

Effects of climate on pollination networks in the West Indies

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Abstract: We studied the effect of climate on the plant-pollinator communities in the West Indies. We constructed plots of 200 m × 5 m in two distinct habitats on the islands of Dominica, Grenada and Puerto Rico (total of six plots) and recorded visitors to all plant species in flower. In total we recorded 447 interactions among 144 plants and 226 pollinator species. Specifically we describe how rainfall and temperature affect proportional richness and importance of the different pollinator functional groups. We used three measures of pollinator importance: number of interactions, number of plant species visited and betweenness centrality. Overall rainfall explained most of the variation in pollinator richness and relative importance. Bird pollination tended to increase with rainfall, although not significantly, whereas insects were significantly negatively affected by rainfall. However, the response among insect groups was more complex; bees were strongly negatively affected by rainfall, whereas dipterans showed similar trends to birds. Bird, bee and dipteran variation along the climate gradient can be largely explained by their physiological capabilities to respond to rainfall and temperature, but the effect of climate on other insect pollinator groups was more obscure. This study contributes to the understanding of how climate may affect neotropical plant-pollinator communities.

Key Words: bees, birds, betweenness centrality, Diptera, functional groups, insects, plant–animal interactions, mutualisms, rainfall, temperature

INTRODUCTION

Climate is known to affect the distribution of organisms and their capability to establish interactions (Hawkins *et al.* 2003, Hegland *et al.* 2009). For instance, it is widely accepted that plant-pollinator assemblages differ along geographical (Cruden 1972, Kay & Schemske 2003, Kearns 1992, Kessler & Krömer 2000, Krömer *et al.* 2006, Olesen & Jordano 2002, Ollerton & Cranmer 2002, Ollerton *et al.* 2006, Primack 1983) and climatic gradients (Arroyo *et al.* 1982, Dalsgaard *et al.* 2009, Devoto *et al.* 2005, Medan *et al.* 2002), particularly temperature and rainfall (Arroyo *et al.* 1982, Dalsgaard *et al.* 2009, Devoto *et al.* 2005, Hegland *et al.* 2009, Medan *et al.* 2002). A widespread pattern often observed is a decrease in insect pollinator species richness at low temperatures and high humidity (Arroyo *et al.* 1982,

Cruden 1972, Devoto *et al.* 2005, Elberling & Olesen 1999, Hodkinson 2005, Kearns 1992, Olesen & Jordano 2002, Tanaka & Tanaka 1982). However, not all insect groups are affected equally (Arroyo *et al.* 1982, Janzen 1973, Janzen *et al.* 1976, Kearns 1992, Warren *et al.* 1988). For example, a widely cited global pattern is that flies replace bees in cooler and wetter habitats (Arroyo *et al.* 1982, Devoto *et al.* 2005, Elberling & Olesen 1999, Kearns 1992, Medan *et al.* 2002, Warren *et al.* 1988).

Compared with most insects, the activity of vertebrates is less constrained by rainfall and temperature, and vertebrates therefore gain importance as pollinators in wet and cold conditions (Cruden 1972, Dalsgaard *et al.* 2009, Kay & Schemske 2003, Kessler & Krömer 2000, Krömer *et al.* 2006, Stiles 1978). For instance, in the New World, hummingbirds become especially important pollinators where insect species richness and activity are reduced due to low temperatures and high rainfall (Aizen 2003), often encountered in mountains (Cruden 1972, Dalsgaard *et al.* 2009, Stiles 1978). There are several

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reports of plant species that are visited exclusively by hummingbirds in the highlands while visited by insect and hummingbird species at lower elevations, e.g. *Buddleja brasiliensis* in south-eastern Brazil (Sazima *et al.* 1996), *Costus* spp. in Central America (Kay & Schemske 2003), bromeliads in the Andes (Kessler & Krömer 2000, Krömer *et al.* 2006) and plant–hummingbird assemblages in the West Indies (Dalsgaard *et al.* 2009).

The aim of this study is to examine the effect of climate on pollinator richness and importance in pollination networks in the West Indies. The West Indies has a pollinator-limited flora (Spears 1987) subject to major disturbances (Dalsgaard *et al.* 2007), e.g. periodic hurricanes known to disrupt plant–pollinator associations (Rathcke 2000, Rivera-Marchand & Ackerman 2006). Although plant–hummingbird assemblages from the West Indies have been thoroughly studied (Dalsgaard *et al.* 2008, 2009; Kodric-Brown *et al.* 1984, Lack 1973), entire plant–pollinator communities have been neglected (although see Percival 1974), and no study has addressed the effect of climate on interactions between plants and pollinators in these islands. We used a network approach to examine and compare plant–pollinator communities across gradients in rainfall and temperature, and hypothesized that: (1) bird species richness would be less affected by rainfall and temperature than insect richness; (2) the response of the different insect groups will be complex, mirroring previously observed patterns, with bee diversity higher in dry and warm sites, and dipteran diversity higher in cooler, wetter habitats. In order to assess the importance of each of the functional groups of pollinators, we used several metrics: (1) proportion of interactions established; (2) proportion of plants visited in each community; and (3) topological importance, measured as proportional betweenness centrality (BC). By using these complementary measures we are able to reveal any potential change in pollinator importance along the climatic gradient. Moreover, this allows us to identify whether rainfall or temperature has a stronger effect on the pollination assemblages in the West Indies.

METHODS

Study sites

Plots with dimensions of 200 m × 5 m were delimited in distinct habitats at two altitudes in the islands of Dominica, Grenada (Lesser Antilles) and Puerto Rico (Greater Antilles), i.e. a total of six plots (Table 1). In Dominica, we sampled in the coastal scrub forest south of Pointe Michel and at the montane thicket-elfin woodland on the ridge towards Boeri Lake in the UN World Heritage Site of Morne Trois Pitons National Park; in Grenada in a coastal dry scrub woodland in the north-east part of the

Mt. Hartman Protected Area/Grenada Dove sanctuary and in a montane elfin woodland at the very top of Mt. Qua Qua in Grand Etang National Park; and in Puerto Rico in the coastal dry scrub forest of Guánica State Forest and UN Biosphere Reserve and at the montane thicket on the top of Monte de Guilarte State Forest. The lowland sites were situated in subtropical dry scrub forests, characterized by warm temperatures, mostly sunny days and low humidity. They are composed primarily of deciduous trees, shrubs and some cactus species. Some of the species, particularly in the Dominican lowlands, although native to the West Indies, are weedy species. The highland sites were situated in montane thicket-elfin woodlands, which are cooler, windier and with a higher rainfall, often being misty, especially in the early morning. These communities were composed mainly by evergreen short trees, herbs, epiphytes and palms. The relatively short vegetation at both lowland and highland habitats allowed us to sample the entire plant–pollinator assemblage.

The mean annual temperature of each site was calculated using the 0.65 °C per 100 m wet adiabatic lapse rate as in Buckley & Roughgarden (2006), taking the mean annual temperature at the closest weather station of each site on each island and calculating the resulting temperature at the elevation of each site (Table 1). The sites ranked in altitude from 9 m to 1154 m, mean annual temperature from 18 °C to 27 °C and mean annual rainfall from 799 mm to 7506 mm (Table 1). These differences in rainfall and temperature enabled us to study the diversity and topological importance of different pollinator groups along a climatic gradient.

Sampling methodology

We conducted our fieldwork between April and July 2005 (Dominica) and between March and June 2006 (Grenada and Puerto Rico). These months encompass the end of the dry and the beginning of the rainy season. We identified all plant species in flower within our study sites and observed their flowers for bird and insect visitation. Since most plant species did not flower for the entire fieldwork period, plants were sampled according to the length of their flowering.

We used a semi-random sampling methodology for our observations of flower visitation. We divided our plots into 10 × 5-m segments and randomly chose a sampling order and segment for each plant species (Dominica) or a starting segment and observed all plant species not previously observed before moving on to the subsequent segment, etc. (Grenada and Puerto Rico). In order to record as many visitors as possible, we restricted the observations of each plant species to different individuals and at different times of the day, preferably. Observations were conducted in fair weather conditions between 06h00 and 18h00 (Dominica) and between 06h00 and

Table 1. Description of the study sites from the West Indies. Total P = the number of plants observed in each site (i.e. total number of plant species in flower), P Visited = the number of plant species which received visits during our observations. A = Total number of pollinator species; Insect = Number of insect pollinator species; Insect Obs = Hours of insect observations; Av. Ins. Obs. = Average observation time (h) of each plant in each site for insects; Bird Obs. = Hours of bird observations; Av. Bird Obs. = Average observation time (h) of each plant in each site for birds. Rainfall data were collected by the Forestry and Wildlife Division of Dominica, by the Forestry Department, Grenada Ministry of Agriculture and the Departamento de Recursos Naturales y Ambientales of Puerto Rico. Mean annual temperature at each study site was calculated using the wet adiabatic lapse rate (0.65 °C per 100 m) as in Buckley & Roughgarden (2006), the mean annual long-term sea-level temperature close to each of our lowland study sites (NOAA National Weather Service) and the elevation of each study site.

	Dominica Lowland	Dominica Highland	Grenada Lowland	Grenada Highland	Puerto Rico Lowland	Puerto Rico Highland
Altitude (m)	9	813	38	705	10	1154
Rainfall (mm)	1905	7506	1287	3868	799	1914
Temperature (°C)	27.1	21.9	27.2	22.9	25.4	17.7
Total P	26	30	24	32	37	47
P Visited	25	24	18	23	26	28
A	64	20	39	39	35	29
Insect	61	16	37	34	32	26
Insect Obs	28.3	25.7	34.3	57.2	45.2	67.8
Av. Ins. Obs.	1.09	0.86	1.43	1.79	1.22	1.44
Bird Obs	96.0	120.0	126.0	247.5	253.0	351.5
Av. Bird Obs.	3.69	4.00	5.25	7.73	6.84	7.48

14h00 (Grenada and Puerto Rico). The visitation of insects (and other small-sized potential pollinators) was recorded during 10-min observation periods (a total of 275 h) at a distance of approximately 2 m from the flowers, while birds (and other large-sized potential pollinators) were monitored during 30-min periods (a total of 1215 h) from a distance of approximately 10 m (Tables 1 and 2). We recorded only floral visitors which touched the flower's reproductive organs, and thus may be regarded as potential pollinators.

Plant species were identified after Lack *et al.* (1997) and with the help of several experts. Plant species which received no visits were excluded from the analysis (Table 1). Bird species were visually identified after Raffaele *et al.* (1998). Bees were classified into families after Michener (2000), lepidopterans after Smith *et al.* (1994) and the rest of the insect groups after Triplehorn & Johnson (2005). Vouchers are kept at Aarhus University. A full list of the species included in the analysis is given in Appendix 1 and 2, and the networks will be deposited at the Interaction Web database (<http://www.nceas.ucsb.edu/interactionweb>) for open use.

Potential methodological biases

There were two potential methodological biases in this study. First, we were comparing communities belonging to islands of different sizes, which may affect species number and composition (MacArthur & Wilson 1967). However, total pollinator species richness is not related to island size ($r_s = -0.50$, $P > 0.05$; two-tailed Spearman correlation analysis). Instead, there were

strong, statistically significant relationships with rainfall and temperature (see Results).

A second potential bias was the difference in sampling effort between birds and insects. Birds were observed for a longer time than insect species (1215 h versus 275 h). This may inflate the importance of birds when compared with insect species. Nevertheless, a relative increase or decrease in visitation of birds or insect groups along the rainfall/temperature gradients are unaffected by differences in sampling effort between birds and insects. Hence, although caution should be taken when comparing the overall importance of birds versus insect species, the observed trends within groups along the climate gradient are genuine.

Data analyses

In our analyses, we focused on birds and insects since these groups accounted for more than 99% of the total species composition and interactions. The remaining 1% was comprised of lizards. Insects were further subdivided into bees, wasps, dipterans, lepidopterans and coleopterans. Other insect groups (hemipterans and thysanopterans) were represented by very few individuals and only in few sites and, due to their small number, were not analysed separately.

We calculated the proportional species richness of each pollinator group as the number of species belonging to that group out of the total number of species present in the community. In this way we can quantify how much each group accounts for the total biodiversity at each site. We measured different aspects of the importance of each pollinator group at each site as follows: (1) in order

to have a measure of their activity, we calculated the proportion of interactions established by each pollinator group in each community; (2) to quantify their flower feeding niche width, we estimated the proportion of plant species which were visited by each pollinator group in each site; and (3) to determine their topological importance for the cohesion of the network we calculated their proportional betweenness centrality. Betweenness centrality (BC) of species i was calculated in Pajek (<http://pajek.imfm.si/doku.php>) as

$$BC_i = 2 \sum_{j < k; i \neq j} [(g_{jk}(i)/g_{jk})/((n-1)(n-2))]$$

where n is the number of species in the community, g_{jk} is the number of shortest paths linking any two species, and $g_{jk}(i)$ is the number of those shortest paths which pass through species i (de Nooy *et al.* 2005, Wasserman & Faust 1994). BC ranges from zero, when there are no shortest paths passing through the focal species, to one, when the focal species is the only connection between all other species in the community, i.e. its extinction would lead directly to complete network fragmentation. Therefore, high- BC pollinator groups are important for the cohesion of the community. BC and other centrality measures have recently been used to identify potential keystone species in ecological communities (Estrada 2007, Jordan *et al.* 2006, Martín González *et al.*, in press). To calculate the centrality of each pollinator group, we summed the BC scores of all species belonging to a given group and divided by the total BC sum of all species in the network.

Since sampling effort was not equal for all communities, for all response variables we used proportional values in the analysis, as also done in similar studies (Devoto *et al.* 2005). Alternatively, we could use absolute numbers and add sampling effort as a predictor variable into the analysis. However, due to the number of communities sampled ($n = 6$), it is preferable to keep the number of predictor variables as low as possible. Hence, our decision was to use proportions rather than absolute numbers. Prior to analysis, rainfall was log-transformed and all proportional variables arcsine square root-transformed. All variables were normally distributed (Kolmogorov–Smirnov test). We examined the relationships between the response variables against rainfall and temperature using both single and multiple regression analysis in SPSS 15.0 (SPSS Inc., Chicago, USA). Although multiple regression has the advantage of taking into account the effect of rainfall and temperature simultaneously, the lower number of degrees of freedom in the multiple regression analysis may cause otherwise significant relations to become non-significant. Therefore, significant results in both single and multiple regressions are considered. Multicollinearity was not an issue in the multiple

regressions, since in all cases VIF < 1.2 and Tolerance > 0.8 .

RESULTS

Networks ranged in size from 68 pollinator and 25 plant species in the Dominican lowland to 27 pollinator and 24 plant species in the Dominican highland. Pollinator species diversity, number of interactions established, number of plants visited and mean BC of each group also varied considerably among communities (Table 2).

For each pollinator group, we analysed how variation in pollinator richness and importance related to each climatic factor using different regression models (Table 3). Although birds did not have any significant relationship with the climatic variables, they did show some marked and near-significant tendencies, particularly with rainfall. Bird proportional species richness remained relatively constant along the gradients, but they tended to have a higher proportion of interactions on the wetter and cooler end of the gradient (Table 3). Birds also visited a higher proportion of plant species and had a higher BC towards the wet end of the gradient in the single regressions (Table 3).

In contrast, for insects the proportional number of interactions significantly decreased with increasing rainfall when the single regression was performed (Table 3). However, none of the other variables was significant, although proportional species richness and proportional betweenness centrality (in single regressions) of insects were strongly affected by rainfall (Table 3).

Within insects, different functional groups showed significant and contrasting responses to climate, especially rainfall (Figure 1, Table 3). Bees were strongly and negatively affected by increasing rainfall: all variables observed (proportional species richness, proportional number of interactions, proportional number of plants visited and proportional BC) significantly decreased with rainfall both in the single and multiple regressions (Figure 1, Table 3). However, bees did not show any significant trend along the temperature gradient (Figure 1, Table 3).

The responses of wasps were different from those of bees. Wasp proportional species richness increased with rainfall, although their proportional BC decreased, when single regressions were performed (Figure 1, Table 3). The other variables did not show any significant trend (Figure 1, Table 3).

Dipterans had significantly lower proportional species richness in warmer sites, both in single and multiple regressions (Table 3). They were in fact the only insect group affected significantly by temperature. Moreover, their BC increased significantly with rainfall both with single and multiple regressions (Figure 1, Table 3).

Table 2. Absolute values of species richness and measure of pollinator importance for each pollinator group at each site. BC = betweenness centrality; Dipt. = dipterans; Lep. = lepidopterans; Col. = coleopterans.

	Birds	Insects	Bees	Wasps	Dipt.	Lep.	Col.
Number of species							
Dominica Lowland	3	65	11	4	14	22	3
Dominica Highland	4	21	0	6	6	1	1
Grenada Lowland	2	40	12	4	5	15	1
Grenada Highland	3	42	4	4	13	10	3
Puerto Rico Lowland	3	33	8	2	7	8	4
Puerto Rico Highland	3	27	1	3	11	5	4
Number of interactions							
Dominica Lowland	16	127	24	7	25	45	3
Dominica Highland	21	37	0	6	12	1	6
Grenada Lowland	5	52	24	6	5	30	1
Grenada Highland	11	48	12	5	15	20	4
Puerto Rico Lowland	8	55	21	3	8	9	4
Puerto Rico Highland	15	50	18	3	15	6	4
Number of plant species visited							
Dominica Lowland	10	24	10	3	15	11	3
Dominica Highland	11	21	0	3	10	1	6
Grenada Lowland	4	18	11	3	5	14	1
Grenada Highland	8	21	8	2	9	11	5
Puerto Rico Lowland	6	23	16	3	7	8	3
Puerto Rico Highland	11	25	18	3	10	4	3
Group BC							
Dominica Lowland	0.24	0.81	0.30	0.04	0.09	0.25	0.00
Dominica Highland	0.43	0.44	0.00	0.00	0.20	0.00	0.23
Grenada Lowland	0.04	1.18	0.51	0.19	0.00	0.48	0.00
Grenada Highland	0.34	0.76	0.21	0.01	0.15	0.29	0.10
Puerto Rico Lowland	0.19	0.53	0.08	0.35	0.00	0.00	0.00
Puerto Rico Highland	0.28	0.74	0.64	0.00	0.10	0.00	0.00

Lepidopterans were the only insect group which did not show any significant trend with rainfall or temperature.

Finally, for coleopterans the proportion of visited plants and proportional BC increased with rainfall, although the former only in the single regressions (Figure 1, Table 3). They were unaffected by temperature.

DISCUSSION

In this study, we have examined the response of the main pollinator groups to climatic gradients in six plant-pollinator networks on three islands in the West Indies. Besides reporting proportional species richness of each pollinator group, we also used several complementary parameters describing their importance as pollinators, including both simple proportions of interactions or plant species visited, and a more sophisticated network measure, i.e. betweenness centrality. All these different measures provide valuable information about how pollinators change in their patterns of interaction along the climatic gradient, giving us a stronger analytical background to support our conclusions than could be obtained by simple species counts alone.

As expected, rainfall and temperature significantly affected the composition and importance of pollinators, but in different ways, depending upon the functional group considered. Overall, rainfall was the more critical for most of the groups, being the main driver of pollinator change along the climatic gradient. A reason for this might be that the lowest temperature at our sites (c. 18 °C) is relatively high, whereas the highest rainfall (c. 7500 mm y⁻¹) is extremely wet and might therefore be a constraining factor for some insect pollinators. Yet, humidity was also found to be the main driver of pollinator turnover in a similar study in Patagonia, South America (Devoto *et al.* in press). Moreover, humidity has, at the macro-ecological scale, also been shown to be the most important factor determining invertebrate richness in warm climates (Hawkins *et al.* 2003). Still, not all pollinator groups responded equally along the gradient.

In concordance with studies from Central and South America, birds tended to become, although not significantly, more important as rainfall increases. This is probably because birds have a high energy demand and therefore feed on flowers even during rain, whereas insect pollinators are inactive under these conditions (Cruden 1972, Dalsgaard *et al.* 2009). The importance of birds as pollinators in wet areas is further supported by a higher

Table 3. Results of the simple and multiple regressions. For each response variable (% species richness, % plant species visited, % interactions, and % BC), the effect of the predictor variables is based on a comparison of three regression models containing: (1) mean annual rainfall (MAR); (2) mean annual temperature (MAT); (3) multiple regression models containing MAR and MAT. For each model, the standardized coefficients and their significance level is indicate for each of the predictor variables, as well as the model fit based on R_{adj} and P-value. ** $P < 0.025$, * $P < 0.5$. Dipt. = Diptera; Lep. = Lepidoptera; Col. = Coleoptera.

Taxa	Model	% Species richness				% Interactions				% Plant species visited				% BC			
		MAR	MAT	R_{adj}	P	MAR	MAT	R_{adj}	P	MAR	MAT	R_{adj}	P	MAR	MAT	R_{adj}	P
Birds	1	0.67		0.31	0.15	0.77		0.49	0.07	0.80		0.55	0.06	0.66		0.29	0.16
	2		-0.60	0.20	0.21		-0.65	0.28	0.16		-0.53	0.11	0.28		-0.51	0.07	0.31
	3	0.51	-0.39	0.29	0.28	0.60	-0.41	0.55	0.14	0.70	-0.25	0.49	0.17	0.54	-0.29	0.17	0.35
Insects	1	-0.79		0.52	0.06	-0.82*		0.60	0.04	-0.36		-0.09	0.49	-0.73		0.42	0.10
	2		0.63	0.24	0.18		0.67	0.31	0.15		0.64	0.26	0.17		0.18	-0.21	0.74
	3	-0.64	0.37	0.55	0.14	-0.66	0.40	0.69	0.08	-0.12	0.59	0.04	0.44	-0.79	-0.14	0.25	0.30
Bees	1	-0.83*		0.61	0.04	-0.91**		0.79	0.01	-0.88**		0.72	0.02	-0.84*		0.63	0.04
	2		0.76	0.46	0.08		0.24	-0.18	0.65		0.14	-0.23	0.79		-0.06	-0.25	0.91
	3	-0.62	0.50	0.82	0.03	-0.98**	-0.16	0.76	0.06	-0.99*	-0.26	0.72	0.07	-1.0**	-0.48	0.83	0.03
Wasps	1	0.83*		0.61	0.04	0.72		0.39	0.11	-0.30		-0.14	0.57	-0.82*		0.59	0.05
	2		-0.38	-0.07	0.46		0.02	-0.25	0.96		0.51	0.08	0.30		0.71	0.38	0.12
	3	0.81	-0.05	0.48	0.17	0.87	0.38	0.39	0.22	-0.11	0.47	-0.21	0.62	-0.64	0.45	0.74	0.06
Dipt.	1	0.57		0.15	0.24	0.70		0.37	0.12	0.41		-0.04	0.42	0.93**		0.82	0.01
	2		-0.90**	0.76	0.02		-0.72	0.40	0.11		0.10	-0.24	0.84		-0.61	0.22	0.19
	3	0.24	-0.80*	0.76	0.05	0.49	-0.52	0.53	0.15	0.54	0.32	-0.24	0.64	0.81**	-0.29	0.88	0.02
Lep.	1	-0.67		0.31	0.15	-0.48		0.04	0.34	-0.51		0.08	0.30	-0.10		-0.24	0.85
	2		0.67	0.30	0.15		0.70	0.36	0.12		0.70	0.37	0.12		0.63	0.24	0.18
	3	-0.47	0.47	0.39	0.22	-0.23	0.60	0.22	0.32	-0.27	0.60	0.26	0.30	0.18	0.70	0.04	0.44
Col.	1	-0.15		-0.22	0.78	0.63		0.24	0.18	0.85*		0.64	0.03	0.92**		0.80	0.01
	2		-0.67	0.32	0.14		-0.64	0.25	0.18		-0.37	-0.08	0.48		-0.29	-0.15	0.58
	3	-0.50	-0.88	0.44	0.19	0.44	-0.46	0.28	0.29	0.83	-0.03	0.52	0.15	0.96*	0.10	0.74	0.06

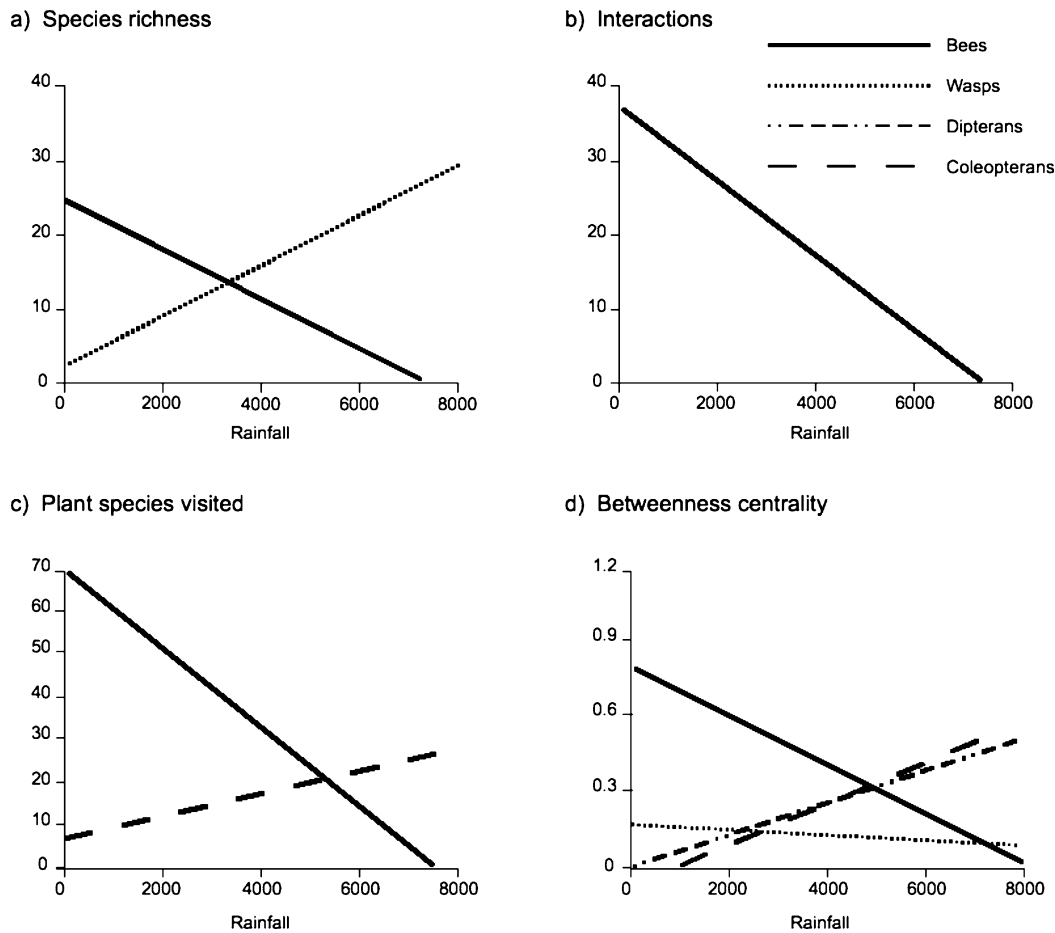


Figure 1. For the insect groups, the relationships between rainfall and the studied measures: pollinator species richness (a); pollinator group's number of interactions (b); pollinator group's number of plant species visited (c); and pollinator group's topological importance as betweenness centrality (BC) (d). Notice that raw values were used for the figures whereas transformed values were used for the analyses. Only significant relationships are shown, i.e. $P < 0.05$.

proportion of plants adapted to ornithophily in humid areas (Aizen 2003, Dalsgaard *et al.* 2009). This tendency of birds was coupled with an overall significant decrease in the importance of insects with increasing rainfall.

Within insects, the two major insect pollinator groups (bees and dipterans) showed opposite responses to climate, and thus partially replaced each other. The higher importance of dipterans at colder and wetter sites is not necessarily because of any selective preference from the flies, but because they are less affected than other insect groups by these factors (Kearns 1992). The reason may be their low energetic requirements, ability to sun-bask and use of heliotropic flowers (Arroyo *et al.* 1982, Kearns 1992, Kevan & Baker 1983). In contrast all variables observed for bees were greatly affected by increasing rainfall. Bees are very energy-demanding insects which require constant foraging for their nest building and offspring provisioning (Kearns 1992, Warren *et al.* 1988). High rainfall and low temperatures are unfavourable to their foraging (Cruden 1972, Kearns 1992, Michener

2000, Roubik 1989) and their nests are susceptible to fungal and bacterial diseases in high humidity conditions, which may be the reasons for their peak in diversity in dry, warm climatic zones (Michener 2000, Ollerton *et al.* 2006, Roubik 1989). Hence, the importance of bees at the wet end of our gradient decreases drastically, mirroring the global trend in bee species richness.

Whereas the trends shown by bees and dipterans can be explained by direct responses to climate, the effects of rainfall and temperature on the minor pollinator groups is more obscure. Wasp diversity increased with rainfall, mainly due to a higher diversity of pompilids. However, other non-climatic factors such as availability of hosts, strongly determine the distribution of these species. Interestingly, although more diverse in species at wetter sites, the interactions that they established were peripheral to the community, i.e. they visited relatively specialized plants. Lepidopterans did not show any significant trend. Lacking a general response to climate, non-thermoregulatory factors seem to have a

greater effect on lepidopterans (Warren *et al.* 1988). Finally, regardless of the expected lower species richness of coleopterans with increasing rainfall (Janzen 1973, Warren *et al.* 1988), coleopterans gained importance at this end of the gradient. However, since this group was formed by only a few individuals these results should be taken cautiously.

In conclusion, the effects of climate in pollinator species distribution and interaction patterns in the West Indies are complex. As in other geographic areas, most pollinator groups are affected by climate in terms of species richness and importance. The general trends found in our work are consistent with those found in similar studies, both from tropical (Cruden 1972, Kay & Schemske 2003) and temperate mainland assemblages (Arroyo *et al.* 1982, Devoto *et al.* 2005, Kessler & Krömer 2000, Krömer *et al.* 2006, Medan *et al.* 2002, Sazima *et al.* 1996, Warren *et al.* 1988). Most of these patterns can be directly explained by the pollinators' physiological capabilities to respond to rainfall and temperature. However, climate can also indirectly affect pollinators by controlling, for example, habitat heterogeneity, plant flowering patterns, floral productivity and phenotype, or nesting conditions (Devoto *et al.* in press). Understanding how rainfall and temperature affect pollinator species composition and importance is crucial for the preservation of pollination processes under future climatic change scenarios (Devoto *et al.* in press, Hegland *et al.* 2009, Ings *et al.* 2009). In this respect we advocate the use of complementary network measures to document any potential change in the pattern of interactions between plants and their pollinators. This study provides valuable information on pollination communities from the West Indies and on how the pollinator fauna relates to climatic factors in tropical communities.

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Appendix 1. Plant species present at each site.

Dominica lowland

- Asteraceae
Ageratum conyzoides L.
- Bignoniaceae
Tabebuia heterophylla (DC.) Britt.
Tecoma stans (L.) Juss. ex Kunth
- Boraginaceae
Cordia globosa (Jacq.) Kunth
- Euphorbiaceae
 Euphorbiaceae sp. 1
- Fabaceae
Desmodium sp.
Leucaena leucocephala (Lam.) de Wit
Tephrosia noctiflora Bojer ex Baker
- Lamiaceae
 Lamiaceae sp. 1
Leonotis nepetifolia (L.) Ait. f.
- Malpighiaceae
 Malpighiaceae sp. 1
- Malvaceae
Sida acuta Burm. f.
- Melastomataceae
Tetrazygia discolor (L.) DC.
- Myrtaceae
Psidium guajava L.
- Oxalidaceae
Oxalis barrelieri L.
- Rubiaceae
Erithalis fruticosa L.
Morinda citrifolia L.
- Rubiaceae sp. 1
Spermacoce assurgens Ruiz & Pavón
- Solanaceae
Solanum torvum Sw.
- Turneraceae
Turnera ulmifolia L.
- Verbenaceae
Citharexylum spinosum L.
Lantana hodgei/urticifolia
Stachytarpheta cayennensis (L. C. Rich.) Vahl
Stachytarpheta jamaicensis (L.) Vahl

Dominica highland

- Acanthaceae
Blechnum pyramidatum (Lam.) Urb.
- Arecaceae
Prestoea acuminata (Graham) Nicholson
- Asteraceae
Chromolaena macrodon (DC.) Nicolson
- Campanulaceae
Lobelia stricta Sw.
- Cyclanthaceae
Asplundia rigida (Aubl.) Harl.
- Ericaceae
Symphysis racemosa (Vahl) Stearn
- Gesneriaceae
Besleria petiolaris (Griseb.) Urb.
- Heliconiaceae
Heliconia bihai (L.) L.
- Lamiaceae
Hyptis atrorubens Poit.
Hyptis lanceolata Poir.
- Malvaceae
Wercklea tulipiflora (Hook. f.) Fryx.
- Melastomataceae

- Charianthus* sp.
Miconia ernstii Wurd.
Pterolepis glomerata (Rottb.) Miq.
- Rubiaceae
Manettia dominicensis Wernh.
Psychotria urbaniana Steyermark
Schraderia exotica (J. F. Gmel.) Standl.
Spermacoce assurgens Ruiz & Pavón
- Ochnaceae
Sauvagesia erecta L.
- Orchidaceae
Spathoglottis plicata Blume
- Siparunaceae
Siparuna glabrescens (Presl) DC.
- Urticaceae
Pilea parietaria (L.) Blume
- Verbenaceae
Stachytarpheta urticifolia Sims
- Zingiberaceae
Renalmia pyramidalis (Lam.) Maas

Grenada lowland

- Acanthaceae
 Acanthaceae sp. 1
 Acanthaceae sp. 2
- Apocynaceae
Rauvolfia viridis Willd. ex Roemer & Schultes
- Bignoniaceae
Tecoma stans (L.) Juss. ex Kunth
- Boraginaceae
Bourreria succulenta Jacq.
Heliotropium angiospermum Murr.
- Cactaceae
 Cactaceae sp. 1
- Convolvulaceae
Ipomoea batatas (L.) Lam.
- Cucurbitaceae
 Cucurbitaceae sp. 1
- Erythroxylaceae
Erythroxylum havanense Jacq.
- Euphorbiaceae
Croton flavens L.
- Fabaceae
Bauhinia aculeata L.
Chaetocalyx scandens (L.) Urb.
Leucaena leucocephala (Lam.) de Wit
- Malpighiaceae
Stigmaphyllon sp.
- Malvaceae
Melochia nodiflora Sw.
- Plumbaginaceae
Plumbago scandens L.
- Rubiaceae
Randia aculeata L.

Grenada highland

- Aquifoliaceae
Ilex sideroxyloides (Sw.) Griseb.
- Arecaceae
Prestoea acuminata (Graham) Nicholson
- Asteraceae
Mikania micrantha Kunth
- Campanulaceae
Lobelia cirsiifolia Lam.
- Gesneriaceae
Alloplectus cristatus (L.) Mart.

- Heliconiaceae
Heliconia bihai (L.) L.
 Lamiaceae
Hyptis atrorubens Poit.
 Marcgraviaceae
Marcgravia umbellata L.
 Melastomataceae
Charianthus purpureus × *grenadensis*
Nepsera aquatica (Aubl.) Naud.
 Myrtaceae
Myrcia citrifolia (Aubl.) Urb.
 Ochnaceae
Sauvagesia erecta L.
 Passifloraceae
Passiflora sp.
 Rubiaceae
Gonzalagunia hirsuta (Jacq.) Schum.
Malanea macrophylla Bartling ex Griseb.
Psychotria capitata Ruiz & Pavón
Psychotria guadalupensis (DC.) Howard
Psychotria muscosa (Jacq.) Steyermark
Schradera exotica (J. F. Gmel.) Standl.
Spermacoce assurgens Ruiz & Pavón
 Rutaceae
Citrus sp.
 Scrophulariaceae
 Scrophulariaceae sp. 1
 Verbenaceae
Stachytarpheta urticifolia Sims
- Puerto Rico lowland
 Apocynaceae
Pentalimon luteum (L.) Hansen & Wunderlin
 Bignoniaceae
Tabebuia heterophylla (DC.) Britt.
 Cactaceae
Melocactus intortus (P. Mill.) Urb.
Opuntia rubescens Salm-Dyck ex. DC.
Pilosocereus royenii (L.) Byles & Rowley
 Cappariaceae
Capparis flexuosa (L.) L.
 Erythroxylaceae
Erythroxylum areolatum L.
 Euphorbiaceae
Chamaesyce sp.
Croton discolor Willd.
Croton lucidus L.
 Fabaceae
Centrosema virginianum (L.) Benth.
Pictetia aculeata (Vahl) Urb.
Stylosanthes hamata (L.) Taubert
 Malpighiaceae
Stigmaphyllon floribundum (DC.) C. Anderson
 Malvaceae
Melochia tomentosa L.
 Myrtaceae
Eugenia foetida Pers.
 Polygonaceae
Coccoloba krugii Lindau
 Rhamnaceae
Colubrina arborescens (P. Mill.) Sarg.
- Colubrina elliptica* (Sw.) Briz. & Stern
Reynosa uncinata Urb.
 Rubiaceae
Erithalis fruticosa L.
Mitracarpus polycladus Urb.
Stenostomum coriaceum (Vahl) Griseb.
Strumpfia maritima Jacq.
 Sapindaceae
Hypelate trifoliata Sw.
 Verbenaceae
Lantana involucrata L.
- Puerto Rico highland
 Acanthaceae
Justicia martinsoniana Howard
 Aquifoliaceae
Ilex macfadynii (Walp.) Rehd.
 Arecaceae
Prestoea montana (Graham) Nicholson
 Asteraceae
 Asteraceae sp. 1
Bidens cynapiifolia Kunth
Elephantopus mollis Kunth
 Balsaminaceae
Impatiens walleriana Hook.f.
 Begoniaceae
Begonia decandra Pavón ex DC.
 Bromeliaceae
Guzmania berteroniana (Schult. & Schult. f.) Mez
 Campanulaceae
Lobelia portoricensis (Vatke) Urb.
 Cucurbitaceae
Cayaponia racemosa (P. Mill.) Cogn.
 Fabaceae
Desmodium adscendens (Sw.) DC.
Neorudolphia volubilis (Willd.) Britt.
 Lamiaceae
Hyptis sp.
Plectranthus scutellaroides (L.) R. Br.
 Malvaceae
Urena lobata L.
 Melastomataceae
Miconia sintenissi Cogn.
Micranium sp.
 Passifloraceae
Passiflora sp.
 Rosaceae
Rubus sp.
 Rubiaceae
Palicourea crocea (Sw.) Roemer & Schultes
Psychotria berteriana DC.
Schradera exotica (J. F. Gmel) Standl.
Spermacoce assurgens Ruiz & Pavón
Spermacoce ocymoides (Burm.)
 Scrophulariaceae
Schlegelia brachyantha Griseb.
 Solanaceae
Cestrum macrophyllum Vent.
 Zingiberaceae
Reanalimia alpinia (Rottb.) Maas

Appendix 2. Pollinator species and morphospecies present in our sites grouped by order and family whenever the information was available. Morphospecies names are given within each site, e.g. 'Apidae sp. 1' in Dominica lowland is not necessarily the same 'Apidae sp. 1' in Grenada lowland. Vouchers are kept at Aarhus University.

Dominica lowland

Birds

Emberizidae

Coereba flaveola (Linnaeus 1758)

Trochilidae

Eulampis holosericeus (Linnaeus 1758)

Orthorhyncus cristatus (Linnaeus 1758)

Bees

Andrenidae

Andrenidae sp. 1

Andrenidae sp. 2

Andrenidae sp. 3

Apidae

Anthophoridae sp. 1

Anthophoridae sp. 2

Apidae sp. 1

Apidae sp. 2

Apis mellifera (Linnaeus 1758)

Megachilidae

Megachilidae sp. 1

Unknown family

Apoidea sp. 1

Apoidea sp. 2

Wasps

Pompilidae

Pompilidae sp. 1

Pompilidae sp. 2

Scoliidae

Scoliidae sp. 1

Vespidae

Vespidae sp. 1

Dipterans

Chamaemyiidae

Chamaemyiidae sp. 1

Chloropidae

Chloropidae sp. 1

Chloropidae sp. 2

Chloropidae sp. 3

Muscidae

Muscidae sp. 1

Muscidae sp. 2

Syrphidae

Eristalis sp.

Syrphidae sp. 1

Syrphidae sp. 2

Syrphidae sp. 3

Syrphidae sp. 4

Syrphidae sp. 5

Syrphidae sp. 6

Tephritidae

Tephritidae sp. 1

Lepidopterans

Hesperiidae

Hesperiidae sp. 1

Hesperiidae sp. 2

Hesperiidae sp. 3

Lycaenidae

Lycaenidae sp. 1

Lycaenidae sp. 2

Lycaenidae sp. 3

Lycaenidae sp. 4

Lycaenidae sp. 5

Nymphalidae

Agraulis vanillae (Linnaeus, 1758)

Anartia jatrophae (Linnaeus, 1763)

Dryas iulia (Fabricius, 1775)

Junonia evarete (Cramer, 1779)

Marpesia petreus (Cramer, 1776)

Papilionidae

Battus polydamas (Linnaeus, 1758)

Pieridae

Ascia monuste (Linnaeus, 1764)

Pieridae sp. 1

Pieridae sp. 2

Pieridae sp. 3

Pieridae sp. 4

Pieridae sp. 5

Pieridae sp. 6

Tortricidae

Tortricidae sp. 1

Coleopterans

Chrysomelidae

Chrysomelidae sp. 1

Mordellidae

Mordellidae sp. 1

Unknown family

Coleoptera sp. 1

Hemipterans

Aphididae

Aphididae sp. 1

Lygaeidae

Lygaeidae sp. 1

Psyllidae

Psyllidae sp. 1

Psyllidae sp. 2

Unknown family

Hemiptera sp. 1

Thysanopterans

Unknown family

Terebrantia sp. 1

Tubulifera sp. 1

Dominica highland

Birds

Emberizidae

Coereba flaveola (Linnaeus, 1758)

Trochilidae

Cyanophaea bicolor (Gmelin, 1788)

Eulampis jugularis (Linnaeus, 1766)

Orthorhyncus cristatus (Linnaeus, 1758)

Wasps

Platygastridae

Platygastridae sp. 1

Platygastridae sp. 2

Pompilidae

Pompilidae sp. 1

Pompilidae sp. 2

Pompilidae sp. 3

Pompilidae sp. 4

Dipterans

Syrphidae

Syrphidae sp. 1

Syrphidae sp. 2

- Tachinidae
Tachinidae sp. 1
- Tephritidae
Tephritidae sp. 1
Tephritidae sp. 2
- Unknown family
Diptera sp. 1
- Lepidopterans
Hesperiidae
Hesperiidae sp. 1
- Coleopterans
Curculionidae
Curculionidae sp. 1
- Thysanopterans
Unknown family
Terebrantia sp. 1
Tubulifera sp. 1
- Grenada lowland
- Birds
Emberizidae
Coereba flaveola (Linnaeus, 1758)
Trochilidae
Orthorhyncus cristatus (Linnaeus, 1758)
- Bees
Apidae
Apidae sp. 1
Apidae sp. 2
Apidae sp. 3
Apidae sp. 4
Apidae sp. 5
Apis mellifera (Linnaeus, 1758)
- Megachilidae
Megachilidae sp. 1
Megachilidae sp. 2
Megachilidae sp. 3
- Unknown family
Apoidea sp. 1
Apoidea sp. 2
Apoidea sp. 3
- Wasps
Vespidae
Vespidae sp. 1
Vespidae sp. 2
Vespidae sp. 3
Unknown family
Hymenoptera sp. 1
- Dipterans
Bombyliidae
Bombyliidae sp. 1
Unknown family
Diptera sp. 1
Diptera sp. 2
Diptera sp. 3
Diptera sp. 4
- Lepidopterans
Hesperiidae
Chiomara asychis (Stoll, 1780)
Phoebis sp.
Polites sp.
Urbanus obscurus (Hewitson, 1867)
- Lycaenidae
Strymon sp.
- Nymphalidae
Agraulis vanillae (Linnaeus, 1758)
- Anartia jatrophae* (Fabricius, 1775)
Dryas iulia (Fabricius, 1775)
Mestra sp.
- Pieridae
Eurema sp.
Pieridae sp. 1
Pieridae sp. 2
- Sphingidae
Allopos sp.
- Unknown family
Lepidoptera sp. 1
Lepidoptera sp. 2
- Coleopterans
Cupedidae
Cupedidae sp. 1
- Grenada highland
- Birds
Emberizidae
Coereba flaveola (Linnaeus, 1758)
Trochilidae
Eulampis holosericeus (Linnaeus, 1758)
Orthorhyncus cristatus (Linnaeus, 1758)
- Bees
Apidae
Apidae sp. 1
Apidae sp. 2
Apidae sp. 3
Apis mellifera (Linnaeus, 1758)
- Wasps
Pompilidae
Pompilidae sp. 1
Pompilidae sp. 2
Pompilidae sp. 3
Unknown family
Hymenoptera sp. 1
- Dipterans
Chironomidae
Chironomidae sp. 1
- Empididae
Empididae sp. 1
Empididae sp. 2
Empididae sp. 3
- Syrphidae
Syrphidae sp. 1
- Unknown family
Diptera sp. 1
Diptera sp. 2
Diptera sp. 3
Diptera sp. 4
Diptera sp. 5
Diptera sp. 6
Diptera sp. 7
Schizophora acalyprate sp. 1
- Lepidopterans
Gelechioidea
Gelechioidea sp. 1
- Hesperiidae
Chiomara asychis (Stoll, 1780)
Polites sp.
Urbanus proteus (Linnaeus, 1758)
- Nymphalidae
Agraulis vanillae (Linnaeus, 1758)
Dryas iulia (Fabricius, 1775)
Junonia sp.

- Pieridae
 Pieridae sp. 1
 Sesiidae
 Sesiidae sp. 1
 Unknown family
 Lepidoptera sp. 1
 Coleopterans
 Bruchidae
 Bruchidae sp. 1
 Curculionidae
 Curculionidae sp. 1
 Curculionidae sp. 2
 Unknown family
 Coleoptera sp. 1
 Reptilia
 Polychrotidae
Anolis richardii (Duméril & Bibron, 1837)
Anolis aeneus (Gray, 1840)
- Puerto Rico lowland
 Birds
 Emberizidae
Coereba flaveola (Linnaeus, 1758)
 Trochilidae
Anthracothorax dominicus (Linnaeus, 1766)
Chlorostilbon maugaeus (Audebert & Vieillot, 1801)
 Bees
 Apidae
 Apidae sp. 1
 Apidae sp. 2
 Apidae sp. 3
 Apidae sp. 4
 Apidae sp. 5
 Apidae sp. 6
Apis mellifera (Linnaeus, 1758)
 Halictidae
 Halictidae sp. 1
 Wasps
 Pompilidae
 Pompilidae sp. 1
 Vespidae
 Vespidae sp. 1
 Dipterans
 Bombyliidae
 Bombyliidae sp. 1
 Bombyliidae sp. 2
 Bombyliidae sp. 3
 Culicidae
 Culicidae sp. 1
 Curtonotidae
 Curtonotidae sp. 1
 Syrphidae
Eristalis sp.
 Syrphidae sp. 1
 Lepidopterans
 Lycaenidae
 Lycaenidae sp. 1
 Lycaenidae sp. 2
 Lycaenidae sp. 3
 Lycaenidae sp. 4
 Pieridae
Appias punctifera (d'Almeida, 1939)
Eurema palmira (Gundlach, 1881)
Phoebis semae (Linnaeus, 1758)
 Unknown family
 Lepidoptera sp. 1
 Coleopterans
 Cerambycidae
Tilloclytus sp.
 Mordellidae
 Mordellidae sp. 1
 Nitidulidae
Mystrops sp.
 Unknown family
 Coleoptera sp. 1
 Thysanopterans
 Thripidae
 Thripidae sp. 1
 Thripidae sp. 2
 Thripidae sp. 3
 Puerto Rico highland
 Birds
 Emberizidae
Coereba flaveola (Linnaeus, 1758)
 Trochilidae
Anthracothorax viridis (Audebert & Vieillot, 1801)
Chlorostilbon maugaeus (Audebert & Vieillot, 1801)
 Bees
 Apidae
Apis mellifera (Linnaeus, 1758)
 Wasps
 Pompilidae
 Pompilidae sp. 1
 Pompilidae sp. 2
 Vespidae
 Vespidae sp. 1
 Dipterans
 Syrphidae
 Syrphidae sp. 1
 Syrphidae sp. 2
 Syrphidae sp. 3
 Syrphidae sp. 4
 Syrphidae sp. 5
 Tachinidae
 Tachinidae sp. 1
 Unknown family
 Caliptrate sp. 1
 Caliptrate sp. 2
 Diptera sp. 1
 Diptera sp. 2
 Lepidopterans
 Hesperidae
Choranthus sp.
Wallengrenia otho (Smith, 1797)
 Nymphalidae
 Nymphalidae sp. 1
 Nymphalidae sp. 2
 Nymphalidae sp. 3
 Coleopterans
 Chrysomelidae
 Chrysomelidae sp. 1
 Curculionidae
Baridinae sp.
Phyllotrox sp.
 Unknown family
 Coleoptera sp. 1
 Hemipterans
 Reduviidae
 Reduviidae sp. 1
 Thysanopterans
 Phlaeothripidae
 Phlaeothripidae sp. 1