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ARTICLE

Disease Ecology

# Food web structure and microenvironment affect Chagas disease vector infection and abundance in a rural landscape

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## Abstract

Vector-borne pathogen transmission is shaped by multiple abiotic and biotic factors. Understanding the relative importance of these factors on vector abundance and infection is important for developing vector-borne disease control strategies. The crown of the *Attalea butyracea* palm provides a natural arboreal mesocosm suitable for studying how food web relations and microclimate affect Chagas disease vectors of the genus *Rhodnius*, which feed on vertebrate blood and interact with many vertebrate and invertebrate species, vegetation, and detritus within the palm crown. We performed a cross-sectional, observational study of *A. butyracea* crowns using a community ecology network approach to evaluate abiotic and biotic conditions associated with *Rhodnius pallescens* abundance and infection with *Trypanosoma cruzi*, the Chagas disease etiologic agent. We collected 1098 *R. pallescens* from 105 *A. butyracea* crowns in rural landscapes of Panama. In a palm subset ($N = 49$), we recorded microclimate and habitat conditions and counted vertebrate and invertebrate species in order to characterize palm crown food webs. We used food web metrics, namely Generality (average number of prey per predator) and Vulnerability (average number of predators per prey) to evaluate associations between palm community trophic structure, vector predators, vector blood meal species composition, vector abundance, and vector *T. cruzi* infection. Field data analyzed with generalized linear models showed that vector abundance and infection in a given palm crown were influenced by a combination of geographic location, land-use type, palm crown animal community composition, and microhabitat conditions. Vector abundance was negatively associated with increased overall palm crown community diversity. However, vector abundance was positively associated with the invertebrate predator and mammal community. *R. pallescens* Vulnerability score, which measures predation pressure on the vector within the palm crown, was positively associated with vector abundance. Vector infection with *T. cruzi* was positively associated with

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mammal presence; vectors in palms with mammals were about 25 times more likely to be infected with *T. cruzi* compared with vectors in palms without mammals. Our findings suggest that a holistic study of food webs and environmental variables at the local scale can provide useful information for vector-borne disease management across a wide habitat range.

**KEYWORDS**

Chagas disease, community ecology, disease ecology, food web, multihost pathogen, palm tree, *Rhodnius pallescens*, triatomine bugs, *Trypanosoma cruzi*, vector-borne disease

# INTRODUCTION

Understanding relationships between biological community diversity and vector-borne infectious disease transmission is critical for predicting how these pathogens emerge in response to anthropogenic environmental change (Civitello et al., 2015; Johnson et al., 2015; Keesing et al., 2010; Ostfeld & Keesing, 2000a; Pongsiri et al., 2009). Many studies of vector-borne disease-community relationships focus on whether "dilution" or "amplification" of pathogen transmission occurs in response to increased or decreased reservoir host diversity indices, respectively (Civitello et al., 2015; Johnson et al., 2008, 2013; Johnson & Thieltges, 2010; LoGiudice et al., 2003). Food webs, which represent an entire animal and/or plant community trophic network, are less studied in relation to infectious diseases, but could provide holistic insight into the relative effects of direct and indirect ecological interactions on vector-borne disease transmission.

Trophic network diagrams and their food web metrics can illustrate how interactions with surrounding species can indirectly or directly influence pathogen–vector–host relationships (e.g., Salathé & Jones, 2010; White et al., 2017), allowing an understanding of how ecological communities as a whole, beyond single species interactions, influence pathogen transmission in situ. Network metrics used to describe complex feeding structures and interactions in food webs include species Diversity (number and evenness of species), Generality (the number of taxa a species eats), and Vulnerability (the number of taxa that feed on a species) (Schoener, 1989; Yoon et al., 2004). These predator–prey interactions can be applied to the study of vector-borne diseases because they influence ecological community structure (Bruno & Cardinale, 2008; Müller & Brodeur, 2002; Rosenheim et al., 1995) and can be associated with disease risk, either directly (e.g., predator consumption of infected vectors) or indirectly (e.g., modifying vector behavior; Finke, 2012; Moore et al., 2010). Predator interactions have also been important in the context of biological vector-control methods (Carlson et al., 2009; Ostfeld & Holt, 2004; Snyder & Wise, 1999). Vector populations may be negatively impacted by different invertebrate or vertebrate predators through indirect interactions associated with their hosts from various trophic levels. Therefore, food web-level metrics such as community Network Generality and Vulnerability may be useful to identify if and how animal community structure influences vector-borne pathogen transmission within a particular ecosystem.

Microenvironmental conditions such as temperature, relative humidity (RH), and microhabitat structure are also important determinants of vector abundance and infection status (Carcavallo, 1999; MacDonald, 2018; Paaijmans et al., 2010; Randolph & Storey, 1999; Shaw et al., 2003; Stresman, 2010). Both temperature and humidity influence vector and parasite interactions, survival, and development, as well as vector behavior and contact rates with hosts (Burri et al., 2011; Elliot et al., 2015; Evans et al., 2019; MacDonald, 2018; Randolph & Storey, 1999; Shaw et al., 2003; Vail & Smith, 2002). Meanwhile, habitat composition and structure can alter local species communities, host space use, and vector–host or vector–predator contact rates (Carlson et al., 2009; Talbot et al., 2019; Weterings et al., 2018).

In this study, we use a palm-associated Chagas disease model system to measure how variations in food web structure, microhabitat, and microclimate influence vector-borne pathogen transmission in a rural landscape. Chagas disease is caused by *Trypanosoma cruzi*, a protozoan parasite that is primarily transmitted among domestic and wild mammals, including humans, by blood-feeding triatomine bugs (Hemiptera: Reduviidae). *Rhodnius pallescens* is the principal Chagas disease vector in Panama, where the bugs feed on a variety of sylvatic and domestic vertebrates, including humans (Christensen et al., 1980; Pineda et al., 2008). *Rhodnius* spp. primarily inhabit the crowns of palm trees; the large-crowned *Attalea butyracea*, for example, is abundant in anthropogenically disturbed landscapes and is often infested with *R. pallescens* (Abad-Franch & Monteiro, 2007; Abad-Franch et al., 2009, 2015; Barrett, 1991; Romaña et al., 1999; Whitlaw & Chaniotis, 1978). The palm crown's unique physiognomy and micro-abiotic and biotic conditions maintain a relatively stable environment for triatomine bug survival (Dias et al., 2008; Gurgel-Gonçalves et al., 2003; Lent & Wygodzinsky, 1979; Teixeira et al., 2001). Palm petiole bases, epiphytic and creeping plants, inflorescences, infructescences, and the organic debris that gathers among them collectively create a suitable environment to shelter and feed the palm crown animal community, including triatomines (Abad-Franch et al., 2010, 2015; Rodríguez et al., 2018; Urbano et al., 2015).

Within the palm crown, *T. cruzi* is transmitted to wild mammals primarily via contact with the feces of infected triatomine bugs or via ingestion (i.e., predation) of infected bugs (Lent & Wygodzinsky, 1979; Schofield, 1994). Several mammal and bird species that inhabit the palm crown ecotope provide regular food supply for the triatomines (Battirola et al., 2017; Dias et al., 2008; Gurgel-Gonçalves et al., 2003; Lahey & Gunnels, 2013; Santos et al., 2003). Opossums, which often provide blood meals for palm-dwelling triatomines, are adapted to living in palm crowns, as well as in areas with human disturbance, and they are also highly competent *T. cruzi* reservoirs (Gaunt & Miles, 2000; Noireau et al., 2009; Olifiers et al., 2005; Pineda et al., 2008; Yeo et al., 2005). In addition to providing blood meals for triatomine bugs and serving as reservoir hosts for *T. cruzi*, many palm-dwelling mammals are also potential predators of *R. pallescens* (e.g., via grooming). Invertebrate predators, such as spiders, centipedes, and scorpions, are also associated with palm crown habitats (Couturier et al., 1996; Gurgel-Gonçalves et al., 2006; Santos et al., 2003), but their role in triatomine predations is less understood. *A. butyracea* palms are suitable arboreal model systems for evaluating the relationships between community structure, microhabitat, and vector-borne disease because each palm crown harbors a largely discrete animal community; the system is, in a way, analogous to a pond ecosystem.

In previous studies, deforestation has been linked to an increase in *Rhodnius* spp. abundance (Gottdenker et al., 2011; Santos et al., 2021) and *T. cruzi* infection (Gottdenker et al., 2012) in *Attalea* palms. The underlying mechanism of this pattern may be connected to changes in the palm crown community and microenvironmental conditions. Identifying these mechanisms is essential to understanding the sylvatic cycle of Chagas disease across the Americas, including central Panama, and how it changes in response to human land use, land conversion, and deforestation.

We hypothesize that *R. pallescens* abundance and infection with *T. cruzi* in *A. butyracea* palm crowns will (1) increase as palm crown species diversity decreases and (2) increase with a greater presence of blood meal host species. In particular, we predict that *T. cruzi* infection rates in *R. pallescens* will be positively associated with abundance of *T. cruzi*-competent mammalian blood meals (e.g., opossums).

We predict that *R. pallescens* Generality will be higher (more hosts available) in palms located in disturbed habitats that attract synanthropic or transient mammals such as opossums, thereby increasing bug abundance and *T. cruzi* infection rates. We also predict that palms found within less disturbed habitat will maintain greater community diversity and lower vector abundance and *T. cruzi* infection probability because of higher invertebrate predator species presence (i.e., greater *R. pallescens* Vulnerability). Finally, we hypothesize that greater *R. pallescens* abundance is supported 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), which contributes to intra-crown environmental stability preferred by triatomines. Palms with increasing microhabitat complexity will provide more stable microclimate conditions for this species, with an ideal temperature between 25 and 28°C, centering around 27°C, and an average RH of 70% with a range of 60%–85% (Elliot et al., 2015; Guarneri et al., 2003; Luz et al., 1999; Okasha, 1964; Schilman & Lazzari, 2004).

# METHODS

## Study sites

The study was conducted in districts of La Chorrera (8°52′49″ N, 79°47′0″ W) and Capira (8°45′0″ N, 79°52′12″ W), which are located in Panama Oeste province and Santa Fe district (8°30′ N, 81°04′ W), located in Veraguas province. This ecoregion consists of lowland and montane tropical moist forest (Holdridge, 1967). The habitat within the region is a mixture of agriculture (cattle ranching with cropland), forest remnants, human settlements, and different successional stages of regenerating forest (Condit et al., 2001; Ibáñez et al., 2002). Santa Fe is the highest in elevation at roughly 430 m above sea level (asl), while La Chorrera and Capira are 81 and 119 m asl, respectively. La Chorrera and Capira are mosaics of pastureland for crop farming and cattle grazing, patches of early to mid-secondary forest succession that were previously abandoned pastures, forest remnants, and peridomestic areas. The habitat within Santa Fe is less disturbed and consists of a larger amount of forest cover in addition to pasture and peri-domiciliary sites (defined below).

Within each district, sites representing gradients of human-modified land-use types were identified and were classified as peridomestic, pasture, and forest remnants (Figure 1). Peridomestic habitat was classified as being either within designated yards (i.e., fencing or evidence of a barrier) in areas of human settlement or within 100 m from a house; cattle pastures were defined as

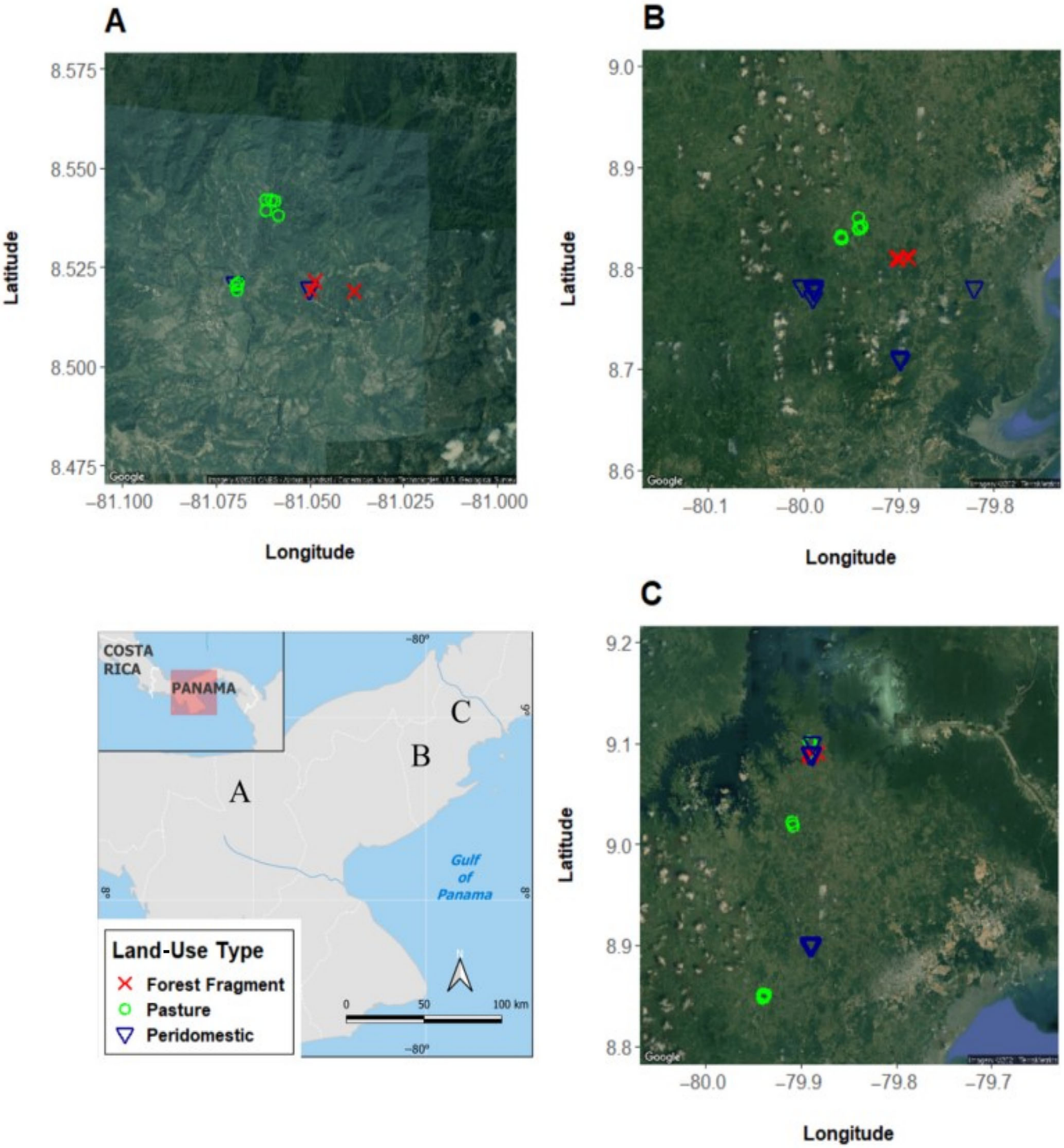


**FIGURE 1** Palm sampling locations across different land-use types throughout central Panama. Symbols (some are overlapped) represent sampled palms from Forest remnants, Pastures, and Peridomestic land-use areas within three localities: (A) Santa Fe, (B) Capira, and (C) La Chorrera.

cleared areas designated for cattle grazing; and forest remnants were classified as patches of mid to late secondary forest surrounded by land that had been deforested for agriculture or cattle. These three landscape classes were distinguished in the field during initial scouting surveys and verified through satellite imagery.

## Study timeline

We sampled a total of 105 *A. butyracea* palms. Palms ($N = 89$) were sampled during the wet season (June–July) between 2013 and 2016 and from June to November 2017. In the dry season (December–May), 16 palms were sampled across Capira ($N = 13$) and La Chorrera ($N = 3$). Palm crown community sampling occurred during midday hours of 1100–1600 h.

## Palm selection and crown access

Palms were sampled within each land-use type at each district. Selection was limited by accessibility (a palm walking distance with a ladder and gear and two field personnel), palm crown canopy architecture, and climbing safety precautions related to crown height. Each *Attalea* palm crown was accessed using a combination of a collapsible 6-m ladder or climbing harness with anchored support to the palm trunk. As such, we sampled every *A. butyracea* palm that met the following logistical criteria: (1) landowner permission was obtained; (2) the palm crown was accessible with a 6-m extension ladder, or a climbing harness anchored to the trunk; and (3) the terrain immediately around the palm allowed access and ladder/harness placement. A total of 105 palms met these criteria and were sampled for *R. pallescens*. Of these palms, 49 were also sampled for animal species community composition and microclimate conditions (described below).

## Vector collection

*R. pallescens* were captured using mouse-baited traps adapted from Noireau et al. (2002). A total of three traps were placed throughout each palm crown (one mouse/trap), out of direct sunlight, and checked every 24 h for three days (Abad-Franch et al., 2000; Gottdenker et al., 2011). Upon checking each trap, *R. pallescens* were collected and individually stored in microtubes in 95% ethanol (EtOH) for molecular analysis. Traps were resupplied with food (a mix of dry cat food and fruit) and water-soaked cotton balls for the mice. For palm crowns higher than 6 m, a telescopic pole was used to place vector traps within the crown.

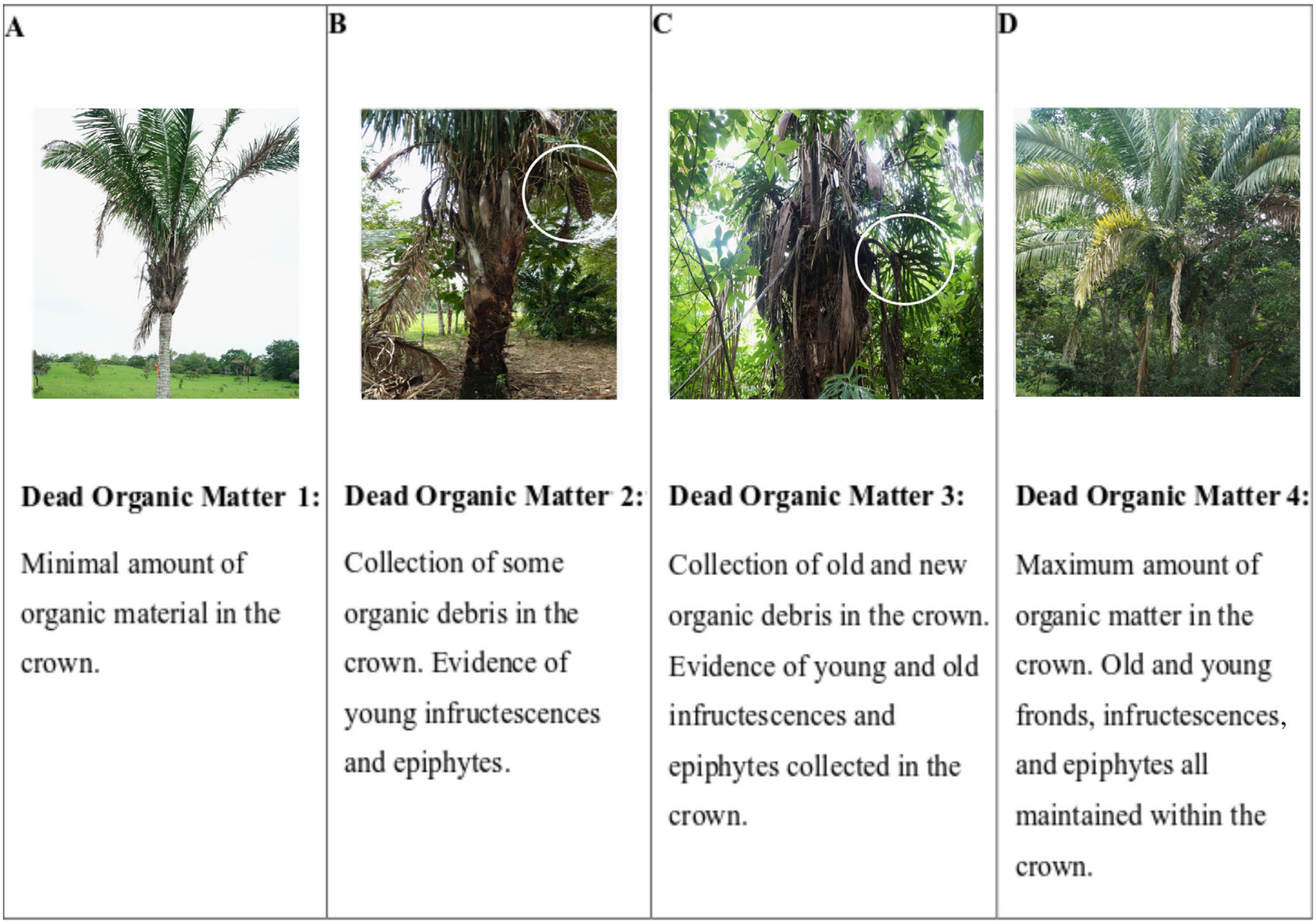
## Microhabitat and microclimate data collection

We recorded the following microhabitat conditions of 49 palm crowns: (1) percent canopy cover (percentage of forest cover measured at 5 m distance from the sampled palm at the four cardinal locations); (2) palm height (height from base of trunk to top of crown [in meters]); (3) number of connected trees (count of other trees physically connected to the sampled palm); (4) presence of infructescence (yes/no); and (5) number of epiphytic plants (see Appendix S1 for measurement details). We also measured the level of dead organic matter (DOM), a method adapted from Abad-Franch et al. (2005) in which the amount of organic matter found in the crown is ranked on a scale ranging from 1 (little to no fibrous matter) to 4 (profuse fibrous matter) (Figure 2). Using these microhabitat conditions collectively, we created an index of palm crown complexity, in which higher levels of organic matter, epiphytic plants, and infructescence contribute to a palm with high level of organic matter at the crown base (Abad-Franch et al., 2005).

Microclimate conditions (average relative humidity [%RH] and average temperature) were collected from a subset of palms ($N = 42$) using data loggers (Reed R6020, Wilmington, NC, USA and HOBO, Cape Cod, MA, USA). Loggers were deployed while *R. pallescens* trapping occurred and prior to palm crown community sampling. We placed three data loggers in each palm within frond crevices throughout the crown. Each logger measured temperature and %RH every minute for 3 days.

## Palm crown community collection

After sampling *R. pallescens* and microclimate and microhabitat conditions, palm crown invertebrate and vertebrate communities were sampled by actively searching for three consecutive days for 30 min per palm. During periods of heavy rains, palm sampling would resume on the following dry day. Each 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. Vertebrate biomaterials (e.g., hair, nests, feathers) were collected as an indicator of vertebrate presence. 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 at the base of the palm. During frond beating and dead organic removal, researchers would collect all invertebrates using forceps and a handheld vacuum. Dead organic material was also collected in a 0.9-L (1 quart) Ziploc bag and brought to the lab to sift for invertebrates with a colander (mesh size 0.08 cm [1/32 in.]). All invertebrates were stored separately in 95% EtOH. All specimens were processed at the Smithsonian Tropical Research Institute, Naos station, in Panama City, Panama.



**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 infructescences and epiphytes.

**Dead Organic Matter 3:** Collection of old and new organic debris in the crown. Evidence of young and old infructescences and epiphytes collected in the crown.

**Dead Organic Matter 4:** Maximum amount of organic matter in the crown. Old and young fronds, infructescences, and epiphytes all maintained within the crown.

**FIGURE 2** Measured characteristics and dead organic matter (DOM) scale of the palm crown microhabitat. DOM ranged from low (A) to high (D). Infructescence (B, white circle) and epiphytic plants (C, white circle) were also among the characteristics measured.

## Species identification and food web construction

All invertebrate species were identified to the lowest possible taxonomic resolution. Once taxonomically identified, individuals were grouped into morphospecies and trophic species. Trophic species were generally defined as those that share predator and prey species (Briand & Cohen, 1984). For each palm community, a binary feeding matrix was constructed. The matrix consisted of all species (in both rows and columns) found in the crown and denotes either a feeding interaction (coded 1) or no feeding interaction (coded 0) between species. Feeding interactions were determined by observations in the field, natural history, and prior studies of consumer–resource interactions for each morphospecies. Interactions were weighted by species abundance. Food webs were created using the computer software Network3D version 1.0 (Williams, 2010; Yoon et al., 2004). Network3D measures trophic composition, network complexity, and structural characteristics of a given community. Specifically, we looked into the network metrics Generality and Vulnerability at both the community level and at the individual (i.e., *R. pallescens*) level (described below).

## Molecular analyses

### Blood meal analysis

We conducted next-generation sequencing (NGS) to identify vertebrate blood meals from *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. We used 12S rRNA gene-specific primers for vertebrates with bar codes (Glenn et al., 2019; Humair et al., 2007) and designated Operational Taxonomic Units for species identification using QIIME v1.9 (Caporaso et al., 2010) with a custom reference database. This method was also used to further confirm the presence of any vertebrates that were initially detected through signs such as nest, hair, fur, or feathers. For a conservative estimate of blood meal source, we eliminated species hits receiving ≤10% of total read hits for the sample. Because the focus of this study was detecting blood meals of wild animals living in 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.

### Trypanosome detection

We detected *T. cruzi* presence using a polymerase chain reaction (PCR) targeting 330 base-pair (bp) fragments from the kinetoplast minicircle DNA (kDNA) using the protocol for PCR conditions outlined in Wincker et al. (1994). The primers used were 121 (5′-AAATAATGTACGGG(T/G) GAGATGCATGA-3′) and 122 (5′-GGTTCGATFGGGGT rGGTGTAA TATA-3′). PCR products (5 μl) were electrophoresed on a 2% agarose gel stained with GELSafe dye and run at 86 V. Gels were evaluated under ultraviolet light for the presence of 330-bp bands. Positive and negative controls were run in each reaction.

## Data analysis

All statistical analyses were performed using the software R 3.5.3 (R Core Team, 2021).

## Missing data

Instances of missing climate data occurred in 18 palms due to data logger malfunctions, animal interference, extreme weather, and equipment loss in deep crevices between palm fronds. We also suffered data loss due to multiple instances of stolen equipment. To handle the values of missing data, we used the R package Amelia II (Honaker et al., 2011), which is based on running an expectation maximization 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 data sets.

## Palm crown community variables

To investigate the influence of the palm crown community on *R. pallescens* abundance and infection with *T. cruzi*, we quantified both the palm crown community and species-level network metrics 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 ($D = 1 - ((\Sigma n(n-1))/(N(N-1)))$), which indicates the number of animal species and their relative abundance at a particular location, 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) (Schoener, 1989; Williams & Martinez, 2000).

In addition, we analyzed the network specific to *R. pallescens*, which was focused on the interaction metrics between *R. pallescens* and the surrounding members of the animal community. Similar to the community-level metrics, we focused on prey and predator interactions with *R. pallescens*, which is also measured by Vulnerability (number of predators of *R. pallescens*) and Generality (number of *R. pallescens* hosts) in each palm crown. We included the community-wide network metric as a proxy for additional underlying or indirect factors stemming from other trophic species that are otherwise overlooked when only incorporating specific predators and blood meal host species of *R. pallescens*. In addition, we included presence/absence and abundance data for particular species of interest for *R. pallescens*, such as presence of host/vertebrate blood meal taxa. This included reptiles, birds, and mammals (further separated into coendu [porcupine], tamandua [anteater], bat, and opossum) that were detected in the palm crown via visual detection (i.e., individual sighting or biomaterials present), and then were later confirmed by blood meal identification from triatomines collected in the same palm (when those data were available). Other species of interest were invertebrates that possibly predate on *R. pallescens*: scorpions, spiders, centipedes, and whip spiders.

## Statistical models

To assess the effects of microclimate, microhabitat, and species community on the response variables abundance and infection (1, infected; 0, not infected) of *R. pallescens* for each palm, we used generalized linear mixed models (Bolker et al., 2009). Our models predicting *R. pallescens* abundance used a negative binomial error distribution and a log link function. The negative binomial distribution is an extension of the Poisson distribution useful to analyze count data that are overdispersed, which we observed in our *R. pallescens* abundance data. For our model predicting *R. pallescens* infection, the binary outcome of infection (infected/not infected) was fitted with a logistic regression with a logit link function. We treated study sites (Santa Fe, Capira, and La Chorrera) and land-use types (Pasture, Peridomestic, and Forest remnant) as fixed variables because their effects remained constant for different individual *R. pallescens* within each palm, and because we were interested in the effects of land-use type and location on both response variables. In our model predicting *T. cruzi* infection, we treated Palm ID as a random variable to account for any random variation associated with repeated measurements for each palm.

To build our hypothesis-driven model, we first explored the correlation between the explanatory variables and *R. pallescens* abundance and infection with *T. cruzi*. Explanatory variables included: land-use type (Pasture, Peridomestic, and Forest remnant), location (La Chorrera, Capira, and Santa Fe), microhabitat (number of connected trees, % canopy cover, palm height, DOM, presence of infructescences, and number of epiphytic plants) and microclimate conditions (average temperature and average %RH), number and type of predatory invertebrates collected from the palm crown (scorpion, tarantula, whip spider, and centipede), number and type of vertebrates observed via crown dissection (mammal, bird, and reptile), blood meal identity (coendu, tamandua, bat, and opossum), or a combination of both direct observation and/or blood meal identity, and palm crown community metrics (community and *R. pallescens*-level Generality and Vulnerability) (see Appendix S1: Table S1 for variable details).

For the initial variable exploration, we used Pearson correlations to investigate the direction and strength of relations between continuous explanatory variables and the response variable abundance. Point-biserial correlations were used to investigate continuous and categorical explanatory variables, including the response variable infection. Variables that were less associated with the driving hypotheses and did not have a significant relationship ($p > 0.05$) with either response variable or that were highly correlated with another explanatory variable were removed from further analysis. We tested collinearity between continuous predictor variables using the variance inflation factor (VIF, package “mctest”; Imdad & Aslam, 2020), and we omitted any strongly correlated variables of VIF > 2.9. In addition to VIF, we investigated variable tolerance, which indicates the proportion of variance in a particular independent variable unrelated to other variables in a model.

Model selection was based on multimodel inference using corrected Akaike information criterion for small sample sizes ($\text{AIC}_c$, Burnham & Anderson, 2004) (see Appendix S1: Tables S3 and S4 for model selection). Using R package “MuMin” (Barton, 2020), we “dredged” our global model, which included the variables selected by the initial exploratory analysis and generated a top-model set based on the criterion that $\Delta\text{AIC}_c < 4$. For each dependent variable, we base inference on the top-model set by (1) averaging parameter estimates across models, using Akaike weights to favor estimates from better-performing (smaller $\text{AIC}_c$) models; and (2) computing unconditional standard errors and confidence intervals that account for model selection uncertainty (Burnham & Anderson, 2004). This approach also helps avoid model overparameterization and minimize the effects of uninformative parameters (Arnold, 2010; Grueber et al., 2011).

# RESULTS

## Vector abundance, infection, and blood meal composition

A total of 1098 *R. pallescens* were collected from 105 palms throughout three study sites and three land-use classes (La Chorrera: $N = 43$; Pasture, $N = 14$, Peridomestic, $N = 16$, Forest remnant, $N = 13$; Capira: $N = 47$; Pasture, $N = 21$, Peridomestic, $N = 20$, Forest remnant, $N = 6$; and Santa Fe: $N = 15$; Pasture, $N = 8$, Peridomestic, $N = 4$, Forest remnant, $N = 3$). Overall, we found *R. pallescens* in 81% (85 of 105) of palms sampled (Table 1). The percentage of palms infested with *R. pallescens* was highest in Santa Fe, with 93% of palms infested by an average of 19.1 bugs. The percentage of palms infested by *R. pallescens* was consistently high (>60%) across all land-use types except for Forest remnants in Capira (33%). Average *R. pallescens* abundance per palm differed significantly among locations (Kruskal–Wallis $\chi^2 = 7.18$, $\text{df} = 2$, $p = 0.03$) and land-use types (Kruskal–Wallis $\chi^2 = 6.41$, $\text{df} = 2$, $p = 0.04$) (Figure 3A,B). There were consistently more nymphs than adults trapped across palm sites (Pearson's $\chi^2 = 27.14$, $\text{df} = 2$, $p < 0.05$) and land-use types (Pearson's $\chi^2 = 33.21$, $\text{df} = 2$, $p < 0.05$).

Of the 1098 *R. pallescens* captured, 476 individuals were tested for *T. cruzi*. Overall, *T. cruzi* infection was detected in 38% (181 of 476) of *R. pallescens* (Appendix S1: Table S2). The proportion of *R. pallescens* infected with *T. cruzi* varied significantly among locations (Fisher's exact test $p = 0.00$) and was highest in Santa Fe (74 of 130; 57%) compared with La Chorrera (52 of 186; 28%) and Capira (54 of 160; 33%) (Figure 4A). The proportion of *R. pallescens* infected with *T. cruzi* also varied significantly among land-use types (Fisher's exact test $p = 0.00$) and was typically higher in Forest remnant (16 of 26; 61%) and Peridomestic (110 of 261; 42%) compared with Pasture palms (50 of 181; 28%) (Figure 4B).

NGS from 240 individual bugs across 31 palms in Capira ($N = 9$), Santa Fe ($N = 8$), and La Chorrera ($N = 14$)

**TABLE 1** Patterns of *Attalea butyracea* palm infestation with *Rhodnius pallescens* triatomine bugs across three locations and three land-use types in central Panama.

| Location and habitat | *N* | Percentage of palms infested with *Rhodnius* (95% CI) | Total no. *Rhodnius* captured | Mean no. *Rhodnius* captured per infested palm (95% CI) | Total no. adult *Rhodnius* captured | Total no. *Rhodnius* nymphs captured | Nymph:adult ratio |
|---|---|---|---|---|---|---|---|
| La Chorrera | | | | | | | |
| Pasture | 14 | 85 (54 to 97) | 98 | 8.1 (3.9 to 12.2) | 7 | 91 | 13 |
| Peridomestic | 16 | 81 (53 to 95) | 142 | 11.8 (3.0 to 20.5) | 17 | 94 | 5.5 |
| Forest remnant | 13 | 92 (62 to 99) | 187 | 15.5 (8.2 to 22.8) | 8 | 139 | 17.4 |
| Total | 43 | 86 (70 to 92) | 427 | 11.8 (7.8 to 15.8) | 32 | 324 | 10.1 |
| Capira | | | | | | | |
| Pasture | 21 | 71 (47 to 88) | 72 | 4.8 (2.3 to 7.2) | 4 | 57 | 14.3 |
| Peridomestic | 20 | 90 (67 to 99) | 327 | 18.1 (5.2 to 31.0) | 36 | 126 | 3.5 |
| Forest remnant | 6 | 33 (6 to 76) | 4 | 2.0 (−2.0 to 6.0) | 2 | 2 | 1 |
| Total | 47 | 74 (60 to 85) | 403 | 11.5 (4.4 to 18.5) | 42 | 185 | 4.4 |
| Santa Fe | | | | | | | |
| Pasture | 8 | 100 (60 to 100) | 82 | 10.25 (4.0 to 16.5) | 13 | 54 | 4.2 |
| Peridomestic | 4 | 100 (40 to 100) | 150 | 37.5 (24.5 to 50.5) | 22 | 46 | 2.1 |
| Forest remnant | 3 | 67 (12 to 99) | 36 | 18 (0.0 to 51.0) | 4 | 7 | 1.7 |
| Total | 15 | 93 (70 to 99) | 268 | 19.1 (10.6 to 27.6) | 39 | 107 | 2.7 |
| Total all locations | 105 | 81 (72 to 88) | 1098 | 12.9 (9.3 to 16.6) | 113 | 616 | 5.4 |

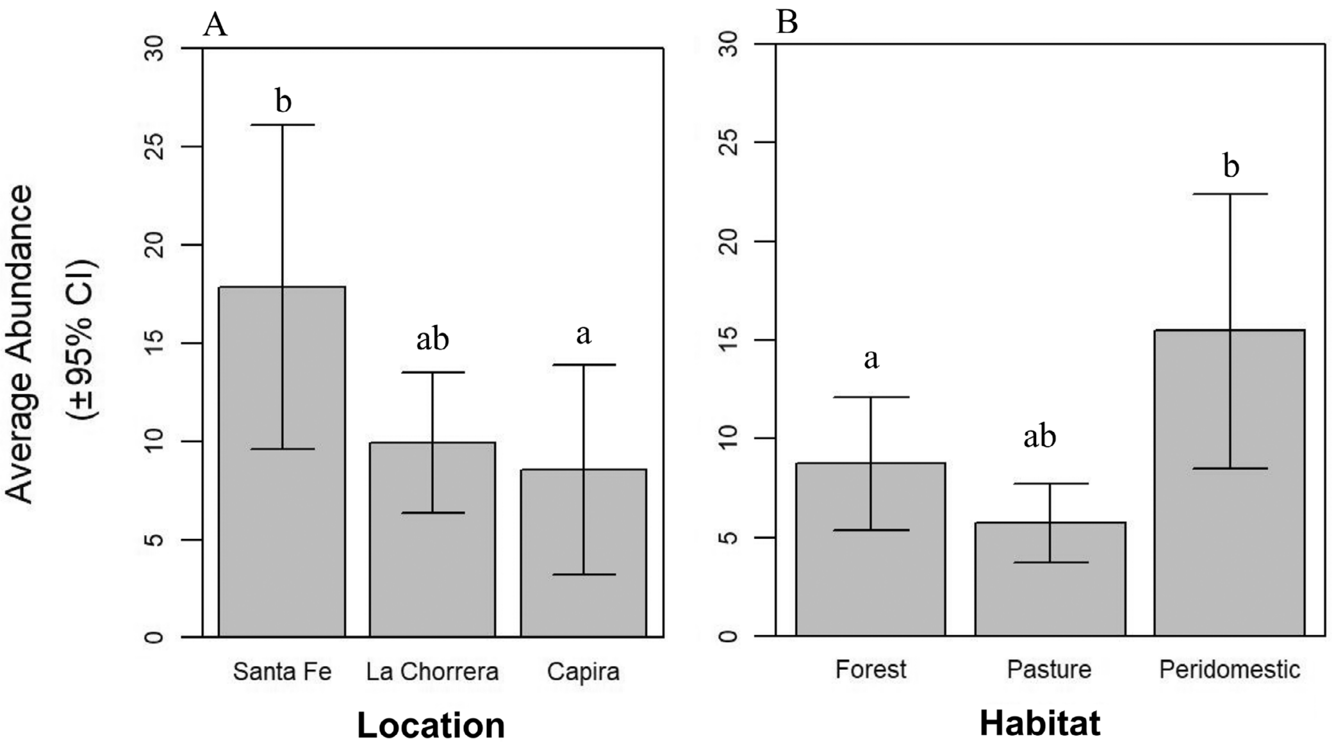


**FIGURE 3** Average *Rhodnius pallescens* abundance in *Attalea butyracea* palms sampled across three locations (A) and three land-use type habitats (B). Dunn's post hoc test reveals the average abundance between locations Santa Fe (17.9 ± 16.9) and Capira (8.6 ± 19; $p = 0.02$) and Forest (8.7 ± 12.5) and Peridomestic habitats (15.5 ± 22.7; $p = 0.04$) differed significantly. Single lowercase letters 'a' and 'b' above a data bar indicate those average bug abundances are significantly different from one another, but 'ab' above a data bar denotes that the average bug abundance does not differ from a nor b.

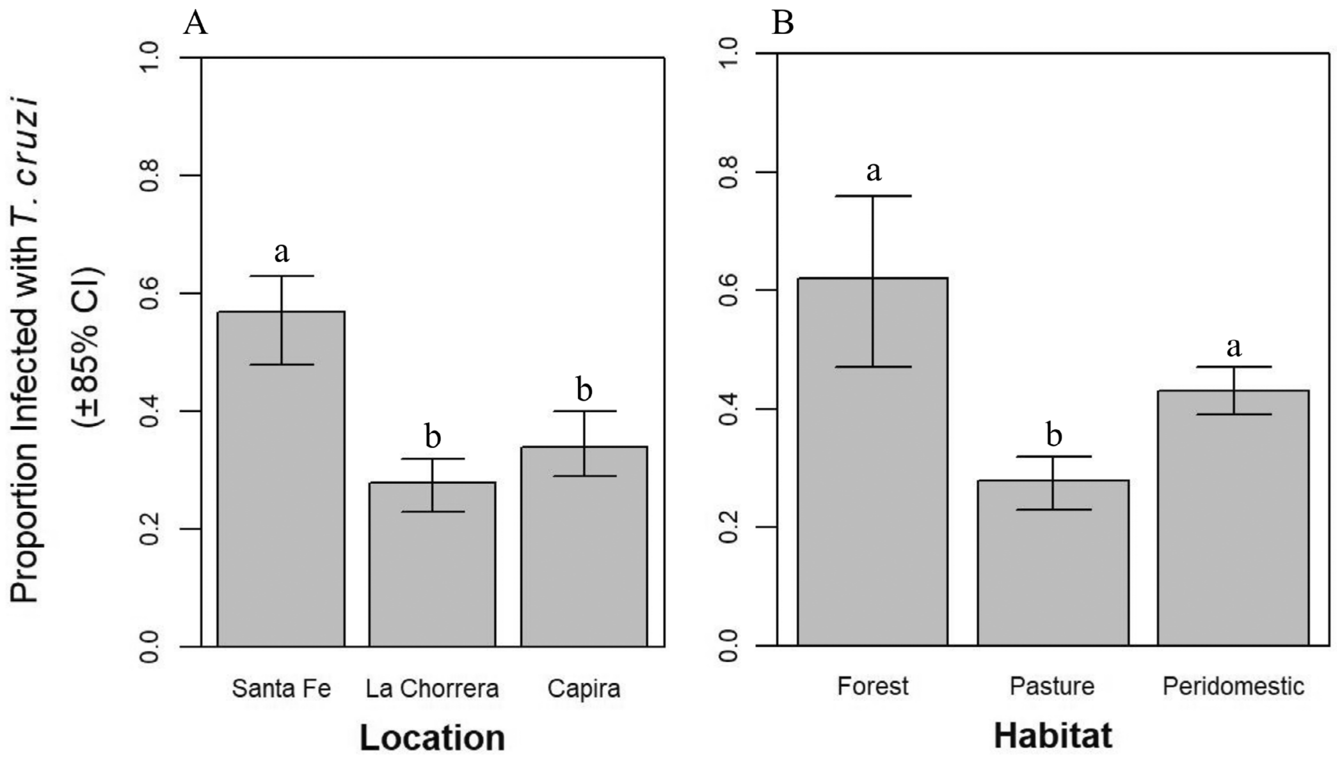


**FIGURE 4** Proportion of *Rhodnius pallescens* infected with *Trypanosoma cruzi* across three locations (A) and three land-use type habitats (B). Fisher's pairwise test reveals the proportion infected between locations Santa Fe and Capira and Santa Fe and La Chorrera and habitats Forest and Pasture and Pasture and Peridomestic differed significantly.

(Figure 5A–C) identified blood meals from 73% (176 of 240) of captured individuals. Overall, a total of seven orders were identified, including 15 genera and nine species. Wild mammal species dominated blood meal composition (87%, 153 of 176, particularly those belonging to the Order Didelphimorphia: 63%, 112 of 176) across all locations and triatomine development stages as compared with bird 11% (19 of 176) and reptile 1.7% (3 of 176) blood meals (Appendix S1: Table S3). Blood meal richness at the level of order and genus was highest in La Chorrera (six orders, 10 genera), followed by Capira and Santa Fe (five orders, seven genera). Across land-use types, triatomines fed from a more diverse host taxa assemblage in Pasture and Peridomestic palms compared with Forest-remnant palms (Appendix S1: Table S4).

Of the 240 *R. pallescens* that underwent blood meal analysis, 175 individuals were tested for *T. cruzi* infection and 45% (79 of 175) were *T. cruzi* positive. Of the 79 total individuals that were positive, 70% (55 of 79) had fed from species in the Order Didelphimorphia (marsupials), followed by sylvatic Rodentia 18% (14 of 79). In total, *T. cruzi*-infected marsupial blood meals were confirmed for 30% (55 of 175) of vectors (Figure 6; see also Appendix S1: Tables S3 and S4).

## Food web network metrics

A total of 49 palms were sampled for species community from La Chorrera ($N = 29$), Capira ($N = 15$), and Santa Fe ($N = 5$). Palm crown network metrics were calculated at the community level (Network Generality and Vulnerability) and *R. pallescens* level (*R. pallescens* Generality and Vulnerability), and overall Diversity (Simpson's *D*), for each palm and across each land-use type: Forest remnant ($N = 18$), Pasture ($N = 14$), and Peridomestic ($N = 17$) (Table 2). Of the network metrics, only community-level Network Generality differed across land-use types, with a significant difference between Pasture and Peridomestic palms (Kruskal–Wallis $\chi^2 = 8.0481$, $df = 2$, $p = 0.02$). A lower community-level Generality score in Pasture palms means that there were fewer prey species per consumer compared with palms in Peridomestic sites.

## Correlation analysis for model selection variables

In addition to species community, microclimate and microhabitat variables were also collected from each of the 49 palms. Of the community variables of interest, the

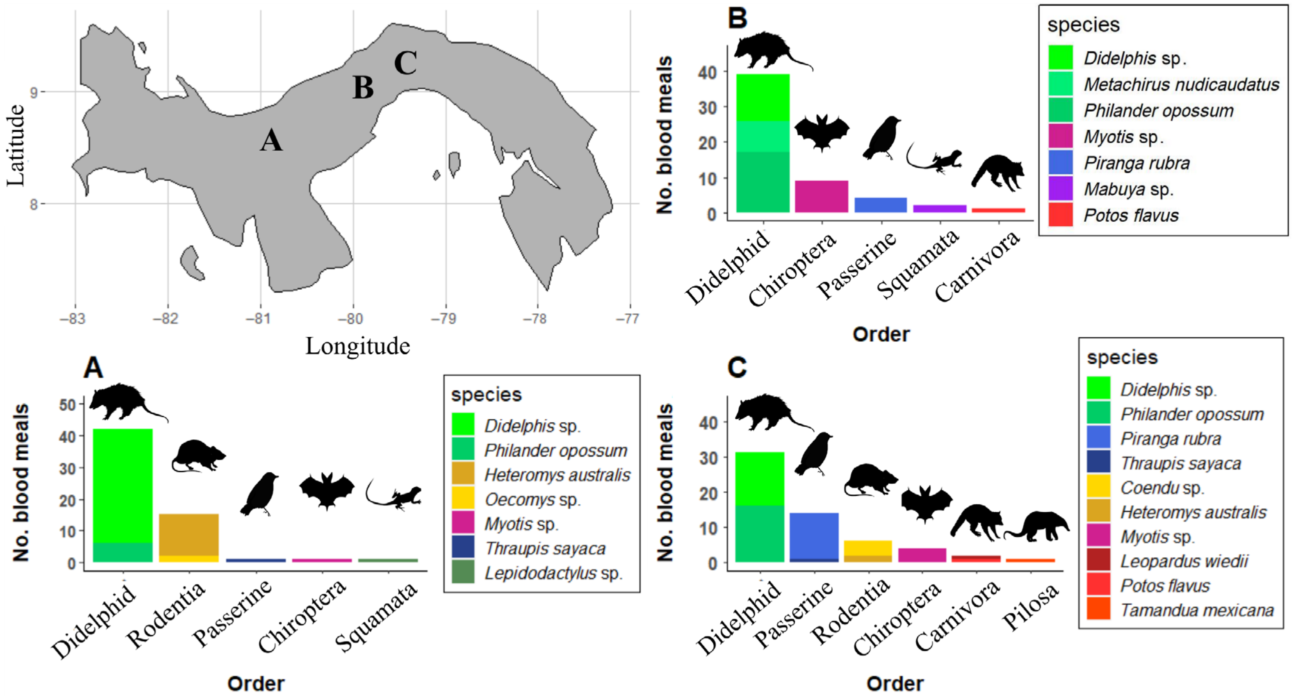


**FIGURE 5** Vertebrate blood meal composition (order and species) identified from *Rhodnius pallescens* individuals collected from *Attalea butyracea* palms of three localities in central Panama: (A) Santa Fe ($N = 60$ individuals), (B) Capira ($N = 55$ individuals), and (C) La Chorrera ($N = 58$ individuals).

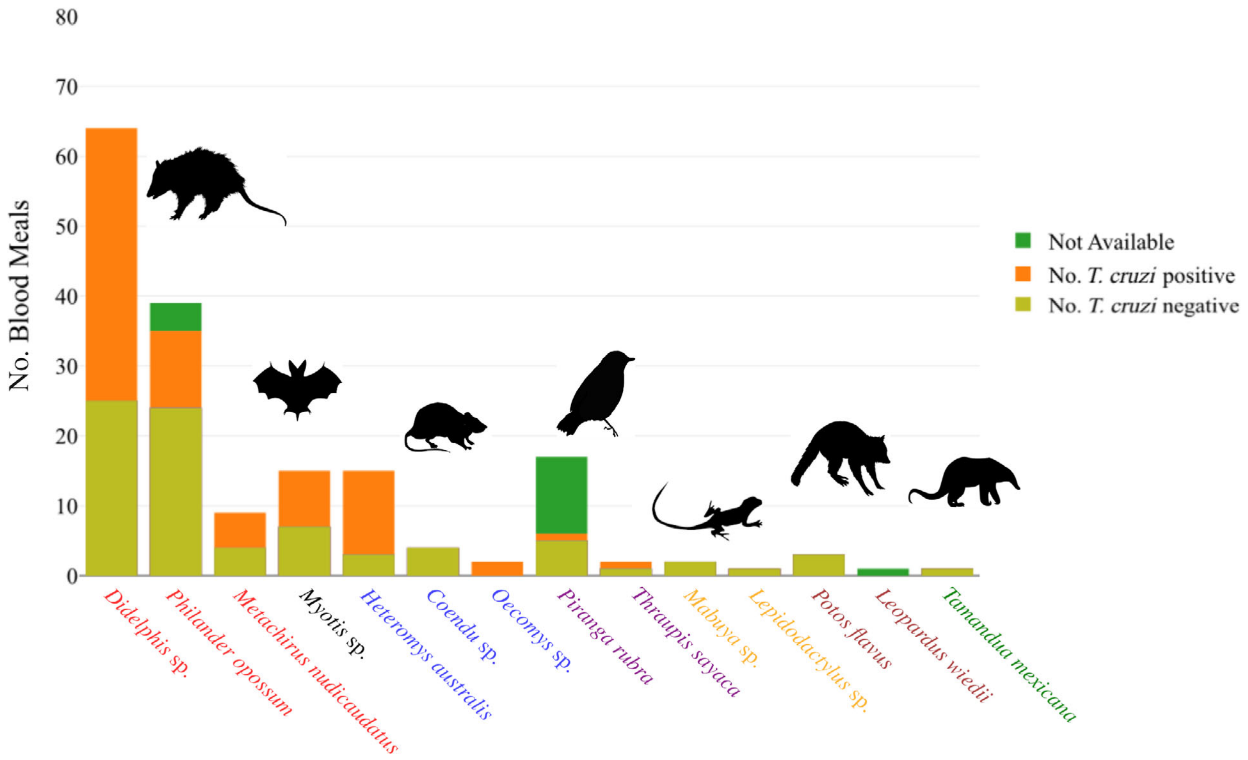


**FIGURE 6** Overall blood meal composition and infection status (*Trypanosoma cruzi* positive/negative) of *Rhodnius pallescens* ($N = 175$) from *Attalea butyracea* palms of three localities in central Panama. Blood meal Order Didelphidmorpha (red): *Didelphis* sp., *Metachirus nudicaudatus*, *Philander opossum*; Order Chiroptera (black): *Myotis* sp.; Order Rodentia (blue): *Coendu* sp., *Heteromys australis*, *Oecomys* sp.; Order Passeriformes (purple): *Piranga rubra*, *Thraupis sayaca*; Order Squamata (yellow): *Mabuya* sp., *Lepidodactylus* sp.; Order Carnivora (brown): *Potos flavus*, *Leopardus wiedii*; Order: Pilosa (green): *Tamandua mexicana*.

**TABLE 2** Palm crown food web network metrics at the palm crown level and relative to *Rhodnius pallescens*.

| Metric | Forest ($N = 18$) | Pasture ($N = 14$) | Peridomestic ($N = 17$) |
|---|---|---|---|
| Network Generality | | | |
| Median (IQR) | 1.11 (0.93–1.28) | 0.93 (0.87–1.04) | 1.19 (1.09–1.38) |
| Mean (±SD) | 1.13 (±0.28) | 0.97 (±0.22) | 1.22 (±0.22) |
| Range | 0.77–1.72 | 0.56–1.46 | 0.82–1.65 |
| Network Vulnerability | | | |
| Median (IQR) | 0.36 (0.16–0.56) | 0.42 (0.31–0.53) | 0.44 (0.35–0.53) |
| Mean (±SD) | 0.43 (±0.18) | 0.42 (±0.09) | 0.47 (±0.15) |
| Range | 0.24–0.99 | 0.26–0.56 | 0.28–0.81 |
| Generality (*R. pallescens*) | | | |
| Median (IQR) | 0.11 (0.00–0.28) | 0.51 (0.24–0.60) | 0.39 (0.00–0.62) |
| Mean (±SD) | 0.16 (±0.19) | 0.46 (±0.29) | 0.40 (±0.34) |
| Range | 0.00–0.64 | 0.00–0.96 | 0.00–1.02 |
| Vulnerability (*R. pallescens*) | | | |
| Median (IQR) | 0.72 (0.14–0.91) | 1.12 (1.00–1.17) | 1.03 (0.86–1.25) |
| Mean (±SD) | 0.60 (±0.40) | 1.03 (±0.34) | 0.93 (±0.49) |
| Range | 0.00–1.00 | 0.00–1.45 | 0.00–1.51 |
| Simpson's diversity | | | |
| Median (IQR) | 0.84 (0.79–0.88) | 0.83 (0.77–0.87) | 0.81 (0.62–0.83) |
| Mean (±SD) | 0.83 (±0.07) | 0.81 (±0.09) | 0.73 (±0.16) |
| Range | 0.63–0.91 | 0.57–0.91 | 0.33–0.88 |

Abbreviation: IQR, interquartile range.

proportion of invertebrate predators, specifically spider taxa, was the highest across all palms and locations (Figure 7A,B). During our initial correlation analysis, we also blended similar covariates that shared direction in their association with the response variables to avoid redundancy and overparameterization. Blood meal and potential vertebrate predator species were grouped as "mammals" (opossum, bat, tamandua, and coendu), lizards and amphibians were combined as "herptiles," and invertebrate predators (spiders, scorpions, and whip spiders) were "invertebrates." We omitted any remaining variables with high VIFs (high multicollinearity) such as network measurements that correlated strongly with the presence and abundance of particular species (i.e., correlation between "invertebrates" and "Network Vulnerability" or "mammals" and "*R. pallescens* Vulnerability" or "Generality").

Regarding microenvironmental measurements, the average palm crown ranged from 25 to 28°C and 79%–98% RH across all habitat types and locations. Results of the Pearson correlation for the model selection variables indicated that average temperature and %RH had alternating, weak associations with *R. pallescens* abundance; %RH and vector abundance had a negative relationship ($r = -0.17$, $p = 0.23$), whereas temperature and abundance had a positive relationship ($r = 0.26$, $p = 0.07$) (see also Appendix S1: Figure S1). Regarding palm physiognomy, the Pearson correlation indicated that increasing

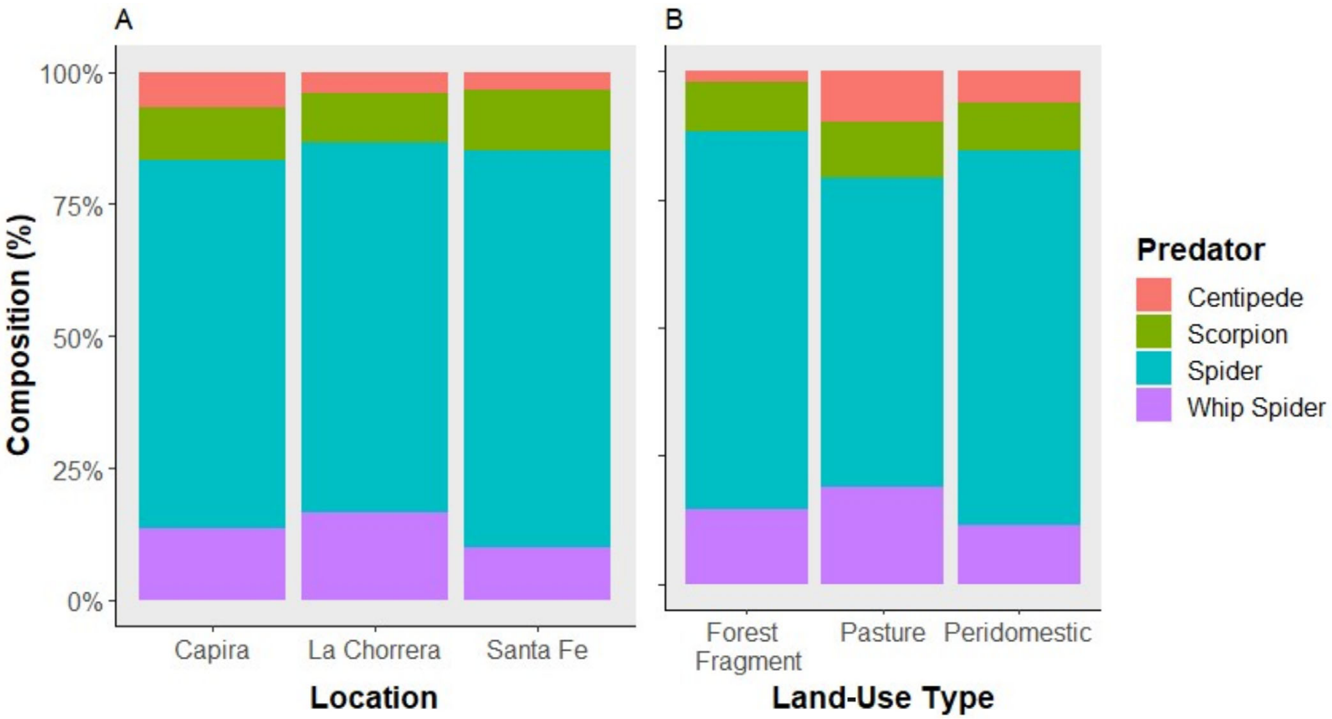


**FIGURE 7** Invertebrate predator community composition in *Attalea butyracea* palms across (A) three location and (B) three land-use types in central Panama. Spider abundance dominated predator communities across all palms sampled.

DOM (as a binary variable 1–2) had a slight positive association with abundance ($r = 0.17$, $p = 0.23$).

Of the community components, we found that the presence of mammals within the palm was positively associated with vector infection ($r = 0.15$, $p = 0.01$), whereas the presence of herptiles showed a negative association with infection ($r = -0.20$, $p < 0.00$). In addition to mammals, the number of invertebrate predators was also positively, but weakly, associated with vector abundance ($r = 0.22$, $p = 0.13$). Of the network measurements, "*R. pallescens* Vulnerability" had a positive association with abundance ($r = 0.46$, $p < 0.00$), whereas community Diversity had a negative association with abundance ($r = -0.45$, $p < 0.00$) (for correlation plots, see Appendix S1: Figures S2 and S3).

## Abiotic, community, and food web factors associated with vector abundance and infection

Our mixed-effects models exploring *R. pallescens* abundance and *T. cruzi* infection were based on covariates selected through the correlation reanalysis and meaningful biological inference related to palm crown fauna, microenvironmental conditions, location, and habitat (for model rankings, see Appendix S1: Tables S5 and S6). According to the top-model set averages, a combination of the palm crown community, microhabitat, microclimate, and locality did indeed influence vector abundance (Table 3) and, to a lesser extent, vector probability of infection (Table 4). Regarding the palm crown community composition and trophic network, model averaging predicts a 41% (85% CI 25%–53%) decrease in vector abundance for every ~12% (1 SD) increase in palm crown community Diversity (Simpson's *D*). We also found about 3.1 (2.19–4.37) as many *R. pallescens*, on average, in a palm with *R. pallescens* Vulnerability 1.29 (mean ± 1 SD) as in a palm with Vulnerability 0.84 (mean) (Figure 8a). The abundances of vectors and their potential invertebrate predators were positively correlated; on average, each additional predator in a palm crown was associated with a 5% (85% CI 2%–8%) increase in vector density (Figure 8b).

Potential blood meals (i.e., vertebrates) had little to no effect on *R. pallescens* abundance. Although nonsignificant, the presence of an additional mammal was predicted to

**TABLE 3** Model-averaged parameter estimates (conditional average) from a model set (negative binomial error distribution and log link function) predicting *Rhodnius pallescens* abundance within palms based on community data collected from 49 *Attalea butyracea* palms.

| Term | Estimate | SE | 85% CI | *p* | Importance[a] |
|---|---|---|---|---|---|
| Intercept | 1.07 | 0.56 | 0.25 to 1.88 | 0.06 | |
| Locality | | | | | 0.93 |
| Capira | (Ref.) | … | … | … | |
| La Chorrera | 0.94 | 0.32 | 0.48 to 1.41 | 0.00 | |
| Santa Fe | 1.32 | 0.42 | 0.70 to 1.91 | 0.00 | |
| Habitat | | | | | 0.41 |
| Forest remnant | (Ref.) | … | … | … | |
| Pasture | −1.08 | 0.49 | −1.79 to −0.37 | 0.03 | |
| Peridomestic | −0.48 | 0.43 | −1.11 to 0.15 | 0.27 | |
| Microhabitat | | | | | |
| RH | 0.30 | 0.15 | 0.09 to 0.51 | 0.04 | 0.45 |
| DOM | 0.90 | 0.41 | 0.25 to 1.47 | 0.04 | 0.65 |
| Community | | | | | |
| Mammals | 0.36 | 0.30 | −0.08 to 0.8 | 0.14 | 0.26 |
| Invertebrates | 0.05 | 0.02 | 0.02 to 0.08 | 0.02 | 0.70 |
| Herps | −0.13 | 0.18 | −0.39 to 0.12 | 0.45 | 0.27 |
| Birds | −0.34 | 0.32 | −1.81 to 0.13 | 0.30 | 0.26 |
| Network | | | | | |
| Vulnerability (*R. pallescens*) | 1.13 | 0.23 | 0.81 to 1.48 | 0.00 | 1.00 |
| Diversity | −0.53 | 0.16 | −0.76 to −0.29 | 0.00 | 0.93 |

Abbreviations: DOM, dead organic matter; RH, relative humidity.

[a] Sum of model Akaike weights across all models in which the variable is included; ranges from 0.0 to 1.0.

**TABLE 4** Model-averaged parameter estimates (conditional average) from a model set (binomial error distribution and logit link function) predicting *Rhodnius pallescens* infection with *Trypanosoma cruzi* in *Attalea butyracea* palms of central Panama.

| Term | Estimate | SE | 85% CI | *p* | Importance[a] |
|---|---|---|---|---|---|
| Intercept | −0.58 | 1.24 | −2.37 to 1.21 | 0.64 | |
| Locality | | | | | 0.38 |
| Capira | (Ref.) | … | … | … | |
| La Chorrera | −0.26 | 0.97 | −1.65 to 1.14 | 0.80 | |
| Santa Fe | 1.44 | 1.31 | −0.46 to 3.34 | 0.27 | |
| Habitat | | | | | 0.84 |
| Forest remnant | (Ref.) | … | … | … | |
| Pasture | −4.91 | 1.61 | −7.23 to −2.59 | 0.00 | |
| Peridomestic | −1.92 | 1.23 | −3.7 to −0.14 | 0.12 | |
| Microhabitat | | | | | |
| Temperature | 0.27 | 0.48 | −0.42 to 0.96 | 0.57 | 0.32 |
| Community[b] | | | | | |
| Mammal presence | 3.21 | 1.26 | 1.39 to 5.03 | 0.01 | 0.83 |
| Herp presence | −1.15 | 0.91 | −2.45 to 0.15 | 0.20 | 0.38 |
| Invertebrate presence | 0.27 | 0.42 | −0.35 to 0.88 | 0.53 | 0.38 |
| Bird presence | −0.58 | 1.10 | −2.16 to 0.10 | 0.60 | 0.35 |

[a] Sum of model Akaike weights across all models in which the variable is included; ranges from 0.0 to 1.0.

[b] Reference level for each group is "absence."

increase mean *R. pallescens* abundance by 43% (Figure 8c), whereas the presence of an additional bird or herptile was predicted to decrease mean abundance by 29% and 12%, respectively.

We also detected geographic variation in vector abundance; there were, on average, 3.7 (85% CI 2.0–6.8) and 2.6 (85% CI 1.6–4.1) times more *R. pallescens* in Santa Fe and La Chorrera, respectively, than in Capira.

In regard to the microenvironmental conditions within and surrounding the palm, we found that *R. pallescens* may benefit from palm crown structural and climate conditions. Palms with increased DOM supported about 2–3 times as many *R. pallescens*, on average, than palms with reduced DOM. Also, we found a ~30% average increase in bug abundance for every ~5.5% increase in RH (with substantial uncertainty, though: 85% CI 9.4%–66.5%). Lastly, palms within Pasture habitat types saw a decrease by about 66% (85% CI 31%–83%) in *R. pallescens* abundance compared with Forest remnants (Table 3, Figure 8C).

Our mixed-effects model predicting vector infection probability further suggests that the likelihood of *R. pallescens* infection with *T. cruzi* is influenced mainly by habitat type and palm crown community factors, as implied by the top-performing model (Appendix S1: Table S6, Model 1). Bugs caught in Pasture and Peridomestic palms were 135.6 times and 6.8 times, respectively, less likely to be infected with *T. cruzi* than bugs caught in Forest-remnant palms. Uncertainty about these large effect estimates was however substantial (Table 4). Finally, vectors dwelling in palms with mammals present were about 25 (85% CI 4.02–153) times as likely to be infected compared with palms without mammals.

## DISCUSSION

The objectives of this study were to (1) identify major abiotic and biotic drivers of *R. pallescens* abundance and infection with *T. cruzi* within *Attalea* palms in central Panama, and (2) identify mechanisms of increased *R. pallescens* abundance and *T. cruzi* infection in rural landscapes in central Panama. We also investigated how animal community structure can shape multihost pathogen risk (Johnson & Thieltges, 2010; Johnson et al., 2008; Keesing et al., 2010; Roche et al., 2012). To understand both abiotic and biotic drivers of infection and abundance, we used results from community and environmental surveys, blood meal identification, and molecular analysis of *T. cruzi* infection. Our results indicated that, similar to previous studies (Gottdenker et al., 2011, 2012), vector abundance and the likelihood of vector infection are associated with land-use type, with additional influential factors being geographic location, the invertebrate and vertebrate community, and environmental conditions within the palm crown.

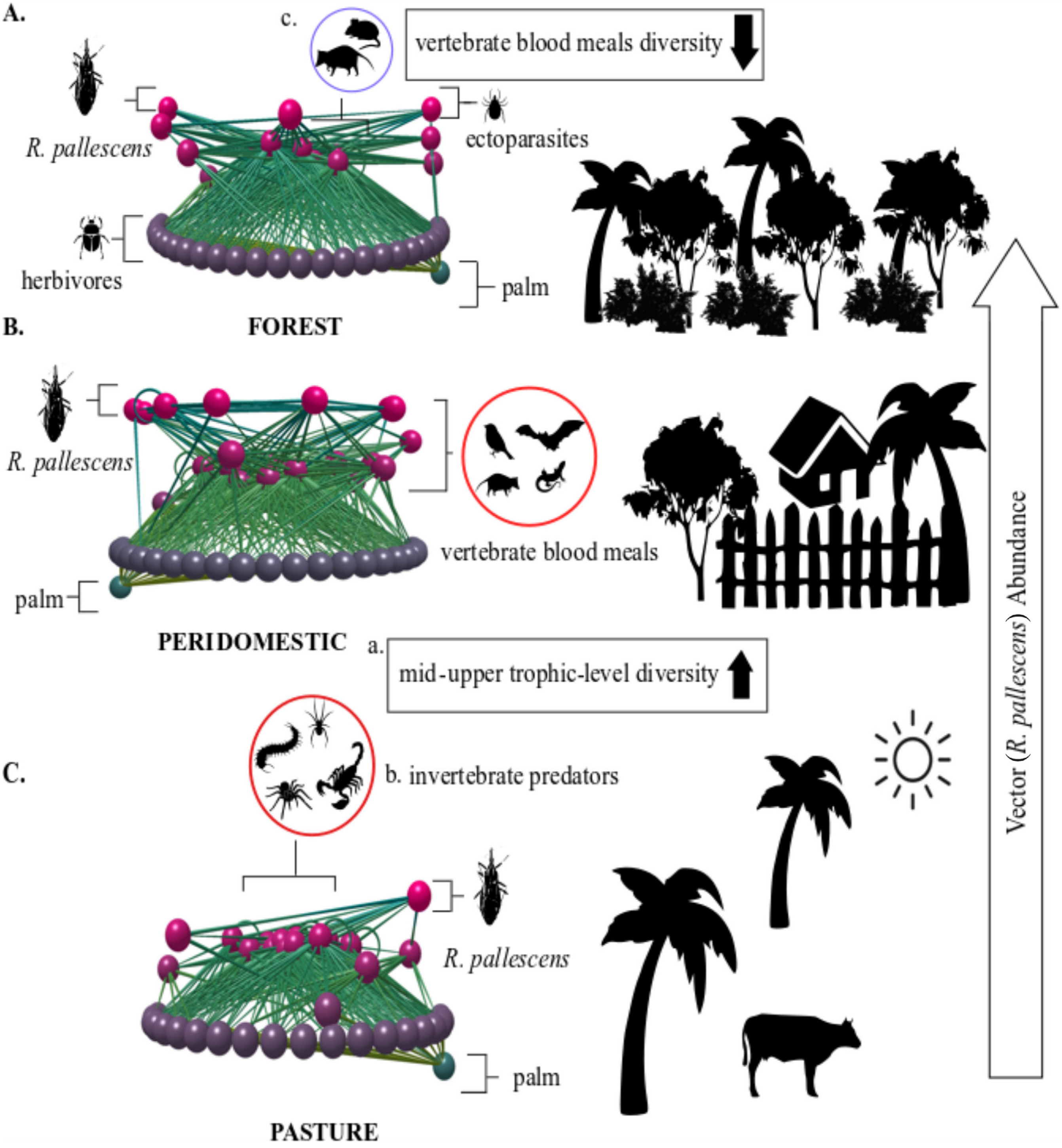


**FIGURE 8** Detailed trophic networks for (A) Forest remnant, (B) Peridomestic, and (C) Pasture palms, averaged across all palms sampled in their respective land-use type. Networks demonstrate that community and trophic structure varies across land-use type. Nodes represent morphospecies, node height represents trophic level (i.e., lower level are herbivores, higher levels are ectoparasites), and the degree of node clustering resembles a species Generality (number of host or prey species per consumer; a node clustered more closely with surrounding nodes has a higher Generality score). Network components that varied across land-use types and influenced *Rhodnius pallescens* abundance and probability of infection with *Trypanosoma cruzi* are circled in red and blue, respectively. Vulnerability, which positively influences *R. pallescens* abundance, is associated with an increase in mid-upper trophic-level diversity (red circles), which was more characteristic of Pasture and Peridomestic palms.

In response to the land-use disturbance gradient, *R. pallescens* abundance in palms is predicted to decrease with the intensity of deforestation. This finding is consistent with a previous study in Panama where abundance of *R. pallescens* was greater in early secondary forest and mid-secondary forest remnants compared with contiguous forest and pasture palms (Gottdenker et al., 2011). However, the response of palm-associated *Rhodnius* spp. populations to land-use disturbance may vary depending on geographical regions. In eastern Amazonia, *Rhodnius* spp. were more abundant in pasture palms than in either peridomestic palms or, especially, Forest-remnant palms (Santos et al., 2021). Variation of *Rhodnius* spp. response to local environmental disturbances and the time since disturbance (e.g., patch isolation time, time since deforestation in pasture) require further investigation across different geographic regions.

Land use was also a significant predictor of vector infection. *R. pallescens* in Pasture palms, followed by Peridomestic palms, had a lower *T. cruzi* infection probability compared with individuals captured in Forest-remnant palms, similar to previous findings in this area of central Panama (Gottdenker et al., 2012). The decrease in vector infection rates was not associated with vector abundance (Appendix S1: Figure S3C). We found that blood meal diversity in Forest-remnant palms was lower than palms in Pasture and Peridomestic sites, and consisted mostly of mammalian blood meals, particularly from rodents and marsupials. Blood meals from *R. pallescens* found in Pasture and Peridomestic palms were more diverse and included birds, which are not competent hosts for *T. cruzi* (see Appendix S1: Table S4). This finding demonstrates a possible dilution effect in which an increase in host diversity reduces the importance of the primary host (in this case, marsupials) within the host community or decreases the probability that a competent host contacts an infected vector (Keesing et al., 2006; Ostfeld & Keesing, 2000a, 2000b; Schmidt & Ostfeld, 2001). Our results support prior findings suggesting that host blood meal species diversity and composition are factors that influence *T. cruzi* vector infection rates (Gottdenker et al., 2012).

Our research also suggests that in addition to the diversity of blood meals, particular elements of the trophic network, namely invertebrate predators and the presence of mammals, reveal specific community-level factors driving *R. pallescens* abundance and infection probabilities. In support of our hypothesis, our study suggests that increased overall animal (vertebrate and invertebrate) community diversity, measured as the palm crown Simpson's diversity, negatively impacts *R. pallescens* abundance. In a previous study of the *Attalea* palm crown community (C.P. Varian, unpublished data), species community diversity was high (Simpson's $D > 0.80$) in both forest remnants and pasture palms (albeit slightly higher in forest remnants), but the palm crown trophic structure differed between habitats. This finding suggests that, although the number and relative abundance of species in the palm crowns stay relatively consistent, community composition and trophic structure in the palm crowns vary across land-use type and location (Figure 8). Indeed, pasture palms had higher mid-trophic-level species diversity in palm crowns, which included invertebrates and some smaller vertebrate predators (e.g., lizards and geckos) that are not considered competent reservoirs for *T. cruzi* (but see Botto-Mahan et al., 2022) and potentially predate on triatomine vectors (Botto-Mahan et al., 2022). Although pasture and peridomestic palms contained network characteristics favorable to *R. pallescens* abundance (i.e., greater number of invertebrate predators), they still maintained a lower abundance compared with forest palms. This demonstrates that a combination of factors, such as trophic community characteristics within the palm and environmental conditions (as we mention further in this *Discussion*), likely drive *R. pallescens* abundance. Of community variables, vertebrate and invertebrate taxa, particularly potential invertebrate predators such as spiders and scorpions, influenced both vector infection rates and abundance. Mammalian blood meals are associated with an increase in *T. cruzi* vector infection rates, particularly opossum blood meals, which have been consistently identified as a major blood meal source of palm-dwelling triatomines and are highly competent reservoir hosts for *T. cruzi* (Christensen et al., 1980; Gaunt & Miles, 2000; Pineda et al., 2008; Yeo et al., 2005). The positive association between *T. cruzi* infection and mammal presence was also supported by our finding that vectors from sites with decreased blood meal diversity consisting mainly of mammals had higher infection probability. These observations suggest that variation in *R. pallescens* infection prevalence in palms is driven primarily by host community composition (Ostfeld & Keesing, 2000a, 2000b; Schmidt & Ostfeld, 2001).

Although mammal or invertebrate presence in palms was not directly tied to vector abundance, we did see evidence of an indirect association between the three factors, as indicated by the network measurement "*R. pallescens* Vulnerability." In our study, the Vulnerability measurement refers to predators of *R. pallescens*, which include all vertebrates (which also serve as vector blood meals) in addition to invertebrate predators (e.g., spiders, scorpions). All taxa fed upon by *R. pallescens* can also be potential predators of triatomine vectors via grooming or ingestion. The significance of "*R. pallescens* Vulnerability" (number of predators per prey) as an influential factor for increased vector abundance overshadows the impact of any particular taxon. Although certain blood meal species were associated with *R. pallescens* abundance (data not shown), and previous studies have identified triatomine infestation as important to vector abundance (see Abad-Franch et al., 2005, 2010; Rabinovich et al., 2011), the metric "Vulnerability" indicates that some combined aspect of predator presence also influences triatomine abundance.

Invertebrate predator presence is often associated with decreased pathogen-transmission risk (Carlson et al., 2009; Finke, 2012; Keesing et al., 2006; Ostfeld & Holt, 2004; Snyder & Wise, 1999). Although the effects of arthropod predation on triatomine bugs remain relatively understudied, jumping spiders (C.P. Varian, personal observation, 2017) and lizards (Ramírez et al., 2013) are potential predators of triatomines and other reduviids. Interestingly, in our study, particularly members of the invertebrate community, such as scorpions and spiders, had a positive impact on vector abundance. We observed that scorpions, a potential predator, were also positively associated with *R. pallescens* abundance, and their presence may not necessarily translate to higher predation rates on *R. pallescens*. Hemolymphagy has been observed between individuals of some triatomine species and cockroaches, suggesting an important survival strategy for the development of starved bugs (Durán et al., 2016; Schmidt et al., 2019). Other, nontriatomine Reduviidae have also been observed to feed on hemolymph from scorpions when cohabitating in leaf litter (Lira et al., 2016; Morocoima et al., 2011; Stevenson & Stohlgren, 2015). The positive association between scorpions' presence and *R. pallescens* abundance may be explained by scorpions being a food source for triatomines in areas devoid of vertebrate blood meals. Scorpions were common across all habitat types, particularly where fronds connect at the base of the palm crown. Another explanation for the *R. pallescens*–scorpion association may be that other interactions such as intraguild predation or competition between predator species outweigh the potential impacts of vector abundance control by predators (Müller & Brodeur, 2002; Snyder et al., 2006). An additional possibility is that *R. pallescens* and invertebrate predators share a preference for microhabitat conditions provided by the palm crown, since scorpions found in *Attalea* palms are considered "bark scorpions" (families Buthidae and Hemiscorpiidae) and are known to inhabit trees or tight crevices (McReynolds, 2008; Stockmann, 2015).

Predators have been linked to reduced disease risk by preying on vectors. However, predators can also alter pathogen transmission (resulting in increased or decreased transmission) via nonconsumptive effects on invertebrate vectors (Finke, 2012). 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 the community from combined or additive effects such as shared preference for microhabitat or that mammals who modify palms increase potential places to hide for spiders and scorpions.

Overall, the significant effects of invertebrate presence on *R. pallescens* abundance suggest there may be a positive indirect relationship between scorpion and spider predators on triatomines and disease risk, which requires further investigation. It is worth noting that increased vulnerability and community diversity within palm crowns had opposing effects on abundance. This result reemphasizes the potential indirect effects that other cohabiting community members may have on vector abundance and ultimately infection status. While increasing evidence has been revealing associations between other community members and triatomines (e.g., triatomine hemolymphagy from cockroaches and anti-predator defense against lizards; Ramírez et al., 2013), it will be essential to continue to investigate predatory and nonpredatory relationships under controlled conditions.

Vector abundance across location and land-use type is also influenced by microenvironment characteristics of the palm crown and its immediate surroundings. Characteristics such as increased DOM, surrounding canopy cover, and number of connected trees can stabilize temperature fluctuations and reduce temperature and RH extremes throughout the day within *Attalea* palms, providing a buffer to changes in ambient climate conditions (Padukone, 2016). Such microhabitat conditions can stabilize the microclimate, which may positively influence *R. pallescens* abundance, which has been observed in other studies as well (Abad-Franch et al., 2010; Dias et al., 2011; Urbano et al., 2015). In our study, microclimate conditions within the palm were consistently within the "ideal" temperature and relative humidity for triatomines, regardless of land-use type, although Pasture palms exhibited greater climate fluctuations in a 24-h cycle than Peridomestic and Forest palms. Collectively, these findings suggest that increased microclimate stability within the palm crown is positively associated with *R. pallescens* abundance, which we observed before in pasture palms (Padukone, 2016).

## Implications of study results for vector-borne disease management

Our study suggests that underlying mechanisms of *R. pallescens* abundance and infection include the local microenvironment, the animal community, and the food web structure within each individual palm crown. Although it has been suggested that landscape-level disturbance may modulate microclimate conditions with cascading effects on vector-borne diseases, we observed that palm crown microhabitat and microclimate conditions varied widely irrespective of the land-use type.

Focusing on the individual-tree scale may be a feasible option when implementing vector-control methods in palms located within peridomestic or Forest-remnant areas within central Panama. For example, instead of targeting landscape-scale changes in a region, vector-control measures could target palm-specific conditions to reduce vector abundance. Based on previous findings related to palm-dwelling vector control (Abad-Franch et al., 2010, 2015; Santos et al., 2021), managing host and predator communities by manipulating the palm crown DOM may be a key strategy for reducing *R. pallescens* abundance and infection with *T. cruzi* in central Panama.

Furthermore, determining the specific components of the palm crown community that influence *R. pallescens* abundance and *T. cruzi* infection rates could reveal whether a particular species, such as a fungus or predator, functions as a potential biocontrol agent, in a particular land-use type or palm crown type. Invertebrate predator abundance, host and community diversity, and palm crown complexity are all factors to consider when designing Chagas disease control measures. Future research should be done to determine the efficacy and feasibility of managing these characteristics within crowns, and the logistics of implementing biocontrol will require additional field experiments. For example, it would be useful to compare *Rhodnius* abundance to measure changes in *Rhodnius* abundance after experimentally removing DOM from palms or limiting access of terrestrial vertebrates to palm crowns (Santos et al., 2021).

## Study limitations

This research was limited by study design implementation, including finding replicate sampling sites across locations, and palm crown accessibility. Palm selection was limited by terrain conditions and landowner consent, while microclimate data collection within palm crowns was a complicated task that resulted in damaged or missing data loggers and, in turn, missing microclimate data.

Although previous studies of Chagas vector abundance within palm crowns did not investigate all potential explanatory variables simultaneously, as we do here, our 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. Future research should include seasonality, particularly the effects of seasonal fluctuation on the palm crown and ambient microclimate conditions, as they likely have a larger influence on abundance and infection than we report in this paper. Additionally, because palm crown conditions can vary across land-use types, there may be overlap in the microhabitat and microclimate conditions attributed to “Pasture,” “Peridomestic,” or “Forest” habitat classifications. For example, some Forest-remnant palms had grazing cattle, and some Peridomestic palm surroundings resembled those of Forest remnant or Pasture palms.

# CONCLUSION

This study addresses the impacts that land use, microhabitat, and local community conditions have on vector abundance and vector infection with a multihost pathogen. By combining measures of animal community, food web structure, and microenvironmental conditions, we attempted to evaluate the complexity of vector–pathogen–host relationships in situ. The presence of vertebrates that can provide vector blood meals in palm trees continues to be an indicator of *R. pallescens* abundance and, potentially, vector infection with *T. cruzi*. However, the significance of potential invertebrate predators, primarily scorpions and spiders, on abundance and infection, respectively, indicates that predators may have varying impacts on disease risk. Our results also contribute to ongoing studies on the use of food web metrics in vector-borne disease studies, and they suggest that community interactions can influence parasite transmission. In other words, aspects of the community as a whole may more strongly impact disease transmission than the impacts of individual species. Studying disease vectors within naturally occurring, discrete mesocosms can be helpful in developing further research hypotheses on community ecology and the effects of land-use-level and local-level characteristics on vector-parasite dynamics. Thus, continuing this area of research on the complexities of microenvironment and food web structure will be essential for predicting and managing multihost vector-borne pathogens.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Varian et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.17899688.

## ETHICS STATEMENT

Mi Ambiente: SE/A-93-13, SE/AP-27-16. Smithsonian Tropical Research Institute (STRI) Institutional Animal Care and Use Committee: 2013-0601-2016-02, 2016-0801-2019-A1. University of Georgia Institutional Animal Care and Use Committee: A2016 05-009-R2.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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