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Invisible Architecture of Tephritids (Diptera): A Chemically Mediated Exploration of Ecological Structure in Tropical Orchards of Northern Cameroon

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Abstract

Understanding the ecology of tephritid communities is essential for developing sustainable pest management strategies in tropical fruit-based agroecosystems. This study assessed relative abundance and the efficacy of four male-specific semiochemical lures (methyl eugenol (ME), cue-lure (CU), terpinyl acetate (TA), and trimedlure (TR)), across two agroecological zones (AEZs) in Cameroon: the Sudano-Sahelian savannah (AEZ 1) and the High Guinea savannah (AEZ 2). Nine tephritid species were recorded, including two previously unreported in these AEZs (*Ceratitis punctata* and *C. fasciventris*). Despite a shared species pool, community structure differed significantly between AEZs. In AEZ 2, *Bactrocera dorsalis* accounted for over 90% of captures, reflecting its invasive dominance. This was amplified by the high specificity of ME, which almost exclusively attracted *B. dorsalis*. Conversely, AEZ 1 supported a more balanced assemblage dominated by *B. dorsalis*, *Zeugodacus cucurbitae*, and *Ceratitis cosyra*, particularly in dry AEZ rich in cucurbit crops. Thus, CU was effective in capturing cucurbit-associated species (*Z. cucurbitae*, *Dacus* spp.), while TR and TA attracted a broader range of *Ceratitis* species. These findings highlight the value of multi-lure trap systems in accurately revealing tephritid community composition and support the need for agroecologically tailored Integrated Pest Management (IPM). Promoting the use of semiochemical surveillance in smallholder systems will require institutional support to offset lure costs. Such strategies can improve early detection and targeted control of key tephritid pests, ultimately enhancing crop protection in vulnerable agricultural landscapes of various sub-Saharan Africa countries.

Keywords

Male Lure, *Bactrocera dorsalis*, *Ceratitis cosyra*, *Zeugodacus cucurbitae*, Agroecosystems, Pest Surveillance

1. Introduction

Fruit flies (Diptera: Tephritidae) are among the most economically significant phytophagous pests worldwide, infesting a wide range of fruits and vegetables and causing substantial pre- and post-harvest losses [1]-[3]. Their destructive potential is attributed to a combination of biological traits, including broad host range [4], high fecundity, and strong dispersal ability [5]-[7]. Damage occurs when female oviposit into host fruit, and larval feeding rapidly degrades fruit tissue, leading to unmarketable produce [7]-[9].

In sub-Saharan Africa, tephritid outbreaks are driven not only by the abundance of cultivated and wild host plants, weak surveillance infrastructure, and inadequate management strategies [10] [11], but also by biological invasions. Two highly aggressive invasive tephritid species *Bactrocera dorsalis* and *Zeugodacus cucurbitae*, both of Asian origin have rapidly colonized much of the region, and fundamentally may reshaping tephritid communities [12] [13].

In Cameroon, tephritid infestations are widespread and severe. Overripe and attacked fruits often accumulate in orchards, markets, and disposal sites, serving as persistent reservoirs that sustain local tephritid populations [12]. Economically important species belong primarily to four genera: *Bactrocera*, *Ceratitis*, *Dacus*, and *Zeugodacus* [9] [13]. Among these, *Bactrocera dorsalis* and *Ceratitis cosyra* are the major pests of mango [14] and guava [15] [16], whereas *Dacus bivittatus*, *Dacus ciliatus*, *Dacus punctatifrons*, and *Zeugodacus cucurbitae* inflict considerable damage on cucurbit crops [9] [13].

Beyond direct yield losses, tephritid infestations also generate substantial indirect costs, particularly due to quarantine restrictions and trade barriers. The continued reliance on broad-spectrum insecticides is becoming increasingly unsustainable because of the development of resistance, growing environmental and human health concerns, the accumulation of toxic residues on fruits, and the inaccessibility of immature stages of tephritids that remain concealed within host tissues [5] [17]-[20]. As a result, Integrated Pest Management (IPM) strategies incorporating semiochemical attractants such as methyl eugenol (ME), cue-lure (CL), trimedlure (TML), and terpinyl acetate (TA), have gained importance, both for surveillance and, in some cases, for population suppression [3] [21]-[23]. Among these, ME is the most widely validated and operationalized semiochemical within IPM programs, particularly through the Male Annihilation Technique (MAT), owing to its exceptional attractiveness and specificity for *Bactrocera dorsalis* males [24]. Despite their proven effectiveness, the adoption of these tools remains limited in Cameroon, primarily due to a lack of awareness, accessibility, purchasing capacity, and context-specific recommendations tailored to smallholder farmers, most of whom operate under resource-constrained conditions.

Developing effective IPM programs requires a comprehensive understanding of the local ecology of tephritid communities, including species composition, abundance patterns, and species-specific responses to male-targeted lures. This study seeks to address critical knowledge gaps in tephritid ecology in Cameroon by: 1) characterizing the diversity of male lures-responsive tephritid species, 2) assessing their ecological community structure, and 3) evaluating the efficacy and selectivity of major male lures across the studied agroecosystems.

2. Materials and Methods

2.1. Study Area and Sampling Period

Field data were collected during two years, from 2021 to 2022, in five orchards located in two agroecological zones (AEZs) of Cameroon. These orchards, previously described in [2], were not treated with insecticides. Detailed agroclimatic and edaphic profiles of each AEZ are also available in [2].

AEZ 1 (Sudano-Sahelian Savannah) included two orchards situated in Ngong and Mbé, while AEZ 2 (High Guinea Savannah) comprised three orchards located in Malang, Manwi, and Marza. Each selected orchard covered at least five hectares and featured mixed tropical fruit trees, with mango (*Mangifera indica* L.) and guava (*Psidium guajava* L.) as the dominant species. All orchards were accessible and suitable for long-term ecological monitoring.

2.2. Trap and Lure Configurations

A total of four tephritid traps were installed at each sampling point, each baited with one of four male-specific lures: methyl-eugenol (ME), cue-lure (CU), trimedlure (TR), and terpinyl acetate (TA) [21] [25] [26]. Every trap contained the organophosphate insecticide dichlorvos (2,2-dichlorovinyl dimethyl phosphate, DDVP) as the killing agent. Traps were hung about 1.5 m above ground on sturdy fruit-tree branches. To minimize odor interference and edge effects, trap placement followed a standardized layout: the first trap was positioned 30 m inside the orchard boundary, and the remaining traps were set at 50 m intervals [27]. The **Figure 1** illustrates the typical trap configuration.

2.3. Sampling and Trap Maintenance

A total of 16 traps was installed in each orchard (4 replicates × 4 lure types). The lures and DDVP insecticide were replaced every six weeks, resulting in eight complete sampling cycles per year in each orchard [28]. Sterile gloves were used

Methyl eugenol | Cue-lure | Terpinyl acetate | Trimedlure

Figure 1. Tephri-traps baited with male-specific lures to tephritids in five orchards in Cameroon during the 2021-2022 sampling period. From left to right, the traps contain: methyl eugenol (ME), cue-lure (CU), terpinyl acetate (TA), and trimedlure (TR), each paired with a DDVP-based insecticide.

during all handling procedures to prevent cross-contamination between attractants. To reduce ant predation and interference from other organisms, a thick layer of automotive grease was applied to the branches used to suspend the traps [29]. Captured tephritid specimens were collected weekly and individually preserved in labeled entomological tubes containing 70% ethanol. All samples were then transported to the Zoology Laboratory of the University of Ngaoundéré for taxonomic identification.

2.4. Identification Procedure

Tephritid specimens were sorted under a stereomicroscope and identified to species level using standard morphological keys [30]. Additional identifications were carried out to confirm initial determinations at the French Agency for Food, Environmental and Occupational Health & Safety (ANSES) in Montpellier, France, and at the Royal Museum for Central Africa (RMCA) in Tervuren, Belgium.

2.5. Assessment of Alpha Diversity

Alpha diversity was assessed using a tripartite approach that included: rarefaction analysis (species accumulation curves), rank-abundance (Whittaker) curves, and complementary diversity indices [31].

Rarefaction curves were used to evaluate sampling completeness, with a 95% asymptotic plateau considered indicative of adequate sampling effort [32].

Species abundance distributions were visualized using rank-abundance curves, where log-transformed abundance is plotted against species rank, in order to analyze patterns of dominance and evenness [33].

Quantitative assessment of diversity was based on three complementary indices:

- Shannon-Wiener diversity index (H'), $H' = -\sum\left(p_i \ln p_i\right)$;
- Simpson's diversity index $(1-D)$, $D = \dfrac{1}{\sum p_i^2}$;
- Pielou's evenness index (J'), $J' = \dfrac{H'}{\ln S}$;

where p_i is the proportion of individuals belonging to tephritid species i, and S is the total species richness [31] [34] [35].

The Shannon-Wiener index ranges from 0 to ln(S), indicating maximum diversity. Higher values of H' and $1 - D$ reflect greater diversity and more balanced communities. Pielou's evenness index, ranging from 0 to 1, indicates more equitable species distribution when values are closer to 1.

2.6. Assessment of Beta Diversity

Beta diversity between AEZs and orchards was evaluated using the Jaccard similarity index:

$$J(\mathrm{A},\mathrm{B}) = \frac{a}{a+b+c};$$

where a is the number of species shared by orchards A and B, b is the number of species unique to orchard A, and c is the number of species unique to orchard B [36]. The index ranges from 0 (no species shared) to 1 (identical species composition). Pairwise similarity values were compiled into a matrix and visualized as a heatmap using a yellow-orange-red (YlOrRd) gradient scale from 0 to 100% to to illustrate the degree of species overlap.

2.7. Evaluation of Lure Efficacy and Selectivity

To evaluate lure efficacy, the mean number of tephritids captured per trap and per sampling day was calculated for each male lure across all orchards. Statistical comparisons of abundance were performed using analysis of variance (ANOVA), followed by Tukey's post hoc test ($p < 0.05$), using XLSTAT software.

Selectivity was assessed by calculating the relative abundance of each species per male lure. The proportion of total captures attributed to each tephritid species was used to determine lure specificity and performance for targeted surveillance.

3. Results

3.1. Alpha Diversity

3.1.1. Rarefaction Analysis Curve

Species accumulation curves plateaued across all five orchards, indicating that the sampling effort, measured by cumulative sampling days, was sufficient to capture the local pool of male tephritid species and to support robust ecological analyses (**Figure 2**). The asymptotic trend consistently observed in the curves of each orchard confirms that further sampling would likely yield only marginal gains in species detection.

3.1.2. Whittaker Analysis Patterns

The Whittaker diagram highlighted patterns of dominance within the tephritid communities studied across the AEZs. In particular, in AEZ 2, the steep slope of the curves reflected a highly unbalanced community, overwhelmingly dominated by *Bactrocera dorsalis* (**Figure 3**). Conversely, the flatter curves observed in AEZ

1, notably in Ngong, indicated a more equitable species distribution, with several major pest species contributing significantly to community structure, especially *B. dorsalis*, *Ceratitis cosyra*, and *Zeugodacus cucurbitae* (**Figure 3**).

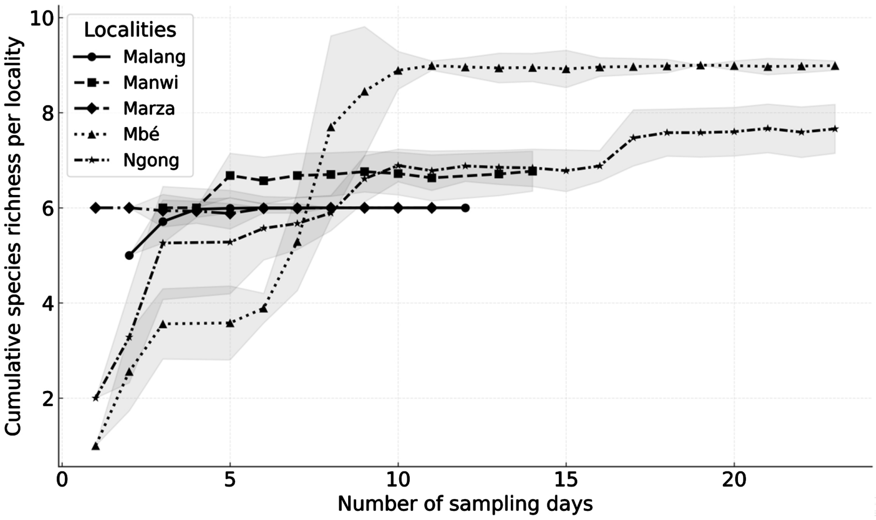

Figure 2. Species accumulation curves illustrating the cumulative tephritid species richness during the 2021-2022 sampling period in five orchards located across two agroecological zones (AEZs) in Cameroon: two orchards in AEZ 1 (Mbé and Ngong), and three in AEZ 2 (Marza, Manwi, and Malang).

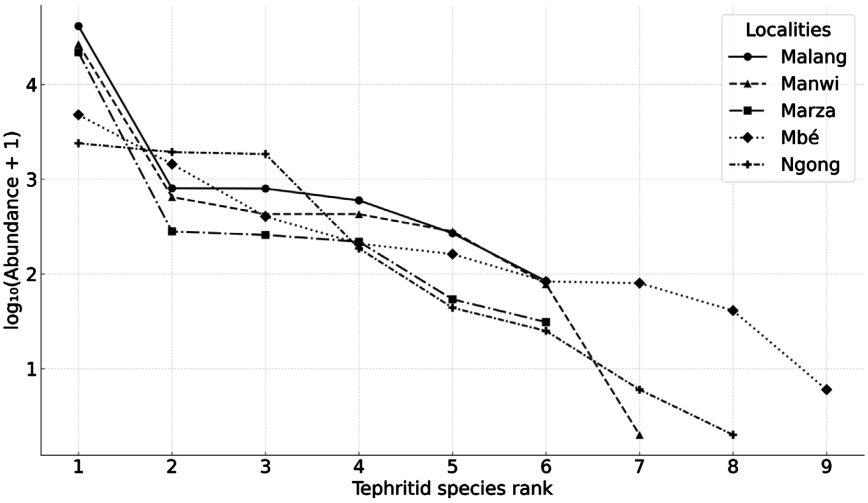

Figure 3. Rank-abundance curves of tephritid communities in five orchards across two agroecological zones (AEZs) in Cameroon: two in AEZ 1 (Mbé, Ngong), and three in AEZ 2 (Marza, Manwi, and Malang), during the 2021-2022 sampling period. Species are ranked from the most to the least abundant, with abundance expressed as Log10 (abundance + 1).

3.1.3. Assessment of Diversity Indices

Diversity indices revealed marked variations between the AEZs (**Figure 4**). Orchards located in AEZ 1 exhibited high values for the Shannon-Wiener diversity index, Simpson's index, and Pielou's evenness index, indicating tephritid communities that were both species-rich and evenly distributed (**Figure 4**). In contrast, diversity indices were significantly lower in AEZ 2, reflecting the numerical dominance of a single species and consequently a low evenness within each orchard (**Figure 4**).

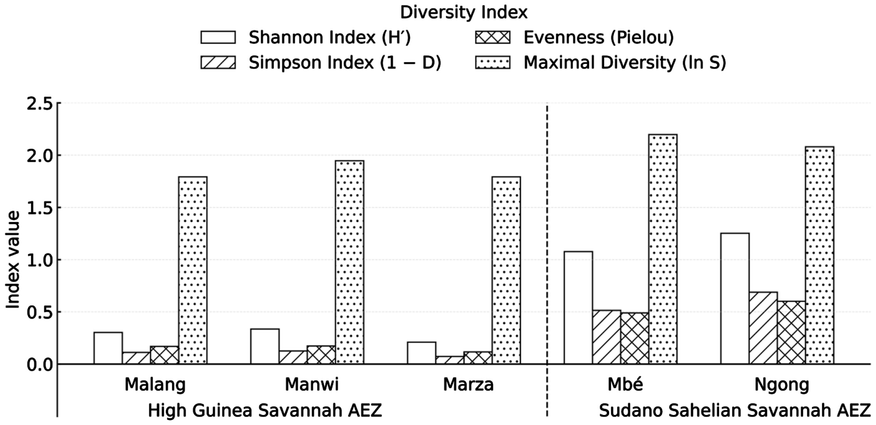

Figure 4. Values of diversity indices: H’, 1-D, and J’, associated with tephritid communities in five orchards located in two agroecological zones (AEZs) in Cameroon: two orchards in AEZ 1 (Mbé and Ngong) and three orchards in AEZ 2 (Marza, Manwi, and Malang), during the 2020-2021 sampling period.

3.2. Evaluation Beta Diversity

Jaccard similarity index values revealed high similarity within AEZ (J > 0.85), suggesting that shared species were more abundant than unique species within each AEZ (**Figure 5**). In contrast, similarity values between AEZs were notably lower (~0.60), indicating a relatively weak ecological differentiation of tephritid communities between AEZs.

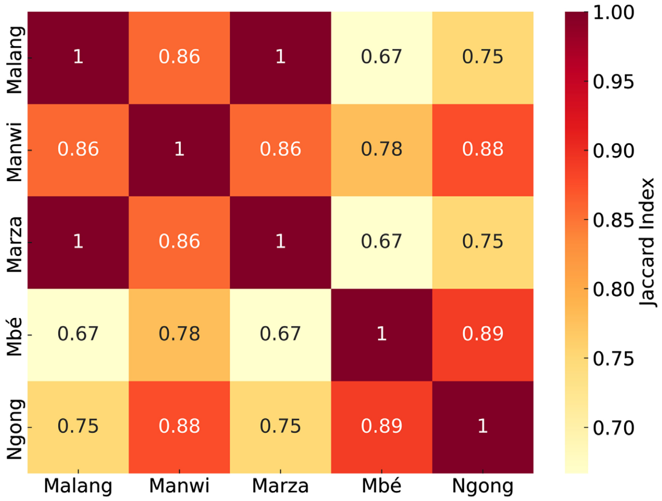

Figure 5. Heatmap showing pairwise Jaccard similarity index among tephritid communities in five orchards across two agroecological zones (AEZs) in Cameroon: two orchards in AEZ 1 (Mbé and Ngong) and three orchards in AEZ 2 (Marza, Manwi, and Malang), during the 2021-2022 sampling period. Color intensity reflects the degree of similarity, with higher intensity indicating greater similarity.

3.3. Lure Effectiveness

A total of nine male tephritid species were recorded across all surveyed orchards. Among them, *Ceratitis bremii* and *C. punctata* were absent from AEZ 2 (**Figure 6**; Supplementary material **Table S1**).

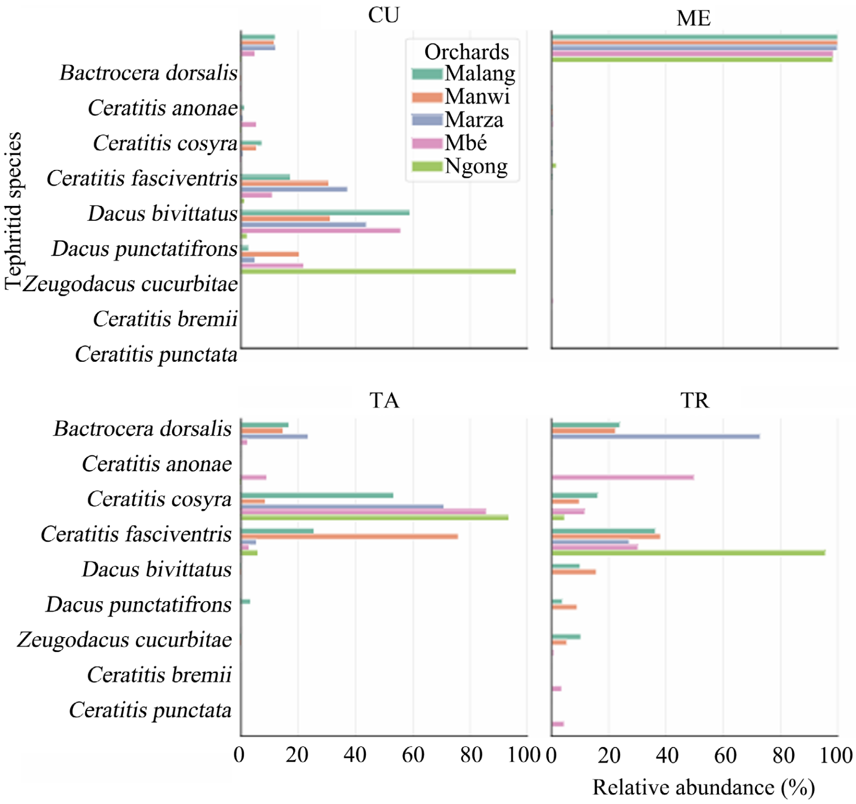

Figure 6. Grouped horizontal bar plots by four male-specific lures: cue-lure (CU), methyl eugenol (ME), trimedlure (TA), and terpinyl acetate (TR), across five orchards located in two agroecological zones (AEZs) of Cameroon: two orchards in AEZ 1 (Mbé and Ngong) and three orchards in AEZ 2 (Marza, Manwi, and Malang), during the 2021-2022 sampling period. Bar length represents relative abundance (%).

Each male-specific lure exhibited significantly distinct selectivity profiles ($p < 0.05$), strongly influencing species composition assessments and underscoring the strategic importance of multi-lure trapping systems for comprehensive ecological surveillance and integrated tephritid management (**Figure 6**; Supplementary material **Table S2**).

Methyl eugenol (ME) demonstrated exceptionally high attractiveness and specificity toward *Bactrocera dorsalis*, accounting for over 99% of captures across all orchards (**Figure 6**), reflecting the species' overwhelming numerical dominance under ME-based monitoring conditions (Supplementary material **Table S1** and **Table S2**). Nevertheless, its relative abundance varied significantly between AEZs ($p < 0.05$), with lower representation in AEZ 1, particularly at Ngong and Mbé, compared to AEZ 2, where this species peaked with averages exceeding 1000 individuals per trapping event (Supplementary material **Table S1** and **Table S2**).

Cue-lure (CU) exhibited moderate but variable performance, with significantly high capture rates at Ngong (16.76 ± 4.64) and markedly low rates at Mbé (3.69 ± 0.33) (Supplementary material **Table S2**). This lure attracted several cucurbit-associated species, notably *Zeugodacus cucurbitae*, *Dacus punctatifrons*, and *D. bivittatus*.

Trimedlure (TR) and terpinyl acetate (TA) displayed broader and less specific attraction profiles, capturing a more diverse assemblage of *Ceratitis* species, including *C. cosyra*, *C. anonae*, and *C. fasciventris*, along with a limited number of *B. dorsalis* individuals (**Figure 6**). This generalist attractant behavior reinforces their complementary role in species detection, particularly for less dominant or lure-insensitive tephritids.

Ceratitis cosyra and *Z. cucurbitae* were well represented in AEZ 1, accounting for over 30% and 25% of total captures, respectively in Ngong (Supplementary material **Table S1**). Notably, this orchard has experienced an intensification of cucurbit cultivation, particularly of sweet melon (*Cucumis melo* L.). In contrast, *C. anonae*, *C. fasciventris*, *D. punctatifrons*, and *D. bivittatus*, although widely distributed across sites, exhibited low responsiveness to the studied lures, with capture rates generally below 5% (Supplementary material **Table S1**).

4. Discussion

The present study provides a comprehensive assessment of the community structure of tephritids and the performance of male-specific lures across two agroecological zones (AEZs) in Cameroon. By integrating multi-lure trapping strategies with various quantitative species diversity metrics, tephritid community studied was strongly shaped by agroecological conditions [2], while male lure effectiveness varied considerably depending on host plants used. These findings challenge the effectiveness of standardized surveillance protocols and highlight the need for ecologically adapted Integrated Pest Management (IPM) frameworks [37] [38].

The observed saturation of species accumulation curves confirms the robustness of the sampling [32], ensuring the reliability of ecological parameter comparisons across AEZs.

Although the incubation of attacked fruits is a labor-intensive yet accurate method for confirming host plant use [14], male lure-based trapping offers a more inclusive and cost-effective approach for monitoring adult populations, particularly for the detection and management of major pest species [3] [6] [24] [37]. The detection approach based on methyl eugenol (ME), cue-lure (CU), terpinyl acetate (TA), and TR revealed significant, context-dependent variation in performance. This enabled the identification of nine tephritid species, including previously unreported species such as *C. punctata*, and *C. fasciventris* [29]. The absence of *Perilampsis* sp., *Bactrocera mesomelas* and *Notoma biocolatum*, which were recorded in previous studies, may reflect differences in male lure selectivity [29].

Despite a shared species pool, clear contrasts were observed in species diversity and community structure across AEZs.

Methyl eugenol (ME) demonstrated outstanding efficacy in areas dominated by *Bactrocera dorsalis*, confirming its high specificity. However, in AEZ 2, this pest accounted for more than 90% of captures [2] [22] [24] [25], indicating its ecological dominance and establishment, pattern consistent with previous studies documenting the invasion and displacement effects of *B. dorsalis* across sub-Saharan Africa [11] [39] [40]. This dominance was particularly pronounced in the orchards of Malang, Manwi, and Marza, suggesting a homogenized community structure under intense pest pressure [41].

By contrast, AEZ 1, characterized by dry climatic conditions and a high presence of cucurbit crops, supported a more balanced assemblage dominated by *B. dorsalis*, *Ceratitis cosyra*, and *Zeugodacus cucurbitae*, particularly in the orchard of Ngong. This pattern may reflect habitat heterogeneity, including broader host plant or altitude-related climatic differences that mitigate interspecific interactions and promote niche partitioning [3] [13]. The higher evenness and species richness observed in this AEZ do not corroborate previous fruit incubation studies, which identified *C. cosyra* as the primary mango pest in this zone [2].

Cue-lure (CU) proved essential for monitoring *Z. cucurbitae* and *Dacus* spp., especially in cucurbit-dominated zones, while trimedlure (TR) and terpinyl acetate (TA) were important for detecting *Ceratitis* spp., despite lower overall catch rates [24]. These results suggest the necessity of deploying mixed-lure systems in tephritid surveillance programs. Sole reliance on ME, as implemented in many *B. dorsalis*-infested areas, risks underrepresenting non-responsive or secondary pest species catching and thereby underestimating true community diversity and pest risk.

In high-diversity settings like AEZ 1, mixed-lure approaches can enhance detection accuracy, improve early warning systems, and support more nuanced pest management strategies [42].

From a management perspective, the dominance of *B. dorsalis* in AEZ 2 supports the implementation of Male Annihilation Technique (MAT) using ME in conjunction with strict orchard sanitation [42]. In contrast, the complex species assemblage in AEZ 1 calls for diversified IPM approaches, including multi-lure trapping, host sanitation, and possibly augmentative biological control. The success of such strategies, however, hinges on institutional support, grower education, and access to affordable lures and traps [10].

5. Conclusions

This study highlights the spatial heterogeneity of tephritid communities across tropical agroecosystems and underscores the pivotal role of agroecological context in shaping both community structure and responsiveness to male-specific semiochemical lures. It also demonstrates the methodological complementarity between male-lure-based trapping, which is highly effective for detecting mobile adult tephritid populations.

Findings from this survey reveal that no single lure, whether sex-specific or generalist, nor any standardized protocol can, in isolation, effectively capture the full species pool. Consequently, integrated and zone-specific strategies, combining a diversity of attractants, are essential for accurate surveillance and sustainable pest management.

Incorporating these insights into local IPM frameworks offers a promising pathway to strengthen national phytosanitary capacity, enhance crop protection, and reduce reliance on synthetic insecticides. This is especially critical in smallholder farming systems, where limited resources and high vulnerability necessitate pest control solutions that are not only effective and affordable but also ecologically sound.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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Supplementary Material

Table S1. Relative abundance (%) of nine tephritid species captured in five orchards located in two agroecological zones (AEZs) of Cameroon: two orchards in AEZ 1 (Mbé and Ngong) and three orchards in AEZ 2 (Marza, Manwi, and Malang), during the 2021-2022 sampling period.

Tephritid species	High Guinea Savannah AEZ			Sudano Sahelian Savannah AEZ	
	Malang	Manwi	Marza	Mbé	Ngong
Bactrocera dorsalis	94.23	93.49	96.30	66.42	37.22
Ceratitis anonae	0	0.01	0	2.88	0.02
Ceratitis bremii	0	0	0	0.55	0.08
Ceratitis cosyra	1.82	0.27	1.23	20.02	28.62
Ceratitis fasciventris	1.35	2.27	0.23	1.14	2.88
Ceratitis punctata	0	0	0	0.07	0
Dacus bivittatus	0.61	1.49	0.96	1.10	0.37
Dacus punctatifrons	1.81	1.49	1.13	5.59	0.67
Zeugodacus cucurbitae	0.19	0.98	0.13	2.23	30.15
Total abundance	44058	28598	22673	7213	6432

Table S2. Mean number of tephritid individuals ± standard deviation captured per trap per sampled day, with minimum and maximum values in parentheses, in five orchards located in two agroecological zones (AEZs) of Cameroon: two orchards in AEZ 1 (Mbé and Ngong) and three orchards in AEZ 2 (Marza, Manwi, and Malang). Values were obtained for four male lures (CU: cue-lure; ME: methyl eugenol; TA: trimedlure; TR: terpinyl acetate), during the 2021-2022 sampling period. Superscript letters indicate statistically significant differences within each community between male lures, while numbers indicate significant differences within each male lure between communities, both based on post hoc tests ($p < 0.05$).

Male lures	High Guinea Savannah (AEZ 2)			Sudano-Sahelian Savannah (AEZ 1)	
	Malang	Manwi	Marza	Mbé	Ngong
CU	14.46 ± 4.73 (0 - 400) [c2]	15.01 ± 1.95 (1 - 91) [d3]	8.49 ± 1.52 (1 - 64) [b2]	3.69 ± 0.33 (0 - 33) [a2]	16.76 ± 4.64 (0 - 273) [e2]
ME	1415.45 ± 280.99 (1 - 4807) [e4]	1058.04 ± 198.31 (1 - 4123) [d4]	772.57 ± 147.54 (1 - 3226) [c4]	36.58 ± 6.56 (0 - 377) [b4]	22.17 ± 4.88 (0 - 317) [a4]
TA	20.62 ± 3.34 (1 - 134) [e3]	14.72 ± 2.96 (1 - 96) [c2]	9.62 ± 2.80 (1 - 94) [a3]	11.01 ± 2.09 (0 - 159) [b3]	17.04 ± 3.92 (0 - 250) [d3]
TR	8.38 ± 1.48 (1 - 60) [e1]	3.62 ± 0.71 (1 - 24) [c1]	3.68 ± 0.68 (1 - 10) [d1]	1.03 ± 0.23 (0 - 12) [b1]	0.21 ± 0.07 (0 - 4) [a1]