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Canopy assemblages and species richness of planthoppers
(Hemiptera: Fulgoroidea) in the Ecuadorian Amazon

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Canopy assemblages and species richness of planthoppers (Hemiptera: Fulgoroidea) in the Ecuadorian Amazon

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Abstract. Planthopper (Hemiptera: Fulgoroidea) diversity inhabiting Neotropical terre firme forests is poorly known but may comprise one twentieth of the known World planthopper diversity. This study estimates planthopper diversity of the terre firme forest canopy using multiple measures. Samples were collected by canopy fogging at two localities in the Ecuadorian Amazon terra firme forest (Orellana province) Tiputini Biodiversity Station and Reserva Etnica Waorani. Fogging was conducted during three seasons (wet, transitional, and dry) between 1994 and 2006. The total planthopper collection encompasses 17,951 specimens in 15 families, and from these specimens 638 morphospecies were recognized. EstimateS diversity software was used to determine seven alpha diversity estimators that predicted an average alpha diversity of 793 morphospecies. Beta diversity estimators supported limited overlap between localities in the study and predicted that diversity of the sampling sites composes roughly 1/3 of the known planthopper diversity for all Central and South America.

Key words. Auchenorrhyncha, Fulgoromorpha, planthoppers, canopy arthropods.

Introduction

Invertebrates, especially arthropods, constitute much of the Earth's biota and few places equal Neotropical forests for arthropod biodiversity (Wilson 1992; Simpson and Cracraft 1995). Insects account for over 1 million described species, or about 66% of all animal species (Zhang 2011; IUCN 2011), and predictions of total insect species richness range from 3.8 to 30 million species (Erwin 1983a, Fonseca 2009), with most undescribed species in the tropics.

Planthoppers (Hemiptera: Auchenorrhyncha: Fulgoroidea) have an extant world diversity of approximately 13,000 species in 2,300 genera and 21 families (Bartlett et al. 2018; Bourgoin 2019). In the Neotropics, known planthopper diversity is 2,107 species in 464 genera and 16 families (Table 1). Planthoppers are phytophagous except that immatures of Achilidae and Derbidae (and possibly others) feed on fungal hyphae. Other planthopper taxa are understood to be phloem feeders, associated with their plant host(s) for all life stages, including mating, for which substrate-born vibration signals play an important role (e.g., Ossiannilsson 1949; Claridge 1985a, b; Drosopoulos and Claridge 2006; Tishechkin 2008). Host preference varies among planthopper families, and is often poorly documented, although host specialization is deemed common (Wilson et al. 1994, Nickel 2003). Caliscelidae and Delphacidae are primarily grass and sedge feeders (Wilson et al. 1994), and would not be expected in arboreal settings, but the remaining 14 families are expected to occur in the forest canopy. In the temperate region, larger-bodied planthoppers are usually univoltine, with small-sized taxa—such as Delphacidae—

Table 1. Planthopper taxa recognized from Ecuador canopy fogging samples (excluding doubtful identifications and subsequently described taxa).

Family	Genus
Acanaloniidae	<i>Acanalonia</i> Spinola
Achilidae	<i>Amblycratus</i> Uhler, <i>Cionoderella</i> Fennah, <i>Opsiplanon</i> Fennah, <i>Phypia</i> Stål, <i>Pseudhelicoptera</i> Fowler, <i>Sevia</i> Stål
Achilixiidae	<i>Bebaiotes</i> Muir
Cixiidae	<i>Bothriocera</i> Burmeister, <i>Cixius</i> Latreille, <i>Haplaxius</i> Fowler, <i>Melanoliarius</i> Fennah, <i>Mnemosyne</i> Stål, <i>Pintalia</i> Stål
Delphacidae	<i>Tetrasteira</i> Muir, <i>Ugyops</i> Guérin-Méneville
Derbidae	<i>Anotia</i> Kirby, <i>Cedusa</i> Fowler, <i>Cenchrea</i> Westwood, <i>Cobacella</i> Fennah, <i>Derbe</i> Fabricius, <i>Dysimia</i> Muir, <i>Herpis</i> Stål, <i>Mysidia</i> Westwood, <i>Otiocerus</i> Kirby, <i>Paramysidia</i> Broomfield, <i>Patara</i> Westwood, <i>Pseudomysidia</i> Metcalf, <i>Sayiana</i> Ball
Dictyopharidae	<i>Hyalodictyon</i> Fennah, <i>Lappida</i> Amyot and Serville, <i>Megadictya</i> Melichar, <i>Mitrops</i> Fennah, <i>Paralappida</i> Melichar, <i>Plegmatoptera</i> Spinola, <i>Taosa</i> Distant
Flatidae	<i>Anormenis</i> Melichar, <i>Ormenis</i> Stål, <i>Carthaeomorpha</i> Melichar, <i>Poekilloptera</i> Latreille
Fulgoridae	<i>Calyptoproctus</i> Spinola, <i>Cathedra serrata</i> (Fabricius), <i>Cladodiptera</i> Spinola, <i>Diacira</i> Walker, <i>Enchophora</i> Spinola, <i>Enhydra</i> Walker, <i>Episcius</i> Spinola, <i>Hypaepa</i> Stål, <i>Learcha</i> Stål, <i>Lystra</i> Fabricius, <i>Odontoptera carrenoi</i> Signoret, <i>Oeagra</i> Stål, <i>Paralystra</i> White, <i>Protachilus</i> Fennah, <i>Scaralis</i> Stål
Issidae	<i>Buca</i> Walker, <i>Dracela</i> Signoret, <i>Oronoqua</i> Fennah, <i>Thionia</i> Stål
Lophopidae	<i>Hesticus</i> Walker
Nogodinidae	<i>Biolleyana</i> Distant, <i>Bladina</i> Stål, <i>Colpoptera</i> Burmeister, <i>Nogodinia</i> Stål, <i>Varciopsis</i> Jacobi, <i>Vutina</i> Stål
Ricaniidae	<i>Cotrades</i> Walker, <i>Pharsalus</i> Melichar, <i>Semestra</i> Jacobi
Tropiduchidae	<i>Alcumena</i> Schmidt, <i>Amapala</i> Melichar, <i>Arenasella</i> Schmidt, <i>Colgorma</i> Kirkaldy, <i>Dichoneura</i> Lethierry

multivoltine (Nickel 2003; Bartlett et al. 2011, 2014). Similar patterns are expected in the Neotropics.

Here we investigate planthopper diversity from canopy fogging samples taken at two sites in the eastern forests of Ecuador in the Amazon Basin by Erwin between 1996 and 2006. We investigate alpha and beta diversity, seasonal abundance, basic life history patterns, and population demographics from these samples of canopy planthoppers. This is part of a larger project (by TLE) to investigate the biodiversity of the Neotropical forest canopy (e.g., Lucky et al. 2002; Erwin et al. 2005, Erwin and Geraci 2009; Erwin and Zamorano 2016, 2017; Erwin et al. 2017).

Materials and Methods

Study location. Two sites in Ecuador were sampled: the Tiputini Biodiversity Station (00° 39' 25" S, 076° 27' 10" W) in the Yasuní National Forest, and Reserva Etnica Waorani, Onkone Gare Station (00° 39' 10" S, 076° 26' 00" W) near the Piraña field station (hereafter Tiputini and Onkone Gare, respectively). The sites are 35 kilometers apart.

The study sites are described in detail by Pitman (2000), and subsequently also by Lucky et al. (2002) and Erwin et al. (2005). They are situated at the northwestern margin of the Amazon basin along the eastern base of the Andean range. The soil conditions are typical of a tropical forest, acidic and low in cations. Both sites are dominated by terre firme forest blocks, disrupted by streams that intersect throughout. Swamps, floodplains, and successional forest also dot the landscape, but make up less than 10% of the region. The forest consists of a multi-tiered collection of trees, saplings, lianas, and shrubs with an underdeveloped epiphytic community. The canopy generally reaches 30 m in height and

emergent trees can reach up to 50 m. Important woody families in the tropics are the same as seen in Yasuní. An extrapolation of an inventory of Yasuní's shrubs and trees estimates approximately 3,100+ species in the park and ethnic reserve (Pitman 2000). A road has been installed near the Tiputini site for oil exploration.

Study design. Canopy fogging samples were collected by TLE between 1994 and 2006 (see, e.g., Lucky et al. 2002; Erwin et al. 2005). A sampling year consisted of a wet season, a dry season, and a transitional season instead of a calendar year. The dry and wet seasons run approximately from November to April and May to October, respectively (Lucky et al. 2002). Dry season samples were collected in January–February, wet season samples in June–July, and transitional season samples taken in late September–October.

Collection methods. Canopy fogging techniques have been previously described (Erwin 1983a, b; Lucky et al. 2002; Erwin et al. 2005; Erwin and Geraci 2009) and will be briefly detailed here. At both Tiputini and Onkone Gare a 100 m × 1000 m transect area was established in terre firme forest, along which 10 perpendicular cross transects, 100 m long, were set 100 m apart. Along each of the cross transects, 10 3x3 m permanent fogging stations were randomly established and used consistently throughout the multiyear project. The heterogeneous distribution of tree trunks in the cross transects prevented a systematic, or statistically random, layout of sheets. Sheets were placed within 5 m of the cross transect center line (either side), suspended 1 m above the ground (to limit potential contamination from the forest floor and undergrowth). The suspended sheets were each provided with a central collection bottle to form a cone shaped collection device, with the bottle filled with 70% ethyl alcohol. Specimens on the sheets were washed into the collection bottles with ethyl alcohol to avoid damage. The total area sampled was 9,250 m² of the 100,000 m² (0.1 km²) transect area.

Canopy fogging envelops the canopy in an UV degradable insecticide to knock arthropods into the sample collection sheets. Fogging is performed between 0345 and 0500 hours to limit impacts of both rainfall and wind on sample effectiveness. The sheets were collected three hours from the time of fogging to allow specimens to drop from the canopy. Sample stations were numbered and were reused for subsequent sampling years. Sample sorting usually took place in Ecuador by students and volunteers, although some samples were first transported to the US. Samples were divided into taxonomic working groups and counted (twice) before being distributed to other researchers.

Sampling began in January 1994 and has continued intermittently as funding and the political climate of Ecuador allow. Three years of sampling for Onkone Gare (900 samples) and one year for Tiputini (300 samples) were available for use in this project, for a potential count of 1,200 samples. However, some samples were subsequently dispersed during the intervening 14 years, and only 952 (Onkone Gare 726 and Tiputini 226) complete samples were available for this study.

Focal study group. All adult planthoppers (Fulgoroidea) from the samples were sorted and identified to morphospecies. Planthoppers were sorted to family primarily using O'Brien and Wilson (1985) to lower taxonomic units as practicable, and finally to morphospecies. Other taxonomic literature was consulted for identification below family (Metcalf 1938, 1945; Fennah 1945, 1950, 1952, 1954, 1978, 1982, 1984; O'Brien 1982, 1987a, b; 1988; Emeljanov 1989, 1992, 1993, 1996, 1999, 2011; Porion 1994, Gnezdilov and O'Brien 2008, Donovall 2008). Since taxonomic resources pertinent to planthoppers in Ecuador are sparse, we used keys from family classification revisions (e.g., Fennah 1954) and faunistic studies (e.g., Metcalf 1945) from nearby regions, regional faunal lists (e.g., Bourgoin 2019) and reference specimens from natural history collections to effect identifications. As family-level assignment of some planthoppers has recently changed (e.g., Cladodipterini from Dictyopharidae to Fulgoridae, Emeljanov 2011; *Pharsalus* Melichar and *Silvanana* Metcalf from Issidae to Ricaniidae, Gnezdilov 2009; Colpopterini from Issidae to Nogodinidae, Gnezdilov 2012), the most recent family-level assignment was used. Portions of the material were also recognized to genera (Table 2). Data were compiled into a morphospecies-by-sample abundance matrix. Morphospecies were used because many specimens represent undescribed taxa and assignment to formal species designations would have been time-prohibitive and without discernable improvement to the biodiversity metrics that were the goal of this study (Oliver and Beattie 1996). External features (not genitalic dissections) were used to define morphospecies. It is anticipated that the use of morphospecies will tend to underrepresent sample diversity, especially if cryptic species

Table 2. Family level planthopper diversity worldwide and in the Neotropics with numbers of morphospecies and specimens found in Ecuador canopy fogging samples (Tiputini and Onkone Gare combined; numbers of world and Neotropical taxa adopted from O'Brien and Wilson (1985), Bourgoin (2019), Bartlett et al. (2018), and O'Brien, (unpublished).

Family	World		Neotropics		Canopy Samples	
	Genera	Species	Genera	Species	Morpho-species	Specimens
Acanaloniidae	7	83	7	59	2	23
Achilidae	160	511	48	111	113	2070
Achilixiidae	2	24	1	8	10	256
Caliscelidae	76	229	10	20	0	0
Cixiidae	230	2508	31	280	95	2765
Delphacidae	419	2226	68	266	8	3186
Derbidae	163	1686	41	410	143	4800
Dictyopharidae	156	732	41	120	26	325
Eurybrachidae	41	193	0	0	0	0
Flatidae	292	1433	64	280	22	422
Fulgoridae	143	761	68	268	57	158
Gengidae	2	4	0	0	0	0
Hypochthonellidae	1	1	0	0	0	0
Issidae	192	1024	14	43	103	2890
Kinnaridae	25	116	13	53	2	18
Lophopidae	48	164	2	6	7	35
Meenoplidae	23	161	0	0	0	0
Nogodinidae	94	367	13	70	20	458
Ricaniidae	63	443	6	10	7	68
Tettigometridae	14	87	0	0	0	0
Tropiduchidae	186	659	37	103	23	477
Totals	2337	13412	464	2107	638	17951

occur (particularly in the Cixiidae and Derbidae). Alternatively, sexual dimorphism (particularly for some derbids) could inflate the number of observed taxa. In the results and discussion, all references to planthoppers 'species' from the canopy refer to morphospecies.

Specimens from the study are deposited in three collections: National Museum of Natural History, Washington D.C., USA [USNM], University of Delaware, Newark, Delaware, USA [UDCC], and the Pontificia Universidad Católica del Ecuador, Quito, Ecuador [QCAZ].

Biodiversity measures. Biodiversity estimators are used to predict actual diversity based on observed samples. EstimateS (Version 8.2.0) (Colwell 2005) was used to calculate seven biodiversity estimators. All seven estimators were used because there was no clear choice as to which estimators were most appropriate for canopy fulgoroids. The diversity estimators were ACE mean (Chao and Lee 1992; Chao et al. 1993), ICE mean (Chao et al. 2000), Chao 1 mean (Chao 1984), Chao 2 mean (Chao 1984, 1987), Jackknife 1 mean (Burnham and Overton 1978, 1979), Jackknife 2 mean (Burnham and Overton 1978, 1979), and Bootstrap mean (Smith and van Belle 1984). ACE and Jackknife 1 and 2 are abundance-based estimators that rely on morphospecies abundances to determine final diversity. ICE and Chao 1 and 2 are incidence-based estimators that rely on presence/absence data for final diversity predictions. Bootstrapping subsamples randomizes data for calculating estimates. Estimators are provided for the combined dataset, Tiputini and Onkone Gare individually, and partitioned among the wet, dry, and transitional seasons.

Cumulative observed species and alpha diversity estimators were plotted against samples to construct species accumulation curves. If sampling is adequate for biodiversity estimation, the curve is expected to initially exceed an asymptote then level off as each successive sample progressively yields fewer previously unobserved species; a substantively increasing curve suggests that additional samples are required. A second indicator of sampling completeness is the numbers of “rare” species (singletons—represented by one individual in the combined samples—and doubletons, represented by two individuals) which decline as sampling becomes more complete.

Beta diversity was calculated using the software program Spade (Chao and Shen 2010). Beta diversity comparisons were made both between sites (Tiputini and Onkone Gare) for combined data and within each season (wet, dry, and transitional). Three sets of data with varying levels of cutoffs of rare data were examined. Morphospecies that appeared in at least 5% or 10% thresholds of total samples were examined in a separate analysis. The 5% cutoff contained 163 morphospecies and the 10% cutoff contained 93 morphospecies. Indices used were Sørensen’s similarity index, Bray-Curtis dissimilarity and Jaccard’s similarity coefficient. Sørensen’s similarity index examines the number of species shared between the samples over the combined population. Values range between 0 and 1 with 0 indicating no shared species and 1 being identical species composition. Bray-Curtis examines the dissimilarity of two communities by dividing the total number of species not shared over the entire population of both communities. Values range between 0 and 1 where 0 means the two sites have the same composition, and 1 means the sites do not share any species. Jaccard’s tests community similarity using presence/absence data and assumes the population has been thoroughly sampled. Values range from 0 to 1 with 0 sharing no species and 1 sharing all species. Jaccard’s and Sørensen’s were calculated using incidence, while Bray Curtis was calculated using abundance data.

Results

The 952 canopy samples examined contained 17,951 planthopper specimens (average 14.96 specimens/sample), representing 15 of the 16 planthopper families found in the Neotropics (Table 2, only Caliscelidae were absent). Three years of fogging at Onkone Gare produced 12,516 planthopper specimens (average 13.97 per sample). Tiputini produced 5,435 planthopper specimens (average 18.12 per sample) in one year of sampling.

Alpha diversity. A total of 638 morphospecies was recognized with 573 from Onkone Gare and 432 morphospecies in Tiputini (Table 3). There were 367 morphospecies shared between the two sites (58%); 206 were unique to Onkone Gare (32%) and 65 were unique to Tiputini (10%). There were 150 singletons (24%) and 67 doubletons (10%).

Species accumulation curves in all instances failed to reach an asymptote. Species richness estimates were highest for the combined data (Fig. 1, Table 4), with Onkone Gare predicting a higher richness than Tiputini (Fig. 2 and 3, Table 4). Predicted richness values were lowest for the bootstrap mean estimator, and highest for the Jack 2 mean estimator. For combined data, the predicted values varied from

Table 3. Summary statistics for planthopper diversity in Ecuador canopy fogging samples.

	Onkone Gare	Tiputini	Combined Sites
Samples	726	226	952
Specimens	12516	5435	17951
Morphospecies	573	432	638
Shared Species	—	—	367
Unique Morphospecies	206	65	—
Singletons	149	104	150
Doubletons	53	77	67

Table 4. Ecuador canopy fogging Alpha-diversity estimator values for planthoppers in six sampling categories.

	Combined Data Set	Onkone Gare	Tiputini	Wet Season	Dry Season	Transitional Season
Number of Samples	952	726	226	313	344	295
Number of Individuals	17951	12516	5435	7202	5167	5582
Number of Observed Species	638	573	432	504	445	459
Singletons Mean	150	149	126	147	134	116
Doubletons Mean	67	53	58	57	60	66
ACE Mean	782.3	715.9	552.9	650.5	578.5	555.9
ICE Mean	785.1	716.1	567.4	662.0	590.6	564.4
Chao 1 Mean	802.3	777.2	565.5	689.0	591.1	558.6
Chao 2 Mean	803.6	780.4	591.7	694.9	622.7	564.4
Jack 1 Mean	792.9	725.8	569.5	660.6	587.6	581.7
Jack 2 Mean	876.8	823.7	649.2	754.3	674.4	634.6
Bootstrap Mean	707.5	639.7	492.9	573.1	508.1	516.9
Average Estimator Value	793	740	570	669	593	568

707.5–876.8 and averaged 793 species. Average predicted species richness was 740 species for Onkone Gare and 570 for Tiputini. It appears that the number of samples had a central influence on both the observed and predicted richness values since species accumulation curves had not reached an asymptote and numbers of species always increased substantively with increased sampling.

The numbers of samples were more similar among the three seasonal categories (Table 5). The average number of specimens per sample was highest for the wet season (23.0), followed by the transitional (18.9) and dry season (15.0). Predicted species richness is highest in the wet season (average estimator value 669 species), followed by dry (593) and transitional (568). This result indicates that planthopper species richness is highest during the wet season (supporting common wisdom for planthoppers), and similar between the dry and transitional seasons.

Beta diversity. Complementariness of the fauna varied between the two sites based on index used, and variations were more pronounced when individual seasons were compared (Table 6). Beta diversity analysis was conducted using metrics that took both incidence and abundance into account. Due to the nature of the data, with a high number of rare taxa, the certain indices used would conflict when compared to the remaining indices.

When the full collections from the two sites (726 samples and 226 samples) are compared, the overlap is higher than any other comparison. Of the 638 species present 367 morphospecies were shared between the two sites, which encompassed nearly 85% of the species at Tiputini (367/432 at Tiputini). Onkone Gare alone contained 573 morphospecies, and the disparity between the sites in total morphospecies was expected from the disproportionate levels of sampling.

Table 5. Morphospecies richness of sample locations by season.

Season	Locality					
	Onkone Gare			Tiputini		
	Samples	Species	Specimens	Samples	Species	Specimens
Wet	214	633	4012	99	361	1442
Dry	287	821	4364	57	185	803
Transitional	225	800	4140	70	212	3190

Table 6. Within season comparisons of Ecuador canopy fogging Beta-diversity index values for planthoppers found at Tiputini and Onkone Gare. Comparisons are made for all data and for data limited to species found in more than 5% or more than 10% of sample locations.

	All data	5% or greater	10% or greater
Onkone Gare vs Tiputini			
Jaccard Incidence	0.5752	0.4954	0.4531
Sørensen Incidence	0.7303	0.6626	0.6237
Bray Curtis	0.5384	0.5019	0.5012
Tiputini Wet vs Onkone Gare Wet			
Jaccard Incidence	0.5218	0.4038	0.3457
Sørensen Incidence	0.6858	0.5757	0.5138
Bray Curtis	0.6190	0.5838	0.5640
Tiputini Dry vs Onkone Gare Dry			
Jaccard Incidence	0.3596	0.3814	0.3000
Sørensen Incidence	0.5289	0.5522	0.4615
Bray Curtis	0.2888	0.2644	0.2477
Tiputini Transitional vs Onkone Gare Transitional			
Jaccard Incidence	0.3747	0.3889	0.3378
Sørensen Incidence	0.5452	0.5600	0.5051
Bray Curtis	0.4174	0.4020	0.3886

The wet season was more diverse than the dry or transitional seasons (Table 4). For the wet seasons Onkone Gare had substantively more morphospecies than Tiputini (633 and 361 respectively, Table 5), and shared 263 morphospecies, the most for an individual season. The incidence-based estimators (Jaccard and Sørensen) produced results similar to all season results (Table 6). The abundance-based estimator, Bray Curtis, contrastingly, indicated that assemblages are less similar in the wet season than during all season comparisons.

Table 7. Morphospecies richness for Yasuní ground based collecting methods. Specimens were collected over four days and five nights in Yasuní National Park (April 25–29, 2005) using light trapping, hand collection, and sweep netting targeting fulgoroids. Specimens were collected by Dr. Charles Bartlett, Nate Nazdrowicz, and Dawn Chang.

Family	Number of Morphospecies	Number of Specimens
Achilidae	51	403
Cixiidae	57	285
Delphacidae	16	128
Derbidae	23	60
Dictyopharidae	18	54
Flatidae	10	39
Fulgoridae	14	32
Issidae	1	1
Kinnaridae	1	15
Nogodinidae	1	1
Tropiduchidae	2	3
Total	194	1021

The dry season saw a reduction in the morphospecies diversity of Tiputini relative to Onkone Gare with 185 to 420 respectively with 160 of those being shared (leaving Tiputini with 25 unique morphospecies). The incidence estimators (Table 6) decreased suggesting low similarity between the sites. However, the Bray Curtis index indicated that the two communities were strongly similar, the strongest indicator for similarity of all the indexes. This disparity between the incidence and abundance estimators highlights the issue of dependency on a single estimator for Beta diversity.

The transitional season saw a slight increase in the Tiputini species count while Onkone Gare stayed stable at 212 and 419 morphospecies respectively. Of the 212 morphospecies at Tiputini, 172 were found at Onkone Gare. The incidence indexes indicated a 2/5 to 1/2 similarity and the Bray Curtis was slightly higher at 3/5 similarity.

When the data are restricted to morphospecies that appear in at least 5% or 10% of the samples, complementarity decreases in the four treatments (combined, wet, dry, and transitional) (Table 6). The effect is stronger in the 10% threshold. These restricted data also increasingly reduced the variance seen in comparison of values between the treatments. The limiting of rare or possibly transient taxa may produce a more realistic comparison of the canopies given the incomplete sampling.

Discussion

Alpha diversity. Species accumulation curves for the individual sample sites and the combined sites failed to reach asymptotes indicating that additional samples are needed to assess canopy planthopper diversity. The high percentage of rare morphospecies taxa (23.5% singletons, 10.5% doubletons) indicates that canopy planthoppers remain incompletely sampled, as the percentage of rare taxa should decline as sampling becomes more complete (Colwell and Coddington 1994; Longino et al. 2002).

When examined separately, Onkone Gare was the more diverse of the two sites. This may reasonably be an artifact of sample size - Onkone Gare had three times the sampling of Tiputini. The observed morphospecies count for Onkone Gare was 573, while Tiputini contained 432, a difference of 141 morphospecies. Onkone Gare averaged 740 predicted morphospecies, which was slightly lower than the predicted value for both sites, 793. Onkone Gare had a lower average species per sample average for the two sites (13.97) compared to Tiputini (18.12).

The wet season was most species rich of the seasons, with an average of 504 morphospecies observed of 669 predicted species (Table 4). The transitional season had 459 morphospecies observed and 568 predicted species then the dry season with 445 observed and 593 predicted species. The dry season's higher predicted total compared to the transitional season was counterintuitive, as species richness was expected to correlate with rainfall.

Our alpha diversity findings are consistent with work conducted in Papua New Guinea (Novotny and Basset 1999). They examined the richness of insect herbivores on 15 species of *Ficus* Linnaeus (Rosales: Moraceae) in rainforest and coastal areas. The sampling techniques, by hand and aspiration, produced 779 herbivorous insects out of 44,900 individuals. Despite their high number of collected individuals the species accumulation curves also failed to reach an asymptote.

The variation in the seasonal data are also consistent with many other tropical insect groups. Wolda (1988) demonstrated that most (>80%) insects have a seasonal component to their presence at Barro Colorado Island (Panama), and fewer than half (39%) appeared in samples year-round. Seasonal peaks for different insect groups also appear year-round, as opposed to temperate climates where most taxa are restricted to peaks in the "warm" season.

The taxon composition of canopy planthoppers appears to differ from that found using ground-based collection methods. Over four days and five nights (April 25–29, 2005) in Yasuní National Park, three collectors (Charles Bartlett, Nate Nazdrowicz and Dawn Chang) used sweeping, beating, and lights targeting planthoppers (Bartlett, unpublished data). They collected 1,021 individuals and 194 planthopper morphospecies in 11 families (Table 7). Perhaps the most striking differences in taxon composition are that the Delphacidae were more species rich (16 vs. 8 morphospecies) in the ground-based collecting methods, and the Issidae were dramatically more abundant and species rich in the canopy samples, with only a single specimen found using ground-based methods, compared to 3,175 specimens (~16%) and 101

morphospecies (~18%) in the canopy. This serves as an example of the influence of sampling methods on taxon composition and suggests that the canopy samples alone may ultimately underestimate true planthopper species richness.

Beta diversity. Overall, the beta diversity analysis for season showed varying levels of consensus, with contradictory patterns emerging in some cases where indices behaved contrary to each other. All estimators are sensitive to high numbers of rare taxa, making comparisons between them difficult. In comparisons where there were large differences in morphospecies (i.e., transitional season) beta diversity estimators were more likely to provide conflicting results. Overall, the varying levels of similarity (or dissimilarity) seen are expected in an under sampled community. By limiting the data tested with thresholds of 5% or 10% presence greater consensus can be reached by limiting the influence of rare or transient taxa.

The beta diversity estimators for the combined sites behaved predictably in terms of the alpha diversity. During the alpha diversity analysis, the rare taxa limited the estimator's ability to reach asymptote. Again, the rare taxa increased uncertainty of the beta estimators. The canopy planthoppers distribution is sufficiently unknown that multiple estimators are valuable. The diversity of the planthoppers in the canopy appears to have a seasonal component to their life history that is not explored here. During the wet season, which exhibits the highest diversity, it is possible that there are more specialists or generalists as forest fauna responds to the increased precipitation. The Tiputini collections from the wet season may responded this effect, reflected in total abundance with over 3,000 individuals compared to 2,200 in the dry and transitional combined. The large difference in abundance by season is sizable compared to Onkone Gare. Onkone Gare had an even spread of individuals with the wet season containing 4,140, dry with 4,012, and transitional with 4,364.

The wide diversity of trees in the Amazon coupled with their sparse occurrence ensures that the composition of the canopy varies greatly between the two sites. If this disparity were solely a product of sampling, the wet season would have also followed the same pattern.

Composition of canopy samples. In the canopy samples, seven families made up 82.6% of the morphospecies and 74.4% of the specimens observed. By morphospecies these were Derbidae (22.4% of planthopper morphospecies), Achilidae (17.7%), Issidae (16.2%), Cixiidae (14.9%), Fulgoridae (8.9%), Dictyopharidae (4.1%), and Tropiduchidae (3.6%). This roughly corresponds to the known Neotropical diversity of these families, in which the most diverse taxa are Derbidae (18.2% of described Neotropical planthopper species), Flatidae (14.2%), Delphacidae (12.7%), Cixiidae (12.5%), Fulgoridae (12.4%), Issidae (7.2%), and Dictyopharidae (6.7%). Differences in observed versus expected species richness among families may suggest differences in the ratios of described-vs.-undescribed taxa. The relatively low richness of delphacids in the canopy is due to delphacids are mostly grass and sedge feeders and would not be expected to occur in the canopy; but no obvious explanation can be provided for the apparent low diversity of flatids in the canopy.

Taxonomic representation within families was remarkable. Within the Cixiidae (Cixiinae), Cixiini and Pentastirini were abundant and Pintaliini unexpectedly abundant and diverse. The Issidae were represented largely by Issini near *Thionia* Stål, whose diversity in the canopy samples far exceeds that expected based on described *Thionia* species. There were also a series of unusual issid taxa such as *Buca* Walker (Fig. 4E) and *Oronoqua* Fennah representing several new species, and at least one undescribed genus, recently described as *Waorania* Gnezdilov and Bartlett (Fig. 4C). Lophopidae was represented by seven morphospecies of *Hesticus* Walker (Fig. 4A), a genus known from only three described species. *Hesticus* was excluded from the Lophopidae by Soulier-Perkins (1997, 2000), but has not yet been placed elsewhere (tentatively included in the Tropiduchidae by Emeljanov 2013a). Achilixiidae were represented by 10 morphospecies of *Bebaiotes* Muir (Fig. 4F), a genus known from eight described species. Dictyopharidae were largely represented by the macropterous Dictyopharinae. The Cladodipterini (*Diacira* Walker, *Cladodiptera* Spinola and *Protachilus* Fennah), recently reassigned from Dictyopharidae to Fulgoridae (Song et al. 2011; Emeljanov 2011, 2013b), were represented by eight morphospecies and 90 specimens. Ricaniidae were represented by taxa similar to *Semestra* Jacobi, *Cotrades* Walker and *Pharsalus* (Fig. 4B, D) the latter moved to Ricaniidae from Issidae by Gnezdilov (2009). Nogodinidae was represented by *Biolleyana* Distant, *Bladina* Stål, *Nogodinia* Stål, *Varciopsis* Jacobi and *Vutina*

Stål, plus a large number of *Colpoptera* Burmeister (Colpopterinae transferred to Nogodinidae from Issidae by Gnezdilov (2012).

Within Delphacidae, 3,160 of 3,186 specimens represented four species in Asiracinae, a basal subfamily, two of which were subsequently described (Barringer and Bartlett 2011), and the remaining two are evidently *Ugyops* Guérin-Méneville (or *Canyra* Stål, see Barringer and Bartlett 2011). The plant hosts of Asiracinae possibly are Pteridophyta (found as epiphytes in the canopy), unlike Delphacinae, which feed mostly on graminoids (Wilson et al. 1994). *Tetrasteira vulgaris* Barringer and Bartlett was the most abundant species in the canopy samples, represented by 3009 specimens. The remaining four species were Delphacinae, three of which were single specimens, possibly transients, but the remaining species is an undescribed genus near *Stobaera* Stål represented by 21 specimens.

Within Fulgoridae, *Calyptrorhynchus* Metcalf species were best represented, with *Cathedra* Kirkaldy, *Enchophora* Spinola, *Enhydra* Walker, *Episcius* Spinola, *Learcha* Stål, *Lystra* Fabricius, *Odontoptera* Carreno, *Oeagra* Stål, *Paralystra* White and *Scaralis* Stål also found. Several specimens appear to represent new genera. Our impression is that the Fulgoridae were more sparsely represented in these samples than anticipated, and some of the expected large taxa (e.g., *Phenax* Germar, *Fulgora* Linnaeus) were entirely absent (similarly, cicadas appear sparse among the samples). It is likely that these large Auchenorrhyncha may successfully jump clear of the sample collection area (even if subsequently knocked down), and therefore are underrepresented.

Among all planthopper families, wing polymorphism was absent. Most planthopper families have species with brachypterous and macropterous forms (or are entirely brachypterous); but among the canopy samples, all planthoppers were macropterous. We also observed an apparently low rate of parasitism with only 27 specimens (one Issidae, one Cixiidae, 25 Derbidae) parasitized by Hymenoptera: Dryinidae or Strepsiptera (Lepidoptera: Epipyropidae were not observed; internal parasites such as Diptera: Pipunculidae were not sought).

Future Perspectives

A total of 638 fulgoroid morphospecies was observed and 793 was predicted using the average of seven estimators. The predicted total species richness of canopy planthoppers that represents 33% of the described Neotropical planthopper fauna (793 predicted / 2,107 described) was found in only 9,250 m² of forest, excluding vegetation layers near the ground. Yet a sampling area of 4.88×10^{-8} (or 0.0000004888%) of the forest canopy was found to harbor a diversity of 37% of known planthopper species richness of the entire Amazon basin.

Bartlett and O'Brien (unpublished data), based on preliminary work with the canopy samples, estimated that up to 70% of the fauna in the canopy was undescribed. This suggests that the 793 estimated species represent ~6% of the known diversity (793 estimated species out of 13,412 known species worldwide). This also implies that 555 of the estimated 793 morphospecies are undescribed. Since the initiation of this project, three new planthopper genera (*Loisirella* Holzinger, Holzinger and Egger, Cixiidae; *Pentasteira* Barringer and Bartlett, Delphacidae; *Waorania* Gnezdilov and Bartlett, Issidae) and seven new species have been described from these samples (Barringer and Bartlett 2011; Holzinger et al. 2013; Gnezdilov et al. 2016; Gnezdilov and Bartlett 2018), with the balance still to be considered (Fig. 4).

If Erwin's (1982) calculation for diversity is applied to Fulgoroidea, an estimate of Neotropical species diversity can be made. With an estimated 50,000 species of trees in the Neotropics, and 60–80% of planthoppers being host specific, a species richness of 30,000 to 40,000 planthoppers may be estimated for the Neotropics (50,000 trees species * 0.6 or 0.8 host affinity), assuming each tree species has only specialized planthopper species associated with it. However, this level of host specificity is based on temperate records, and Novotny et al. (2002) have suggested that host specificity in the tropics is lower than the temperate region; but even if host specificity were only 25%, this would predict 12,500 planthopper species in the Neotropics, which is equivalent to the currently known richness of planthoppers worldwide (Bartlett et al. 2018; Bourgoin 2019).

It is the authors' hope that this work will spur further research on Fulgoroidea, not only on this material, but also in the Neotropical regions as a whole. A wealth of opportunities to pursue this work

from morphological and genetic approaches can further elucidate the identities of the morphospecies and any patterns within.

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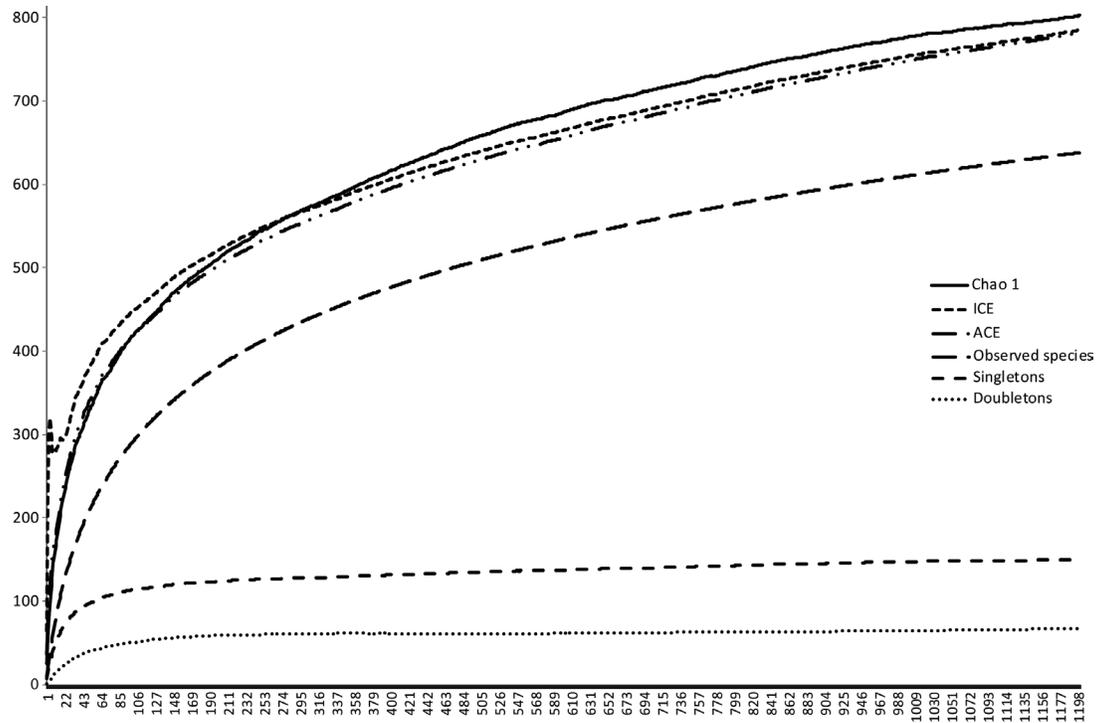


Figure 1. Combined species discovery curve for 952 planthopper canopy fogging samples (two sites, four collecting years) including select estimators of diversity. Total observed morphospecies was 638, with 24% represented as singletons. The averaged value of the diversity estimators is 793 species. Curves for species observed and diversity estimators failed to reach an asymptote.

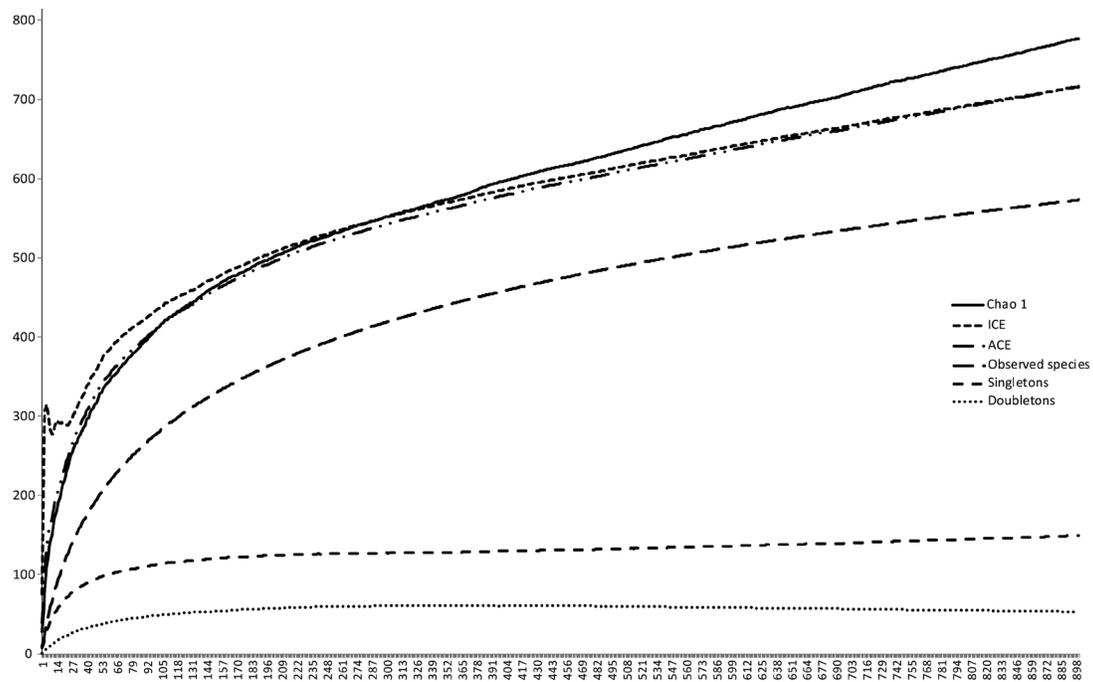


Figure 2. Combined species discovery curve for 726 planthopper canopy fogging samples from Onkone Gare (three collecting years) including select estimators of diversity. Total observed morphospecies was 573, with 26% represented as singletons. The averaged value of the diversity estimators is 740. Curves for species observed and diversity estimators failed to reach an asymptote.

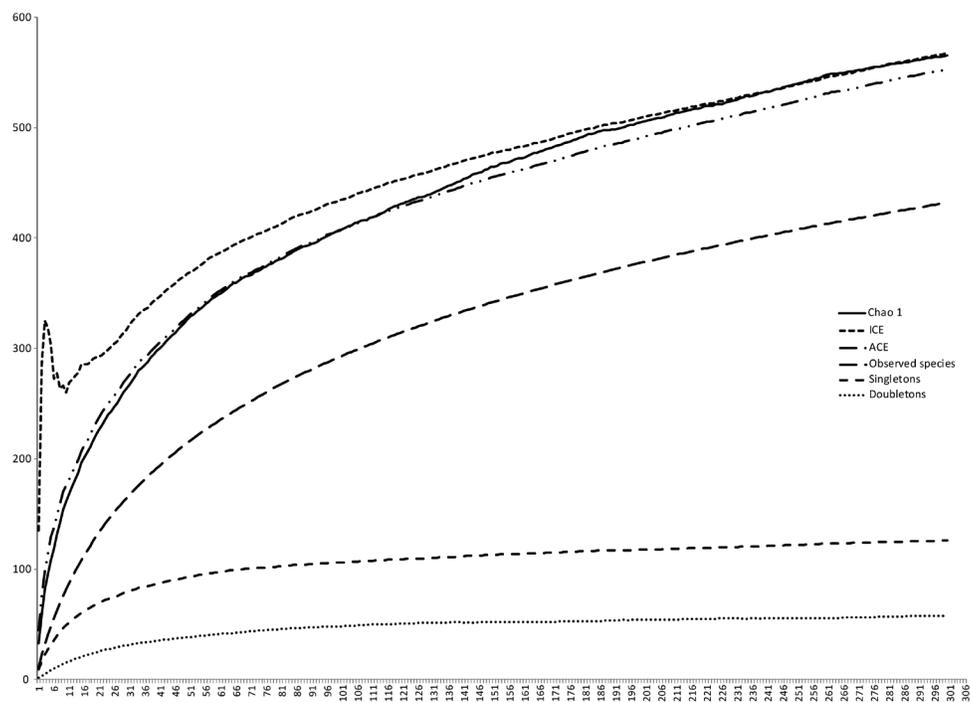


Figure 3. Combined species discovery curve for 226 planthopper canopy fogging samples from Tiputini (one collecting year) including select estimators of diversity. Total observed morphospecies was 432, with 29% represented as singletons. The averaged value of the diversity estimators is 570. Curves for species observed and diversity estimators failed to reach an asymptote.

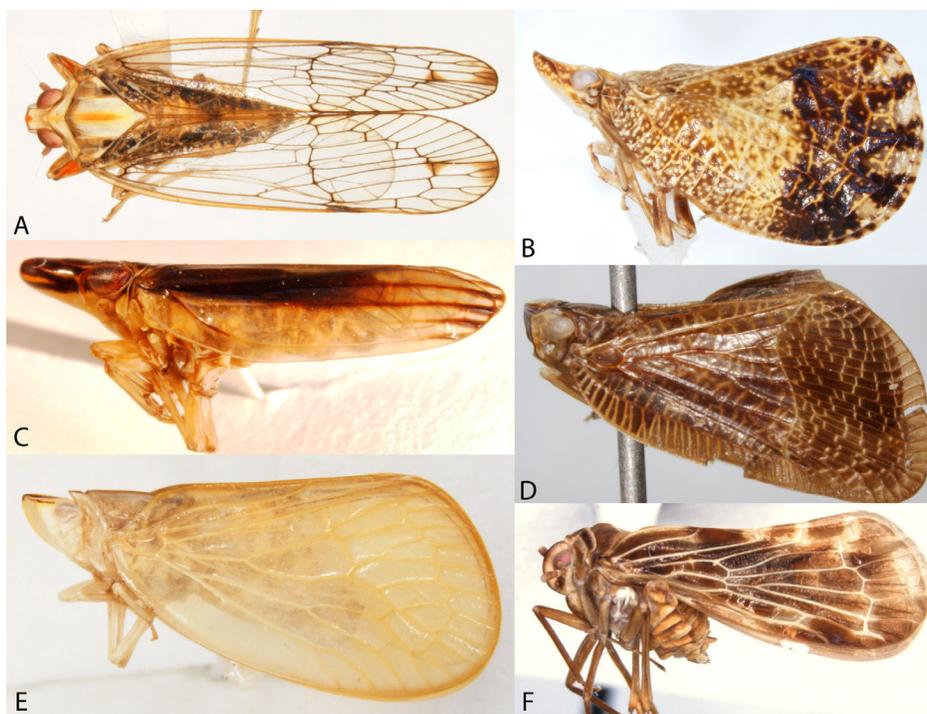


Figure 4. Example planthopper taxa from canopy fogging samples. **A)** *Hesticus* sp. (Lophopidae). **B)** Pharsalinae (Ricaniiidae), probably *Pharsalus*. **C)** Issidae, *Waorania jaguarina* Gnezdilov and Bartlett. **D)** Ricaniiidae. **E)** *Buca asymmetrospinata* Gnezdilov, Bartlett and Bourgoin (Tropiduchidae: Elicinae). **F)** *Bebaiotes* sp. (Achilixiidae).