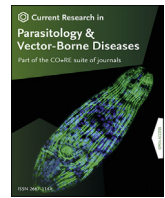


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Triatoma costalimai, a neglected vector of *Trypanosoma cruzi* in the Cerrado savannas of South America: A comprehensive review

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ABSTRACT

Triatoma costalimai is a little-known triatomine-bug species whose role as a vector of Chagas disease remains poorly understood. To address this gap, we conducted a comprehensive review of the literature and assessed the evidence base from a public-health perspective. We found 89 individual documents/resources with information about *T. costalimai*. DNA-sequence and cytogenetic data indicate that *T. costalimai* belongs, together with *Triatoma jatai*, in a distinct clade within the ‘pseudomaculata group’ of South American *Triatoma*. *Triatoma costalimai* is probably a narrow endemic of the Cerrado on the upper Tocantins River Basin and associated ranges/plateaus; there, the species thrives in the sandstone/limestone outcrops typical of the “Cerrado rupestre” (rocky-soil savanna) and “mata seca decídua calcária” (limestone-soil dry forest) phytophysiognomies. Wild *T. costalimai* appear to feed on whatever vertebrates are available in rocky outcrops, with lizards and rodents being most common. There is persuasive evidence that house invasion/infestation by *T. costalimai* has increased in frequency since the 1990s. The bugs often carry *Trypanosoma cruzi*, often defecate while feeding, have high fecundity/fertility, and, under overtly favorable conditions, can produce two generations per year. Current knowledge suggests that *T. costalimai* can transmit human Chagas disease in the upper Tocantins Basin; control-surveillance systems should ‘tag’ the species as a potentially important local vector in the Brazilian states of Goiás and Tocantins. Further research is needed to clarify (i) the drivers and dynamics of house invasion, infestation, and reinfestation by *T. costalimai* and (ii) the genetic structuring and vector capacity of the species, including its wild and non-wild populations.

1. Introduction

Chagas disease is caused by *Trypanosoma cruzi*, a protozoan parasite primarily transmitted by blood-feeding bugs known as triatomines (WHO, 2002, 2021). In spite of impressive progress towards curbing incidence, the disease is still among the most relevant public-health concerns in Latin America (Rojas de Arias et al., 2022); recent estimates suggest that 6–7 million people are chronic *T. cruzi* carriers, that close to 170,000 become infected each year, and that the disease kills about 9000 people annually (GBD, 2019). Vectors can infect humans through direct contact or via food contamination; transmission through other routes (mother-to-child, blood transfusion, organ transplantation, and laboratory accidents) is far less frequent (Rassi et al., 2010;

Shikanai-Yasuda & Carvalho, 2012; Dias et al., 2016). Massive insecticide-spraying campaigns have virtually eliminated non-native, domestic populations of two “primary” disease vectors, *Triatoma infestans* and *Rhodnius prolixus*, from large areas of Meso and South America (Rojas de Arias et al., 2022). However, over 100 native vector species maintain widespread *T. cruzi* transmission cycles from the USA to Patagonia, and many can act as “secondary” vectors of human Chagas disease (Waleckx et al., 2015; Abad-Franch & Gurgel-Gonçalves, 2021; Rojas de Arias et al., 2022). This has led to the suggestion that vector-borne *T. cruzi* transmission cannot be completely interrupted, and that continuous surveillance will be critical to sustain Chagas disease control in the long run (Abad-Franch, 2016; Rojas de Arias et al., 2022).

Although locally native triatomine-bug species are now the key

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targets of entomological surveillance throughout most of the Americas, we know very little about the vast majority of “secondary” vectors (Lent & Wygodzinsky, 1979; Noireau et al., 2005; Guhl et al., 2009; Waleckx et al., 2015; Abad-Franch, 2016; Monteiro et al., 2018; Abad-Franch & Gurgel-Gonçalves, 2021; Gürtler & Cecere, 2021; Gürtler et al., 2021). To roughly illustrate the bias toward “primary” vectors (namely, *T. infestans*, *R. prolixus*, *Triatoma dimidiata*, and *Panstrongylus megistus*) in the literature, we carried out PubMed searches using two different query strings. When using ‘(Triatominae [MeSH Major Topic])’, we recovered 3713 records; to exclude publications likely dealing with the four “primary” vectors, we modified the query string to ‘((Triatominae[MeSH Major Topic]) NOT (infestans[Title/Abstract]) NOT (prolixus[Title/Abstract]) NOT (dimidiata[Title/Abstract]) NOT (megistus[Title/Abstract]))’ and recovered 1477 records. This suggests that, as of June 2022, over 60% of studies on the Triatominae in PubMed focused on the four “primary” vector species. In other words, while each “primary” vector species has likely been the subject of ~560 PubMed papers on average, each of the other 150 species known to science has probably been the subject of, also on average, 9–10 papers. One might conclude that, in a fairly concrete sense, these understudied triatomine-bug species are neglected vectors of a neglected disease, and that they collectively merit extra attention from the scientific community.

Of particular public-health and academic interest are locally native species that comprise non-wild populations capable of spawning infestation foci in or around houses, the environments where vector-human contact almost invariably occurs (Waleckx et al., 2015; Abad-Franch, 2016; Gürtler & Cecere, 2021; Gürtler et al., 2021; Rojas de Arias et al., 2022). Examples include *Triatoma barberi*, *Triatoma brasiliensis*, *Triatoma sordida*, *Triatoma pseudomaculata*, *Triatoma maculata*, *Rhodnius ecuadoriensis*, and many others (Abad-Franch et al., 2013; Waleckx et al., 2015; Abad-Franch, 2016; Abad-Franch & Gurgel-Gonçalves, 2021; Gürtler & Cecere, 2021; Rojas de Arias et al., 2022). One such species is *Triatoma costalimai*, which infests houses and peridomestic structures in parts of central Brazil (Brito et al., 2017a) and has recently been described as a cause of “public health concern” (Teves et al., 2019). Here, we present a comprehensive review and synthesis of what is known about the systematics, ecology, and bionomics of *T. costalimai*, with an emphasis on (i) critically assessing the evidence base from a public-health perspective and (ii) identifying knowledge gaps that may hamper control-surveillance and thus require further attention.

2. Document search and selection strategy

In March–April 2022, we searched 13 bibliographic databases, including one dedicated to triatomines and Chagas disease (BibTri v 3.0), and 137 Brazilian academic repositories (see Supplementary Table S1). We searched for the expression “*Triatoma costalimai*” (or “*T. costalimai*”) anywhere in the ‘Text’; when search engines did not have this option, we made the search as inclusive as possible by, e.g., searching in the ‘Title OR Abstract’. We set no date or language limits, and updated our search in June 2022.

After removing duplicate records, we sequentially screened Titles and Abstracts to (i) select all documents including the phrase “*Triatoma costalimai*” (or “*T. costalimai*”) and (ii) exclude all documents clearly having no relation with the topic of this review. We read the full text of the remaining documents, excluded those that contained no information about *T. costalimai*, and retained those that did. Using these ‘focal documents’, we then screened (i) the documents cited in the reference lists and (ii) the documents in which, according to Google Scholar, our ‘focal documents’ had been cited; we also updated this latter procedure in June 2022. Finally, we added references that we knew contained information about *T. costalimai* but had not been recovered in our search.

Database searches recovered 70 unique documents/resources with information about *T. costalimai*; to these, we added 19 extra sources for a total of 89 items: 59 peer-reviewed journal articles and 30 further documents or resources including theses, dissertations, books, book

chapters, meeting abstracts, and databases (see Supplementary Text S1). Additional selected references on Chagas disease and its vectors or on the ecological, geological, or land-use contexts of the Cerrado (the tropical savanna biome where *T. costalimai* occurs) were also used.

3. Systematics and evolution of *Triatoma costalimai*

3.1. An overview of phenotypic characters

Triatoma costalimai was described in 1958 (not “1959”, as often misquoted) by Verano & Galvão (1958) after bugs caught in southeastern Tocantins, Brazil (Fig. 1). Adults are medium-sized (25.5–26.5 mm long), black or dark-brown bugs with orange-reddish markings along the dorsal outer margins of the connexival segments, on the forewings and, in some specimens, on the neck and posterior lobe of the pronotum (Fig. 2) (Verano & Galvão, 1958; Lent & Wygodzinsky, 1979; Gonçalves et al., 2013; Galvão & Gurgel-Gonçalves, 2015). Although there is variation in color patterns and forewing size (Verano & Galvão, 1958; Vendrami, 2017; Vendrami et al., 2021), adult *T. costalimai*’s phenotype is overall easy to distinguish from those of its sister species, *Triatoma jatai* (Teves, 2012, 2018; Gonçalves et al., 2013), and other South American *Triatoma* spp. (Verano & Galvão, 1958; Lent & Wygodzinsky, 1979; Galvão & Gurgel-Gonçalves, 2015). Humans and machine-learning algorithms succeeded, respectively, in 70.6% and 91.3% of identification tasks involving adult *T. costalimai*, with misidentification perhaps somewhat biased towards members of Monteiro et al.’s (2018) ‘pseudomaculata complex’ such as *Triatoma williami*, *Triatoma guazu* or *Triatoma arthurneivai* (Gurgel-Gonçalves et al., 2017, 2021; Khalighifar et al., 2019; Abdelghani et al., 2021). A few studies have described in some detail other anatomical structures of adult *T. costalimai*, including the scutellum and external genitalia, as well as the characteristics of eggs and nymphs (Lent & Jurberg, 1980; Obara et al., 2007a, b; Raigorodski et al., 2011; Teves, 2012; Müller, 2013; Gonçalves et al., 2013; Santos, 2019; Teves et al., 2020). While these studies overall confirm that phenotypic traits can be used to distinguish *T. costalimai* from other South American species of *Triatoma*, their findings were not discussed in the broader systematic context that would allow inference about the phylogenetic affinities of the species. Lent & Wygodzinsky (1979) cautiously suggested that *T. costalimai* may belong in a broad ‘infestans complex’ encompassing most South American species of *Triatoma*. Thirty years later, Schofield & Galvão (2009) included *T. costalimai* in what they called the ‘matogrossensis subcomplex’, which turned out to be a non-monophyletic assemblage of species genetically close to *T. pseudomaculata* (*T. williami*, *T. guazu*, *Triatoma baratai*, and *Triatoma deaneorum*) and *T. sordida* (*Triatoma matogrossensis*, *Triatoma jurbergi* and *Triatoma vandae*), but not particularly close to *T. costalimai* itself (see Monteiro et al., 2018 and below).

3.2. Cytogenetics

The diploid chromosome complement of *T. costalimai* ($2n = 20$ autosomes + XX/XY sex chromosomes = 22) is by far the most common in species of the ‘South American Triatomini lineage’ (sensu Monteiro et al., 2018); it is also found in species of the ‘dispar’ and ‘North American’ lineages (including species in *Triatoma*, *Paratriatoma*, *Panstrongylus*, and *Dipetalogaster*), as well as in the Rhodniini (Pita, 2013, 2017; Alevi et al., 2015; Alevi, 2017; Monteiro et al., 2018; Panzera et al., 2021). This trait, therefore, is barely informative with regard to the systematics of *T. costalimai*. More useful is the fact that ribosomal DNA (rDNA) clusters are located in one autosomal pair in *T. costalimai* and *T. jatai* (Pita et al., 2016). Even if common across South American *Triatoma* species, this character state suggests that *T. costalimai* and *T. jatai* are more distantly related to *T. matogrossensis* and allies (*T. sordida*, *Triatoma rosai*, *Triatoma garciabesi*, *T. jurbergi* and *T. vandae*), whose rDNA clusters are on the sex chromosomes, than they are to, e., *T. pseudomaculata* and allies (*T. williami*, *T. guazu*, *T. baratai*, *T. deaneorum*, *T. arthurneivai*, and

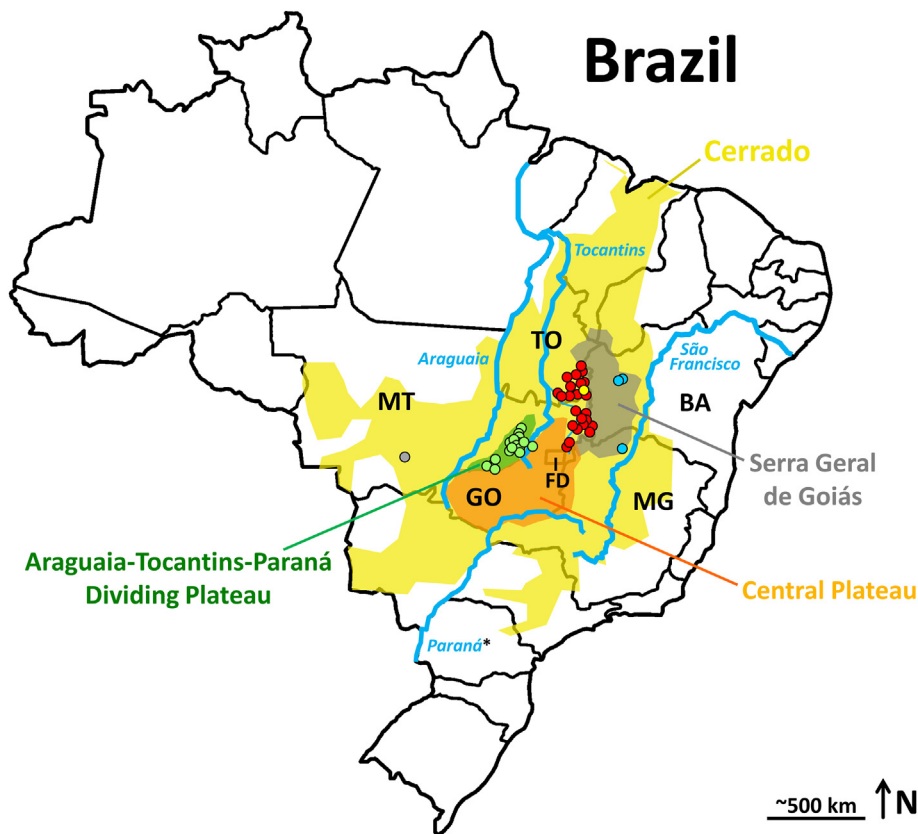


Fig. 1. Distribution of *Triatoma costalimai*. All confirmed records fall within the Brazilian Cerrado biome (yellow shape), which covers the middle-upper Tocantins River Basin and the ranges and plateaus that delimit that basin – including the Serra Geral range (grey shape), the Brazilian Central Plateau (orange shape), and the Araguaia-Tocantins-Paraná Dividing Plateau (green shape). Yellow circle: the species' type-locality, Aurora do Tocantins (see main text), state of Tocantins (TO). Red circles: other confirmed records in southeastern Tocantins and northeastern Goiás (GO); records marked with red and yellow circles fall within the Sub-basin of the northerly-flowing Paranã River, a tributary of the upper Tocantins not to be confused with the southerly-flowing Paraná River (asterisk). Green circles: confirmed records from central Goiás. Blue circles: confirmed records from western Bahia (BA) and northern Minas Gerais (MG), in the São Francisco River Basin. We are aware of no confirmed record from within the Federal District (FD). The grey circle highlights the only, apparently unconfirmed record west of the Araguaia River in Mato Grosso (MT). Note that, in this illustrative map, the location and extent of rivers, ranges, plateaus, and biomes, as well as administrative boundaries and site locations, are all approximate. See Section 4.1. *Macroscale patterns: biogeography* for references and details.

Triatoma wygodzinskyi or *Triatoma rubrovaria* and allies (*Triatoma carvalhoi*, *Triatoma circummaculata*, *Triatoma guasayana*, *Triatoma klugi*, *Triatoma patagonica*, and *Triatoma pintodiasi*) (Pita, 2013, 2017; Pita et al., 2016; Panzera et al., 2021). Results by Bardella et al. (2016) also suggest that the patterns of AT-rich (DAPI+) and GC-rich (CMA+) regions in *T. costalimai*'s heterochromatin are similar to those seen in *T. guazu* (which may be a *T. williami* variant; see Correia et al., 2022) and *T. carvalhoi*, but distinct to those in *T. matogrossensis*. However, *T. wygodzinskyi*, *T. rubrovaria*, *T. guasayana*, or *T. klugi* have yet another pattern, which is shared by *T. matogrossensis* relatives *T. garciabesi* and *T. vandae* and by the distantly-related *Triatoma boliviana* and *T. brasiliensis* (Bardella et al., 2016).

3.3. Molecular phylogenetics

The results discussed in the two previous sections illustrate how morphological and cytogenetic characters have been of limited value for clarifying the systematic position and phylogenetic relations of *T. costalimai*. Since the late 1990s, DNA-sequence analyses have contributed substantially to our understanding of the systematics and evolution of triatomines (Abad-Franch & Monteiro, 2005; Monteiro et al., 2018) including *T. costalimai*.

Hypša et al. (2002) were the first to include *T. costalimai* (one bug of unspecified origin) in a molecular phylogenetics study. Maximum parsimony (MP) and distance analyses of ~500 base pairs (bp) of the mitochondrial 16S rDNA suggested that *T. costalimai* is likely basal to the clades ((*T. williami*, *T. guazu*) (*T. pseudomaculata*, *T. arthurneivai*) (*T. jurbergi* (*T. matogrossensis*, *T. sordida*, *T. garciabesi*))), but also that it probably does not belong in any of them. These early findings have received overall support from most subsequent studies, including those using mitochondrial and nuclear DNA and those adding sequences from further species and specimens (see below). However, the availability of sequences from just a few loci, the analytical approaches used in some

studies, and, as we will see, doubts about the origin and taxonomic identity of some specimens mean that important uncertainties remain.

Sainz et al. (2004), for example, analyzed 12S and 16S rDNA sequences of *T. costalimai* originally from Goiás, Brazil, and recovered them as likely basal (albeit with relatively weak support) to the clades ((*T. williami* *T. guazu*) (*T. sordida*, (*T. garciabesi*, *T. matogrossensis*))). de Paula et al. (2005) included the 16S rDNA sequence of *T. costalimai* by Hypša et al. (2002) in their MP analyses and recovered, again with weak support, the clade (*T. costalimai* (*T. pseudomaculata*, *T. arthurneivai*)), thus suggesting clear differences between *T. costalimai* on the one hand and *T. matogrossensis* and allies on the other. The maximum-likelihood (ML) reanalysis of the data of Hypša et al. (2002) by Schofield & Galvão (2009), however, did not provide support for a particularly close relation between *T. costalimai* and the pair *T. arthurneivai*-*T. pseudomaculata*, but neither did it support the view that *T. costalimai* is closely related to *T. matogrossensis* and allies.

Bayesian analyses by Gardim et al. (2013) (see also Gardim, 2010, 2013) included *T. costalimai* originally from Tocantins, Brazil, and sequences of two mitochondrial protein-coding genes (*cytb* and *cox1*); they recovered overall low-resolution trees with weak node support in which *T. costalimai* tends to appear as a relatively isolated taxon, and about as close to *T. matogrossensis* and allies as it is to phylogenetically more distant taxa such as, e.g., *T. infestans*, *T. brasiliensis*, or *Triatoma juazeirensis*. A few years later, Teves et al. (2016) (see also Teves, 2018) used 16S and *cox1* mitochondrial sequences and Bayesian phylogenetic analyses and recovered a well-supported (*T. costalimai*, *T. jatai*) clade in a polytomy with three further clades, each also well supported (*T. williami*, *T. guazu*) ((*T. matogrossensis*, *T. vandae*) (*T. sordida*, *T. guasayana*)); and (*T. circummaculata* (*T. rubrovaria*, *T. carvalhoi*)).

Justi et al. (2014a, 2016) increased taxonomic coverage (albeit excluding *T. jatai*) and used mitochondrial and nuclear sequences in a series of Bayesian phylogenetic analyses; unfortunately, a detailed examination of metadata associated with bugs identified as *T. costalimai*

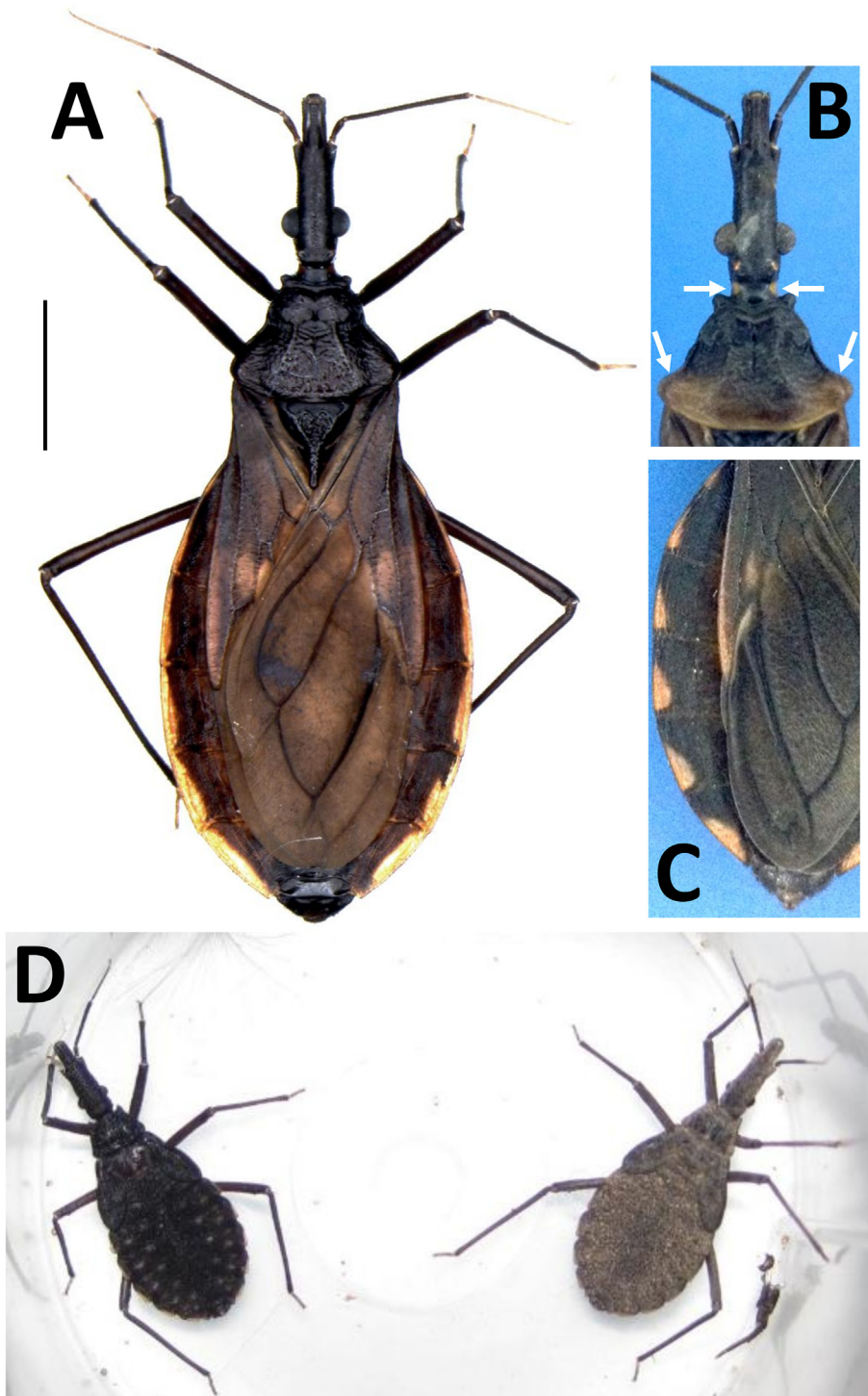


Fig. 2. The overall phenotype of *Triatoma costalimai*. **A** Adult female (photo: de Paiva VF & Belantini T; <https://www2.fcfar.unesp.br/#1/triatominae/subfamilia-triatominae/triatoma/triatoma-costalimai/>; Creative Commons license CC BY-NC-ND 4.0; <https://creativecommons.org/licenses/by-nc-nd/4.0/>). **B** A specimen with orange markings on the neck and posterior lobe of the pronotum (arrows) (photo: RG-G). **C** The connexivum of a specimen with triangular orange-reddish blotches similar to those described in type specimens – and particularly in females, with males said to have “narrower” orange-reddish markings (Verano & Galvão, 1958, p. 202) more similar to those in panel A (photo: RG-G). **D** Two *T. costalimai* nymphs; the darker bug on the left molted in the laboratory and shows the overall black color of the cuticle, whereas the lighter-colored bug on the right, which was collected in a limestone outcrop, is covered with limestone dust-particles, apparently as a means of camouflage (photo: RG-G). Scale-bar in panel A: ~5 mm.

and the position of those bugs in phylogenetic trees raises some doubts about how to interpret the results. First, a bug labeled as “*T. costalimai_42*” is said to have been collected in “Chiquitania, Cochabamba, Bolivia” (cf. Table 1 of Justí et al., 2014a); besides the fact that the Bolivian Chiquitania does not include territory in the Department of Cochabamba, “*T. costalimai_42*” is genetically very different from another bug, labeled as “*T. costalimai_35*” and said to be from “Posse, GO, Brazil” (Justí et al., 2014a; b, 2016). In fact, genetic distances between the “*T. costalimai_42*” 16S rDNA sequence (GenBank: KC248998.1) and those determined from field-caught *T. costalimai* (Goiás, Tocantins and

Bahia, i.e. covering most of the known range of the species; see Fig. 1) seem to be larger than the distances between those *bona fide T. costalimai* and *T. jatai* (Vendrami, 2017; Vendrami et al., 2021). We also noticed that a specimen labeled as “*T. costalimai*” in Figure 1 of Justí et al. (2016) occupies the position that in Figure 1 of Justí et al. (2014a) is occupied by a specimen apparently from “Mataral, Cochabamba, Bolivia” and labeled “*Triatoma sp_50*” – the position basal to the clade including *T. rubrovaria*, *T. circummaculata* and *T. carvalhoi*. Overall, then, it is difficult to interpret these findings with confidence. Specifically in relation to Bolivian material, a thorough assessment of the morphology and genetics of



Fig. 3. The ecotopes of wild *Triatoma costalimai* in northeastern Goiás, Brazil. **A** A rocky-soil stretch of Cerrado savanna, illustrating the overall appearance of the “Cerrado rupestre” phytophysognomy. **B** and **C** Limestone outcroppings within deciduous dry forest, illustrating the habitat of *T. costalimai* in the “mata seca decídua calcária” phytophysognomy (photos: RG-G).



Fig. 4. Ecotopes of synanthropic *Triatoma costalimai* populations in northeastern Goiás, Brazil. **A** A peridomestic limestone outcropping adjacent to a chicken coop and used by chickens and their chicks. **B** A peridomestic limestone outcropping adjacent to a pigsty (photos: RG-G).

field-collected, carefully vouchered specimens will be required to clarify the bugs’ taxonomic status and their relations with *T. costalimai* and other *Triatoma* species.

More recently, [Kieran et al. \(2021\)](#) combined DNA-sequence fragments from “*T. costalimai*_35” (16S, GenBank: KC248997.1; and 18S, GenBank: KC249101.1) and “*T. costalimai*_42” (28S, GenBank: KC249149.1) in ML and Bayesian analyses. Despite the mixing of sequences from two bugs that likely belong in distinct taxa (see [Justi et al., 2014b](#); [Vendrami, 2017](#); [Vendrami et al., 2021](#)), these analyses recovered a relatively well-supported (*T. costalimai*, *T. jatai*) clade basal to another, low-resolution clade including *T. pseudomaculata* and allies plus *T. sordida* and allies, but also two species that seem to be phylogenetically more distant: *T. guasayana* of the ‘rubrovaria complex’ and *Triatoma petrocchia* of the ‘brasiliensis complex’ ([Monteiro et al., 2018](#); [Kieran et al., 2021](#)).

[Monteiro et al. \(2018\)](#) put forward the hypothesis that *T. costalimai* and *T. jatai* form a cohesive, distinct cluster that shares a most recent common ancestor with *T. pseudomaculata*, *T. williamsi*, *T. guazu*, *T. baratai*, *T. deaneorum*, *T. arthurneivai*, and *T. wygodzinskyi*, i.e. the ‘pseudomaculata group’ of species in the ‘sordida clade’ of South American Triatomini.

While our review of the evidence base highlights important uncertainties, the chromosome location of rDNA clusters and DNA-sequence data seem to overall point in the same direction, suggesting that *T. costalimai* and *T. jatai* may be best seen as representing an independent species complex (the ‘costalimai complex’) within the ‘pseudomaculata species group’ of South American species of *Triatoma* ([Monteiro et al., 2018](#)).

3.4. Population genetic diversity

Very little is known about the levels of inter-population genetic diversity and structuring in *T. costalimai*. Preliminary analyses by [Vendrami \(2017\)](#) and [Vendrami et al. \(2021\)](#) suggest that there is some degree of mitochondrial DNA differentiation between two population clusters, one to the west and south (central Goiás and Minas Gerais) and the other to the north and east (eastern Tocantins/Goiás and Bahia) of the species’ distribution ([Fig. 1](#); see also [Teves, 2012](#)). These results will need to be confirmed, and perhaps qualified, with more DNA-sequence data – ideally including, besides wider population sampling, other mitochondrial genes and fast-evolving nuclear markers such as ribosomal internal

transcribed spacers, microsatellites, or genome-wide single-nucleotide polymorphisms (e.g., Marcilla et al., 2001; Abad-Franch & Monteiro, 2005; Fitzpatrick et al., 2008; Monteiro et al., 2018; Hernández-Castro et al., 2022).

4. Ecology of *Triatoma costalimai*

4.1. Macroscale patterns: biogeography

We first note that the type-locality of *T. costalimai*, often quoted as “Taguatinga” (e.g., Gonçalves et al., 1993, p. 329), was given by Verano and Galvão as “Distrito de Manhã, Município de Taguatinga (Goiás)” (Verano & Galvão, 1958, p. 203). The “Manhã” district of Taguatinga changed its status to municipality, under the name of “Aurora do Norte”, in the early 1960s (IBGE, 1970); later on, the state of Goiás was divided into two states, Goiás and Tocantins, and “Aurora do Norte”, which belongs to the latter, was renamed “Aurora do Tocantins” (IBGE, 2008). “Aurora do Tocantins, state of Tocantins, Brazil” is therefore the current name of the type-locality of *T. costalimai*; it lies in the core Cerrado biome of Neotropical savannas (Fig. 1), and entomological-surveillance records suggest that *T. costalimai* is particularly common there (Brito et al., 2017a). Incidentally, records of *T. costalimai* from “Taguatinga, Federal District, Brazil” (Ceccarelli, 2018; Ceccarelli et al., 2018a, b) appear to be due to confusion between two localities bearing the same name – a municipality in Tocantins, where *T. costalimai* does occur, and an administrative region of the Federal District, from where we found no confirmed records (see Maeda et al., 2012; Minuzzi, 2016; Minuzzi-Souza et al., 2017; and below).

Since the description of the species, confirmed records of *T. costalimai* occurrence consistently cluster in the upper Tocantins River Basin and associated ranges/plateaus, always to the east of the Araguaia River main channel (Fig. 1) (Sherlock & Serafim, 1972; Mello & Borges, 1981; Mello, 1982; García-Zapata et al., 1985; García-Zapata & Marsden, 1992; Elias et al., 1994; Marsden et al., 1994; Carcavallo et al., 1999; Lorosa et al., 1999a, b; Silveira et al., 2001; de Oliveira, 2006; de Oliveira & Silva, 2007; Gurgel-Gonçalves et al., 2012a, b; Machiner, 2012; Machiner et al., 2012; Pereira, 2012; Teves, 2012, 2018; Leite, 2013; Pereira et al., 2013; Ribeiro et al., 2021; Souza et al., 2014; Minuzzi, 2016; Brito et al., 2017a, 2021; Ceccarelli, 2018; Ceccarelli et al., 2018a, b; Minuzzi-Souza et al., 2017; Teves et al., 2019). As far as we are aware, the only record to the west of the Araguaia is an unconfirmed record from “Dom Aquino”, state of Mato Grosso (Fig. 1) – a record that Ceccarelli et al. (2018b) attribute to Gurgel-Gonçalves et al. (2012a) but cannot be found in that report. To our knowledge, the entomological surveillance system of Mato Grosso has never reported *T. costalimai* from the state, including data for 2000–2010 (see Pereira, 2012; Pereira et al., 2013) and 2011–2021 (M.F. Martins, Secretaria Estadual de Saúde do Mato Grosso, pers. comm.). Souza et al. (2014) extended *T. costalimai* occurrence records to the Cerrado of northern Minas Gerais on the eastern slope of the Serra Geral de Goiás, which separates the Tocantins and São Francisco Basins (Fig. 1; see also Vendrami, 2017; Brito et al., 2021; Vendrami et al., 2021). As discussed above, a bug identified as “*T. costalimai*” was seemingly collected in Bolivia (either in the Chiquitania or in the Department of Cochabamba), hundreds of kilometers west of the Araguaia and well beyond the limits of the Cerrado, but there are substantial doubts as to the taxonomic status of the specimen (see above and Justi et al., 2014a, b, 2016; Vendrami, 2017; Vendrami et al., 2021).

Taken as a whole, then, and in spite of some uncertainties, the evidence suggests that *T. costalimai* is most likely a narrow endemic of the Cerrado associated with the upper Tocantins River Basin and the ranges and plateaus that delimit that basin, i.e., the Serra Geral de Goiás, the Brazilian Central Plateau, and the Araguaia-Tocantins-Paraná Dividing Plateau (Fig. 1). We note that records from northeastern Goiás and southeastern Tocantins (yellow and red circles in Fig. 1) fall within the drainage (Sub-)basin of a northerly-flowing tributary of the Tocantins, the Paraná River – not to be confused with the much larger, southerly-

flowing Paraná River (see Fig. 1 and Espirito-Santo et al., 2009). Factors that contribute to setting the northern limits of the range of *T. costalimai* are not quite as obvious and remain to be investigated. *Triatoma costalimai* is, therefore, a species with a relatively restricted distribution in the core Cerrado biome (Fig. 1) (Sherlock & Serafim, 1972; Mello & Borges, 1981; Mello, 1982; García-Zapata et al., 1985; García-Zapata & Marsden, 1992; Elias et al., 1994; Marsden et al., 1994; Carcavallo et al., 1999; Lorosa et al., 1999a, b; Silveira et al., 2001; de Oliveira 2006; de Oliveira & Silva, 2007; Gurgel-Gonçalves et al., 2012a, b; Machiner, 2012; Machiner et al., 2012; Pereira, 2012; Teves, 2012, 2018; Leite, 2013; Pereira et al., 2013; Ribeiro et al., 2021; Souza et al., 2014; Minuzzi, 2016; Brito et al., 2017a, 2021; Ceccarelli, 2018; Ceccarelli et al., 2018a, b; Minuzzi-Souza et al., 2017; Teves et al., 2019).

4.2. Mesoscale patterns: landscapes

All confirmed records of *T. costalimai* are from areas dominated by Cerrado landscapes with sandstone and/or limestone outcrops, including the “Cerrado rupestre” (rocky-soil savanna) and “mata seca decídua calcária” (limestone-soil deciduous dry forest) phytophysiognomies (Fig. 3). This is true for the Tocantins Basin proper (including the Paraná Sub-basin and the Araguaia-Tocantins-Paraná Dividing Plateau) and for the São Francisco Basin in northern Minas Gerais and western Bahia (Lacerda-Filho et al., 1999; da Silva & Scariot, 2003; Scariot & Sevilha, 2005; Lima, 2008; Ribeiro & Walter, 2008; Espirito-Santo et al., 2009; dos Santos et al., 2012; Lobo et al., 2013; Dantas, 2017). It is important to emphasize that the absence of *T. costalimai* records from other sites in the states of Tocantins, Goiás, Bahia, and Minas Gerais (as well as from neighboring Mato Grosso and the Federal District; see Fig. 1) is not due to the absence of surveys: there are thousands of records, derived from routine entomological surveillance and research projects, of many other triatomine-bug species in these administrative regions (see, e.g., Sherlock & Serafim, 1972; Lustosa et al., 1984; Silveira et al., 1984; Silva et al., 1991, 1995; Diotaiuti et al., 1995; de Oliveira, 2006; de Oliveira & Silva, 2007; Gurgel-Gonçalves et al., 2012a, b, c; Maeda et al., 2012; Pereira, 2012; Leite, 2013; Pereira et al., 2013; Souza et al., 2014; Vinhaes et al., 2014; Galvão & Gurgel-Gonçalves, 2015; Minuzzi, 2016; Brito et al., 2017b, 2021; Browne et al., 2017; Ceccarelli, 2018; Ceccarelli et al., 2018a, b; Minuzzi-Souza et al., 2017; Ribeiro et al., 2019, 2021). Also important is the absence of *T. costalimai* records from areas where “Cerrado rupestre” and/or “mata seca decídua calcária” are present, including parts of Goiás, Mato Grosso, Minas Gerais, or Bahia (see Fig. 1 and, e.g., IBGE, 2004; Lima, 2008; Espirito-Santo et al., 2009; Gomes et al., 2011; Françoso et al., 2015; Almeida et al., 2018). Further, directed field sampling would however be needed to see if *T. costalimai* is indeed absent from those areas – which, if confirmed, would suggest that hitherto unidentified factors drive the species’ absence at sites with landscapes suitable for its occurrence. Examples of candidate factors are (i) geographical barriers, such as perhaps the sedimentary lowlands and main channels of the Araguaia River to the west, the Tocantins River to the north, and the São Francisco River to the east; and (ii) competing rock-dwelling species, such as perhaps *T. williamsi* or *Triatoma melanica* (Lent & Wygodzinsky, 1979; Monteiro et al., 2018; Abad-Franch & Gurgel-Gonçalves, 2021).

The preference of *T. costalimai* for rocky-soil landscape formations (Fig. 3) may also have a bearing on the response of the species to anthropogenic land-use change. In the current context of widespread transformation of the Cerrado into large agribusiness farms (Aquino & Miranda, 2008; Françoso et al., 2015; Potapov et al., 2021; Song et al., 2021), rocky-soil patches can act as “islands” of suitable habitat (including the mineral substrate and the associated vegetation and fauna) for wild *T. costalimai* populations (see Schofield et al., 1980; Brito et al., 2017a; and also Lacerda-Filho et al., 1999; Bonvicino et al., 2002; da Silva & Scariot, 2003; Scariot & Sevilha, 2005; Pacheco & Olmos, 2006, 2010; Werneck, 2006; Camargo & Aguiar, 2007; Martins, 2007; Aquino & Miranda, 2008; Lima, 2008; Ribeiro & Walter, 2008; Espirito-Santo

et al., 2009; Gomes et al., 2011; Recoder et al., 2011; dos Santos et al., 2012; Lobo et al., 2013; Purificação et al., 2013; Vieira et al., 2013; Ribeiro, 2015; Mews et al., 2016; Dantas, 2017; Almeida et al., 2018; Arcela, 2019). Thus, *T. costalimai* might be less vulnerable to the effects of deforestation and land-use change than other, sympatric triatomine-bug species primarily associated with tree habitats such as, e.g., *T. sordida* or *T. pseudomaculata* (Abad-Franch & Gurgel-Gonçalves, 2021). This hypothesis, however, remains to be tested (Schofield et al., 1980; Brito et al., 2017a).

4.3. Microscale patterns I: ecotopes

As discussed above, wild *T. costalimai* populations are associated with the sandstone or limestone rock outcrops typical of the “Cerrado rupestre” and “mata seca decídua calcária” (Verano & Galvão, 1958; Lent & Wygodzinsky, 1979; Schofield et al., 1980; Mello, 1982; Barrett, 1991; Carcavallo et al., 1998; Machiner, 2012; Machiner et al., 2012; Vendrami, 2017; Teves et al., 2019; Abad-Franch & Gurgel-Gonçalves, 2021) (Fig. 3). Schofield et al. (1980) wrote that *T. costalimai* nymphs were “fairly common” in limestone outcrops within dry-forest patches of northeastern Goiás and southeastern Tocantins; the nymphs hid “within the drier cracks between the rocks” and covered their black-colored cuticle with pale-grey limestone dust (see Fig. 2). This use of material drawn from the environment as a means of camouflage, which is seen in nymphs of a few further Triatomini (Zeledón et al., 1973; Weirauch, 2006; Ramírez et al., 2013; Monte et al., 2014), suggests that *T. costalimai* is adapted to, and hence likely evolved in, rocky-substrate microhabitats. Mello (1982) also reported the association of wild *T. costalimai* with limestone outcrops in northeastern Goiás; it is important to emphasize that Mello (1981, 1982) also studied more than 325 non-rocky ecotopes in the same fieldwork areas but found *T. costalimai* in none of them – including 100 trees (some with *T. sordida* and/or *T. pseudomaculata*), 96 palms (some with *Rhodnius neglectus* and *T. sordida*), 102 bird nests (some with *Psammolestes tertius*) or 29 armadillo burrows (no bugs found). Similarly, Gurgel-Gonçalves et al. (2012c) did not find *T. costalimai* in the 118 palms they investigated within the species’ range in Goiás, Tocantins, Bahia, and Minas Gerais – and 50 of which were infested with *R. neglectus*. On the other hand, we are aware of no field survey reporting the occurrence of other triatomine-bug species, save *T. jatai*, in the rocky-outcrop ecotopes used by *T. costalimai* (Schofield et al., 1980; Mello, 1981, 1982; Teves, 2012, 2018; Machiner, 2012; Machiner et al., 2012; Gonçalves et al., 2013; Vendrami, 2017; Teves et al., 2019). *Triatoma williamsi*, which seems to be rupicolous too (Abad-Franch & Gurgel-Gonçalves, 2021), has however been recorded in areas of Goiás where *T. costalimai* also occurs (de Oliveira, 2006; de Oliveira & Silva, 2007), raising the possibility of interspecies competition for rocky-outcrop habitats.

4.4. Microscale patterns II: hosts

Field observations and blood-meal analyses suggest that, in the wild, *T. costalimai* associates mainly with rodents, lizards and marsupials (see Abad-Franch & Gurgel-Gonçalves, 2021 and below). Here, we present an overview of the vertebrates that may share rocky-outcrop ecotopes with wild *T. costalimai* across its range in the Cerrado and are, therefore, actual or potential hosts for the species.

4.4.1. Rodents

The bugs used by Verano & Galvão (1958) in the description of the species were collected in August 1955 among limestone rocks occupied by “mocós”, i.e. caviid rodents of the genus *Kerodon*. Because a single *Kerodon* species was known at the time, this was interpreted as evidence of association between *T. costalimai* and the Caatinga rock cavy, *Kerodon rupestris* (Lent & Wygodzinsky, 1979; Miles, 1979; Carcavallo & Martínez, 1985; Espínola, 1985; Carcavallo et al., 1998; Galvão & Gurgel-Gonçalves, 2015; Catzefflis et al., 2016). We now know that the species of *Kerodon* that

co-occurs with *T. costalimai* in the Tocantins-Paraná Sub-basin (red circles in Fig. 1) is instead the Cerrado climbing cavy, *Kerodon acrobata*, probably a Paraná Sub-basin narrow endemic specializing on limestone outcroppings covered by “mata seca decídua calcária” (Moojen et al., 1997; Bezerra et al., 2010; Zappes, 2014; Zappes et al., 2014; Portella, 2015; Portella & Vieira, 2016; Roach, 2016). Preliminary nuclear DNA-based evidence suggests, however, that a *K. rupestris* population likely occurs at the northernmost tip of the range of *T. costalimai* (Zappes, 2014); *K. rupestris* may also co-occur with *T. costalimai* in northern Minas Gerais and western Bahia (see Catzefflis et al., 2016 and blue circles in Fig. 1). Mello (1982) caught “*Oryzomys eliurus*”, “*Calomys callosus*” and “*Thrichomys apereoides*” in rocky outcrops with *T. costalimai*. Current knowledge suggests that, except for northern Minas Gerais, *Thrichomys apereoides* does not occur within the range of *T. costalimai*; instead, *Thrichomys pachyurus* and *Thrichomys* aff. *inermis* (plus perhaps *Thrichomys* aff. *apereoides* in western Bahia) likely co-occur with *T. costalimai* (Nascimento et al., 2013; Roach & Naylor, 2016). Within *Calomys*, the known ranges of *Calomys callosus* (Dunnum et al., 2016), *Calomys expulsus* (Bonvicino & Geise, 2016), and *Calomys tener* (Leite & Patterson, 2016a) overlap that of *T. costalimai* (Fig. 1). “*Oryzomys eliurus*” (Mello, 1982, p. 236) likely refers to a species of *Oligoryzomys*; since the systematics of this genus is still controversial, with some authors not accepting “*Oligoryzomys eliurus*” as a valid taxon (see, e.g., Agrellos et al., 2012; da Cruz et al., 2019; Hurtado & D’Elia, 2019), we simply note that several *Oligoryzomys* species have been reported from within the range of *T. costalimai*; for example, distribution maps from the International Union for Conservation of Nature (IUCN) suggest that *Oligoryzomys moojeni* (Weksler, 2019a), *Oligoryzomys stramineus* (Weksler & Bonvicino, 2017) or *Oligoryzomys rupestris* (Weksler, 2019b), as well as *Oligoryzomys utariensis*/*O. eliurus* (Leite & Patterson, 2016b) and perhaps others, all may co-occur with *T. costalimai* (see also Agrellos et al., 2012; da Cruz et al., 2019; Hurtado & D’Elia, 2019). Other rodents associated with rocky-soil environments in the Cerrado include species of *Necomys*, *Thalpomys*, *Ceratomys*, *Rhipidomys*, *Galea*, and likely some further taxa (see, e.g., Lacher & Alho, 2001; Bonvicino et al., 2002; Camargo & Aguiar, 2007; Carmignotto & Aires, 2011; Ribeiro, 2015; Gutierrez & Marinho-Filho, 2017).

4.4.2. Marsupials

Mello (1982) captured *Didelphis albiventris* in limestone outcrops occupied by *T. costalimai*. *Monodelphis domestica*, *Micoureus demerarae*, *Gracilianus agilis*, *Thylamys karimii*, *Crytonanus agricolai*, and possibly other marsupial species, may also use rocky-soil habitats in the Cerrado biome (Lacher & Alho, 2001; Bonvicino et al., 2002; Camargo & Aguiar, 2007; Carmignotto & Aires, 2011; Ribeiro, 2015; Gutierrez & Marinho-Filho, 2017).

4.4.3. Lizards

Lizards, and in particular species of *Tropidurus*, are among the most common vertebrates in the limestone/sandstone outcroppings of the “Cerrado rupestre” and “mata seca decídua calcária” where *T. costalimai* thrives (see, e.g., Werneck, 2006; Werneck & Colli, 2006; Camargo & Aguiar, 2007; Recoder et al., 2011). Schofield et al. (1980) indeed noted that “*Tropidurus* sp.” were likely major hosts for *T. costalimai* living among limestone rocks in dry-forest patches. *Tropidurus oreadicus*, *Tropidurus torquatus*, *Tropidurus montanus*, and *Tropidurus itambere* have been recorded in sites within the range of *T. costalimai*. Other lizard taxa potentially interacting with wild *T. costalimai* include species of, among others, *Ameiva*, *Cnemidophorus*, *Mabuya*, *Tupinambis*, *Anolis*, *Phyllorhynchus*, *Gymnodactylus*, *Hemidactylus*, *Hoplocercus*, *Cloeadactylus*, and *Vanzosaura* (Werneck, 2006; Werneck & Colli, 2006; Camargo & Aguiar, 2007; Recoder et al., 2011). We note that recent studies suggest that some lizards may act as ‘silent hosts’ of *T. cruzi* (Botto-Mahan et al., 2022).

4.4.4. Other vertebrates

Armadillos and primates have been mentioned as possible blood sources for wild *T. costalimai* (Schofield et al., 1980; Lorosa et al., 1999a; Abad-Franch & Gurgel-Gonçalves, 2021). Schofield et al. (1980) noted

that *Callithrix* marmosets were common in the limestone-soil dry forests they studied; the ranges of both *Callithrix penicillata* (Valle et al., 2021) and *Callithrix jacchus* (Valença-Montenegro et al., 2021) overlap that of *T. costalimai*, and species of *Sapajus* capuchins (Lima et al., 2017) and *Alouatta* howlers (Cortés-Ortiz et al., 2003) might also use dry forests growing on rocky substrates in the Cerrado. Close interactions between these diurnal, tree-living primates and *T. costalimai* may, however, be limited. Armadillos, on the other hand, are terrestrial and may often be available to the bugs; species of *Dasytus*, *Euphractus*, *Cabassous*, *Tolypterus*, and perhaps *Priodontes* might interact with *T. costalimai* in the wild (Camargo & Aguiar, 2007; Carmignotto & Aires, 2011; Gutierrez & Marinho-Filho, 2017). Lorosa et al. (1999a, b) also reported “bird” blood meals in *T. costalimai*. Many bird species can use rocky-soil Cerrado and dry-forest environments within the range of *T. costalimai* (e.g., Camargo & Aguiar, 2007; Martins, 2007; Pacheco & Olmos, 2006, 2010; Purificação et al., 2013; Vieira et al., 2013); we suggest that ground-nesting taxa are more likely to be fed upon by ground-dwelling *T. costalimai* than tree-nesting taxa. Examples of ground-nesting birds recorded within the range of *T. costalimai* include the greater rhea (*Rhea*), vultures (*Coragyps*, *Cathartes*, *Sarcoramphus*), guans (*Penelope*), tinamous (*Crypturellus*, *Nothura*), owls (*Athene*), nighthawks (*Chordeiles*, *Lurocalis*, *Podager*), nightjars (*Nyctidromus*, *Hydropsalis*, *Eleothreptus*), nunbirds (*Monasa*, *Nonnulla*), and several smaller birds in, e.g., *Geositta*, *Arremon*, *Porphyrospiza*, *Tersina*, or *Streptoprocne* (Camargo & Aguiar, 2007; Martins, 2007; Pacheco & Olmos, 2006, 2010; Purificação et al., 2013; Vieira et al., 2013). We finally stress that other vertebrate taxa, from snakes and amphibians to carnivores, anteaters and bats, might on occasion be fed upon by wild *T. costalimai* – which, as other active-foraging, ‘stalker’ triatomine-bug species (Abad-Franch & Gurgel-Gonçalves, 2021), probably feeds opportunistically on the vertebrates that become available in the bugs’ rocky-outcrop ecotopes. Most of the time, those vertebrates happen to be rodents and lizards, yet the highly diverse fauna of the Cerrado likely offers, at least for the time being (Strassburg et al., 2017), numerous alternatives.

We close this section on vertebrate hosts by noting that the results of blood-meal studies mentioned above should be interpreted with much caution (Barrett, 1991). First, precipitin tests have low taxonomic resolution and can yield false-positive results; secondly, none of the reports published to date describes the use of reaction controls, either positive or negative (see Schofield et al., 1980; Lorosa et al., 1999a, b; and also Barrett, 1991; Rabinovich et al., 2011; Georgieva et al., 2017).

Taken as a whole, the evidence on the ecology of wild *T. costalimai* we reviewed strongly suggests that it is a truly rupicolous (rock-dwelling) triatomine specialized in exploiting rocky-outcrop microhabitats (and the vertebrates that use them) in the “Cerrado rupestre” and “mata seca decídua calcária” (Fig. 3) of the core Cerrado biome in the upper Tocantins Basin and associated ranges/plateaus (Fig. 1), where other triatomine-bug species, such as *T. sordida*, *T. pseudomaculata*, *R. neglectus*, or *Ps. tertius*, exploit trees, palms, or arboreal vertebrate nests (Lent & Wygodzinsky, 1979; Miles, 1979; Carcavallo & Martínez, 1985; Espínola, 1985; Carcavallo et al., 1998; Barrett, 1991; Abad-Franch & Gurgel-Gonçalves, 2021). The ecological relations of *T. costalimai* with potentially competing species, such as the sympatric and also rupicolous *T. jatai* or *T. williami*, remain to be investigated.

4.5. Synanthropic populations

Triatoma costalimai also exploit human-made microhabitats. House invasion by adult bugs is common in Tocantins and has also been recorded, with varying frequencies, in Goiás, Minas Gerais and Bahia (Sherlock & Serafim, 1972; García-Zapata et al., 1985; García-Zapata & Marsden, 1992; Elias et al., 1994; Marsden et al., 1994; Lorosa et al., 1999a, b; Silveira et al., 2001; de Oliveira, 2006; de Oliveira & Silva, 2007; Souza et al., 2014; Brito et al., 2017a, b, 2021; Minuzzi-Souza et al., 2017; Vendrami, 2017) (Figs. 1 and 4). There are also reports of breeding colonies (i.e. with nymphs) inside houses (Brito et al., 2017a)

or, more often, in peridomestic ecotopes including (i) rock outcrops close to houses and/or associated with chicken coops, pigsties, or corrals, and (ii) human-made structures such as chicken coops or sheds/storerooms (García-Zapata et al., 1985; Marsden et al., 1994; de Oliveira, 2006; de Oliveira & Silva, 2007; Rossi, 2014; Rossi et al., 2015; Brito et al., 2017a; Teves et al., 2019; Vendrami, 2017) (Fig. 4). In southeastern Tocantins, *T. costalimai* was found hiding among peridomestic rocks, but not in timber piles; in northeastern Goiás, two nymphs were caught (one in a chicken coop, one in a shed or storeroom) in a rural area where over 1000 *T. sordida* were found infesting chicken coops, sheds/storerooms and other wooden structures (Teves, 2012; Rossi, 2014; Rossi et al., 2015). Rodents, birds, and perhaps humans, dogs, cattle and horses might provide blood meals to domestic/peridomestic *T. costalimai* (Lorosa et al., 1999a, b; Rabinovich et al., 2011; Georgieva et al., 2017); we re-emphasize, however, that the results of these blood-meal analyses have to be interpreted with caution (see above and Barrett, 1991). Even if these observations might suggest that, when they colonize human environments, *T. costalimai* tend to select stony structures resembling their natural rocky-outcrop ecotopes (Fig. 4), possible associations between microhabitat substrate/structure, vertebrate-host availability, and occupancy by synanthropic *T. costalimai* remain uncharted (see, e.g., Valença-Barbosa et al., 2014).

5. Medical relevance of *Triatoma costalimai*

Broadly speaking, the medical/epidemiological relevance of triatomine bugs can be seen as depending on three major, species-specific, interacting factors (Lent & Wygodzinsky, 1979; WHO, 2002; Gürtler & Cecere, 2021; Gürtler et al., 2021; Ribeiro et al., 2021): (i) *geographical range*, with more widely-spread species usually more relevant; (ii) *synanthropism*, with species more prone to invade and/or colonize human environments usually more relevant; and (iii) *bionomics*, loosely defined as the set of intrinsic traits that govern the probability of vector-borne *T. cruzi* transmission, e.g., the species’ typical fecundity/fertility, development time and lifespan, infection frequency, blood-feeding preferences and dynamics, or feeding-defecation time (Gürtler & Cecere, 2021; Gürtler et al., 2021). Below we briefly survey what is known about these three factors for *T. costalimai*.

5.1. Geographical range

As discussed above, the evidence base suggests that *T. costalimai* is a narrow endemic of the rocky-soil “Cerrado rupestre” and “mata seca decídua calcária” phytophysiognomies of the core Cerrado in the upper Tocantins Basin and associated ranges/plateaus (Fig. 1). From a broad-scale, continental perspective, the range of *T. costalimai* is hence rather limited; compared with more widely-distributed taxa such as *T. dimidiata* or *T. infestans* (or even *T. sordida* or *T. pseudomaculata*), *T. costalimai* might by this criterion be seen as relatively unimportant. From a more local perspective, however, *T. costalimai* is fairly widespread across the upper Tocantins Basin (a region of 12.4 million hectares with well over one million residents; Ferreira & Tokarski, 2007) and extends towards parts of the São Francisco Basin in northern Minas Gerais and western Bahia (Fig. 1). Within that area, the species’ synanthropism and bionomics interact to determine its epidemiological relevance.

5.2. Synanthropism

Recent (21st century) records show that *T. costalimai* frequently invades, and at times colonizes, houses and peridomestic structures (see Section 4.5. *Synanthropic populations*). In Goiás, Machiner et al. (2012; see also Machiner, 2012) reported higher infestation frequency, higher bug-trapping success, and more bug catches per unit effort in rocky ecotopes located around houses than in similar rocky ecotopes located in the wild, suggesting that *T. costalimai* colonies were probably denser in the former – and particularly in rocks close to chicken coops or pigsties

(Fig. 4). These observations also suggest that peridomestic rock-outcrop bugs were using resources derived from human activities (such as domestic animal husbandry; see Fig. 4), and we therefore consider them to be synanthropic. In 2000–2003, entomological surveillance reported synanthropic *T. costalimai* in 25 municipalities of Goiás (de Oliveira, 2006; de Oliveira & Silva, 2007). In southeastern Tocantins, house invasion by adult, mainly female, *T. costalimai* seems to peak in the cool-dry season (Brito, 2015; Brito et al., 2017a), and in northeastern Goiás nymph catches were much more productive, especially for first-stage nymphs, in the warm-rainy season (Machiner, 2012; Machiner et al., 2012). Of the more than 400 indoor infestation events recorded in 2005–2014 in Tocantins, less than 10% involved nymphs; detection of synanthropic *T. costalimai* was much less frequent outdoors (53 events), but nymph involvement was more common there (43% of the events), including a colony with over 250 nymphs infesting a chicken coop (Brito, 2015; Brito et al., 2017a). Overall, we found records of *T. costalimai* from 41 municipalities of Goiás, Tocantins, Bahia, and Minas Gerais; by 2010, these municipalities had ~500,000 residents, more than 120,000 of whom were living in rural areas (see Supplementary Table S2). These recent data show that *T. costalimai* can, and does, invade, occupy, and at times colonize human-made habitats, thus lending further support to the idea that the species is a locally important vector of Chagas disease across its distribution range (Rojas de Arias et al., 2022).

There is, however, an apparent contradiction between this latter statement (and the data that support it) and the conclusion, either explicit or implicit, of 20th century studies on Chagas disease and its vectors in central Brazil – the conclusion that *T. costalimai* was probably not a relevant vector of human Chagas disease (see, e.g., Schofield et al., 1980; Mello, 1982; Lustosa et al., 1984; Silveira et al., 1984; García-Zapata et al., 1985; Silva et al., 1991, 1995; García-Zapata & Marsden, 1992; Elias et al., 1994; Marsden et al., 1994). This contradiction arises, at least in part, from the fact that records of synanthropic *T. costalimai* were indeed very rare in the databases of the 20th century. Surveillance data show, for example, that none of the more than 60,000 triatomine bugs caught in or around houses in Goiás and Tocantins during 1976–1980 (Lustosa et al., 1984) or in Tocantins during 1984–1988 (Silva et al., 1991) was identified as *T. costalimai*. Local-scale surveys also suggested that the species was seldom found in human environments (Mello, 1981, 1982; García-Zapata et al., 1985; García-Zapata & Marsden, 1992; Elias et al., 1994; Marsden et al., 1994; Silveira et al., 2001). In the late 1990s, Lorosa et al. (1999a) noted the “high incidence” (p. 411) of synanthropic *T. costalimai* in northeastern Goiás; this seems to be the first report suggesting that infestation of human environments by *T. costalimai* can be locally common. As outlined above, this suggestion has been widely confirmed by 21st century data from Goiás (de Oliveira, 2006; de Oliveira & Silva, 2007; Machiner, 2012; Machiner et al., 2012) and Tocantins (Brito, 2015; Brito et al., 2017a). The possible drivers of this apparent increase of domestic/peridomestic infestations with *T. costalimai* have not been investigated; as we have seen, extensive land-use change in the Cerrado might have a bearing on this phenomenon (Schofield et al., 1980; Brito et al., 2017a). A related, uncharted aspect of the process of occupation of human environments by *T. costalimai* is the response of synanthropic populations to control interventions; the recent rise of infestation records suggests, however, that selective insecticide-spraying does not suppress infestation-reinfestation pressure in Tocantins and Goiás (de Oliveira, 2006; de Oliveira & Silva, 2007; Machiner, 2012; Machiner et al., 2012; Brito, 2015; Brito et al., 2017a, b).

Taken as a whole, therefore, the evidence shows that *T. costalimai* is capable of invading and colonizing houses and peridomestic structures, and suggests that the realization of this synanthropic potential has become more frequent since the beginning of the 21st century. While one might argue that any triatomine-bug species with these capabilities should be considered as a potential vector of human Chagas disease, there are some species-specific features, often grouped under the label of ‘bionomics’, that modulate the bugs’ capacity to transmit *T. cruzi* to people and, consequently, their medical relevance.

5.3. Bionomics

Although there is an overall dearth of empirical studies on the bionomics of *T. costalimai*, two important aspects have been covered in the literature: infection with *T. cruzi* and the bugs’ life-cycle and reproductive potential.

5.3.1. Infection with *Trypanosoma cruzi*

Using xenodiagnosis techniques, Schofield et al. (1980) showed that *T. costalimai* is susceptible to infection with *T. cruzi*, and one year later Mello & Borges (1981) reported natural infection in a wild bug (see also Mello, 1982). Since these early reports, several studies have assessed natural infection frequency in field-caught *T. costalimai*; the results show that infection is relatively common, with *T. cruzi* detected in about 13% of more than 1300 bugs tested (Elias et al., 1994; Marsden et al., 1994; Lorosa et al., 1999a; Silveira et al., 2001; de Oliveira, 2006; de Oliveira & Silva, 2007; Machiner, 2012; Machiner et al., 2012; Brito et al., 2017a; Minuzzi-Souza et al., 2017; Teves et al., 2019). The two studies in which results were reported separately suggest that infection is more common among adult (~23%) than among immature bugs (~10%) (Brito et al., 2017a; Teves et al., 2019). Teves et al. (2019) detected *T. cruzi* in 64% of 53 bugs caught in a periurban rocky outcrop; 21 isolates derived from those bugs were all typed as TcI. Mello (1982) found *T. cruzi* in rodents (identified as “*Thrichomys apereoides*”; see Section 4.4. *Microscale patterns II: hosts*) and marsupials (*D. albiventris*) caught in rock outcroppings occupied by *T. costalimai* and in which no other triatomine species was found. These observations suggest that *T. costalimai* is a vector of *T. cruzi* in the parasite’s wild cycles, and that, in some cases, TcI transmission in those cycles can be very intense. Dias-Lima & Sherlock (1997) fed 62 *T. costalimai* on a *T. cruzi*-infected guinea pig and subsequently detected the parasite in 43 (69.3%) of the bugs.

Key to interpreting these results on infection with *T. cruzi* is the fact that they are all based on optical microscopy, which has low sensitivity (20–50%) for detecting the parasite in its vectors (Minuzzi-Souza et al., 2018); infection indices given above are therefore, in all likelihood, gross underestimates of true *T. cruzi* infection frequencies. Other aspects of vector–pathogen interactions, such as the dynamics of infection with different parasite lineages, do not seem to have been investigated in *T. costalimai*. Importantly, Dias-Lima & Sherlock (1997) reported that 30 of the 100 nymphs they tested defecated while blood-feeding, a trait that is critical to efficient vector-borne *T. cruzi* transmission (Gürtler et al., 2021).

5.3.2. Life-cycle and reproductive potential

We found four studies reporting on the life-cycle of *T. costalimai*; while the overall impression is that the species develops very slowly (Schofield et al., 1980; Dias-Lima & Sherlock, 1997; Teves, 2018), the results of Isac et al. (2000) suggest that, when allowed to feed frequently on mammal blood (with restrained mice offered daily) and without competition (with each bug in an individual container), *T. costalimai* can complete development from egg to adult in 4–5 months. Teves (2018) fed *T. costalimai* weekly on mice and reported that nymph development from first to fifth stage took about 5 months; fifth-stage nymphs were followed for about three extra-months, during which none molted into adult. Schofield et al. (1980) and Dias-Lima & Sherlock (1997) fed the bugs on chicken/rooster blood and reported first-to-fifth stage development times of about 14–16 months on average; complete development times were not reported for fifth-stage nymphs, but apparently were in excess of 5 months – with Dias-Lima & Sherlock (1997) stating that the bugs took “years” to reach adulthood. Egg incubation times were more similar across studies (from 21 to 33 days), suggesting that blood sources and feeding schedules can have strong effects on post-hatching development times in laboratory-reared *T. costalimai*. Mouse-fed *T. costalimai* females laid, on average, about 75 eggs (range: 9–169) over a 30-day period (Isac et al., 2000); fertility was high too, with 80–90% of eggs hatching successfully (Schofield et al., 1980; Dias-Lima & Sherlock, 1997; Isac et al.,

2000). Finally, Isac et al. (2000) reported that *T. costalimai* can survive from about one to over 4.5 months (first-stage and fifth-stage nymphs, respectively) without feeding. Taken together, these results suggest that, when conditions are favorable, the bionomic traits of *T. costalimai* do not differ substantially from those reported for *T. infestans*, *T. brasiliensis* or *T. sordida* (e.g., Guarneri et al., 2000). At least in this rather specific sense, then, we may conclude that *T. costalimai* is as well (pre-)adapted to survival and reproduction in human-made habitats (such as jars in laboratories) as are those three major domestic vectors of human Chagas disease (Guarneri et al., 2000; Rojas de Arias et al., 2022).

In summary, current knowledge about the geographical range, synanthropism, and bionomics of *T. costalimai*, even if still fragmentary, is overall more compatible with the view that the species is a potentially important local vector of human Chagas disease than with the alternative view that the species has little-to-no medical relevance. Notably, while 20th century studies largely supported the latter view, more recent data tend to support the former; this apparent trend towards growing epidemiological relevance suggests that *T. costalimai* is likely bound to join the list of major “secondary” vectors of Chagas disease in Brazil.

6. Conclusions and outlook

We have presented a comprehensive review of the literature on *T. costalimai*, a neglected vector of *T. cruzi* in the Cerrado savannas of central Brazil. Our critical appraisal not only provides an updated synthesis of what is known about the species – in addition, by revealing previously unrecognized patterns and placing previously disconnected observations in a coherent framework, it also offers novel insight on several little-understood aspects of the evolution, systematics, biogeography, population ecology, and medical relevance of *T. costalimai*. Below and in Table 1 we summarize our main conclusions and outline a set of hypotheses and recommendations that, we hope, may guide future academic and operational research on the biology and control-surveillance of *T. costalimai*.

- *Triatoma costalimai* shares a most recent common ancestor with *T. jatai*; closest to this pair are probably the species in the ‘pseudomaculata group’ of Monteiro et al. (2018), not those in the non-monophyletic ‘matogrossensis subcomplex’ of Schofield & Galvão (2009). The chromosomal location of rDNA clusters provides

particularly compelling evidence for this hypothesis. Phenotypic and genetic data overall suggest that *T. costalimai* and *T. jatai* may be best seen as forming a distinct complex within the ‘pseudomaculata group’, which would then encompass the ‘pseudomaculata complex’ and a new ‘costalimai complex’ (Monteiro et al., 2018).

- There are signs of genetic and phenotypic differentiation within *T. costalimai*; further research is needed to (i) describe intraspecific variation and population genetic structuring/connectivity, and (ii) assess whether genetic-phenotypic variation is associated with variation in synanthropic behavior across populations.
- *Triatoma costalimai* is most likely a narrow endemic of rocky-soil Cerrado phytophysiognomies (the “Cerrado rupestre” rocky savanna and the “mata seca decídua calcária” limestone dry forest) scattered across the upper Tocantins River Basin and associated ranges/plateaus; the geographical span of the species is, hence, relatively limited (Figs. 1 and 3).
- *Triatoma costalimai* is most likely a truly rupicolous (rock-dwelling) species adapted to life in sandstone/limestone outcroppings (Fig. 3) where rodents, lizards and, to a lesser extent, opossums are the bugs’ main hosts; however, the vertebrate fauna potentially available to wild *T. costalimai* in the Cerrado is astoundingly diverse, and further research is needed to clarify bug-host relations.
- The association with rocky-soil habitat patches might help *T. costalimai* to endure land-use change better than do tree-living, sympatric species such as *T. sordida* and *T. pseudomaculata*; this possibility, however, remains to be investigated.
- Synanthropic *T. costalimai* also seem to prefer stone-like ecotopes, including peridomestic rock outcroppings (Fig. 4); field research is needed to see if the presence of such outcroppings can help pinpoint dwellings at higher risk of infestation by the species. More generally, the patterns and drivers of habitat selection by synanthropic *T. costalimai* are yet to be thoroughly investigated.
- Within its range, *T. costalimai* invades, infests, and reinfests houses and peridomestic structures with increasing frequency. Infection with *T. cruzi* is common among these bugs, and there are data suggesting that, at least under overtly favorable conditions, the species has bionomic characteristics similar to those of well-known vectors of human Chagas disease.
- Even if still fragmentary, the evidence base suggests, in sum, that *T. costalimai* is a potentially important local vector of human Chagas

Table 1

The evolution/systematics, ecology, and medical relevance of *Triatoma costalimai*: a summary of major findings and key references.

Topic	Major findings	Key references
Evolution and systematics	1. <i>Triatoma costalimai</i> is a phenotypically distinct species with moderate population-level variability 2. <i>Triatoma costalimai</i> and <i>T. jatai</i> form a distinct, moderately divergent phylogenetic clade - the putative ‘costalimai species complex’ 3. The putative ‘costalimai complex’ is most likely sister to the ‘pseudomaculata complex’ of the ‘pseudomaculata species group’ (both <i>sensu</i> Monteiro et al., 2018)	Verano & Galvão (1958); Lent & Wygodzinsky (1979); Gonçalves et al. (2013); Vendrami et al. (2021) Hypša et al. (2002); Sainz et al. (2004); Gardim et al. (2013); Justi et al. (2014a, b, 2016); Teves et al. (2016); Kieran et al. (2021); Vendrami et al. (2021); see also Monteiro et al. (2018) Hypša et al. (2002); Bardella et al. (2016); Pita et al. (2016); Monteiro et al. (2018); Panzera et al. (2021)
Ecology	4. <i>Triatoma costalimai</i> is a narrow endemic of the Cerrado savanna on the upper Tocantins River Basin and associated ranges/plateaus 5. <i>Triatoma costalimai</i> is a truly rupicolous species adapted to limestone/sandstone outcroppings in the “Cerrado rupestre” (rocky-soil savanna) and “mata seca decídua calcária” (limestone-soil dry forest) phytophysiognomies 6. <i>Triatoma costalimai</i> , an active-foraging ‘stalker’ species, is an eclectic feeder capable of exploiting a wide range of vertebrate hosts, from lizards to mammals, in wild and non-wild microhabitats	Verano & Galvão (1958); Carcavallo et al. (1999); de Oliveira & Silva (2007); Gurgel-Gonçalves et al. (2012a); Souza et al. (2014); Brito et al. (2017a); Ceccarelli et al. (2018a); Monteiro et al. (2018); Ribeiro et al. (2021) Verano & Galvão (1958); Lent & Wygodzinsky (1979); Schofield et al. (1980); Mello (1982); Barrett (1991); Carcavallo et al. (1998); Abad-Franch & Gurgel-Gonçalves (2021) Lent & Wygodzinsky (1979); Schofield et al. (1980); Mello (1982); Barrett (1991); Carcavallo et al. (1998); Lorosa et al. (1999a, b); Rabinovich et al. (2011); Georgieva et al. (2017); Abad-Franch & Gurgel-Gonçalves (2021) Gurgel-Gonçalves et al. (2012a); Brito et al. (2017a); Ceccarelli et al. (2018a); Ribeiro et al. (2021)
Medical relevance	7. The distribution range of <i>Triatoma costalimai</i> covers at least 41 municipalities (in four Brazilian states) with about 0.5 million residents 8. <i>Triatoma costalimai</i> invades, infests and re-infests houses and peridomestic structures - and is doing so with increasing frequency since the 1990s 9. <i>Triatoma costalimai</i> often carry <i>Trypanosoma cruzi</i> , often defecate while feeding, have high fecundity/fertility, and can produce 1–2 generations per year; these bionomic traits are similar to those reported for major human disease vectors including <i>T. infestans</i>	Lorosa et al. (1999a); de Oliveira & Silva (2007); Machiner et al. (2012); Brito et al. (2017a); Teves et al. (2019) Schofield et al. (1980); Mello & Borges (1981); Dias-Lima & Sherlock (1997); Guarneri et al. (2000); Isac et al. (2000); Brito et al. (2017a); Teves et al. (2019); see also Abad-Franch & Gurgel-Gonçalves (2021)

disease across its range (Rojas de Arias et al., 2022). In terms of the working classification of Chagas disease vectors outlined by Abad-Franch (2016), public-health managers working within the distribution area of *T. costalimai* (Fig. 1) should consider that:

- (i) *Triatoma costalimai* is a native species with widespread wild populations and hence cannot be eliminated;
- (ii) Records of non-wild *T. costalimai* populations are common, and apparently becoming more frequent;
- (iii) Non-wild *T. costalimai* populations can spawn infestation foci inside and around houses;
- (iv) Most infestation foci do not seem to involve breeding colonies, but instead result from invasion of human-made structures by individual bugs, usually adults; importantly, however, adult bugs often carry *T. cruzi*, and breeding colonies – which can be hard to detect (Valença-Barbosa et al., 2014) – have indeed been reported.

These final considerations suggest that municipal, state, and federal managers in charge of Chagas disease prevention should (i) explicitly ‘tag’ *T. costalimai* as a specific target of control and surveillance actions, including education/communication and community engagement, across the species’ range; and (ii) set up and run long-term control-surveillance programmes aimed, on the one hand, at detecting and eliminating foci of domestic/peridomestic infestation by *T. costalimai* (or other triatomines) and, on the other, at providing due access to diagnosis and, if needed, integral medical care to any person exposed to contact with the bugs (Abad-Franch, 2016; Rojas de Arias et al., 2022). The scientific community, in turn, should strive to (i) further elucidate the genetic structuring and vectorial capacity of wild and non-wild *T. costalimai* populations; and, in collaboration with public-health managers and stakeholder communities, (ii) help understand the dynamics of invasion, infestation, and reinfestation of human habitats by *T. costalimai*, including the species’ responses to land-use change, the patterns and drivers of microhabitat selection by wild and non-wild populations, and the effects of control interventions on domestic/peridomestic infestation foci.

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Data availability

The data supporting the conclusions of this article are included within the article and its supplementary files.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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