



# *Trioza erytreae* (Del Guercio, 1918) and the Interaction with Its Hosts: A Review

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**Abstract:** The cultivation of citrus in the Mediterranean region is of considerable economic importance. The viability of this industry is contingent upon a number of factors, with adequate phytosanitary management being of particular significance. During the last decade, the geographical range of the invasive psyllid, *Trioza erytreae* (Del Guercio, 1918), has expanded to the mainland territories of Portugal and Spain. *Trioza erytreae* acts as a vector for the Huanglongbing disease (HLB). This review presents the current knowledge about the hosts of the psyllid and their attractiveness and suitability. A classification of the hosts according to their suitability, as assessed in the literature, is provided. The attributes of the hosts and the methods used to assess their suitability are described, as well as the climatic factors that affect the psyllid–host interaction. The review emphasises the importance of a comprehensive evaluation of the interactions between the psyllids and their hosts to develop and implement more effective strategies for controlling *T. erytreae*.

Keywords: citrus; huanglongbing; HLB; insect-plant interaction; psyllid; Rutaceae

### 1. Introduction

The citrus industry is the most important fruit sector in the world, with an annual production exceeding 166 million tonnes [1]. The industry is currently being confronted with an incredibly devastating bacterial disease that is rapidly disseminating globally: the Huanglongbing (HLB) disease. HLB is caused by *Candidatus* Liberibacter spp. bacteria, which clog the phloem and limit the flow of nutrients in the tree, thereby affecting its development, fruit production, and quality. The two functional vectors that transmit C. Liberibacter are the psyllids *Diaphorina citri* (Kuwayama, 1908) (Hemiptera: Liviidae), mainly present in the Asian and American continents, and *Trioza erytreae* (Del Guercio, 1918) (Hemiptera: Triozidae), mainly present in the African continent. The two vectors have recently reached the European continent, posing a threat to Mediterranean citriculture. *Diaphorina citri* is spreading from the East, having been detected in Israel and Cyprus [2,3], while *T. erytreae* is spreading from the West, with observations in the Iberian Peninsula dating back to 2014 in the north-western region near the coastline [4,5].

The Mediterranean basin is one of the few citrus-producing regions that has not been affected by HLB. To date, no positive results have been obtained from the HLB tests conducted in Europe on both vectors [3,6,7]. The potential spread of these harmful insects in the Mediterranean region represents a substantial concern for citrus growers, as their presence could facilitate the rapid dissemination of the HLB disease. The spread



Academic Editor: Elena Gonella

Received: 12 November 2024 Revised: 30 December 2024 Accepted: 31 December 2024 Published: 4 January 2025

Citation: Magalhães, T.; Duarte, A.; Pereira, J.A.; Marques, N.T. *Trioza erytreae* (Del Guercio, 1918) and the Interaction with Its Hosts: A Review. *Agriculture* **2025**, *15*, 101. https://doi.org/10.3390/ agriculture15010101

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/ licenses/by/4.0/). of *D. citri* carrying *C*. Liberibacter has been rapid in the citrus-producing regions on both American continents over the 15-year period since HLB was first identified. This has resulted in a 74% reduction in citrus production and a 62% decline in the number of citrus producers in Florida [8], which serves to demonstrate the destructive capacity of this disease. The management of HLB requires the elimination of infected plants [9] and a significant alteration in cultural practices [10]. Several control strategies for this disease have been tested, such as the injection of antibiotics into the stem, thermotherapy, and the application of endophytes. However, no treatment has been shown to be effective in controlling HLB [11–13].

The control of psyllid vectors represents a primary concern for the citrus industry. Aidoo [14] comprehensively outlined the main management strategies. These strategies encompass the use of chemical control, applying insecticides during peak flushing periods [15], and biological control, with the release of the parasitoids *Tamarixia dryi* (Waterston, 1922) [16,17], and *T. radiata* [14]. The release of *Tamarixia dryi* has been undertaken in France, Spain, and Portugal, encompassing all territories that have been infested and contingent on the relevant government authorities [4,7,18–22]. Furthermore, novel strategies based on entomopathogens [23] and kaolin applications [24] are currently under investigation.

The presence of *T. erytreae* in the Iberian Peninsula represents a significant challenge to the protection of Europe's main citrus producers. A multitude of factors, including climatic conditions [25], the presence of natural enemies [26], chemical treatments, and host plants, exert a substantial influence on the survival and development of *T. erytreae*. The insect exhibits a high degree of dependency on its hosts, as they play a pivotal role in its establishment, development, and dissemination. Moreover, the adult psyllid has a limited lifespan (85 h) when deprived of its hosts [27-29]. In the absence of the bacteria, the psyllid's direct damage to citrus hosts is considered negligible [30,31]. Nevertheless, nurserymen have reported it to be of significant consequence, as the pit gall symptoms that form in citrus leaves during nymph development impact the plants' eligibility for commercialisation [30,31]. A deeper understanding of the *T. erytreae* host range may facilitate the design of more efficacious control strategies and the advancement of psyllid epidemiological studies, given the pivotal role of the interactions between the vector, the plant, and the pathogen. This review provides an update on the current knowledge regarding the interaction between *T. erytreae* and its hosts, with a particular focus on the factors influencing its establishment, oviposition, and development.

#### 2. *Trioza erytreae* Hosts

*Trioza erytreae* feeds and develops mainly on Rutaceous plants [30,31]. *Trioza erytreae* lays its eggs on the tips of young shoots. The nymphs hatch and settle on the underside of the developing leaves, where they complete their five-instar development before a new flying adult emerges. During its development, the nymphs form "pit galls", which are circular or oval-shaped depressions on the underside of the leaf. The pit galls are perfectly fitted to the nymph, and on the upper side of the leaf, they are visible as convex bulges [30,32].

The Aurantioideae subfamily, which is part of the Rutaceae family, comprises 33 genera. The *Citrus* genus, which is part of this subfamily, comprises the preferred *T. erytreae* hosts [32]. Three species from the Rutaceae, namely the two Aurantioideae, *Clausena anisata* [(Willd.) Hook.fil., De Wild. & Staner] and *Citrus* × *limon* (L.) Burm, along with *Vepris lanceolata* [(Lam.) G.Don] (non-Aurantioideae), have been historically linked with *T. erytreae*, as they were the first psyllid hosts to be documented in the literature [21,30,31,33–35]. The first host to be recorded was *Citrus* × *limon*, which was formally described in 1918 in Eritrea [36]. Almost all species and varieties within the *Citrus* genus serve as hosts, including those used as rootstocks [37]. The term 'suitability' is used to refer to the host's ability to support all stages of psyllid development until the emergence of a new generation. The suitability of some citrus species remains inconclusive, as is the case of *C. australasica* (F.Muell) [21], or even contradictory, as observed in *C. trifoliata* (L.) [21,37] and *C. japonica* (Thunb.) [21,25].

Plants from other genera of the subfamily Aurantioideae outside the *Citrus* genus were described as suitable hosts. These included *Murraya paniculata* [(L.) Jacq.] and *Glycosmis pentaphylla* [(Retz.) Corrêa], which are commonly used as ornamentals [38]. There is a lack of consensus regarding the suitability of certain Aurantioideae hosts for the growth of the psyllid. For instance, *C. anisata* has been reported as a suitable host in some studies [21,30,39,40], while in others, it has been identified as unsuitable due to the absence of oviposition [33]. Similarly, *Calodendrum capense* [(L.fil.) Thunb.], which has been described as a suitable host [39], has been deemed unsuitable in other studies [21,30,34]. Suitable Rutaceae hosts identified outside the Aurantioideae subfamily were *V. lanceolata* and *Zanthoxylum capense* [(Thunb.) Harv] [21,30,34].

Possible host species outside the Rutaceae family are *Ficus* spp. (L.) [41], including *Ficus sycomorus* (L.) (Moraceae family) [42], *Pygeum africanum* (Hook.fil.) (Rosaceae family) [42], *Stephania abyssinica* [(Dill. & A.Rich.) Walp.] (Menispermaceae family) [41,42], and *Diospyros mespiliformis* (Hochst. ex A.DC.) (Ebenaceae family) [41]. *Trioza erytreae* has only been documented to feed on these hosts and to be the likely cause of leaf pit gall symptoms. However, there is no evidence to suggest that nymphal development or the emergence of a new generation of psyllids has occurred [41,42]. Therefore, in light of the current knowledge, these species can only be considered as non-reproductive hosts or as feeding hosts (Table 1).

Carrot plants [*Daucus carota* subsp. sativus (Hoffm.) Schübl. & Martens] were also evaluated as possible hosts for the transmission of '*Candidatus* Liberibacter solanacearum' to sour orange plants [*C. aurantium* (L.)]. However, despite oviposition, *T. erytreae* was unable to complete its life cycle [43].

As outlined in the preceding paragraphs, the available data support the classification of *T. erytreae* as oligophagous. The collected data indicate that hosts outside the Rutaceae family are non-viable hosts. Some of these non-viable hosts may have the potential to be used in psyllid control measures. For instance, researchers have suggested using *Nicotiana tabacum*, a non-viable host, near citrus orchards as a control measure for *D. citri* [44].

Table 1 provides a concise overview of the *T. erytreae* host suitability data that have been tested to date. The hosts were classified according to their attractiveness to the psyllid and their suitability as hosts, based on an evaluation of the results described in the literature.

**Table 1.** Summary of *T. erytreae* hosts, including the host name and common name, as well as host suitability classification in the following categories: "Attraction", "Survival", "Oviposition", "Nymphal Development", "Adult Emergence", and "Host Classification". Where "+ + + + + " represents the highest suitability, "+ + + + " high suitability, "+ + + + " good suitability, "+ + " medium suitability, "+" low suitability, "- " almost no suitability, "- - " no suitability. The "Host Category" indicates host support for the *T. erytreae* life cycle; "R" represents the "reproductive hosts", where the full life cycle is supported by the host; "NR" represents the "non-reproductive hosts", where oviposition is observed but the full life cycle cannot be completed; "F" represents the solely "feeding hosts", where oviposition was tested but not supported. The "NR/R" combination represents hosts where oviposition was supported, but the following stages were not analysed (reproductivity was not ascertained); the "F/NR" combination represents hosts where feeding was observed, and oviposition was not analysed (oviposition support was not ascertained). The designation "NT" indicates that the host comparison studies have not been conducted, while "NC" indicates that they are not classifiable.

Host; Common Name	Attraction	Survival	Oviposition	Nymphal Development	Adult Emergence	Host Classification	Host Category	References
Family: Rutaceae; Subfa	mily: Aurantioid	eae; Genus: Citr	rus					
<i>Citrus × limon</i> [(L.) Burm. f.]; <b>Lemon</b>	+ + + + +	+ + + + +	+ + + + +	+ + + + +	+++++	+ + + + +	R	[15,21,31,33,34,37,40, 45–56]
Citrus × latifolia (Yu.Tanaka); Tahiti lime	+ + + + +	NT	+ + + + +	NT	NT	++++*	R	[48,49]
<i>Citrus medica</i> (L.); <b>Citron</b>	+ + + + +	+ + + + +	+ + + + +	+ + + + +	NT	+ + + + +	R	[21]
<i>Citrus × aurantiifolia</i> [(Christm.) Swingle]; <b>Lime</b>	+ + + +	+ + +	+ + + +	+ + +	NT	+ + + +	R	[21,25,48,49,51]
<i>Citrus trifoliata × Citrus × sinensis;</i> <b>Citrange</b>	+	+ + + + +	+ + + + +	NT	NT	+ + + + **	NR/R	[37]
<i>Citrus macrophylla</i> (Wester)	+ + + + +	+	+ + + + +	NT	NT	+ + + + **	NR/R	[37]
Citrus ×sinensis [(L.) Osbeck]; Sweet orange	+ + +	+++	+ + +	+ + +	+ + +	+ + +	R	[21,25,27,28,31,37,40, 41,46,48–50,56–64]
<i>Citrus reticulata</i> (Blanco); <b>Mandarin</b>	+ + +	++	+ + +	+++	NT	+ + +	R	[21,25,37,41,48–51,56]

Table 1. Cont.

Host; Common Name	Attraction	Survival	Oviposition	Nymphal Development	Adult Emergence	Host Classification	Host Category	References
Citrus reticulata × Citrus × sinensis; Tangor	+ + +	+++	+ + +	+++	+	+ + +	R	[21,25,48,49,56,60]
Citrus reticulata × Citrus × paradisi; Tangelo	+++	NT	+ + +	NT	NT	+ + + *	R	[40,48,49,61]
Citrus × paradisi (Macfadyen); Grapefruit	++	+ + +	++	+++	NT	+ +	R	[21,25,48,49,56,60]
<i>Citrus maxima</i> [(Burm.) Merril]; <b>Pomelo</b>	+	+ + +	+	+ + +	NT	+ +	R	[21]
<i>Citrus reshni</i> (Engl) Yu. Tanaka; <b>Cleopatra mandarin</b>	+	+++	+	NT	NT	+ **	NR/R	[37]
<i>Citrus japonica</i> (Thunb.); <b>Kumquat</b>	+ +	+	+		NT	+	NR	[21,25]
<i>Citrus trifoliata</i> × <i>Citrus</i> reticulata; <b>Citrandarin</b>	+	+	+ +	NT	NT	+ **	NR/R	[37]
Citrus trifoliata (L.)	+	+			NT	_	F	[21,25,37]
<i>Citrus australasica</i> (F.Muell.); <b>Caviar lime</b>	+	+			NT	_	F	[21]
<i>Citrus × aurantium</i> (L.); <b>Sour orange</b>	+	+ + ***	+ + ***	+ + ***	+ + ***	+ + ***	R	[25,41,43,50,52]
Citrus × jambhiri (Lush.); <b>Rough lemon</b>	+ + +	NT	NT	NT	NT	NC	R	[41,65,66]

Table 1. Cont.

Host; Common Name	Attraction	Survival	Oviposition	Nymphal Development	Adult Emergence	Host Classification	Host Category	References
Citrus × paradisi x Citrus trifoliata; <b>Citrumelo</b>	NT	NT	NT	NT	+ + + + +	NC	R	[40]
Family: Rutaceae; Subfa	mily: Aurantioid	eae; Genus: Oth	er than <i>Citrus</i>					
<i>Murraya koenigii</i> [(L.) Spreng.]	+++++	NT	+ + + + +	+ + + + +	+ + + +	+ + + + +	R	[39,40]
Clausena anisata [(Willd.) Hook.fil., De Wild. & Staner]	+ + +	++++	++++	+ + + + +	+ +	+ + + +	R	[21,27,28,30,33,34,39, 40,42,57,62,67]
<i>Murraya paniculata</i> [(L.) Jacq.]	+	+ + +	+	+	NT	+	R	[21]
<i>Glycosmis pentaphylla</i> [(Retz.) Corrêa]	NT	NT	NT	NT	NT	NC	F/NR	[30]
<i>Triphasia trifolia</i> [(Burm.fil.) P.Wilson]	NT	NT	NT	NT	NT	NC	F/NR	[30]
Family: Rutaceae; Subfa	mily: Other than	Aurantioideae						
Vepris lanceolata [(Lam.) G.Don]; White ironwood	+ + + + +	+ + + + +	+ + + + +	+ + + + +	+ + +	++++	R	[21,27,30,33,34,67]
<i>Vepris nobilis</i> [(Delile) Mziray]	+ + +	NT	+ + +	+ + + + +	+ + +	+ + +	R	[39]
<i>Zanthoxylum capense</i> [(Thunb.) Harv.]	+	+ + +	+ +	+ +	+	+ +	R	[21,30,33,34,67,68]
Vepris bilocularis [(Wight & Arn.) Engl.]	+	NT	+ + + + +	+	+ + +	+ +	R	[39]
Calodendrum capense [(L.fil.) Thunb.]; Cape chestnut	+ +	+	+	_	_	_	R	[21,33,34,39]
Zanthoxylum asiaticum [(L.) Appelhans, Groppo & J.Wen]	+	+	+		NT	_	NR	[21]

Table 1. Cont.

Host; Common Name	Attraction	Survival	Oviposition	Nymphal Development	Adult Emergence	Host Classification	Host Category	References
<i>Vepris</i> Comm. (ex A.Juss.)	NT	NT	NT	NT	NT	NC	R	[21,69]
Ruta graveolens (L.); English rue	NT	NT	NT	NT	NT	NC	NR	[30]
<i>Agathosma ciliaris</i> [(L.) Druce]	NT	NT	NT	NT	NT	NC	NR	[30]
Choisya ternata (Kunth); Mexican orange	NT	NT	NT	NT	NT	NC	F/NR	[70]
Family: Other than Ruta	ceae							
Morus alba (L.); <b>Mulberry</b>	+	NT	NT	NT	NT	NC	F/NR	[47]
Tropaeolum majus (L.); Garden nasturtium	+	NT	NT	NT	NT	NC	F/NR	[47]
Daucus carota subsp. sativus (Hoffm.) Schübl. & Martens; Carrot	+	+	+		NT	_ /***	NR	[43]
<i>Stephania abyssinica</i> [(Dill. & A.Rich.) Walp.]	NT	NT		NT	NT	NC	F	[39,41,42]
Ficus sycomorus (L.)	NT	NT		NT	NT	NC	F/NR	[39,42]
Ficus thonningii (Blume)	NT	NT		NT	NT	NC	F	[39]
Diospyros mespiliformis (Hochst. ex A.DC.)	NT	NT	NT	NT	NT	NC	F/NR	[41]
<i>Pygeum africanum</i> (Hook.fil.)	NT	NT	NT	NT	NT	NC	F/NR	[42]

NC denotes that the classification is not applicable; \* classification based only on two tested categories; \*\* comparison study limited to rootstocks; \*\*\* the only comparison made regarding the oviposition was for sour orange and a non-Rutaceae host (a more comprehensive analysis involving additional hosts would be necessary to classify this host) [43]; \*\*\*\* In the case of carrot, classification has been applied despite the species not being a viable host. However, it is important to note that this is based on a single study [43].

With regard to the *Citrus* genus, which comprises more than 30 species, only 17 have been evaluated as potential hosts for *T. erytreae*. Ten of the species have been classified as having high to highest suitability for *T. erytreae*. The highest suitability was identified for lemon ( $C. \times limon$ ), citron (C. medica), and lime ( $C. \times aurantiifolia$ ) (Table 1). The two most widely cultivated citrus trees [1], sweet orange ( $C. \times$ sinensis) and mandarin (C. reticulata), were classified as having good host suitability (Table 1). Additionally, *Clausena anisata* and *M. koenigii* (L.) Spreng., two additional species within the Aurantioideae subfamily, were classified as having high and highest suitability, respectively (Table 1).

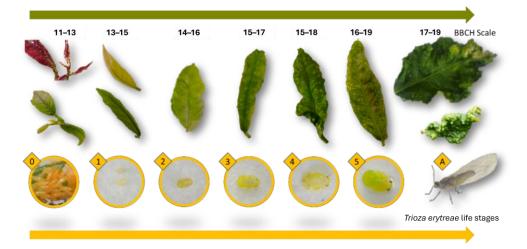
It appears that species belonging to the Rutaceae family that are not part of the Aurantioideae subfamily are less suitable for *T. erytreae*. Only two members of the *Vepris* genus exhibited a suitability classification above the medium level (Table 1).

In view of the paucity of studies on hosts outside the Rutaceae family, it is not yet possible to conclude that they are unsuitable. However, current evidence suggests that the hosts examined so far are unsuitable (Table 1).

While the majority of citrus hosts exhibited comparable levels of attractiveness and suitability for oviposition (Table 1), two hosts, namely citrange (*C. trifoliata*  $\times$  *C.*  $\times$  *sinensis*) [37] and *Vepris bilocularis* [(Wight & Arn.) Engl.] [39], exhibited a low level of attraction and a high oviposition rate. This suggests that these hosts possess a quality that allows for optimal oviposition without attracting *T. erytreae* (Table 1).

## 3. Host Characteristics and Their Influence on *Trioza erytreae* Development

The suitability of a host for *T. erytreae* depends on intrinsic and extrinsic factors. The following aspects related to young flushes are particularly important in determining host suitability: the intensity of flushing, the timing of flushing, leaf length, shoot length, and tissue softness/succulence. Additionally, the nutritional status, age, and phytosanitary condition of the host plant are of considerable importance. The significance of these host traits resides in the requirement of young leaves and shoots for successful oviposition and nymph development [28,57,58,64,69,71] (Figure 1).



**Figure 1.** The various stages of leaf development and the symptoms of infestation by *Trioza erytreae*, along with the developmental stages of the psyllid. The upper half of the figure depicts the leaf appearance and phenological stages of *Citrus* × *limon* according to the Biologische Bundesanstalt, Bundessortenamt und CHemische Industrie (BBCH) scale [72] when infested with the *T. erytreae* stages. The lower portion of the figure depicts the developmental stages of *Trioza erytreae*: stage 0—eggs; stage 1—first instar nymph; stage 2—second instar nymph; stage 3—third instar nymph; stage 4—fourth instar nymph; stage 5—fifth instar nymph; and stage A—adult.

The phytosanitary status of the host plant exerts an influence on the flushing rhythm and the nutritional status of the shoots and leaves, which, in turn, affects the growth and development of psyllids. For example, a decrease in leaf nitrogen levels substantially hampered psyllid development [59]. Additionally, in a  $C. \times$  *sinensis* orchard, the presence of chlorotic young shoots caused a high mortality rate of *T. erytreae*. Furthermore, the surviving nymphs were observed to exhibit reduced size and flattened morphology, along with an extended period of developmental stages [59], contrary to a more rapid spread of *T. erytreae* observed in young, healthy, and vigorous trees [61].

*Trioza erytreae* shows a tendency to transit between suitable hosts in the vicinity of citrus orchards, contingent upon the availability of fresh flush growth. The prevalence of psyllids is higher when citrus orchards undergo alternate flushes with out-of-season flushes in hosts situated outside the orchards [58,62,68]. Therefore, the development of *T. erytreae* is facilitated when a host plant produces young flushes throughout the year [69]. *Citrus* × *limon* is a highly attractive host for psyllids due to the continuous formation of young flushes throughout the year, which provides consistent opportunities for settlement and growth [58,73].

The nymphs of *T. erytreae* can move over a distance of 300 mm in search of optimal feeding spots, which are characterised by the presence of young flushes and soft tissues [57]. The greater the hardness of the tissue, the longer the nymphs will spend searching, thereby increasing the probability that the nymphs will become dehydrated, preyed upon, or parasitised [57]. In comparison to nymphs developing on either side of leaves (softer tissues), fewer nymphs complete their development on branches (harder tissues), which are characteristic of lemon and satsuma mandarin trees [73], tend to attract a higher number of psyllids [60]. As the leaf matures and grows, a reduction in the hatching rate of the eggs and the survival of the nymphs is observed. Therefore, mature, longer, and larger leaves of the leaves, which impairs the eggs' ability to absorb water, a vital requirement for their survival [59,74].

*Trioza erytreae* is able to extend its longevity and the pre-oviposition period in the absence of young flushes. However, this phenomenon has only been observed to occur for a limited duration of time [58]. In citrus orchards in South Africa, a high flushing intensity rendered the plant highly attractive to *T. erytreae*, while a low number of young flushes resulted in a high mortality rate for the psyllid. This indicates that the number of flushes is an important factor in the psyllid's attraction to the host plant [61,64].

The timing of flushing is of pivotal relevance, as when it coincides with optimal climatic conditions for *T. erytreae* development, significant population peaks are observed [58]. The efficacy of parasitoids in targeting *T. erytreae* is enhanced when psyllid population levels are high [75].

Previous studies have demonstrated that plants infected with HLB flush at different periods in comparison to their healthy counterparts [76]. Having both healthy and HLB-infected plants exhibiting asynchronous flush periods provides more favourable conditions for psyllid proliferation [58]. This aspect should be considered in the management of HLB-affected orchards.

To ensure its own survival and reduce conspecific competition for resources, *T. erytreae* avoids flushes with high levels of infestation. This behaviour contributes to insect dispersal, leading to the search for new, uncolonized shoots. In their study, Van den Berg et al. [77] observed a positive correlation between the number of eggs, nymphs, and adults on the host and the dispersion rate.

Pruning is a cultural practice that regulates the growth of new shoots [73]. Heading cuts stimulate the development of new shoots [78] and make citrus trees more attractive to psyllids. Topping is an operation that consists of multiple heading cuts applied to the top of the trees [73], thereby inducing the development of numerous new shoots and attracting psyllids [79]. This operation has already been tested to control D. citri in conjunction with the application of insecticides to the pruned trees [79]. Furthermore, deficit irrigation has been shown to extend the period during which the citrus plant exhibits no flushes. This was evidenced in lemon orchards subjected to deficit irrigation over a 12-week period during the winter, although the same procedure did not affect sweet orange trees [71]. It can be reasonably deduced that the cultivation of sweet oranges and lemons in the same orchard or in adjacent orchards is not recommended, given that lemon trees exhibit continuous flushing [73]. During the flushing period of the sweet orange tree, an influx of insects migrating from the lemon trees to the orange trees has been observed, leading to an increase in the psyllid population [58]. A comprehensive understanding of citrus flushing cycles and effective management techniques is essential for the implementation of cultural practices that mitigate *T. erytreae* populations.

#### 4. The Influence of Climatic Conditions on *Trioza erytreae* and Its Hosts

The climatic variables exert an influence on the duration of insect development [30,32,69], as well as on the intensity and timing of host flushing [80]. The two main studies described in this section were conducted in climatically controlled conditions, and both used *C*. × *limon* as the *T. erytreae* host [5,55]. Other studies do not specify the citrus host [30,32,54] or are based on field studies on sweet orange (*C*. × *sinensis*) orchards [63,64]. It has been established that the duration of the developmental process, from the egg stage to the adult stage, is significantly influenced by temperature [5,55]. The optimal temperature range for the growth of the *T. erytreae* population is between 18 °C and 24 °C [5,55]. This aligns with the spring average daily temperature range of 12 °C to 20 °C in subtropical regions, where citrus trees produce a considerable number of short shoots [80].

Temperatures above 27 °C or below 10 °C severely delay or prevent the completion of the *T. erytreae* life cycle, and if the temperature is constant at 10 °C, 27 °C, or 30 °C, the life cycle is not completed [5]. It is well documented that citrus hosts enter a state of dormancy when the daily average temperatures fall below 12 °C [80]. Therefore, temperatures below 10 °C will restrict the development of both the host and the psyllid. While temperatures above 30 °C appear to exert a deleterious effect on the psyllid, the same does not occur with regard to host flushing, given that citrus hosts produce long new shoots at daily average temperature ranges between 25 °C and 35 °C [80]. The specific conditions required for each developmental stage have been the subject of considerable research. The pre-oviposition period, at 25 °C, lasts between 3.4 and 10.5 days [5]. The viability of eggs is compromised when temperatures are below 8 °C and above 33 °C [5]. The successful development of eggs and nymphs is contingent upon a temperature range of 15 °C to 24 °C [5,55]. Aidoo et al. [55] observed that the mortality rate of the first nymphal instar was highest at 15 °C and lowest at 18 °C, whereas the third instar exhibited the highest survival rates at 20 °C.

The duration of the *T. erytreae* life cycle is also subject to the influence of humidity. Recent studies conducted under controlled conditions showed that at a relative humidity of 65% and at a temperature of 15 °C, the development period is 56.23 days, whereas at 24 °C, it is reduced to 19.95 days. Similarly, at a temperature of 15 °C and a relative humidity of 70%, the developmental period is 46.7 days, whereas at 25 °C, it is reduced to 23.9 days [5,55]. With respect to nymphal development, no development was observed at a constant temperature of 25 °C when both 40% RH and 90% RH were maintained. In these conditions, the psyllid only reached the third instar stage, and the time taken for

pre-oviposition and egg hatching was extended. However, at 70% RH, the entire life cycle of the psyllid was completed in 23.9 days [5].

The influence of climatic conditions on insect development times also has an indirect impact on the overall population size of *T. erytreae* [49,63,70]. High mortality rates have been attributed to hot and dry summer days [30]. A 100% mortality rate of eggs and first-instar nymphs was observed when temperature and humidity parameters, reported as the saturation deficit index (SD), were 45 mbars or higher. At 35 mbars, the mortality rate was 70%, while at 15 mbars, it decreased to 10% [21]. As a result, Catling [64] introduced the term "lethal days" to describe periods when values exceeded 34.6 mbars, which had a significant impact on egg viability and the first instar stage of development [55,64].

Studies carried out before 1970 utilising citrus branches (the species of citrus is not specified) have demonstrated that the requisite duration for egg hatching is 7–9 days, with a range of 5–17 days during summer and winter conditions, respectively. The nymphal stage lasted, on average, 20-27 days, with summer conditions requiring 18 days and winter conditions requiring 34 days [30,32,54]. Additionally, the lifespan of the adult insect during periods of warm weather ranges from 26 to 36 days [32]. More recent studies conducted under controlled conditions showed a similar trend to the aforementioned branch studies, with slight differences. The eggs hatched, on average, between 7.2 and 13.5 days after oviposition, while the development of nymphs lasted from 16.4 to 33.4 days [5]. The specified timeframes are specific to constant temperatures of 15 °C and 25 °C, respectively. Pérez-Otero et al. [5] additionally observed that female adults outlive male adults across all tested temperatures. The mean survival of female specimens was 44.2 days at 15 °C, while the mean survival of male specimens was 17.2 days at 25 °C. In citrus plants cultivated in temperate climates, the duration from bud break to complete leaf development is 60 days when daily average temperatures exceed 13 °C [81]. This timeframe enables T. erytreae to generate at least one generation. Under optimal climatic conditions, two generations may occur per flushing season [58].

It is necessary to evaluate the climatic conditions in relation to the region's orography, as well as the presence or absence of suitable hosts, to identify the geographic regions where *T. erytreae* can thrive. This systematic approach enables the delineation of regions where *T. erytreae* may be able to establish and proliferate, thereby facilitating the prompt implementation of protective measures [16,82,83].

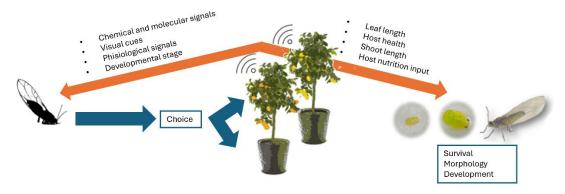
## 5. Methods to Study *T. erytreae* Host Attraction and Suitability and Their Applications

Several methodologies have been employed in order to facilitate a comprehensive understanding of insect–host interaction and host suitability. These include population surveys, choice tests, no-choice tests, studies of insect development and morphometrics, and chemical and molecular interaction studies. Some studies focus on the factors that guide *T. erytreae* to the host, while others focus on the factors that affect the insect's survival and growth subsequent to the selection of a host (Figure 2).

In population surveys, hosts are sampled within a defined geographical area and time range to record the presence and/or symptoms of *T. erytreae*. This approach enables the determination of the psyllid's natural preference. Such surveys may be designed at a national level or at the level of individual orchards.

Extensive population surveys constitute a valuable initial step in identifying the hosts of the psyllids and discerning their preferences [4,41,84]. To illustrate, a national-level survey conducted in Uganda documented the proportion of each host species in the total number of identified infested plants. The findings demonstrated that mandarins (*C. reticulata*) were the preferred host (66.7%), followed by sour orange (*C. aurantium*) and

rough lemon *C.* × *jambhiri* (Lush.) (both with 13.3%), in addition to the least-attractive sweet orange variety "Washington Navel" (6.7%) (*C. sinensis*) [41]. In the same study, three non-Rutaceae plants were identified as bearing galls and *T. erytreae* adults, namely *Stephania abyssinica* (Dill. & A. Rich) Walp. var. *tomentella* (Oliv.) Deils (Menispermaceae family), *Diospyros mespiliformis* (Ebenaceae family), and *Ficus* spp. (Moraceae family). However, the absence of the observation of nymphs [41] indicates the necessity for further investigation to ascertain the suitability of these hosts for *T. erytreae*.



**Figure 2.** Host effect on *Trioza erytreae*. Orange arrows represent host cues/signals; blue arrows represent insect decision pathways.

The study of psyllid populations at the orchard level offers considerable advantages in terms of the information they provide regarding host attractiveness and their suitability to *T. erytreae.* This is primarily due to the reduced edaphoclimatic and orographic variability observed in such studies. The results of studies conducted in multi-species orchards have provided valuable insights into host attractiveness for *T. erytreae*. The findings of Samways and Manicom [60] demonstrated that the 'Valencia' cultivar (*C.* × *sinensis*) exhibited a higher mean number of branches with eggs and *T. erytreae* adults in comparison to the 'Navel' orange (*C.* × *sinensis*), the 'Ortanique' tangor (*C. reticulata* × *C.* × *sinensis*), and the grapefruit (*C.* × *paradisi* (Macfadyen)). Conversely, a comparable study conducted by Van den Berg et al. [25] found that the 'Navel' orange was more attractive than the 'Valencia' orange, which demonstrates how variables inherent to the experimental field and methodology may influence the results.

A considerable number of mandarin cultivars (*C. reticulata*), along with their hybrids, tangor (*C. reticulata*  $\times$  *C.*  $\times$  *sinensis*) and tangelo (*C. reticulata*  $\times$  *C.*  $\times$  *paradisi*), were evaluated for their attractiveness for *T. erytreae* in different multi-species orchards [48,51,77]. The findings of these studies indicate that mandarins have a high degree of intra-species variability in terms of attractiveness for *T. erytreae*. The "Satsuma" subgroup of cultivars, including 'Owari', 'Saigon', and 'Wase', was found to be highly attractive to the psyllid. In contrast, the cultivars 'Dancy', 'Fortune' (a 'Dancy' hybrid), and tangelo hybrid cultivars, such as 'Page' and 'Osceola', show a low attractiveness for *T. erytreae* (Table 2) [48,51,77].

Host: Common Name; <i>Species;</i> Grou 'Cultivar'/ Variety	ıp; Subgroup;	Attractiveness	Oviposition	Survival	Nymph Development	Adult Emergence
Family: Rutaceae; Subfamily: Aurantioideae; G	Genus: Citrus					
Citrus reticulata (Blanco); Mandarin						
Mandarin hybrid (Clementine $ imes$ Ponkan); 'Frem	iont'	1H [48], 1M [51]	1M [48], 1L [51]	NA	NA	NA
Mandarin hybrid (Satsuma $ imes$ King) 'Kara'		1H [48]	1H [48]	NA	NA	NA
	'Saigon'	1H [48]	<b>1H</b> [48]	NA	NA	NA
	'Wase'	1H [48]	<b>1H</b> [48]	NA	Development    NA   I	NA
Satsuma	'Owari'	1H [48]	<b>1H</b> [48]	NA	NA	NA
	'Saint Jean'	<b>1M</b> [48]	1M [48]	NA	NA	NA
	'Kowano'	<b>1M</b> [48]	<b>1L</b> [48]	NA	NA	NA
Ponkan		<b>1M</b> [48]	<b>1H</b> [48]	NA	NA	NA
Classerting	Clementine	<b>1M</b> [48]	1M [48]	NA	NA	NA
Clementines	Clemenules	1 <b>M</b> [56]	1M [56]	1M [56]	NA NA NA NA <b>1M</b> [21] NA	
Willowleaf mandarin		1 <b>M</b> [21]	1M [21]	1M [21]	1 <b>M</b> [21]	NA
Madagascar		1H [48]	1M [48]	NA	NA	NA
King of Siam		1 <b>M</b> [48]	<b>1L</b> [48]	NA	NA	NA
Green Rind		1L [25]	NA	NA	NA	NA
	'Fairchild'	<b>1M</b> [48]	1M [48]	NA	NA	NA
Mandarin hybrid (Clementine x Tangelo)	'Osceola'	1 <b>M</b> [48]	<b>1L</b> [48]	NA	NA	NA
	'Page'	1L [48]	<b>1L</b> [48]	NA	NA	NA
Mandarin 'Dancy'		1L [48]	<b>1L</b> [48]	NA	NA	NA
Mandarin hybrid (Clementine $ imes$ Dancy) 'Fortun	e'	<b>1L</b> [48]	<b>1L</b> [48]	NA	NA	NA
Mandarin 'Emperor'		1L [25]	NA	NA	NA	NA

Table 2. Host attractiveness and effect on different stages of Trioza erytreae infestation.

Table 2. Cont.

Host: Common Name; <i>Species</i> ; Group 'Cultivar'/ Variety	; Subgroup;	Attractiveness	Oviposition	Survival	Nymph Development	Adult Emergence
Total		7H [41,48], 11M [21,25,48,51,56], 6L [25,48]	4H [48], 9M [21,37,48,56], 7L [48,51]	<b>3M</b> [21,56]	<b>2M</b> [21]	NA
<i>Citrus</i> × <i>sinensis</i> [(L.) Osbeck]; <b>Sweet orange</b>						
	'Valencia'	1H [60], 1M [25], 4L [41,48,56]	1H [60], 2L [48,56]	1 <b>M</b> [56]	NA	<b>1M</b> [40]
	'Hamlin'	1M [48]	1M [48]	NA	NA	NA
Common	'Pineapple'	1M [48]	1L [48]	NA	NA	NA
oranges	'Mid Season'	1M [25]	NA	NA	NA	NA
	'Mouton'	1L [25]	NA	NA	NA	NA
	'Oom Louis'	1L [25]	NA	NA	NA	NA
	'Pera'	1L [25]	NA	NA	NA	NA
Navel	'Navel'	1H [25], 1M [60]	1 <b>M</b> [60]	NA	NA	NA
oranges	'Navelina'	1H [56]	1M [56]	1M [56]	NA	NA
Total		3H [25,56,60], 7M [21,25,48,60], 5L [25,48,56]	1H [60], 4M [21,48,56,60], 3L [48,56]	<b>3M</b> [21,56]	1 <b>M</b> [21]	<b>1M</b> [40]
<i>Citrus</i> $\times$ <i>limon</i> [(L.) Burm. f.]; <b>Lemon</b>						
	'Lisbon'	1H [48]	<b>1H</b> [48]	NA	NA	NA
	'Eureka'	1H [48]	1H [48]	NA	NA	NA
	'Villafranca'	<b>1H</b> [51]	<b>1M</b> [51]	NA	NA	NA
	'Fino 49'	1 <b>M</b> [56]	1L [56]	1M [56]		
Total		<b>8H</b> [21,33,47,48,50–52], <b>1M</b> [56]	4H [21,33,48], 1M [51], 1L [56]	2H [21,34], 1M [56]	1H [21], 1M [34]	<b>2H</b> [34,40]
<i>Citrus × aurantiifolia</i> [(Christm.) Swingle]; <b>Lime</b>						
	'Mexican'	<b>1H</b> [51], <b>1L</b> [48]	1H [51], 1L [48]	NA	NA	NA
	'Likeland'	1H [48]	1H [48]	NA	NA	NA

Table	<b>2.</b> C	Cont.
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Host: Common Name; <i>Species;</i> Grou 'Cultivar'/ Variety	ip; Subgroup;	Attractiveness	Oviposition	Survival	Nymph Development	Adult Emergence
Total		<b>2H</b> [48,51], <b>2M</b> [21,25], <b>1L</b> [48]	2H [48,51], 1M [21], 1L [48]	1 <b>M</b> [21]	1M [21]	NA
Citrus × paradisi (Macfadyen); Grapefruit						
	'Red Blush'	<b>1M</b> [48]	1 <b>M</b> [48]	NA	NA	NA
	'Shambar'	1M [48]	1M [48]	NA	NA	NA
	'Marsh'	1L [48]	1L [48]	NA	NA	NA
	'Star Ruby'	1 <b>M</b> [56]	NA	NA	NA	NA
Total		4M [21,25,48,56], 2L [48,60]	3M [21,48], 2L [48,60]	<b>1M</b> [21]	1M [21]	NA
Citrus reticulata $ imes$ Citrus $ imes$ sinensis; <b>Tangor</b>						
	'Ortanique'	2H [48,56], 1M [60]	1H [56], 2M [48,60]	1M [56]	NA	NA
	'Murcott'	1L [25]	NA	NA	NA	NA
Total		2H [48,56], 2M [21,60], 1L [25]	1H [56], 2M [48,60]	<b>2M</b> [21,56]	1M [21]	NA
Citrus × aurantium (L.); Sour orange		1H [43], 1M [41], 3L [25,50,52]	1H [43]	1H [43]	1H [43]	NA
Citrus maxima [(Burm.) Merril]; <b>Pomelo</b>		1L [21]	1L [21]	1M [21]	1L [21]	NA
Citrus reticulata $ imes$ Citrus $ imes$ paradisi; <b>Tangelo</b>						
	Minneola	1H [48]	<b>1H</b> [48]	NA	NA	1L [40]
	Orlando	1L [48]	1L [48]	NA	NA	NA
Total		1H [48], 1L [48]	1H [48], 1L [48]	NA	NA	<b>1L</b> [40]

Table 2. Cont.

Host: Common Name; <i>Species</i> ; Group; Subgroup; 'Cultivar'/ Variety	Attractiveness	Oviposition	Survival	Nymph Development	Adult Emergence
Citrus trifoliata × Citrus reticulata; <b>Citrandarin</b>					
Forner-Alcaide 5	1L [37]	1 <b>M</b> [37]	1L [37]		NA
Forner-Alcaide 517	1L [37]	1L [37]	1L [37]	NA	NA
Total	2L [37]	1M [37], 1L [37]	<b>2L</b> [37]	NA	NA
Citrus trifoliata (L.)					
Flying Dragon	1L [37]	NA	1L [37]	NA	NA
Total	<b>3L</b> [21,25,37]	<b>10</b> [21]	<b>2L</b> [21,37]	10 [21]	NA
Citrus japonica (Thunb.);	1M [25],	1L [21]	1L [21]	10 [21]	NA
Kumquat	1L [21]	1L [41]	<b>IL</b> [ <b>2</b> 1]	10 [21]	INA
Citrus ×latifolia (Yu. Tanaka);	<b>1H</b> [48]	<b>1H</b> [48]	NA	NA	NA
Tahiti lime			411 [01]	111 [01]	NT A
Citrus medica (L.), Citron Citrus macrophylla (Wester)	1H [21] 1H [37]	1H [21] 1H [37]	1H [21] 1L [37]		NA NA
Citrus australasica (F.Muell.); Caviar lime	1L [21]	10 [21]	1L [37]		NA
Citrus reshni (Engl) Yu.Tanaka; Cleopatra mandarin	1L [21] 1L [37]	10 [21] 1M [48]	1L [21] 1L [37]		NA NA
Citrus trifoliata × Citrus × sinensis; Citrange	1L [37]	1H [48]	1H [37]		NA
Citrus (L.) **	1H [25]	NA	NA		NA NA
<i>Citrus × jambhiri</i> (Lush.); <b>Rough lemon</b>	<b>1M</b> [41]	NA	NA		NA
Citrus × paradisi × Citrus trifoliata; <b>Citrumelo</b>	NA	NA	NA		1H [40]
Family: Rutaceae; Subfamily: Aurantioideae; Genus: Other than <i>Citrus</i>	INA	INA	INA	INA	I <b>II</b> [40]
ramity: Rutaceae; Subramity: Aurantioideae; Genus: Other than Citrus	111 [01]				
<i>Clausena anisata</i> [(Willd.) Hook.fil., De Wild. & Staner]	1H [21], 1M [39],	<b>2H</b> [ <b>21</b> , <b>39</b> ],	1H [21],	<b>211</b> [21 24 20]	<b>2M</b> [34,39],
Ciuusenii unisuu [(Willd.) Hook.iii., De Wild. & Statter]	11vi [39], 1L [33]	1L [33]	1M [34]	Development     NA     NA     NA     NA     NA     10 [21]     10 [21]	1L [40]
					1H [39],
Murraya koenigii [(L.) Spreng.]	1H [39]	1H [39]	NA	1H [39]	1M [39], 1M [40]
Murraya paniculata [(L.) Jacq.]	1L [21]	1L [21]	1M [21]	1L [21]	NA
Family: Rutaceae; Subfamily: Other than Aurantioideae			<b>t</b> 1		
Vepris lanceolata [(Lam.) G.Don]; White ironwood	<b>2H</b> [21,33]	<b>2H</b> [21,33]	<b>2H</b> [21,34]	<b>2H</b> [21,34]	1M [34]
Zanthoxylum capense [(Thunb.) Harv.)]	<b>2L</b> [21,33]	1M [33], 1L [21]	<b>2M</b> [21,34]		<b>1L</b> [34]
Vepris nobilis [(Delile) Mziray]	1M [39]	1M [39]	NA		1M [39]
Vepris bilocularis [(Wight & Arn.) Engl.]	1L [39]	1H [39]	NA		1M [39]
Zanthoxylum asiaticum [(L.) Appelhans, Groppo & J.Wen]	1L [21]	1L [21]	1L [21]		NA

#### Table 2. Cont.

Host: Common Name; <i>Species</i> ; Group; Subgroup; 'Cultivar'/ Variety	Attractiveness	Oviposition	Survival	Nymph Development	Adult Emergence
Family: Other than Rutaceae					
Daucus carota subsp. sativus (Hoffm.) Schübl. & Martens; Carrot	1L [43]	1L [43]	1L [43]	10 [43]	NA
Tropaeolum majus (L.); Garden nasturtium	1L [47]	NA	NA	NA	NA
Morus alba (L.); Mulberry	1L [47]	NA	NA	NA	NA
Ficus thonningii (Blume)	NA	10 [39]	NA	NA	NA
Ficus sycomorus (L.)	NA	1O [39]	NA	NA	NA
Stephania abyssinica [(Dill. & A.Rich.) Walp.]	NA	10 [39]	NA	NA	NA

"Total" represents the sum of all comparisons described for each host; it should be noted that the number of comparisons may exceed those specified in the aforementioned subgroups, as some studies do not specify the assayed cultivar or variety; NA means "Not Applied"; OLMH nomenclature: "O" represents a value of zero, "L" represents low comparative values, "M" represents intermediate comparative values, and "H" represents high comparative values. The number preceding the OLMH nomenclature represents the number of hosts classified. This number is sometimes higher than the number of references, as some studies compared more than one variety of the same species. \*\* "*Citrus*" represents studies where the host was mentioned as "citrus miscellaneous crosses".

The attraction of *T. erytreae* to *Citrus* × *limon* has been well documented [85]. In an orchard of sour oranges (*C. aurantium*), a single *C.* × *limon* tree was found to have twice the number of psyllids in yellow sticky traps compared to the other traps placed near sour oranges [50]. In contrast to *C.* × *sinensis* and *C. reticulata* cultivars, different *C.* × *limon* cultivars have been observed to consistently exhibit high levels of attraction and oviposition rates [48,51]. The 'Fino 49' lemon was the sole exception, as despite the high oviposition rate when grafted onto the Carrizo citrange (*C. trifoliata* × *C.* × *sinensis*) rootstock, there was a low oviposition rate when grafted in other tested rootstocks [56] (Table 2). It can be inferred that for certain citrus species, the attraction and oviposition by the psyllid are less dependent on the cultivar, probably due to a lower genetic variability of these species [86].

The host's characteristics and the signals they release to either attract or repel the psyllid can also be explored through choice experiments. The results of choice test studies performed in a controlled environment have provided insights into the characteristics of psyllids that influence their preference and attraction. The study revealed that the sex of the psyllid may exert an influence on its attraction towards a host. In a dual-choice settlement assay, the probability of selecting a sour orange (*C. aurantium*) was 39% for males and 19% for females [52].

A choice experiment study showed that leaf softness affects the oviposition rates of *T. erytreae*; however, it had no impact on the settling behaviour of the psyllid [33,53]. Furthermore, choice experiment studies revealed that no oviposition occurred on leaves with a hardness rating exceeding 90 g/mm [53]. Hardness values represent the weight required for a 0.254 mm diameter flat-tipped pin to puncture 1 mm of leaf tissue [53,87].

A choice test and a no-choice test were used to compare the attraction and oviposition of *T. erytreae* on ungrafted rootstocks. The results showed *C. macrophylla* as the most appealing host, while 'Carrizo' citrange (*C. trifoliata*  $\times$  *C.*  $\times$  *sinensis*) exhibited the highest oviposition rate [37]. The lowest incidence of oviposition was observed in *C. trifoliata*, which was identified as the least attractive host [37]. The available evidence indicates that citrus rootstocks may affect the volatile profiles of the host scion, which may, in turn, affect the attraction of psyllid pests to them [88]. It can also affect the suitability of the scion for *T. erytreae*, affecting both attractiveness and oviposition rate. Some cultivars appear to be more affected, as evidenced by the case of 'Fino 49' *C.*  $\times$  *limon* [56].

The use of no-choice experiments, in which the insect is presented with a single host option, enables the study of the host's suitability, as well as the survival and behaviour patterns of the insects after settlement. This approach provides valuable data for epidemiological studies, including the number of adults that form in a new generation [34] and the number of generations that form in a year [58].

In a no-choice experiment, Aidoo et al. [39] observed oviposition differences among eight non-citrus hosts from the Rutaceae family. *Clausena anisata* had the highest percentage of flushes with eggs (52%), while *C. capense* had the lowest values (24%). *Ficus thonningii*, *F. sycomorus*, and *S. abyssinica* showed no oviposition. The carrot (*D. carota* subsp. *sativus*) was found to be unsuitable as no nymphs were able to reach the adult stage [43].

Studies on the morphometrics of *T. erytreae* developing in different hosts have provided insights into the host species' impact on the development of the psyllid. A comparative analysis was conducted on five non-citrus hosts from the Rutaceae family. The results showed that *C. capense* yielded the fewest and smallest adults of *T. erytreae*, *Clausena anisata* the second highest number and the largest adults, and *Murraya koenigii* the highest number of emerged adults with sizes similar to those formed in *Clausena anisata* [39]. Additionally, the morphology and size of *T. erytreae* wings [40] also differed across distinct host species, which could potentially influence the psyllid's ability for flight and dispersal.

The attraction of psyllids to hosts is influenced by plant volatiles. Valterová et al. [89] conducted a study on the psyllid Dyspersa apicalis Foerster, which belongs to the Triozidae family, across a diverse range of host species. The study examined the psyllid's feeding and oviposition preferences in relation to the volatiles derived from the hosts and concluded that the least attractive host species exhibited a higher limonene content. In citrus, the concentration of volatiles in young leaves was higher than in mature leaves despite the absence of any change in their attractiveness when assessed using a choice test [66]. Nevertheless, these findings suggest that the higher concentration of volatiles in young leaves may increase the likelihood of *T. erytreae* detecting them in field settings. Among the volatiles produced by the hosts, the terpenes appear to play a role in their attractiveness to T. erytreae [66]. The volatile profile of both young and mature leaves of  $C. \times jambhiri$ , specifically (S)-(-)-limonene, sabinene, and  $\beta$ -ocimene, was used as synthetic blends, isolated and in various ratios, in choice tests. These volatiles were more effective at attracting *T*. erytreae when combined with others from the plant's volatile profile rather than when used alone [66]. The leaves of Vepris lanceolata [(Lam.) G. Don] have a lemony scent similar to that of  $C \times limon$  [(L.) Burm. f.], which may be linked to the high attractiveness and high rate of *T. erytreae* oviposition observed in this plant species [21,33] (Table 1). In light of these promising results, plant-based volatiles (acetic acid, (R)-(+)-limonene, sabinene, an ocimene isomer mix comprising cis-ocimene and ß-, myrcene, ethyl butyrate, methyl salicylate, and p-cymene) have been incorporated into yellow-sticky traps to attract T. erytreae. However, in field conditions, this addition proved ineffective [90].

An analysis of the volatiles of non-host plants revealed that *T. erytreae* avoided the volatiles of guava (*Psidium guajava* L.), garlic (*Allium sativum* L.), and lemongrass (*Cymbopogon citratus* (DC.) Stapf) [65]. Studies suggested that the practice of interplanting citrus trees with guava (*P. guajava*) in open fields decreased the populations of *D. citri* in the orchards. However, the effects were not evident under controlled greenhouse conditions [91,92]. It would be interesting to study the impact of intercopping guava, garlic, and/or lemongrass in citrus orchards on *T. erytreae* to ascertain the repelling effect in field conditions.

The majority of studies on the interaction of *T. erytreae* with its hosts have been focused on the analysis of plant volatiles. Nevertheless, a recent study performed by our research group that used a no-choice experimental design and proteomic analysis found that the proteomic response of lemon and sweet orange plants to *T. erytreae* was distinct. The proteomic response of sweet orange plants to the psyllid was more pronounced and extensive [46]. This study suggests that citrus host plants adjust their proteome in response to *T. erytreae* infestation, which may be related to host suitability.

#### 6. Final Remarks and Future Perspectives

The objective of this review was to provide a synthesis of the existent knowledge regarding the hosts of *T. erytreae* and their interaction with the psyllid. Despite the extensive research conducted on *T. erytreae*, further research is required to elucidate the host influence on nymphal development and adult emergence. This encompasses the analysis of the quantity and proportion of hatching eggs and nymphs, nymph development time, adult emergence, and morphometrics of emerged adults. Understanding insect–host interactions at the molecular level is essential for developing effective control strategies for the psyllid. The formulation of efficacious artificial diets for *T. erytreae* and the improvement of diets already tested, such as the one proposed by Russell and Pelz-Stelinsk [93] for *D. citri*, may facilitate the study of the effects of isolated diet compounds on the psyllids. This could potentially result in the development of an effective strategy for controlling psyllid populations.

A major challenge identified in this review was the gap in knowledge on the molecular aspect of this specific insect-host interaction. Omics-based approaches provide a comprehensive understanding of the interactions between insects and plants [94]. The application of omics approaches to the study of *D. citri* has facilitated a more profound understanding of the host's response to the psyllid infestation [95,96]. Furthermore, the identification of characteristic proteins related to psyllid phenotypes [97] and development stages has been made possible [98]. A meta-analysis of omics on the molecular profiles of citrus hosts would also be advantageous in identifying potential molecular correlations with *T. erytreae* preferences. This approach has been employed to study citrus hosts tolerant to HLB [99].

Another major challenge identified in this review was the dispersed nature of the data and the diverse types of reporting on *T. erytreae* interaction with its hosts. Hence, the construction of an accurate database on potential *T. erytreae* hosts is of significant importance, as it facilitates informed decision-making regarding citrus management strategies, including control policies, breeding programs, research lines, and orchard management [14]. In addition, the implementation of a standardised methodology for the reporting of *T. erytreae* populations to a centralised repository would contribute to a more complete and accessible knowledge base of the psyllid populations, behaviour, and hosts, improving the precision of the prediction models, as was already developed for *D. citri* and HLB [16,100].

**Author Contributions:** Writing—original draft preparation, T.M.; writing—review and editing, N.T.M., A.D., J.A.P. and T.M. All authors have read and agreed to the published version of the manuscript.

**Funding:** This study was financially supported by the "European Union Horizon 2020" through the research project grant agreement ID: 817526 (Pre-HLB "Preventing HLB epidemics for ensuring citrus survival in Europe."). Tomás Magalhães gratefully acknowledges the financial support of "Fundação para a Ciência e Tecnologia" (FCT—Portugal), through the PhD scholarship 2020.07798.BD ("Understanding host preference of *Trioza erytreae* (Del Guercio) by a multi-omics approach") (https://doi.org/10.54499/2020.07798.BD). Additional funds were from programmes supported by FCT/MCTES (PIDDAC) for MED UIDB/05183/2020 (doi: 10.54499/UIDB/05183/2020), and UIDP/05183/2020 (doi: 10.54499/UIDP/05183/2020), for CHANGE LA/P/0121/2020 (doi: 10.54499/UIDP/00690/2020 (doi: 10.54499/UIDB/00690/2020) and UIDP/00690/2020 (doi: 10.54499/UIDP/00690/2020), and for SusTEC LA/P/0007/2020 (doi: 10.54499/LA/P/0007/2020).

Data Availability Statement: Not applicable.

**Acknowledgments:** The opinions, findings, conclusions, and recommendations expressed in this material are those of the authors alone.

Conflicts of Interest: The authors claim no conflicts of interest.

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