The significance of climate in the pollinator dynamics of a tropical agroforestry system

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Abstract

Even though many globally important tropical agroforestry crops are partially or completely dependent on insect pollination, the conditions influencing pollinator abundance in these systems are often incompletely understood. This is particularly the case for cocoa midges (Diptera: Ceratopogonidae), which are essential for cocoa pollination and thus yield, but agro-ecological management frequently neglects them. We report the first assessment of cocoa midge population dynamics from two Caribbean countries across a full year, and relate this to seasonal climate variables.

We used static suction traps along transects to sample insects monthly, from six cocoa farms across three Caribbean islands, with a particular focus on known pollinators of cocoa. A total of over 87,000 insects were captured, including more than 1800 cocoa midges. Midges were present in all months of the survey and on all sites, but typically comprised less than 2% of the total insects caught. At least twelve different species of cocoa midges were identified from this survey. The previous month's rainfall positively predicted cocoa midge absolute abundance and further analysis also revealed a relationship between rainfall and relative midge abundance. In particular, during drought periods, midge numbers were very low, consistent with their larval ecology. Humidity and mean daily maximum and minimum temperatures did not relate to midge abundance. Rainfall negatively influenced the Shannon-Weaver index. The findings highlight the possible threat of droughts to cocoa pollination services and the importance of proactive farm management to support them.

Keywords: pollination; biodiversity; rainfall; agroforestry; Ceratopogonidae; agroecology

1 Introduction

Extensive research been carried out on factors impacting pollinator distribution and abundance in semi-natural and agricultural systems in temperate regions over recent decades (Vanbergen and The Insect Pollinators Initiative, 2013; Rader *et al.*, 2016). Far less work, in comparison, has taken place in study systems located in the tropics, especially the Caribbean islands. More information is needed about pollination in the tropics, as these areas are likely to be affected severely by climate change (Intergovernmental Panel on Climate Change, 2014), which may impact negatively on ecosystems services and lead to reduced yields (Settele *et al.*, 2016) and therefore impact incomes and livelihoods.

One system of particular interest in this respect is cocoa (*Theobroma cacao* L.): a major tropical agroforestry crop with rising demand worldwide and of high value to growers, who are often resource-poor smallholders. Yields of this crop depend upon successful transfer of pollen between flowers; pollinator exclusion in some cultivars has been found to decrease fruit set to zero (Bos *et al.*, 2007). Recent studies have shown significant pollination limitation in several regions (Groeneveld *et al.*, 2010; Forbes and Northfield, 2017). Pollination is achieved primarily by midges (Diptera: Ceratopogonidae) (Billes, 1941; Posnette, 1944) with other small Diptera such as Cecidomyiidae and similar insects making possible secondary contributions (Salazar-Díaz and Torres-Coto, 2017). Cocoa flowers are relatively small (10 mm long), with a specialized morphology that restricts which insects can pollinate them successfully. As a consequence, relatively few taxa can be effective pollinators, and evidence indicates that Ceratopogonidae are most effective at carrying sufficient pollen to ensure successful pollination (Toledo-Hernández *et al.*, 2017).

This crop often forms part of a diverse agroforestry system, and as such the potential to support invertebrate and vertebrate biodiversity on cocoa farms is considerable (Bisseleua *et al.*, 2009). However, published surveys of biodiversity, and particularly midge diversity, from cocoa plantations in the Caribbean – where cocoa farms are often medium-sized and grown alongside shade and fruit trees – are rare compared with those from other parts of world (Winder, 1978; Frimpong *et al.*, 2009; Frimpong *et al.*, 2011; Deheuvels *et al.*, 2014). Consequently, there is much still unknown about the abundance and species composition of cocoa pollinators in this region. It is currently very difficult to predict the impact of global change on pollination services in cocoa plantations generally, and in the Caribbean in particular. It has previously been hypothesized that rainfall, due to its impact on soil and vegetation moisture, is an important factor affecting cocoa pollination (Entwistle, 1958; Toledo-Hernández *et al.*, 2017), because Ceratopogonidae larvae develop primarily in moist, decomposing vegetable matter such as cocoa pods and leaf litter (Winder, 1978; Adjaloo *et al.*, 2013). This has not yet been tested in the Caribbean despite the fact that Caribbean countries are expected to experience decreased rainfall in future (Intergovernmental Panel on Climate Change, 2014).

Understanding the link between on-farm conditions and cocoa midge abundance is key to targeting farm management to ensure continuing pollination services and support yields. As cocoa suffers a pollination deficit (Groeneveld *et al*., 2010), there is increasing interest in targeting management to increase cocoa pollinator abundance globally.

This study sought to determine the abundance and species diversity of cocoa midges on three islands in the Caribbean (Trinidad, Tobago and Jamaica), evaluating their phenology in relation to the seasons. This enables consideration of the interaction between climate and farm management in safeguarding future pollination services in this important system. In particular, we studied the relationship between various climatic factors (rainfall, humidity and mean maximum/minimum daily temperatures) and adult midge populations from six farms. We also explored the relationship between climate and variability in overall invertebrate diversity within and between these locations. Our specific hypotheses were as follows:

1. Rainfall over the previous month is a significant predictor of absolute and relative cocoa midge (Ceratopogonidae) abundance.
2. Rainfall is a weaker predictor of Cecidomyiidae (secondary pollinator) abundance (because they do not normally reproduce in moist, rotting vegetable material).
3. Humidity is a positive predictor of insect and specifically Ceratopogonidae abundance.
4. There is a weak link, if any, between temperature and Ceratopogonidae and Cecidomyiidae abundance (because temperature is relatively seasonally uniform in the Caribbean).

2 Materials and methods

2.1 Sites

We sampled from four sites in Trinidad and Tobago (two on Trinidad from February 2013 to January 2014, two on Tobago from March 2014 to February 2015) and two sites in Jamaica from October 2013 to September 2014, with details of locations, cocoa cultivars grown and farm size contained in Table 1. The sampling periods were free from hurricanes and severe tropical storms. Both Trinidad and Jamaica experienced droughts during the sampling period, but it is difficult to find years in which none of the three islands experienced some level of drought.

The wet seasons in both Trinidad and Tobago and Jamaica occur from approximately May/June to October/November, and mean temperatures are broadly equivalent: the mean temperature for Trinidad during the sampling period was 27.9°C (range 19.6 – 32.1 °C, Tobago was 27.8°C (range 21.8 – 31.2 °C) and Jamaica was 25.6°C (range 20.2 – 32.4°C).

2.2 Static suction traps

Battery-powered suction traps with a bespoke design (Acis R&D, Plymouth, UK) to collect small, fragile flying insects were used. A full description of the traps is included in Appendix A and shown in Fig. S1. They were suspended in trees at approximately head-height (between 1.2 m and 1.7 m above the ground), a height at which trees also exhibit significant flowering.

2.3 Sampling

Five traps were deployed on each site, regularly spaced along transects of 40 m (i.e. 10 m apart). Transects were selected based on accessibility and compatibility with farm activities, where possible encompassing both “edge” and “central” parts of the plantation. Traps were suspended from the nearest cocoa tree branch to the 10 m transect point that was at suitable height. Trapping took place for a 72 h period each month for 12 months on each site, with daily collections of insects during the trapping period. Traps were deployed at consistent locations along the transect at the start of each monthly trapping period. Samples were stored in >90% ethanol, in individual 30 ml screw-topped tubes marked with location, date and trap number within the transect.

Insects were identified to order level, and family where possible, with particular emphasis on small Diptera. The dominant observed species of Ceratopogonidae were identified to species level; Cecidomyiidae, as potential secondary pollinators extremely abundant flies in the samples, were also counted and analyzed but not identified beyond family level. Non-insect invertebrates (e.g. spiders) were recorded and identified to class level, but not analyzed.

2.4 Statistical analyses

Statistical analyses were performed in R version 3.2.4 via RStudio version 0.99.893 (R Development Core Team, 2008). Insect diversity was calculated using the order level as a proxy for total diversity (shown by Biaggini *et al.* (2007) to be valid), as it was not possible to identify all taxa in the samples to the same degree of taxonomic specificity in all countries. The order-level diversity was expressed as a Shannon-Weaver index (H') (Shannon, 1948), calculated as per Equation 1.

$$H' = -\sum_{i=1}^{S} p_i ln(p_i)$$

(Equation 1)

In which *S* is the species (or order) richness and *p* is the probability of each taxon occurring in the sample.

Ceratopogonid and Cecidomyiid numbers, the % of total daily sample comprising Ceratopogonidae, insect diversity and overall trap catches were tested for relationships with climate data for the regions during the sampling period using long-term climate datasets from the Jamaican Meteorological Service (Meteorological Society of Jamaica, 2015) and the Trinidad and Tobago Meteorological Office (Trinidad and Tobago Meteorological Service, 2017). Both of these organizations provide daily data on air temperature and humidity collected from automated weather stations at fixed locations and calculated from hourly data recordings, one being located at the OR site. The Jamaican Meteorological Service also collects rainfall data from a national network of monitoring locations, with rainfall being checked at 07:00 daily. Rainfall data for Trinidad and Tobago is collected from the two Meteorological Office weather stations at airports daily.

Initial explorations of the four climatic variables (rainfall, humidity, high temperatures, low temperatures) indicated a high degree of cross-correlation between them. Consequently, a Principle Components Analysis (PCA) was performed in the four climatic variables to account for this and reduce the number of variables required in the model. The PCA revealed that 99.5% of the variance of these explanatory variables were accounted for by PC1, which comprised a 99.9% contribution from the rainfall variance and less than 2% from each other variable (Fig. S2; Table S1). PC2 comprised 96.4% of the humidity variance. Further analysis thus proceeded using only PC1, which was dominated by rainfall and PC2, which was dominated by humidity but also incorporated a contribution from daily mean minimum temperature. Using PC1 and PC2, a multiple regression was performed with total number of insects, and number of Ceratopogonidae and Cecidomyiidae (all log-transformed), Shannon at order level, and

Ceratopogonidae as a % of the total catch, but in all cases including trap identity within each site as a random factor, as there were indications of high site-to-site variability which did not relate to any measured variable (Fig. S3).

3 Results

Each trap caught a mean of 91.5 ± 2.1 (mean ± s.e.m.) insects per 24-hour period. The highest catch recorded was from the L'Eau Estate (LE), Tobago, in April, with 529 insects in a single trap over a 24-hour period; while some low catches were recorded these were sometimes due to degradation of the samples. Some samples had to be excluded as rainfall had caused the ethanol to be diluted, resulting in decomposition of insect material, or because sample tubes degraded in storage, causing leakage and damage to contents. Some months had incomplete data sets due to an equipment failure and time commitments of farmers. Consequently, analysis was based on 955 samples (out of a total theoretical planned of 1080), comprising a total of 87387 arthropods. Diptera dominated the samples (a mean of 69.1 ± 0.6 %). Ceratopogonidae were not abundant, but were present on every site surveyed, and in every month throughout the survey, comprising a mean of 1.9 ± 0.07 % (mean ± s.e.m.) of the total sample, with up to 31 individuals per trap (a mean of 2.0 ± 0.1). This was not significantly different between Trinidad (2.1 ± 0.2%), Tobago (1.8 ± 0.08%) and Jamaica (1.9 ± 0.02%).

The sites in Trinidad, Tobago and Jamaica showed some significant differences in diversity at the Order level (Fig. 1a). Overall, the private farm in Trinidad (GC) had the lowest diversity at order level (0.71) whereas a private farm in Tobago (LE) had the highest (0.96). The highest regular catches of Ceratopogonidae came from the government site (LR) in Trinidad, with 3.6

midges per trap per month (Fig. 1b). This was also the largest farm involved in the study. However, a private farm (PR) in Tobago yielded the two individual highest Ceratopogonidae catches (31 and 24 insects, both during October 2014).

Catches of Ceratopogonidae were typically higher during the wet season (Fig. 2). Conversely, flowering in cocoa does not relate predictably to rainfall except during extreme drought (Fig. S4). Observations of the study sites in 2014-15 (Bridgemohan, unpublished data) provided more detailed information about flowering phenology. On Trinidad, the cocoa trees reached peak flowering numbers during September 2014 (with a second, smaller flush in June, despite May 2014 having less than 20mm rainfall). The September flush saw flower numbers per tree increase by 2-3 times relative to the mean. On Tobago, the flowering peaks were recorded during May-June and November, with the highest number of flowers 1.7 times the mean. In Jamaica, the peaks of flowering occurred during April-June (dry season) and November, with the peak flowering presenting 2.4 times the mean flower number per tree. In all cases, peaks of flowering occurred both during rainy periods and during extended dry periods, which would coincide in the latter case with low midge numbers.

The initial simple regressions indicated significant associations between rainfall and Ceratopogonidae catches (positive; Fig. 3a) and H’, the Shannon diversity at order level (negative; Fig. 3b) (linear regression, Ceratopogonidae: $t = 3.551$, $p = 0.0004$; H’: $t = 9.807$, $p < 0.0001$), and humidity and numbers of Cecidomyiidae per trap (positive; Fig. 3c), and H’ (negative; Fig. 3d) (linear regression, Cecidomyiidae: $t = 3.261$, $p = 0.0012$; H’: $t = 3.866$, $p = 0.00012$). There was also a negative association between the daily minimum temperature and the number of Cecidomyiidae caught (Fig. 3e) (t = 3.058, p = 0.0023) but there was no significant relationship between any of the other climatic variables and any of these measures. The PCA revealed that most of the variability in climate data relates to the rainfall, with humidity a minor component, and the temperature variables more minor still (Table S2, Fig. S2).

The multiple regressions (summarized in Table S3) provided more information, revealing that Ceratopogonidae could be predicted by PC1 significantly (PC1 was largely comprised of rainfall) (F_1 = 15.36, p < 0.0001, significant at α = 0.01) but after Bonferroni correction for multiple tests, not PC2 (comprised largely of humidity) (F_1 = 4.0045, p = 0.0457, significant at α = 0.01) (Fig. 4a,b). Cecidomyiidae, conversely, were not predicted by PC1 or PC2 (PC1: F_1 = 0.0010, p= 0.975; PC2: F_1 = 0.713, p = 0.3988) (Fig. 4c,d). Total insects were not predicted by either variable after Bonferroni correction (PC1: F_1 = 5.701, p = 0.0172 NS at α = 0.01; PC2: F_1 = 3.425, p = 0.0645) (Fig. 4e,f). Ceratopogonidae as a % of the total catch was predicted only by PC1 (F_1 = 7.98, p = 0.00482) but not PC2 (F_1 = 1.11, p = 0.291) (Fig. 4g,h). The insect diversity, as measured by H', was strongly predicted by PC1 (i.e. associated with rainfall) (F_1 = 96.70, p < 0.0001) but not PC2 (F_1 = 5.87, p = 0.0156, NS at α = 0.01) (Fig. 4i,j). This accords generally with the initial analyses, indicating that rainfall predicted some variables but humidity and temperature did not remain as significant predictors after accounting for the cross-correlation with rainfall.

Species of Ceratopogonidae identified from trap catches in Trinidad and Jamaica are listed in Table S4, with some being new records for the respective countries. Almost all the Ceratopogonidae caught were found to be *Forcipomyia* or *Dasyhelea*, both genera associated with cocoa pollination (*Forcipomyia* particularly so) (Winder and Silva, 1972; Winder, 1978; O'Doherty and Zoll, 2012). Further detailed study of the Jamaican samples revealed that 41% of the Ceratopogonidae were of just three species (*F. pictoni*, *F. bicolor* and *F. genualis*), though the proportions differed between the two sites (FP had more *F. bicolor* and OR had more *F. genualis*) (Fig. 5). Furthermore, the frequencies of *F. bicolor* and *F. genualis* were not strongly correlated within a site; in some months one was relatively numerous and the other nearly or entirely absent (Fig. 6). Different species assemblages were found on each island, but past literature (see Table S4) indicates that most of the species found are likely to be cosmopolitan across the Caribbean region.

4 Discussion

Cocoa is highly dependent on pollination by small Diptera, in particular Ceratopogonidae (Posnette, 1944; O'Doherty and Zoll, 2012). Safeguarding cocoa pollination services in order to support crop yields and farmer incomes requires an understanding of the insects' ecology, the factors underpinning their population dynamics, and the resilience of their populations in different sites and regions. In this study, we monitored pollinators as part of the invertebrate fauna across three Caribbean islands, and found that their numbers fluctuate substantially across the year, but according to predictable patterns relating to recent rainfall.

We established that cocoa midges were present on all the cocoa farms surveyed throughout the year, even partway through the dry season, and at no time were Ceratopogonidae entirely absent. This is similar to the result found by Frimpong *et al.* (2011) in Ghana, but repeated across multiple islands in the neotropics and including some larger farms. Comparing to a smaller dataset collected on the same sites in a different year (Bridgemohan et al. unpublished) evaluating flowering phenology, we found that that their peak numbers often coincide with intensive periods of cocoa flowering (Fig. S4 a, b), but that the synchrony is not exact, with cocoa flushes also occurring at times when midge numbers are typically low. This indicates a need to actively manage plantations for pollinators during the flowering seasons to ensure sufficient pollinators are present when they are most needed.

The relationship between cocoa midge populations and recent rainfall also fits with the results of Frimpong *et al.* (2011), but we specifically included analysis of the relationship between these variables over the sampling period, providing new information and specifically as it relates to the Caribbean. Our findings correspond well with existing knowledge about the larval stages of Ceratopogonidae. The majority of Ceratopogonidae larvae are semi-aquatic or moisture-loving, developing in damp, organic-rich substrates such as leaf litter, moss, bromeliads and especially rotting cocoa pods and slices of banana stem (Winder and Silva, 1972; Winder, 1978). Our findings indicate cocoa midge abundance relates primarily to rainfall, probably due to the need for moist refugia during the larval stage (which comprises the majority of their approximately 28-day life-cycle) (Soria and Wirth, 1977). Moisture at ground level is predicted to affect the availability of nesting sites for the midges at dry times of year limiting larval development and possibly survival. During the dry season, damp, decomposing cocoa pods, leaf litter, etc. become increasingly unavailable, forcing insects to breed in limited refugia. Population recovery occurs rapidly when rains return, suggesting that some species may enter a partial diapause when moisture conditions drop. In contrast, we did not find a comparable relationship between abundance of Cecidomyiidae on farms and recent rainfall.

This group mostly does not have free-living larvae (most develop inside plant galls and some associated with cocoa flowers live in the *dry* exocarp of pods (Young, 1985)) and therefore drying of the soil and litter layers will affect this group to a lesser extent. Cecidomyiidae are relatively frequently recorded from cocoa flowers (Salazar-Díaz and Torres-Coto, 2017), are attracted to steam distillate of cocoa flowers (Young *et al.*, 1989; Young and Severson, 1994), and a few species do provide pollination services (Young, 1985). However, the majority of this taxon are poor transporters of pollen, have very long legs which preclude complete entry into the anther hoods of cocoa flowers, and tend to deposit pollen on staminodes rather than stigmas (Kaufmann, 1973). Consequently, they are normally considered poor pollinators (Entwistle, 1958) unless their populations are very high.

An alternative possibility that could account for the relationship between rainfall and midge numbers is a third factor, e.g. forage availability, which is affected by rainfall and goes on to alter midge populations. Saunders (1959) discovered that presence of cocoa flowers increases the longevity of female midges, but native Ceratopogonidae species are found worldwide and predate the introduction of cocoa in many countries (Winder, 1978) so there is no evidence cocoa flowers are essential for midge survival. Cocoa midges may use other sources of nectar as well, and many plants have reduced nectar secretion during hot, dry periods (Leiss and Klinkhamer, 2005), reducing potential food availability; however, this would only impact older, feeding adults, not larval development or freshly eclosed young adults.

The relationship between rainfall and the overall insect diversity is a different one, with diversity generally negatively relating to the Shannon-Weaver index. It is likely this is due to the index measuring evenness of taxa; wet conditions are likely to favor the samples being dominated by a few highly abundant groups such as non-biting midges or thrips, which will serve to lower the diversity measure.

Our study also included consideration of temperature and its possible impacts. However, temperature has relatively subtle fluctuations year-round in the Caribbean islands where we sampled. Consequently, we found it did not impact significantly on cocoa midge numbers in our study. However, we did note an association (negative) with Cecidomyiidae numbers, in which lower mean daily minima predicted higher Cecidomyiidae trap catches. One possibility is an acute effect of cooler temperatures, resulting in more resting behavior in trees, where the traps were placed.

We therefore recommend that ecological management of cocoa estates should focus on moisture retention on cocoa farms, providing refugia for Ceratopogonid larvae to continue to develop, even during the dry season. This could include creation of specific areas of cocoa pods or banana pseudostem, either piled up or placed within a shallow depression to reduce drying; this has been effective in Australia for improving pollination services. In that case, the pollination limitation was primarily due to lack of breeding medium on the plantations, which suffered low rainfall and were heavily irrigated (Forbes and Northfield, 2017). Banana pseudostem has been recommended for pollinator habitat in Ghana, where the presence of banana or plantain intercrops promotes midge abundance (Frimpong *et al.*, 2011). Other suggested interventions could include irrigation where it is environmentally appropriate; investigation of biochar; and addition of cover crops (particularly legumes) at ground level to reduce evaporation. Midges are thought to be limited in their dispersal ability (Kaufmann, 1975), so we recommend that the arrangement of breeding substrate takes this into account, with refugia provided throughout the plantation.

While considering the limitations of the sampling duration, our findings fit within the existing understanding that cocoa agroforestry is vulnerable to climate change (Wanger, 2014): altered weather patterns put these environments at increased risk of prolonged drought during dry seasons (Intergovernmental Panel on Climate Change, 2014). Our findings indicate that dry periods reduce cocoa midge abundance acutely, but more information is needed to extrapolate the implications were the regions under study to suffer multiple successive extreme dry seasons. *Forcipomyia* spp. persisted at low levels through the dry seasons we studied (which were considered in Trinidad and Jamaica to be drier than average) and recovered numbers on return of precipitation. However, the importance of rainfall in midge numbers highlights the need for farm management that is sensitive to this requirement, especially during drought periods.

There remain large gaps in our understanding of the species' ecology and population dynamics in different parts of the world. In this study we have investigated the spatio-temporal dynamics and diversity of Ceratopogonid cocoa pollinators, other small Diptera and other invertebrates in Caribbean cocoa estates. By sampling over the year we demonstrated that, while Ceratopogonids never disappear entirely and represent a small proportion of the total invertebrate fauna, the numbers show considerable variability within and between sites throughout the year. Our data indicate that the temporal variability is related primarily to rainfall. Reasons for the differences between sites may be more complex, relating to a combination of factors including elevation and slope, soil type, intercropping, shade, undergrowth and management type, which we were unable to address in full with this study alone. More research to examine these factors is desirable, in order to establish which are most important in determining midge numbers and, ultimately, pollination efficacy.

Overall, our data indicate a larger variation between sites within an island than between islands, in terms of the number of insects caught and the percentage of those that are possible cocoa pollinators. While each island has its own climatic patterns, soil types and endemic and indigenous species, the size of local midge populations relate more to the individual farms than to any consistent differences between islands. Our data indicate that of temperature, humidity and rainfall, the key factor influencing this is the recent rainfall.

5 Conclusions

We found that, in accordance with the ecology of the family, recent rainfall correlated with both overall invertebrate abundance on Caribbean cocoa estates, and of Ceratopogonid abundance specifically. Ceratopogonid abundance varied greatly between sites, but typically was less than 2%; even sites where the percentage was towards the lower end of this range produced cocoa successfully.

Provision of midge breeding substrate on cocoa farms is already commonly promoted by agronomists to farmers (Somarriba Chávez *et al.*, 2010), where disease control permits (as rotting cocoa pods can be a source of black pod infection). We add to this the suggestion that farmers may be able to increase pollinating midge numbers and their resilience on estates by encouraging moisture retention in refugia throughout the dry season.

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Supporting information

Appendix A – Details of suction trapping methodology, additional results, supplementary tables and figures

Tables

Table 1. Information about the sites studied

Farm (reference)	Location	Approx. elevation (m asl)	Government/Private	Size (ha) (approx.)	Trapping dates	System
La Reunion, Trinidad (LR)	10° 35′ 30″ N 61° 18′ 15″ W	22	Government	200	February 2013 – February 2014	Mixed varieties of cocoa (mostly TSH), some intercropping with banana
Gran Couva, Trinidad (GC)	10° 25′ 17″ N 61° 20′ 8″ W	76	Private	7	February 2013 – February 2014	Cocoa intercropped with mixed fruit trees; TSH varieties
L'Eau, Tobago (LE)	11° 12′ 54″ N 60° 37′ 54″ E	10	Private	2	March 2014 – February 2015	Rehabilitated estate with TSH and fruit trees.
Providence, Tobago (PR)	11° 12′ 11″ N 60° 43′ 53″ W	124	Private	1.2	March 2014 – February 2015	Farm under restoration, mostly TSH and some ICS accessions.
Highgate/ Orange River, Jamaica (OR)	18° 13′ 59″ N 76° 52′ 55″ W	136	Government	111	November 2013 – November 2014	Cocoa intercropped with mixed fruit trees; varieties ICS1, 60, 95, PA150, TSH, IMC67

Boscobel, Jamaica (FP)	18° 22' 53" N 76° 58' 17" W	176	Private	44	November 2013 – November 2014	Cocoa intercropped with coconuts; varieties ICS1, 60, 95

Figure legends

Fig. 1 (a) H’, Shannon-Weaver diversity index calculated at order level for the six sites. Letters above bars indicate statistically indistinguishable sites; (b) mean number of Ceratopogonidae individuals caught per month on each site.

Fig. 2 Mean Ceratopogonidae catches per trap, per 24h period, over the year for each site, and total rainfall (mm) in the 30 days preceding the sampling that month.

Fig. 3 Significant simple regressions between temperature variables and output variables: (a) rainfall and Ceratopogonidae catches (t = 3.551, p = 0.0004); (b) humidity and Cecidomyiidae catches (t = 3.261, p = 0.0012); (c) mean daily minimum temperature and Cecidomyiidae catches (t = 3.058, p = 0.0023); (d) rainfall and H’ (t = 9.807, p < 0.0001); (e) humidity and H’ (t = 3.866, p = 0.00012).

Fig. 4 Influence of principle components (PC) 1 and 2 on (a) total number of Ceratopogonidae caught per trap, per day (PC1, significant relationship, p < 0.0001); (b) total number of Cecidomyiidae caught per trap, per day; (c) total insects caught per trap, per day; (d) Ceratopogonidae as a percentage of the total trap catch, per trap, per day (PC1 significant, p =0.00482); (e) insect diversity as H’ (PC1 significant, p < 0.0001).

Fig. 5 Relative percentages of the three commonest *Forcipomyia* species from the two sites in Jamaica, demonstrating site-to-site variability in species dominance (OR = Orange River; FP = private farm near Boscobel).

Fig. 6 Month-to-month changes in abundance of two *Forcipomyia* species across both sampled sites in Jamaica.