EFFECTS OF ANTHROPOGENIC LAND USE ON PALM CROWN COMMUNITY NETWORKS AND IMPLICATIONS FOR CHAGAS DISEASE ECOLOGY

by

CHRISTINA PILAR VARIAN

(Under the Direction of Nicole Gottdenker)

ABSTRACT

In order to manage or predict infectious disease in response to anthropogenic disturbance, it is essential to understand how pathogen transmission is affected by changes in local abiotic and biotic conditions. The objective of this study is to investigate how land use influences microclimate and species communities in Panama and address how these changes collectively affect the Chagas disease vector *Rhodnius pallescens* that transmits parasite *Trypanosoma cruzi*. The vector *R. pallescens* is associated with the ubiquitous palm, *Attalea butyracea*, and transmits *T. cruzi* across domestic and sylvatic mammalian host, including humans. The risk of Chagas disease increases in areas of anthropogenic disturbance, yet underlying mechanisms require further investigation and may be related to altered microclimate and species communities within the Attalea palm. The key hypotheses of the study are 1) palm crown species community composition, structure, and function are impacted by land use change and disturbed communities have a higher instance of generalist, disturbance tolerant species, and 2) *R. pallescens* abundance and infection are driven by communities that have a decrease in habitat sensitive, invertebrate predator species and are sustained by resilient vertebrate hosts (particularly mammals). This study was conducted throughout central and west-central Panama across the disturbance gradient pasture, peridomestic, and forest fragment. A total of 1098 *R. pallescens* individuals were collected from 106

Attalea palms and 490 individuals were tested for *T. cruzi*. Blood meal analysis was conducted on 240 individuals. Forty-nine palm crown communities were sampled, and 2952 specimens were captured and identified. Food web networks of the palm crown community were created using network software from blood meal and community survey data and combined with microclimate conditions. A generalized mixed effects model was conducted to determine the abiotic and biotic drivers of both *R. pallescens* abundance and infection with *T. cruzi*. Results indicate disturbance does alter communities via shifts in community structure and function which both directly and indirectly influences *R. pallescens* abundance and infection with *T. cruzi*. These results demonstrate that community-level characteristics are a contributing factor to variations in multi-host vector-borne pathogen transmission, particularly in response to land use changes.

INDEX WORDS: Community ecology, Food web ecology, *Attalea butyracea*, *Rhodnius pallescens*, Chagas disease, Anthropogenic disturbance, Disease ecology, Panama

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DEDICATION

THIS IS DEDICATED TO MY FAMILY: LUCI, JIM, MAYA, THOMAS, NEPHEW MILES, VITEK, AND CAT BAGHEERA, ESPECIALLY TO MY GRANDMA BLANCHE AND BELOVED DOG MAGGIE MAE. I LOVE YOU ALL.

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CHAPTER 1

INTRODUCTION

1.1 Background and Research Aim

Anthropogenic land use disturbance is broadly associated with an increase or shift in vector-borne disease transmission. These changes in transmission may be a consequence of altered ecological communities and/or microenvironmental conditions, as they respond to disturbance (Felicia Keesing et al. 2010; Pongsiri et al. 2009; Ostfeld and Keesing 2000a; Johnson, Ostfeld, and Keesing 2015). Increasing evidence suggests that changes in species community structure and composition are tied to multiple emerging infectious diseases for both humans (i.e. Lyme Disease) and animals (i.e. Anuran trematode *ribeiroia ondatrae* (Johnson et al. 2013) which validates the importance of understanding how species function and interact, both direct and indirect, within a community and how that may influence the transmission of pathogens. It also addresses the need to integrate concepts from community and food web ecology with disease ecology in future research directions (Johnson, de Roode, and Fenton 2015; Poulin 2010). For instance, infectious disease studies heavily focus on the vector-host-pathogen dynamics, however this disease triad exists within a wider community context across multiple scales (i.e. within host, across populations). Addressing these scales across disciplines is extremely complicated. For example, metacommunity and dispersal dynamics as well as network topology and size, which are components of community and food web ecology, all require PhD investigations of their own. However taking small steps toward integrating these concepts have been beneficial for having a better understanding of pathogen transmission (Lafferty et al. 2008a), reducing the risk of infectious disease in humans (Sokolow et al. 2015), and biocontrol of disease vectors via conserving community integrity (Klapwijk et al. 2016). In another example of this integration approach, food web networks of communities found in natural mesocosm can be used as a tool to investigate community-level characteristics (i.e. non- vector, host, parasite) and their cascading indirect effects on pathogen transmission (Chapter 2). My research goal is to incorporate an in-depth look into species communities and their response to both disturbance at the local and landscape level and how these responses ultimately influence a multi-host vector-borne disease. Interests driving this research involve the natural history and function of species and their communities, natural methods of disease vector control using predator populations, and conservation of community function by means of landscape conservation. Questions driving this research include: How does land use change influence community structure and function? Can community food web networks reveal underlying drivers (direct and indirect) of multi-host vector-borne disease transmission? How can community integrity act as biocontrol and is it predictable and reliable? To address these questions, I investigate the Attalea palm – Chagas disease in central Panama as a study system. I combine both field and laboratory components to study both the ecology of the disease and palm crown community in order to develop a better understanding of the multiple biotic and abiotic drivers of multi-host vector-borne disease transmission.

1.2 Attalea Palm crown – Chagas Disease as a study system

The Attalea palm crown can be viewed as a natural mesocosm which also provides an ideal opportunity to thoroughly investigate species communities as they are impacted by various gradients of disturbance. The palm is ubiquitous across central Panama and provides food and shelter materials for both humans and domestic animals (Aguilar and Condit 2001; Bernal et al. 2010). Palms also play an essential role in the canopy ecosystem as they are important to invertebrate and vertebrate communities as sites for food and refugia, especially for transient species throughout areas of deforestation (Battirola et al. 2017; Lahey and Gunnels 2013; Inga, Vásqua, and Riva, 1996). In central Panama, the *Attalea* palm is associated with the Chagas disease vector, *Rhodnius pallescens* (Order Hemiptera, Family Reduviidae) and the palms presence has been positively linked with disease risk (Whitlaw and Chaniotis 1978; Christensen et al. 1980). *Rhodnius pallescens* is hematophagous and feeds from a variety of sylvatic and domestic vertebrates including humans. One particular taxonomic group, mammals, serve as both blood meals and predators (i.e. via grooming) of *R. pallescens*, as well as reservoir hosts for the etiological agent of Chagas disease, *Trypanosoma cruzi*. *Trypanosoma cruzi* transfers between vertebrate host and vector primarily via contact with infected vectors and their feces (Romaña et al. 1999b; Whitlaw and Chaniotis 1978). Given these conditions, palms serve as replicate communities across varying degrees of deforestation with which to address multiple ecological drivers of Chagas disease. Previous studies have pointed out that gradients of deforestation are associated with an increase in *R. pallescens* abundance and infection with *T. cruzi* (Gottdenker et al. 2011; Gottdenker et al. 2012). I investigate the mechanisms driving this pattern and hypothesize that an increase in abundance and infection is attributed to community and microenvironment conditions within the palm crown.

In Chapter 3, I investigate the *Attalea* palm crown to determine associations between land use disturbance and community assembly. The objective was to determine whether community assembly and the food web network within the *Attalea butyracea* palm crown is influenced by land use types characteristic of central Panama: pasture, peridomestic, and forest fragments and local scale environmental variables such as palm crown microclimate and microhabitat conditions. We tested the hypotheses that palm crowns in increasingly disturbed sites will have decreased species richness and an altered community structure such as higher network connectivity (higher connections due to increased generalist species in disturbed sites), as well as an increased presence of omnivores, and a decrease in invertebrate predators. I accessed palms using various climbing techniques and the sampled the invertebrate (and indirectly the vertebrate) species community. All individuals were stored in 95% ethanol and later identified to recreate the palm crown food web. Overall, results indicate that land use disturbance does alter communities but via shifts in structure and function rather than disassembly of the community.

In chapter 4, I incorporate the palm crown community metrics and microenvironment results from chapter 3 to determine whether such factors influence the Chagas disease vector, *R. pallescens,* abundance and infection with *T. cruzi*. We tested the following hypotheses that *R. pallescens* abundance is driven by an increase in palm crown microhabitat complexity (i.e. greater number of leaves, dead organic matter, etc.) associated with optimal microclimate conditions of temperatures between 25-28 C and average RH of 70% (Luz, Fargues, and Grunewald 1999; Okasha 1964) and an increase in vertebrate blood meals and decrease in invertebrate predators. Additionally, that infection with *T. cruzi* is driven by a decrease in overall community diversity (i.e. potential for dilution of pathogen transmission due to non-competent hosts (Kathleen LoGiudice et al. 2003a; Ostfeld and LoGiudice 2003). I focused on food web network characteristics, in particular network generality and vulnerability, which refer to the proportion of predator and prey species, to determine whether community-level effects can transcend to scales and specifically impact *R. pallescens* and infection via means of indirect (and direct) pathways. Across central Panama*,* *R. pallescens* were captured and tested for *T. cruzi* and blood meals were investigated to determine vertebrate species fed upon within the palm crown. A generalized linear mixed effects model was performed to determine the effect of multiple explanatory variables on *R. pallescens* abundance and infection with *T. cruzi*. Results indicated that host and predators communities, as well as microhabitat conditions influence *R. pallescens* abundance and infection with *T. cruzi* and demonstrate that community-level characteristics are a contributing factor to variations in multi-host vector-borne pathogen transmission. Determining such drivers can help implement feasible ways of *R. pallescens* vector control in rural regions of central Panama, such as palm crown management.

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CHAPTER 2

NETWORK APPROACH TO DETECT INDIRECT EFFECTS ON PATHOGEN TRANMISSION[1]

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ABSTRACT

Indirect interactions are prevalent in ecological communities and their effects have varying consequences on the transmission of pathogens. Although indirect interactions are often analyzed in more discrete interaction-specific community modules, it may lose the context within which these interactions exist in the real world. Community networks in the form of food webs have been increasingly used in disease ecology to demonstrate how parasites incorporated into a community framework reshape our understanding of parasite transmission. We expand on the food web network approach in disease ecology as a tool to investigate indirect pathways of pathogen transmission in a larger community context. We review literature regarding indirect interactions and their impacts on pathogen transmission and use the Attalea palm crown community as a model food web to address the effects of 'peripheral species' (species part of ecosystem food webs that are not directly involved in pathogen transmission) on disease transmission. The *Attalea* palm is associated with the disease vector *Rhodnius pallescens* and its hosts, mammalian vertebrates. The palm serves as a unique mesocosm for both vector, host, and invertebrate/vertebrate species community. Using the *Attalea* palm-Chagas disease model, we apply hypothetical scenarios to investigate how incorporating these species in the form of a food web network can expand how we view indirect and direct interactions and their consequences on parasite transmission.

KEYWORDS Indirect effects, Pathogen transmission, Food webs, Network ecology, Vector-borne disease.

2.1 INTRODUCTION

Indirect effects are defined as the impact of one species on another mediated by the presence of an intermediary species (Wootton 1994**)**. Existing evidence suggests that these effects can play critical roles in shaping parasite transmission in animal and plant communities, because indirect interactions are ubiquitous across ecosystem networks and should therefore not be overlooked. However, many approaches only incorporate the indirect effects stemming from the immediate surrounding species. We review the range and diversity of indirect effects described within the existing disease ecology literature and apply concepts from ecological networks to investigate effects driven by community-wide interactions. We also discuss the applications of a network approach in real world systems (i.e. biocontrol in agriculture). Lastly, we apply a network framework to illustrate effects of indirect interactions on disease transmission using a multi-host vector-borne parasite, *Trypanosoma cruzi*, cause of Chagas disease in humans, as a model system. We will not be focusing on parasite-mediated direct and indirect effects as this has already been reviewed extensively (Hatcher, Dick, and Dunn 2006) and because parasites can also directly and indirectly play a role in their own transmission across hosts (i.e. modify host behavior). Rather, we focus beyond the parasite-host-vector community and consider the effects of other species within the larger ecological community where pathogen transmission takes place using a network approach in the form of food webs. This holistically conceptual approach to understand risks that the non- host, vector, or pathogen species has on parasite transmission have potential applications for infectious disease management or surveillance.

2.2 Indirect Interactions and pathogen responses

We define an indirect effect in parasite/pathogen transmission as when a parasite's ability to infect its host(s) is influenced by a third (or more) species outside the parasite - host linkage. This third species can either elicit a change in host or parasite density (density-mediated indirect effect) or host/parasite trait (e.g. behavioral or morphological; trait-mediated indirect effect or interaction modifications). Two types of indirect interactions commonly referred to are *interaction chain* and *interaction modification*. An *interaction chain* refers to a series of direct interactions between species that are connected by an intermediary species (Strauss 1991). In the simplest case of a parasite interaction chain, a species within the community indirectly influences a parasite by changing the density or traits of the parasite's host or hosts. For example, a predator species indirectly influences the transmission dynamics of a parasite by changing the density of its prey (also the parasite's host). So, when a predator consumes a prey, it reduces the density of hosts available to parasite infection. This is demonstrated in the "Healthy Herd Hypothesis", where predators selectively consume weakened and parasitized individuals, thereby keeping the remaining population healthy by reducing the number of interactions between a parasite and host (Packer et al. 2003)**.** This has been found in both aquatic and terrestrial systems in which predators can indirectly help prevent the spread of disease (Hudson, Dobson, and Newborn 1992; Duffy et al. 2005)**.**

An interaction modification (sometime referred to as a trait-mediated indirect) arises when the trait of a host is altered (e.g. morphological or behavioral) in response to the presence of, or interaction with, another species within the community (i.e. a predator) (Wootton 2002; 1994)**.** An example are predator-avoidance mechanisms, in which a prey/host responds to a potential predator by reducing activity or altering body size (Van Buskirk and Yurewicz 1998; Semlitsch 1990). Some larval anurans decrease their activity when exposed to various aquatic predators (i.e. fish and larval-staged dragonflies) in mesocosm experiments (Thiemann and Wassersug 2000; Rohr et al. 2015; Orlofske et al. 2014; Raffel et al. 2010). Additionally, prolonged predator exposure had driven changes in body morphology in *Rana clamitans* and *Pseudacris regilla* (Relyea 2001). A reduction in tadpole activity and changes in tadpole development was associated with increased parasite infection (Thiemann and Wassersug 2000)**.** Habitat selection behavior by prey/host is another example of avoidance mechanism. In the Daphnia system, Daphnia select habitat along the water column which is driven by a tradeoff between both anti- predator and parasite response behavior. Daphnia that reside higher along the water column are more exposed to predators, while Daphnia that remain closer to the sediment are more exposed to parasitic spores

(Decaestecker, De Meester, and Ebert 2002). Beyond the two main types of indirect interactions, indirect effects can be further distinguished by their context within the ecological community. These include variations of interaction chains and interaction modifications (Table 2.1). In the following sections, we will discuss these community specific cases and the types of indirect effects that arise in relation to parasite transmission.

Intraguild predation

When competing species that share a resource also consume each other, they are demonstrating intraguild predation (G A Polis, Myers, and Holt 1989; Robert D. Holt and Polis 1997). In theory, intraguild predation (IGP) can occur between any species competing for a shared resource that belong to the same guild (although their interactions are asymmetric). IGP combines the interactions of both predation and competition and is considered prevalent across various ecological systems. In the context of parasite infection, a predator "competes" with parasites for a shared resource (i.e. the host) but can also consume the parasite simultaneously when it consumes the host (Borer, Briggs, and Holt 2007). For example, in an aquatic mesocosm experiment, the intraguild predator dragonfly larvae can consume both trematode parasite (*Riberoia ondatrae*) and tadpole host (Rohr et al. 2015). In a terrestrial agricultural system, parasitized aphid species can also be consumed by predators (i.e. coccinellidae) (as discussed in Müller and Brodeur 2002). However, the overall impacts of IGP on parasite-host interactions are variable and can be a consequence of the study system (i.e. species richness, function, and environmental variability) and can either decrease or increase parasite transmission, as demonstrated in (Orlofske et al. 2012; Rohr et al. 2015; Müller and Brodeur 2002). Referring back to the mesocosm experiment in Rohr et al. 2015 using tadpole hosts, cercarial parasites, and their odonate predators (i.e. dragonflies and damselflies), intraguild predation between the dragonfly and parasite failed to reduce tadpole infection by a parasitic cercariae because the dragonfly consumed healthy individuals instead of consuming infected individuals. This reduced the dragonfly's ability to decrease contact rate between parasite and host. The mechanism here depended on prey selection (infected vs. uninfected) by the dragonfly and predator-mediated response by the tadpole host (trait and behavior modification of tadpole to dragonfly). Additionally, the effects of biocontrol on pest communities can be dampened by IGP among multiple introduced predators as discussed in Müller and Brodeur 2002.

Trophic cascade

Effects that spread across multiple trophic levels within a community and are mediated through consumer-resource interactions resembles a trophic cascade. Trophic cascades are conventionally perceived as traveling down the food chain whereby the effects of top-trophic level species loss propagate down to lower trophic level species (Ripple et al. 2016; Gary A Polis et al. 2000). Top down trophic cascades are predator-driven, whereas bottom-up cascades are resource-driven (Hunter and Price 1992).

Top-down trophic cascade

Cascading effects generated at high trophic levels can indirectly influence the interactions between parasite and host. Some trophic cascades have been initiated or enhanced by anthropogenic disturbances because they are associated with a decline in vertebrate predator populations (i.e. top-trophic level species) in which predators were intentionally removed or a population suffers from loss of their habitat or decline in habitat quality (as discussed in Pace et al. 1999). As a result of predator loss, prey densities can increase and then succumb to density-dependent diseases. For instance, in the purple urchin (*Strongylocentrotus purpuratus*) populations in the Channel Islands of Southern California, overharvesting of the urchins' predators such as the large spiny lobster (*Panulirus interruptus*) and the sheephead (*Semicossyphus pulcher)* resulted in denser purple urchin populations. Denser urchin populations then suffered a higher mortality caused by the bacteria *Vibrio* (Lafferty 2004). In terrestrial systems, a reduction in rodent predator populations was tied to a potential increase in rodent-borne zoonotic disease agents (Ostfeld and Holt 2004). As rodent predations decline, higher rodent densities increase exposure rate of rodent-borne disease agents which can pose a risk as spillover to humans (Mills et al. 1999).

The impact of trophic cascades on disease dynamics can also depend on environmental conditions. In the *Aedes* mosquito vector-dengue virus system, Aedes larval and adult stages take place in both aquatic and terrestrial environments, respectively. While their population dynamics are vulnerable across environments and developmental stages, Weterings, Umponstira, and Buckley (2018) described that *Aedes* mosquito population dynamics in Thailand are controlled by the predator community. The impact of the predator community as biocontrol agents on Aedes was influenced by trophic cascades which in turn was dependent on landscape conditions.

Bottom-up trophic cascade

While several examples of bottom-up trophic cascades can be identified, a common example referred to in the context of disease ecology is resource supplementation. Resource supplementation (i.e. wildlife feeding, agricultural run-off) can be traced along trophic levels in a bottom-up trophic cascades which can directly influence host space use, body condition and immune response traits, which in turn can change host-parasite dynamics (Becker Daniel J. and Hall Richard J. 2014; Pulkkinen and Ebert 2004; Bradley and Altizer 2007; Becker, Streicker, and Altizer 2015; Suzán et al. 2015)

For example, resource provisioning can lead to host aggregation which can increase density-dependent disease transmission across hosts (Krasnov, Khokhlova, and Shenbrot 2002; Krkosek 2010; Murray et al. 2016). Resource provisioning can also indirectly affect host-parasite dynamics by changing the density and/or traits of the predators, competitors, and/or parasites of the host (Civitello et al. 2018; Murray et al. 2016). Furthermore, particular species that respond positively to resource supplementation or pulsed resources (i.e. seasonal variations in resources) can ultimately dominate in abundance in these communities and as a result influence the overall community composition and structure (Galbraith et al. 2015; Murray et al. 2016)

Lastly, other evidence also demonstrates that bottom-up and top-down work simultaneously. In the extensively studied multi-host-*Ribeiroia ondatrae* trematode disease system, agricultural run-off facilitates a bottom-up trophic cascade because it increases food resources for the intermediate snail host and increased snail density is positively associated with tadpole infection (Rohr et al. 2008; Pieter T. J. Johnson et al. 2007). Alternatively, other resource-level characteristics, such as resource quality (i.e. leaf-litter nutrient content), has been demonstrated to propagate effects via multiple pathways working simultaneously by directly affecting hosts and facilitating indirect predator-mediated effects (P. R. Stephens et al. 2016; J. P. Stephens et al. 2017; Stoler and Relyea 2013).

Life-History and Exploitative Facilitation

When two species are exploiting the same resource (for example, parasite and predator exploit the same host/prey) those two species are indirectly competing with each other (exploitative competition) or in some cases benefiting from one or the other (exploitative mutualism) (Matsuda, Abrams, and Hori 1993). While exploiting the same resource is conventionally viewed as a competitive interaction, some evidence also finds exploiting the same resource as facilitative (i.e. life-history facilitation). In other words, instead of indirectly reducing the density of a competing species by reducing the density of the shared resource, the resource (host) is attacked at different life stage in that it facilitates the consumption/infection at later stages by a subsequent predator or parasite. For example, host susceptibility to predation increases after exposure to a pathogen because of a compromised immune system, energy allocation, or changes in behavior (Ramirez and Snyder 2009). Alternatively, susceptibility to pathogens can increase after exposure to predators as observed in some systems such as the herbivorous beetle (*Leptinotarsa decemlineata*) (Ramirez and Snyder 2009). Or systems where exposure to parasites may influence the susceptibility to other parasites such as in field vole (*Microtus agrestis*) populations (Telfer et al. 2010). In the Daphnia system, predator-induced defenses changed Daphnia morphology however, these morphs were also more vulnerable to infection by a yeast parasite (Yin et al. 2011)

Apparent competition

Multiple prey species can sometimes indirectly depress each other's populations by increasing the abundance of a shared natural enemy (Robert D. Holt 1977). When a shared natural enemy is a parasite or pathogen, a highly infectious host can reduce the number of other, more susceptible hosts within the community (Power and Mitchell 2004). For example, variations in host community competency can influence the persistence of disease because if highly competent hosts dominate a community, then there will be a higher transmission risk and potential for spillover to other species (P. T. J. Johnson and Thieltges 2010; Pieter T. J. Johnson et al. 2013; Keesing, Holt, and Ostfeld 2006; Ostfeld and Keesing 2000b; 2000a; LoGiudice et al. 2003; Power and Mitchell 2004). In particular, if a host species amplifies a vector or pathogen, it can increase the risk of disease transmission to the remaining susceptible hosts. In a study conducted on host community diversity and the tick-borne louping ill virus, it was demonstrated that combinations of hosts influenced virus persistence (Gilbert et al. 2001). The 3-host community consisting of deer, hare, and grouse in upland Britain varied in vector and parasite competency which "led to" an apparent competition between hosts. Deer amplified the tick vector, grouse amplified virus, while hare amplified the tick and virus. Combinations of hosts and their density affected the persistence of the louping ill virus in grouse, which alone suffers high virus-induced mortality. In aquatic systems, the exotic brown trout is an asymptomatic host to the protozoan *Myxobolus cerebralis*, yet native trout in the western US can suffer a population decline in response to the protozoan, reducing competition for the exotic brown trout and facilitating disease spread (see Hay et al. 2004). Apparent competition has also been observed in plant systems in which host-specific variations in disease transmission drives disease severity, rather than host susceptibility (Cobb, Meentemeyer, and Rizzo 2010). Within tree communities of the California coast redwood forests, sudden oak death (SOD) is caused by the pathogen *Phytophthora ramorum* and affects a variety of tree species including oaks (*Quercus spp*.) and bay laurel (*Umbellularia californica*). Although both hosts are equally susceptible to SOD, apparent competition among tree species results in a greater mortality among tanoak species in contrast to bay laurel. A positive feedback by resistant bay laurel increases their densities which sustains the SOD pathogen and can ultimately change the overall tree composition within the affected regions.

2. 3 EXPANDING ON INDIRECT EFFECTS – A NETWORK APPROACH

The aforementioned indirect effects cover some of the major pathways of non- host, vector, parasite species and the impacts they have on disease dynamics. Overall, it points out that certain types of pathways are more commonly acknowledged when discussing indirect effects and disease. For instance, interactions such as predation and competition, which are considered to be “negative” interactions, are regarded to have a particularly strong impact on community structure and dynamics and therefore receive considerably more attention (Stier et al. 2016; Sih et al. 1985; Pieter T.J. Johnson et al. 2010; Hatcher, Dick, and Dunn 2006; Bruno and Cardinale 2008). Other interactions, such as facilitative interactions, are also investigated less despite evidence of their significance (Stachowicz 2001; Bruno, Stachowicz, and Bertness 2003; Bertness and Callaway 1994; Stanton 2003). This general bias for negative interactions can possibly be explained by their potential in applied methods for controlling diseases, such as biocontrol in agricultural systems (R. D. Holt and Hochberg 2001). Another observation is that communities are often simplified into modules or motifs (a subset of species within a community) which is a method to reduce complexity (as demonstrated in R. D. Holt and Hochberg 2001; Baiser, Elhesha, and Kahveci 2016). These modules typically portray an interaction triad containing the parasite, vector and host, or/and sometimes an intermediary species, or resource. While this approach is ideal for analyzing isolated mechanisms or to use as a proxy for larger communities (i.e. Brose, Berlow, and Martinez 2005), it can be taken out of the community context within which these interactions exist. A deeper investigation into whole communities that involve non-host and non-predator species can offer additional insight into indirect interactions only possible when incorporating a larger community breadth as outlined by (Pieter T. J. Johnson, Ostfeld, and Keesing 2015; P. T. J. Johnson, de Roode, and Fenton 2015).

Diseases viewed in a network framework

Food web modules, which are used to represent whole community interaction networks, are commonly assembled by nodes (species) that are connected by links (interactions) and are used to trace bioenergetic flows or other characteristics of interest (i.e. biomass) (Fath and Patten 1999). Food web modules can further be used as an essential tool to investigate both indirect and direct interactions (Borrett, Whipple, and Patten 2010; Patten 1995; Jordán and Scheuring 2004), particularly because of the unique visualization it provides of the community structure and trophic composition. More recently, food webs have been used to demonstrate how parasites are embedded in complex community webs and are an essential component in determining trophic relationships (Lafferty et al. 2008; Poulin 2010) as well as the shaping of communities which, in turn, are shaped by the species community itself (Poulin 1999; Hatcher, Dick, and Dunn 2006; Lafferty et al. 2008; Chen et al. 2008; Sander, Wootton, and Allesina 2015; Dunne et al. 2013). We expand on the growing use of networks on disease ecology by applying a food web network approach to a vector-borne multi-host parasite system Chagas disease.

Chagas Disease as A Study System

The Chagas disease system in central Panama is an ideal study system with which to apply a food web approach because the palm crown can be viewed as an ecosystem unit that has defined boundaries and supports the existence of *R. pallescens* vector- *T. cruzi* parasite- vertebrate host within a larger community network. Chagas disease is caused by the protozoan parasite *Trypanosoma cruzi* which is transmitted by the triatomine vector (Family Reduviidae). In central Panama, the primary vector, *Rhodnius pallescens*, is associated with the crown of the royal palm *Attalea butyracea* (Whitlaw and Chaniotis 1978; Christensen et al. 1980). The palm crown supports a diverse invertebrate and vertebrate species community that acts as a unique arboreal mesocosm *in situ*. *Rhodnius pallescens* feeds from a variety of vertebrate hosts, with taxa ranging from mammalian to reptilian species (Kieran et al. 2017; Pineda et al. 2008; Vasquez et al. 2004). The transmission of *T. cruzi* occurs when a host comes in contact with contaminated vector feces (which can occur while *R. pallescens* takes a blood meal from a host) or during consumption of the vector by the host during activities such as grooming.

We examine the food web of the multi-host vector-borne Chagas disease study system to explore how the perception of parasite transmission is influenced by the community network and the structure of direct and indirect interactions surrounding the *R. pallescens* vector, and the consequences it has on parasite transmission. We explore hypothetical examples of the palm crown community to investigate various responses by the parasite *T. cruzi* to these various potential direct and indirect (trait and density - mediated) pathways that incorporate all species (basal to top trophic levels). This approach has implications for revealing potential underlying mechanisms of vector-borne disease transmission that may otherwise be overlooked (Sander, Wootton, and Allesina 2015). Viewing the palm community as a web also helps visualize the extent of the species interaction diversity, structure, and interconnectedness as it potentially exists in the real world and how species outside the main host- vector- parasite triad influences the transmission of this multi-host vector-borne pathogen.

We used data based on preliminary research collected from 5 felled trees in 2013 (*unpublished data)* and reconstructed a food web network using the software Network3D developed by Yoon et al. 2004. The output, a generalized hypergraph, shows a general palm crown community with the species represented as nodes connected by consumer relationships (links) that are structured hierarchically to resemble various trophic levels (Figure 2.1 A-E). Feeding relationships were determined by field observations and literature on natural history. *Rhodnius pallescens* directly interacts with its blood meals (vertebrates) and invertebrate and vertebrate predators (which can also be hosts) (Figure 2.2). Using this simple food web, we can initially observe that increasing the node degree of the host-vector-predator relationships to incorporate indirect effects quickly incorporates the entire community of the crown, making an initial suggestion of the high interconnectedness within the crown (Figure 2.3). We can also hypothetically identify individual indirect effects that occur (i.e. apparent competition etc.) as it exists simultaneously with other interaction types and its influence on shaping the outcome of pathogen transmission using hypothetical scenarios (Table 2.2) and gives examples of tracing particular indirect interactions to basal or intermediate trophic level species, which tend to be overlooked in disease interactions webs. Perhaps most importantly, the web can be used as a tool to generate hypotheses for future research regarding species interactions and pathogen transmission.

How can food webs change the way parasite transmission is viewed?

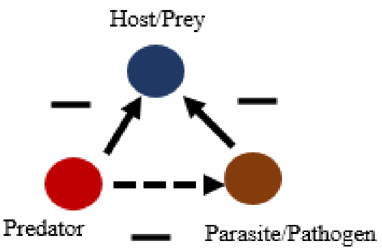
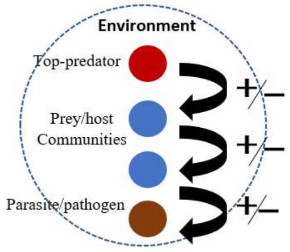
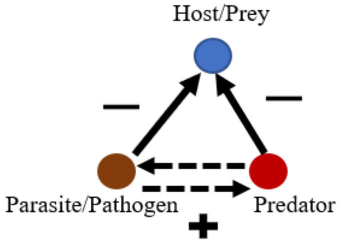
In this simple palm crown network, we can observe that indirect interactions do not exist in isolation, as outlined in Figures 2.1 and Table 2.2, where degrees of separation between nodes is low and because a pathogens involvement in many linkage pathways across hosts and non-hosts can make them more susceptible to community-wide changes. However, this observation is likely specific to small mesocosms, such as palm crowns, where the overlap of species occurrences can be high due to the unique structure and general heterogeneity of the *main* body of the crown. In larger more vast communities, effects of isolated indirect pathways may be dampened as the links between species lengthens (Abrams et al 1996). The palm crown network can also change the perspective of transmission outcomes and acknowledge alternative routes of trophic transmission. In an intimate community setting such as the palm crown, alternative routes of transmission (mammalian host species overlap in the crown) may be more easily observed. Based on Table 2.2, various trophic species overlap in interactions multiple times, indicating that alternative pathways may exist, which have potential repercussions in *T. cruzi* response. Alternative routes of transmission can also be identified in a network framework such as dead-end hosts, or other hosts with varying degrees of competency. Because consumption of parasites is not uncommon, they can be transferred across trophic levels through various ways (i.e. passive or active consumption). Lastly, food web networks can allow you to investigate changes in species composition and the impacts they may have on pathogen transmission. For example, seasonal changes in species abundance or local extinctions can remove species (nodes) or add nodes and change the structure of the food web. Trophic structural changes can also influence indirect interaction pathways that can be traced more easily in a network framework. This may be particularly important because habitat disturbance can have drastic changes on species communities and therefore its network.

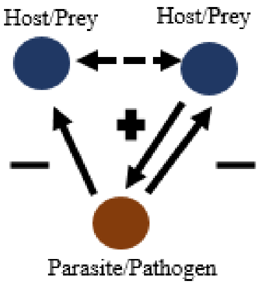
2.4 CONCLUSION

Acknowledging indirect interactions in a community is essential, particularly when those effects impact the transmission of a vector-borne pathogens. Food web networks have been utilized to study parasite transmission within a community context and can be further used as a tool to identify how indirect and direct effects, stemming from the surrounding species community, influence pathogen transmission. Although focusing on single interactions and their effects on pathogens reduce the complexity of studying entire communities, it isolates the interaction from the surrounding community context and, as a consequence, it may fail to acknowledge underlying mechanisms, or other indirect controls on transmission. In our example, we are able to visualize and identify how other non -host, vector, parasite and the immediately surrounding species and potentially impact pathogen transmission through hypothetical indirect and direct effect scenarios. It also suggests that the transmission of *T. cruzi* may can be influenced by a broader range of species other than reservoir host composition and allows us to generate hypotheses for future research questions. This study also demonstrates that researching diseases out of the context of its community can have negative consequences for the development of vector control and disease prevention. While increasing studies acknowledge the importance of addressing species communities in disease research, the time and effort to conduct such studies can be daunting.

2.5 TABLES AND FIGURES

Table 2.1. General overview of indirect interactions and examples of pathogen responses.

	INDIRECT EFFECT ON PARASITE	**MECHANISM**	**Pathogen Response**	**EXAMPLE**
	**INTRAGUILD PREDATION**	*Predator-mediated:* Predator consumes both host and parasite (competitor).	Negative (especially if the predator is a dead-end host)	Predator (dragonfly) competes with parasite (*Ribeiroia ondatrae)* for a shared resource (tadpole). *Orlofske et al. 2012; Rohr et al. 2015*
	**TROPHIC CASCADE**	*Top trophic-level predator or resource-mediated:* Effects transcend multiple trophic levels	Positive or Negative	Impact of predator community on the *Aedes* mosquito – Dengue virus transmission is dependent on the degree of landscape disturbance *Weterings, Umponstira, and Buckley 2018*
	**EXPLOITATIVE/LIFE HISTORY FACILITATION**	*Predator or parasite - mediated:* Exposure to predator/parasite facilitates exposure to subsequent predator/parasites	Positive	Initial exposure of Daphnia to a predator (i.e. fish) or pathogen facilitates predation or infection by the other (Yin et al. 2011b)

	**APPARENT COMPETITION**	Host species negatively impact each other by amplifying a shared pathogen/parasite	Positive	Invasive grey squirrel amplifies parapoxivirus which is detrimental to native red squirrel in the UK. *(Tompkins, White, and Boots 2003)*

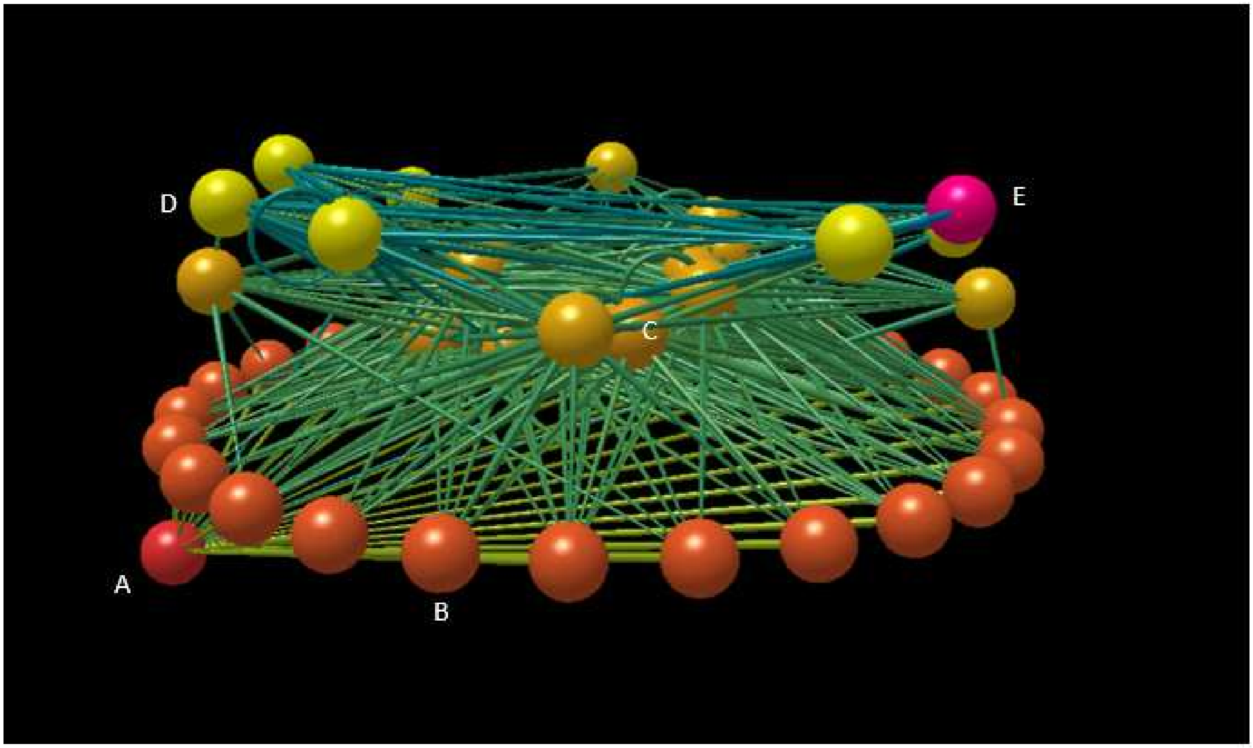


Figure 2.1. The Attalea palm crown community network (A-palm; B – herbivores (i.e. beetles); C – omnivores/low trophic level predators; D – omnivores/high trophic level predators). *Rhodnius pallescens* is represented by the pink node (E).

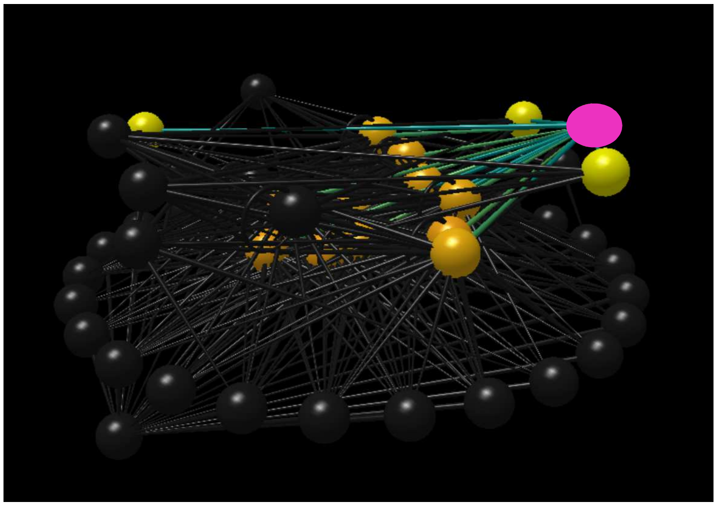


Figure 2.2 Direct linkages between *R. pallescens* (pink) high trophic-level blood meals (yellow) and arthropod predators/mid-trophic level blood meals (orange). These linkages represent consumer-resource relationships with *R. pallescens*.

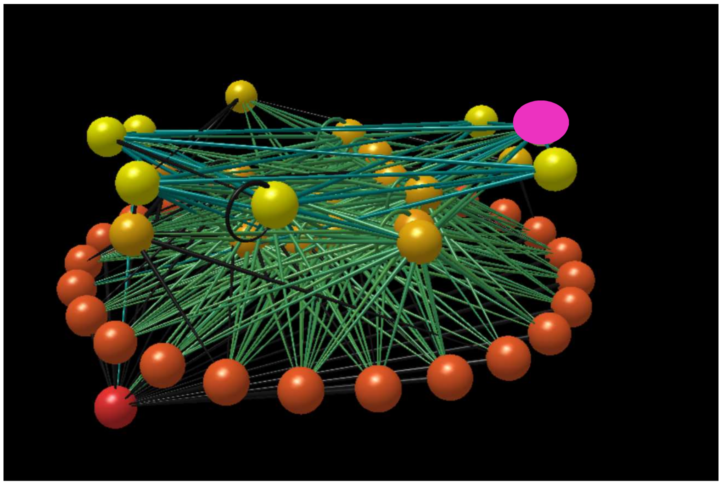


Figure 2.3. Indirect linkages with *R. pallescens*. The secondary node degree from *R. pallescens* (pink) involves all species present in the palm crown.

Table 2.2 The Attalea palm crown food web, direct and indirect effects of the food web and hypothetical outcomes of *T. cruzi.*

Trophic level	Trophic species	Interaction with *R. pallescens*	Mechanism	Hypothetical *T. cruzi* transmission response	Network 3D Reference Letter
Basal	Attalea palm	Indirect	Provides shelter to the hosts	+	A
Top	Humans	Indirect	Habitat modification of palm crown alters microhabitat/microenvironment and host availability	+ or -	NA
Top	Vertebrate hosts	Direct	Predation/accidental ingestion of *R. pallescens* while grooming	-	C/D-E
Top	Vertebrate hosts	Indirect	Inter-intra specific competition for resources		C-D
Top	Vertebrate hosts	Indirect	Predation (not *R. pallescens*)	+	C-D
Top	Vertebrate hosts	Indirect	Modification of palm crown (i.e. nest building)	+/-	D
Mid	Arachnid predators	Direct	Predation of *R. pallescens*	-	C-E
Top/Mid	Invertebrate predators	Indirect	Intraguild predation	+	C-C, C-D, D-D
Top/Mid	Generalist	Indirect/direct	Interference/exploitative competition: Competition for shared resources and/or shared natural enemies induce behavioral changes	+	B-C-D
Top	*R. pallescens*	Direct	Life history facilitation Avoidance behavior at different life stages may decrease questing behavior	-	E-D
Top-low	All	Indirect	Trophic cascade		B-C-D
Basal	Herbivore/Omnivores	Indirect	Apparent mutualism lessened predation pressure by presence of alternative prey	+	B-C-D
Basal	Herbivore/Omnivores	Indirect	Apparent competition Increase risk of predation by a shared predator	-	E-B
NA	*R. pallescens*	Indirect	Mutualism	+	

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CHAPTER 3

IMPACTS OF LAND USE ON ANIMAL COMMUNITIES IN ARBOREAL MESOCOSMS: A NETWORK APPROACH[2]

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[2] Varian, Christina. To be submitted to Food Webs.

ABSTRACT

Anthropogenic disturbance is broadly associated with influencing community diversity, composition, and trophic structure across tropical marine and terrestrial ecosystems. These community-level effects can have repercussions on ecosystem services such as protection from infectious disease, in part due to both loss of natural habitat and declines in biodiversity. Although studying impacts of disturbance on species communities within natural settings as well as well distinguished mesocosms outside of controlled environmental conditions can be difficult to observe, these studies can provide valuable insight on natural community responses to ongoing land use changes. We studied the impacts of a land use disturbance gradient on the species community diversity, and network structure, of the *Attalea butyracea* palm crown across central Panama and made inferences of both spatial and environmental effects on community assembly and species co-occurrences. We hypothesized that increasing disturbance will drive an overall decrease in community diversity and a shift in both community structure and function. We collected 2952 specimens from 49 palm crown communities across forest fragments, peridomestic, and pasture sites across 3 locations within central and west-central Panama using a combination of canopy community sampling techniques and identification of vertebrate species in the palm based on direct observation of animals, animal sign, and molecular identification of blood meals taken by hematophagous triatomine bugs. Community composition varied as a function of land use type, but community diversity and the number of nonsignificant species co-occurrences stayed relatively the same across different habitats. Analysis of the food web network also suggests that some feeding guilds did vary significantly. Also, while investigation on the community assembly processes suggests that environmental filtering is a major underlying mechanisms that influences variation in community composition across land use types. These findings indicate that land use disturbance can influence communities outside of taxonomic diversity but can also influence palm crown community function. Understanding how these palm crown communities respond to disturbance has larger implications for land use management, particularly in relation to control

of the Chagas disease insect vector which primarily inhabits the *A. butyracea* palm crown across central Panama.

KEYWORDS: Arboreal communities, Community ecology, Network ecology, *Attalea butyracea*

3.1 INTRODUCTION

Land use change is a major cause of biodiversity loss influencing the number of species, species composition and abundance (community diversity) as well as alter feeding relationships (trophic structure) within a community (Turner 1996; Takano et al. 2014; Allan et al. 2019), particularly within the tropics (Martinez et al 2009, Gibson et al 2011). In the face of unprecedented rates and degrees of land use change, understanding community-level responses to anthropogenic disturbance can help identify not only the changes in community diversity and food webs but also the underlying mechanisms that influence patterns in community assembly which ultimately drive ecosystem functions, particularly ecosystem services regarding human and animal welfare such as protection from infectious disease transmission. A reduction in habitat suitability for a species with a low tolerance for habitat disturbance can lead to a reduced community diversity and more homogenized community composition dominated by habitat generalist species that have a higher capacity to exploit a wide range of environmental conditions and resources (see ecological niche Hutchinson 1957, Clavel, Julliard, and Devictor 2011; Futuyma and Moreno 1988; Devictor, Julliard, and Jiguet 2008; McKinney and Lockwood 1999). Such shifts in community composition are reportedly widespread and support for more tolerant species over "specialist" species diversity in response to disturbance has been observed across a variety of terrestrial systems including mammal, bird, amphibian, and arthropod communities (Devictor et al. 2008, 2007; Lea, Luiselli, and Politano, n.d.; McIntyre et al. 2001, Prist, Michalski, and Metzger 2012).

Alongside shifts in animal community composition, trophic structure can also be impacted by land use changes. Larger vertebrates are particularly vulnerable to habitat fragmentation (Prist, Michalski, and Metzger 2012; Cardillo et al. 2005, Urquiza-Haas et al. 2009, Pimm et al 1988) and habitat disturbance is associated with a decrease in invertebrate and vertebrate predator species, resulting in a loss of high trophic level consumer diversity (Holt et al. 1999, Cagnolo 2009, Gibb and Hochuli 2002). Predator absence from fragmented sites can have cascading indirect or direct impacts on lower trophic level species densities via shifts in predator-prey dynamics (Duffy 2003; Dobson et al. 2006, Dorresteijn et al 2015) resulting in shifts toward an herbivore-dominated trophic structure concomitant with simplified landscapes (i.e. Enemy Hypothesis; Root 1973, also see Dorresteijn et al 2015). However, lower trophic level species communities can be more resilient to disturbance, as some taxa of smaller herbivores, granivores, and omnivores are observed to persist within habitat disturbance gradients (McIntyre et al. 2001, Croci et al. 2008; Evans et al. 2011) better than large-bodied species (Stork et al 2009). In regards to trophic position and size, omnivores, which have a wider diet range, may be less impacted by disturbance because of the ability to switch diets and have been found to be equally abundant across all land use types as observed in some invertebrate and vertebrate communities (McIntyre et al. 2001, Gray et al, Silva et al 2016).

Shifts in species composition (trophic and non-trophic) can also influence the structure of community networks **(**Gonzalez, Rayfield, and Lindo 2011, Morris Rebecca J. 2010). In trophic networks (i.e. food webs) species are represented by nodes that are connected by links which can represent a variety of interaction types. As habitat fragmentation reduces the occurrence of particular taxonomic groups, it can also reduce network size and complexity (Valladares, Cagnolo, and Salvo 2012). Network complexity is the number of links in a network which can be measured using the conventional metrics Connectance (L/S^2), the proportion of realized interactions among all possible ones (May 1972, 1973), and Linkage Density (L/S), the average number of links per species (Pimm et al 1991). These metrics indicate the degree of connectedness between species within a community and even indicate species generalism (species feeding from multiple links) as they interact closely with most other species (Gonzalez et al 2010). Disturbed habitats may show an increase in generalist species and therefore an overall greater community network connectance. Recent studies have demonstrated that habitat fragmentation is linked to an increase in connectance (Valladares, Cagnolo, and Salvo 2012; Hagen et al. 2012), attributed to the changes in the proportion of generalist to specialist species (Dunne 2006). However, alternative evidence reports that connectance can either increase or decrease in response to disturbance (Heleno, Devoto, and Pocock 2012; Tylianakis et al. 2010), thus continued investigation is needed.

The previous evidence suggests that habitat disturbance can influence both community composition and structure, however determining whether response in communities is indeed a factor of land use change or alternatively a result from random variation (i.e. sampling design) requires a deeper investigation into the mechanistic drivers of community assembly. Similar studies regarding community composition and structure across environmental or spatial gradients stress the importance of differentiating whether ecological processes, such as niche (deterministic) assembly processes (i.e. environmental filtering or competition) or neutral processes (stochastic or random variation) plays a role in the variation in community response. For instance, based on studies statistically comparing species communities using beta-diversity, communities can be less similar to each other than is expected, suggesting that more stochastic processes such as dispersal or ecological drift are a driving factor; or more similar to each other than is expected, suggesting that deterministic, or niche-based processes are driving community composition and structure. Differentiating ecological process is the underlying mechanism is essential for understanding whether indeed communities respond to environmental changes or whether variation in communities is by chance.

3.2 METHODS

Study location, sites and habitat types

The study was conducted across the central Panama provinces of Panama Oeste and Veraguas. Within these provinces, we specifically chose sites within the La Chorrera (8°52′49″N 79°47′0″W), Capira (8°45′0″N 79°52′12″W), and Santa Fe (8°30′N 81°04′W) districts (Figure 3.1). This region of western and central Panama is characterized as montane and lowland tropical moist forest, respectively

(Holdridge 1967). Santa Fe is the highest site in elevation at roughly 430 m above sea level while La Chorrera and Capira sit at 81 m and 119 m above sea level, respectively. The habitat within these regions are comprised of varying levels of disturbance that consist of agriculture (cattle ranching with cropland), human settlements, and regenerating forest landscapes (Condit et al 2001, Ibanez et al 2002). La Chorrera and Capira are comprised mainly of pastureland for crop farming and cattle grazing, patches of early to mid-secondary forest succession which were previously abandoned pastures, forest remnants, and peri-domiciliary areas. The habitat within Santa Fe was less disturbed and comprised of late secondary growth in addition to pasture and peri-domiciliary sites.

Palms chosen for canopy sampling were selected across a disturbance gradient roughly categorized into peri-domiciliary, cattle pasture, and regenerating forest patches. Palms within peri-domiciliary habitat were located within designated yards (i.e. fencing or evidence of a barrier) in areas of human settlement which were less than 100 meters from a house; cattle pastures were cleared areas designated for cattle grazing; and forest remnants were abandoned pastures undergoing early to mid-secondary succession. Replicate palms from comparable habitats were chosen at each location with a total of 14 palms selected in pasture; 17 palms in peridomestic; and 18 palms in forest fragments, with 49 palms examined in total. For palm sampling selection, palms were scouted for and detected from a main road within each land use type. Further selection was limited by accessibility of the palm crown canopy and climbing safety precautions (i.e. crowns that were too high to reach). In particular, due to the hilly terrain at each location, relatively flat ground was essential for proper sampling by ladder as well as ladder stability. Another limiting factor was the requirement of written permission from the landowners, who were often absent. After these limitations were accounted for, the remaining palms were exhaustively sampled.

Palm crown community sampling

Field data collection

A total of 49 palms were sampled during the wet season (June-July) from 2013-2016 and from June-November 2017, although several palms were also sampled across habitat types during the dry season (Dec.-May) in 2017. Sampling occurred during midday hours of 1100-1600. The palm crown was accessed using a combination of an aluminum ladder and climbing harness with anchored support to the palm trunk using the girth hitching technique. The crown communities were sampled for 30 minutes over 3 consecutive days, although during periods of heavy rains palm sampling would resume on a following dry day. The palm crown was dissected systematically, starting from the removal of the outer older fronds and ending at the center of the crown. Younger fronds, which were stronger and more difficult to remove, were cut at the base and removed using a battery-powered reciprocating saw. Invertebrate specimens were vacuumed using a handheld battery-powered vacuum (BioQuip Products, Inc., Rancho Dominguez, CA, USA) upon detection either during frond removal while in the crown or during "frond beating" and dead organic removal. This involved beating the fronds and extracting dead organic material, allowing all materials to fall on a tarp on at the base of the palm. During frond beating and dead organic removal, a field assistant would collect all invertebrates and place them in a jar containing ethyl acetate. Dead organic material was also collected in a 1- quart sized Ziploc bag and later brought to the lab further to sift for invertebrates with a colander (mesh size 1/32 inches). All invertebrates were later stored in 95% EtOH. Vertebrate signs (i.e. hair, nests, feathers) were also collected as an indicator of vertebrate presence in the community. All specimens were processed at the Smithsonian Tropical Research Institute, Naos station, in Panama City, Panama.

Species identification and food web

All invertebrate species were identified to the lowest taxonomic resolution possible. However, we put a particular emphasis on invertebrate predator species identification. Once identified to the lowest taxonomic resolution, individuals were grouped into morphospecies and trophic species. Trophic species are species that are grouped together because they share the same predators and prey species (Briand and Cohen 1984). A binary feeding matrix was constructed for each palm community. A binary feeding matrix consists of a matrix of species (in both row and column) found in the crown and describes whether the there is a feeding interaction (1) or no feeding interaction (0) between species. Feeding interaction was determined by observations from the field, natural history and literature of consumer-resource interactions for each morphospecies and weighted by species abundance. Food webs were created using the computer software Network3D version 1.0 (Yoon et al. 2004, Williams 2010) and a food web was generated for each palm crown. Network3D measures trophic composition and network complexity and structural characteristics of a given community.

Environmental variables

For each palm crown, we collected the following microhabitat conditions: % surrounding canopy cover (percentage of forest cover measured at 5 m distance from the sampled palm at the four cardinal locations), palm stem height (base of trunk – top of crown (m)), number of connected trees (count of other trees physically connected to the sampled palm), level of dead organic matter (DOM; scale 1 (low) – 4 (high), presence of infructescence (yes/no), and number of epiphytic plants.

Next Generation Sequencing

Captured *R. pallescens* (N=240) underwent gut dissection and blood meal analysis using Next Generation Sequencing to identify vertebrate blood meals fed on by *R. pallescens* through targeting the 12S rRNA gene specific for vertebrates following the protocol outlined in (Kieran et al. 2017). This method was also used to confirm the presence of any vertebrates that were initially detected through signs such as nest, hair, fur or feathers, as well as detect the presence of cryptic vertebrates, found within the palm crown during the community sampling period. Because the main focus of NGS was detecting blood meals of wild animals associated with the *Attalea* palm, blood meal hits from humans, house mouse (*Mus* *musculus*)-the species used in the triatomine traps, or domestic animals were omitted from the final crown food web. For a conservative estimate of blood meal source, we eliminated species hits receiving ≤10% of total read hits for the sample. Only sylvatic vertebrates that can possibly be found in the palm crown were included in the final analysis.

Evaluation of sampling efficiency

A comparison between community sampling techniques was conducted between palm felling and palm 3-day climbing/dissecting. Because it was not feasible to consistently cut down palms in the field (which was the prior technique in 2013) alternative methods were required. Communities collected from 5 felled palms from forest fragment (N = 1; La Chorrera), pasture (N = 1; La Chorrera), and peridomestic (N = 3; Capira) collected in 2013 were considered baseline communities from which to compare the adequate number of sampling days for the dissection technique. Felled palms were thoroughly investigated for approximately 2 hours and across each habitat type. We later compared sample completeness (sample coverage) between felling and 3-day sampling of palms from the same location and season to determine whether sample coverage was roughly the same (package iNEXT, Hsieh, Ma, and Chao. 2019, Chao et al 2014) and to compare the adequacy of 3-day sampling to felling. Sample completeness is based on a mixture of sample-based rarefaction and extrapolation of species accumulation curves (Chao and Jost 2012; Chao et al. 2014)

Data Analysis

Community Diversity and Composition

To determine community assembly and trophic network of the palm crown we quantified species diversity, trophic composition and interactions. We used the measurements: species richness and abundance for each palm (Simpson's Diversity) and compared compositional similarity within palms across all land use types (β-diversity). We further used the null model approach to determine whether β-diversity is an effect of random sampling design or a response to environmental filters (see Myers et al.

2015). We also investigated feeding relationships to infer trophic level and feeding guild composition, network complexity (Connectance, L/S, and Linkage Density L/S^2) and species association patterns (co-occurrences) to inquire on the various community-level response to levels of deforestation. All statistical analysis was performed using the software R 3.5.3. (RStudio Team 2016).

For each palm crown examined, we calculated Simpson's Diversity Index ($D = 1 - (\Sigma (n(n-1)/(N(n-1))$) which is an index of community diversity that evaluates species richness and abundance. We also calculated community dissimilarity (β-diversity) using the presence/absence based Jaccard's Dissimilarity Index for all palm crowns across each land use type (package *vegan*, function 'vegdist'; Oksanen 2019). To examine the effect of land use type on community composition (based on the Jaccard's Dissimilarity outout), we conducted a non-parametric multivariate analysis of variance (PERMANOVA; function 'adonis') and determined whether there is a significant difference in community composition across forest fragment, pasture, and peridomestic locations. Additionally, we examined the homogeneity of the species communities within land use types to account for effects of species dispersal among palms within land use types (ANOVA, function 'betadisper') because significant differences in communities across land use gradients can actually be caused by different within-land use type variation (heterogeneity of dispersal) (see Warton et al. 2012). Community composition across and variation within land use type was also visualized using a nonmetric multidimensional scaling (NMDS) ordination using Bray-Curtis dissimilarity, which further accounted for species abundances.

Environmental variables

In addition to regional effects such as land use type, we investigated effects of local scale palm crown micro- climate and habitat variables on community composition. We used the distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) to estimate how well additional continuous explanatory parameters account for the variation in community distance matrices (i.e. Bray-Curtis) (package *vegan*, function 'capscale'; Oksanen 2019). We looked at a community model constrained by all environmental variables and then proceeded to omit any insignificant variables using forward stepwise regression (function ‘ordiR2step’) (See Myers 2013). We excluded the effect of land use type before analyzing the effects of the rest of the micro- environmental variables to account for the main effect that was previously looked into.

Palm Crown Food Webs – Trophic Dynamics and Interaction Network

The palm crown trophic network was analyzed using the computer software Network3D version 1.0 (Williams 2004, Yoon 2010) and a food web was generated for each palm crown. Network3D measures trophic composition, feeding relationships and network structure characteristics (i.e. species count, links per species, connectance, fraction of each trophic level and guild) of a given community. For each palm, we used species richness, relative abundance and feeding relationships as input data. Of the results, we focused on species richness (species count), and feeding dynamics such as trophic composition (TL1 – primary producer -TL5 quaternary consumer), structure (basal, intermediate, and top species), network complexity: links per species, and connectance (actual links occurring out of the possible links that could occur, and feeding guild (i.e. herbivore, omnivore). We compared the output of each variable across land use type using non-parametric Kruskal-Wallis test to investigate whether trophic variables significantly varied in response to land use disturbance. We also compared community diversity and composition of each trophic level across and within land use types. Detecting trophic responses to disturbance may explain observed variation in community composition across land use type and vice versa or can indicate that they respond independent of each other.

Species Association Patterns

We lastly investigated species association patterns using pairwise co-association across each land use type (package *cooccur*, function ‘cooccur’; Griffith et al 2016). We focused on the count, structure, and composition of association types (positive, negative, and random) and its variation across gradients to determine whether shifts in association occurred as well as the directional outcome of those shifts.

Community Assembly Mechanisms

It is possible to utilize the measurements of community composition (Colwell and Winkler 1984, Gotelli and Graves 1996, Ulrich and Gotelli 2007) to determine whether ecological processes, such as neutral and niche assembly processes influenced our observed β-diversity. Initially, β-diversity can be compared with null β-diversity ("null model approach"; Chase et al 2011) in order to differentiate whether the observed variation in community composition (observed β-diversity) is indeed a factor of random variability (expected β-diversity), or whether the results are from changes in the underlying structure attributed to assembly processes such as niche-related (deterministic) processes. For example, aside from using null β-diversity as a comparison with observed β-diversity to determine whether random variability influences community composition we also use β-deviation (which is the difference between observed and null β-diversity) to investigate the direction of deviation in community composition. The direction of β-deviation is informative of communities being more similar than by chance (negative null deviation) or less similar than expected by chance (positive deviation value). Large deviations suggest that communities are structured by non□neutral assembly mechanisms, such as environmental filtering (negative values; communities more homogenous than expected by chance) or competitive interactions (positive values; communities more homogenous than expected by chance) (Chase 2010, Chase and Myers 2011).

To determine whether β-diversity across land use types was a product of random sampling effect (i.e. sample size for each land use type) or from a community assembly mechanism, such as deterministic or stochastic assembly processes, we used the null model approach and generated null communities for each palm (package *Metacom*, Dallas 2018). The output, expected β-diversity, was compared with the observed β-diversity generated from our field data (β-deviation). B-deviation is effect size from the variation of observed and null B diversity and is the difference between the observed and mean expected dissimilarity divided by the standard deviation of the expected value (Myers et al. 2013).

3.3 RESULTS

Sampling efficiency: higher for 3-day sampling than palm felling

Overall, sampling completeness was higher for the 3-day sampling than with palm felling (Supplementary Information; Figure 2, A-C). The sample coverage of the reference palms for forest (75%), pasture (87%) and peridomestic (87%) palms had an overall average coverage of 83% using the palm felling technique. The compared sample coverage of palms using the 3-day technique for forest (100%), pasture (80%), and peridomestic (83%) had an average completeness of 87%. Based on the similar coverage of the 3-day sampling to that of palm felling, it was determined that 3-day climbing/dissecting technique was adequate for sampling the palm crown community.

Palm crown community

Forty-nine *A. butyracea* palms were sampled for community analysis across pasture (N=14), peridomestic (N=17), and regenerating forest patch (N=18). A total of 2952 specimens (including incidence of vertebrate signs) were collected consisting of 70 Families that were identified to 91 Genera. All individuals were categorized into 52 morphospecies and their respective trophic levels and feeding guild (previous reference *Supplementary Information, Table 3.1*).

Community Diversity and Composition Within and Across a Land Use Gradient

Palm crown species diversity (Simpson's Diversity index) was highest in forest fragments (D = 0.826) and similar in pasture (D = 0.810) with a slight decrease in peridomestic palms (D = 0.73). Results further indicate that community composition did vary as a function of land use type (Table 3.1). However, the effect was weak ($R^2 = 0.10$). Community composition within all trophic levels except for Trophic Level 5 species also varied as a function of land use type. Furthermore, community composition within land use type did not vary and displayed similar homogeneity, which was similar with community composition within each trophic level (Table 3.2). Although the overall species composition of each trophic level did vary as a function of land use type and the composition within displayed similar homogeneity, the proportion of each trophic level making up the entire community did not significantly differ. Comparison of community composition across and variation within land use types was also visualized using a nonmetric multidimensional scaling (NMDS) ordination and Principal Components Analysis (PCoA) (Figure 3.2 A-B) which further reiterates that differences in community composition as a function of land use type was not a result of compositional heterogeneity across palms within land use type.

Trophic structure in Response to Land Use Gradient

Mid-trophic level diversity (Simpson's Diversity index) was highest in pasture palms (D = 0.61) compared to forest fragment (D = 0.49) and peridomestic (D = 0.43). Feeding guild varied significantly across land use type (Figure 3.6).The fraction of herbivores significantly decreased (Kruskal-Wallis chi-squared = 11.712, df = 2, p-value = 0.002863), and the fraction of omnivores (Kruskal-Wallis chi-squared = 7.4131, df = 2, p-value = 0.02456) significantly increased from forest to pasture palms. Network connectance (Kruskal-Wallis chi-squared = 8.1493, df = 2, p-value = 0.017) and generality (Kruskal-Wallis chi-squared = 8.0481, df = 2, p-value = 0.01788) also increased from forest to pasture palms (Figure 3.7). Remaining network variables such as: species count (Kruskal-Wallis chi-squared = 2.2, df = 2, p-value = 0.3), links per species (Kruskal-Wallis chi-squared = 0.49, df = 2, p-value = 0.7), fraction top level species (Kruskal-Wallis chi-squared = 0.82, df = 2, p-value = 0.66), fraction intermediate species (Kruskal-Wallis chi-squared = 3.27, df = 2, p-value = 0.19), fraction basal species (Kruskal-Wallis chi-squared = 3.4, df = 2, p-value = 0.18) were not significant.

Pairwise Species Associations Across Land Use Type

The number of species associations varied land use type. Out of the potential 1326 pair associations, there was a greater number of significant (occurred > 1) species co-occurrences in forest fragment (583 pairs) compared to peridomestic (505 pairs) and pasture (322 pairs). The composition of species associations as well as type of associations (i.e. positive, negative, random) also varied across land use type (Table 3.3). The richness and diversity of species co-occurrences declined with increasing deforestation as well as percent positive associations. Although negative interactions were present in peridomestic and forest fragment sites, pasture sites did not have negative species associations.

Environmental Drivers of Community Composition

Microhabitat variables displayed a wide variation within land use types but only significantly differed for a subset of those variables (*not shown*). Our distance-based redundancy analysis of the micro environmental variables suggested that palm crown micro- habitat variables account for a small but significant amount of variation in community composition when effects of land use (8% of variation, F=1.28, P=0.02) was accounted for. Dead organic matter explains 2.6% (P=0.006), number of connected trees explains for 4.0% (P=0.0034), and average palm crown temperature explains for 5.3% (P=0.042) of compositional variation. Unrecorded variables accounted for the remaining variation in community composition.

Testing Community Assembly Mechanisms

The results from comparing null and observed β-diversity indicate that observed β-diversity was consistently more dissimilar than what was expected across all land use types (Figure 3.4 A). Furthermore, β-deviation values were all positive, however the magnitude of deviation remained slightly above zero. Deviation in pasture sites was variable and did not show a strong trend of aggregated or homogenized communities (Figure 3.4 B). Across all trophic levels, the observed β-diversity deviated from expected β-diversity, however the magnitude of deviation was small, roughly within +2 of -2 (Figure 3.5A-D). The largest deviation was observed for the species community at trophic level 5 within pasture palms that had a deviation value at (-3).

3.4 DISCUSSION

We investigated the potential impacts of land use types on the *Attalea butyracea* palm crown community composition and network structure. Overall, we found that the palm crown species community is primarily dominated by arthropod species, particularly arthropods that are considered agricultural pests, compared to vertebrate taxa. We also found that there were moderate differences in both species diversity and elements of the trophic network structure of the *Attalea* palm crown community in response to land use type. In the investigation on the environmental process driving variation in community composition also indicates that niche-related processes, rather than neutral, influence communities across pasture, peridomestic and forest fragment areas.

Community Diversity and Composition and Trophic Structure Within and Across Land Use Types

Contrary to our prediction, we found that pasture palms did not have a lower diversity or distinctly more homogenized communities compared to peridomestic and forest patch sites. While community diversity was high across land use types, composition actually varied as a function of land use type. As indicated by the NMDS plot, although some pasture and forest palm communities showed some similarities, palms within peridomestic sites could be similar to either those found in pasture and forest (*see* Figure 3.1). This is a likely a reflection of the variation in palm microhabitat variables found in peridomestic areas, which can either resemble palms found in forest fragments or pasture, depending on its surrounding conditions. Similarly, species communities within each trophic level were also varied as a function of land use type, except for TL5. These species, which are all vertebrate species (i.e. opossum, bat, tamandua), are able to move freely across land use types, using palms as refuge, and would likely not be as affected by changes in habitat as was observed in lower trophic level species. However, lower trophic level species communities, particularly mid-trophic level species, did vary as a function of land use type, notably combined with an increase in pasture sites. While these species include invertebrate predators such as spiders and scorpions, they were generally more diverse than bottom-trophic level species (i.e. herbivores) and may have been able to maintain a higher diversity in more disturbed (i.e. pasture) sites than herbivores. Alternatively, their high diversity is maintained through redundant species. For example, one species is replaced by another in pasture vs. forest remnants, but the diversity stays the same. Other studies regarding habitat fragmentation or urbanized areas sometimes observe an increase in species richness (McKinney 2008) or a change in community composition, particularly within arthropod communities (i.e. edge effect) (Gibb and Hochuli 2002). In such communities, although predator diversity is typically higher in less disturbed areas (Thorbek 2004, see also Haddad et al 2009) some generalist predators, such as spider and ground beetle species, can persist in agricultural farmland and thus are useful in the biocontrol of crop pest species (Snyder et al *date*). In some instances of arthropod communities, it's not richness that varies across disturbance gradients but the functional groups that are more heavily impacted (Sattler et al. 2010) as will be discussed in a later section.

Using the beta-diversity null model approach to determine palm crown community assembly processes, we detected that indeed deterministic processes drove variation in community composition across land use types although the magnitude of these processes were small. While our null model suggested that community variation was not a result of random variation (stochasticity), the slightly positive was small and suggests that communities were overall more heterogeneous across palms than expected, hinting that some species may have aggregated in response to environmental filtering. Alternatively, across trophic levels the magnitude and direction of beta-deviation varies, albeit consistently small. These results only suggest that species across trophic levels respond differently to land use change that is driven by different assembly processes. For example, while most communities in TL2-4 are more heterogenous then expected, once again suggesting that they are assembled via environmental processes (niche/deterministic), species in TL5 displays a strong stochastic/neutral assembly process. This means that the distribution of these species is more homogenous, and less influenced by the surrounding environment. As previously mentioned, these species (birds, bats, opossums) can move around more easily and are less restricted to environmental variation caused by the variation in land use types. Relevant literature has demonstrated that finding community assembly responses to environmental disturbance may not always change in a predictable or consistent direction and is likely to vary across different systems (Dormann et al 2017, Newbold et al 2016) (Berry et al 2008, Kitching et al 2013, Solar et al 2015) and studies comparing the processes driving community assembly have determined that a mixture of both spatial and environmental variables contribute to patterns in community assembly (Siefert 2013), or can contribute differently across latitudinal, elevational, or disturbance gradients (Myers 2013, Tello 2015). When comparing community assembly within tropical and temperate forest plots, spatial variables in tropical communities had a stronger effect whereas within temperate communities, environmental factors had a stronger influence on community assembly (Myers et al 2013). Across land use gradients, we find that environmental variables become more important with increased land use intensity (Wearn 2019). Further studies of the effects on land use gradients have suggested that environmental filters are more important as disturbance increases, suggesting that variation in habitat at finer scales may cause species to persist closer to their biological tolerances (Wearn et al 2019);other studies indicate that disturbance did not influence community assembly (Myers et al 2015).

Network Structure and Feeding Guilds in Response to Land Use Type

Omnivory and connectance were also higher in pasture sites, supporting our prediction that species communities within increasingly deforested areas generally had a wider diet range compared to the communities within more forested areas. This supports other studies that have observed similar findings regarding a steady presence of omnivore species (McIntyre et al. 2001, Gray et al, Silva et al 2016) and increased connectance (i.e. Valladares, Cagnolo, and Salvo 2012) within altered habitats. Contrary to our prediction and other evidence, herbivory was higher in forest than in pasture, which we expected to be lower due to an increase in predator diversity in forests. However, this pattern could be explained by the decrease in surrounding vegetation within pasture sites as well as presence of epiphytes in the palm crown and on the stem. Also, contrary to what we expected, the consumerism index (generality) was higher in forest palms. In this system, omnivory and generality were not positively correlated with each other as was assumed. A higher fraction of generality in forest patches can be a result from the higher fraction of herbivores, which was observed, which would have been collectively greater than that of the highly omnivorous pasture palm community. It is not suspected that increased generality in forest fragments was due to an increase in predator diversity, since there was no difference in the proportion of top trophic-level species or insectivorous species across land use type.

Pairwise Species Associations Across Land Use Type

Although the number and type of significant species associations did shift across land use type, we did not see an increase in randomized associations as was expected. Randomized species co-occurrences are often associated with anthropogenic disturbance resulting in a degradation in community structure (Bhat and Magurran 2007, Burkle, Marlin, and Knight 2013). However, our results may indicate that pasture palms are not necessarily disassembled communities but have reassembled and readapted and function as a different community driven by a resilient species community. This reinforces the previous findings that although community richness and composition across disturbances varies, it shifts from its original function, but is not necessarily ecologically “degraded”.

Effects of Regional vs. Local Scale Environmental Drivers of Community Composition

We found that the effect on community composition was stronger across land use type rather than the variables at the local scale. Compared to the local scale, which in this study refers to individual palm crown characteristics, impacts on ecological communities driven by larger-scale effects can be associated with land use history, disturbance intensity, or degree of habitat heterogeneity, all of which are known to influence species assembly process (as discussed in Hendrickx et al. 2007; Aviron et al. 2005). Other potentially influential variables at the local scale including productivity (i.e. within the palm crown), size of the land use area, or proximity to other natural resources (i.e. streams), which are also known to influence species assemblage, were not measured in this study.

Management Implications

Because pathogens, hosts and vectors are embedded within a community network, tying together functional and taxonomic variations with disease transmission can bridge the gap between disease and community ecology. In this study, we observed that there is both taxonomic and trophic variation of animal communities in palm crowns across land use type that can influence community function in these palms. For instance, reduction in surrounding canopy plant biomass can result in a decrease in herbivore species, thereby shifting a community to one that is dominated by higher trophic level omnivory. *Rhodnius pallescens*, the Chagas disease vector, is observed to be positively associated with increasing deforestation throughout central Panama (Gottdenker et al 2011). However, the mechanisms behind this increase could ultimately be related to species community structure and function within the *Attalea* palm crown. In other studies, community patterns have been tied to shifts in infectious disease dynamics but have mainly focused on a subset of the community rather than as a whole. This study serves as an ideal stepping-stone for a more holistic approach to ask additional questions relating to an entire community and its relationship to vector-borne disease transmission across a deforestation gradient. It is also possible that particular community characteristics associated with each land use type are major drivers of kissing bug abundance and infection prevalence (i.e. presence of host blood meals) ---determining these characteristics are essential for vector control.

Research Limitations

In this study, we were primarily limited to palms that could be safely accessed using a ladder and harness which proved to be major barriers preventing the collection of a more robust community sample that would have included taller palms. Lastly, tropical canopy arthropods, which made up a majority of these communities, are notoriously difficult to sample (Lowman 2012).

3.5 CONCLUSION

Land use disturbance is heavily associated with a decrease in biodiversity, a disassembly of communities, and a loss in community function. We used a palm crown study system to demonstrate that although gradients of landscape disturbance are indeed associated with shifts in community composition and function, it did not drastically reduce community diversity. This reiterates the point gathered from other community ecology studies which suggest that measuring the impacts of disturbance on communities should not just focus on taxonomic diversity but should include other community variables such as functional traits. These variables can further infer whether functional redundancy occurs irrespective of taxonomic differences or how disturbance can maintain highly diverse communities but have species replacement, creating distinct shifts in community function. Lastly, researching community characteristics representative of land use types has the potential to combine both abiotic and biotic factors that drive emerging infectious diseases.

Permits: Mi Ambiente: SE/A-93-13, SE/AP-27-16

STRI IACUC: 2013-0601-2016-02, 2016-0801-2019-A1

UGA IACUC: A2016 05-009-R2 (double check)

3.6 TABLES AND FIGURES

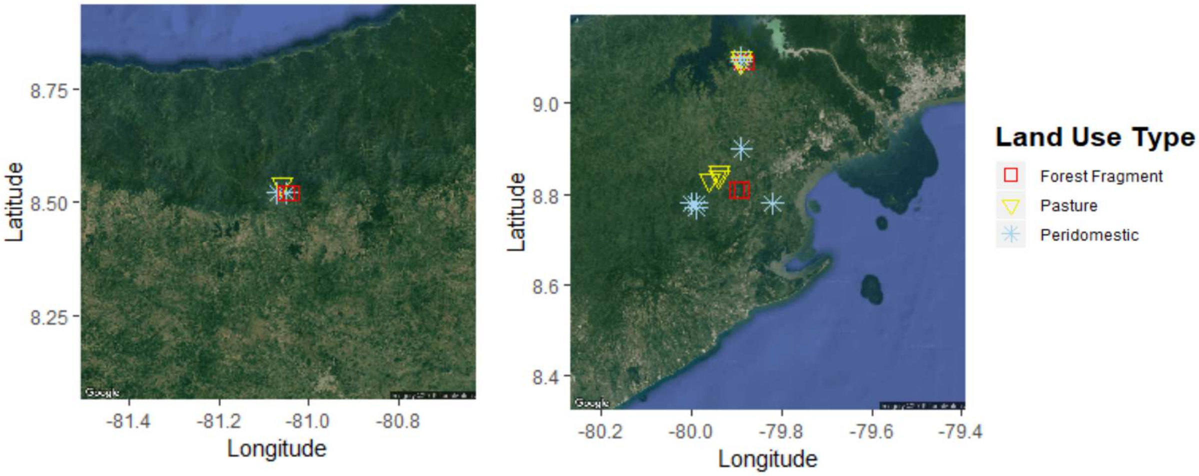


Figure 3.1. Three main districts Santa Fe (left) and Capira and La Chorrera (right) where palm sites were selected across a land use gradient.

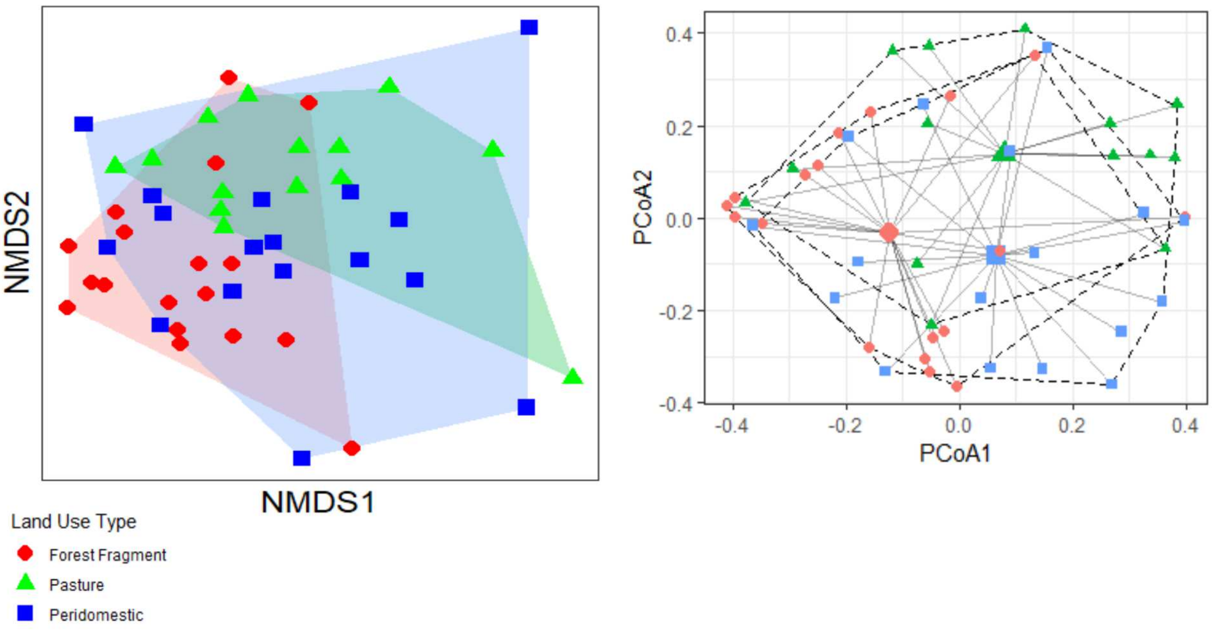
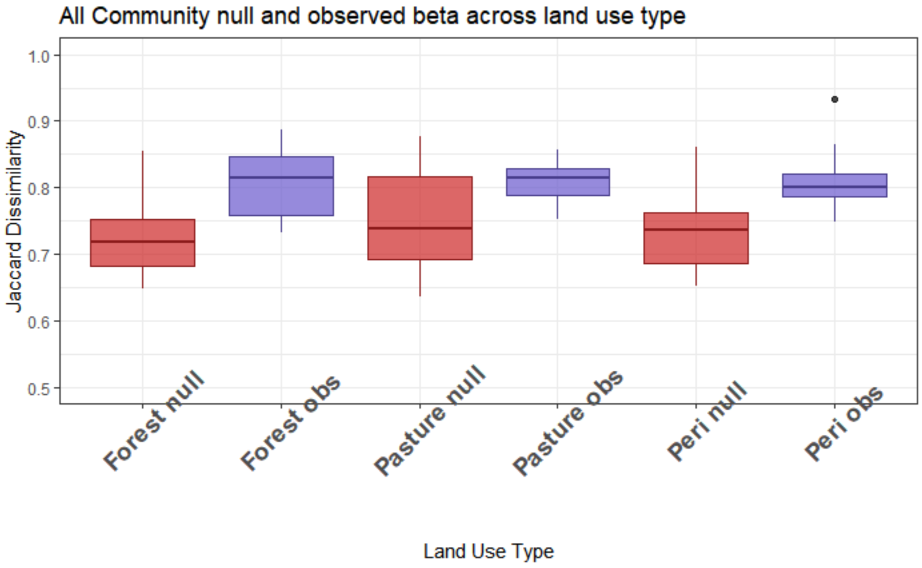


Figure 3.2 A-B. Comparison of communities across (A) and the compositional variation within (B) land use type. Community composition does vary as a function of land use type however within displayed similar homogeneity.

A.



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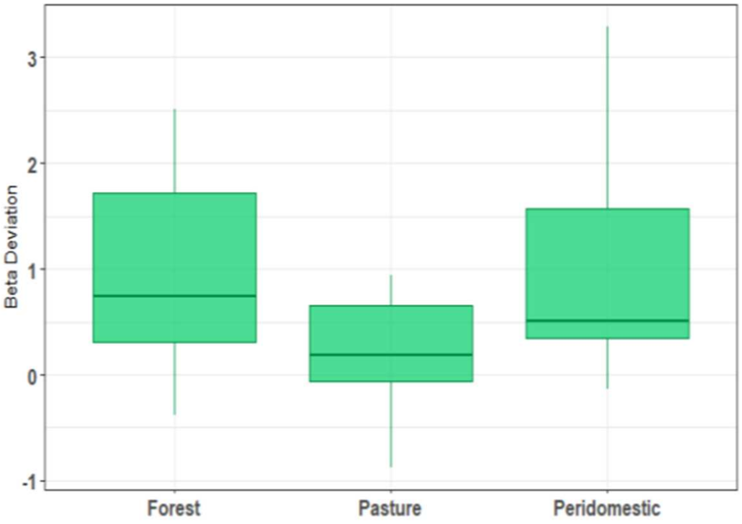
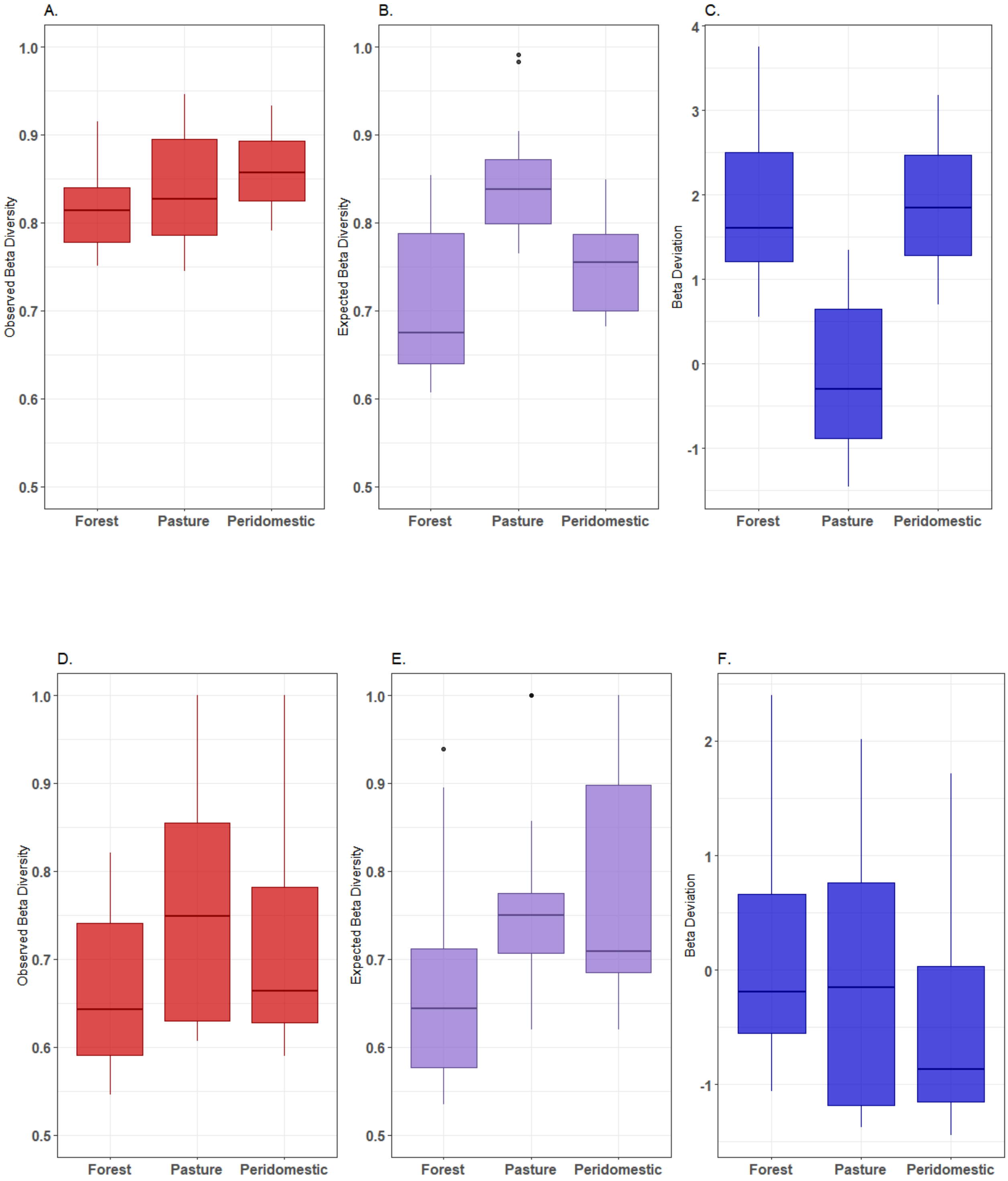


Figure 3.3 A-B. (A.) Observed and expected (null) beta diversity across land use type. (B). Beta-deviation (difference between observed beta-diversity from expected beta-diversity) for communities for each land use type.


A.
Observed Beta Diversity
1.0
0.9
0.8
0.7
0.6
0.5
Forest
Pasture
Peridomestic
B.
Expected Beta Diversity
1.0
0.9
0.8
0.7
0.6
0.5
Forest
Pasture
Peridomestic
C.
Beta Deviation
4
3
2
1
0
-1
Forest
Pasture
Peridomestic
D.
Observed Beta Diversity
1.0
0.9
0.8
0.7
0.6
0.5
Forest
Pasture
Peridomestic
E.
Expected Beta Diversity
1.0
0.9
0.8
0.7
0.6
0.5
Forest
Pasture
Peridomestic
F.
Beta Deviation
2
1
0
-1
Forest
Pasture
Peridomestic

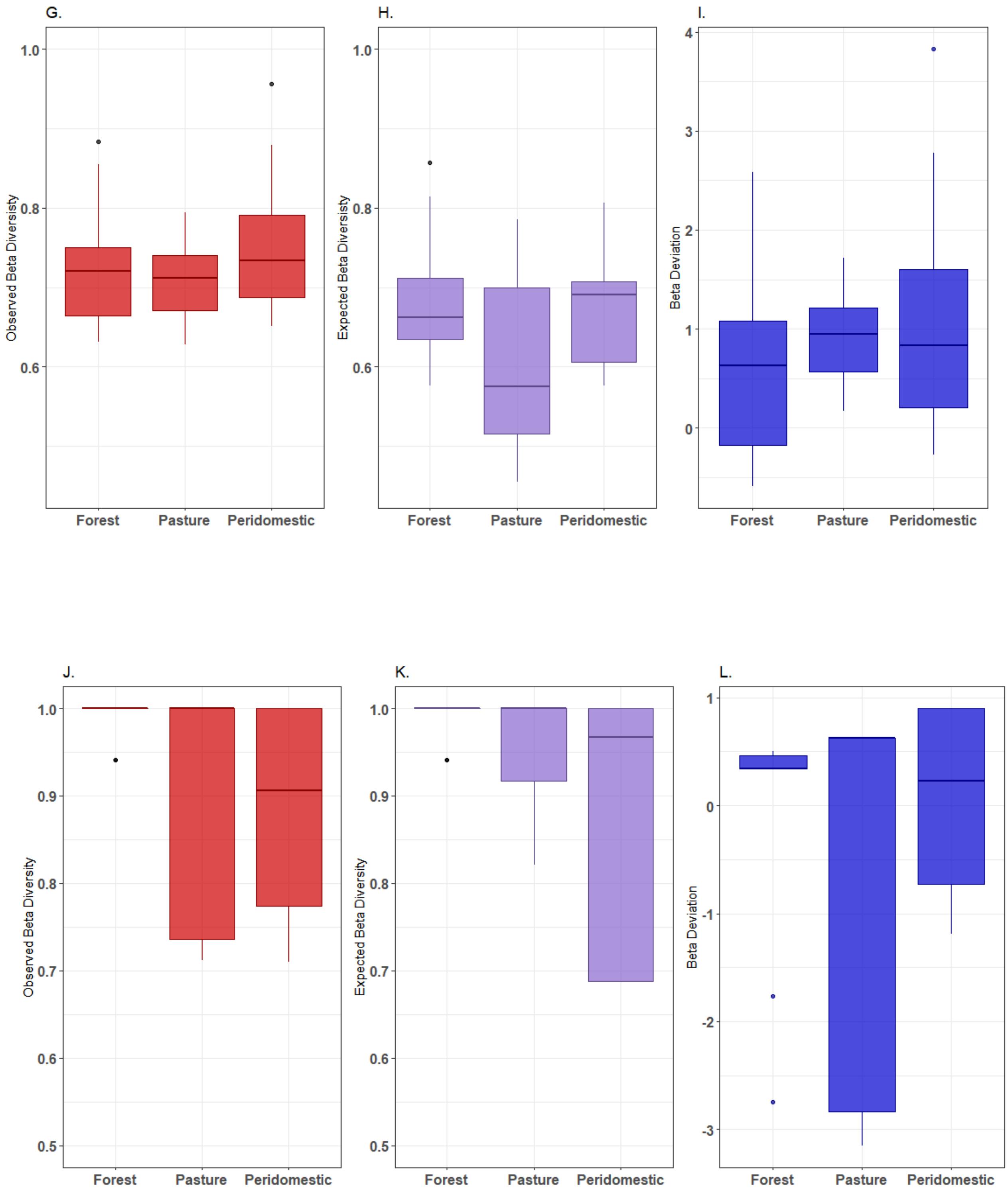


Figure 3.4 A-D. Beta - Observed, Null and Deviation across (A-C) trophic level 2, (D-F) trophic level 3, (G-I) trophic level 4, and (J-K). trophic level 5.

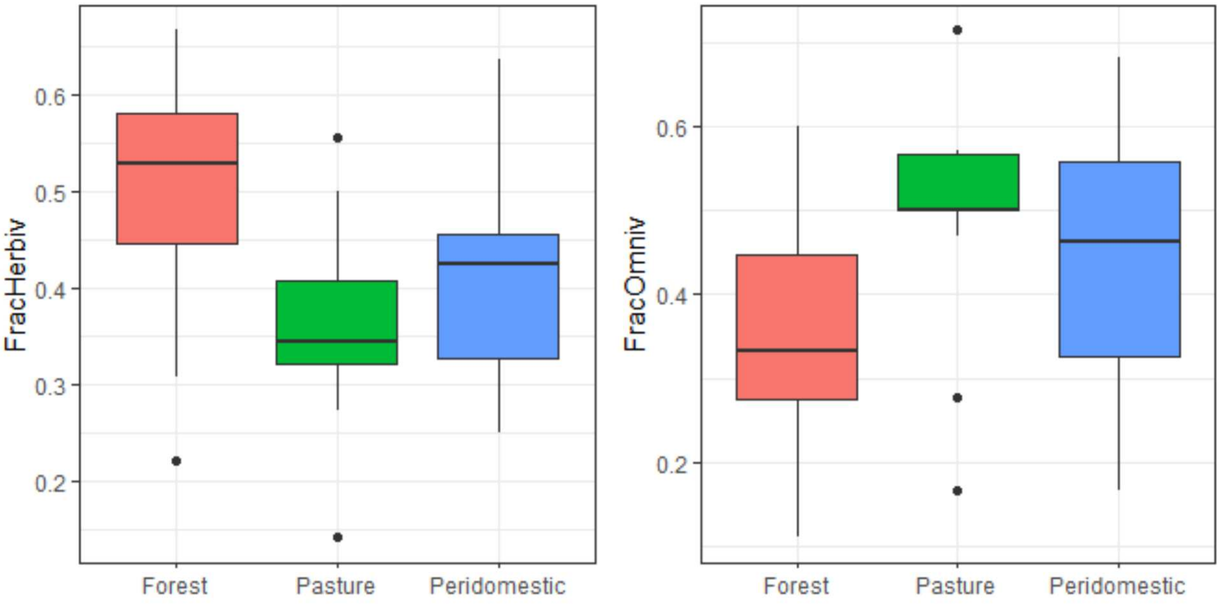


Figure 3.5. Fraction herbivore (left) and omnivore (right) species across land use type. Both guilds varied significantly (Kruskal-Wallis $\chi 2 = 11.7$, df = 2, $p < 0.00$; Kruskal-Wallis $\chi 2 = 7.4$, df = 2, $p < 0.03$, respectively).

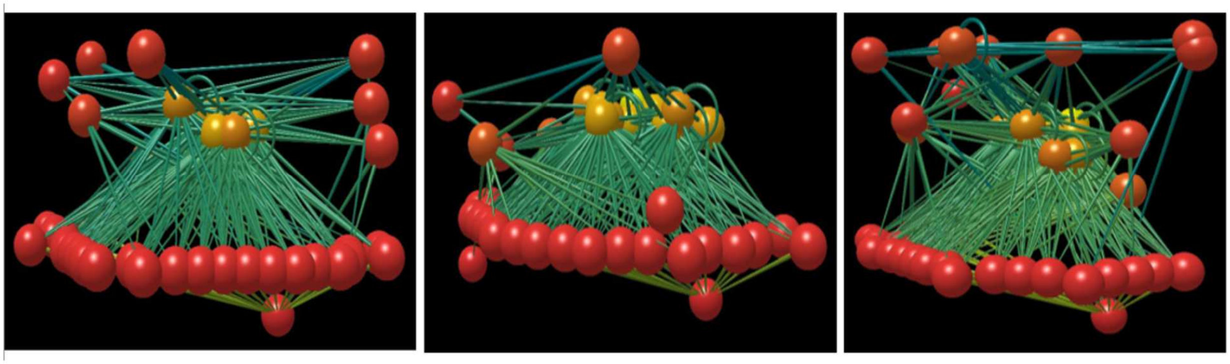


Figure 3.6. Network 3D representing average connectivity and generality for forest fragment (left), pasture (middle), and peridomestic (right) palms. Nodes represent trophic species and node height represents trophic level. Color represents generality (the number of other nodes it feeds from) and depth (clustering) represents species connectivity. The connectance (number of realized links out of links

possible) is represented by the high clustering of species, which is greater in the pasture palms. Node color (red, orange, yellow) indicates generality score (low, med, high) which is greater in forest palms.

Table 3.1. PERMANOVA results investigating the variation community composition, and composition across trophic levels, as a function of land use type.

	DF	Sum of Squares	F.Model	R^2	Pr(>F)
Community	2	1.2	2.5	0.10	0.01
TL2	2	1.02	1.8	0.07	0.03
TL3	2	1.42	4.4	0.18	0.01
TL4	2	1.1	2.8	0.11	0.01
TL5	2	0.22	0.80	0.09	0.57

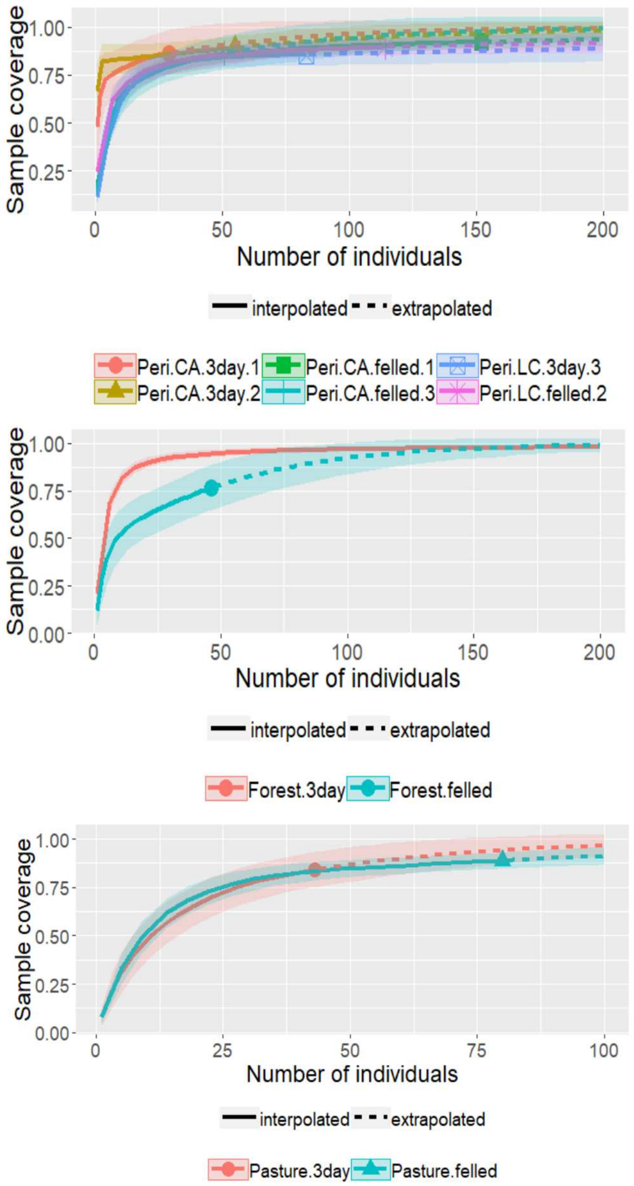
Table 3.2. ANOVA results indicating the variation in community composition and composition across each trophic level, within each land use type.

	DF	Sum of Squares	Means Square	F value	Pr(>F)
Community	2	0.01	0.002	0.33	0.70
TL2	2	0.02	0.01	0.80	0.50
TL3	2	0.40	0.02	1.40	0.30
TL4	2	0.02	0.01	0.91	0.41
TL5	2	0.15	0.08	2.75	0.09

Table 3.3. Proportion of association types within palm crown communities across land use type.

LAND USE TYPE	% PAIRS SIGNIFICANT	% POSITIVE	% NEGATIVE	% RANDOM
FOREST FRAGMENT	**44%**	**1.3%**	**0.1%**	**42%**
PASTURE	**25%**	**.1%**	**0**	**23%**
PERIDOMESTIC	**38%**	**.1%**	**0.2%**	**35%**

3.7 SUPPLEMENTARY INFORMATION



SI Figure 3.1. Sampling coverage for palm felling and 3-day dissection technique for peridomestic (A), forest fragment (B), and pasture (C) palms.

SI Table 3.1. Identification from Order to Genus species and trophic information of the species in the Attalea palm.

ORDER	**FAMILY**	***Genus species***	**COMMON NAME**	**TROPHIC GROUPING**
Scorpiones	Buthidae	*Centruroides granosus*	Bark Scorpion	Predator, carnivore/insectivore
	Hemiscorpiidae	*Opisthacanthus elatus*	Bark Scorpion	Predator, carnivore/insectivore
Ixodida	Ixodidae	NA	parasite/tick	Parasite
Trombidiformes	Erythraeidae	NA	parasite/mite	Parasite
Amblypygi	Phrynidae	*Phrynus gervaisii*	Spider: Whip Spider	Predator, insectivore
		Phrynus barbadensis	Spider: Whip Spider	Predator, insectivore
		NA	Spider: Whip Spider	Predator, insectivore
Araneae	Salticidae	*Metacyrba punctata* (Peckham & Peckham, 1894)	Spider: Jumping	Predator, insectivore
		Xanthofreya arraijanica (Chickering, 1946)	Spider: Jumping	Predator, insectivore
		Leptofreya bifurcata (F. O. Pickard-Cambridge, 1901)	Spider: Jumping	Predator, insectivore
		Corythalia sp.	Spider: Jumping	Predator, insectivore
		Habronattus paratus (Peckham & Peckham, 1896)	Spider: Jumping	Predator, insectivore
		Corythalia spiralis (F. O. Pickard-Cambridge, 1901)	Spider: Jumping	Predator, insectivore
		Corythalia sulphurea (F. O. Pickard-Cambridge, 1901)	Spider: Jumping	Predator, insectivore
		Colonus sp.	Spider: Jumping	Predator, insectivore
		Corythalia sulphurea Petrunkevitch, 1925	Spider: Jumping	Predator, insectivore
		Menemerus bivittatus (Dufour, 1831)	Spider: Jumping	Predator, insectivore

		Eustiromastix frontalis (Banks, 1929)	Spider: Jumping	Predator, insectivore
		Frigga pratensis (Peckham & Peckham, 1885)	Spider: Jumping	Predator, insectivore
		Lyssomanes jemineus (Peckham, Peckham & Wheeler, 1889)	Spider: Jumping	Predator, insectivore
		Breda milvina (C. L. Koch. 1846)	Spider: Jumping	Predator, insectivore
		Pachomius dybowskii (Taczanowski, 1871)	Spider: Jumping	Predator, insectivore
		NA	Spider: Jumping	Predator, insectivore
	Scytodidae	*Scytodes sp.*	Spider: Spitting	Predator, insectivore
		NA	Spider: Spitting	Predator, insectivore
	Gnaphosidae	*Zimiromus sp.*	Spider: Ground	Predator, insectivore
		Zimiromus iotus	Spider: Ground	Predator, insectivore
		NA	Spider: Ground	Predator, insectivore
	Tetragnathidae	*Leucauge sp.*	Spider: Long-jawed Orb Weavers	Predator, insectivore
		Dolichognatha sp.	Spider: Long-jawed Orb Weavers	Predator, insectivore
		NA	Spider: Long-jawed Orb Weavers	Predator, insectivore
	Selenopidae	*Selenops sp.*	Spider: Flying	Predator, insectivore
		NA	Spider: Flying	Predator, insectivore
	Ctenidae	*Ctenus spp.*	Spider: Wandering	Predator, insectivore
		Cupiennius spp.	Spider: Wandering	Predator, insectivore
		Acanthoctenus spp.	Spider: Wandering	Predator, insectivore
		NA	Spider: Wandering	Predator, insectivore
	Corinnidade	*Castianeira dentata*	Spider: Antmimic/Ground/Swift Sac Spider	
		Castianeira sp.	Spider: Antmimic/Ground/Swift Sac Spider	

		NA	Spider: Antmimic/Ground/Swift Sac Spider	
	Anyphaenidae	*Hibana sp.*	Spider: Ghost Sac Spiders	Predator, omnivore
		NA	Spider: Ghost Sac Spiders	Predator, omnivore
	Thomisidae	*Misumenoides sp.*	Spider: Crab	Predator, carnivore/insectivore
		Strophius sp.	Spider: Crab	Predator, carnivore/insectivore
		NA	Spider: Crab	Predator, carnivore/insectivore
	Philodromidae	*Apollophanes puntipes*	Spider: Running Crab Spider	Predator, carnivore/insectivore
		NA	Spider: Running Crab Spider	Predator, carnivore/insectivore
	Caponiidae	*Nops largus*	Spider: NA	Predator, carnivore/insectivore
		NA	Spider: NA	Predator, carnivore/insectivore
	Lycosidae	*Hogna tivior*	Spider: Wolf	Predator, carnivore/insectivore
		NA	Spider: Wolf	Predator, carnivore/insectivore
	Araneidae	*Araneus sp.*	Spider: Orb Weaving	Predator, carnivore/insectivore
		Eustela sp.	Spider: Orb Weaving	Predator, carnivore/insectivore
		Eriophora sp.	Spider: Orb Weaving	Predator, carnivore/insectivore
		Micrathena sexpinosa	Spider: Orb Weaving	Predator, carnivore/insectivore
		Nephila clavipes	Spider: Orb Weaving	Predator, Insectivore
		NA	Spider: Orb Weaving	Predator, carnivore/insectivore
	Senoculidae	*Senoculus sp.*	Spider: Bark Hunter	
		NA	Spider: Bark Hunter	
	Sparassidae	*Olios sp.*	Spider: Huntsman	Predator, carnivore/insectivore

		NA	Spider: Huntsman	Predator, carnivore/insectivore
	Segestriidae	*Ariadna spp.*	Spider: Tube Web	Predator, carnivore/insectivore
		NA	Spider: Tube Web	Predator, carnivore/insectivore
	Clubionidae	NA	Spider: Sac Spider	Predator, carnivore/insectivore
	Oxypodidae	*Peucetia spp.*	Spider: Lynx	Predator, carnivore/insectivore
		NA	Spider: Lynx	Predator, carnivore/insectivore
	Theraphosidae	*Psalmopoeus pulcher*	Tarantula	Predator, carnivore/insectivore
	NA	NA	Spider: unidentified	Predator, carnivore/insectivore
Opiliones	NA	NA	Harvestmen	Predator, omnivore, generalist
Coleoptera	Chrysomelidae	*Pachymerus cardo*	Leaf Beetle (Bruchid)	Herbivore
		Speciomerus giganteus		
	Subfamily: Chrysomelinae and Eumolpinae	*Myochrus sp.*	Leaf Beetle	Folivore
		Colaspis sp.,	Leaf Beetle	Folivore
		Calligrapha sp.	Leaf Beetle	Folivore
		NA	Leaf Beetle	Folivore
	Superfamily: Curculionoidea		**Snout and Bark Beetles**	
	Curculionidae: Molytinae and Baridinae	*Homalinotus sp.*	Weevil: Snout/Bark Beetle	Herbivore
		NA	Weevil: Snout/Bark Beetle	Herbivore
	Brachyceridae:Erirhininae	NA	Weevil: Marsh	Herbivore
	Elateridae	NA	Click-Beetle	Omnivore
	Scarabidae	*Cyclocephala amazona*	Masked Chafer	Herbivore, geophagia

		Onthphagus sp.	Dung Beetle	Coprophagous, decomposer, (some) necrophagous
		Coprini tribe	Dung Beetle	Coprophagous, decomposer, (some) necrophagous
		NA	Dung Beetle	Coprophagous, decomposer
	Tenebrionidae	*Armalia sp.*	Darkling Beetle	Generalistic omnivores, detritivore
		Talanus sp.	Darkling Beetle	Generalistic omnivores, detritivore
		Xystropus californicus	Darkling Beetle	Generalistic omnivores, detritivore
	Carabidae	NA	Ground Beetle	Predator, omnivore, insectivore
	Staphylinidae	*Lathrobium sp*	Rove Beetle	Omnivore, detritivore
		NA	Rove Beetle	Omnivore, detritivore
	Superfamily: Cucujoidea		**Sap, Bark, Fungus Beetles**	
	Endomychidae	*Trochoidea sp.*	Handsome Fungus Beetle	Fungivore
		Acinaces sp. (lebasii)	Handsome Fungus Beetle	Fungivore
		NA	Handsome Fungus Beetle	Fungivore
	Erotylidae	*Aegithus clavicornis*	Pleasing Fungus Beetle	Fungivore
		NA	Pleasing Fungus Beetle	Fungivore
	Phalacridae	NA	Shining Flower Beetle	Fungivore, palynophagous
	Silvanidae	NA	Silvan Flat Bark Beetle	Fungivore
	Nitidulidae	*Cyllodes sp*	Sap Feeding Beetle	Herbivore, detritivore

		NA	Sap Feeding Beetle	Herbivore, detritivore
	Passandridae	*Catogenus sp.*	Flat Bark Beetle	Ectoparasitic
	Cerambycidae	NA		
		NA	Long-horned Beetle	Phytophagous, xylophagous
	Lampyridae	NA	Lightening Bug	Herbivore, Omnivore
Hemiptera	**Superfamily Lygaeoidea**		**Seed Bugs and Allies**	
	Rhyparochromidae	*Cryphula sp.*	Dirt-colored Seed Bug	Herbivore
		Valtissius sp.	Dirt-colored Seed Bug	Herbivore
		NA	Dirt-colored Seed Bug	Herbivore
	Lygaeidae	*Ochrostomus sp.*	Seed Bugs	Herbivore
		NA	Seed Bugs	Herbivore
	Superfamily Coreoidea		**Leaf-footed Bugs and Allies**	
	Rhopalidae	NA	Scentless Plant Bug	Herbivore
	Coreidae	NA	Leaf-footed bugs	Herbivore
	Superfamily Pentatomoidea		**Shield bugs, Chust bugs, and Stink bugs**	
	Scutelleridae	*Camiurus sp.*	Jewel Bug	Herbivore
		NA	Jewel Bug	Herbivore
	Pentatomidae	*Antiteuchus sp.* (*panamensis*?)	Stink Bug	Herbivore
		NA	Stink Bug	Herbivore
	Plataspidae	*Brachyplatys subaneus*	Shield Bug	Herbivore
		NA	Shield Bug	Herbivore
	Superfamily Pyrrhocoroidea		**Bordered Plant Bugs**	

	Largidae	*Largus sp.*	Bordered bugs	Phytophagous
		NA	Bordered bugs	Phytophagous
	Pyrrhocoridae	*Dysdercus sp.*	Cotton Stainers	Phytophagous, (sometimes) omnivore
		NA	Cotton Stainers	Phytophagous, (sometimes) omnivore
	Reduviidae	Rhodnius pallescens	kissing bug	Hematophagy
		Triatoma dimidiata	kissing bug	Hematophagy
		Salyavatinae spp.	Termite assassin bug	Insectivore
		Reduvius spp.	Masked Assassin Bug	Insectivore
		NA	Assassin bug	Insectivore
	Fulgoridae	NA	Peanut-headed Bug	Herbivore
Hymenoptera	Apidae	*Trigona sp.*	Bee	Carnivore
		Euglossa sp.	Bee	Nectarivore
		Eufriesea sp.	Bee	Nectarivore
	Formicidae	*Camponotus ager*	Carpenter Ant	Omnivore
		Odontomachus bauri	Trap Jaw Ant	Carnivore
		Linepithema humile	Argentine Ant	Omnivore, trophic generalist
		Nesomtrmex sp.	Ant	
		Paratrechina caeciliae	Ant	Omnivore
		Azteca sp.	Ant	Herbivore
		Tapinoma ramulorum	Ant	Omnivore
		Camponotus brettesi	Ant	Omnivore
		Crematogaster nigropilosa	Acrobat Ant	Insectivore
		Pseudomyrmex sp.	Bullhorn Acacia Ant	Herbivore
Diptera	Stratiomyiidae	NA	Fly	Herbivore, Detritivore
	Drosophilidae		Fly	Herbivore, Detritivore
Blattodea	NA	NA	Cockroach	Omnivore, Insectivore (opportunistic)

	NA	NA	Termite	Herbivore
Orthoptera	NA	NA	Cricket/Grasshopper	Omnivore
Mantodea	NA	NA	Mantis	Predator, carnivore/insectivore
Phasmatodea	NA	NA	Walking Stick	Herbivore
Squamata	NA	NA	Snake	Predator, Carnivorous
	NA	NA	Lizard/Gecko	Omnivore, insectivore
Oligochaeta	NA	NA	Segmented Worm	Decomposer, geophagia
Dermaptera	NA	NA	Earwig	Omnivore, Insectivore, Decomposer
Chilopoda	NA	NA	Centipede	Predator, carnivore/insectivore
Aves (Class)	NA	NA	Bird	Omnivore, insectivore
	Cardinalidae	Piranga rubra	Bird	
	Thraupidae	Thraupis sayaca	Bird	
	Tyrannidae	Sayornis phoebe	Bird	
	Turdidae	Turdus grayi	Bird	
Lepidoptera	NA	NA	Grub; larval stage	Herbivore, (very few) Carnivores
Coleoptera	NA	NA	Grub; larval stage	Herbivore
Diplopoda	NA	NA	Milipede	Detritivore, Herbivore
Pseudoscorpion	NA	NA	Pseudoscorpion	Predator, Insectivore
Armadillidae			pill bugs	Herbivore, Detritivore
Didelphimorpha	Didelphidae	Philander opossum	opossum	
		Metachirus nudicaudatus	opossum	
		Didelphis marsupialis	opossum	
		Didelphis virginiana	opossum	

Rodentia	Cricetidae	Oecomys bicolor	Arboreal Rice Rat	
	Rodent sign	NA	rodent	
	Erthizontidae	*Coendu sp.*	rodent: Coendu	Herbivore

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CHAPTER 4

IMPACTS OF FOOD WEB STRUCTURE AND MICROHABITAT CONDITIONS ON TRIATOMINE ABUNDANCE AND TRYPANOSOME INFECTION IN CENTRAL PANAMA[3]

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ABSTRACT

Vector-borne pathogen transmission is shaped by multiple abiotic and biotic factors. Understanding the relative importance of these factors for vector abundance and infection is important to develop effective vector-borne disease control strategies. In this study, we apply a community ecology network approach to study abiotic and biotic conditions associated with abundance of the Chagas disease vector *Rhodnius pallescens* and vector infection with *Trypanosoma cruzi,* the cause of Chagas disease, within the crown of the royal palm tree (*Attalea butyracea*), which serves as an important vector habitat. We sampled 105 palms and collected 1098 *R. pallescens* in rural landscapes of three provinces in central and western Panama. We surveyed microclimate and habitat conditions of the *A. butyracea* palm and surveyed the food web by surveying animal (vertebrate and invertebrate) species within palm crown community for a subset of palms (N = 49) using a variety of canopy sampling techniques in order to characterize the food web of each palm. Of the food web characteristics, we used food web metrics, namely generality (the average number of prey per predator), and vulnerability (the average number of predators per prey) to evaluate associations between palm community trophic structure, vector predators, and blood meal composition with vector abundance and *T. cruzi* infection. We used a generalized linear mixed effects model to evaluate associations between the composition of the palm crown community, microclimate, and microhabitat on *R. pallescens* abundance and infection with *T. cruzi.* We found that vector abundance was influenced by both microhabitat (dead organic matter) and microclimatic (temperature, relative humidity) conditions within the palm crown, and was also positively associated with the presence of scorpions and negatively associated with increased community diversity. *T. cruzi* infection in the vectors was positively associated with vector developmental stage and the presence of spiders within the palm community. Although the probability of infection increased if *R. pallescens* fed from a mammal (particularly opossum and rodent), it actually decreased when mammal sign was present in the palm crown, but mammals were not present in vector blood meals from that palm. Furthermore, both abundance and infection were also associated with palm geographic location in central Panama. Our results emphasize the importance of incorporating the food web community measures, particularly the presence of reservoir hosts and potential predators, because it may modify the understanding of vector borne disease transmission, particularly combined with effects of microclimate and habitat conditions. Although complex, a holistic study of the local environment surrounding zoonotic disease vectors will be essential in management, monitoring, and prediction of disease risk, particularly in response to anthropogenic disturbance.

KEYWORDS: *Attalea butyracea*, *Rhodnius pallescens*, *Trypanosome cruzi*, Chagas disease, Disease ecology, Community ecology

4.1 INTRODUCTION

A reduction in biodiversity can drive emergence of arthropod-borne infectious diseases via changes in vector interactions with the surrounding species community (Pongsiri et al. 2009; Ostfeld and Keesing 2000; Felicia Keesing et al. 2010; Pieter T. J. Johnson, Ostfeld, and Keesing 2015). Changes in a vector's host or predator communities have been empirically associated with an increase or dilution in parasite transmission due to changes in contact between vectors and their potential hosts and predators (LoGiudice et al. 2003; P. T. J. Johnson and Thieltges 2010; Pieter T. J. Johnson et al. 2013; 2008). Food webs, which represent an entire animal and/or plant community trophic network, can be used to investigate how ecological communities as a whole, beyond single species interactions, influence pathogen transmission *in situ*. For instance, network diagrams can demonstrate how interaction with surrounding species can indirectly influence pathogen-vector-host relationships. Network metrics often used to describe complex feeding structures and interactions in food webs include species diversity (number and evenness of species), generality (the average number of prey per predator), and vulnerability (the average number of predators per prey) (Schoener 1989). These predator-prey interactions are important to investigate because they influence overall ecological community structure (Bruno and Cardinale 2008; Müller and Brodeur 2002; Rosenheim et al. 1995) and are also tied to influencing disease risk, either directly (i.e. consuming infected vectors) or indirectly (i.e. modifying vector behavior) (Finke 2012). Predator interactions have also been important in the context of applied natural vector control (i.e. biocontrol; (Snyder and Wise 1999). In the context of vector-borne multi-host pathogens, host species at different trophic levels can vary in their competence to transmit a pathogen to a vector, and vector populations may be negatively impacted by other invertebrate or vertebrate predators. Therefore, food web metrics such as community network generality and vulnerability are useful methods to identify or predict if and how animal community structure influences vector-borne pathogen transmission within a particular habitat.

Abiotic microenvironmental conditions such as temperature, relative humidity, and microhabitat structure are also important determinants of vector abundance, behavior, and infection status (Paaijmans et al. 2010; Randolph and Storey 1999; Carcavallo 1999; Shaw et al. 2003). In tick vectors, drier conditions decrease questing height, which then alters the host composition of tick meals and the subsequent infection probability for rodents (Randolph and Storey 1999; Burri et al. 2011). Meanwhile, temperature influences the mean distance travelled by ticks and the percentage of time in questing posture (Vail and Smith 2002). In mosquitos, temperature and precipitation as well as gradients of anthropogenic disturbance, such as deforestation and agricultural landscapes, have been associated with increased rates of development of the malaria parasite (*Plasmodium* spp.) within vectors as well as distribution and vectorial capacity of the *Anopheles* mosquito vector (Stresman 2010; Paaijmans Krijn P. et al. 2012). Similarly, increasing temperatures, along with urbanization, are associated with increased risk in Dengue fever (Wu et al. 2009). Clearly, microclimate is a principal determinant of arthropod vector abundance and infectious disease transmission. Empirical evidence linking animal species community and micro-environmental conditions with multi-host vector-borne disease transmission in natural systems suggests that both abiotic conditions (microhabitat/microclimate) and direct biotic interactions (food web networks) are important for predicting consequences of environmental changes on disease transmission (Weterings, Umponstira, and Buckley 2018)

Here, we study how variations in both the species community and microenvironment influence abundance and infection status of the principal Chagas disease vector in Panama, *Rhodnius pallescens* (subfamily Triatominae) in *Attalea* palms. *R. pallescens* is hematophagous and feeds from a variety of sylvatic and domestic vertebrates including humans. In Panama, *R. pallescens* inhabits palm crowns, principally the crown of the royal palm (*Attalea butyracea*), which is abundant across anthropogenically disturbed landscapes (Whitlaw and Chaniotis 1978; Barrett 1991; Romaña et al. 1999; Fernando Abad-Franch et al. 2015; 2009; Fernando Abad-Franch and Monteiro 2007). There is a frequent association between palm crowns and the triatomine tribe *Rhodniini* in part due to the palm's unique structural attributes and the micro-abiotic and biotic conditions provided; rendering the palm an ideal ecotope for triatomine infestation. Preferences for the palm crown ecotope are also shared with other taxa (Battirola et al. 2017; Santos et al. 2003; Lahey and Gunnels 2013; Gurgel-Gonçalves et al. 2006). The presence of various mammals (i.e.marsupials) and birds (*Thraupis* spp.) are also found within the crown and they provide a regular food supply for triatomines. Because of this co-adaptation, the presence of triatomine blood meals is associated with higher infestation probability (see Abad-Franch et al. 2010). In particular, opossums are known to be heavily associated with infestation and infection of palm dwelling triatomines due to the co-evolved adaptation to palm crowns, their adaptability to anthropogenic disturbance, and high competency as reservoirs for *T. cruzi* infection (Noireau, Diosque, and Jansen 2009; Gaunt and Miles 2000b; Yeo et al. 2005; Olifiers, Gentile, and Fiszon 2005). Invertebrate predators, such as spiders, centipedes, and scorpions, are also associated with palm crown conditions (Couturier et al. 1996; Santos et al. 2003; Gurgel-Gonçalves et al. 2006), however, their role as triatomine predators is less known. In the palm crown, *T. cruzi* is transmitted between wild mammal hosts and vectors primarily via contact with infected vectors and their feces or via oral ingestion (i.e. predation) of infected vectors (Lent and Wygodzinsky 1979; Schofield 1994). In addition to being blood meals and reservoir hosts for the Chagas disease agent *Trypanosoma cruzi*, many mammals inhabiting palm crowns are also potential predators of *R. pallescens.*

The *T. cruzi*-triatomine vector-palm system is a useful model to study impacts of vectors and vector-borne pathogen responses to variations in both food web structure and microenvironmental conditions. In previous studies within central Panama, deforestation has been linked to an increase in *R. pallescens* abundance and infection with *T. cruzi* (Gottdenker et al. 2011; 2012) and the mechanism driving this pattern may be attributed to changes in palm community and microenvironmental conditions. Identifying these mechanisms is essential to understand the sylvatic cycle of Chagas disease in central Panama. Palm crown physiognomy such as palm height, number of leaves, epiphytic plants and volume of organic matter, can be indicators of triatomine infestation in palms and have been positively associated with the relative density and distribution of some triatomine species (Urbano, Poveda, and Molina 2015; Fernando Abad-Franch et al. 2010; 2015). In laboratory settings, studies have also shown that temperature and humidity fluctuation regimes influence triatomine population density, distribution, development, mortality, and behavior as well as the interaction between trypanosome and triatomines (Luz, Fargues, and Grunewald 1999; Urbano, Poveda, and Molina 2015; Guarneri et al. 2003; Schilman and Lazzari 2004; Elliot et al. 2015). For example, increasing temperatures are associated with *T. cruzi* growth and triatomine diuresis and biting rate, all of which can influence the transmission of the parasite (Okasha 1964). Despite these studies regarding palm tree conditions and triatomine infestation, further investigation into the palm crown species community is lacking and can provide the next step in understanding the sylvatic cycle of Chagas disease in central Panama and potential means of vector control and disease prevention. Studying the food web network in palm crowns can give a general insight into the trophic relationships that exist within the palm tree, and how they might drive Chagas disease transmission.

In this study, we aim to evaluate biotic and abiotic factors related to kissing bug abundance and *T. cruzi* vector infection by investigating whether changes in community composition, network, and palm microhabitat and microclimate influence the risk of Chagas disease transmission. Determining these drivers can help implement feasible ways of *R. pallescens* vector control in rural regions of central Panama, such as palm crown management (see Abad-Franch 2015). We hypothesize that *R. pallescens* abundance and infection with *T. cruzi* will increase with a decrease in palm crown species diversity, an increase in the presence of overall blood meals, a decrease in host blood meal diversity and increase in highly competent mammalian blood meals (e.g. opossums). Furthermore, we predict *that R.* pallescens abundance will be lower when there are higher numbers of predator species in the palm crown (i.e. greater *R. pallescens* vulnerability). We also hypothesize that *R. pallescens* abundance is favored by a palm crown microhabitat with increased "complexity" (i.e. greater number of leaves, organic matter at the base of the crown, and presence of fruits, etc.). We predict that palms with increasing microhabitat complexity will be associated with ideal microclimate conditions for this species- between 25-28 C, centering around 27 C, and average RH of 70%, or a range of 60-85%, thereby supporting greater abundances of *R. pallescens* (Luz, Fargues, and Grunewald 1999; Okasha 1964). We also predict that palms in gradients of disturbance that attract synanthropic or transient mammals, will increase *R. pallescens* generality and will subsequently increase their abundance and infection and palms found within less disturbed habitat will maintain greater community diversity and lower vector abundance and infection because of higher invertebrate predator species presence.

4.2 METHODS

Study location and sites

The study was conducted across the western-Central Panama provinces of Panama Oeste and Veraguas. Within these provinces, we chose sites within the La Chorrera (8°52′49″N 79°47′0″W), Capira (8°45′0″N 79°52′12″W), and Santa Fe (8°30′N 81°04′W) districts. This ecoregion is considered lowland and montane tropical moist forest, respectively (Holdridge 1967). The habitat within these regions is comprised of a mosaic of agriculture, forest remnants, human settlements, and different successional stages of regenerating forest (Condit et al 2001, Ibanez et al 2002). Within each location, palm selection was further assessed from a main road throughout gradients of deforestation represented by peridomestic, pasture, and forest fragment land use types (Figure 1). These three landscape classes were distinguished in the field and verified through satellite imagery (Google Earth 2012). The *Attalea butyracea* palm crowns were identified in these landscape classes, and landowner permission was obtained for palm sampling. Final palm selection for *R. pallescens* sampling was limited by accessibility of the palm crown. This included palm crown height limited by sampling techniques (*discussed in later section).* Palms chosen for subsequent community sampling were further limited by terrain conditions which was also restricted by palm crown community sampling techniques. Given these initial limitations, all remaining palms were opportunistically sampled for *R. pallescens* and, permitting, community and microclimate conditions. All palms were sampled during the wet season (June-July) from 2013-2016 and from June-

November 2017, although 16 palms were also sampled in Capira (N=13) and La Chorrera (N=3) across habitat types during the dry season (Dec.-May) in 2017. Palm crown community sampling occurred during midday hours of 1100-1600.

Sampling for Rhodnius pallescens

Rhodnius pallescens were captured using a modified mouse-baited trap adapted from (Noireau et al. 2002). A total of three traps were placed within each palm and throughout the crown, out of direct sunlight, and checked every 24 hours for three days. This sampling method was adopted from Abad-Franch et al. 2000 and Gottdenker 2011. Each day when checking the trap, *R. pallescens* were collected and stored in 95% EtOH for molecular analysis. Traps were resupplied with food (a mix of dry cat food and fruit) and water (water-soaked cotton balls) for the mice (1 mouse/trap). The *Attalea* palm crown was accessed using a combination of a 20 ft aluminum ladder or climbing harness with anchored support to the palm trunk. For palm crowns higher than 20 ft, a collapsible pole device was used to place the traps within the crown (IACUC approval 2013-0601-2016-02; 2016-0801-2019-A1).

Microhabitat and Microclimate Conditions

For a subset of palms (N=49) we collected information on the species community within the crown as well as microhabitat and microclimate conditions. Palm traits can vary drastically across habitat type, therefore it was essential to collect information pertaining to the architectural characteristics of the palm. For each palm crown, we collected the following microhabitat conditions: % surrounding canopy cover (percentage of forest cover measured at 5 m distance from the sampled palm at the four cardinal locations), palm stem height (base of trunk – top of crown (m)), number of connected trees (count of other trees physically connected to the sampled palm), level of dead organic matter (DOM; scale 1 (low) – 4 (high), presence of infructescence (yes/no), and number of epiphytic plants (Figure 2A-D). These microhabitat conditions were an index of palm crown complexity, in which higher levels of organic matter, epiphytic plants, and infructescence contribute to a palm that had a high level of organic matter at the crown base adapted from Abad-Franch et al., 2005. Microclimate conditions such as average relative humidity (%RH) and average temperature (*Celsius*) were also collected from within the palm crown using data loggers (Reed R6020, Wilmington, North Carolina, and HOBO, Cape Cod, Massachusetts; USA) that were placed in palm frond crevices throughout the crown (3 loggers per crown) for a subset of palms (N=52). Data loggers measured temperature and % RH every minute for 3 days prior to palm crown community sampling.

Community Collection

After sampling *A. butyracea* for *R. pallescens* with modified Noireau traps, the crown communities were sampled by active direct searching for an additional 3 consecutive days for 30 minutes per palm, although during periods of heavy rains palm sampling would resume on a following dry day. The palm crown was dissected systematically, starting from the removal of the outer older fronds and ending at the center of the crown. Younger fronds, which were stronger and more difficult to remove, were cut at the base and removed using a battery-powered reciprocating saw. Invertebrate specimens were vacuumed using a handheld battery-powered vacuum (BioQuip Products, Inc., Rancho Dominguez, CA, USA) upon detection either during active frond removal while in the crown or during “frond beating” and dead organic removal. Frond beating consisted of beating the fronds and extracting dead organic material, allowing all materials, including invertebrates, to fall on a tarp on at the base of the palm. During frond beating and dead organic removal, a field assistant would collect all invertebrates using forceps and a hand-held vacuum. Dead organic material was also collected in a 1- quart sized Ziploc bag and later brought to the lab further to sift for invertebrates with a colander (mesh size 1/32 inches). All invertebrates were later stored in 95% EtOH. Vertebrate signs (i.e. hair, nests, feathers) were also collected as an indicator of vertebrate presence in the community. All specimens were processed at the Smithsonian Tropical Research Institute, Naos station, in Panama City, Panama.

Species identification and food web

All invertebrate species were identified to the lowest taxonomic resolution possible. However, we put a particular emphasis on invertebrate predator species identification. Once identified to the lowest taxonomic resolution, individuals were grouped into morphospecies and trophic species. Trophic species are species that are grouped together because they share the same predators and prey species (Briand and Cohen 1984). A binary feeding matrix was constructed for each palm community. A binary feeding matrix consists of a matrix of species (in both row and column) found in the crown and describes whether the there is a feeding interaction (1) or no feeding interaction (0) between species. Feeding interaction was determined by observations from the field, natural history and literature of consumer-resource interactions for each morphospecies and weighted by species abundance. Food webs were created using the computer software Network3D version 1.0 (Yoon et al. 2004, Williams 2010) and a food web was generated for each palm crown. Network3D measures trophic composition and network complexity and structural characteristics of a given community. Specifically, we looked into the network metrics species count, links/species, connectance, Fraction Top, Intermediate, Basal, generality, vulnerability and *R. pallescens* vulnerability and generality.

Molecular Analysis

Blood meal analysis

We conducted Next Generation Sequencing to identify vertebrate blood meals fed on by *R. pallescens* following the protocol outlined in (Kieran et al. 2017). Captured *R. pallescens* used for blood meal analysis underwent gut dissection and DNA was extracted from guts using Phenol-Chloroform-Isoamyl alcohol. This method targets the 12S rRNA gene specific for vertebrates and designates an Operational Taxanomic Unit (OTU) for species identification. This method was also used to confirm the presence of any vertebrates that were initially detected through signs such as nest, hair, fur or feathers found within the palm crown during the community sampling period. Because the main focus of NGS was detecting blood meals of wild animals associated with the *Attalea* palm, blood meal hits from humans, house mouse (*Mus musculus*)-the species used in the triatomine traps, or domestic animals were omitted from the final analysis of the palm crown food web. For a conservative estimate of blood meal source, we eliminated species hits receiving ≤10% of total read hits for the sample. Only sylvatic vertebrates that can possibly be found in the palm crown were included in the final analysis.

Trypanosome detection

We detected the presence of *Trypanosoma cruzi* using polymerase chain reaction which targeted the 330 base pair fragments from the kinetoplast minicircle DNA using the protocol for PCR conditions outlined in Morel et al. 1994. The primers used were 121 (5' – AAATAATGTACGGG(T/G)GAGATGCATGA – 3') and 122 (5'-GGTTCGATFGGGGTrGGTGTAA TATA-3'). PCR products (5 ml) were mixed with loading dye and electrophoresed on a 2% agarose gel stained with GELSafe dye at 86 volts and evaluated by ultraviolet light for the presence of bands of a length specific for *T. cruzi* (330 bp). Positive and negative controls were run for each reaction.

Missing Data

Instances of missing data occurred in palms (N=18) when data loggers measuring temperature and humidity were deployed within the palm crown for multiple days but malfunctioned or were lost after wild and domestic animal intervention, extreme weather, or had fallen into deep crevices between the palm fronds. To handle the values of the missing data, we used the R package *Amelia II* (Honaker, King, and Blackwell 2011) which is based on running an expectation maximization (EM) algorithm of incomplete multivariate datasets to create multiple imputed data that contain missing values. Our final values of %RH and average temperature within palms are based on the average values from 10 imputed datasets.

Data Analysis

All statistical analysis was performed using the software R 3.5.3 (RStudio Team 2015).

Community Network Analysis and Microenvironment Variables

To investigate the influence of the palm crown community on *R. pallescens* abundance and infection with *T. cruzi*, we looked into both the palm crown community and species -level network metrices using the output from the software Network3D (Williams 2010, Yoon et al. 2004). Network measurements at the community level include community diversity (calculated by the Simpson's Diversity Index ($D = 1 – (\Sigma (n(n-1)/(N(n-1))$), richness (no. of species), GeneralitySD (the number of prey in a community, normalized by links/species) and VulnerabilitySD (the number of predators in a community, normalized by links/species) (see Williams and Martinez 2013). Alternatively, we looked at the network specific to *Rhodnius pallescens* which focused on the interaction between *R. pallescens* and the surrounding members of the species community. Similar to the community-level, we focused on prey and predator interactions with *R. pallescens* which is also measured by vulnerability (number of *R. pallescens* consumers) and generality (number of *R. pallescens* hosts) of each palm crown. We included the community- wide network metric as a proxy for additional underlying factors stemming from other trophic species, which may otherwise be overlooked when only incorporating specific predators and blood meal species of *R. pallescens*. In addition, we included abundance data of particular species of interest for *R. pallescens*, such as count data of individual host/vertebrate blood meal taxa: reptiles, bird, mammal (further separated into coendu, tamandua, bat, opossum) as well as potential invertebrate predator species: scorpion, spider, tarantula, centipede, whip spider. It is obvious that some network characteristics will correlate strongly with the presence and abundance of particular species (i.e. "spider" positively correlated with network vulnerability or "mammal" is correlated with *R. pallescens* vulnerability and generality). To also account for the effects of microenvironment on both response variables, we incorporated the aforementioned microhabitat and microclimate covariates (see *Supplementary Information Table 4.1*).

Model Structure

To assess drivers of microclimate, microhabitat, and community on the response variables *abundance* and *infection* (1-*infected*, 0-not *infected*) of *R. pallescens* for each palm, we applied a generalized linear mixed-effects model (GLMM). These mixed models are flexible for complex and mixed data types including those with non-normal distributions or nonlinear responses to various predictor variables (Bolker et al. 2009). In our models, *R. pallescens* abundance fit the negative binomial distribution with a log link function. Negative binomial is an extension of Poisson distribution and fits count data that is overdispersed as was observed for the *R. pallescens*. Furthermore, the binary outcome of infection (infected/not infected) was fitted with a logistic regression with a logit link function. For both models, palm ID was treated as random variable to account for the random variation attributed to the palms selected and was further nested by '*R. pallescens* ID' in our infection model to account for the random variation in the *R. pallescens* that were collected across sampled palms. The locations Santa Fe, Capira, and La Chorrera, and land use types pasture, peridomestic, and forest fragment, were treated as fixed variables because the effects from these variables remain constant for every *R. pallescens* collected from a selected palm therefore would not vary randomly between individuals, also, because we were interested in the effects that both land use type and location have on both response variables.

To build our hypothesis-based model, we explored the correlation between the aforementioned explanatory variables and between explanatory and response variables. During the initial variable exploration, Pearson correlation was used to investigate the direction and strength between continuous explanatory variables and the response variable *abundance*. Point-Biserial correlations was used to investigate continuous and categorical explanatory variables, including the response variable *infection*. Explanatory variables were re-standardized to improve model output interpretability and reduce multicollinearity and variables that did not have a significant relationship with either response variable or was highly correlated with another explanatory variable was removed from further analysis. Collinearity between the continuous predictor variables was investigated using the variation inflation factor (VIF) and omitted any strongly correlated variables using (VIF > 2.9) In addition to VIF, we investigated *variable tolerance*, which indicates the percent of variance in that variables that cannot be accounted for by other predictors. Determination of the final model for abundance (equation 1) and infection (equation 2) was based on hypothesis-based testing and using the Akaike Information Criterion (AIC) for model selection, which combines information and maximum-likelihood theories to find models with the best compromise between model fit and complexity (Burnham and Anderson 2004). The final model represented the best fit between lower AIC value, and least complexity (to avoid overparameterization) with AIC value better supported by the data (see *Supplementary Information Tables 4.2 and 4.3*). The final model assumptions and diagnostics were also verified using the *DHARMa* package (Hartig 2019) and further confirmed model fit using residual plots for the full model using a simulation-based approach.

Equation 1:

$NAbundance_{ij} \sim negative\ binomial\ distribution\ (\mu_{ij})$

$E(NAbundance_{ij}) = \mu_{ij}$

$Log\ link(\mu_{ij}) = (1|palm\ site) + location_{ij +} habitat_{ij} + community\ diversity_{ij} + scorpion_{ij} + R.\ pallescens\ vulnerability_{ij} + dead\ organic\ material_{ij}$

Where $NAbundance_{ij}$ is the jth observation in palm i, and i = 1, 2, 3, …49.

Equation 2:

$N(InfectionStatus_{ij}) \sim\ binomial\ distribution\ (\mu_{ij}\ (1- \mu_{ij}))$

$E(InfectionStatus_{ij}) = \mu_{ij}\ (1- \mu_{ij})$

$Logit\ link\ ((\mu_{ij}\ (1- \mu_{ij})) = Location_{ij} + nymph/adult_{ij} + mammal_{ij} + Spider_{ij} + (1|palm\ site:\ bug.ID)$

Where $Nprop.infected_{ij}$ is the jth bug in palm i, and i = 1, 2, 3, …49.

4.3 RESULTS

Sampling for R. pallescens and vector infection

A total of 1098 *R. pallescens* were captured from 105 palms across gradients of anthropogenic disturbance in La Chorrera (N=42; pasture N=13, Peridomestic N=16, forest fragment N=13), Capira (N=47; pasture N=21, peridomestic N=20, forest fragment N=6), and Santa Fe (N=16; pasture N=8, peridomestic N=5, forest fragment N=3) (Table 4.1 A). Overall, we recovered *R. pallescens* from 81% (85/105) of palms. The percentage of palms infested with *R. pallescens* was highest in Santa Fe (93%) compared to Capira (74%) and La Chorrera (84%) and on average, the number of *R. pallescens* captured from infested palms ranged from 11.5 (95% CI 4.5 – 18.4) in Capira to 19.1 (95% CI 10.6 – 27.6) in Santa Fe. Across all land use types the percentage of palms infested by triatomines was consistently high (>%60) except for palms found in forest fragment in Capira (%33) (Table 4.1 B). There was consistently a greater number of nymphs than adults across location (Pearson's $\chi^2 = 27.14$, df = 2, $p<0.05$) and land use type (Pearson's $\chi^2 = 33.21$, df = 2, $p<0.05$). Also, the nymph:adult ratio varied across location, with the number of nymphs per adult being overall lower throughout land use types within Santa Fe. The colonization index of palms (number of palms with nymphs/number of palms with *R. pallescens*) was relatively high throughout all locations and habitat types, ranging from .88 in Santa Fe pasture to 1.0 in multiple locations and land use types, although was lowest in Santa Fe forest fragment at .50. Of nymphs collected, there were fewer N4 and N5 stages found within palms compared to stages N1-N3 across all locations and habitat types (*Supplemental Information Table 4.4*).

Of 1098 *R. pallescens* captured, a total of 476 individuals were tested for *T. cruzi*. Overall, *T. cruzi* infection was detected in 38% (181/476) of *R. pallescens* (Table 4.2 A). A low overall infection rate, compared to the similar study by Gottdenker et al (2012), may be due to the incorporation of the N1 and N2 stage nymphs that were collected but were still uninfected. The proportion of *R. pallescens* infected with *T. cruzi* was highest in Santa Fe 57% (74/130) compared to La Chorrera 28% (52/186) and Capira 34% (54/160). Overall, the proportion of infected adults was higher than nymphs across all locations and land use types, except in peridomestic and forest fragment palms found within Capira and Santa Fe, respectively, where the proportion of infected nymphs was higher (Table 4.2 B). Furthermore, the percentage of bugs infected was typically higher in forest fragment and peridomestic compared with pasture palms across all locations. Proportion infected did vary across nymph stages across location and land use types, and at times infection rate was higher at a nymphal stage than at the adult stage among individuals collected within the same palm (see *Supplementary Information Table 4.5*). Overall, with increasing nymphal stage, the probability of infection also increased, with the highest probability of infection at the adult stage; although we did detect a sharp increase from stages N1 to N2 (Figure 4.3).

Blood meal analysis

Next Generation Sequencing was conducted on 240 individual bugs across 31 palms in Capira (N = 9), Santa Fe (N = 8), and La Chorrera (N = 14). Blood meals from sylvatic species were identified from 73% of captured individuals (174/240). Of the blood meals where more than one species source had been identified, we used the most recent sylvatic blood meal for the community analysis as a species recently found in the palm crown. Overall, a total of 7 Orders were identified, including 15 genera and 9 species. Blood meal richness at the level of Order and Genus was highest in La Chorrera (6 Orders, 10 Genera), followed by Capira and Santa Fe (5 Orders, 7 Genera). Mammalian species, particularly those belonging to the Order Didelphimorphia, dominated blood meal composition (>50%) across all locations compared to bird, lizard blood meals (Figure 4.4 A-C; see *supplementary Information Table 4.6*).

Of the 240 *R. pallescens* that underwent NGS, 177 individuals were tested for infection with *T. cruzi* across Capira (N=73), La Chorrera (N = 44) and Santa Fe (N = 60) and 45% tested positive (79/177). Of the 79 total individuals that were positive, 70% (53/79) had most recently fed from Order Didelphimorpha. In total, marsupial blood meals were confirmed for 27% (53/193) of the positive cases (Figure 4.5). For our final infection model, we exclusively focused on blood meal and infection of nymphal stages N3 – N5 and adult because we had a more complete test results of larger nymph stages given the difficulty in gut dissection of early stages.

Community and Microenvironment: Associations with R. pallescens abundance and T. cruzi infection

A total of 49 palms were sampled for species community, microclimate, and microhabitat variables from La Chorrera (N = 29), Capira (N = 15), and Santa Fe (N = 5). Of the invertebrate predators of interest, the proportion of spider taxa was the highest across all palms and locations (Figure 4.6 A-B). Correlation plots further indicated which components of food web network, vertebrate and invertebrate species composition, and microenvironmental conditions were significantly positively or negatively associated with *R. pallescens* abundance and *T. cruzi* infection and identified (Figure 4.7 A-F). Of the microhabitat conditions, increasing dead organic matter was the only variable that was positively associated with *R. pallescens* abundance. The average palm crown temperature ranged from 25-28 C across all locations and 79 – 98 %RH, however, we did not find a significant association between response variables and the average temperature and relative humidity within the palm crown. A shorter study was conducted on a subset of palm microenvironment conditions in June and July 2015, which included both ambient and palm crown temperature and % RH comparison and diurnal fluctuations (Padukone, 2015, *unpublished MS thesis, Princeton University*). Results from this study concluded that relative to the ambient conditions, intra-palm microclimate experienced lower maximum and greater minimum temperature and %RH creating more stable conditions and a buffer from the external environment. In particular, changes in temperature and RH range relative to ambient temperature was greatest in pasture palms compared to peridomestic and forest palms. It was also concluded that the microclimate conditions observed in palms were influence by microhabitat conditions, such as organic matter and number of connected trees, rather than the land use type *per se*. For our current model, we focused on average temperature and %RH of palms and discuss the potential impacts of dampened microclimate conditions and reduced temperature and humidity ranges and variation on triatomines in a later section.

After initial variable exploration, final explanatory variables included: habitat type (nominal; *pasture, peridomestic, forest fragmentation),* location (nominal; *La Chorrera, Capira, Santa Fe*) and dead organic matter/DOM (ordinal *with 4 levels*).Of the community components, we found a significant positive relationship between '*mammal*' presence including '*coendu*', '*tamandua*', '*bat*', and '*opossum*' and vector abundance but alternatively, mammal sign presence had a negative relationship with infection. Infection additionally had a negative and positive relationship with '*lizards*' and '*birds*', respectively. Invertebrate predators '*spider'* and '*scorpions*' had a positive relationship with infection and abundance, respectively, however infection was further positively associated with predators '*phyrinidae*', and '*chilopoda*'. Lastly, networks metrics: *R. pallescens*: '*generality*', '*vulnerability*' and network '*vulnerability*' were positively associated with abundance and infection, respectively. Overall community '*diversity*' was negatively related to vector abundance and '*R. pallescens abundance*' positively associated with infection. All correlations were conducted using a Pearson and Biserial correlation test for abundance and infection, respectively (Figure 4.7 A-F). All significant variables had a p-value no greater than 0.05. Multicollinearity between particular variables, for instance '*R. pallescens* generality' and mammalian variables or invertebrate predator variables and '*network vulnerability*', were reduced by checking the variation inflation factor (VIF< 2.9) in the final model (*see Supplementary Information Table 4.2 and 4.3*).

Covariates were further reduced after checking multicollinearity. After reducing covariates, the final variables included were scorpion (*count*), spider (*count*), mammal (*count*), *R. pallescens* vulnerability, generality, crown diversity and species richness (*continuous*), *R. pallescens* abundance (*count*), and *R. pallescens* nymph adult stage (*nominal*).

Generalized Linear Mixed Model Results

We built a model to predict *R. pallescens* abundance and infection status as an effect of both abiotic and biotic drivers that were based on the collective information gathered from laboratory diagnostics NGS (e. g. verification of mammals/blood meals), PCR (e.g. proportion infected with *T. cruzi*), and field collection on palm crowns (e.g. vector abundance, community, microclimate, and microhabitat).

Our model suggests that *R. pallescens* abundance is an effect of location and habitat type as well as community diversity, in particular the presence of blood meals and to a lower degree invertebrate predators, including scorpions (Figure 4.8 A-B). There is a predicted increase of vectors within palms located in Santa Fe ($p = 0.007$) and La Chorrera ($p = 0.001$) along with the presence of blood meals and some invertebrate predators (*R. pallescens* vulnerability) ($p<0.001$), particularly scorpions ($p = 0.034$). However, vector abundance decreases in pasture palms ($p = 0.023$) and communities with a higher Simpson's diversity ($p = 0.005$). Although an increase in abundance was associated with high levels of dead organic matter (DOM = 4), this relationship was not as significant as the aforementioned covariates. The proportion of variance explained by the fixed factors alone was (marginal $R^2 = 0.55$) while the proportion of variance explained by both the fixed and random factors remained unchanged (conditional $R^2 = 0.55$).

We also determined that the probability of an infected *R. pallescens* individual is influenced by location, particularly in palms found in Santa Fe where probability of infection increases ($p = 0.008$); and also, particular members of the palm crown community, such as spiders ($p = 0.03$). Although we detected a positive association between '*mammals'* and probability of infection when using blood meal composition results only, the variable 'mammals' as a proxy for mammal diversity within the palm crown community indicated a decrease in the probability of infection. For example, the presence of mammals detected during our palm crown surveys indicated mammals were present in the palm but were not necessarily fed upon. In our final model, mammal diversity actually decreased the odds of infection in *R. pallescens* individuals as did the presence *R. pallescens* nymphs ($p = 0.025$) (Figure 4.9 A-B). The proportion of variance explained by the fixed factors alone was fairly high (marginal $R^2 = 0.636$) while the proportion of variance explained by both the fixed and random factors was higher (conditional $R^2 = 0.79$). When blood meal and infection results of *R. pallescens* individuals were used only and omitted the palm crown community metrics such as mammal diversity, the model suggested that blood meal diversity, particularly opossum and rodent blood meals combined ($p = .058$), increased probability of infection, although this effect was less significant when the model included location (p = 0.03) and stage of triatomines (p = 0.09).

4.4 DISCUSSION

Our study aimed at disentangling the abiotic and biotic drivers of *R. pallescens* abundance and infection with *T. cruzi* within *Attalea* palms in central Panama in order to identify mechanisms of increased *R. pallescens* abundance and *T. cruzi* infection associated with deforestation in central Panama. We also investigate how community structure can shape multi-host disease risk (Roche et al. 2012; Achee 2006; Pieter T. J. Johnson et al. 2008; P. T. J. Johnson and Thieltges 2010; Felicia Keesing et al. 2010). To understand both abiotic and biotic drivers of infection and abundance, we used results from community, blood meal, and molecular analysis of *T. cruzi* infection. We found that both *R. pallescens* abundance and infection are indeed influenced by habitat conditions, both stemming from within the palm crown and the surrounding habitat, as well as across locations. We also found that *T. cruzi* vector infection was largely driven by diversity and composition of the animal (vertebrate and invertebrate) community within the palm crown.

Land use and site factors influencing vector abundance and infection

Anthropogenic disturbance across central Panama continues to be a significant factor in *R. pallescens* abundance and infection. In response to forest fragments and peridomestic land use types, *R. pallescens* abundance is predicted to increase (Figure 8B) which is consistent with the previous observation of abundance in early-secondary forest and mid-secondary forest fragments compared to contiguous forest (Gottdenker et al. 2011). Furthermore, our model associates pasture palms with a significant decrease in *R. pallescens* abundance. This observation is likely due to more drastic changes in the microclimate conditions within pasture palm crowns which in turn could also be associated with a decrease in surrounding vegetation (i.e. number of connected trees, canopy cover, etc.) and will be discussed in the following section. Despite land use type being significant for *R. pallescens* abundance, we did not observe land use type to influence infection probability with *T. cruzi*.

There were also regional differences in abundance and probability of infection. In Santa Fe, which is further west than La Chorrera and Capira, there were higher percent of infested palms and a greater average number of triatomines per infested palm and although nymphal stages are predicted to decrease probability of infection, there was an increase in both infected nymphs and adults within the Santa Fe palms. An increase in infected individuals across triatomine stage, particularly among nymphs, may reflect on the variation of infection and blood meals across *R. pallescens* stages and location. In Santa Fe, the overall blood meal composition was less diverse for both nymphs and adults who primarily fed from opossums and sylvatic rodents compared to individuals found in Capira and La Chorrera, which had a more diverse blood meal composition (see *Supplementary Material Table 6*). This diet on mainly rodents and marsupials may explain for the increased infection rate for both nymphs and adults which is backed by our model that had used blood meal results only which indicated that both rodent and opossum blood meals combined was positively associated with the probability of infection. Although this model indicated host availability positively influenced *T. cruzi* infection, it did not single out a particular taxonomic group as a significant driver (i.e. rodents, marsupials, etc.) although opossums did dominate blood meal composition.

Community diversity associated with vector abundance and infection

Biodiversity and emerging infectious disease have been heavily researched in recent decades and studies often associate increased disease risk as a consequence of declining diversity (Ostfeld and Keesing 2000; F. Keesing, Holt, and Ostfeld 2006). Our research demonstrates that in addition to overall diversity, particular elements of the trophic network, namely invertebrate predators and vertebrate blood meals, are significant in both positively and negatively driving *R. pallescens* abundance and probability of infection. In support of our hypothesis, our study suggests that increased community diversity, measured as the palms crown Simpson's Diversity, negatively impacts *R. pallescens* abundance. In a previous study on the

Attalea palm crown community (Varian, *unpublished)*, species community diversity was high (Simpsons diversity index > .80) in both forest fragments and pasture palms (albeit slightly higher in forest fragments) but the trophic structure differed in palm crowns from these habitats. This suggests that although the number of species and their abundance stay relatively consistent, community composition and trophic structure varies across land use type as well as location. Indeed, pasture palms were characterized as having higher mid-trophic level species diversity, which includes invertebrate and some smaller vertebrate predators (e.g. lizards and geckos) that potentially predate on triatomines. Because palms within pasture habitats were also negatively associated with abundance, these results may be driven by community characteristics within the palm, in addition to crown microhabitat conditions, as we mention further in this discussion.

Of the community variables, particular vertebrate and invertebrate taxa influenced both abundance and infection. While the presence of mammals (indicated by the detection of mammals signs whose presence was additionally confirmed using blood meal analysis) in the palm crown community increased *R. pallescens* abundance, it actually was associated with a decreased predicted probability of infection. The model result regarding probability of infection is counterintuitive since mammals, particularly opossums, are reservoirs for *T. cruzi.* However, when alternatively, modeling infection using confirmed mammalian blood meals only and omitting presence indicated by the mammal signs detected in the palms (which weren't always confirmed with NGS), mammals did have a positive association with increased infection probability. This suggests that although mammals may be present in the palm crown, they will only have a positive effect on infection probability if they are fed upon by *R. pallescens*. In other words, mammal detection in the palm may not directly result in increased *R. pallescens* infection, potentially due to mammals leaving a palm crown, or movement of the mammal, before being fed upon by triatomines. A negative association between the probability of infection and mammal presence could be driven by mammal behavior in the palm crown (i.e. nest making) that could attract other species which have a potential indirect negative influence on *R. pallescens* (i.e. competition for space, predation, etc.)

Alternatively, mammal (vertebrate predators) well as potential invertebrate predators, were positively associated with vector abundance, which was reflected in the covariate '*R. pallescens* vulnerability'. In our study, vulnerability refers to predators of *R. pallescens*, which includes all vertebrates (which are also blood meals) in addition to invertebrate predators (e.g. spiders, scorpions). Our prediction on the relationship between abundance and mammals was supported and is consistent with the literature as synanthropic species such as opossums have been consistently identified as a major blood meal source of palm dwelling triatomines (Gaunt and Miles 2000a; Yeo et al. 2005; Pineda et al. 2008; Christensen et al. 1980) particularly because they are resilient to gradients of anthropogenically disturbed landscapes. Alternatively, these blood meals can also act as *R. pallescens* predators. Furthermore, the significance of '*R. pallescens* vulnerability' as an influential factor for increased vector abundance overshadows the significance of any particular taxa. Although individual blood meal species composition was initially associated with *R. pallescens* abundance (Figure 7A) and previous studies identify host accessibility and triatomine infestation as important to vector abundance (see Abad-Franch et al 2005, 2010; Rabinovich 2011), the metric 'vulnerability' indicates that some aspect of predator presence also influences triatomines. Interestingly, scorpions, which were considered an invertebrate predator, were actually a positive driver of abundance, so 'vulnerability' having a positive effect on abundance may be a result of the combined impact of blood meal and scorpion, or the presence of another invertebrate predator. Although, this combination was alternatively modeled (i.e. mammal and scorpion separately), those model AIC scores were still ranked lower than '*R. pallescens* vulnerability'. Both increased vulnerability and community diversity had opposing effects on abundance suggesting, that a greater number of species in the palm crown community that are unrelated to *R. pallescens* predator or prey, may have an indirect negative influence on *R. pallescens*.

Potential Invertebrate predators on infection and abundance

Although effects of arthropod predation on kissing bugs is relatively understudied, jumping spiders (*personal observation*) and lizards (Ramírez, González, and Botto-Mahan 2013) are potential predators of triatomines and other reduviids. We observed that scorpions, a potential predator, were positively associated with *R. pallescens* abundance, therefore its presence may not necessarily translate to higher predation rates on *R. pallescens*. Haemolymphagy has been observed between some triatomine species and cockroaches, suggesting an important survival strategy for the development of starved kissing bugs (Durán et al. 2016; Schmidt, Dorn, and Klotz 2019). Other reduviids (non-triatomines) have also been observed to feed from scorpions under cohabitation in leaf litter (Lira, Araújo, and Albuquerque 2016; Morocoima et al. 2011; Stevenson and Stohlgren 2015). This indicates that the positive association with *R. pallescens* abundance may be supported by scorpions due to potential haemolymphagy in areas devoid of vertebrate blood meals. Scorpions were commonly found across all habitat types, so their presence was reliable, particularly where fronds connect at the base of the palm crown. The positive association may be also be due to other interactions such as intraguild predation or competition between predator species, that outweigh the potential impacts on vector abundance control by predators (Snyder et al. 2006; Müller and Brodeur 2002). It can also be a preference by both *R. pallescens* and scorpions for similar microhabitat conditions provided by the palm crown, since the scorpions found in the Attalea palms are considered ‘bark scorpions’(Families Buthidae and Hemiscorpiidae) and are known to inhabit trees or tight crevices (McReynolds 2008; Stockmann 2015).

While invertebrate predator presence is recognized to mainly alleviate disease risk (Moore, Borer, and Hosseini 2010; Finke 2012; Carlson et al. 2009), spider presence and an increase in infection seems like another counterintuitive result because spiders, which are often vector predators, could possibly decrease pathogen transmission indirectly by decreasing vector abundance. In the instance when a predator increases infection probability, the predator likely impacts pathogen transmission via non-consumptive methods such as alter vector behavior (Finke 2012). For example, predators have been linked to decreasing disease risk by preying on vectors (Snyder and Wise 1999) however, predators can increase disease risk via non□consumptive effects such as altered transmission rates, vector birth rates, and/or non□predation vector mortality, which are predicted to have more variable outcomes (Finke

2012). In this system, one way that spiders can potentially impact *R. pallescens* infection is by predating on uninfected nymph stage and increasing the proportion of adults, who are more likely to be infected. Spiders may also have an indirect consumptive effect on *R. pallescens* by predating on a species that competes for space within the palm crown. This result may also indicate an interaction with other components of community from combined or additive effects such as shared preference for microhabitat as with hosts or that mammals who modify palms increasing potential places to hide for the spider.

With respect to land use type, the effect of vulnerability, scorpion, and diversity on *R. pallescens* abundance was consistently lowest in pasture palms compared to forest and peridomestic palms across locations (Figure 4.8B). The positive impact of scorpions and blood meals was greatest in forest palms, and the negative impact of diversity on abundance was also greatest in forest palms. Forest palms *per se* were not a significant driver in abundance, suggesting that community characteristics such as presence of blood meals, community diversity, and scorpion predators may be the underlying driver of the observed increased abundance in forest fragments compared to peridomestic and pasture.

Overall, the significant effects of scorpion and spider occurrence on *R. pallescens* abundance and trypanosome infection, respectively, suggests there may be a positive indirect relationship between scorpion and spider predators on triatomines and disease risk, both of which requires further investigation. This result reemphasizes the potential impacts that other cohabiting community members may have on vector abundance and ultimately infection status. While increasing evidence finds associations between other community members and triatomines (i.e. cockroaches – haemolymphagy, anti-predator defense and lizards (i.e. Ramirez et al 2013) it is will be essential to continue to investigate predatory and non-predatory relationships under controlled conditions.

Effects of microhabitat and microclimate on abundance and infection

Our observations regarding abundance and infection across location and land use type are also influenced by microenvironment characteristics of the palm crown and its immediate surroundings. We investigated palm-level conditions to determine whether microclimate and microhabitat conditions drive what is observed at the landscape level. Previous studies have linked palm crown characteristics such as increased dead organic matter, surrounding canopy cover, and number of connected trees to stabilize temperature fluctuations and reduce temperature and relative humidity extremes throughout the day in *Attalea* palms (Padukone, 2015, *unpublished MS thesis, Princeton University*). Results from that study concluded that such microhabitat conditions created more stable microclimate conditions which positively influenced the *R. pallescens* abundance. Furthermore, dead organic matter, palm height, epiphyte cover, were similarly associated with increased infestation and density in *Attalea* palms found in Brazil and Ecuador, and Colombia, respectively (Abad-Franch 2010, Urbano et al 2015). Urbano (2015) also noted that microclimate stability influences greater numbers of juvenile vector stages. This collective evidence suggests that microclimate stability and increased humidity, influenced by greater organic matter and forest cover, drives *Rhodnius* abundance. Our model results continue to suggest that land use type influences abundance and pasture palms are associated with decreased *R. pallescens* abundance. Overall, microclimate conditions within the palm were consistently in the 'ideal' range for both temperature (average 27.37 C and relative humidity (average %RH 84.83), regardless of land use type. However, pasture palms experienced a greater fluctuation in both temperature and relative humidity throughout a 24hr cycle than peridomestic and forest palms. This evidence suggests that greater microclimate fluctuations within the palm crown and a greater fluctuation relative to the ambient temperature and %RH negatively influences *R. pallescens* abundance, which was observed in pasture palms (Padukone 2015, unpublished). Overall, all palms were observed to be a consistent buffer from ambient temperature and although the palms sampled across land use type had an ideal average temperature and relative humidity for *Rhodnius* infestation, the conditions relative to their surroundings requires a deeper investigation. Because all palms maintained average ideal microclimate conditions, we did not find an association between increased palm crown complexity, microclimate, and abundance, although there is evidence that increased organic matter and canopy cover dampens the microclimate range relative to their external surroundings.

Our study did find that increased palm crown complexity in the form of dead organic matter continues to be positively associated with *R. pallescens* abundance (p=0.07) but was not significant when community metrices were included in the model, which may be attributed to the inclusion of blood meals into the model. Pasture palms had the highest range in microclimate fluctuation with the palm relative to ambient temperatures.

Lastly, our study further suggests that underlying factors that drive the pattern of *R. pallescens* abundance and infection are conditions of the local microenvironment of the palm crown as well as the animal community context within the individual palm crown. Landscape-level disturbance has been associated with establishing microclimate conditions, with cascading effects on vector-borne diseases, but we observed that palm crown microhabitat and microclimate conditions varied widely irrespective of the land use type. Focusing on this local scale may be more feasible when implementing vector control methods in peridomestic palms within central Panama. For example, instead of targeting landscape scale changes in a region, *targeting palm-specific conditions at local levels may be more effective* as a control measure Based on previous studies that focused on triatomine vector control with palm trees (Abad-Franch 2015) and the findings of this research, managing host and predator communities and the palm crown dead organic matter may be the key factor to limiting *R. pallescens* abundance and infection with *T. cruzi* in central Panama. Biocontrol has been of particular interest throughout this research. Determining which components of the palm crown community influenced *R. pallescens* abundance and infection could reveal whether a particular species functioned as a potential biocontrol agent or whether community function as whole that was representative of a particular land use type or palm crown type Predator abundance was associated with more forested sites and conserving these sites might help control Chagas disease within central Panama. However, determining the efficacy and feasibility of managing these characteristics within crowns and implementing biocontrol will require additional field experiments. For example, reducing dead organic matter and the inhabitation of hosts by cleaning palm crown debris vs. maintaining a diverse predator community would be an interesting next approach to disentangle the best methods to control *R. pallescens* and infection with *T. cruzi* within rural areas of central Panama.

This research was limited by study design implementation including finding replicate sampling sites across locations, and palm crown accessibility. This was because choosing palm sites were primarily limited by terrain conditions and landowner consent. Furthermore, collecting microclimate data within palm crowns is a complicated task which resulted in damaged or missing data loggers. Alternatively, our results may be a consequence of missing microclimate data. Although the aforementioned studies did not investigate all potential explanatory variables simultaneously, as we do here, these results might further indicate that microhabitat and community characteristics have stronger effects on vector abundance and infection. Seasonality was not included in our model since a majority of palms were sampled in the wet season and therefore, we did not have a large enough sample size to include the dry season. Future research should focus on seasonality, particularly regarding fluctuation in the palm crown and ambient microclimate conditions, as they likely have a larger influence on abundance and infection than we report in this paper.

4.5 CONCLUSION

This study continues address the impact that human activities have on multi-host vector-borne disease via altering microhabitat and local community conditions associated with Chagas disease in central Panama. We also demonstrate that incorporating community measurements can alter our understanding of disease transmission as well as predator roles on decreasing disease risk. By adopting a community approach with existing evidence linking microclimate and microhabitat data to triatomine infestation, we acknowledge the complexity that surrounding community members have on vector-pathogen-host relationships and realize continued work down this avenue of research is essential for predicting and managing disease. For example, the presence of blood meals in palm trees continues to be an indicator of *R. pallescens* abundance and infection with *T. cruzi*, however the significance of potential predators, primarily scorpions and spiders, on abundance and infection respectively, indicates that predators have varying impacts on disease and also change how we view vectors with the surrounding community members. Our results also contribute to ongoing scientific studies regarding the use of food web metrics to imply that community interactions can have an influence on transmission rather than just immediate hosts and predators of the vector or parasite of interest. This may be because aspects of the community as a whole may have a stronger impact on disease transmission rather than studying the impacts of individuals species groups, thereby also changing the results of the model.

Also, we demonstrate that studying palm crowns as mesocosms can be helpful in developing further research hypotheses on community ecology or *R. pallescens* ecology and the interaction between land use-level and local-level characteristics on vector-parasite dynamics. Although we conducted this research in an uncontrolled environmental setting, it brings the research closer to understanding what occurs in 'real world' situations.

Permits: Mi Ambiente: SE/A-93-13, SE/AP-27-16

STRI IACUC: 2013-0601-2016-02, 2016-0801-2019-A1

UGA IACUC: A2016 05-009-R2

4.6 TABLES AND FIGURES

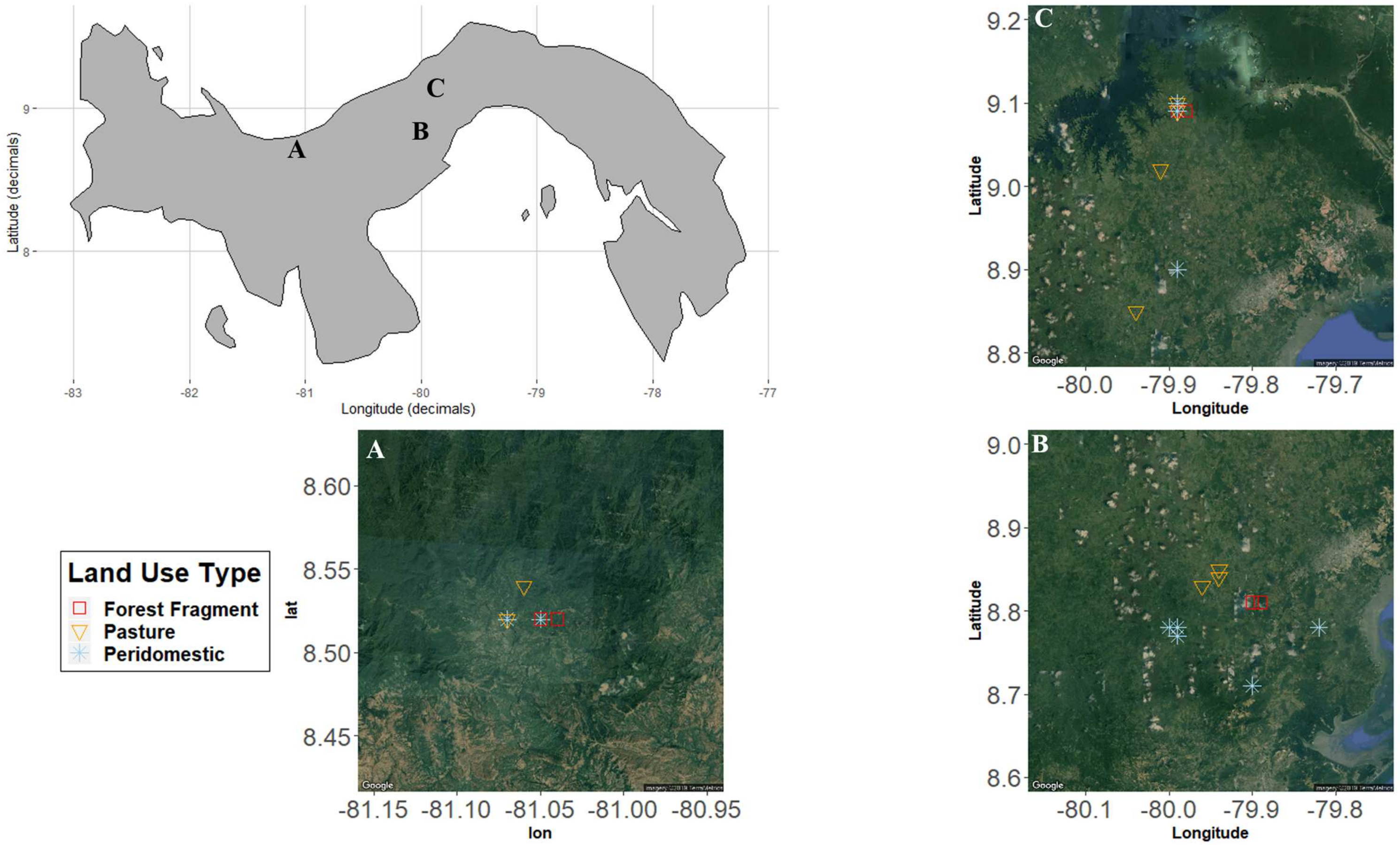


Figure 4.1 Palm sampling locations across different land use types throughout central Panama. Symbols (some are overlapped) represent sampled palms from forest fragments, pastures, and peridomestic land use areas within **(A)** Santa Fe, **(B)** Capira, and **(C)** La Chorrera.

A 	**B** 	**C** 	**D** 
Dead Organic Matter 1: Minimal amount of organic material in the crown.	*Dead Organic Matter 2:* Collection of some organic debris in the crown. Evidence of young infructescence and epiphytes	*Dead Organic Matter 3:* Collection of old and new organic debris in the crown. Evidence of young and old infructescence and epiphytes collected in the crown.	*Dead Organic Matter 4:* Maximum amount of organic matter in the crown. Old and young fronds, infructescence and epiphytes all maintained within the crown.

Figure 4.2 Measured characteristics and dead organic matter scale of the palm crown microhabitat. Dead organic matter ranged from low (A) to high (D). Infructescence (B, white circle) and epiphytic plants (C, white circle) were also among the characteristics measured.

Table 4.1 A-B. Infestation patterns of triatomines within palms across **(A)** location and across **(B)** land use types within location.

A.

***R. pallescens* abundance**	**La Chorrera (N=42 palms)**	**Capira (N=47 palms)**	**Santa Fe (N=15 palms)**	**Total (N = 105 palms)**
% Palms infested with Rhodnius (95% CI)	86% (70% - 92%)	74% (60% - 85%)	93% (70% - 99%)	81% (72% - 88%)
Total no. Rhodnius captured	427	403	268	1098
Mean no. Rhodnius captured in infested palm/Location (95% CI)	11.8 (7.8-15.8)	11.5 (4.5-18.4)	19.1 (10.6 - 27.6)	12.9 (9.3-16.6)
Total No. Adults captured	32	42	39	113
Total No. Nymphs captured	324	184	107	615
Colonization Index**	10.12	4.38	2.74	5.44

B.

R. pallescens **abundance**	**La Chorrera (N=42 palms)**			**Capira (N=47 palms)**			**Santa Fe (N=16 palms)**			**Total (N=105 palms)**
	Pasture (N=13)	Peridomestic (N=16)	Forest Fragment (N=13)	Pasture (N=21)	Peridomestic (N=20)	Forest Fragment (N=6)	Pasture (N=8)	Peridomestic (N=5)	Forest Fragment (N=3)	
% Palms infested with Rhodnius (95% CI)	85% (54% - 97%)	81% (53% - 95%)	92% (62% - 99%)	71% (47% - 88%)	90% (67% - 99%)	33% (6% - 76%)	100% (60% - 100%)	100% (40% - 100%)	67% (12% - 99%)	**81% (72% - 88%)**
Total no. Rhodnius captured	98	142	187	72	327	4	82	150	36	**1098**
Mean no. Rhodnius captured in infested palm (95% CI)	7	8.87	11	3.4	16.35	0.6	10.25	37.5	18	**12.9**
Total No. Adults captured	7	17	8	4	36	2	13	22	4	**39**
Total No. Nymphs captured	91	94	139	57	126	2	54	46	7	**107**
Nymph : Adult Ratio	13	5.52	17.35	14.25	3.5	1	4.15	2.09	1.75	**5.44**
Colonization Index**	1.00	0.92	1.00	0.93	1.00	1.00	0.88	1.00	0.50	**0.95**

** No. palms with nymphs/no. palms with triatomines

Table 4.2 A-B. Triatomine infection patterns across **(A)** location and across **(B)** land use types within location.

A.

R. pallescens infection and stage	**La Chorrera (N=25 palms)**	**Capira (N=16 palms)**	**Santa Fe (N=13 palms)**	**Total (N=54 palms)**
% *R. pallescens* infected with *T. cruzi* (95% CI)	28% (22% - 35%) (N=186)	34% (27% - 42%) (N=160)	57% (48% - 65%) (N=130)	38% (34% - 42%) (N=476)
% nymphs infected with *T. cruzi* (95% CI)	23% (18% - 31%) (N=158)	34% (26% - 42%) (N=122)	46% (37% - 56%) (N=95)	33% (28% - 37%) (N=375)
% adults infected with *T. cruzi* (95%CI)	54% (36% - 70%) (N=28)	37% (23% - 53%) (N=38)	86% (71% - 94%) (N=35)	57% (48% - 67%) (N=101)
% palms with infected *R. pallescens* (95% CI)	64% (45% - 80%) (N=25)	63% (39% - 82%) (N=16)	85% (58% - 96%) (N=13)	69% (56% - 80%) (N=54)

B.

***R. pallescens* infection and stage**	**La Chorrera (N=26 palms)**			**Capira (N=16 palms)**			**Santa Fe (N=13 palms)**			**Total (N=55)**
	Pasture (N=13)	Peridomestic (N=16)	Forest Fragment (N=13)	Pasture (N=21)	Peridomestic (N=20)	Forest Fragment (N=6)	Pasture (N=8)	Peridomestic (N=5)	Forest Fragment (N=3)	
% *R. pallescens* infected with *T. cruzi* (95% CI)	27% (18% - 39%) (N=78)	27% (19% - 38%) (N=95)	31% (10% - 61%) (N=13)	17% (8% - 30%) (N=54)	43% (33% - 53%) (N=105)	100% (5% - 100%) (N=1)	40% (27% - 55%) (N=50)	65% (52% - 76%) (N=68)	83% (51% - 98%) (N=12)	**38%** **(33% - 43%)** **(N=476)**
% nymphs infected with *T. cruzi* (95% CI)	24% (15% - 36%) (N=71)	23% (14% - 33%) (N=79)	25% (4% - 64%) (N=8)	16% (7% - 30%) (N=51)	46% (35% - 59%) (N=71)	0	32% (20% - 48%) (N=44)	53% (38%-69%) (N=43)	87% (47% - 99%) (N=8)	**33%** **(28% - 34%)** **(N=375)**
% adults infected with *T. cruzi* (95%CI)	57% (20% - 89%) (N=7)	50% (26% - 75%) (N=16)	60% (17% - 93%) (N=5)	33% (2% - 88%) (N=3)	35% (20% - 53%) (N=34)	100% (5% - 100%) (N=1)	100% (52% - 100%) (N=6)	87% (67% - 97%) (N=24)	75% (22% - 99%) (N=4)	**57%** **(47% - 67%)** **(N=101)**
% palms with infected *R. pallescens* (95% CI)	50% (20% - 80%)	64% (32% - 88%)	60% (17% - 93%)	33% (6% - 76%)	89% (50% - 99%)	100% (5% - 100%)	83% (37% - 99%)	100% (47% - 100%)	50% (3% - 98%)	**69%** **(54% - 80%)**

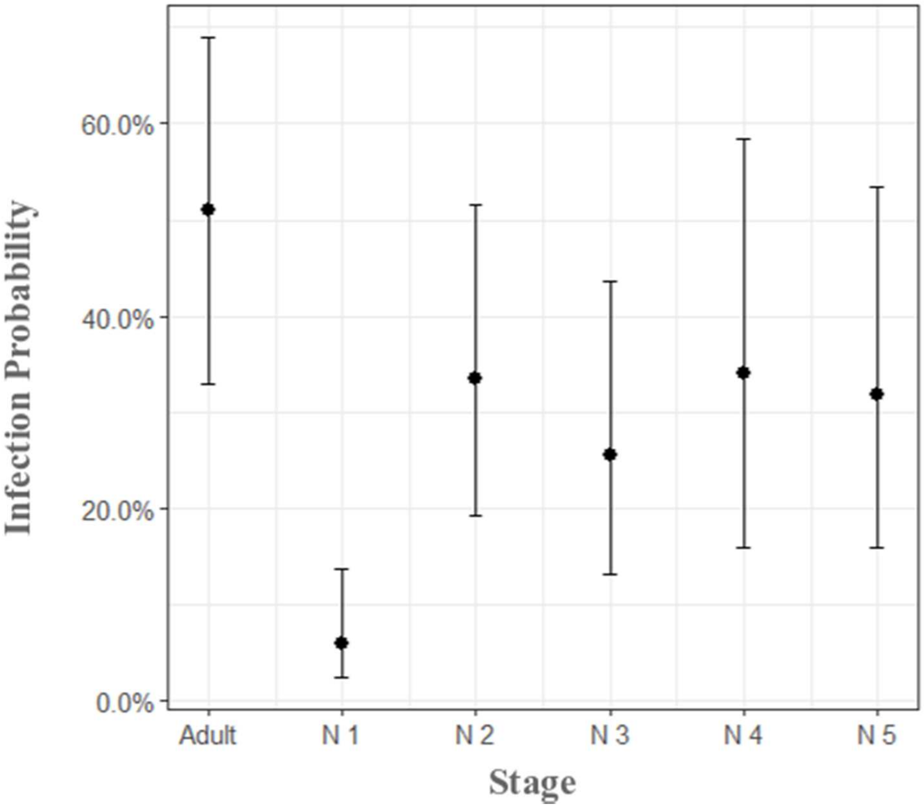


Figure 4.3 Predicted effects of triatomine stage on the probability of infection. The probability of infection is predicted to generally increase as nymphal stage increases, resulting in the highest probability of infection at the adult stage.

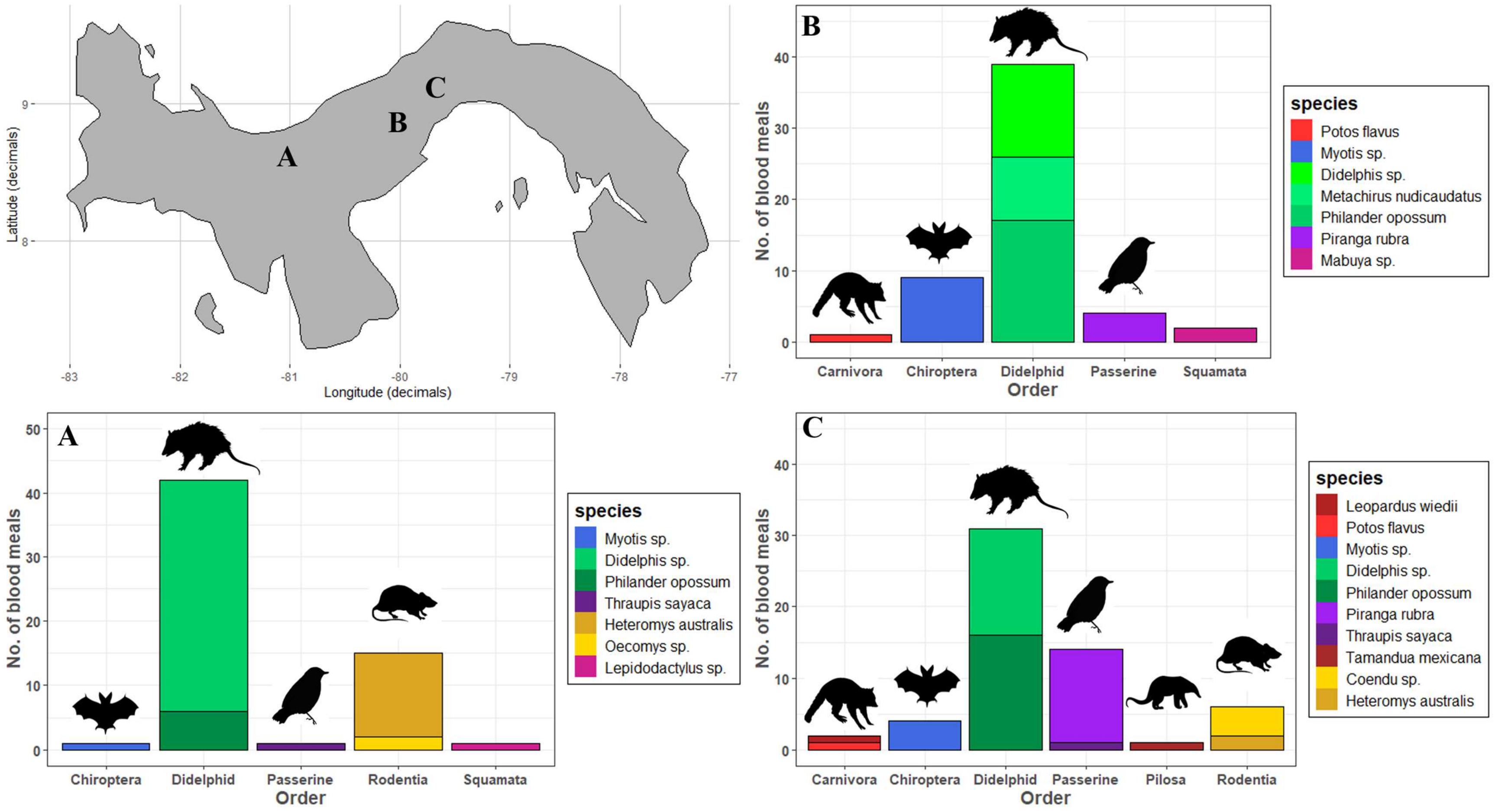


Figure 4.4 A-C. Vertebrate blood meals composition (Order and species) identified from *R. pallescens* individuals collected from **(A)** Santa Fe (N=60 individuals), **(B)** Capira (N=55 individuals), and **(C)** La Chorrera (N=58 individuals).

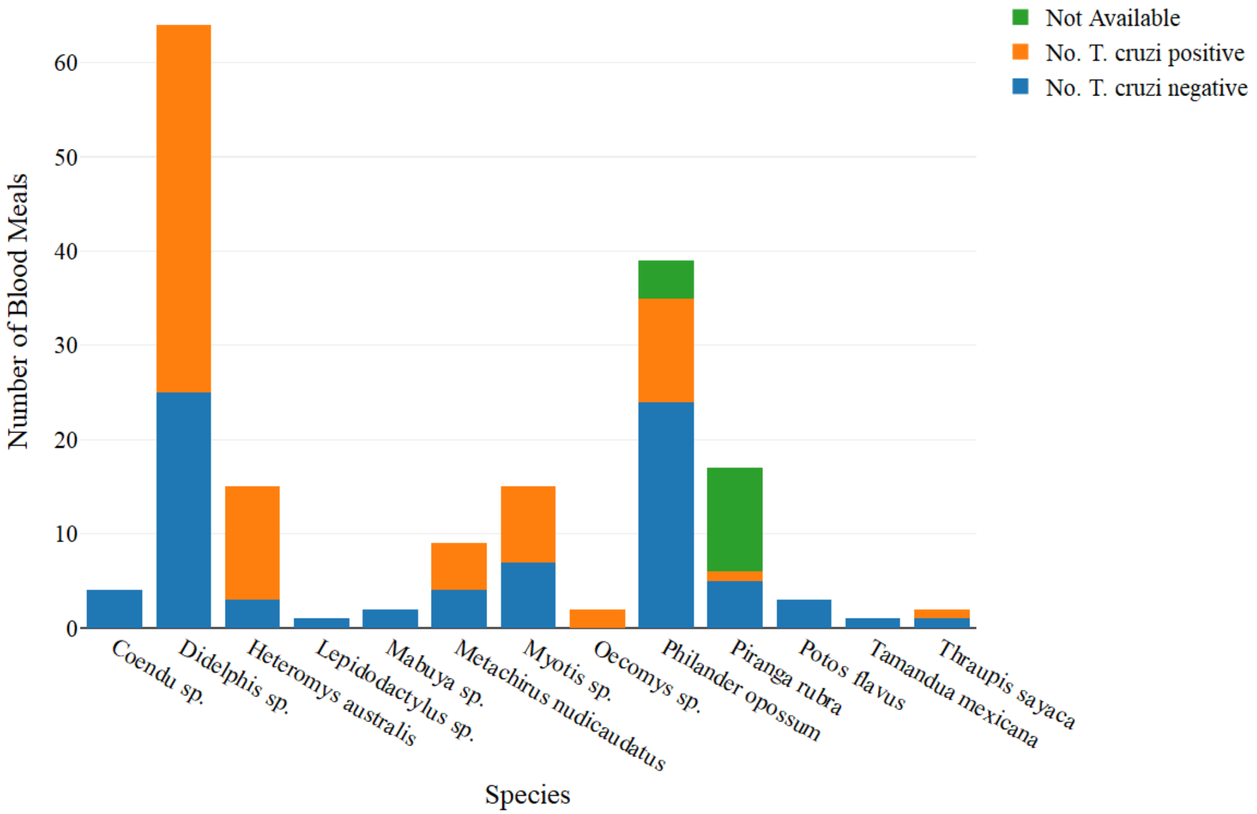


Figure 4.5 Overall blood meal composition and infection status (*T. cruzi* positive/negative) of *R. pallescens*.

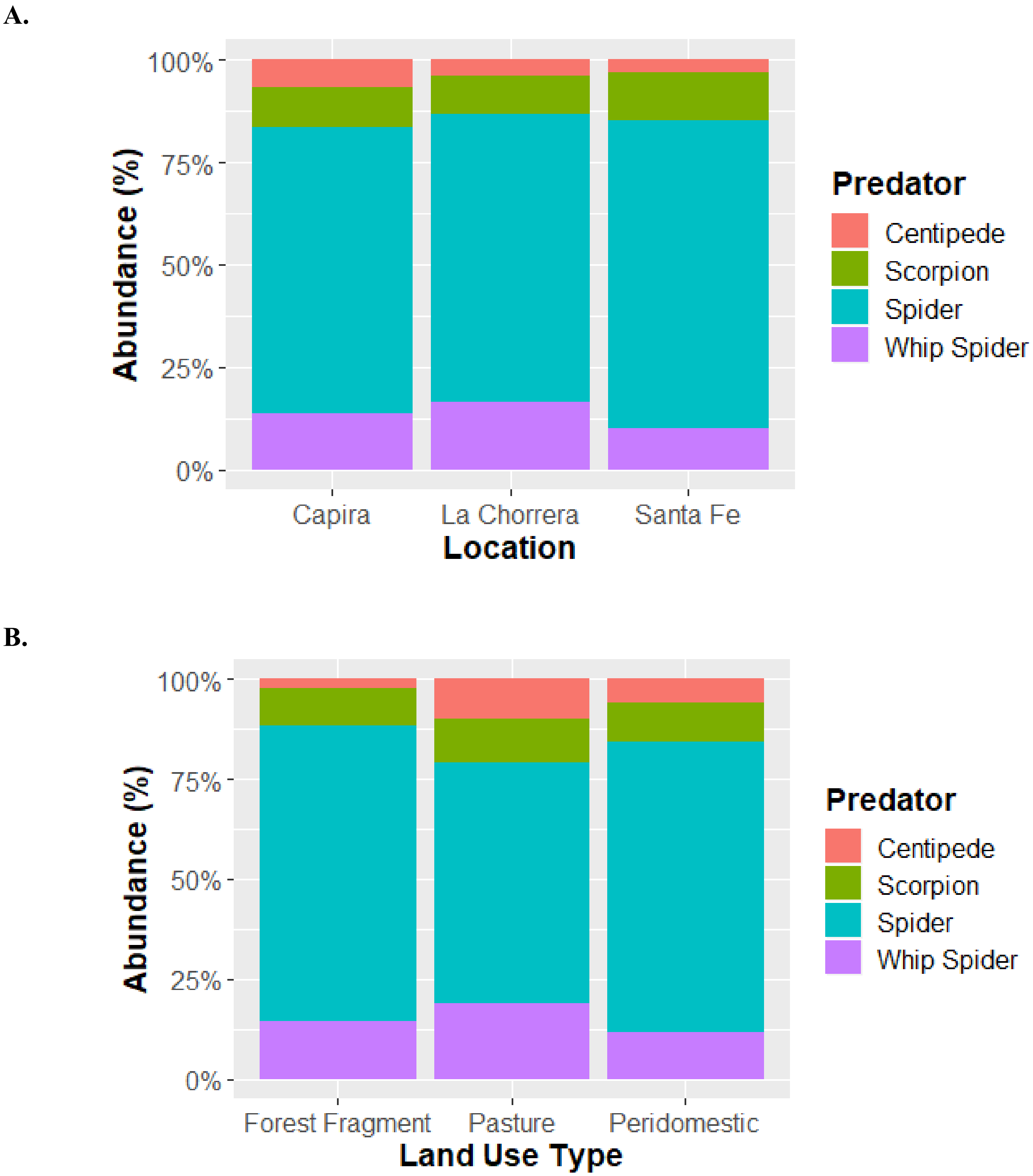
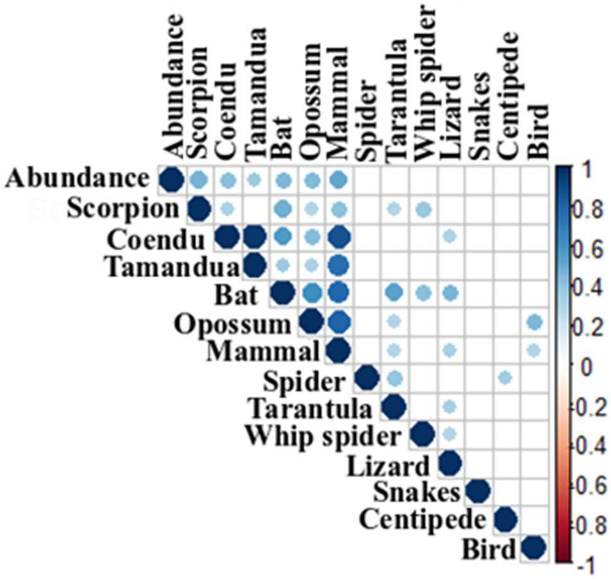
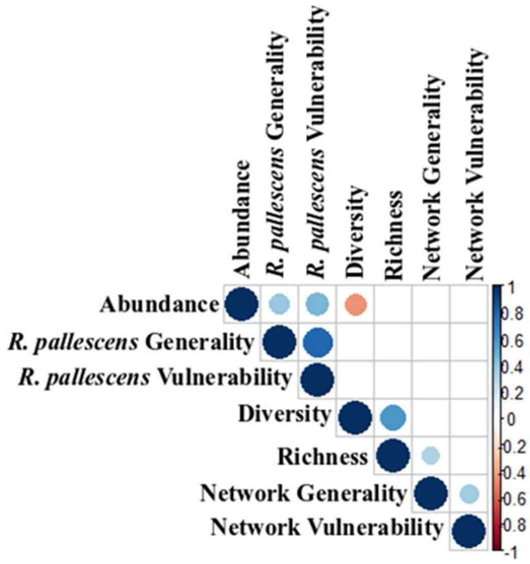


Figure 4.6 A-B. Predator community composition across **(A)** location and **(B)** land use type. Spider abundance dominated predator communities across all palms sampled.

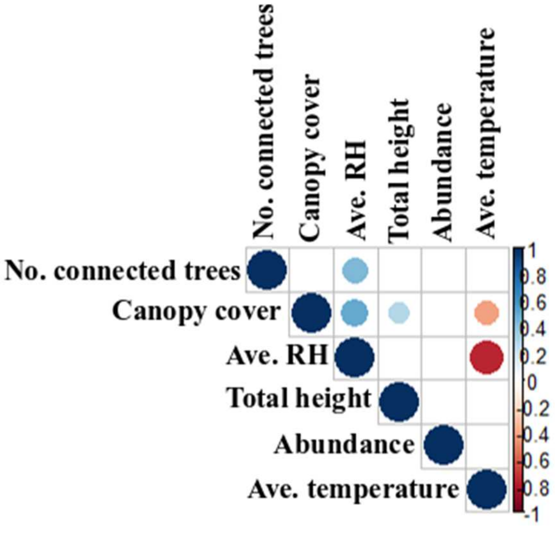
A.


Abundance
Scorpion
Coendu
Tamandua
Bat
Opossum
Mammal
Spider
Tarantula
Whip spider
Lizard
Snakes
Centipede
Bird
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

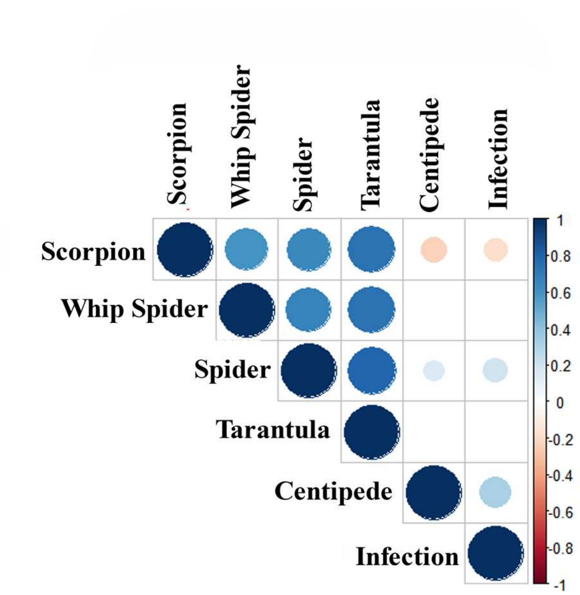
B.


Abundance
R. pallescens Generality
R. pallescens Vulnerability
Diversity
Richness
Network Generality
Network Vulnerability
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

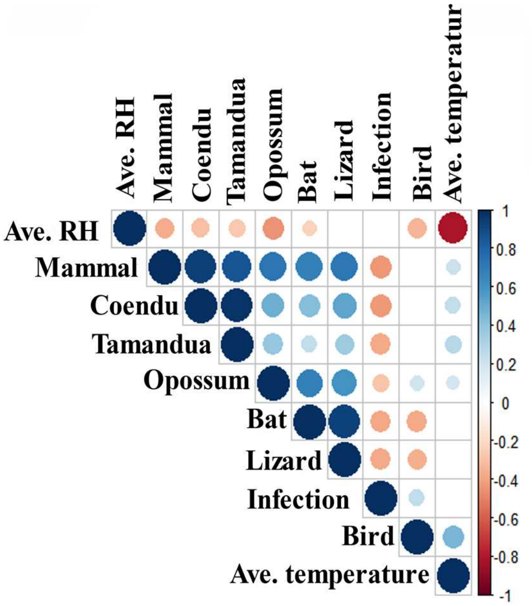
C.


No. connected trees
Canopy cover
Ave. RH
Total height
Abundance
Ave. temperature
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

D.


Scorpion
Whip Spider
Spider
Tarantula
Centipede
Infection
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

E.


Ave. RH
Mammal
Coendu
Tamandua
Opossum
Bat
Lizard
Infection
Bird
Ave. temperatur
Ave. temperature
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

F.

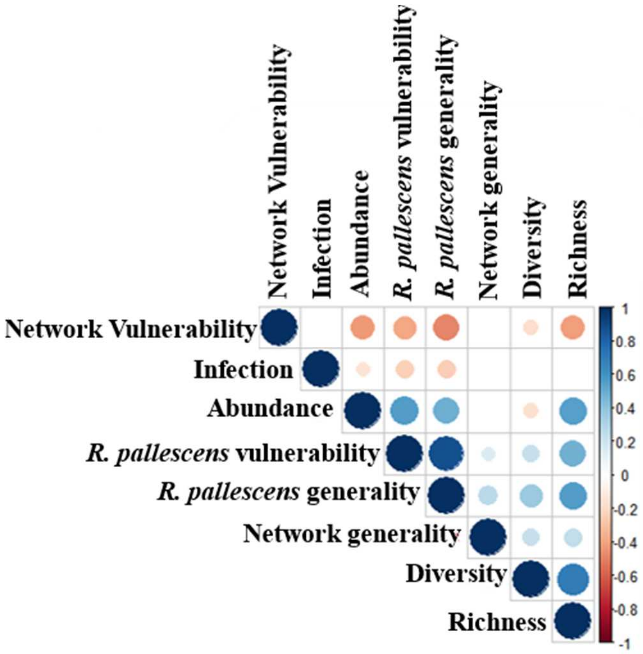
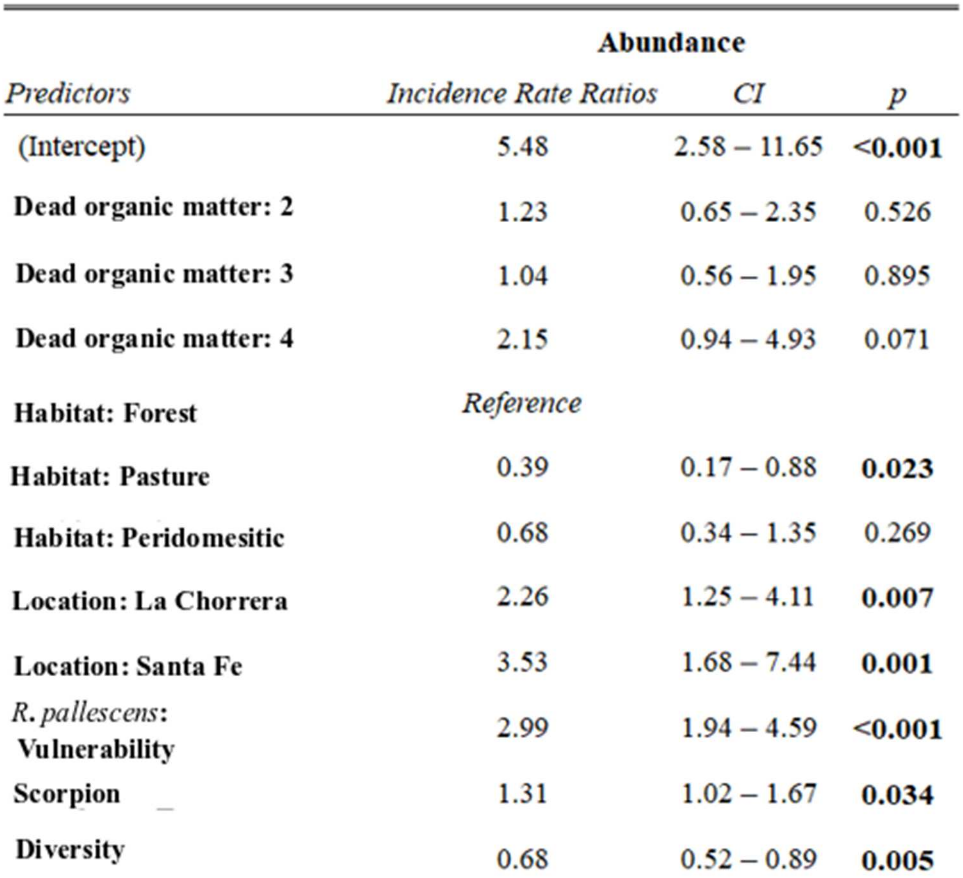

Network Vulnerability
Infection
Abundance
R. pallescens vulnerability
R. pallescens generality
Network generality
Diversity
Richness
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1

Figure 4.7 A-F. Correlation between *R. pallescens* abundance and **(A.)** palm crown community including blood meals and invertebrate predators **(B.)** food web network metrics and **(C.)** microhabitat and microclimate conditions. Correlation plots between the binary response variable *T. cruzi* infection and **(D.)** invertebrate predator community, **(E.)** blood meal community, and **(F.)** food web network metrics. A blank square indicates no significant correlation.

A.



	Abundance		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	5.48	2.58 – 11.65	**<0.001**
Dead organic matter: 2	1.23	0.65 – 2.35	0.526
Dead organic matter: 3	1.04	0.56 – 1.95	0.895
Dead organic matter: 4	2.15	0.94 – 4.93	0.071
Habitat: Forest	*Reference*		
Habitat: Pasture	0.39	0.17 – 0.88	**0.023**
Habitat: Peridomesitic	0.68	0.34 – 1.35	0.269
Location: La Chorrera	2.26	1.25 – 4.11	**0.007**
Location: Santa Fe	3.53	1.68 – 7.44	**0.001**
R. pallescens: **Vulnerability**	2.99	1.94 – 4.59	**<0.001**
Scorpion	1.31	1.02 – 1.67	**0.034**
Diversity	0.68	0.52 – 0.89	**0.005**

B.

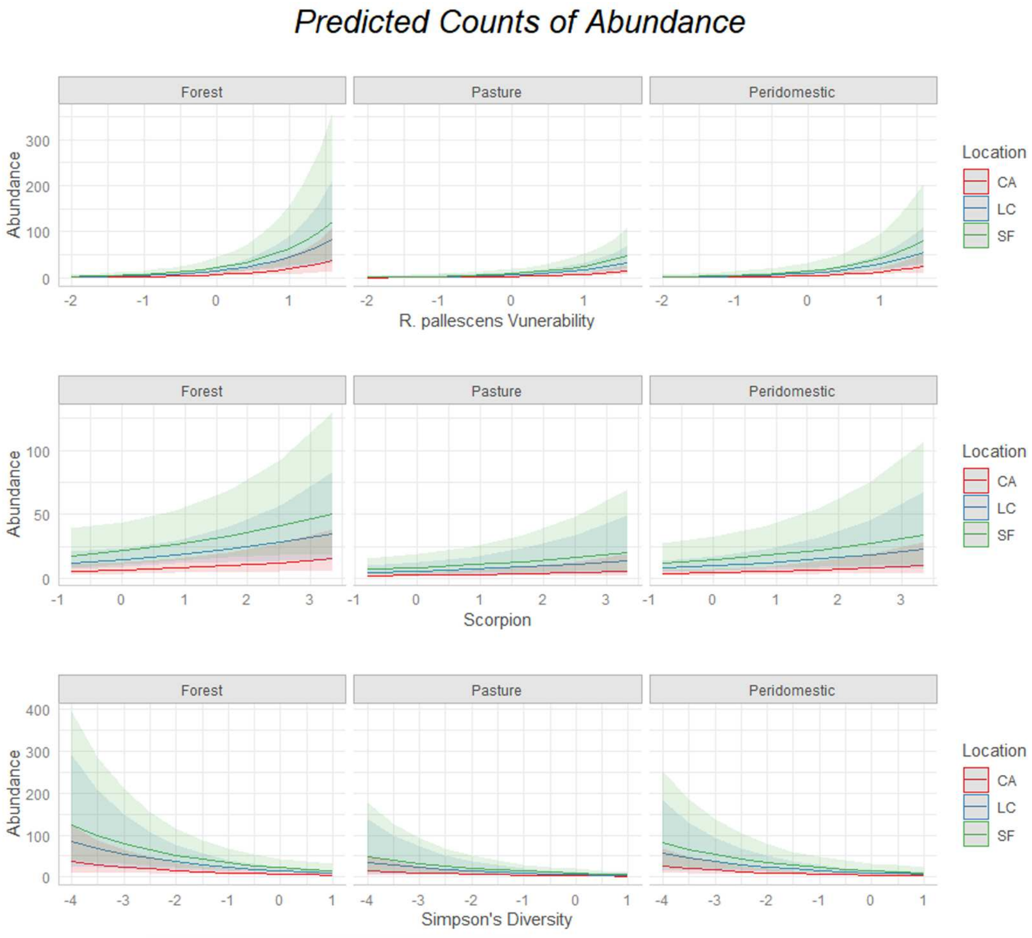
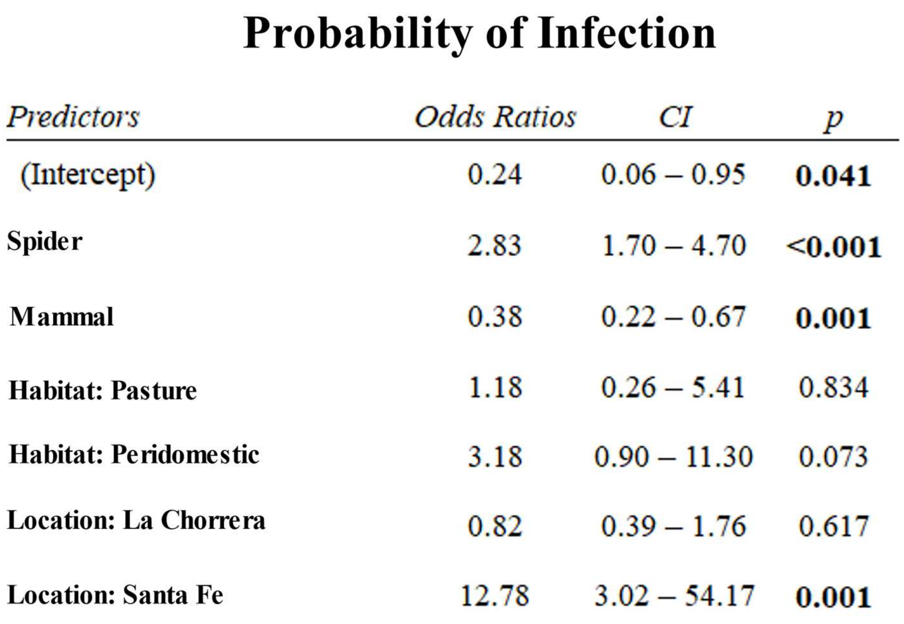


Figure 4.8 A-B. (**A.**) Best fit model for glmm predicting *R. pallescens* abundance. Incidence rate ratio refers to an increased risk in abundance given the predictor variables. **(B).** Marginal effects (predicted values) of each community predictor variables on *R. pallescens* abundance across location (CA – Capira, LC – La Chorrera, SF – Santa Fe) and land use type.

A.



Probability of Infection

Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.24	0.06 – 0.95	**0.041**
Spider	2.83	1.70 – 4.70	**<0.001**
Mammal	0.38	0.22 – 0.67	**0.001**
Habitat: Pasture	1.18	0.26 – 5.41	0.834
Habitat: Peridomestic	3.18	0.90 – 11.30	0.073
Location: La Chorrera	0.82	0.39 – 1.76	0.617
Location: Santa Fe	12.78	3.02 – 54.17	**0.001**

B.

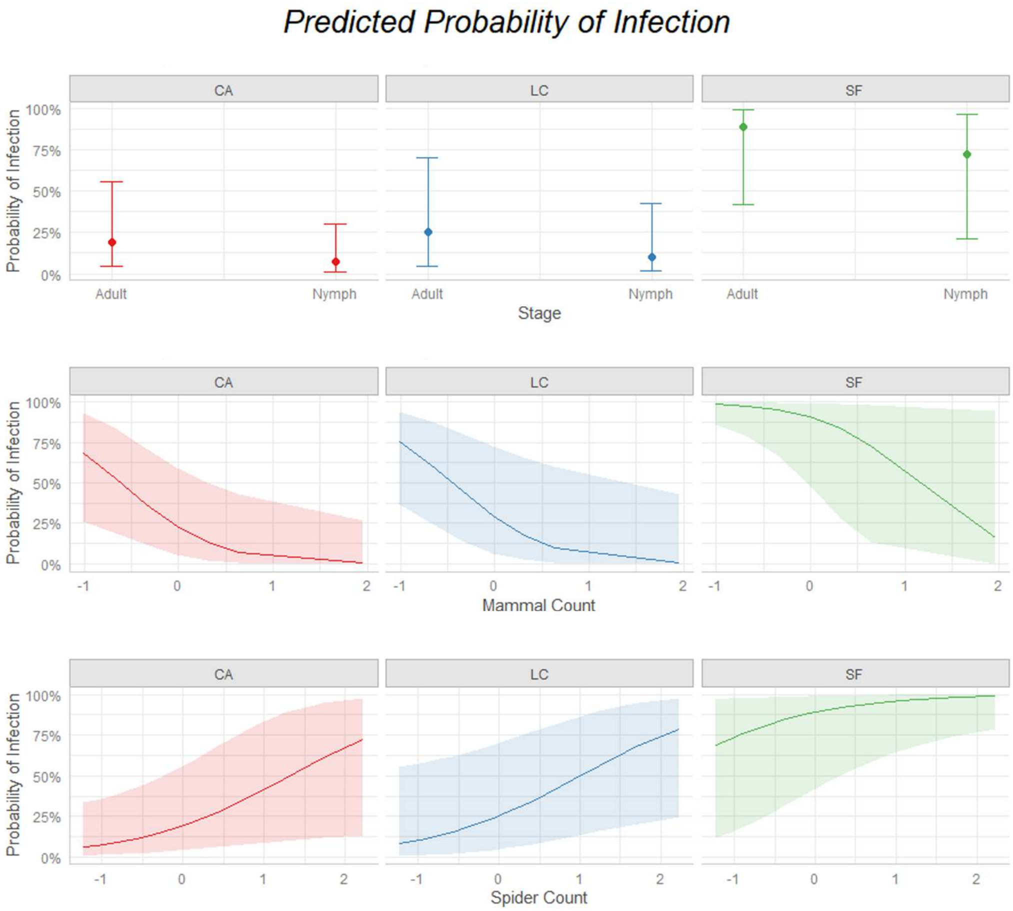


Figure 4. 9A-B. (A.) Best fit glmm predicting probability of infection (odds ratio). **(B.)** Marginal effects (predicted effects) of each predictor variables on the probability of infection across location (CA – Capira, LC – La Chorrera, SF – Santa Fe).

4.7 SUPPLEMENTAL INFORMATION

SI Table 4.1 Predictor variables used to model *R. pallescens* abundance and *T. cruzi* infection

VARIABLE	**DESCRIPTION**
Community:	**Species collected from the palm crown**
Scorpions	No. of scorpions collected
Whip Spider	No. of whip spiders collected
Spider	No. of spider collected
Centipede	No. of centipedes collected
Bird	No. of birds detected
Mammal*	Total no. of all mammals detected
Coendu	No. of coendu detected
Opossum	No. of opossums detected
Bat	No. of bats detected
Tamandua	No. of tamandua detected
Lizard	No. of lizards detected
Network:	**Metrics from food web output**
R. pallescens Vulnerability	The number of taxa that feed on *R. pallescens* (Dunne 2009, 2004)
R. pallescens Generality	The number of taxa that *R. pallescens* feeds from (i.e. blood meals) (Dunne 2009, 2004)
Network VulnerabilitySD	Variability in the standardized number of predators in a network (Dunne 2009, 2004)
Network GeneralitySD	Variability in the standardized number of prey in a network (Dunne 2009, 2004)
Simpson’s Diversity	Number and abundance of species in a community
Species Richness	Number of species in a community
Microclimate:	
Average Relative Humidity	Average %RH within crown recorded over 72 hour period
Average Temperature	Average temperature within crown recorded over 72 hour period
Microhabitat:	
% Canopy Cover	percentage of forest cover measured at 5 m distance from the sampled palm at the four cardinal locations
Total Height	Measured from base of trunk – top of crown (m)
No. of Connected Trees	Number of other trees physically connected to the sampled palm

Dead Organic Matter (DOM)	Presence of dead organic matter; scale 1 (low) – 4 (high)
Location	Santa Fe, La Chorrera, or Capira
Land Use Type	Peridomestic, pasture, or forest fragment
Palm ID	Palm identification
Bug ID	*R. pallescens* identification

* Presence also verified with NGS results

SI Table 4.2 Model selection explaining for *R. pallescens* abundance in Attalea palms using Akaike Information Criterion.

Model Parameters	**df**	**AIC**
null	3	358.21
Average temperature	4	358.14
Habitat	5	357.85
Location	5	357.07
Habitat + Location	7	354.13
Habitat + Location + Diversity	8	351.49
Habitat + Location + Diversity + Mammals	9	341.42
Habitat + Location + Diversity + DOM + Mammals	12	344.34
Habitat + Location + Diversity + DOM + Mammals + Scorpions	13	341.03
Habitat + Location + Diversity + DOM + *R. pallescens* vulnerability	12	321.07
Habitat + Location + Diversity + DOM + Scorpion	12	342.44
Habitat + Location + Diversity + DOM + Scorpions + Coendu + Tamandua + Bat + Opossum	16	344.14
Habitat + Location + Diversity + DOM + Scorpions + Coendu + Tamandua + Bat	15	345.94
Habitat + Location + Diversity + DOM + Scorpions + Coendu + Tamandua	14	344.30
Habitat + Location + Diversity + DOM + Scorpions + Coendu	13	343.83
Habitat + Location + Diversity + DOM + Scorpions	12	342.44
Habitat + Location + Diversity + DOM + Scorpions + *R. pallescens* vulnerability	13	318.82
ALL: Location + Habitat + Average temperature + DOM + *R. pallescens* vulnerability + Scorpion + Simpson + Mammal	15	321.82

SI Table 4.3 Model selection explaining for *T. cruzi* infection in Attalea palms using Akaike Information Criterion. Alternative models not shown in the table did not converge and were omitted.

Model Parameters	**df**	**AIC**
null		204.1
Location + Bat + Centipede +Spider + Bird + Stage	10	160.84
Location + Bat + Spider + Bird + Stage	9	161.45
Location + Mammal + Spider + Stage	8	158.88

SI Table 4.4 Nymphal stages of *R. pallescens* collected across location and land use type. Exact nymphal stages are missing from 17 palms in Capira, 7 palms in La Chorrera, and 1 palm in Santa Fe.

	La Chorrera (N=47 palms)			**Total**	**Capira (N=48 palms)**			**Total**	**Santa Fe (N=15 palms)**			**Total**	**Total**
	Pasture (N=21)	Peri-domestic (N=20)	Forest Fragment (N=6)		Pasture (N=15)	Peri-domestic (N=16)	Forest Fragment (N=17)		Pasture (N=8)	Peri-domestic (N=4)	Forest Fragment (N=3)		
No. N1 Collected	20	30	0	**50**	25	13	33	**71**	20	15	1	**36**	**157**
No. N2 Collected	17	45	0	**62**	20	26	51	**97**	14	6	1	**21**	**180**
No. N3 Collected	8	21	0	**29**	27	34	26	**87**	8	17	1	**26**	**142**
No. N4 Collected	3	18	0	**21**	8	14	14	**36**	4	3	1	**8**	**65**
No. N5 Collected	5	12	0	**17**	10	7	15	**32**	7	5	3	**15**	**64**
No. Adults Collected	3	36	1	**39**	7	17	8	**32**	13	22	3	**38**	**109**

SI Table 4.5 Proportion of infected *R. pallescens* individuals at each stage across location and land use type.

	La Chorrera (N=26 palms)			**Total**	**Capira (N=16 palms)**			**Total**	**Santa Fe (N=13 palms)**			**Total**	**Total (N=55)**
	Pasture (N=10)	Peri-domestic (N=11)	Forest Fragment (N=5)		Pasture (N=6)	Peri-domestic (N=9)	Forest Fragment (N=1)		Pasture (N=6)	Peri-domestic (N=5)	Forest Fragment (N=2)		
Proportion N1 positive	0.076 (1/13)	0.083 (1/12)	0.00	**0.08 (2/25)**	0 (0/20)	0.54 (6/11)	0.00	**0.19 (6/31)**	0.05 (1/20)	0.2 (3/15)	0.00	**0.11 (4/36)**	**0.13 (12/92)**
Proportion N2 positive	0.21 (3/14)	0.29 (7/24)	0.00	**0.26 (10/38)**	0.13 (2/15)	0.71 (20/28)	0.00	**0.51 (22/43)**	0.46 (6/13)	0.6 (3/5)	1 (2/2)	**0.55 (11/20)**	**0.42 (43/101)**
Proportion N3 positive	0.15 (4/26)	0.26 (6/23)	0 (0/3)	**0.19 (10/52)**	0.25 (2/8)	0.44 (4/9)	0.00	**0.35 (6/17)**	0.33 (1/3)	0.76 (10/13)	1 (1/1)	**0.7 (12/17)**	**0.32 (28/86)**
Proportion N4 positive	0.25 (2/8)	0.076 (1/13)	0.33 (1/3)	**0.16 (4/24)**	0.33 (1/3)	0.27 (3/11)	0.00	**0.28 (4/14)**	0.5 (1/2)	1 (4/4)	1 (1/1)	**0.85 (6/7)**	**0.31 (14/45)**
Proportion N5 positive	0.7 (7/10)	0.42 (3/7)	0.5 (1/2)	**0.57 (11/19)**	0.6 (3/5)	0 (0/12)	0.00	**0.17 (3/17)**	1 (5/5)	0.5 (3/6)	1 (3/3)	**0.78 (11/14)**	**0.5 (25/50)**
Proportion Adult positive	0.57 (4/7)	0.5 (8/16)	0.6 (3/5)	**0.53 (15/28)**	0.33 (1/3)	0.35 (12/34)	1 (1/1)	**0.37 (14/38)**	1 (6/6)	0.84 (21/25)	0.75 (3/4)	**0.85 (13/35)**	**0.58 (59/101)**

SI Table 4.6. Blood meal identification and proportion infected for nymphal stage (N1 and N2 included) and adult stage across location and land use types.

Blood meal identification		**Capira**			**La Chorrera**			**Santa Fe**			
		Nymph No. blood meals (infected/no. tested)	**Adult** No. blood meals (infected/no. tested)	Overall Proportion Infected	**Nymph** No. blood meals (infected/no. tested)	**Adult** No. blood meals (infected/no. tested)	Overall Proportion Infected	**Nymph** No. blood meals (infected/no. tested)	**Adult** No. blood meals (infected/no. tested)	Overall Proportion Infected	**Overall no. of blood meals identified** **(infected/no. tested)**
Mammalia	Didelphid	38 (16/36)	1 (0/1)	.43 (16/37)	27 (8/26)	4 (4/4)	.4 (12/30)	29 (19/21)	13 (11/13)	.88 (30/34)	112 (58/101)
	Chiroptera	9 (7/9)	0	.77 (7/9)	5 (1/5)	0	.2 (1/5)	1 (0/1)	0	0	15 (8/14)
	Carnivora	2 (0/2)	0	0	1 (0/1)	0	0	0	0	0	3 (0/3)
	Rodentia	0	0	0	5 (0/5)	0	0	11 (10/11)	4 (4/4)	.93 (14/15)	20 (14/20)
	Pilosa	0	0	0	1 (0/1)	0	0	0	0	0	1 (0/1)
Reptilia	Squamata	2 (0/2)	0	0	0	0	0	1 (0/1)	0	0	3 (0/3)
Aves	Passerine	4 (0/4)	0	0	6 (0/4)	1 (1/1)	.2 (1/5)	0	1 (1/1)	1 (1/1)	13 (2/10)

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CHAPTER 5

CONCLUSIONS AND FUTURE DIRECTIONS

5.1 SUMMARY OF FINDINGS

This study shows that land use change does impact species community composition, structure and function. However, instead of community 'disassembly', as communities within disturbed areas are often considered to be, we find that community composition, structure and function shift, while maintaining a high level of diversity. Using a food web of these communities, we investigated how community-level characteristics, along with microenvironment conditions, influence the abundance of the Chagas disease vector, *Rhodnius pallescens*, and infection with the parasite *Trypanosoma cruzi*. We concluded that microhabitat conditions, such as dead organic matter, and particularly top trophic level community members (i.e. vector hosts) as well as community predators (i.e. spiders) contributed to patterns in abundance and infection. Dead organic material provides refuge for vectors in addition to a stable microclimate which would be essential to support a greater number of individuals. Also, the presence of opossums was positively correlated with abundance which adds to the ongoing evidence that opossums are associated with triatome vector in the palm crown ecotope. Although opossums were not found to be significantly associated with *T. cruzi* infection, network generality, which is an indication of blood meal/host composition (i.e. bats, opossums), was. Interestingly, network vulnerability, which is an indication of potential invertebrate predators (i.e. whip spiders, centipedes), was negatively associated with *T. cruzi* infection. In particular, lizards were identified as a negative driver in infection, which suggests that lizards dilute the transmission of the parasite as an incompetent host or is a component predator of infected individuals.

5.2 PALM CROWNS AS IDEAL MESOCOSM

Palm crowns provided an ideal mesocosm within which to study communities within a defined boundary. The Attalea palm is ubiquitous across the landscape disturbance gradient throughout central Panama, which enables communities to be investigated in natural conditions under various 'treatments' of land use change. Furthermore, palms provide services to humans, and wild and domestic animals. Under these conditions, and the palms association with Chagas disease, we were able to investigate a mesocosm that is also significant to humans and animals health. It would be interesting to continue to research the community dynamics of the palm crown but the difficulty in ascending palms is discouraging. Developing techniques to more properly access these communities will requires additional time and money.

5.3 IMPLICATIONS FOR VECTOR DISEASE CONTROL

Biocontrol has been of particular interest throughout this research. Determining which components of the palm crown community influenced *R. pallescens* and infection could reveal whether a particular species functioned as a potential biocontrol agent or whether community characteristics as whole, and that was representative of a particular land use type or palm crown type, could function as a type of vector management. Conducting laboratory studies between infected and uninfected *R. pallescens*, especially behavioral studies, would also be an interesting avenue for future research. Furthermore, palm crown management could also be included in additional studies. Cleaning palm debris from within the crown and below the palm could deter host species or *R. pallescens* themselves. Further trapping and removing some species from the community and observing the impacts of the remaining community and on *R. pallescens* abundance would be interesting to conduct in the field, although it could also be modeled using the Network3D software.

5.4 LIMITATIONS

The field work component of this study was extremely limited to the accessibility of locations throughout central Panama. Also, palms are extremely hard to sample. Given ideal weather conditions, additional barriers included palm height, uneven terrain, angry domestic animals, soggy and slippery palms, loosing gear into the black abyss of the palm crown, scary and dangerous animals lurking in the palm crown, scary and dangerous animals actually attacking from the palm crown, and just ants and bees. Although I don't address these issues in the chapters, the palm crown community is an incredibly dangerous place and I was considered a major threat to all of the species living in the crown. At times, it did hinder my ability to sample, especially when bees knew that I wanted to collect them. Although wearing protective gear did help at times it did increase the danger of climbing in and out of the palm.

5.5 CONTRIBUTION

This study intimately investigates the palm crown, its community, and physiognomy to provide a better understanding of how multiple factors need to be addressed when understanding pathogen transmission. It also promotes landscape conservation by linking aspects of biocontrol and increased *R. pallescens* predator abundance. Predator abundance was associated with more forested sites and conserving these sites can help control Chagas disease within central Panama.