Time is the hidden variable in all of this.*

The research conducted for this dissertation clearly documents the multifaceted, multi-scalar and bi-directional relationship between humans and *A. butyracea* palms. However, even these framings capture only pieces of the entire network of actors and drivers of this disease. The specific causes and effects that we can infer from these papers varies by the scale at which they are conducted—regional studies mask the household-level decisions (and decision makers) that drive regional effects, and individual and household level studies do not capture the full extent of local decisions. Also, by choosing to focus on the palm, we do not consider drivers of sylvatic transmission cycles within the crown itself (before the palm-level view), or the drivers of human-to-human transmission cycles (after the palm-level view). All these sections are part of the same continuous assemblage, but we are only able to look at certain aspects at a time, and critically, *only looking at one section does not tell the whole story*, and *the choice of which part to examine may introduce bias or be driven by disciplinary bias.*

I suggest that time is the silent variable in the assemblage of Chagas disease from my own background in infectious disease epidemiology. I would argue that the biomedical goal for infectious disease is to look at how transmission is actively occurring or possibilities for future transmission to instigate prevention and mitigation strategies. Public health scientists do not look far into the past for drivers of active transmission. From a socionatural perspective I suggest that is shortsighted, which brings me to my second conclusion.

Conclusion 2: The social and economic processes that are driving present-day Chagas disease transmission were centuries in the making, but are still active today.

While the external social and political processes that have physically and economically remade Panama have been extensively studied (Carse 2014, Cooke 2005, Herrera 2001), my goal in this research was first to quantify the human-palm interaction at multiple scales to gain an understanding of the interactions and then to address this in the context of landscape change. Given the slow growth and long lifespans of the *A. butyracea* palm, I have come realize that the social processes affecting current transmission risk of Chagas disease go back much further than I suspected. In a very real sense, the geographical area at most risk for Chagas transmission in Panama is due to another non-human species that does not enter into the typical Chagas cycle: cows. As stated in the introduction, cattle ranching has informed cultural and physical changes in Panama, and especially in what is now the Panama and Panama Oeste provinces, since the Spanish colonialists introduced cattle in the 1500s (Chapter 1). Given the slow growth and long lifespan of *A. butyracea* palms, the high abundance of *A. butyracea* in our study region, and particularly in the Panama Oeste Province, are not recent occurrences. It is likely that the transmission risk we see today is due to centuries of agricultural practices, driven by national and international powers and interests. This leads me to my final conclusion.

Conclusion 3: Individuals and households overwhelmingly bear the burden and the responsibility to protect themselves against Chagas disease, but they are not the root cause of the landscape disturbance that is causing elevated Chagas risk due to proximity of palms.

The co-production of Chagas disease in central Panama is inherently politically and socially linked due to the history of land use in this region. However, the landscape change that is the result of global power dynamics are realized at the local, household scales. Individuals who contract Chagas disease due to close proximity of mature *A. butyracea* palms are sick due to wide-reaching landscape change that was outside of their control and may even have occurred before they were alive. Yet the responsibility to protect themselves is placed squarely at the household level, whether through education campaigns by Ministry of Health Vector Control staff (personal observation) or through the implementation of household barriers to entry of infectious bugs (Dell’Arciprete et al. 2014, Ferral et al. 2010, Gunn et al. 2018, Herber and Kroeger 2003).

This type of approach is the norm for the biomedical model of disease transmission, because it halts (or aims to halt) the meeting of the only two actors of interest: the pathogen, and the susceptible population. However, by not looking at disease transmission as complex, scale-dependent, and inherently social phenomenon, we are unable to perceive and address the root causes. Until an expanded approach to the study of disease is taken, we will not truly be in the prevention business as outbreaks continue; we will be stuck in this cycle of damage control.

REFERENCES

Balslev, H. & U. Blicher-Mathiesen. 1991. La ‘Palma Real’de la Costa Ecuatoriana (Attalea colenda, Arecaceae), un Recurso poco Conocido de Aceite Vegetal. In *Las Plantas e El Hombre: Memorias del Primer Simposio Ecuatoriano de Etnobotánica y Botánica Económica. Herbario QCA-PUCE, Quito,* 47-62.

Carse, A. 2014. *Beyond the Big Ditch: Politics, Ecology, and Infrastructure at the Panama Canal*. Cambridge, MA: The MIT Press.

Castree, N. 2001. Socializing Nature: Theory, Practice, and Politics. In *Social Nature: Theory, Practice, and Politics,* eds. N. Castree & B. Braun. Malden, MA: Blackwell Publishing.

Cooke, R. (2005) Prehistory of native Americans on the Central American land bridge: Colonization, dispersal, and divergence. *Journal of Archaeological Research,* 13**,** 129-187.

Dell’Arciprete, A., J. Braunstein, C. Touris, G. Dinardi, I. Llovet & S. Sosa-Estani (2014) Cultural barriers to effective communication between Indigenous communities and health care providers in Northern Argentina: an anthropological contribution to Chagas disease prevention and control. *International Journal for Equity in Health,* 13**,** 6.

Dyer, J. L., S. Tanner, J. Velasquez Runk, C. Mertzlufft, N. Gottdenker (2016) Deforestation, Dogs, and Zoonotic Disease. *Anthropology News,* e92-e95.

Ferral, J., L. Chavez-Nunez, M. Euan-Garcia, M. J. Ramirez-Sierra, M. R. Najera-Vazquez & E. Dumonteil (2010) Comparative field trial of alternative vector control strategies for non-domiciliated Triatoma dimidiata. *Am J Trop Med Hyg,* 82**,** 60-6.

Gunn, J. K. L., K. C. Ernst, K. E. Center, K. Bischoff, A. V. Nunez, M. Huynh, A. Okello & M. H. Hayden (2018) Current strategies and successes in engaging women in vector control: a systematic review. *BMJ Glob Health,* 3**,** e000366.

Herber, O. & A. Kroeger (2003) Pyrethroid-impregnated curtains for Chagas’ disease control in Venezuela. *Acta Tropica,* 88**,** 33-38.

Herrera, G. C. (2001) On cattle and ships: Culture, history and sustainable development in Panama. *Environment and History***,** 201-217.

Wade, D. T. & P. W. Halligan (2004) Do biomedical models of illness make for good healthcare systems? *BMJ* 329**,** 1398-1401.

Wright, S. J. & H. C. Duber (2001) Poachers and Forest Fragmentation Alter Seed Dispersal, Seed Survival, and Seedling Recruitment in the Palm *Attalea butyraceae,* with Implications for Tropical Tree Diversity. *Biotropica,* 33**,** 583-595.

APPENDIX A.

PALM SAMPLE DISTRIBUTION BY PREDICTIVE VARIABLE FOR THE MODELS CONSIDERED (CHAPTER 2)

Predictive Variables		***Study Area***		**Model 1**		**Model 2 (1km)**		**Model 2 (2km)**	
Abiotic:				***n=160***		***n=193***		***n=173***	
	Avg. Precipitation								
	min:	1672.77		1849.39		1849.39		1849.39	
(mm)	max:	3390.20		3243.72		3243.72		3243.72	
	mean:	2414.13		2416.46		2420.21		2417.34	
	std. dev.:	272.42		250.55		232.82		243.33	
	Holdridge Life Zones	*km^2*	*%*	*n*	*%*	*n*	*%*	*n*	*%*
bh-P	Premontane Moist Forest	511.86	5.57	3	1.875	3	1.55	3	1.73
bh-T	Tropical Moist Forest	4535.25	49.36	102	63.75	127	65.80	112	64.74
bmh-P	Premontane Wet Forest	1766.29	19.22	28	17.5	36	18.65	31	17.92
bmh-T	Tropical Wet Forest	1842.39	20.05	21	13.125	21	10.88	21	12.14
bp-MB	Lower Montane Rainforest	0.65	0.01	0	0	0	0	0	0
bp-P	Premontane Rainforest	323.23	3.52	1	0.625	1	0.52	1	0.58
bs-T	Tropical Dry Forest	208.58	2.27	5	3.125	5	2.59	5	2.89
	Total:	9188.25							
	Avg. Temperature								
	min:	21.28		22.2		22.2		22.2	
(°C)	max:	27.62		27.41		27.41		27.41	
	mean:	25.92		26.21		26.24		26.22	
	std. dev.:	1.03		0.69		0.64		0.67	

Soils	km^2	*%*	*n*	*%*	*n*	*%*	*n*	*%*
Andols	175.46	1.95	2	1.25	2	1.09	2	1.16
Cambisols	2677.21	29.72	25	15.63	25	13.66	24	13.87
Gleysols	312.45	3.47	2	1.25	2	1.09	2	1.16
Nitisols	5794.41	64.33	131	81.88	154	84.15	145	83.82
Regosols	14.59	0.16	0	0	0	0	0	0
Vertisols	33.05	0.37	0	0	0	0	0	0
Total:	9007.17							

Biotic:

Land Cover Type	km^2	*%*	*n*	*%*	*n*	*%*	*n*	*%*
Mature Forest	2309.35	25.18	23	14.375	24	12.44	24	13.87
Secondary Forest	2763.58	30.13	59	36.875	69	35.75	62	35.84
Grassland	2824.00	30.79	65	40.625	77	39.89	68	39.31
Planted Crops/Timber	293.88	3.20	3	1.875	4	2.07	4	2.31
Populated Area	463.41	5.05	10	6.25	19	9.84	15	8.67
Wetlands	375.97	4.10	0	0	0	0	0	0
Surface Water	70.36	0.77	0	0	0	0	0	0
No Vegetation	72.17	0.79	0	0	0	0	0	0
	9172.72							

Anthropogenic Disturbance	km^2	*%*	*n*	*%*	*n*	*%*	*n*	*%*
Little to None	2862.37	31.21	26	16.25	27	13.99	27	15.61
Minimal	2356.28	25.69	52	32.5	60	31.09	55	31.79
Moderate	3426.81	37.36	72	45	87	45.08	76	43.93
Maximum	527.26	5.75	10	6.25	19	9.84	15	8.67
Total:	9172.72							

APPENDIX B.

SURVEY QUESTIONS ANALYZED FOR HUMAN-PALM INTERACTION STUDY[4]

(CHAPTER 4)

Demografía

¿Cuántas personas viven en su casa? ________________

[Indique el nombre, sexo, edad, y educación de las personas que viven en la casa]

			Persona entrevistada	Otras personas en la casa				
	Instrucciones	Formato						
4.	¿Hasta qué curso ha completado en la escuela?	0=Ninguno, 1=Primaria incompleta, 2=Primaria completa, 3=Educación media, 4=Secundaria 5=Universitaria						

Características de la vivienda

37.		¿Qué tipo de vegetación se encuentra cerca de su casa?	Distancia desde la vivienda (metros)	Notas
		No hay vegetación		
		Palmas reales		
		Árboles frutales		
		Arbustos y plantas ornamentales		
		Malezas		
		Hortalizas		
		Palmas de coco		
		Otras ______________________		

---

[4] These questions are drawn from a larger survey that was the collaborative work of many researchers, including partners at Panamanian government institutions (see Dyer et al. 2016). As of this writing the full survey has yet to be analyzed, and its intellectual property cannot be shared. Only the questions analyzed in Chapter 4 of this body of work are shown.

PRACTICAS

12. ¿Por qué va al monte? (anotar todas las respuestas)
    1. Tala de árboles / Árboles de cosecha
    2. Plantas medicinales
    3. Cazar animales
    4. Comida (frutas, insectos, otras plantas) del monte
    5. Otro uso de plantas
    6. Tumbar y quemar para potreros
    7. Tumbar y quemar para agricultura
    8. A pasar hacia otro lugar
    9. Otro _______________

LAS PALMAS

33. ¿Son útiles las palmas o los materiales de las palmeras para usted? (1=Si, 2=No)
____

34. ¿De qué manera son útiles las palmas para usted o su familia? (Nota todas las repuestas)

A. Comida para personas
B. Comida para animales
C. Materiales de construcción
D. Uso tecnológico (ejemplo: escoba, sombrero)
E. Uso medicinal
F. Uso cosmético
G. Uso cultural
H. Uso ornamental
I. Otro ________________

35. ¿Prefiere algún tipo particular de palma? (Anotar todas las respuestas)

____