November 2008

The effects of intrinsic and extrensic factors on floral visitation of Xanthosoma undipes in Monteverde, Costa Rica

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The Effects of Intrinsic and Extrinsic Factors on Floral Visitation of *Xanthosoma undipes* in Monteverde, Costa Rica.

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Abstract:

Both intrinsic and extrinsic floral characteristics exert important influences on floral visitation. The average distance between flowering plants, the number of flowering plants, and the spadix temperature were assessed to determine the influence of these intrinsic and extrinsic floral factors on floral visitation in *Xanthosoma undipes* in Monteverde Costa Rica. Observations were made for seven nights in which the distances between all flowering plants, abundances of all morphospecies of arthropods present and spadix temperatures were taken. Both the number of plants in flower and the average distance between flowers did appear to have an effect on flower visitation among pollinators. As the number of male inflorescences open in a night increased, the number of scarabs per inflorescence tended to decrease ($p = 0.0687$). It was also found that as the average distance between plants increased, the number of scarabs per inflorescence increased ($p = 0.0374$). On the other hand, arthropod abundances showed no correlation with either the number of plants in flower ($p = 0.1911$) or the average distance between flowering plants ($p=0.1881$), which suggests a lower degree of specialization among interlopers than the *Cyclocephala* pollinators. The inflorescences sexual identity, an intrinsic factor, did have an effect on visitor composition. Diversity in male inflorescences was significantly higher than diversity in female inflorescences ($H'_{males}=1.5097$, $H'_{females}=0.6466$. $t= 15.826$, $F = 1.964$). This study showed that both intrinsic and extrinsic factors are important in floral visitation in *X. undipes*, and different floral factors have differing effects on interloper and scarab visitation. Understanding the effects of both intrinsic and extrinsic factors in floral visitation is important because plant pollination directly affects plant reproduction and therefore directly affects plant fitness.

Resumen:

Tantas características florales intrínsecas como extrínsecas ejercen influencias importantes en la visitación floral. La distancia promedio entre plantas con flores, el número de flores por planta y la temperatura del espádice fueron tomados para medir la influencia de estos factores intrínsecos y extrínsecos en la visitación floral en *Xanthosoma undipes* en Monteverde, Costa Rica. Se realizaron observaciones durante siete noches en la cual la distancia entre todas las plantas con flores, abundancia de todas las morfoespecies de artrópodos presentes y la temperatura de espádice fue tomada. Tanto el número de plantas con flores como la distancia promedio entre flores parece tener un efecto en la visitación de flores por parte de polinizadores. En cuanto el número de inflorescencias masculinas abiertas por noche aumenta, el número de escarabajos por inflorescencia tiende a disminuir ($p= 0.0687$). Se encontró también que al aumentar la distancia entre plantas, el número de escarabajos por planta también aumenta ($p= 0.0374$). Por otro lado, la abundancia de artrópodos no muestra correlación con el número de plantas en flor ($p= 0.1911$) o la distancia promedio entre plantas con flor ($p= 0.1881$), lo que sugiere un bajo grado de especialización entre otros organismos que visitan la planta que los polinizadores *Cyclocephala*. La identidad sexual de las inflorescencias, factor intrínseco, tiene un efecto en la composición de visitantes. La diversidad en inflorescencias masculinas es mayor que la diversidad encontrada en las femeninas ($H'_{males}=1.5097$, $H'_{females}=0.6466$. $t= 15.826$, $F = 1.964$). Este estudio muestra que tanto los factores intrínsecos como los extrínsecos son importantes en las visitas a *X. undipes*, y diferentes factores florales tienen diferentes

efectos en la visitación por escarabajos y otros organismos. Entender los efectos de ambos factores en la visitación floral es importante debido a que la polinización afecta directamente la reproducción de la planta, por lo tanto afecta directamente también su éxito reproductivo.

Introduction:

Floral visitation is affected by many factors, both intrinsic and extrinsic (Garcia-Robledo *et al*. 2005). Intrinsic factors include factors such as flower size, color, temperature, or sexual identity of the flower. Some extrinsic factors include climate, neighboring plant species and pollinator abundance as well as floral distribution and the number of plants in flower. The effects of floral distribution and the number of plants in flower are unclear and may change depending on the pollination system of the plant in question (Bosche & Waser 2001, Garcia-Robledo *et al*. 2005). In the bumblebee pollinated flower *Alstroemeria auria*, density did not explain variations in pollen receipt (Aizen 1997), but in the beetle pollinated flower *Xanthosoma daguense*, rates of pollinator visitation have been shown to increase with increasing average distance between inflorescences (Garcia-Robledo *et al.* 2005). Floral offer, or the number of flowers in a given area, is an important extrinsic factor that has been shown to have an effect on floral visitation. For example, an increase in floral offer leads to a decrease in the number of pollinators per inflorescence in *Xanthosoma dangues* (Garcia-Robledo *et al*. 2005). Limited research exists on the effects of the number of plants in flower and distance between inflorescences on visitation in *X. undipes.*

Many aroids possess a thermogenic inflorescence, meaning that the inflorescence heats up to above air temperature. In *Xanthosoma undipes* temperatures peak around 35 degrees Celsius (Goldwasser, 1987). This suggests that inflorescence temperature may be an important intrinsic factor in determining flower visitation. It is commonly believed that heat itself does not provide the primary attractant to the pollinators; rather a sweet odor, which is volatized by the heat, is believed to attract the pollinators (Dormer 1960 in Goldwasser 1987). Few studies have directly measured how differences in spadix temperature may affect pollinator visitation in *X. undipes*.

Sexual identity may also be an important intrinsic factor in plant visitation. In the bumblebee pollinated plant *Alstroemeria auria*, it was found that female biased patches had higher rates of visitation than male dominated patches. On the other hand, sexual identity did not explain variations in pollen receipt (Aizen 1997). Although *Alstroemeria* and *Xanthosoma* have very different pollination systems and therefore flower sex may effect visitation differently in the two plants (Bosche & Waser 2001, Garcia-Robledo *et al.* 2005).

In addition to pollinators, many interlopers visit *Xanthosoma* inflorescences (Cochran 1997, Goldwasser 1987). An interloper is an organism that takes advantage of and benefits from a mutualism to the detriment of the mutualism (Goldwasser 1987). This high abundance and visibility of interlopers in *X. undipes* provides a unique opportunity for the study of the interaction between intrinsic and extrinsic factors and interloper visitation rate. Previous research on inflorescence temperature and interloper communities in *Xanthosoma jacquinii* has shown no correlation between the two (Cochran 1997). No previous research on interloper visitation and any other intrinsic or extrinsic floral factor were found.

In this study I will assess the effects of intrinsic and extrinsic factors on inflorescence visitation by looking at inflorescence temperatures, inflorescence sex, floral distribution and the number of inflorescences in flower. I hypothesized that such intrinsic and extrinsic factors would have an effect on floral visitation in *X. undipes*. I predicted that differences in inflorescence temperatures, inflorescence sex, average distance between inflorescences and the number of inflorescences in flower would be correlated with changes in the abundance of pollinators and interlopers in *X. undipes*.

Materials and Methods:

Study Organisms:

X. undipes is pollinated by beetles of the genus *Cyclocephala*, in the family Scarabidae (Goldwasser 1987, Goldwasser 2000). Two species of *Cyclocephala* pollinators are found in the Monteverde region, *C. sexpunctata*, which is a dirty yellow color with dark spots and *C. nigerrima*, which is completely black. Both pollinators are similar in size and behavior (Goldwasser 2000). The inflorescence is in flower for two nights, on the first night the inflorescence opens and the spadix begins heating up around 4:00 pm, volatizing a sweet odor. The scarabs, attracted by this odor, land on the spadix and descend into a closed, kettle-like structure formed by the spathe at the base of the flower, where they cannot be seen by an outside observer. While in the kettle the scarabs eat a ring of sterile flowers provided by the inflorescence, mate, and feed on nectar. Late the next afternoon the spadix heats again, and the male flowers begin to grow pollen. The heat signals the scarabs to leave the kettle, and crawl up the spadix, which is covered in pollen. The beetle then flies to another flower; thus completing pollen transfer (Garcia-Robledo *et al.* 2005; Goldwasser 1987; Goldwasser, 2000).

Study Site:

The plot was found in Monteverde Costa Rica, near the Monteverde Cloud Forest Preserve. The site measured approximately 80m squared and was mostly cleared of its primary vegetation. The distance between neighboring *X. undipes* plants varied, with some plants clumped and others standing alone.

Procedure:

Upon arrival, the site was systematically searched for open flowers. The number of open inflorescences as well as the distance between all flowering plants was measured, and the open inflorescences were sexed. Females were distinguished by having a clean, white spadix. Males had a slightly yellowed spadix, often with arthropods present. Next one male and one female inflorescence were chosen at random by assigning numbers to all the plants in flower and picking a numbered card out of a stack of cards of corresponding numbers. If only one sex was present, two randomly chosen flowers from the same sex were observed. If only one flowering plant was present, that inflorescence was observed alone, for twice the number of observations. Once one male and one female were

selected, the selected plants were marked with white flagging tape in order to facilitate finding them in the dark.

Inflorescences were observed in 10 minute intervals, between 4:00 and 6:30pm. Inflorescences were observed starting on the quarter hour and observed for 10 minutes. All observations after dark were made with a red light, in order to avoid disturbing the arthropods present. After 10 minutes of observation I moved to the randomly chosen flower of the opposite sex, and started observations on that flower at the next quarter hour. The abundance of each morphospecies present in each inflorescence during the time of observation, as well as the temperature of the spadix was recorded during each observation. All non-*Cyclocephala* species were considered interlopers.

On two separate occasions a male inflorescence was collected after the night's observations were made in order to facilitate arthropod identification. A male inflorescence was chosen so as not to affect the ratio of male to female inflorescences that would be present the following night. The inflorescence was cut off the plant, put in a large zip lock bag and put in the freezer overnight. The following day the arthropods contained in the inflorescence were counted and identified to morphospecies.

Analysis:

The average distance between flowering plants and average inflorescence temperatures were calculated. Abundances for each observation period were standardized for differing observation numbers by interpolating to the smallest number of observations. The Spearman rank correlation was run between the total number of flowers in a night and the total abundance of scarabs in the same night. In addition the Spearman rank correlation was run between intrinsic and extrinsic plant factors (the number of male flowers, average distance between plants, total number of flowers, average temperature of male inflorescences, average temperature of female inflorescences) and abundances of different arthropod communities (Abundance of scarabs per night, abundance of arthropods per night, abundance of scarabs in both male and female inflorescences and abundance of interlopers in male and female inflorescences). The overall community diversity of male inflorescence communities and female inflorescence communities were compared using the Shannon-Weiner index and results were compared using a modified t-test. Total abundances of each species of arthropod in males and female communities were compared using a Chi-squared test for independence.

Results:

Extrinsic Factors and Visitation:

TABLE 1: The number of plants in flower was recorded on seven separate nights and the average distance between all flowering plants was calculated. The averages on days 5 and 6 were not calculated due to the presence of only one flowering plant.

Night #	Total # of open inflorescences	Males open	Females open	Average distance between flowering plants
1	6	4	2	24.94 m.
2	2	1	1	47.80 m.
3	2	1	1	53.80 m.
4	5	3	2	29.72 m.
5	1	1	0	
6	1	1	0	
7	3	0	3	22.18 m.

It was found that the total number of plants in flower and the average distance between plants were not correlated (Rho = -0.7016, p = 0.1203, df = 6).

The number of male inflorescences open in a night was not correlated with total arthropod abundance in male plants on that night (Rho= -0.3381, p = 0.5122, df = 5). In addition the number of male inflorescences in a night was not correlated with total abundance of scarabs in a night, but the data did show a negative trend (Rho = -0.7775, p = 0.0687, df = 5).

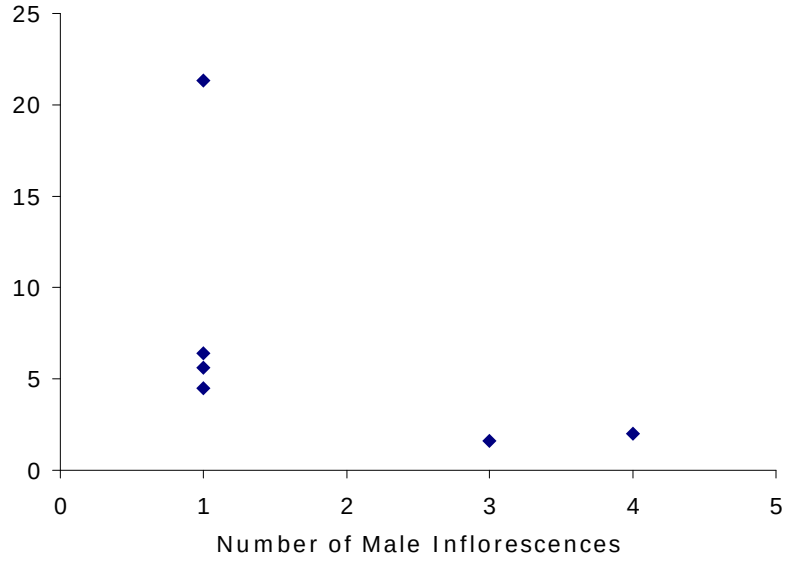

FIGURE 1: Number of male inflorescences open on a given night correlated with the abundance of scarabs observed in male inflorescences that same night. A negative trend was found (Rho = -0.7775, p = 0.0687).

The number of plants in flower per night was not correlated with the total number of arthropods found that night (Rho = 0.6179, p = 0.1911, df = 5). On the other hand, a negative trend was observed between the number of plants in flower on a given night and the abundance of scarabs observed on the same night (Rho = -0.6910, p = 0.0856, df = 6).

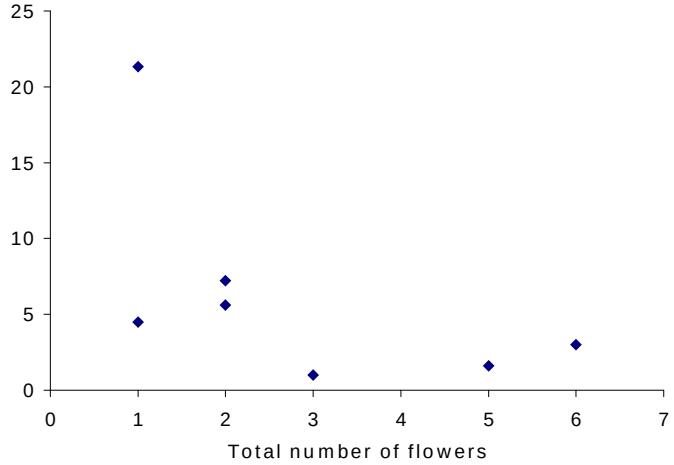

FIGURE 2: The total number of plants flowering on a given night correlated with the total abundance of scarabs on the same night. A negative trend was found between the two (Rho = –0.6910, p = 0.0856).

The average distance was not correlated with the abundance of scarabs in males (Rho = 0.80, p = 20, df = 3) or females (Rho = -0.6325, p = 0.3675, df=3). Finally, the average distance was not correlated with the abundance of arthropods (Rho = 0.700, p = 0.1881, df = 4), but an increase in the average distance between inflorescences did correlate with an increase in the total abundance of scarabs (Rho = 0.900, p=0.0374, df=4).

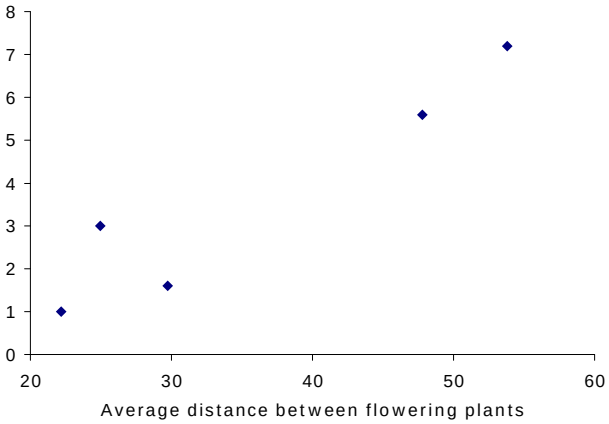

FIGURE 3: Average distance between flowering plants on a given night correlated with the total abundance of scarabs found on the same night. A positive correlation was found (Rho = 0.900, p = 0.0374).

Intrinsic factors and visitation:

There was no correlation found between average temperature of the male inflorescence and either interloper abundance (Rho = -0.3143, p = 0.5441, df = 5) or scarab abundance (Rho = 0.2571, p = 0.6228, df = 5).

Diversity was significantly higher in Male inflorescences than female inflorescences (H'males = 1.5097, H'females = 0.6466. t = 15.826, F = 1.964).

The morphospecies present in male and female inflorescences as well as the number of inflorescences in which they were present, their minimum and maximum abundances in the inflorescences and their mean abundance are summarized in Table 2.

TABLE 2: Arthropod community composition of both male and female inflorescences. Percent of inflorescences of the given sex in which the species is found, minimum and maximum abundances of the species in a night in the given sex and the mean abundance of the arthropod species in one night in the given sex.

	Male Inflorescences (N=6)			Females (N=4)		
	% Present	Min-Max	Mean	% Present	Min-Max	Mean
Cyclocephala nigerrima	42.86	0-21	4.67	25	0-1	0.25
Cyclocephala Sexpunctata	100	2-27	7.83	75	0-1	0.75
Diptera sp.	28.57	0-14	2.33	50	0-1	0.25
Diptera larvae	14.28	0-2	0.33	0	-	-
Drosophila	85.71	0-44	22	100	5-44	16.25
Hemipteran sp.	100	11-101	42.33	0.25	0-4	0.25
Miridae	100	39-134	93.33	100	35-184	94.5
Mite	100	2-157	45.83	75	0-5	1.25
Mosquito	14.28	0-1	0.17	25	0-1	0.25
White Moth	14.28	0-1	0.17	0	-	0

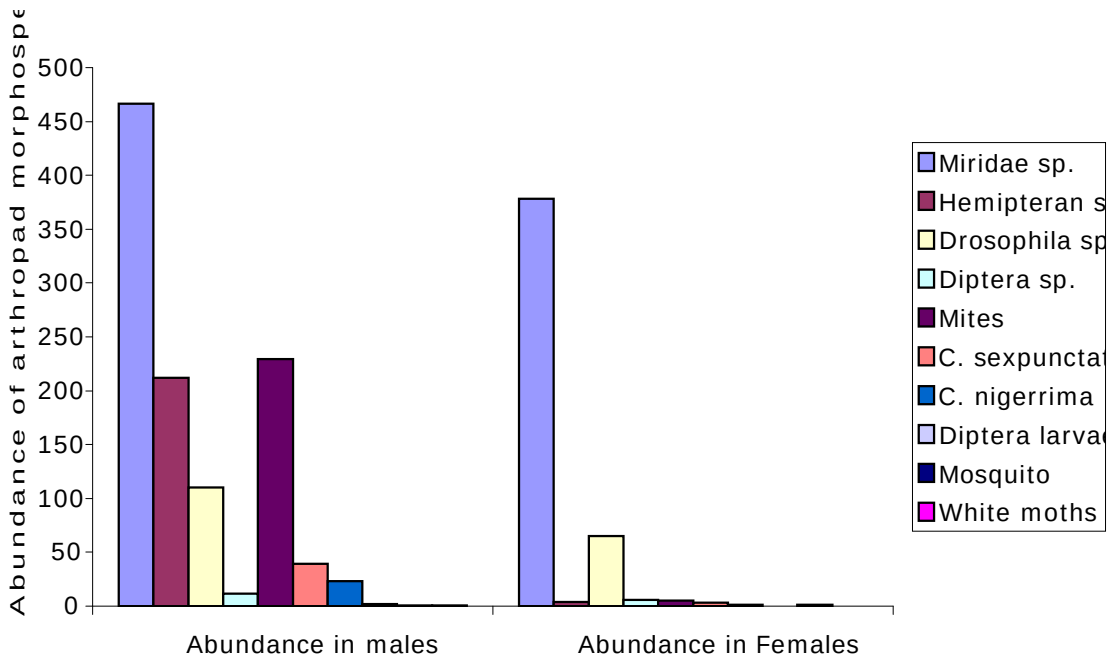

FIGURE 4: The total abundance, for all seven nights, of different arthropod morphospecies in male and female inflorescences is depicted in this graph. Male inflorescences had greater abundances of individuals in the following groups: Miridae ($x^2=9.3074$, $p=0.0023$, $df=1$), O. Hemiptera ($x^2=199.96$, $p < 0.0001$, $df = 1$), *Drosophila sp*. ($x^2=11.5714$, $p= 0.00067$, $df=1$), mites ($x^2 = 214.59$, $p < 0.001$, $df = 1$), *Cyclocephala sexpunctata* ($x^2 = 31.02$, $p < 0.0001$, $df = 1$) and *Cyclocephala nigerrima* ($x^2 = 20.50$, $p < 0.0001$, $df = 1$).
The sexes did not differ in abundances of individuals of the O.Diptera found in their inflorescences ($x^2=1.82$, $p=0.1776$, $df=1$), Diptera larvae ($x^2=1.67$, $p=0.1967$, $df=1$), mosquitoes ($x^2=0.015$, $p=0.920$, $df=1$), or white moths ($x^2=0.833$, $p=0.3613$).

Discussion:

I predicted that both intrinsic and extrinsic factors would show an effect on arthropod visitation to *X. undipes*. I found that average distance between flowering plants on a given night was not correlated with the number of inflorescences on that same night. This allowed me to treat them as independent variables and assess both separately.

Extrinsic Factors:

The negative trend found between the number of plants on a given night and the number of scarabs found per inflorescence on that night shows that the more inflorescences on a given night, the fewer scarabs tended to be found in each inflorescence. Similarly, the negative trend observed between the number of male inflorescences on a given night and the number of scarabs per male inflorescence on the same night shows that the more male inflorescences open on a given night the fewer scarabs that were present per inflorescence. Based on the pollination biology of the plant, a negative trend between the number of female flowers on the previous night and the number of scarabs arriving at

them is probable. It is likely that this trend was not observed in female flowers due to small sample size (seven nights) as well as the inherent difficulty of seeing the scarabs arrive, as opposed the relative ease of seeing the scarabs congregating on the male spadix. Further study is needed to see if these trends are significant, but these data support the observation of Garcia Robledo *et. al* 2005 that on nights with a low number of flowering plants *Cyclocephala* beetles appear to be congregating in the few available inflorescences.

The positive correlation found between the average distance between flowers and the number of scarabs found per inflorescence is consistent with previous results found in *Xanthosoma daguense* (Garcia-Robledo *et al.* 2005). I suggest that this positive correlation is due to increasing distances effectively lowering floral availability from the scarab point of view. *Cyclocephala spp.* have been shown to go to the first available inflorescence of the appropriate sex in some aroids, in this case females (Young 1986). Therefore, with increased distance between inflorescences, it is likely that the number of inflorescences detected by the scarabs decreases, decreasing the floral availability to the beetles and increasing the number of scarabs found in each inflorescence.

Arthropod abundance was not correlated with either the number of flowering plants or the average distance between flowering plants. This could be explained by a lack of host specificity among the interlopers present. If this is the case, then other factors such as the other plant species in the area may be more important. The interloper may be looking for any place to go, and not necessarily another *Xanthosoma* flower.

Intrinsic factors and visitation:

No correlation was found between average temperature of inflorescences and abundances of either scarabs or all arthropods. This is consistent with previous observations on the subject (Cochran 1997, Goldwasser 1987) and suggests the role of heating is indirect. Visitors are likely attracted to the odor volatized by the heat and not the heat itself (Dormer 1960 in Goldwasser 1987).

Male inflorescences displayed higher community diversity than female inflorescences. This difference was due to increased abundance in a few species. This was consistent with field observations, where the spadix of the male flower was often covered with interloper species, while the spadix of the female inflorescence was often clean.

These differences, especially in scarabs, may also be due to the arthropod visibility in the different inflorescences. For example, upon arriving at a female inflorescence a scarab would go into the kettle formed by the spathe and was usually not seen again for the remainder of the night, so if the scarab was not seen arriving it would not be documented in the female inflorescence. On the other hand, in the male inflorescence the scarabs would spend extended periods of time on the spathe and hence were easier to observe. This pattern appeared to be less important among the interloper species present; they appeared to spend more time on the spadix of the female inflorescence and would less often disappear into the kettle of the flower.

In conclusion, both intrinsic and extrinsic factors were important in floral visitation in *X. undipes*, and different factors had differing effects on interloper and scarab visitation.

Future study should increase sample size, in order to find out if any of the trends observed are significant. In addition further study on the visitation patterns and host specificity of the interlopers present in *X. undipes* are needed to fully understand the results shown in this study. This study furthered botanical knowledge of the unique pollination process of *X. undipes*. Understanding the pollination process is extremely important in this, or any other flowering plant, because it directly affects plant reproduction and as such directly affects the fitness of the plant.

Acknowledgements:

I would like to thank Tania Chavarría for the endless help finding study sites, coming up with project ideas and running statistics. Also a huge thank you to Karen Masters for peaking my interest in the *Xanthosoma* pollination system and helping me gain access to my study site. Thank you to the Morrison, Tandy and Calvert property owners for generously allowing me to use their land to conduct this study. Also, an extra huge thank you to Pablo Allen for helping me identify arthropods and run my statistical analyses Finally, thank you to Moncho Calderon for helping me deal with all my computer problems throughout the process.

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