



Chagas Disease in Central America: Recent Findings and Current Challenges in Vector Ecology and Control

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Abstract

Purpose of Review In Central America, most new human *Trypanosoma cruzi* infections (Chagas disease) are vector-borne, primarily by native vector species. Given the importance of vector control in reducing Chagas disease incidence, here, we provide an updated report on the recent advances and the latest research in vector ecology and control in Central America. Our objective is to present a panorama of the current situation that includes vector control program details, recent public health activities and academic research, and current challenges faced by each country and the region as a whole.

Recent Findings With the elimination of the introduced species *Rhodnius prolixus* from the region, the primary vector control challenge is control of native species that move between sylvan and domestic environments, namely *Triatoma dimidiata* and *Rhodnius pallescens*. These species cannot be eliminated from domestic/peridomestic settings in a sustainable way using insecticide alone, as residual members of domestic populations and/or sylvatic foci allow the species to persistently reinfest following insecticide application. Implementation of integrated, multidisciplinary methods for native vector species control has yielded promising results. In particular, projects using the Ecohealth method have been scaled up and expanded to endemic areas in multiple countries through partnerships between international stakeholders and ministries of health (MoHs). Additionally, the recent description of two new triatomine bug species that were once classified as *T. dimidiata* may help to tailor vector control methods to interspecies variations, and the discovery of a dark morph of *R. pallescens* may provide further insight into vector control in Panama. Finally, associations between deforestation and vector *T. cruzi* infection and abundance in Panama call attention to associations between human land use change and Chagas disease risk.

Summary The elimination of *R. prolixus* contributed to significant reductions in human *T. cruzi* infection incidence in Central America over the past 20 years, but native vector species still pose a significant public health threat. New methods and collaborations present promising solutions, but sustained partnerships, long-term commitment, and strong regional leadership are required to see them through.

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Abbreviations

IPCA	Initiative for Chagas Disease Control in Central America
IPCAM	Initiative for Chagas Disease Control in Central America and Mexico
IRS	Indoor Residual Spraying
MoH	Ministry of Health
PAHO	Pan American Health Organization

Introduction

With a combined population of approximately 47 million people [1], Central America is small in size but rich in cultural and ecological diversity; most of the region is considered a biodiversity hotspot [2, 3]. There are 18 triatomine bug species described for the region ([4]; Table 1), and six of them are found exclusively in Central America and Mexico. The species *Rhodnius prolixus*, *R. pallescens*, and *Triatoma dimidiata* are responsible for most current Chagas disease cases in the region, and the remaining species are primarily sylvatic. Given the importance of vector control in reducing the burden of Chagas disease, our objective in this report is to provide an up-to-date, comprehensive review of the current entomological situation of Chagas disease in Central America since it was last formally reviewed [28]. This article is a companion piece to Peterson et al. [29], which covers the current epidemiology of Chagas disease in Central America.

Regional Overview

R. prolixus was once the most epidemiologically important vector species in Guatemala, El Salvador, Honduras, and Nicaragua, but the species was largely eliminated through national vector control programs supported by the Initiative for Chagas Disease Control in Central America (“IPCA,” [30]), which was launched in 1998. *R. prolixus* is believed to be an introduced species in Central America; populations were exclusively domestic with no sylvatic population foci, making regional elimination a realistic target [31]. The vector control strategies used to eliminate *R. prolixus* were modeled after the approach used in the Southern Cone against *Triatoma infestans* (an approach that had come from malaria control [32]): large-scale, three-phase campaigns consisting of a preparatory phase in which multitudinous homes were inspected, followed by an “attack phase,” in which indoor residual spraying (IRS) occurred in infested homes, and concluding with a surveillance phase. Between 2008 and 2012,

Guatemala, Honduras, and Nicaragua were certified by PAHO at the IPCA meetings for interruption of *T. cruzi* transmission to humans by *R. prolixus*, and Mexico, Costa Rica, and El Salvador were certified for elimination of the species between 2009 and 2011 (Mexico officially joined IPCA in 2012, and the acronym thereafter became “IPCAM”). Estimated Chagas disease prevalence for the region decreased from 7% in the 1980s [30] to 0.91% in 2010 [33–35]. In the 2018 annual meeting of IPCAM, Honduras and Nicaragua were certified for the elimination of *R. prolixus*, and Guatemala is likely to be certified in 2019 [36].

With *R. prolixus* largely eliminated from the region, attention has turned to the native species *T. dimidiata*, which is currently the most important *T. cruzi* vector species in all of Central America except Panama. *T. dimidiata* has proven more challenging to control than *R. prolixus*; the ecological characteristics of *T. dimidiata* are quite different from those of *R. prolixus*, which, in Central America, was primarily rural, exclusively domestic, and dispersed only passively. *T. dimidiata*, in contrast, is found in both rural and urban areas, is highly mobile from sylvan to domestic environments, disperses both actively and passively, and is much more widely distributed. Since the year 2000, national efforts to control *T. dimidiata* in Guatemala, El Salvador, Honduras, and Nicaragua have centered around the same IRS-based control strategy used against *R. prolixus*. However, *T. dimidiata* has shown a remarkable ability to reinfest domestic areas following insecticide application [16•, 37, 38], and long-term evaluations have repeatedly shown that IRS-based programs against *T. dimidiata* are effective only in the short term [16•, 37, 39–41, 42•, 43], even when followed by community-based surveillance [44–46].

A particular challenge for the control of *T. dimidiata* is that the species displays tremendous behavioral variation throughout its range, which has made it difficult to design vector control methods tailored to the species. The behavioral variability in combination with high levels of morphological diversity has fueled debate about the status of *T. dimidiata* as a single or multiple species (or subspecies), and several hypotheses of the true systematics of *T. dimidiata* have been proposed [47–50, 51•]. Recently, a genomic analysis revealed strong evidence that *T. dimidiata* is indeed a species complex comprised of three distinct species ([52]; Fig. 1). The three species are *T. dimidiata* and two new species, which have recently been formally described as *Triatoma mopan* [5] and *Triatoma huehuetenanguensis* ([7]; formerly *T. sp. aff.*

Table 1 Vector information for each country in Central America, including recent findings and current challenges related to vector control and ecology

Country (no. of species)	Triatomine species reported ^a	Local names	Recent advances	Current challenges
Belize (4 ^{b,c})	<i>Rhodnius pallescens</i> ^b , <i>R. pictipes</i> ^c , <i>Triatoma dimidiata</i> [*] , <i>T. mopan</i> ^{od}	chinch, bush chinch, chinch bug	<ul style="list-style-type: none"> New cave-dwelling species, <i>T. mopan</i>, described in [5] <i>T. dimidiata</i> collected in the Orange Walk and Corozal districts [6] 	<ul style="list-style-type: none"> Monitor the movements of <i>T. dimidiata</i> in domestic and peridomestic areas Confirm/deny the presence of <i>Rhodnius</i> in sylvan environments
Guatemala (8)	<i>Eratyrus cuspidatus</i> , <i>E. mucronatus</i> , <i>Panstrongylus geniculatus</i> ^o , <i>R. prolixus</i> ^{*^} , <i>T. dimidiata</i> [*] , <i>T. nitida</i> ^o , <i>T. huehuetenanguensis</i> ^{oc} , <i>T. ryckmani</i> ^o	chinche picuda, talaje, telepate (names of the nymphs)	<ul style="list-style-type: none"> New species, <i>T. huehuetenanguensis</i>, described in [7] Ecohealth methods resulted in significant and sustained reduction in <i>T. dimidiata</i> feeding on humans, % of <i>T. cruzi</i>-infected bugs, and in house infestation indices; the latter stayed below 2% for at least 3 years following last intervention [8], and domestic infestation was maintained at <3% and peridomestic infestation at <2% for 5 years beyond the last insecticide spraying [9] 	<ul style="list-style-type: none"> Sustained reduction of domestic and peridomestic infestation and colonization of <i>T. dimidiata</i> Clarify epidemiological importance of newly described species Determine if there are other species in the <i>dimidiata</i> species complex Train MoH staff to carry out integrated vector control measures Monitor domiciliation of <i>T. ryckmani</i> [10] and <i>T. nitida</i> [11]
El Salvador (4)	<i>R. prolixus</i> ^{*^} , <i>T. dimidiata</i> [*] , <i>T. ryckmani</i> ^o , <i>T. nitida</i>	chinche, chinche picuda, chinche pelona (nymphs only)	<ul style="list-style-type: none"> <i>T. dimidiata</i> blood meal analysis revealed that bugs had fed predominantly on humans and birds [12•, 13]. Bugs collected from peridomestic areas were significantly more likely to be infected with <i>T. cruzi</i> than bugs collected from within the house [12•]. <i>T. ryckmani</i> collected inside homes, including sleeping areas [14] <i>T. ryckmani</i> found with human blood meals [14] 	<ul style="list-style-type: none"> Sustained reduction of domestic and peridomestic infestation and colonization of <i>T. dimidiata</i> Vector control in densely populated housing developments Monitor domiciliation of <i>T. ryckmani</i> [14] Clarify if there are other species in the <i>T. dimidiata</i> species complex in the country
Honduras (9 ^c)	<i>E. cuspidatus</i> ^f , <i>E. mucronatus</i> ^f , <i>P. geniculatus</i> ^f , <i>P. rufotuberculatus</i> ^f , <i>R. prolixus</i> ^{*^} , <i>T. dimidiata</i> [*] , <i>T. huehuetenanguensis</i> ^{oc} , <i>T. nitida</i> ^o , <i>T. ryckmani</i> ^o	chinche, chinche picuda	<ul style="list-style-type: none"> <i>T. dimidiata</i> captured in Honduras, El Salvador, and Guatemala had unique feeding preferences, infestation/colonization patterns, and <i>T. cruzi</i> infection rates between countries. Bugs in all countries fed on humans at the same rate though [12•] Analyses of DNA extracted from <i>T. dimidiata</i> collected in Guatemala, El Salvador, and Honduras revealed two <i>T. cruzi</i> DTUs, geographic genetic structure, blood meal sources, and a diverse microbial community, with <i>T. cruzi</i>-infected bugs having higher bacteria species richness than uninfected bugs [15] 	<ul style="list-style-type: none"> Sustained reduction of domestic and peridomestic infestation and colonization of <i>T. dimidiata</i> Housing improvements with local materials to prevent <i>T. dimidiata</i> infestation Assure institutional response to community vector surveillance when the capacity of local health services is limited in new decentralized control program structure Maintain surveillance of <i>T. nitida</i> and other sylvan species in departments where they have been reported Clarify if there are other species in the <i>T. dimidiata</i> species complex in the country
Nicaragua (9)	<i>E. cuspidatus</i> ^o , <i>P. geniculatus</i> ^o , <i>P. rufotuberculatus</i> ^o , <i>R. pallescens</i> ^o , <i>R. prolixus</i> ^{*^} , <i>T. dimidiata</i> [*] , <i>T. dispar</i> ^o , <i>T. nitida</i> ^o , <i>T. ryckmani</i> ^o	chinche, chinche de Chagas	<ul style="list-style-type: none"> Infestation indices that had decreased from 20.6 to 7.0% between 2010 and 2014 had recovered to 14.6% by 2016 [16•] 	<ul style="list-style-type: none"> Sustained reduction of domestic and peridomestic infestation and colonization of <i>T. dimidiata</i> Clarify if there are other species in the <i>T. dimidiata</i> species complex present in the country Monitor potentially invasive sylvan species, such as <i>T. ryckmani</i> and <i>P. geniculatus</i>

Table 1 (continued)

Country (no. of species)	Triatomine species reported ^a	Local names	Recent advances	Current challenges
Costa Rica (12)	<i>Belminus costaricensis</i> , <i>Cavernicola pilosa</i> , <i>E. cuspidatus</i> , <i>Microtriatoma trinidadensis</i> , <i>P. geniculatus</i> ^o , <i>P. rufotuberculatus</i> , <i>R. pallescens</i> ^o , <i>R. prolixus</i> * [^] , <i>T. dimidiata</i> *, <i>T. dispar</i> , <i>T. nitida</i> , <i>T. ryckmani</i>	chinche, chupa sangre	<ul style="list-style-type: none"> • <i>T. cruzi</i>-infected synanthropic animals and triatomine bugs in peri-urban and rural areas, and in an area of heavy ecotourism [17–21] 	<ul style="list-style-type: none"> • Update the current distribution of <i>T. dimidiata</i> infestation of domestic and peridomestic environments • Investigate <i>T. dimidiata</i> in ecotourism areas • Update status of sylvatic <i>R. pallescens</i> populations. • Clarify if there are other species in the <i>dimidiata</i> species complex present in the country
Panama (11)	<i>Belminus herreri</i> , <i>C. pilosa</i> , <i>E. cuspidatus</i> , <i>E. mucronatus</i> , <i>M. trinidadensis</i> , <i>P. geniculatus</i> ^o , <i>P. humeralis</i> , <i>P. rufotuberculatus</i> , <i>R. pallescens</i> * ^o , <i>T. dimidiata</i> ^o , <i>T. dispar</i>	Chinche, chinche mamón, chinche besador, chinche de Chagas	<ul style="list-style-type: none"> • New dark morph of <i>R. pallescens</i> discovered [22] • <i>R. pallescens</i> found colonizing two new palm species [23•] • Deforestation found to be associated with increase vector abundance and <i>T. cruzi</i> infection in <i>R. pallescens</i> [24, 25] 	<ul style="list-style-type: none"> • Develop an integrated control strategy for <i>R. pallescens</i> • Further investigate and define the risk posed by new palm species found to harbor <i>R. pallescens</i>

^a Species reported in [26], unless specified otherwise. *Primary vector of *T. cruzi* to humans. ^oOccasional, secondary or emerging vector of *T. cruzi* to humans. ^b One specimen of *R. pallescens* reported in 1931. Its presence in Belize needs to be confirmed. ^c Just one specimen of *R. pictipes* ever reported. Needs to be confirmed. ^d [5]. ^e Not a native species, and currently believed to be eliminated from the country. ^f [7]. The presence of *T. huehuetenanguensis* in Honduras still needs to be confirmed. ^g [27]. ^h Sporadically invades intradomestic areas (pers. comm., Dr. Empatriz Lugo, Nicaragua MoH Laboratory of Entomology)

dimidiata). In addition to being genomically distinct from *T. dimidiata* sensu stricto (s.s), *T. huehuetenanguensis* has also been found to be a biological species, as it was infertile when crossed with *T. dimidiata* s.s [53].

Taken together, these findings could have implications for Chagas disease risk and control and may partially explain the behavioral variation found among different populations of *T. dimidiata*. Studies are underway to further describe the ecological characteristics of each species, namely their geographic ranges, habitat and feeding preferences, and *T. cruzi* competence and infection burdens. An ecological understanding of each species will allow disease control interventions to be adapted to the appropriate vector species (e.g., barriers to house entry to prevent seasonal intrusion vs. wall plastering to counter colonization by resident populations [54, 55]), and it may also help to focus scarce resources where *T. cruzi* transmission risk is highest.

Country by Country Reports

In the following reports, please note that in general discussion we will use “*T. dimidiata*” to refer to all three members of the *T. dimidiata* species complex, since the exact distribution of each species is still being determined.

Belize

Overview

T. dimidiata is the primary Chagas disease vector species in Belize, where it is distributed throughout all six administrative districts [56]. Low human population density and well-preserved forests have contributed to *T. dimidiata* being primarily sylvatic in the country, and Chagas disease is considered a low risk [57], with domestic infestation by *T. dimidiata* being only seasonal. However, it is believed that human encroachment into previously undisturbed areas may be contributing to increases in *T. dimidiata* domestic infestation [6, 58], and *T. cruzi* seropositive blood units have been found in all six districts [59]. The Cayo and Toledo districts have the highest reported *T. dimidiata* infestation, colonization, and dispersion indices [6, 58, 60]. These districts include the current national capital, and three of the four highest populated cities in the nation.

The current national vector control program primarily deals with the prevention and control of mosquito-borne infections. There is no chemical control program dedicated to *T. dimidiata*, but IRS for malaria control in rural communities sometimes reduces *T. dimidiata* infestations (K. Bautista, pers. comm.). Despite the fact that *T. dimidiata* has never been a vector control target in Belize (K. Bautista, pers. comm.), the

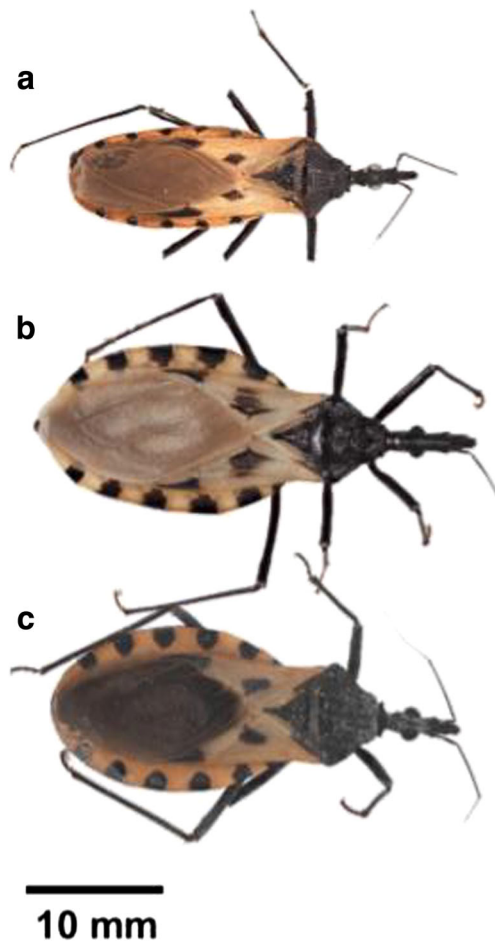


Fig. 1 The three described species of the *Triatoma dimidiata* species complex. **a** *Triatoma huehuetenanguensis*, **b** *Triatoma mopan*, and **c** *Triatoma dimidiata*. All species shown to scale (10 mm). Photos by Silvia Justi and Raquel Lima-Cordón, and reproduced with permission from the authors (Lima-Cordón RA et al. [7], Figure 7, <https://doi.org/10.3897/zookeys.820.27258.figure7>)

country was certified as free of *T. cruzi* transmission to humans by *T. dimidiata* at the IPCAM meeting in 2012 [60].

Recent Activities

Since 2006, two surveys of *T. dimidiata* in Belize have been published covering the Cayo and Toledo districts [58] and the Orange Walk and Corozal districts [6]. The studies, both of which used community-based collection methods, calculated dispersion and infestation indices. In Cayo and Toledo, dispersion indices (number of villages with *T. dimidiata*/total number of villages sampled) of 100% and 89% were found, respectively [58]. Infestation indices (number of infested houses/total number of houses sampled) were upwards of 43% in both districts, and colonization indices (number of houses with nymphs/total number of houses sampled) were 22% in Cayo and 11% in Toledo. *T. cruzi* infection prevalence in the bugs was 23% and 32% in Cayo and Toledo,

respectively [58]. Household infestation was found to be seasonal, and associated with peak activity in the late dry season (April–June). In Corozal and Orange Walk, infested houses were dispersed widely throughout both districts, and dispersion indices were 60% and 48%, respectively. Average *T. dimidiata* infestation index was 15% in Corozal, and 18% in Orange Walk [6]. Risk factors associated with infestation were proximity to street lights and presence of dogs [6]. All bugs collected from domestic areas in Corozal and Orange Walk were adults, suggesting invasion, but not colonization.

In addition, the only specimens of the newly described species *T. mopan* are from a single cave in the Cayo district of Belize, known as the Rio Frio Cave. Interestingly, one of the earliest reports of *T. dimidiata* in Belize originated from the same cave [57], which is within the Mountain Pine Ridge Forest Reserve. The area experiences a large amount of human traffic, as it is a common tourist attraction that is regularly visited by local school groups, and the bugs are known to be active during the day in the presence of human activity. At night, guards sleep in the cave to protect it against vandalism, resulting in human blood meals being available for the bugs both day and night [61]. In preliminary studies of specimens collected in the cave, more than half of the bugs had fed on humans, and some of the specimens were infected with *T. cruzi* [5, 61]. The estimated probability of vector-borne *T. cruzi* transmission upon a single contact is very low [62], but not impossible, and ongoing studies will help to clarify any human health risks associated with *T. mopan*.

Guatemala

Overview

Eight species of triatomine bugs are distributed throughout most of Guatemala ([11]; Table 1), including the newly described species, *T. huehuetenanguensis*. *R. prolixus* was the most epidemiologically important species in the country, but with its elimination, *T. dimidiata* is now the most important vector species. At least one million people in Guatemala live in *T. dimidiata*-endemic areas spanning 15 departments [63, 64], but the current national vector control program is active in just 10 departments [65]. Program activities consist of vector surveillance, residual insecticide application to infested domiciles (data in Table 2), house improvements, and blood bank screening. House improvements occur mainly in the departments of Jutiapa and Chiquimula, which have the highest levels of infestation, and are considered as hotspots of *T. cruzi* transmission to humans.

Chagas disease is a low national health priority in Guatemala, and mosquito-borne diseases such as dengue fever are better known, garner more media coverage, and are generally prioritized over Chagas disease. Insecticide supply shortages are frequent, such that when a focus of *R. prolixus*

Table 2 Vector control data by country

	2015			2016			2017		
	No. of houses inspected	No. of positive houses (no. colonized)	No. of houses sprayed	No. of houses inspected	No. of positive houses (no. colonized)	No. of houses sprayed	No. of houses inspected	No. of positive houses (no. colonized)	No. of houses sprayed
Belize	Not available	na	8419*	na	na	8753*	na	na	9645* [^]
Guatemala ^a	8880	1122		19,853	621		18,311	504	
Honduras ^b	38,705	1489 (295)	40,284	50,767	3654 (875)	53,614	44,274	1769 (81)	37,376
El Salvador ^c	67,630	4444	14,971	164,179	2982	6004	99,241	1870	3246
Nicaragua ^d	Not available	na	na	na	na	na	682	na	574

^a [63, 64, 66]. ^b [27]. ^c [67]. ^d [68]. *Number of houses sprayed for malaria prevention and control by the malaria control unit. All houses sprayed are in rural areas that are endemic for *T. dimidiata*. Since Belize has no dedicated Chagas disease program, there are no vector control records specific to Chagas disease. (K. Bautista, pers. comm.). [^]No. of houses sprayed in 2018: 9496. Data for Costa Rica and Panama were not available

was discovered in 2015, insecticides had to be obtained from Honduras [69]. At the 2018 IPCAM meeting, Guatemala was encouraged to prepare for a 2019 certification for the elimination of *R. prolixus* as a public health problem [36], which might allocate a few more resources toward Chagas disease control in the short term in order to obtain the certification, but in the long term, it may add to a general sentiment that with the elimination of *R. prolixus*, Chagas disease is no longer a problem [70].

Recent Activities

Recent projects using multidisciplinary approaches have yielded promising results for *T. dimidiata* control in the country. These types of approaches (often called the Ecohealth approach [71]) take into account the cultural, epidemiological, and ecological disease transmission scenarios in a given area to identify and sustainably eliminate different risk factors, often while improving the quality of life in the local community. In one study using the Ecohealth approach, Monroy et al. [55, 72] collaborated with villagers and local health personnel in four villages to design a Chagas disease control program that centered around house improvements, but also included reforestation with native trees, chicken coop construction, and chicken vaccination, in addition to a single insecticide application. The program resulted in reductions in *T. dimidiata* infestation that were similar to other villages in which insecticides alone had been applied, but more economical [73, 74] and sustainable [8, 9, 55]. Between 2012 and 2014, the project was expanded to five communities in the department of Chiquimula, and *T. dimidiata* infestation rates were reduced by a factor of 4 [75]. In another study in the Jutiapa department, the network underlying *T. cruzi* transmission in local domestic and peridomestic environments was characterized in order to find new *T. dimidiata* control targets that could complement the application of insecticide (in this study, the approach was called “eco-social-bio” [76]). The authors found that, in addition to the habitat and food sources provided by villagers (blood meals from humans and chickens were detected in 50% and 64% of bugs, respectively), *T. dimidiata* commonly inhabited rodent nests in roof tiles and fed on both rats (24% of bugs) and mice (21% of bugs), some of which were infected with *T. cruzi* (17% of mice and 43% of rats). Additionally, nymphs were found in human sleeping quarters that had fed on both rodents and humans, and the rodents, in turn, were being sustained by fruit trees located in the patio. By providing a picture of the local epidemiological network that was both directly and indirectly sustaining transmission, several opportunities for interrupting *T. cruzi* transmission to humans were identified.

Building on the success of these projects, in 2017, the Alliances for Chagas Elimination in Central America project (“Proyecto Alianzas” in Spanish) was initiated in Guatemala

with the objective of eliminating Chagas disease transmission in remaining hotspots in Central America. The project, which is a collaboration between several international donors, health agencies, research institutions, and the Guatemala MoH, is centered around using an integrated approach that strengthens multiple aspects of Chagas disease control, diagnosis, and treatment in a sustainable way, while also aiming to improve quality of life [77]. The Ecohealth approach is a central part of the vector control component, for which the aim is to increase the number of homes that are protected from *T. cruzi* transmission by *T. dimidiata*, as measured by reduced levels of intradomiciliary infestation and fewer infections in children. The Alliances project is currently being piloted in the municipality of Comapa, Jutiapa, after which the project is to be scaled up and implemented in 48 more villages in Jutiapa [77], and later in other Central American countries.

Honduras

Overview

Eight triatomine species are described for Honduras ([26, 78]; Table 1), and a ninth species, the recently described *T. huehuetenanguensis*, is expected to be present, but remains to be confirmed. The most endemic departments in the country are Comayagua, Copán, Choluteca, El Paraíso, Francisco Morazán, Intibucá, La Paz, Lempira, Ocotepeque, Olancho, Valle, and Yoro, where three triatomine species, *R. prolixus*, *T. dimidiata*, and *T. nitida*, have been found infesting domestic areas. In 2003, the Honduran MoH began a national vector control program targeting *R. prolixus* [79, 80], and in 2010, the species was found for the last time in four villages in the Intibucá and El Paraíso departments [80]. In 2011, Honduras was certified for the interruption of *T. cruzi* transmission by *R. prolixus*, and in 2018, the country was certified for elimination of the species.

T. dimidiata is now the most epidemiologically important species in Honduras, and the species has been reported in 17 of 18 national departments. Domestic invasion of *T. nitida* is occasionally reported in a few departments, but the species is considered insignificant as a Chagas disease vector [68]. The average domestic infestation index in endemic areas has declined from 21.9% in 2004 [81] to 3.5–7.2% between 2014 and 2016 [27], and the current vector control program consists of community-based surveillance, entomological surveys, and insecticide spraying of infested houses ([27]; Table 2). The Honduran MoH has been an innovator in finding ways to overcome limited resources when formulating Chagas disease control strategies (e.g., the use of rapid diagnostic tests, training local village residents to carry out insecticide application, among others), but a 2012 reorganization and decentralization of the national Chagas disease control program has made it challenging for national and local leadership to assure

institutional response to community vector surveillance when the capacity of local health services is limited [45, 82]. House improvements, which are particularly important for sustaining reductions in vector infestation, are a critical area to strengthen in the current program. At the field level, house improvement has been promoted by the MoH and implemented by communities in collaboration with local governments, national institutes (e.g., The Honduran Social Fund/Fondo Hondureño de Inversión Social, [FHIS]), research institutions, and NGOs. Local governments in some endemic areas are able to obtain and distribute materials such as tin roofs and sand to use for plastering cracked mud walls, but the majority of endemic communities remain at high risk of vector infestation.

Recent Activities

Between 2011 and 2014, a multinational project using the Ecohealth approach [75] resulted in 690 house improvements being carried out in 12 Lenca ethnic group settlements in Honduras. The settlements had previously been infested by *R. prolixus* and had later become infested with *T. dimidiata*. It was found that dogs played an important role in the local *T. cruzi* transmission cycle, while humans did not [12•], and infestation indices of 7.0–9.7% were found [83]. All infested homes were constructed using adobe, and in an analysis using models to predict domestic triatomine infestation, the most important predictive factors were house wall material and biological signs of insect presence. The authors found that the models were much better at predicting the absence of infestation than at predicting the presence of infestation, and interestingly, reduced models (to identify dominant causes) were not supported, further suggesting that integrated approaches with multiple targets are needed to control infestation by native vector species.

El Salvador

Overview

Three species of triatomine bugs are found throughout all 14 departments of El Salvador. *R. prolixus* was once widely distributed as well, which is believed to have been introduced to Central America from bugs that escaped from a laboratory colony in San Salvador, El Salvador, around 1915 [31]. In 1955, the first entomological survey was carried out in 137 rural localities throughout the 14 departments of El Salvador. An average triatomine bug domestic infestation index of 26.3% was found, with similar numbers of *R. prolixus* and *T. dimidiata* [33]. From the 1950s to the 1970s, houses in low altitudes were repeatedly sprayed with insecticides for malaria control, which is thought to have reduced triatomine infestation as well [82]. In 1976, all vector control and research activities in the country were halted, due to the

Salvadoran Civil War, and when studies resumed in 1995, *R. prolixus* had disappeared from the country. A number of factors, including the malaria control activities and the replacement of palm thatch roofs with tin roofs, are thought to have indirectly contributed to the elimination of *R. prolixus* in El Salvador [84]. Between 2003 and 2009, the MoH evaluated houses in all areas where *R. prolixus* had been found throughout the country, and did not find any specimens [33]. In 2010, El Salvador was certified at the IPCA meeting for elimination of *R. prolixus* as a public health problem, the first country in the Americas to be certified for elimination of a Chagas disease vector species [85].

The most important *T. cruzi* vector species after the disappearance of *R. prolixus* became *T. dimidiata*, which was targeted in a national vector control program beginning in 2003. The program undertook the same three-phase, insecticide-based approach that was used in neighboring countries against *R. prolixus*, and the national infestation index declined from 19.4% in 2004 to 2.2% in 2012 [81]. Nonetheless, *T. dimidiata* is still widely distributed in the country and continues to persistently infest and reinfest human dwellings. The problem is believed to be exacerbated by the high population density of the country—over six million people live in an area of 21,000 km² [86]. Dense housing developments with limited peridomestic space [82] are thought to facilitate *T. dimidiata* colonization by providing different blood meal sources tightly clustered within and between homes [82]. In these areas, the elimination of vector infestation and associated risk factors is challenging, because it requires improvements to be made to each house in a given sector, necessitating a collective effort. El Salvador has established operational programs in these areas that are carried out by vector control personnel and health promoters, but activities are largely dependent on the capacity of each local health office, facility, or staff, which influences outcomes [45].

The current national Chagas disease control program in El Salvador consists of active and passive (i.e., community) vector surveillance, distribution of promotional materials for house improvements, obligatory notification of all entomological activities and human cases to a central health information database, blood bank screening, and antiparasitic treatment with follow-up. Active vector surveillance is carried out by local health promoters who inspect homes for triatomine bugs and advise residents on changes that can be made in the domicile to reduce infestation risk. Infested homes are sprayed with insecticides if the bugs are found to be infected with *T. cruzi* (recent data is found in Table 2). At the departmental health office, a vector control team monitors and supports these field operations. The Health Research Center (CENSALUD) at the University of El Salvador has carried out some housing improvement projects in collaboration with the MoH, but there is no regular program. In many endemic

areas, Chagas disease control often competes with better-known, mosquito-borne diseases for both financial and human resources. Currently, when older, experienced Chagas disease vector control personnel retire, they are not necessarily replaced. Complicating matters further is that access to communities in some endemic areas is quite limited, due to violence and gangs. As a consequence, health workers and vector control operations cannot be carried out there, leaving the populations in these communities unattended.

Recent Activities

In 2010, the species *Triatoma ryckmani* was first reported in the department of Achuachapán [87] and was subsequently captured in five other departments. The species had been found to be capable of colonizing artificial environments in Guatemala [10], but it was believed to be strictly sylvatic in El Salvador. However, a recent study found specimens with human blood meals in domestic settings (including beds and sleeping areas) in the departments of Santa Ana, La Unión, Usulután, San Miguel, and Morazán between 2011 and 2016 [14]. The sample size of the study was small ($N=69$), but the findings provide preliminary evidence of the emergence of *T. ryckmani* as a potential secondary Chagas disease vector in El Salvador.

Nicaragua

Overview

The primary Chagas disease vector species in Nicaragua is *T. dimidiata*, one of nine triatomine bug species described for the country (Table 1). A 1998–1999 entomological survey found *T. dimidiata* in all departments except the two Caribbean Coast Autonomous Regions, which were not surveyed [88], and in 2017, the species was reported by community residents in 14 of 19 departments [68]. *R. prolixus* was once found throughout eight departments in Nicaragua, but chemical control successfully eliminated the species from the country [89], and *R. prolixus* was last reported in the Matagalpa department in 2013 [90]. Nicaragua was certified for interruption of *T. cruzi* transmission to humans by *R. prolixus* in 2011 and for elimination of the species as a public health problem in 2018 [36]. *R. pallescens* was at one time considered a secondary vector in the departments bordering Costa Rica [91–93], but results from recent entomological and serological surveys have led the MoH to disregard the species as a vector of epidemiological importance [60, 94].

After the successful control of *R. prolixus*, the Nicaraguan MoH began a control program that targeted *T. dimidiata* in the northern departments of Estelí, Jinotega, Madriz, Matagalpa, and Nueva Segovia. In 2009–2010, the MoH inspected 12,195 randomly selected houses in the five departments

and found an average domestic infestation index of 6.7% [60, 90]. After a spray campaign, the index declined to below 5% in all five departments [43], and a community-based surveillance system was rolled out in 2013 to sustain the reduction [46]. During the first 6 months of 2014, the surveillance system detected 1957 houses with *T. dimidiata*, and health personnel visited more than 80% of infested homes to provide advice to the residents and apply insecticides when necessary [90]. The surveillance system was subsequently incorporated into the national guidelines and scaled up to the national level.

Researchers later investigated the sustainability of the vector control program in the department of Estelí and found that infestation indices that had decreased from 20.6 to 7.0% between 2010 and 2014 had increased to 14.6% by 2016 [16•]. The results demonstrated that although the *T. dimidiata* control program in Nicaragua was successful in the short term, the primarily insecticide-based vector control approach used was ineffective for sustaining reductions of *T. dimidiata* infestation over the long term [16•, 43, 46]. The same study also found that application of sublethal levels of agricultural insecticide by villagers to their own houses (to control multiple types of vermin, not necessarily triatomines) at least once a month was associated with reduced odds of *T. dimidiata* reinfestation compared with houses that did not apply insecticide [16•]. The practice of using agricultural insecticide to control vermin in and around the home is common in rural, agricultural areas of Nicaragua and other Central American countries, suggesting that in these areas, villagers may be capable of sustaining vector control in their own homes. More research is needed though to understand if the practice actually prevents *T. dimidiata* domestic infestation/reinfestation.

Recent Activities

Data from the national Chagas disease control program indicate that the capacity of community-based vector surveillance is weakening in Nicaragua. In 2017, 873 houses were reportedly infested by *T. dimidiata* in 14 out of 19 departments (data in Table 2 [68]);. These numbers reflect a noticeable decrease in house infestation reporting rates in comparison with 2014 when nearly 2000 houses were reported with *T. dimidiata* in five departments within 6 months. The decrease likely reflects a diminished capacity of vector surveillance to detect house infestation as opposed to an actual decrease in vector infestation levels, given there have been no large-scale control activities for *T. dimidiata* since 2014. Although community-based surveillance has been found to be ineffective at sustaining reductions in *T. dimidiata* domestic infestation to under 5%, it is still an effective way to identify high-risk areas at a relatively low cost [16•]. Submission of triatomine bugs caught inside the home to the local health post has been found to improve vector detection probabilities in the presence of native vectors [95], and the national program should keep

encouraging community residents to bring triatomine bugs found in and around their homes to the nearest health facilities.

Costa Rica

Overview

Costa Rica has the highest triatomine species richness in Central America, with 12 species described (Table 1 [4];). The country was certified for the elimination of *R. prolixus* in 2011 [85], although the species had only been sparsely distributed in the northwest province of Guanacaste and had not been seen in decades [31]. After the elimination of *R. prolixus*, *T. dimidiata* was the only triatomine species in Costa Rica that regularly infested human homes, making it the most important Chagas disease vector species. *T. dimidiata* is widely distributed throughout Costa Rica, where it is found in domestic, peridomestic, and sylvan environments [96]. A small number of Chagas disease cases in Costa Rica have been attributed to *R. pallescens* [91, 96–98] and *Panstrongylus geniculatus* [91], but neither species is domiciliated; rather, both species tend to visit human homes opportunistically, attracted by artificial light [78, 91, 96]. There is no active vector control program in Costa Rica, but the MoH surveils passively, with home inspections carried out in response to reported domestic vector infestation, and insecticide application if the home is found to be colonized [99].

Urban and peri-urban cases of *T. dimidiata* infestation and Chagas disease are relatively well documented in Costa Rica, with 45% of acute cases registered between 2003 and 2018 being from metropolitan or suburban areas of the capital city of San Jose [100], and 90% of chronic cases between 2014 and 2018 being reported from the San Jose province [101]. Zeledon et al. [102, 103] found infestation indices upwards of 44% in communities less than 10 miles from San Jose, and more recently, a colonization index of 67% was found in a peri-urban area of Heredia province, described below [104]. *T. dimidiata* is known to be an urban and rural species [105–108], and there are mentions of the species in the capital cities of Guatemala, El Salvador, Nicaragua, and Honduras [33]. However, there are few published studies of urban *T. dimidiata* infestation in Central America [16•, 105], and most reports are opportunistic findings [105]. It is possible that data in Costa Rica are biased toward better detection in urban areas due to more available services in those areas. Regardless, the presence of urban vector-borne *T. cruzi* transmission to humans carries implications for disease control, as it necessitates approaches that are adapted to urban communities (e.g., denser housing, different cultural practices and attitudes than in rural areas). Urban infestations in Costa Rica often occur in settlements of poorly constructed homes built on deforested or recently converted land in the peripheries of

cities, where a *T. cruzi* transmission cycle with a native vector species is already established [109]. Zeledón and Rojas [102] were able to reduce domestic and peridomestic infestations in a peri-urban area of Costa Rica by modifying the domestic and peridomestic environments to eliminate artificial ecotopes, similar to integrated approaches used to control *T. dimidiata* in other countries [55]. The authors found that the bugs quickly returned if the modifications were not sustained [103].

Recent Activities

Studies continue to find *T. cruzi*-infected synanthropic animals and triatomine bugs in peri-urban and rural areas [17–20, 104, 110], as in prior studies [105, 111–114], suggesting that the zoonotic *T. cruzi* cycle in the region is well established. A 2015 entomological survey of *T. dimidiata* in a peri-urban community in Heredia province found *T. dimidiata* in 12% of houses surveyed, with 67% of positive houses being colonized, as mentioned above, and 55% of bugs infected with *T. cruzi*, including bugs collected in bedrooms [104].

In the Monteverde region, an ecotourism destination that receives around 250,000 international tourists a year [115], researchers found white-nosed coatis infected with *T. cruzi* [19], and in another study in the region, *T. cruzi*-infected *T. dimidiata* were collected from sylvatic, peridomestic, and domestic environments [18]. Additionally, *T. cruzi*-infected bats were found in Costa Rican national parks for the first time [21]. Interestingly, all *T. cruzi*-infected white-nosed coatis and bats were asymptomatic [19, 21]. Although isolated prevalence studies do not capture spatiotemporal variability, what can be gleaned from these studies is that host and vector species capable of maintaining *T. cruzi* infection are present in and around human homes and areas of human use in Costa Rica, including ecotourism destinations. The probability of acquiring *T. cruzi* infection upon a chance contact with a triatomine bug is very low [62], but an American tourist was infected with *T. cruzi* after vacationing in an ecotourism area in Costa Rica in 2008 [116].

Panama

Overview

There are 11 triatomine bug species identified in Panama (Table 1), with *R. pallescens*, *T. dimidiata*, and *P. geniculatus* being most associated with human *T. cruzi* infection [117]. These species have the widest geographical distribution, spanning most of country's ten provinces. *R. pallescens* is considered to be the most important Chagas disease vector species in the Panama, where it inhabits *Attalea butyracea* palms, which are often found in close proximity to human homes. The palms have a self-contained microclimate,

which regulates *R. pallescens* abundance in the palm crowns, especially in rural deforested landscapes, which are common in the country [118]. High *T. cruzi* infection prevalences have been found in *R. pallescens* populations, with one study reporting *T. cruzi* infection in 80–90% of adult specimens collected from human homes [119].

The only domiciliated vector species in Panama is *T. dimidiata*, which is also found in sylvan environments in the country. The species is most associated with Chagas disease in temperate mountainous regions of Panama, such as the northern parts of the Veraguas province in western Panama [120]. In a recent study of four communities in the Veraguas province, 24.6% of *T. dimidiata* collected in domestic environments had fed on humans, and 21.4% of specimens collected were infected with *T. cruzi* [120]. *P. geniculatus* is a relatively common visitor to human homes in peri-urban and suburban sites adjacent to forested areas, and the species has repeatedly been found infected with *T. cruzi* [121]. Most Chagas disease vector research in Panama is focused on just *T. dimidiata* and *R. pallescens*, and there is a need for a revival of the vector distribution and ecology studies that took place in the latter half of the twentieth century [117] in order to understand contemporary distribution and abundance patterns of other triatomine bug species in the rapidly changing landscapes of Panama.

Panama has never had a formal national Chagas disease control program, and the country is categorized by PAHO as one of four endemic countries in Latin America for which the interruption of vector-borne transmission of *T. cruzi* to humans is not a formally declared public health goal [122]. However, Chagas disease studies, including routine passive and active surveillance for triatomine infestation and in endemic communities, are carried out by members of the Gorgas Memorial Institute for Health Studies (ICGES), in collaboration with the Panama MoH (called MINSA) and the National Technical Commission for the Prevention and Control of Chagas disease, Leishmaniasis and Other Neglected Diseases. The ICGES supports further eco-epidemiological studies in endemic communities as well, and other vector surveillance occurs through projects at research institutions in Panama funded by the National Department of Science, Technology and Innovation (SENACYT).

Recent Activities

Recent studies have found links between *T. cruzi* transmission and deforestation, which is widespread in Panama, and continuing at relatively high rates in some areas. In a series of studies of *T. cruzi* vectors and hosts across a land use gradient, researchers found that deforestation was a risk factor for increased abundance of *R. pallescens* [24], and higher *T. cruzi* infection frequency in the species [25]. The authors also found

that trypanosome infection patterns in *R. pallescens* changed in different land use types [123], and deforestation/forest fragment-associated loss of species diversity and changes in the mammal community structure favored increased abundance of human-adapted wildlife species that are highly competent for *T. cruzi* [25]. Preliminary results of a follow-up study to identify the main *T. cruzi* reservoir species in deforested areas have found opossums (*Didelphis marsupialis*) to be a main reservoir for *T. cruzi*. Opossums are highly competent *T. cruzi* hosts that serve as links between sylvatic and domestic *T. cruzi* cycles in numerous Chagas-endemic regions. These results suggest that deforestation and forest fragmentation are important drivers of increased vector abundance, *T. cruzi* infection and Chagas disease risk in humans.

Other ongoing studies have identified a potentially novel triatomine subspecies and new vector habitats, suggesting that contemporary human *T. cruzi* infection risk may be more geographically widespread in Panama than previously believed. A dark chromatic variation of *R. pallescens* was recently identified in a mountainous region of the Veraguas Province, which was recently found to be a new endemic focus for *T. cruzi* [120]. The bugs had a *T. cruzi* prevalence of 14.3% (single infections) and a *T. rangeli* prevalence of 22.2% (single infections), and 28.6% of bugs were infected with both parasite species [22]. Phylogenetic studies are in process to clarify the systematics of the chromatic variant in order to determine if it is a color morph, or a new species or subspecies.

Specimens of two palm species were found harboring *R. pallescens* populations, revealing new habitats for the vector beyond the *A. butyracea* palm. The first species, *Acrocomia aculeata* (coyol palm), was infested with *R. pallescens* in the Los Santos Province in the Azuero Peninsula, which was the first report of *R. pallescens* in the region. A total of 62 *R. pallescens* and 1 *Eratyrus cuspidatus* were collected from 23% (19/83) of *A. aculeata* palms searched, and 67% of bugs collected were infected with *T. cruzi* (all *R. pallescens* [23]). The second palm species, *Elaeis oleifera*, was found infested with *R. pallescens* in the Panama Oeste province. *E. oleifera* is a native species of oil palm used mainly for medicinal purposes by local populations. Out of 60 palms searched, 13 (21.7%) were infested with *R. pallescens*, and some of the bugs were infected with *T. cruzi* (unpublished data, ICGES). In both palm species, adults and nymphs were found, suggesting colonization.

Concluding Remarks

Although the elimination of *R. prolixus* from Central America contributed to significant reductions in the incidence of human *T. cruzi* infection in the region, national and regional leaders and must still continue to emphasize the importance of

controlling native vector species, namely *T. dimidiata* and *R. pallescens*, which still pose a significant public health threat. Effective vector control is especially critical for the success of national programs working to expand medical interventions in endemic areas, such as screening of pregnant women [124] and treatment coverage [122]. For these programs to be successful, it will be imperative that patients live in a home that is not and will not be infested with the vector in order to avoid reinfection with *T. cruzi* after medical intervention [125].

The seriousness of *T. dimidiata* in particular should not be underestimated considering that human blood meals, acute cases, and domestic infestation by *T. dimidiata* are found in every country in the region, unequivocally indicating a risk. IRS-based vector control strategies reduced *T. dimidiata* domestic infestation to some degree, but in multiple regions, the reductions were unsustainable, and IPCAM has acknowledged that integrated approaches are needed [36]. The Ecohealth approach has been designated by MoHs as a best practice [75], as it is considered less costly and more sustainable than repeated insecticide application for suppressing *T. dimidiata* infestation over the long term, although it has yet to be fully applied to *R. pallescens*. Regardless of the chosen approach, development and implementation of effective native species control measures in Central America will require sustained effort, commitment, and resources from multiple entities over the long term, and it remains to be seen if current efforts will translate to significantly reduced human *T. cruzi* infection burden in the region.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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