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Habitat selection by fruit flies (Diptera: Tephritidae) in a tropical agroecosystem in Papua New Guinea

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Abstract

Habitat selection by fruit flies (Diptera: Tephritidae) along disturbance gradients of tropical agroecosystems has ecological significance. There have been extensive studies of fruit flies in agricultural systems and in natural forests. Here we examined the species preference regarding three vegetation types: cocoa plantation, secondary forest and primary forest, using methyl eugenol (ME) and cue-lure (Cue). We also quantified the efficiency of the two para-pheromones for fruit fly sampling within different habitats. The total number of individuals collected were 685 respectively in cocoa plantation, 1338 in primary reserved forest and 1589 in secondary forest. Species diversity reached its highest value in cocoa plantation ($H=3.59$) followed by secondary forest ($H=3.17$) and least diverse in primary forest ($H=2.94$). Total species richness (pooled data per site) was identical in primary forest and secondary forest (10 species each) but slightly higher in cocoa plantation (12 species). No individuals of *Bactrocera kirki* and *Bactrocera obliqua* were trapped with ME but only in cue-lure. Vice versa, nil individuals of *Bactrocera curvifera* and *Bactrocera laticaudus* were attracted to cue-lure but only to ME. *Dacus longicornis* (1.09 ± 0.162), *Zeugodacus cucurbitae* (3.00 ± 0.61) and *Zeugodacus* sp.n (1.88 ± 0.35) were more responsive to cue-lure than to ME (0.181 ± 0.121 , 1.750 ± 0.463 , 0.592 ± 0.186). Temperature (F -value = 11.34, $p<0.001$) and vegetation (F -value = 3.33, $p<0.05$) had significant effect on the number of individuals trapped in cue-lure. Cue-lure abundance was positively correlated with rainfall, however, there was no significant interaction effect (F -value = 0.50, $p>0.05$). Cue-lure abundance was non-significantly correlated with relative humidity ($r = -0.09$, $p>0.05$). All three abiotic factors did not have any significant interaction with vegetation on ME abundance ($p>0.05$). This study finds that there is low species composition within a typical tropical agroecosystem and thus similar species can be widely distributed across a contiguous habitat. However, the abundance was significant among the three study habitats. Temperature, wet season and seasonal fruit availability exerted ecological impact on fruit fly population and their distribution among the three study sites.

Keywords: fruit flies, tephritidae, agroecosystem, methyl eugenol, cue-lure, diversity

Introduction

Dacine fruit flies are largely distributed in the Australasian and Oceanian regions [1]. Over 190 described species of this subfamily are found in Papua New Guinea (PNG), particularly in the genus *Bactrocera* Macquart and *Dacus* Fabricius [1, 2]. In agriculture, fruit flies are considered major pests of fruits and horticultural crops [3], with 18 species recorded as serious agricultural pests in PNG [4] causing direct damage to host fruits and invading new areas [5-7]. The taxonomy and species identification in PNG is well documented largely due to the work of Drew (1989) and Drew & Romig (2001), while the information on the distribution, biogeography and ecology of fruit fly species is still lacking [8].

Fruit fly studies have been done to compare species richness at the assemblage level [9], sampled using male hormonal attractants: methyl eugenol (ME) and cue-lure (Cue) that have been used also in PNG [10-13]. Several pest fruit fly species in PNG are known to respond to cue (e.g. *Zeugodacus cucurbitae* Coquillett, *Bactrocera trivialis* Drew) or ME (e.g. *Bactrocera dorsalis* Hendel), although over 60% of species are nonresponsive to these lures [13]. That is why new attractants are being developed, including vanillyl acetone, commercially known as zingerone, that attracted the weakly Cue-responsive *Bactrocera obliqua* Malloch, *Zeugodacus atrisetosus* Perkins, *Zeugodacus decipiens* Drew, *Bactrocera jarvisi* Tryon and several 'non-responsive' non-pest species in Australia [13-16].

Further, female fruit flies are attracted to protein hydrolysate [17].

There have been extensive studies of fruit flies in agricultural systems [8] and in natural forests [11, 12] in PNG. Here we examined the species preference regarding three vegetation types: cocoa plantation, secondary forest and primary forest, using methyl eugenol and cue-lure. We also aim to quantify the efficiency of the two para-pheromones for fruit fly sampling in different habitats in PNG.

Materials and Methods

(a) Study sites

The study was carried out around the campus of PNG University of Natural Resources and Environment (PNGUNRE) in Vudal, Gazelle Peninsula of Papua New Guinea (PNG) at 4° 21' 01.90" S and 152° 00' 33.44" E, 51 m a. s. l. [18, 19]. The climate is classified as tropical humid with a 2780 mm average annual rainfall and only mild dry season. The average annual humidity is 77-79%, temperature 27-29°C. The soil type is a calcareous sandy loam with alkaline pH. The sampled vegetation included (1) Crops, (2) Secondary forest, and (3) Primary forest reserve. The crop fields constitute cocoa (*Theobroma cacao*), teak (*Tectona grandis*) and balsa (*Ochroma pyramidale*) plantations to the north-east, vegetable gardens to the east and a cattle farm and paddock situated to the west. Predominant vegetables grown here are cabbages, tomatoes and capsicum, grown all year round. Bananas (*Musa spp.*), mangoes (*Mangifera indica*), star fruits (*Averrhoa carambola*), breadfruit (*Artocarpus altilis*) and other fruit trees are also growing in the vicinity. Cocoa plantation is approximately 30 ha and represents an agricultural monoculture system. Most of the cocoa trees are clonal varieties that has some level of tolerance to pest attacks. The secondary forest contains vegetation regrowth after disturbances from gardening and clear cutting. The common tree species include *Artocarpus altilis*, *Pometia pinnata*, alien *Spathodea campanulata* and bamboos (*Bambusa spp.*), growing over 30 ha. The primary forest is actually a reserved forest that has been preserved for its vital ecosystem services, conservation site for fauna and flora, and research site for academic studies. It has an approximate area of 200 ha. Common tree species include *Pometia pinnata*, *Alstonia scholaris*, *Canarium indicum*, *Inocarpus fagifer*, and *Maniltoa sp.* The three study sites selected represent a representative selection of the vegetation types in the local landscape.

(b) Fruit fly sampling

Adult fruit flies were attracted to two male para-pheromone lures, cue-lure (Cue) and methyl eugenol (ME), used in modified Steiner traps. Six traps were placed along a transect with minimum distance of 10 m between traps at each study site; 3 ME traps and 3 Cue traps. The study sites were more than 500 m apart from each other to avoid overlapping of attractant cues. A total of 18 baited traps were used in this study and were placed strategically to capture the vegetation type which were not continuous but fragmented. Each trap used the lure-and-kill technique [17, 20] where Dichlorvos (DDVP [2,2-dichlorovinyl dimethyl phosphate]) cubes were used as a toxicant [21, 22].

Approximately 2-3 ml of each parapheromone were soaked in a cotton wick and placed inside each trap along with one Dichlorvos cube (BioTrap Australia Pty Ltd, Victoria, Australia) used as killing agent [23] and hung from understorey

tree branches 1.5 m above the ground using string ropes. A new pair of laboratory gloves were used to handle individual types of lures, and the lures were separately prepared in the laboratory before taking them out to the field. All traps at all three study sites were emptied at weekly intervals from 18th June – 16th November 2019. All flies were collected into vials containing 70% ethanol and identified to species using Australian guide book of fruit flies [7], fruit flies in PNG [4] and iNaturalist website (<https://www.inaturalist.org/>). Environmental factors were taken into consideration as they can have adverse effect on distribution. Therefore, daily recordings of temperature, relative humidity and rainfall were taken at the weather station at UNRE campus. Weekly mean values of each factor were then calculated and used for analysis.

(c) Data analysis

We used the R function *aov* (R Core Team, 2013) for Analysis of Variance (ANOVA) to analyse effect of vegetation types and attractants on species richness and abundance of fruit flies. Principal Component Analysis (PCA) was used (function *prcomp*, package *vegan*) to analyse the relationship of different biotic and abiotic variables on the distribution of fruit flies to vegetation types on an ordination scale, function *diversity* (package *vegan*) to calculate diversity index, function *H/log* (package *vegan*) for evenness, function *cor.test* (package *ggplot2*) for Pearson correlation, and function *ggbarplot* (package *ggpubr*) for species abundance. The species diversity of each site was compared using Shannon diversity index (H) and Pielou's evenness (H/log) [24].

Results

We collected a total of 3612 fruit flies representing 13 species from 151 trap-days during sampling. The highest abundance was recorded in primary forest and lowest in cocoa plantation. The abundance of fruit flies caught with ME decreased from primary forest to secondary forest, and particularly a sharp decline in cocoa plantation but not for Cue (fig. 2A). The total number of individuals collected were 685 respectively in cocoa plantation, 1338 in primary reserved forest and 1589 in secondary forest. Species diversity reached its highest value in cocoa plantation (H=3.59) followed by secondary forest (H=3.17) and least diverse in primary forest (H=2.94). The species evenness from high to low followed this order; cocoa plantation (E=0.89), secondary forest (E=0.79) and primary forest (E=0.73). Total species richness (pooled data per site) was identical in primary forest and secondary forest (10 species each) but slightly higher in cocoa plantation (12 species) (fig.1).

The number of individuals trapped in cue-lure and methyl eugenol respectively in cocoa plantation was (ME=116, Cue=107), primary forest (58, 1280) and secondary forest (151, 1438). Vegetation ($F_{\text{value}} = 7.39, p > 0.001$) and lure type ($F_{\text{value}} = 0.00, p > 0.05$) had no significant effect on the number of species trapped. The interaction between these two factors was also not significant ($F_{\text{value}} = 0.00, p > 0.05$). However, the vegetation ($F_{\text{value}} = 6.87, p < 0.01$) and lure type ($F_{\text{value}} = 23.69, p < 0.001$) had significant effect on the number of individuals trapped and the interaction between these two factors was also significant ($F_{\text{value}} = 9.12, p < 0.001$). The most successful lure was ME, attracting $3.27 \pm \text{SE } 0.49$ individuals in an average trap in cocoa plantation, $23.27 \pm \text{SE } 5.98$ in primary forest and $12.61 \pm \text{SE } 3.66$ in secondary forest. Cue-

lure recorded low number of fruit flies, attracting $2.35 \pm SE 0.50$ individuals in cocoa plantation, $1.05 \pm SE 0.25$ in

primary forest, and $1.32 \pm SE 0.17$ in secondary forest.

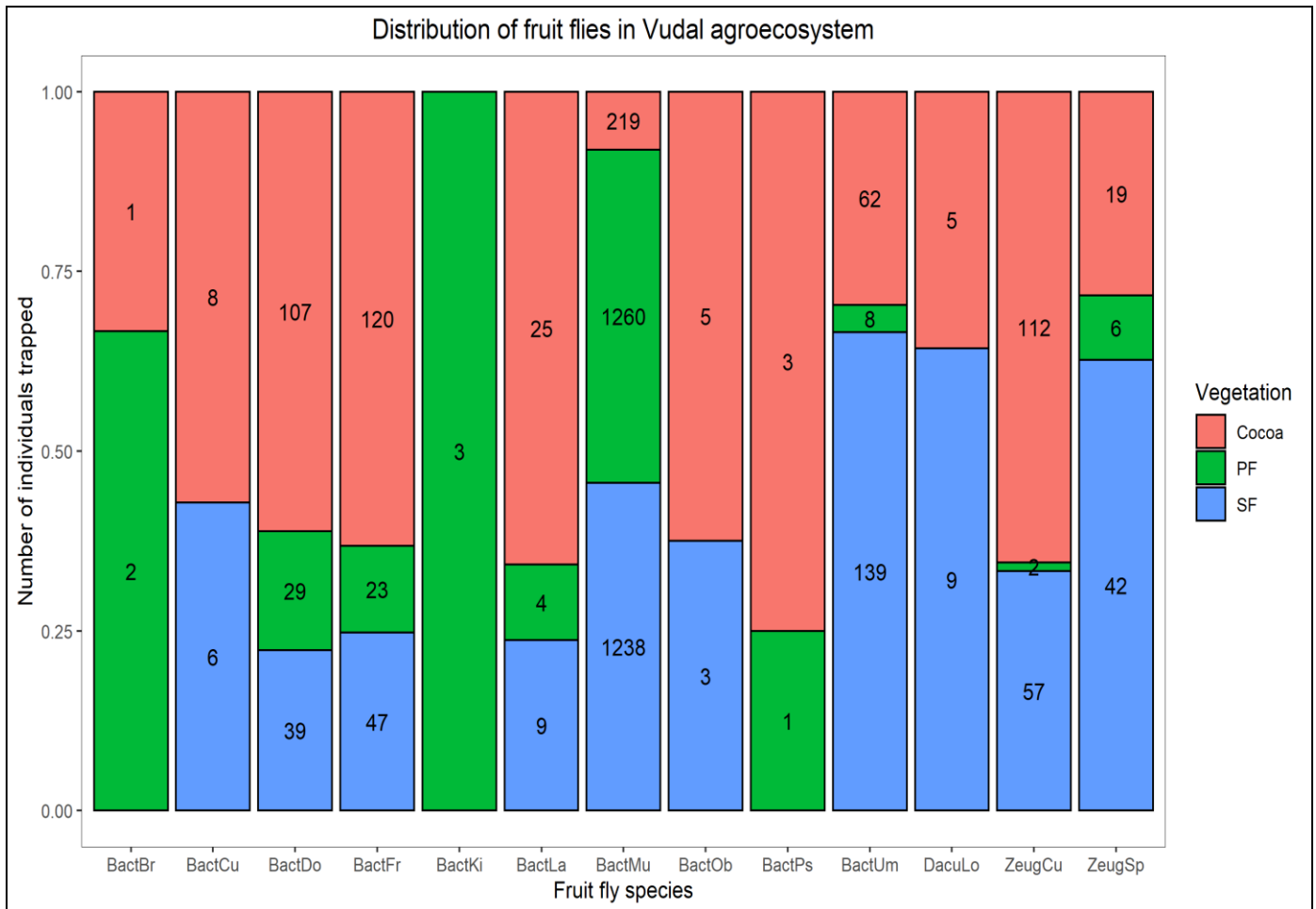


Fig 1: The relative distribution of fruit fly species among the three habitats: cocoa plantation (Cocoa), primary forest (PF) and secondary forest (SF). The number of individuals is given in each column. Full species names: *Bactrocera breviaculeus* (BactBr), *B. kirki* (BactKi), *B. psidii* (BactPs), *B. obliqua* (BactOb), *B. curvifera* (BactCu) and *Dacus longicornis* (DacuLo). The most dominant species was *B. musae* (BactMu) followed by *B. fraunfeldi* (BactFr), *Zeugodacus cucurbitae* (ZeugCu), *B. dorsalis* (BactDo) and *B. umbrosa* (BactUm). Other species such as *B. laticaudus* (BactLa) and *Zeugodacus sp.* (ZeugSp) had moderate numbers.

B. musae greatly contributed to the difference in abundance (2716 indiv.) because on average it was highly abundant in primary forest ($35.00 \pm SE 8.54$, 94.17%) and secondary forest ($34.39 \pm SE 10.77$, 77.91%) while least abundant in cocoa plantation ($6.08 \pm SE 1.38$, 31.82%) (Fig. 2A). Second highest was *B. umbrosa* (209 indiv.) mostly sampled in cocoa plantation ($1.94 \pm SE 0.51$, 9.05%) and secondary forest ($3.86 \pm SE 1.19$, 8.75%) but rarely trapped in primary forest ($0.57 \pm SE 0.17$, 0.59%). Thirdly, *B. fraunfeldi* ($3.75 \pm SE 1.20$, 190 indiv., 17.52%) then followed by *Bactrocera dorsalis* ($3.34 \pm SE 1.31$, 175 indiv., 15.62%) and *Z. cucurbitae* ($3.11 \pm SE 0.69$, 171 indiv., 16.35%) which were predominant in cocoa

plantation but had low numbers in secondary and primary forest. ME attracted the highest number of individuals (23.27 ± 5.98) in primary forest, 12.61 ± 3.66 in secondary forest, and 3.27 ± 0.48 individuals in cocoa. Cue-lure recorded 2.35 ± 0.49 in cocoa, 1.05 ± 0.25 in primary and 1.32 ± 0.17 in secondary forest. Cue-lure abundance was relatively similar for primary and secondary forest but increased in cocoa plantation (fig. 2). Although Cue had low number of individuals, it was successful in trapping rare and exotic species such as *B. kirki*, in primary forest which can be of interest to quarantine and biosecurity.

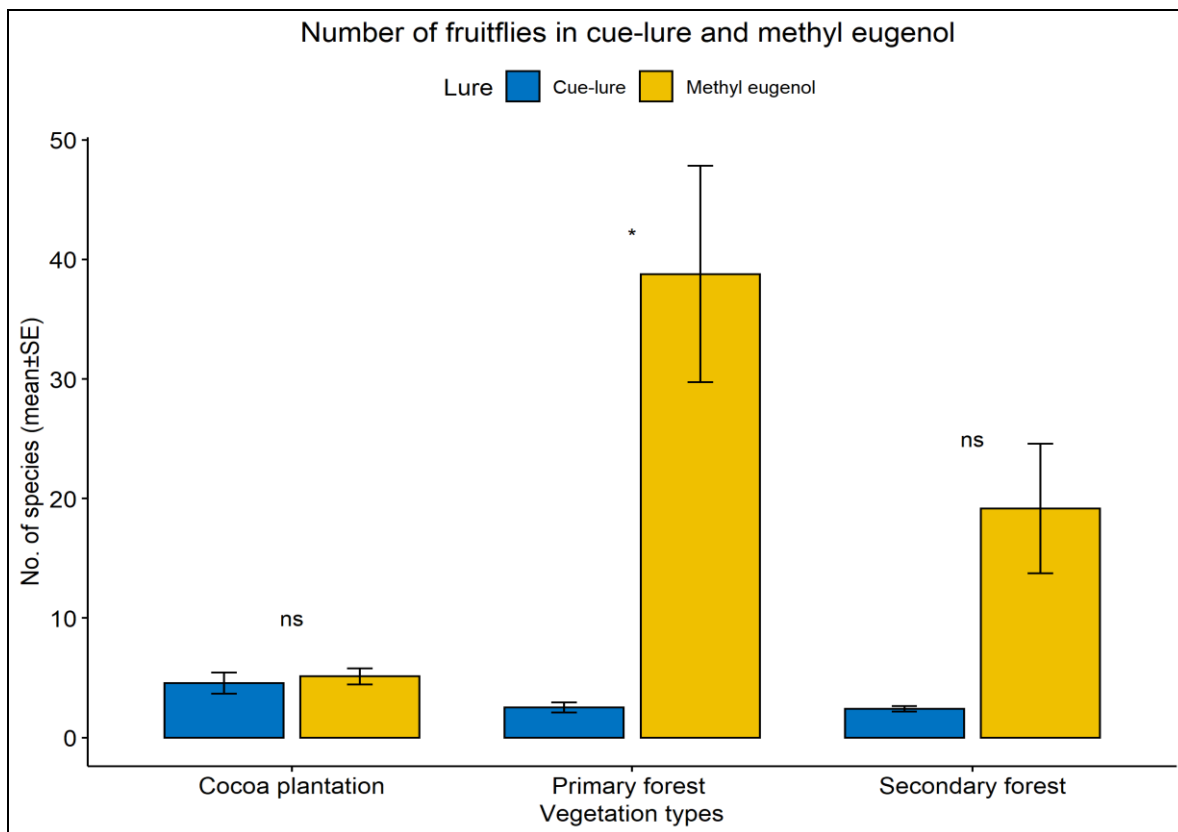


Fig 2A: The number of fruit flies attracted to the two lures in each vegetation type. There are both significant (*) and non-significant (ns) differences at $\alpha = 0.05$ between the two lures at each study site. There was significant difference between ME and CL at primary forest ($p < 0.05$) while non-significant in secondary forest and cocoa plantation ($p > 0.05$).

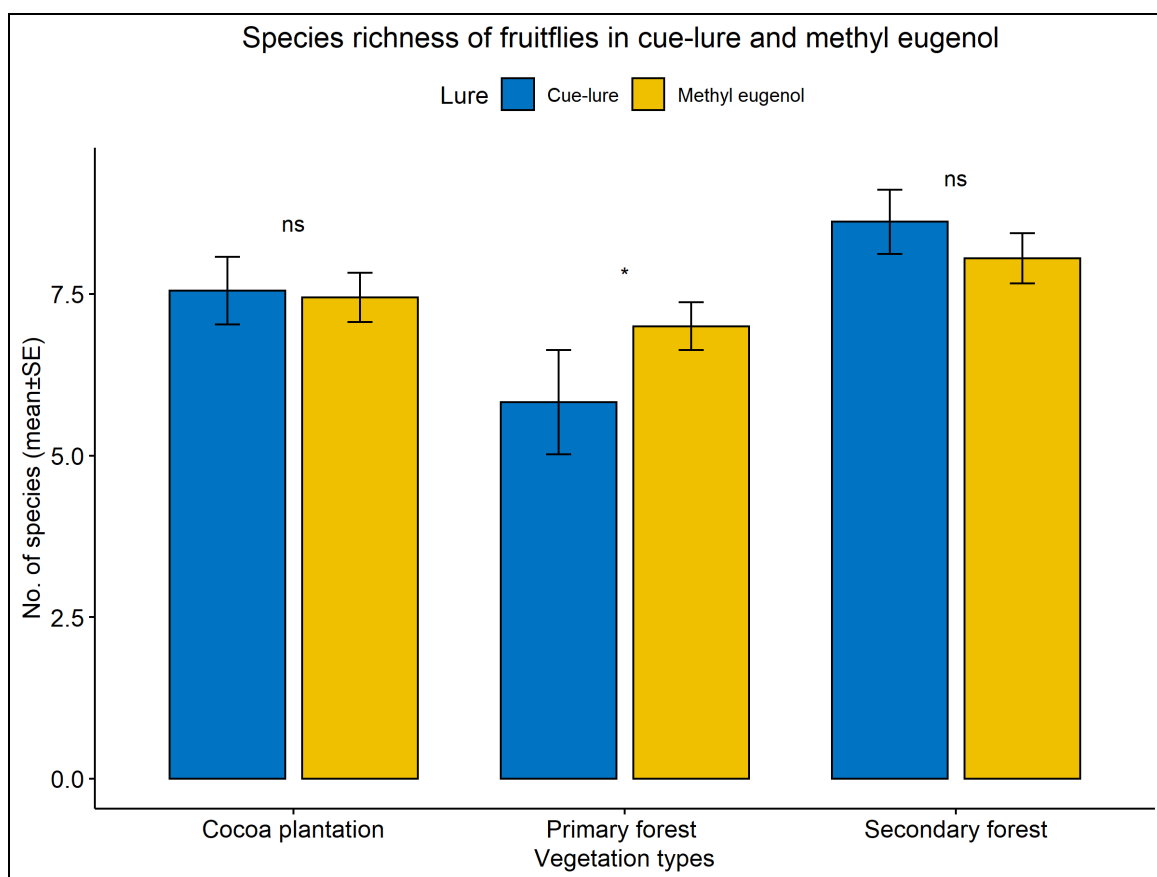


Fig 2B: There is significant difference in number of fruit fly species attracted to cue-lure (Cue) and methyl eugenol (ME) in primary forest ($p < 0.05$). See table 1 for full species list trapped with the two lures. The number of species caught in ME and CL in both cocoa plantation and secondary forest did not differ significantly (ns, $p > 0.05$). Number of species trapped with the two lures was significant in primary forest ($p < 0.05$).

The number of species recorded for cue-lure and methyl eugenol were higher in cocoa plantation (10,10), followed by secondary forest (8,10) and primary forest (6, 5). There is a significant difference in mean number of species between CL and ME in primary forest types ($p<0.05$) (fig. 2B). That is mainly due to the very high number of *B. musae* in relation to other species (fig. 1). Some species such as *B. dorsalis*, *B. fraunfeldi*, *B. laticaudus*, *B. musae*, *B. umbrosa*, *Z. cucurbitae*, and *Z. sp.n* were present in all study sites (fig.1). Two species, *B. breviaculeus* and *B. psidii* were only recorded in cocoa and primary forest. Other three species; *B. curvifera*, *B. obliqua*, and *D. longicornis* were only trapped in cocoa and secondary forest. A cryptic species, *B. kirki*, was only trapped in Primary forest and is considered as an exotic species [7].

The response of different fruit flies to the lures are measured by their abundance. Higher abundance on a specific lure can imply the effectiveness of the lure and preference of the species. Although ME attracted more individuals of specific species, the species diversity was low ($H=3.94$). Cue-lure had a higher species diversity ($H=4.47$) and can be a good sampling tool for long term monitoring of rare and exotic species. The species that were readily attracted to ME were *Z. cucurbitae*, *B. fraunfeldi*, *D. longicornis* and cryptic species like *B. kirki* and *B. psidii*. ME attracted mostly species from genus *Bactrocera*; *B. musae*, *B. umbrosa*, *B. curvifera*, and *B. laticaudus*. Both *B. dorsalis* and *B. obliqua* were attracted to both cue-lure and methyl eugenol.

Table 1: The table shows the number of fruit fly species and their abundance trapped with Methyl eugenol (ME) and Cue-lure (Cue). No individuals of *Bactrocera kirki* and *Bactrocera obliqua* were trapped with ME but only in cue-lure. Vice versa, nil individuals of *Bactrocera curvifera* and *Bactrocera laticaudus* were attracted to cue-lure but only to ME. Total frequency (N) refers to the total count caught in ME and cue-lure. The dash (-) indicates that the species is missing therefore the N belongs to the other attractant. *Dacus longicornis* (1.09 ± 0.162), *Zeugodacus cucurbitae* (3.00 ± 0.61) and *Zeugodacus sp.n* (1.88 ± 0.35) were more responsive to cue-lure than to ME (0.181 ± 0.121 , 1.750 ± 0.463 , 0.592 ± 0.186). The mean (\bar{x}), standard deviation (σ) and standard error (S_E) have also been calculated for each species. Significant means are denoted with codes: $p<0.000^{***}$, $p<0.001^{**}$, and $p<0.05^*$.

| Fruit Fly Species | Total N | Methyl Eugenol (Me) | | | Cue-Lure (Cue) | | |
|--------------------------------|--------------|-----------------------|-----------------|--------------|----------------------|-----------------|--------------|
| | | Mean (\bar{X}) | SD (Σ) | SE (S_E) | Mean (\bar{X}) | SD (Σ) | SE (S_E) |
| <i>Bactrocera breviaculeus</i> | 2 | 1.000 | 1.414 | 1.000 | 0.500 | 0.707 | 0.500 |
| <i>Bactrocera curvifera</i> | 12 | 1.166 ^{***} | 0.389 | 0.112 | - | - | - |
| <i>Bactrocera dorsalis</i> | 37 | 0.945 | 1.985 | 0.326 | 3.783 | 6.688 | 1.099 |
| <i>Bactrocera fraunfeldi</i> | 36 | 1.194 | 2.691 | 0.448 | 4.083 | 6.072 | 1.012 |
| <i>Bactrocera kirki</i> | 3 | - | - | - | 1.000 ^{***} | 0.000 | 0.000 |
| <i>Bactrocera laticaudus</i> | 22 | 1.727 ^{***} | 1.638 | 0.349 | - | - | - |
| <i>Bactrocera musae</i> | 54 | 49.925 ^{***} | 60.448 | 8.226 | 0.388 ^{***} | 1.471 | 0.200 |
| <i>Bactrocera obliqua</i> | 7 | - | - | - | 1.142 ^{***} | 0.377 | 0.142 |
| <i>Bactrocera psidii</i> | 3 | 0.666 | 1.154 | 0.666 | 0.666 | 0.577 | 0.333 |
| <i>Bactrocera umbrosa</i> | 41 | 5.024 | 6.509 | 1.016 | 0.073 | 0.263 | 0.041 |
| <i>Dacus longicornis</i> | 11 | 0.181 | 0.404 | 0.121 | 1.090 | 0.539 | 0.162 |
| <i>Zeugodacus cucurbitae</i> | 36 | 1.750 | 2.781 | 0.463 | 3.000 | 3.664 | 0.610 |
| <i>Zeugodacus sp.n</i> | 27 | 0.592 | 0.971 | 0.186 | 1.888 | 1.825 | 0.351 |

Three meteorological factors; temperature, rainfall and relative humidity were also included in the analysis. Weekly mean values of each factor were calculated from daily recordings at the weather station at UNRE campus. Temperature ($F_{\text{value}} = 11.34$, $p<0.001$) and vegetation ($F_{\text{value}} = 3.33$, $p<0.05$) had significant effect on the number of individuals trapped in cue-lure. The interaction between these two factors was also significant ($F_{\text{value}} = 7.38$, $p<0.001$). Cue-lure abundance was negatively correlated with temperature ($r = -0.19$, $p<0.01$) as evident on the Principle Component Analysis (PCA) graph (fig. 4). Further separation of means showed that the significant differences existed between temperature and primary forest ($t_{\text{value}}=2.38$, $p<0.05$), thus temperature and secondary forest ($t_{\text{value}}=3.68$, $p<0.001$). Rainfall ($F_{\text{value}} = 16.73$, $p<0.001$) and vegetation ($F_{\text{value}} = 3.67$, $p<0.05$) had significant interaction effect on cue-lure abundance ($F_{\text{value}} = 8.69$, $p<0.001$). The significant

differences existed between rainfall and primary forest ($t_{\text{value}}=-3.02$, $p<0.01$), thus rainfall and secondary forest ($t_{\text{value}}=-3.76$, $p<0.001$). Cue-lure abundance was positively correlated with rainfall ($r = 0.23$, $p<0.001$) (fig. 4). However, there was no significant interaction effect ($F_{\text{value}} = 0.50$, $p>0.05$) on cue-lure abundance between relative humidity ($F_{\text{value}} = 2.63$, $p>0.05$) and vegetation ($F_{\text{value}} = 3.16$, $p<0.05$). Cue-lure abundance was negatively correlated with relative humidity ($r = -0.09$, $p>0.05$). All three abiotic factors did not have any significant interaction with vegetation on ME abundance ($p>0.05$). ME abundance was negatively correlated with temperature ($r = -0.1$, $p>0.05$) (fig. 4). ME abundance was positively correlated with rainfall ($r = 0.06$, $p>0.05$) (fig. 4) but very weak. ME abundance was negatively correlated with relative humidity ($r = -0.02$, $p>0.05$) but was also rather weak (fig. 4).

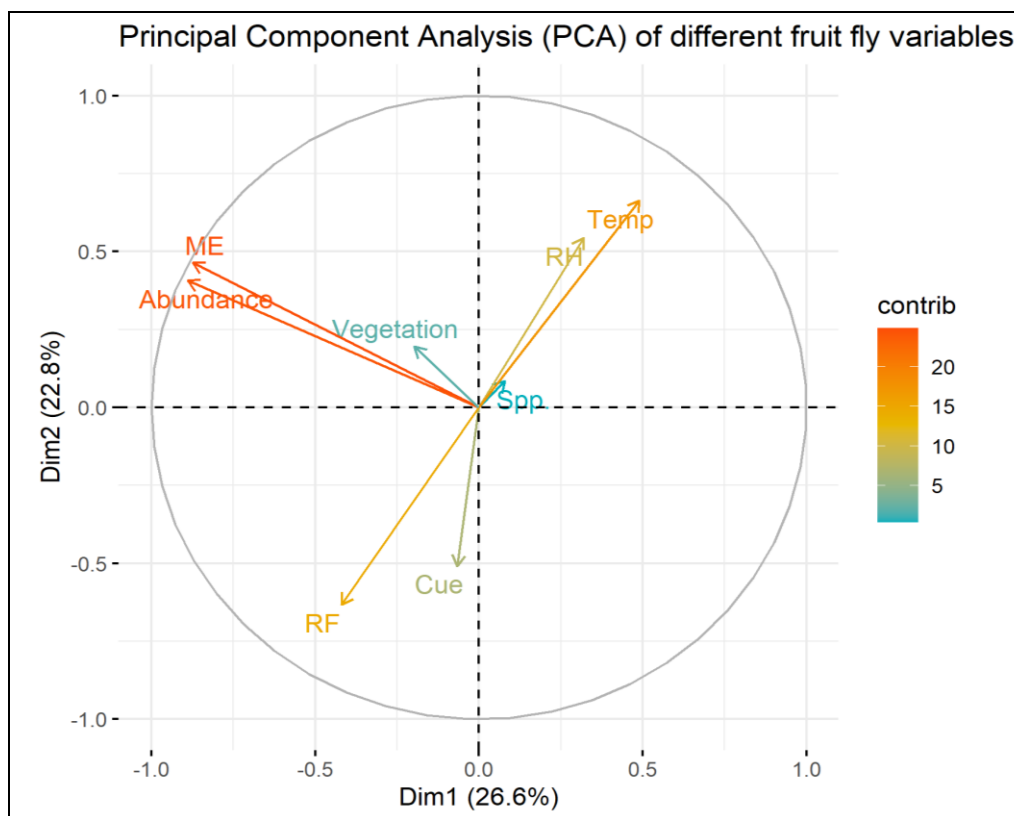


Fig 3: Combined ordinal distribution of different variables in relation to fruit fly abundance and number of species (Spp). Data from both lures, ME and Cue were combined and processed to produce the PCA of different variables. Cue-lure (Cue) abundance is negatively correlated with temperature (Temp) ($r = -0.19, p < 0.01$) and relative humidity (RH) ($r = -0.09, p > 0.05$) while positively correlated with rainfall (RF) ($r = 0.23, p < 0.001$), RH and RF had no effect on ME abundance ($p > 0.05$). However, temperature had significant effect on abundance ($p < 0.05$). There was also a significant interaction effect between temperature and RH on combined abundance ($r = 0.41, p < 0.05$). Number of species (Spp.) was positively correlated with temperature ($r = 0.04, p > 0.05$).

The number of species was positively correlated with temperature ($r = 0.04, p > 0.05$) (fig. 3) but the correlation was very weak. Similarly, there was almost no correlation between number of species and relative humidity ($r = 0.01, p > 0.05$). There was also a very weak correlation between number of species and vegetation ($r = 0.08, p > 0.05$). Vegetation had positive correlation with total abundance ($r = 0.12, p < 0.05$) and ME abundance ($r = 0.13, p < 0.001$) while negative correlation with cue-lure abundance ($r = -0.12, p > 0.05$) and rainfall ($r = 0.02, p > 0.05$). From the five abundant species, there was a significant difference between *B. musae* abundance and temperature ($p < 0.05, r = -0.28$). The abundance of *Z. cucurbitae* was significant with temperature ($p < 0.05, r = -0.40$) and rainfall ($p < 0.05, r = +0.36$). Temperature had a significant effect on *B. fraunfeldti* abundance ($p < 0.05, r = -0.35$) while non-significant on *B. umbrosa* abundance. *B. dorsalis* abundance was positively correlated with rainfall ($p < 0.05, r = +0.44$). However, the meteorological factors did not have any significant effect on the abundance of *B. umbrosa*.

Discussion

We recorded the highest abundance of fruit flies in secondary forest followed by primary reserved forest and cocoa plantation respectively. We generally categorized cocoa plantation and secondary forest as disturbed habitats (production vegetation) and primary forest as undisturbed pristine habitat (non-production vegetation). Our results thus confirm the findings of Virgilio, Backeljau [25] who recorded significantly higher number of fruit flies in disturbed habitats than in pristine forest. The horticultural orchards in an

agroecosystem provides suitable habitats for fruit flies to thrive while trading of agricultural products by humans contributes to the dispersal of tephritid pests [26, 27]. The species richness did not differ between the disturbed and undisturbed habitats suggesting that the variability exist among locations hundreds of kilometres apart rather than between habitats [25]. We found out that there is low species composition within Vudal agroecosystem and thus supports the findings of Novotny, Miller [12] as similar species can be widely distributed across 75,000 km² of a contiguous habitat. As the abundance was quantified using two types of lure traps, we found that methyl eugenol (ME) attracted higher number of fruit flies than cue-lure (Cue) [28-31].

Both Methyl eugenol and Cue-lure are contained phenyl propanoids which is a class of organic compounds having a structure of a C6– C3 skeleton [32]. Most species of Dacinae fruit flies (Diptera: Tephritidae) are readily attracted to Phenyl propanoids [33]. Methyl eugenol occurs naturally in plants while cue-lure is an artificial compound isolated from plant-borne substances [34, 35]. Cue-lure attracted individuals from three (3) genera; *Zeugodacus* (i.e. *Z. cucurbitae*), *Bactrocera* (i.e. *B. fraunfeldti*), and *Dacus* (i.e. *D. longicornis*) including cryptic species like *B. kirki* and *B. psidi* (table 1). Our findings support Metcalf (1990) that male Dacine fruit flies from genera *Bactrocera* Macquart and *Dacus* Fabricius are attracted to cue-lure while other species to ME. According to our results, we found out that ME attracted low number of species ($H = 3.94$) but Cue attracted more fruit fly species ($H = 4.47$) (table 1) [1, 5, 36, 37]. Methyl eugenol attracted mostly species from genus *Bactrocera*; *B. musae*, *B. umbrosa*, *B. curvifera*, and *B. laticaudus*. Both *B. dorsalis* and *B. obliqua*

were attracted to both cue-lure and methyl eugenol. Mature males in genera *Bactrocera* responds quickly to ME therefore it is generally recognized as a more powerful lure than cue-lure [38]. According to ancestral host-hypothesis, lures originated as plant kairomones serving as engagement stimulants to foster mating, while sexual selection-hypothesis suggests that the lures serve as male pheromone progenitor that affects the role of female in choice of mates [39].

The five most abundant species sampled were *B. musae*, *B. umbrosa*, *B. fraunfeldi*, *B. dorsalis* and *Z. cucurbitae*. These species are commonly found in tropical agroecosystems and can easily be sampled with Cu and ME parapheromones [40]. Our study affirms the findings of Gnanvossou, Hanna [40] that temperature positively influenced the abundance of melon fruit fly, *Z. cucurbitae*, while *B. dorsalis* abundance positively correlated with rainfall. The correlation between fruit fly (i.e. *B. musae*) abundance and temperature was negatively correlated whereas positively correlated with rainfall [19, 41]. As the temperature increases, the number of *Z. cucurbitae* decreases and wet season boosted the population of *Z. cucurbitae*. Backing our findings, Tan and Serit [42] recorded peak numbers of *B. dorsalis* males within wet season when starfruit, *Averrhoa carambola*, was fruiting. Starfruit is a common fruit tree grown around Vudal area and generally reaches peak fruiting in October which falls in wet season. Monthly rainfalls have been found to synthetically influenced the population dynamics of *B. dorsalis* [43]. Host plant availability and suitability as well as meteorological factors have proven to have an impact on fruit fly population dynamics and occurrence patterns [44-48]. Fruiting season of breadfruit, *Artocarpus altilis*, in the months of October and November also resulted in peak numbers of breadfruit fruit fly, *B. umbrosa*. The same can be observed in the mango fruit fly, *B. fraunfeldi* where the population peaks in October which is the ripening month of mango, *Mangifera indica*, in lowland Gazelle Peninsula of East New Britain. Fruit flies can adjust their resource searching patterns in response to changes in seasonal distribution of food, spatial and temporal factors [49]. The banana fruit fly, *B. musae*, had the highest abundance due to the study sites being dominated with banana plants growing around the vicinity. The population of *B. musae* also peaked in the month of October which is the fruiting season for most fruit trees. Studies in spatio-temporal dispersion patterns showed that fruit flies can move between habitats on a daily cycle to satisfy their feeding, mating and ovipositional requirements [49, 50]. Temperature was the abiotic factor inversely regulating the temporal population of *B. musae* in our study. High air temperatures can cause physiological stress to adult fruit flies and heavy rains can influence activities of fruit flies [51].

The distribution of species and their population within our three study sites can be attributed to several factors. Some of the species such as *B. musae*, *B. fraunfeldi*, and *B. dorsalis* were trapped in all three vegetation types in considerable numbers suggesting they move between habitats in search for food, mating and refugia [20, 49, 50]. Searching for these resources in some species of fruit flies can be dynamic [49, 52, 53]. Interspecific niche partitioning also plays an important role in the distribution of fruit fly species. According to ecology theory, organisms differ in their use of shared, limiting resources if they are to coexist [50] thus specialization is needed to reduce interspecific competition and promote species coexistence through niche partitioning [54]. Very high number of *B. musae* was recorded in primary forest (94.17%)

which we attributed to the niche being utilized as refugium [20, 49, 50]. Population of *B. fraunfeldi* was notable in cocoa plantation (17.52%) which might suggest that they are attracted to resources provided by cocoa flowers and mucilage [55]. The mucilage from harvested cocoa pods makes up 10% of total cocoa beans, with soluble solids up to 17.78° Bx, pH of 3.43–3.5, and is rich in sugar, minerals, organic acids and phenolic compounds [56]. *Z. cucurbitae* and *B. dorsalis* were mostly trapped in cocoa plantation which we attributed to the food resources provided by cocoa [55, 56]. *B. umbrosa* numbers peaked in secondary forest which is mainly due to sufficient availability of host plant, *A. altilis* [49, 52, 53] and mating purposes as fruiting season also signals congregating females [49, 50]. According to Sati [57], *B. umbrosa* has a narrower host range and only oviposit in *Artocarpus* species under Moraceae family. Few invasive species not endemic to Papua New Guinea (PNG) were collected during the study but had low numbers. Examples of these species were; *B. kirki* which is originally distributed in Western Samoa, American Samoa, Fiji Islands, Tonga, Wallis & Futuna, Niue, and Tahiti, and, *B. laticaudus* which is endemic to Australia [7]. *B. kirki* was responsive to Cue and only three specimens were collected in primary forest thus utilizing the forest niche as refugium [20, 49, 50].

Frugivorous insects like fruit flies can be categorized as monophagous (utilizing a single host plant species); stenophagous (a few closely related species under a single plant family); oligophagous (two or few plant families); or polyphagous (utilizing many plant families). *B. umbrosa* can be classified as oligophagous or specifically stenophagous since it feeds on several species of plants under a single family, Moraceae [7]. *B. dorsalis* is polyphagous or generalist, but shows preference to mango and guava over other fruits, *Z. cucurbitae* (polyphagous) prefers cucurbitaceous plants, but oviposits on other fruits, and *B. oleae* (monophagous) prefer only olives for their development [30]. Both *B. musae* and *B. fraunfeldi* are classified as polyphagous since the former respectively utilizes 16 hosts from nine families, and the latter utilizes 109 hosts from 37 families [7]. According to Novotny, Clarke [11], fruit flies exhibited low host specificity with respect to congeneric plant species but much higher, and similar with respect to both confamilial genera and interfamilial.

A complex of cues from the host plants within the three agro-habitats, parapheromones (Cue/ME), and meteorological factors played an essential role in determining the spatio-temporal population of fruit flies. Since we were using parapheromones for trapping sexually matured male fruit flies, it has to be correlated with changes in their olfactory circuitry [30]. Through evolution, generalist species might have conserved olfactory receptor neurons while specialists would have lost some of these neurons on the expense of others [58, 59]. In our study, both *Z. cucurbitae* ($p < 0.05$, $r = +0.36$) and *B. dorsalis* ($p < 0.01$, $r = +0.44$) had positive correlation with rainfall suggesting that they respond better to olfactory cues during wet season. All three species, *B. musae* ($p < 0.05$, $r = -0.28$), *Z. cucurbitae* ($p < 0.05$, $r = -0.40$) and *B. fraunfeldi* ($p < 0.05$, $r = -0.35$) showed negative correlation suggesting that increase in temperature might have caused physiological stress in adult fruit flies thus lowering their population [51].

Conclusion

This study finds that there is low species composition within a typical tropical agroecosystem and thus similar species can be

widely distributed across a contiguous habitat ^[12]. However, the abundance was significant among the three study habitats; cocoa plantation, secondary forest and primary forest. Several factors influenced the abundance of fruit flies within each habitat. Meteorological factors such as temperature and rainfall exert significant impact on fruit fly population and their distribution among the three study sites. Wet season recorded higher numbers while high air temperature reduces the activity of fruit flies. Host availability and fruiting season contributed positively to peak numbers of fruit flies. Most of the fruit fly species recorded their highest abundance in the month of October which signifies the fruiting season. Specialization and generalization are needed to reduce interspecific competition and promote species coexistence through niche partitioning ^[54]. The matured male species are able to utilize different plant resources and cues for feeding and mating. The luring of matured male fruit flies to parapheromones, Cu and ME, is often correlated with changes in their olfactory circuitry. Finally, the discovery of exotic and invasive species such as *B. kirki* is of quarantine interest.

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