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Chromatic and Morphological Differentiation of *Triatoma dimidiata* (Hemiptera: Reduviidae) with Land Use Diversity in El Salvador

Víctor D. Carmona-Galindo [1,2,*], Claire C. Sheppard [1], Madelyn L. Bastin [1], Megan R. Kehrig [1], Maria F. Marín-Recinos [3], Joyce J. Choi [4] and Vianney Castañeda de Abrego [2]

1 Biology Department, University of Detroit Mercy, Detroit, MI 48221, USA; sheppacc1@udmercy.edu (C.C.S.); bastinml@udmercy.edu (M.L.B.); kehrigmr@udmercy.edu (M.R.K.)
2 Centro de Investigación y Desarrollo en Salud, Universidad de El Salvador, San Salvador CP1101, El Salvador; vianney.monroy@ues.edu.sv
3 Agrobiotechnology Program, Justus Liebig Universität Gießen, 35390 Hesse, Germany; Maria.F.Marin-Recinos@agrar.uni-giessen.de
4 School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, USA; joycejc@umich.edu
* Correspondence: carmonvi@udmercy.edu; Tel.: +1-313-993-1182

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Abstract: Chagas disease is caused by the parasite *Trypanosoma cruzi*, which is transmitted by insect-vectors in the taxonomic subfamily Triatominae and affects approximately 8,000,000 people worldwide. Current mitigation strategies for Chagas focus on insecticides, infrastructure improvements, and management of symptoms, which are largely unsustainable in underserved communities where the disease is widespread. Transmission patterns of vector-borne diseases are known to adaptively respond to habitat change; as such, the objective of our study was to evaluate how the physical characteristics of *Triatoma dimidiata* would vary in relation to land use in El Salvador. We hypothesized that the color and morphology of *T. dimidiata* would change with municipal levels of urban and natural green space, natural green space, and agricultural space, as well as municipal diversity, richness, and evenness of land use types. Our results characterize how *T. dimidiata* color and morphology vary directly with anthropogenic changes to natural and agricultural environments, which are reflective of a highly adaptable population primed to respond to environmental change. Mitigation studies of Chagas disease should exploit the relationships between anthropogenic land use and *T. dimidiata* morphology to evaluate how the transmission pattern of *T. cruzi* and Chagas disease symptomology are impacted.

Keywords: American trypanosomiasis; Central America; eco health; kissing bug; neglected tropical diseases; phenotypic variation; vector ecology

1. Introduction

Chagas disease is a tropical neglected disease [1] caused by the parasite *Trypanosoma cruzi* (Chagas, 1909) [2], which is transmitted by hematophagous insect vectors, which are members of the Triatominae, a taxonomic subfamily of the Reduviidae [3]. Also known as kissing bugs, due to their feeding-behavior to typically bite near the mouth or eyes [2], Triatominae often share shelter with the nesting vertebrates on which they feed [3]. While all Triatominae are potential vectors of Chagas disease [4], only species that are adapted to domiciliary habitats are considered important for human transmission [3,4]. Triatominae species acquire *T. cruzi* when a kissing bug feeds on a mammalian host that is infected with the parasite [5]. The *T. cruzi* parasite is harbored in the gut of the Triatominae vector [6], and transmission to a new host occurs when the kissing bug defecates near the bite-wound following feeding [3,5]. The proximity of the parasite-laden feces to the skin-breakage or mucous membranes facilitates the entry of the *T. cruzi* parasite into the bloodstream of the new host, where it circulates to various tissues and replicates [5].

In humans, Chagas disease has systemic clinical symptoms but mostly targets the heart, digestive system, or both [1,4,7]. The acute phase of infection may be asymptomatic or include prolonged fever, malaise, enlargement of the liver, spleen, and lymph nodes [4]. Cardiomyopathy and digestive mega syndromes are common in the chronic phase [4], but heart failure is often a late term effect of Chagas heart disease [1]. While treatment is available and effective during the early acute phase, Chagas disease is incurable [1,5,6,8]. As many as 8,000,000 people in Latin America have Chagas disease [1], most of whom are unaware that they are infected [4], disproportionately affecting communities in rural areas where poverty is widespread [8]. In domiciliary environments, Triatominae vectors hide in the crevices of earthen walls and thatched roofs [9,10] and emerge at night to feed on inhabitants [11], including humans, domestic animals, and household livestock [12].

Mitigation strategies for Chagas disease include the use of bed nets [8], insecticides [13], infrastructure improvements [13], and therapeutic care [14]. However, these efforts are costly and unlikely economically viable for those communities living in the rural townships where Chagas disease proliferates [15,16]. However, Triatominae species can undergo home range expansions, for example, via anthropogenically aided dispersal (e.g., trade routes), as well as in adaptive response to favorable shifts in habitat suitability brought on by climate change, effectively introducing vectors to new regions [17,18]. The likely consequences of climate change are the northbound expansion of Triatominae vector species home ranges [11] and subsequently autochthonous cases of Chagas in humans [17,18]. Additionally, transmission patterns of Chagas disease can change with anthropogenic alteration of natural environments [19,20]. As such, expanding transdisciplinary collaborations, integrative characterizations, and novel explorations of strategies to mitigate Chagas disease are crucial for advancing the public health of countries that are currently, and in the future, susceptible to this tropical neglected disease [15,16].

Our research objective was to combine Geographic Information System (GIS) tools and image analyses of specimen collections to evaluate the relationship between land use in the Central American country of El Salvador and adaptations of the principal Triatominae species in that country, *Triatoma dimidiata* (Latreille, 1811) [9,12]. While approximately 14% of El Salvador is forested, native tropical forests cover less than 2% of the land area [21,22], and more than 90% of all forested land is privately owned [23]. Forested land in El Salvador persists in a highly fragmented landscape, with agricultural (82% of land area) and urban (4% of land area) spaces [24], which, for the last 30 years, have been marked with negative rates of natural forest regeneration (−0.74% of land area per year on average), sustained deforestation rates (−0.69% of land area per year on average), and net-limited reforestation initiatives (+1.93% of land area per year on average) [23]. As such, we hypothesized that the color and morphology of *T. dimidiata* populations would change with respect to municipal levels of urban and natural green space, natural green space, and agricultural space, as well as the diversity of land use.

2. Materials and Methods

2.1. Image Analysis

The specimens of *T. dimidiata* used in this study were collected during 2013 by the Ministry of Health using national protocols for Chagas disease [25]. A total of 52 individuals of *T. dimidiata* (23 males and 29 females from domiciliary habitats) preserved in ethanol-glycerol solution (19:1) were selected for this study, representing six departments from across El Salvador: Santa Ana (n = 14), Morazán (n = 10), San Vicente (n = 4), La Unión (n = 12), and San Miguel (n = 12). Dorsal and ventral views of all specimens were digitally photographed and used to collect color and morphological measurements using Sigma Scan Pro (v5) sensu [26]. Dorsal structures measured were as follows: wing, spots on dorsal connexivial plates, body, and light region on dorsal connexivial plates. Ventral structures measured were as follows: ventral light region and ventral dark region. Color measurements included: total pixel intensity, average pixel intensity, average red pixel intensity, average blue pixel intensity, and average green pixel intensity. Pixel intensity values are expressed as integers that range from 0 (black) to 255 (white). Morphological measurements included: area, shape, and proportion of the area of a given structure (dorsal or ventral) to body area. Shape was expressed as a deviation from circularity, using Formula (1):

$$S = \frac{P}{2\sqrt{\pi A}} \quad (1)$$

where "*P*" represents the perimeter and "*A*" represents the area of a given structure (dorsal or ventral). Increasing values denote deviations from a circular shape; where a value of 1 represents a (perfect) circle and values > 1 represent elongated shapes (with a long perimeter relative to area).

2.2. Land Use Diversity

The GIS map layer for land use at the municipal level for El Salvador was created by the Salvadoran National Records Center and made available by the GIS Laboratory in the School of Physics at the College of Natural Sciences and Mathematics in the University of El Salvador. The land use GIS shapefile (*.shp) contained information on the distribution of 57 different land use categories in 257 municipalities (of 262 total), distributed across 14 departments (of 14 total) in El Salvador.

Land use types were reorganized under three constructs sensu [16]: urban and natural green space, natural landscapes, and agricultural landscapes. The category of urban and natural green space represented 43 land use types (Table 1), encompassing vegetation classes found in urban, natural, and agricultural habitats. The category of natural landscapes represented 22 land use types (Table 1), encompassing naturally occurring vegetation or habitats. The category agricultural landscapes represented 17 land use types (Table 1), encompassing diverse crops. The richness (S) of land use in each municipality was quantified as the number of land use types represented in that municipality. The diversity (H) of land use in each municipality was quantified using the Shannon–Weiner diversity index (2):

$$H = -\sum p_i * \ln(p_i) \quad (2)$$

where p_i is the proportional abundance of the area occupied by a given land use type (km^2), relative to the total municipal area (km^2). As a measure of equitability, the evenness (J) of land use categories in each municipality was quantified using formula (3):

$$J = \frac{H}{\ln(s)} \quad (3)$$

where *H* is the Shannon–Weiner diversity index of land use types in a given municipality and S is the richness of land use types in that municipality.

2.3. Statistical Analysis

Variation in the color (i.e., total pixel intensity, average pixel intensity, average red pixel intensity, average blue pixel intensity, and average green pixel intensity) and morphological (i.e., both dorsal and ventral area, shape, and proportion of the area of a given structure relative to body area) characteristics of *T. dimidiata* were evaluated as dependent variables to changes in municipal-level land use (i.e., percent urban and natural green-space, percent natural landscapes, percent agricultural landscapes, land use type richness, land use type diversity index, and land use type evenness) using linear regression models. The null hypothesis for a linear regression (H_0: x = 0) was rejected at $\alpha < 0.05$. Data analyses were conducted using the software Statistica, version 13 (TIBCO Software Inc., Palo Alto, CA, USA).

Table 1. Assignments of land use types (from GIS shapefile) for green space evaluations.

Urban & Natural Green Space	Natural Landscapes	Agricultural Landscapes
Fruiting Trees	Deciduous Forest	Fruiting Trees
Deciduous Forest	Riparian Forest	Sugar Cane
Riparian Forest	Mangrove Forest	Coffee
Mangrove Forest	Evergreen Forest	Pineapple Crop
Evergreen Forest	Coniferous Forest	Annually Associated Crop
Coniferous Forest	Mixed Forest	Permanent Herbaceous Crop
Mixed Forest	Semi-deciduous Forest	Staple Grains
Semi-deciduous Forest	Spaces with Sparse Greenery	Vegetables
Sugar Cane	Estuaries	Mosaic of Crops and Pastures
Coffee	Lakes and Lagoons	Other Irrigated Crops
Pineapple Crop	Coastal Lagoons and Estuaries	American Oil Palm Trees
Annually Associated Crop	Beaches, Dunes, and Sandbanks	Cultivated Pastures
Permanent Herbaceous Crop	Marshy Meadows	Natural Pastures
Spaces with Sparse Greenery	Rivers	Monospecific Forest Plantations
Estuaries	Lava Rock	Plantains and Bananas
Staple Grains	Salt Flats	Agroforestry Systems
Vegetables	Aquatic Greenery Around Bodies of Water	Mainly Agricultural Land
Lakes and Lagoons	Beach Shrub Vegetation	
Coastal Lagoons and Estuaries	Sclerophyll or Thorny Vegetation	
"Morrales" in Pastures	Natural Herbaceous Vegetation	
Mosaic of Crops and Pastures	Short Shrub Vegetation	
Other Irrigated Crops	Urban Green Zones	
American Oil Palm Trees		
Cultivated Pastures		
Natural Pastures		
Monospecific Forest Plantations		
Plantains and Bananas		
Beaches, Dunes, and Sandbanks		
Marshy Meadows		
Lava Rock		
Salt Flats		
Agroforestry Systems		
Mainly Agricultural Land		
Aquatic Greenery Around Bodies of Water		
Beach Shrub Vegetation		
Sclerophyll or Thorny Vegetation		
Natural Herbaceous Vegetation		
Short Shrub Vegetation		
Ornamental Plant Nurseries and Others		
Ecotonal Zones		
Construction Zones		
Port Zones		
Urban Green Zones		

3. Results

3.1. Percent Urban and Natural Green Space

There was a positive relationship between urban and natural green space (%) and the following *T. dimidiata* chromatic characteristics: total pixel intensity of spots on the dorsal connexivial plate, average green pixel intensity of the light region on the dorsal connexivial plate, average red pixel intensity of the light region on the dorsal connexivial plate, average green pixel intensity of the ventral light region, average pixel intensity of the ventral light region, total pixel intensity of the ventral light region, and total pixel intensity of the ventral dark region (Table 2). There was a negative relationship between urban and natural green space (%) and the following *T. dimidiata* chromatic characteristics: average blue pixel intensity of spots on the dorsal connexivial plate, average green pixel intensity of spots on the dorsal connexivial plate, average red pixel intensity of spots on the dorsal connexivial plate, average pixel intensity of spots on the dorsal connexivial plate, average blue pixel intensity of the light region on the dorsal connexivial plate, average blue pixel intensity of the ventral dark region, and average pixel intensity of the ventral dark region (Table 2).

Table 2. Linear relationships between municipal urban and natural green space (%) and *T. dimidiata* morphology, where: I = pixel intensity; B = average blue pixel intensity; R = average red pixel intensity; G = average green pixel intensity; and P = proportion of given region to the body area.

Morphology	*p*-Value	Slope (m)	R^2	y-Intercept (b)
B of Spots on Dorsal Connexivial Plate	0.004	−0.625	0.157	117.282
G of Spots on Dorsal Connexivial Plate	0.014	−0.546	0.115	116.442
R of Spots on Dorsal Connexivial Plate	0.003	−0.727	0.159	135.921
Average I of Spots on Dorsal Connexivial Plate	0.004	−0.625	0.152	121.950
Total I of Spots on Dorsal Connexivial Plate	0.033	998.608	0.088	−46,830.4
B of Light Region on Dorsal Connexivial Plate	0.016	−0.558	0.111	117.854
G of Light Region on Dorsal Connexivial Plate	0.047	0.715	0.077	28.914
R of Light Region on Dorsal Connexivial Plate	0.015	1.085	0.112	12.205
Area of Light Region on Dorsal Connexivial Plate	0.001	−1.254	0.415	140.889
Shape of Light Region on Dorsal Connexivial Plate	0.001	−0.010	0.424	1.076
G of Ventral Light Region	0.004	1.283	0.151	−12.355
R of Ventral Light Region	0.004	1.562	0.157	−23.869
Average I of Ventral Light Region	0.015	1.001	0.113	8.418
Total I of Ventral Light Region	0.011	139,131.795	0.123	−10,561,676.07
P of Ventral Light Region	0.001	0.014	0.295	−0.859
Shape of Ventral Light Region	0.011	−0.004	0.121	0.558
B of Ventral Dark Region	0.012	−0.453	0.104	103.325
Average I of Ventral Dark Region	0.036	−0.440	0.085	104.697
Total I of Ventral Dark Region	0.028	516,201.796	0.093	−38,683,702.48
P of Ventral Dark Region	0.001	0.012	0.329	−0.686
Area of Ventral Dark Region	0.001	2.078	0.255	−106.807

There was a positive relationship between urban and natural green space (%) and the following *T. dimidiata* morphological characteristics: ventral light region proportion to the body area, ventral dark proportion to the body area, and ventral dark region area (Table 2). There was a negative relationship between urban and natural green space (%) and the following *T. dimidiata* morphological characteristics: light region on the dorsal connexivial plate area, light region on the dorsal connexivial plate shape, and ventral light region shape (Table 2).

3.2. Percent Natural Green Space

There was a positive relationship between natural green space (%) and the following *T. dimidiata* chromatic characteristics: average blue pixel intensity of spots on the dorsal connexivial plate, average green pixel intensity of spots on the dorsal connexivial plate, average red pixel intensity of spots on the dorsal connexivial plate, average intensity of spots on the dorsal connexivial plate, average blue pixel intensity of the light region on the dorsal connexivial plate, average blue pixel intensity of the ventral dark region, average green pixel intensity of the ventral dark region, and average pixel intensity of the ventral dark region (Table 3). There was a negative relationship between natural green space (%) and the following *T. dimidiata* chromatic characteristics: total pixel intensity of the wing, total pixel intensity of spots on the dorsal connexivial plate, total pixel intensity of the body, total pixel intensity of the ventral light region, and total pixel intensity of the ventral dark region (Table 3).

Table 3. Linear relationships between municipal natural green space (%) and *T. dimidiata* morphology, where: I = pixel intensity; B = average blue pixel intensity; R = average red pixel intensity; G = average green pixel intensity; and P = proportion of given region to the body area.

Morphology	*p*-Value	Slope (m)	R^2	y-Intercept (b)
Total I of Wing	0.030	−69,687.3	0.090	7,219,776
B of Spots on Dorsal Connexivial Plate	0.021	0.150	0.101	55.410
G of Spots on Dorsal Connexivial Plate	0.043	0.135	0.080	62.280
R of Spots on Dorsal Connexivial Plate	0.013	0.187	0.118	63.631
Average I of Spots on Dorsal Connexivial Plate	0.019	0.155	0.105	59.972
Total I of Spots on Dorsal Connexivial Plate	0.038	−290.627	0.083	53,489.16
P of Spots on Dorsal Connexivial Plate	0.011	0.001	0.122	0.023
Area of Spots on Dorsal Connexivial Plate	0.002	0.006	0.414	1.492
Total I of Body	0.041	−134,604.474	0.081	14,808,561.12
Area of Body	0.001	0.689	0.261	225.418
B of Light Region on Dorsal Connexivial Plate	0.030	0.150	0.090	62.137
P of Light Region on Dorsal Connexivial Plate Area	0.002	0.004	0.171	0.247
Area of Light Region on Dorsal Connexivial Plate	0.001	0.266	0.210	17.857
Total I of Ventral Light Region	0.005	−45,385.556	0.148	3,560,541.547
Area of Ventral Light Region	0.010	0.1889	0.124	11.690
Shape of Ventral Light Region	0.037	0.001	0.084	0.120
B of Ventral Dark Region	0.021	0.134	0.103	57.721
G of Ventral Dark Region	0.037	0.037	0.084	61.753
I of Ventral Dark Region	0.028	0.137	0.093	60.223
Total I of Ventral Dark Region	0.010	−179,370.257	0.126	14,037,744.61
Shape of Ventral Dark Region	0.005	0.001	0.147	0.589

There was a positive relationship between natural green space (%) and the following *T. dimidiata* morphological characteristics: spots on the dorsal connexivial plate proportion to the body area, spots on the dorsal connexivial plate area, body area, light region on the dorsal connexivial plate area proportion to the body area, light region on the dorsal connexivial plate area, ventral light region area, ventral light region shape, and ventral dark region shape (Table 3).

3.3. Percent Agricultural Space

There was a positive relationship between agricultural space (%) and the following *T. dimidiata* chromatic characteristics: total pixel intensity of the wing, total intensity of spots on the dorsal connexivial plate, total pixel intensity of the body, average green pixel intensity of the ventral light region, average red pixel intensity of the ventral light region, total pixel intensity of ventral light region, and total pixel intensity of the ventral dark region (Table 4). There was a negative relationship between agricultural space (%) and the following *T. dimidiata* chromatic characteristics: average blue pixel intensity of spots on the dorsal connexivial plate, average green pixel intensity of spots on the dorsal connexivial plate, average red pixel intensity of spots on the dorsal connexivial plate, average pixel intensity of spots on the dorsal connexivial plate, average blue pixel intensity of the light region on the dorsal connexivial plate, average blue pixel intensity of the ventral dark region, average green pixel intensity of the ventral dark region, average red pixel intensity of the ventral dark region, and average pixel intensity of the ventral dark region (Table 4).

There was a positive relationship between agricultural space (%) and the following *T. dimidiata* morphological characteristic: ventral dark region proportion to the body size (Table 4). There was a negative relationship between agricultural space (%) and the following *T. dimidiata* morphological characteristics: spots on the dorsal connexivial plate proportion to the body area, spots on the dorsal connexivial plate area and body area, light region on the dorsal connexivial plate proportion to body area, light region on the dorsal connexivial plate area, light region on the dorsal connexivial plate shape, ventral light region area, ventral light region shape, and ventral dark region shape (Table 4).

Table 4. Linear relationships between municipal agricultural space (%) and *T. dimidiata* morphology, where: I = pixel intensity; B = average blue pixel intensity; R = average red pixel intensity; G = average green pixel intensity; and P = proportion of given region to the body area.

Morphology	*p*-Value	Slope (m)	R^2	y-Intercept (b)
Total I of Wing	0.013	138,490.8	0.117	−5,773,723
B of Spots on Dorsal Connexivial Plate	0.005	−0.315	0.147	84.676
G of Spots on Dorsal Connexivial Plate	0.013	−0.285	0.116	88.780
R of Spots on Dorsal Connexivial Plate	0.002	−0.394	0.173	100.243
Average I of Spots on Dorsal Connexivial Plate	0.004	−0.325	0.153	90.231
Total I of Spots on Dorsal Connexivial Plate	0.017	575.950	0.108	−571.863
P of Spots on Dorsal Connexivial Plate	0.034	−0.001	0.087	0.072
Area of Spots on Dorsal Connexivial Plate	0.005	−0.010	0.144	2.426
Total I of Body	0.017	271,180.95	0.108	−10,579,306.2
Area of Body	0.001	−1.130	0.231	334.973
B of Light Region on Dorsal Connexivial Plate	0.008	−0.318	0.133	91.655
P of Light Region on Dorsal Connexivial Plate	0.004	−0.007	0.155	0.881
Area of Light Region on Dorsal Connexivial Plate	0.001	−0.583	0.333	71.774
Shape of Light Region on Dorsal Connexivial Plate	0.013	−0.003	0.117	0.378
G of Ventral Light Region	0.011	0.599	0.122	58.139
R of Ventral Light Region	0.010	0.725	0.126	62.366
Total I of Ventral Light Region	0.001	91,580.101	0.198	−5,011,035.25
Area of Ventral Light Region	0.020	−0.300	0.103	40.950
Shape of Ventral Light Region	0.007	−0.002	0.137	0.345
B of Ventral Dark Region	0.006	−0.274	0.140	83.318
G of Ventral Dark Region	0.013	−0.271	0.117	87.081
R of Ventral Dark Region	0.020	−0.309	0.104	90.617
Average I of Ventral Dark Region	0.009	−0.282	0.130	86.549
Total I of Ventral Dark Region	0.003	354,006.922	0.162	−19,212,626.2
P of Ventral Dark Region	0.045	0.003	0.078	0.212
Shape of Ventral Dark Region	0.002	−0.002	0.184	0.735

3.4. Diversity of Land Use

There was a positive relationship between the richness of land use and the following *T. dimidiata* chromatic characteristics: total intensity of spots on the dorsal connexivial plate, average green pixel intensity of the body, average pixel intensity of the body, average green pixel intensity of the light region on the dorsal connexivial plate, average red pixel intensity of the light region on the dorsal connexivial plate, average pixel intensity of the light region on the dorsal connexivial plate, average green pixel intensity of the ventral light region, average red pixel intensity of the ventral light region, total pixel intensity of the ventral light region, and total intensity of the ventral dark region (Table 5). There was a negative relationship between the diversity of land use and the following *T. dimidiata* chromatic characteristics: average green pixel intensity of the light region on the dorsal connexivial plate, average red pixel intensity of the light region on the dorsal connexivial plate, average green pixel intensity of the ventral light region, average red pixel intensity of the ventral light region, average pixel intensity of the ventral light region, total pixel intensity of the ventral light region, and total pixel intensity the ventral dark region (Table 6). There was a negative relationship between the evenness of land use and the following *T. dimidiata* chromatic characteristics: average green pixel intensity of the body, average green pixel intensity of the light region on the dorsal connexivial plate, average red pixel intensity of the light region on the dorsal connexivial plate, average pixel intensity of the light region on the dorsal connexivial plate, total pixel intensity of spots on the dorsal connexivial plate, average green pixel intensity of the ventral light region, average red pixel intensity of the ventral light region, average pixel intensity of the ventral light region, total pixel intensity of the ventral light region, and total pixel intensity of the ventral dark region (Table 7).

Table 5. Linear relationships between the richness of land use types (S) and *T. dimidiata* morphology, where: I = pixel intensity; B = average blue pixel intensity; R = average red pixel intensity; G = average green pixel intensity; and P = proportion of given region to the body area.

Morphology	*p*-Value	Slope (m)	R^2	y-Intercept (b)
Total I of Spots on Dorsal Connexivial Plate	0.001	2,315.634	0.250	2,609.797
G of Body	0.014	0.746	0.115	73.120
Average I of Body	0.035	0.591	0.085	71.890
P of Light Region on Dorsal Connexivial Plate	0.026	0.001	0.095	1.000
G of Light Region on Dorsal Connexivial Plate	0.002	11.464	0.171	67.819
R of Light Region on Dorsal Connexivial Plate	0.003	1.820	0.167	78.658
Average I of Light Region on Dorsal Connexivial Plate	0.004	1.096	0.157	68.299
Area of Light Region on Dorsal Connexivial Plate	0.001	−1.150	0.185	46.733
Shape of Light Region on Dorsal Connexivial Plate	0.004	−0.008	0.152	0.313
G of Ventral Light Region	0.043	1.277	0.079	82.125
R of Ventral Light Region	0.050	1.480	0.075	92.586
Total I of Ventral Light Region	0.039	155,914.24	0.082	−630,879.771
P of Ventral Light Region	0.001	0.016	0.195	0.133
Shape of Ventral Light Region	0.031	−0.005	0.090	0.248
Total I of Ventral Dark Region	0.001	1,019,245.636	0.192	−9,883,020.224
P of Ventral Dark Region	0.001	0.016	0.272	0.177
Area of Ventral Dark Region	0.006	2.131	0.142	45.103

Table 6. Linear relationships between the diversity of land use types (H) and *T. dimidiata* morphology, where: I = pixel intensity; B = average blue pixel intensity; R = average red pixel intensity; G = average green pixel intensity; and P = proportion of given region to the body area.

Morphology	*p*-Value	Slope (m)	R^2	y-Intercept (b)
P of Light Region on Dorsal Connexivial Plate	0.022	−0.001	0.101	1.000
G of Light Region on Dorsal Connexivial Plate	0.005	−22.780	0.147	132.510
R of Light Region on Dorsal Connexivial Plate	0.049	−20.485	0.075	146.018
P of Light Region on Dorsal Connexivial Plate	0.043	0.208	0.0796	0.017
Area of Light Region on Dorsal Connexivial Plate	0.028	13.679	0.093	2.941
G of Ventral Light Region	0.005	−29.522	0.150	154.652
R of Ventral Light Region	0.012	−31.269	0.119	171.714
Average I of Ventral Light Region	0.025	−21.263	0.096	135.739
Total I of Ventral Light Region	0.006	−3,458,224.213	0.144	7,979,460.029
Area of Ventral Light Region	0.004	16.402	0.157	−10.050
Shape of Ventral Light Region	0.008	0.107	0.134	−0.026
Total I of Ventral Dark Region	0.013	−13,308,888.17	0.116	30,904,302.68
Shape of Ventral Dark Region	0.016	0.053	0.110	0.525

There was a positive relationship between the richness of land use and the following *T. dimidiata* morphological characteristics: light region on the dorsal connexivial plate proportion to the body area, ventral light region proportion to the body area, ventral dark region proportion to the body area, and ventral dark region area (Table 5). There was a negative relationship between the richness of land use and the following *T. dimidiata* morphological characteristics: light region on the dorsal connexivial plate area, light region on the dorsal connexivial plate shape, and ventral light region shape (Table 5). There was a positive relationship between the diversity of land use and the following *T. dimidiata* morphological characteristics: light region on the dorsal connexivial plate proportion to the body area, light region on the dorsal connexivial plate area, ventral light region area, ventral light region shape, and ventral dark region shape (Table 6). There was a negative relationship between the diversity of land use and the following *T. dimidiata* morphological characteristic: light region on the dorsal connexivial plate proportion to the body area (Table 6). There was a positive relationship between the equitability of land use and the following *T. dimidiata* morphological characteristics: light region on the dorsal connexivial plate area, light region on the dorsal connexivial plate shape, ventral light region shape, and ventral dark region shape (Table 7). There was a negative relationship between the equitability of land use and the following *T. dimidiata* morphological characteristics: light region on the dorsal connexivial plate proportion to the body area, ventral dark region proportion to the body area, and ventral dark region area (Table 7).

Table 7. Linear relationships between the evenness of land use types (J) and *T. dimidiata* morphology, where: I = pixel intensity; B = average blue pixel intensity; R = average red pixel intensity; G = average green pixel intensity; and P = proportion of given region to the body area.

Morphology	*p*-Value	Slope (m)	R^2	y-Intercept (b)
G of Body	0.034	−28.729	0.087	103.812
P of Light Region on Dorsal Connexivial Plate	0.008	−0.001	0.134	1.000
G of Light Region on Dorsal Connexivial Plate	0.001	−77.070	0.240	140.367
R of Light Region on Dorsal Connexivial Plate	0.002	−83.204	0.177	161.349
Average I of Light Region on Dorsal Connexivial Plate	0.008	−44.655	0.132	114.855
Area of Light Region on Dorsal Connexivial Plate	0.001	59.175	0.249	−9.446
Shape of Light Region on Dorsal Connexivial Plate	0.004	0.362	0.152	−0.052
Total I of Spots on Dorsal Connexivial Plate	0.002	−857	0.174	95,860.46
G of Ventral Light Region	0.001	−99.422	0.244	164.561
R of Ventral Light Region	0.001	−110.326	0.211	185.196
Average I of Ventral Light Region	0.002	−76.475	0.178	145.771
Total I of Ventral Light Region	0.002	−10,022,914.6	0.172	8,174,925.742
Shape of Ventral Light Region	0.001	0.377	0.238	−0.071
Total I of Ventral Dark Region	0.001	−47,041,775.7	0.207	36,692,751.55
P of Ventral Dark Region	0.001	−0.628	0.224	0.835
A of Ventral Dark Region	0.032	−74.697	0.089	128.409
Shape of Ventral Dark Region	0.004	0.167	0.157	0.513

4. Discussion

In El Salvador, several chromatic characteristics of *T. dimidiata* populations varied in relation to changing green spaces and land use at the municipal level. The spots on the dorsal connexivial plate of *T. dimidiata* got darker in color in terms of average blue pixel intensity, average green pixel intensity, average red pixel intensity, and average pixel intensity, with the increase of urban and natural green space, natural green space, and agriculture space. Spots on the dorsal connexivial plate got lighter in color in terms of average blue pixel intensity, green pixel intensity, average red pixel intensity, and average pixel intensity, with increasing natural green space. The spots on the dorsal connexivial plate also got lighter in color in terms of average pixel intensity, with increasing natural green space, but got darker with increasing urban and natural green space, as well as agriculture space. Spots on the dorsal connexivial plate got lighter in color in terms of total pixel intensity, with increasing urban, natural green, and agriculture space, as well as evenness of land use, but got darker in color with increasing natural green space and evenness of land use.

The ventral light region of *T. dimidiata* got lighter in color in terms of average green pixel intensity and average red pixel intensity, with increasing urban and natural green space, equitability of land use, and agriculture space, but got darker in color with an increase in diversity of land use, as well as evenness of land use. The ventral light region also got lighter in terms of average pixel intensity, with increasing urban and natural green space but got darker with increasing diversity of land use and evenness of land use. The ventral light region also got lighter in terms of total pixel intensity, with increasing urban and natural green space, agriculture space, and evenness of land use, but got darker with increasing natural green space percentage, diversity of land use, and evenness of land use. The ventral dark region got lighter in terms of average blue pixel intensity, with increasing natural green space, but got darker with increasing urban and natural green space, as well as agriculture space. The ventral dark region got darker in terms of average red pixel intensity, with increasing agriculture space. The ventral dark region got lighter in terms of average green pixel intensity, with increasing natural green space, but got darker with increasing agriculture space. The ventral dark region got lighter in terms of average pixel intensity, with increasing natural green space, but got darker with increasing urban and natural green space. The ventral dark region got lighter in terms of total pixel intensity, with urban and natural green space, as well as agriculture space, but got darker with increasing natural green space, as well as diversity of land use.

The light region on dorsal connexivial plate of *T. dimidiata* got lighter in color in terms of average blue pixel intensity, with increasing natural green space, but got darker in color with increasing urban and natural green space. The light region on dorsal connexivial plate average got lighter in terms of average green pixel intensity, with increasing urban and natural green space, as well as richness of land use, but got darker with increasing diversity of land use, as well as evenness of land use. The light region on dorsal connexivial plate got lighter in terms of average red pixel intensity with increasing urban and natural green space, as well as equitability of land use, but got darker with increasing diversity of land use, as well as evenness of land use. The light region on dorsal connexivial plate got lighter in terms of average pixel intensity, with increasing evenness of land use, but got darker with increasing evenness of land use.

The body of *T. dimidiata* got lighter in color in terms of average green pixel intensity, with increasing equitability of land use, but got darker in color with increasing evenness of land use. The body got lighter in terms of average pixel intensity, with increasing evenness of land use, and got darker in terms of total pixel intensity, with increasing natural green space and agriculture space. The wings of *T. dimidiata* got lighter in terms of total pixel intensity, with increasing agriculture space, but got darker with increasing natural green space.

In El Salvador, several morphological features of *T. dimidiata* populations also varied in relation to changing green spaces and land use at the municipal level. Both the ventral light region, as well as the ventral dark region, increased in size with increasing urban and natural green space, as well as richness of land use. The ventral dark region decreased in size, with increasing evenness of land use. The ventral light region increased in size with increasing natural green space, as well as diversity of land use, but decreased in size with increasing agricultural space. The ventral dark region increased in size with increasing urban and natural green space, as well as richness of land use, but decreased in size, with increasing evenness of land use. The ventral light region increased in size, with increasing diversity of land use, as well as evenness of land use, but decreased in size, with increasing urban and natural green space, agricultural space, and richness of land use. The ventral dark region increased in size, with increasing natural green space, diversity of land use, and evenness of land use, but decreased in size, with increasing agricultural space. The ventral dark region increased in size, with increasing agricultural space.

The shape of the light region on the dorsal connexivial plate of *T. dimidiata* became more elongated with increasing evenness of land use but became more circular with increasing urban and natural green space, agricultural space, and richness of land use. The light region on dorsal connexivial plate increased in area with increasing natural green space, diversity of land use, and evenness of land use, but decreased with increasing urban and natural green space, as well as richness of land use. The body of *T. dimidiata* increased in area with increasing natural green space but decreased in area with increasing agricultural space. The light region on dorsal connexivial plate of *T. dimidiata* increased in proportional size with increasing richness of land use but decreased in size with increasing diversity of land use, as well as evenness of land use. The light region on dorsal connexivial plate increased in area with increasing natural green space, as well as diversity of land use, but decreased in area with increasing agricultural space. The spots on dorsal connexivial plate of *T. dimidiata* increased in area with increasing natural green space but decreased in area with increasing agricultural space. The spots on the dorsal connexivial plate increased in area with increasing natural green space but decreased in area with increasing agricultural space.

Human behavior continually changes how land is used [16]; in recent decades, global croplands, pastures, plantations, and urban areas have all continued to expand [27]. Our study characterized adaptive shifts in the chromatic and morphological variation of *T. dimidiata* populations, with respect to the municipal management and modification of natural and agricultural landscapes in El Salvador. Anthropogenic changes to natural habitats can contribute to directional selection pressures on sylvatic populations [28], which in turn can contribute to variation in terms of morphology as well as species assemblages in both urban and natural environments [29]. An evaluation of *T. infestans* color polymorphism in a rural area of Cordoba Province, Argentina, documented life-history tradeoffs associated with melanic individuals and suggested pleiotropic effects linked to environment-specific adaptations [30]. As such, our findings align with other field studies by suggesting that anthropogenic management and modification of rural and urban environments can exert selection pressures on Triatominae populations in domiciliary habitats [26,30].

It is important to note that morphological studies of Triatominae cryptic species have found that variability corresponds closely with genetic variability [31,32]. Multivariate modeling of Triatominae speciation also points to a rapid process driven primarily by localized ecological factors [33]. As such, the variability of *T. dimidiata* characterized in our study further suggests an understated capacity to adapt to climate change. Climate change studies document that human behavior contributes significantly to global warming, fragmentation of natural environments, and the loss of ecosystem processes and ecological resilience [34]. Global warming has contributed to significant changes to insect morphology, as well as physiological processes, such as development rates [35]. As poikilothermic organisms, insects are highly sensitive to increased global temperatures and exhibit high rates of adaptation [35,36].

While inferential statistics can help identify categorical predictors that significantly describe some of the variation observed in a natural population, ultimately, the integration of biological null-models (e.g., the Hardy–Weinberg principle), with machine learning algorithms, will better serve to characterize anthropogenic contributions to (or interruptions of) evolutionary selective landscapes [37,38]. The ecological and evolutionary response of species populations to anthropogenically-imposed selective pressures vary richly with taxa and region [39–41], but the epidemiological importance of Triatominae vectors will largely depend on their dispersal ability and adaptation to localized environments [42]. As such, the characterization of Triatominae ecotypes (e.g., phenotypic plasticity and genotype $\times$ environment interactions) stand to better conect the current development of machine-learning algorithms for the identification of vector species [43,44] and the eco-epidemiological re-evaluation of Chagas disease [45].

The symptomology of Chagas disease varies greatly in both the acute and chronic phases, ranging from asymptomatic or mild to extreme [46]; however, the causes remain uncharacterized [6]. The relatively small size of El Salvador (21,041 km^2) allows for field studies to document how the behavior, morphology, and physiology of vector species for Chagas disease can change as a result of anthropogenic transformations of both natural and urban environments [9,12,26,30]. Additionally, the limited number of main Triatominae vector-species remaining in-country [47] and the limited number of *T. cruzi* strains in-country [48] further suggest that future field-studies in El Salvador can also begin to explore the relationship between the variation in *T. dimidiata* morphology and the symptomology of Chagas disease, specifically as it relates to the transmission efficacy and differential virulence of *T. cruzi* strains [9,49].

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