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ABSTRACT

The International Tropical Timber Organization (ITTO 2002) estimated that secondary forest make up 60% of all tropical forests. By definition, that means that a majority of tropical forests have gone through succession in the recent past. In the present study I looked at differences between foliage dwelling insects at different stages of succession. A total of eight sweep samples were taken from a regenerating field (RF), a new growth forest (NGF), and an old growth forest (OGF) in San Luis, Puntaranes, Costa Rica to assess the diversity and evenness during the dry season and at an altitude of around 1200 meters. Of 34 morpho-species, the NGF had the greatest amount of diversity and evenness, followed by OGF and finally RF, which suggest that insect foliage sampling and composition analysis has potential to be used for monitoring forests for succession progress and disturbances.

RESUMEN

La Organización Internacional Maderera Tropical (ITTO 2002) estima que los bisques secundarios ascienden a un 60% de todos los bosques tropicales. Por definición, esto significa que la mayoría de los bosques tropicales han pasado por sucesiones en el pasado reciente. En el presente estudio, observe las diferencias entre los insectos que viven en el follaje a diferentes estados de sucesión. Un total de ocho barridas se tomaron en un campo en regeneración (CR), un bosque joven (BJ) y un bosque viejo (BV) en San Luis, Puntarenas, Costa Rica para determinar la diversidad y similitud durante la estación seca a una altitud alrededor de los 1200 metros. De las 34 morfoespecies, el BJ tiene la mayor diversidad y similitud, seguido por el BV y finalmente el CR, lo que sugiere que los insectos del follaje pueden ser usados para el análisis y monitoreo de los progresos de sucesión de los bosque y los disturbios de los mismos.

INTRODUCTION

Humans manipulate forested land to fulfill desires and demands of human consumption (Vitousek *et al*. 1986), however these actions unintentionally affect habitats, watersheds, and biodiversity. Impacting wild habitats not only could hurt wildlife systems but it could cause problems for humans by dampening services we rely on from natural systems such as pollination, dung burial, and pest control. In the U.S.A., alone, wild insects provide $57 billion USD worth of these services (Losey & Vaughan 2006), which could be put at risk without careful land management. Despite the prevalence of forest disturbances, they are still not well understood. However it is obvious that they are causing negative affects on biodiversity and habitats and that balancing trade-offs between satisfying human needs and maintaining habitats and biodiversity requires knowledge about impacts of land use (DeFries *et al* 2004).

The International Tropical Timber Organization estimated that new growth forest makes up roughly 60% of the forest in the tropics (ITTO 2002). This indicates that more than 60% of all tropical forest has been disturbed and is going through succession. However 60% is a conservative estimate considering that the 60% does not include the amount of cleared land that once hosted tropical forest. With succession so abundant across the tropics it is important to understand ecological differences and implications at various stages and to be able to recognize the different stages. Success may be achieved through using bioindicator species or species compositions and findings may be used to choose and monitor conservation efforts. This knowledge can be applied to conservation strategies and may serve useful in situations when resources are limited it is tough to know whether to pick the larger tract of land with newer forest or a smaller tract of older forest.

Arthropod compositions were first suggested for use as bioindicators in 1981 by Pyle *et al.* The short life cycles of arthropods add a higher resolution to the mapping of disturbances than organisms with longer generation times where it would take a couple of decades to see trends in populations. In addition, arthropods tend to be small, easy to handle and transport, and many have very large population sizes. In the present study I took sweep net samples of foliage dwelling insects at three different stages of succession to see if there were differences between community compositions, to establish a baseline for future studies, and to note any potential bioindicator candidates.

METHODS

A total of eight sweep samples were collected from a old growth forest (OGF), a new growth forest (NGF), and a regenerating field (RF) in the Premontane Moist Tropical Forest life zone located in the town of San Luis, Puntaranes, Costa Rica (Holdridge *et al*. 1971). San Luis was first settled in 1915 and by 1940 there was a considerate amount of deforestation and conversion of land for agricultural and pastoral purposes, which left the forests that remain, a mosaic of new growth and old growth fragmented forests.

Three sweep samples were collected from RF, three samples were collected from OGF, and two samples were collected from NGF. Photographs and details about the study sites can be found in Appendix 1-3. Knowing that insect behaviors may change with season and time of day (Janzen 1973), all sample collections occurred between 12:00pm and 2:00pm and during the end of the dry season, between April 23rd and April 28th. The weather at the time of collections varied from direct sunlight to partly cloudy days. The wind strength was about the same during each collection and the foliage was never wet.

To obtain the samples, I swept continuously and consistently walking forward with a sweep net with a diameter of 40cm and a 80cm long handle. The sweep netting lasted 3 minutes for each sample and the same foliage was never swept twice. I operated the sweep net at each site, as expected for sweep sampling, my movements with the sweep net were aimed at catching whatever flying insects were flying or resting on the foliage in my path while retaining insects already caught within the mesh. Each sample was taken at least 25m from the others. Foliage ranging from 5 cm to 250 cm off the ground was swept with the net and often the sweeping damaged plants. Usually foliage ended up in the samples, which made it more difficult to separate the insects. About twenty minutes after the samples were taken, the insects were killed by freezing the sample.

Insects were categorized into 34 taxa (morpho-species). The taxonomic groups specified in this study were chosen based on time constraints and my confidence in my ability to categorize the insects based on my familiarity with insects and available resources. I thoroughly went through each sample separating all insects from plant debris to adequately extract and categorize all insects in the sample.

To compare the diversity between sites, I calculated the Shannon-Weiner index of diversity (H') with the total number of individuals for each site, and then compared the values between all sites. Evenness was also calculated based on this index (H' /Hmax).

RESULTS

I categorized a total of 3997 insects. Through applying the Shannon-Weiner index to the data we found significant differences diversity and evenness between all three types of sample sites. With a Shannon-Weiner diversity index of 2.32 and an evenness of 0.75, the NGF had significantly higher diversity and evenness than the RF (t=9.46, degrees freedom (df) = 741.80, $p < 0.00005$) and the OGF (t = 2.06 , df = 818.57, p = 0.04; Table 1). The field had the lowest diversity and evenness leaving OGF as the intermediate (t = 9.24, df = 3141.86, p <0.0005; Table 1). There are obvious differences between order composition among the sites (chi-squared = 1492.31, df = 12, $p < 0.0001$; Fig. 1).

TABLE 2. Shannon-Weiner index diversity (H') values and evenness (E) values of 34 morpho-species across the three different types of sites. The new growth forest had a higher diversity and evenness than both the old growth forest (OGF) (t = 2.06, df = 818.57, p = 0.0398) and the regenerating field (RF) (t = 9.46, df = 741.80, $p < 0.00005$). The OGF had higher diversity and evenness than the RF (t = 9.24, df = 3141.86, p <0.0005).

	H'	E
Regenerating Field	1.745	0.524
New Growth Forest	2.320	0.750
Old Growth Forest	2.190	0.644

The RF had a total representation of 28 of the 34 taxa (morpho-species), NGF had a total of 20, and OGF had a total of 29. I observed that more that half of each RF sample consisted of leafhoppers (Table 1, Fig. 1). Additionally, the remaining smaller majorities consisted of grasshoppers, flea beetles, miscellaneous dipterans, small parasitic wasps and other miscellaneous hemipterans in RF samples. The majorities among NBF samples consisted of leafhoppers, crane flies, miscellaneous dipterans, ants, and small parasitic wasps. Among the OGF, the majorities appear to be spiders, dipterans, little wasps, beetles, and leafhoppers. Leaf hoppers, appear to have a strong presences across all environments however they have an overwhelming presence in the RF. While the hymenoptera composition of NGF and OGF (28% and 23% respectively) appear to be very similar, it is important to note that 24% of hymenoptera in NGF were ants while only 7% of hymenoptera were ants in the OGF. Also, every adult insect specimen collected possessed wings.

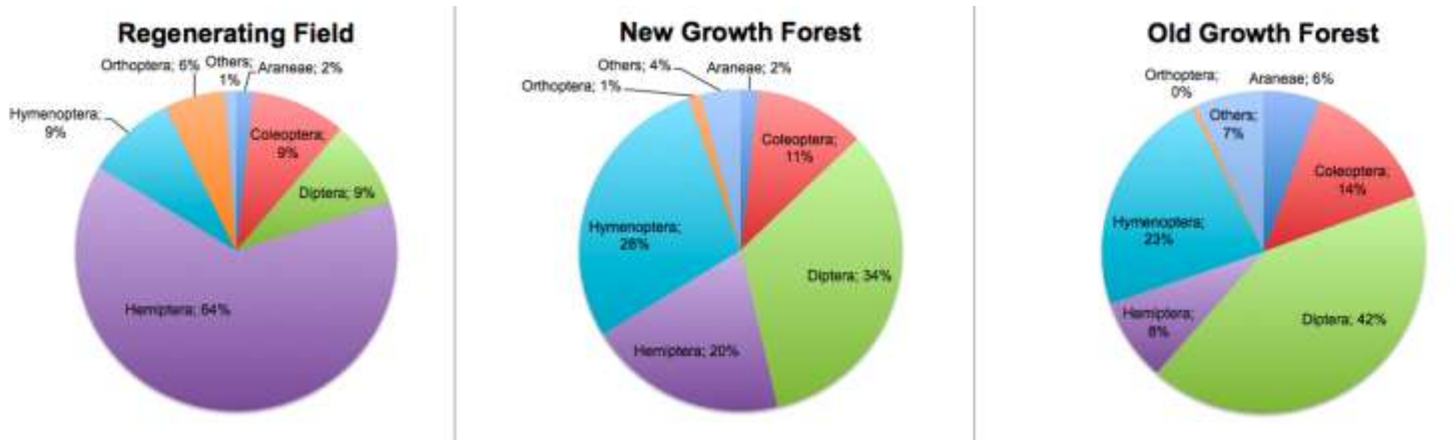

FIGURE 1. Percent composition of foliage dwelling arthropods by order in three different stages of succession. A chi-squared test confirmed significant differences between orders across the three environments (chi-squared = 1492.31, df = 12, p <0.00005). The regenerating field (RF) had a total of 2252 individuals, new growth forest (NGF) had 397, and old growth forest (OGF) had 1344. More detailed categorization based on morpho-species revealed that the NGF had a higher diversity and evenness than both the OGF (t = 2.06, df = 818.57, p = 0.0398) and the RF (t = 9.46, df = 741.80, p < 0.00005). The OGF had higher diversity and evenness than the RF (t = 9.24, df = 3141.86, p <0.0005).

DISCUSSION

NGF was found to have the highest diversity and evenness, contrary to the original prediction that OGF would have the highest diversity and evenness. At first thought, it may seem that NGF had more diversity and evenness because insects from RF and OBF could have just been passing through NGF since an older forest on one side and a pasture on the other side surrounded the NGF site. However it is not necessarily just the morpho-species richness that separated NGF from the other two, it was the lack of domination from a few morpho-species. This is evident when one notices that NGF had the least amount of morpho-species representation, both RF and OGF had at least eight more morpho-species represented. The diversity and evenness indexes appeared to be affected by domination by leafhoppers in the RF and Misc. Diptera and < 5cm parasitic wasps in the OGF samples.

Perhaps this finding could be explained by the extremity of each stage of succession chosen for the study. The RF had existed as a field for many years and had only just begun the process of succession four years ago while the NGF had well progressed through the transition back to forest but was very far from achieving old growth status, and OGF was well established and mature but still needed a relatively few more community developments to achieve pristine forest status. Brown Jr. (1996) portrays a forest disturbance system where the presence of field and edge species dominates pasture areas but wanes as forests age. Leafhoppers have been observed to be fast and prevalent colonizers of grass fields (Novotny 1995) and had a strong presence in the RF samples and weaker presences in the NGF and OGF. At the other side of the spectrum, the OGF, having been a forest for many years, has had time to achieve an established forest community and did not have relatively as many leafhoppers. It can be argued that the NGF, of fifteen years, has more diversity and evenness because it is in a transitional phase where is starting to loose the edge species and host more forest species as the trees develop and the canopy closes.

It would be interesting to see if this higher diversity and evenness found in NGF would hold true if samples were sorted town to species. Coleoptera, Diptera, and hymenoptera are extremely diverse insect groups whose diversity was disproportionately underrepresented in this study.

Additionally the RF appears to be composed of about 75% herbivores, while the NGF is composed of 27% herbivores, and the OGF has a composition of 16% herbivorous morpho-species. The OGF had a large proportion of small parasitic wasps which function at the third trophic level. Spiders are also a third trophic level taxa, which had a notably greater presence in the composition of the OGF arthropods. Perhaps the balance of trophic levels present at each successional indicates complexity or complexity of the community. The greater amount higher trophic levels present may indicate the habitat a higher level of complexity and perhaps productivity in the community since the sustaining higher trophic levels requires more energy at lower trophic levels. Further studies should look to explore this idea.

On a different note, Huston (1982) brings up the idea that nutrient availability greatly affects competition during succession. Through experimentation, he found that one succession tree species to dominate in higher nutrient conditions and not in lower nutrient conditions. Further studies could incorporate soil nutrition or plant composition into the evaluation of insect composition in forest succession since insects often have close interactions with plants and would probably be affected by changes in plant composition.

Differences across the three stages of succession is significant and therefore could be used for monitoring the statuses of forests and disturbances however further samples must be collected and analyzed to provide better species resolution and at more stages of succession.

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TABLE 1. Number of individuals of morpho-species collected in each of eight sweep-samples in San Luis, Puntaranes, Costa Rica across three stages of succession, a four year old regenerating field (RF), a fifteen year old new growth forest (NGF), and an old growth forest (OGF). The NGF had a higher diversity and evenness than both the (OGF) (t = 2.06, df = 818.57, p = 0.0398) and the RF (t = 9.46, df = 741.80, p < 0.00005). The OGF had higher diversity and evenness than the RF (t = 9.24, df = 3141.86, p <0.0005).

Order	Taxon (morpho-species	RF 1	RF 2	RF 3	**RF TOTAL**	NFG 1	NFG 2	**NFG TOTAL**	OG F1	OG F2	OGF3	**OGF TOTAL**
Hemiptera	Leaf Hoppers	44 8	24 7	602	**1297**	28	38	**66**	47	21	18	**86**
Hemiptera	Myridae	11	2	10	**23**	-	-	**-**	-	-	-	**-**
Hemiptera	Red Leaf Hop	2	1	1	**4**	-	-	**-**	-	-	1	**1**
Hemiptera	Misc Hemiptera	36	34	41	**111**	7	6	**13**	10	8	7	**25**
Coleoptera	Flea Beetle	15	2	137	**154**	5	1	**6**	11	10	4	**25**
Coleoptera	Staph	-	5	1	**6**	2	2	**4**	11	5	7	**23**
Coleoptera	Weevil	5		9	**14**	8	9	**17**	24	2	8	**34**
Coleoptera	Misc Beetles	10	16	14	**40**	7	10	**17**	67	15	20	**102**
Diptera	Syrphidae	18	9	6	**33**	-	1	**1**	2	1	1	**4**
Diptera	Sarcophag	6	4	7	**17**	-	1	**1**	1	-	-	**1**
Diptera	Tabanidae	-	1	-	**1**	2	-	**2**	-	-	-	**-**
Diptera	Tipulidae	1	1	-	**2**	11	26	**37**	52	5	16	**73**
Diptera	misc Dip	14	57	74	**145**	45	47	**92**	274	101	113	**488**
Lepidoptera	butterfly	3	3	2	**8**	-	-	**0**	1	1	-	**-**
Lepidoptera	moth	-	2	-	**2**	2	2	**4**	7	3	3	**13**
Odonata	damselflies	3	-	2	**5**	-	-	**0**	-	-	-	**-**
Tricoptera	Tricoptera	2	-	-	**2**	2	-	**2**	6	-	-	**6**
Hymenoptera	Formicidae	2	9	1	**12**	15	12	**27**	11	4	-	**15**
Hymenoptera	Parasitic wasp <0.5cm	19	31	76	**126**	46	31	**77**	123	82	80	**285**
Hymenoptera	misc wasp	13	17	12	**42**	7	2	**9**	2	3	2	**7**
Hymenoptera	misc bee	5	5	12	**22**	-	-	**-**	-	-	-	**-**
Orthoptera	Grasshoppers	64	28	45	**137**	3	-	**3**	2	1	3	**6**
Orthoptera	Katydid	-	2	-	**2**	-	2	**2**		-	1	**1**
Phasmida	Phasmid	-	-	-	**-**	-	-	**-**	1	-	3	**4**
Opiliones	Opilionid	-	-	-	**-**	-	-	**-**	1	-	1	**2**
Isopoda	Isopod	-	-	-	**-**	-	-	**-**	4	4	8	**16**
Gastropod	Snail	-	-	-	**-**	-	-	**-**	13	4	7	**24**
Diplopoda	Millipede	-	-	-	**-**	-	-	**-**	-	-	2	**2**
Thysanoptera	Thrips	-	-	4	**4**	3	-	**3**	8	-	3	**11**
Araneae	Spider Misc	15	8	13	**36**	3	4	**7**	21	24	19	**64**
Araneae	Salticidae	2	1	-	**3**	-	-	**-**	5	3	4	**12**
Blattodea	Cockroach	-	-	1	**1**	1	1	**2**	2	1	1	**4**
Lepidoptera	Caterpillar	-	2	1	**3**	3	2	**5**	3	1	2	**6**
Dermaptera	Dermaptera	-	-		**-**	-	-	**-**	1	1	-	**2**
Total	N	69 4	48 7	107 1	**2252**	200	197	**397**	710	300	334	**1344**
Number of Taxa Present	S	21	23	22		19	18		27	22	25	

APPENDIX 1. The Regenerating Field Site. This field site consists of two four year old regenerating pastures located on the property of University of Georgia's Costa Rican Campus in San Luis. At an altitude of approximately 1150 meters. The first and second field samples were taken from pasture on the southern side (pictured) of the dirt road that runs in between the fields and the third sample was taken from the pasture on the north side of the road. Secondary forest encroaches on the edges of both fields that do not boarder the road. There is one small 10m-25m laguna in each field at the forest edge. The size of the lagunas vary depending on rain. The fields consisted of grasses of plants that were up to a meter in height along with a few scattered trees.

APPENDIX 2. Secondary Growth Forest. This slightly sloped forest site was in between a gently sloped pasture and a steeply sloped primary growth forest in the town of San Luis, Puntaranes, Costa Rica. Understory growth was thin throughout the forest. The canopy is lower and more open than a mature forest. Fifteen years ago this site was used for cow pastures. Since then the site has been left to grow on its own.

APPENDIX 3. Old growth site. These sweep samples were taken from the primary forest surrounding the stream that leads up the often tourist visited San Luis waterfall. The forest has most likely maintained its pristine state because of the remarkably steep inclines 50m to each side of the waterway, which, aside from leaving it untouched for water potability purposes, significantly lowers economic potentials that entail developing the land.