CANOPY ASSEMBLAGES AND SPECIES RICHNESS OF PLANTHOPPERS (HEMIPTERA: FULGOROIDEA) IN THE ECUADORIAN AMAZON

by

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ABSTRACT

The diversity of planthoppers inhabiting the canopy of Terre Firme forests is largely unknown but potentially makes up one twentieth of known World planthopper diversity. This study estimates Neotropical planthopper diversity using multiple measures. Samples were collected by canopy fogging at 2 localities in the Ecuadorian Amazon Terra firme forest (Orellana province) Tiputini Biodiversity Station and Reserva Etnica Waorani. Fogging was conducted during 3 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 identified. EstimateS diversity software was used to determine 7 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 the diversity of the sampling sites composes roughly 1/3 of the known planthopper diversity for all Central and South America.

In addition to diversity estimates, host tree affinity and seasonal preferences were examined for 12 morphospecies in the Reserva Etinica Waorani (Onkone Gare) samples, using the program Presence. The species chosen were from 6 planthopper families and the morphospecies fell into 4 categories: no preferences found, possible hosts tree identified, seasonal components identified, or host tree and seasonal component identified. Applying this study is a first step towards novel

methods to predicting hosts for highly monophagous insects in diverse tropical environments.

Chapter 1

CANOPY ASSEMBLAGES AND SPECIES RICHNESS OF PLANT HOPPERS (FULGOROIDEA) IN THE AMAZON CANOPY OF ECUADOR

1.1 Introduction

Much of the Earth's biota is constituted of arthropods and smaller invertebrates (Wilson 1992, Simpson and Cracraft 1995), and few places exemplify this as well as Neotropical forests. The tropics hold the greatest diversity of not only insects, but also plants, birds, and many other taxa. Insects are by far the most species rich group of tropical terrestrial organisms. This incredible diversity creates unique challenges for science because sampling and categorizing this diversity is a daunting endeavor yet it is critical for our understanding of global biodiversity. Forest surveys of trees produce vast numbers of species, with densities sometimes below an individual per hectare (Whitmore 1998). Each new survey can also produce 10s to 100s of species previously unknown to science. Aside from charismatic megafauna, few groups are adequately catalogued. Insects present a particular problem; although approximately 1 million species are already described, predictions of species richness range from 3.8 to 30 million species (Erwin 1983a, Fonseca 2009). Large charismatic insect groups, such as butterflies, have the most complete species records, but many other groups remain largely unexplored.

Coupled with incomplete species record is a disparity between taxonomists and diversity. It has been estimated that for every invertebrate taxonomist there are 400 known species and another 400 yet undiscovered species, though the latter number may be grossly underestimated (Gaston and May 1992). Estimates place 80% of invertebrate taxonomists in North America and Europe (where the biota is comparatively well known), and roughly 7% in Central Africa and Neotropics where most new species are found (Gaston and May 1992). In contrast, upwards of 50% of the Earth's diversity is found in moist tropical biomes straddling the equator, which only account for 6% of the terrestrial biome (Wilson 1988, 1992). The distance between specimens and expertise increases the difficulty of cataloging the tropic's biological riches.

Hyperdiverse Neotropical forest habitats are in a state of crisis. The past 250 years have a seen human encroachment and technology damage the landscape. Neotropical forests, in particular, are susceptible to conversion from forest to fields for pasturing and crops or unsustainable agricultural practices (Didham et al. 1996, Whitmore 1998). The conversion of habitats, species, and resources into finite valued resources has led to an economic view on the environment, sometimes with the affect that economics supersedes environmental concerns. Banana production in the early 1990s caused large shifts in rainforest use and value driven by global demands (Vandermeer and Perfecto 1995).

The rapid conversion of highly biodiverse tropical forests to anthropogenic landscapes is one factor that has led popularization of the "biodiversity crisis", which emphasizes a high rate of species extinctions (Kareiva and Meyer 2002). Myers and colleagues (2000) work identified 35 biodiversity hotspots of conservation priority. These locations have a combination of areas of high percentages of endemic species and regions threatened with destruction or other forms of encroachment. Conserving these regions would place upwards of 50% of the earth's biodiversity under protection. Destruction of these hotspots and degradation of all habitats pushes diversity down towards a looming extinction crash.

Changes in extinction rates also influence the current diversity situation. It is the general consensus among scientists that the background extinction rate has increased drastically in the past 200 years (Myers 1988, Simpson and Cracraft 1995, Pimm et al. 1995). Historical records for background extinction rates are often based on fuzzy math, using fossils and records of current extinctions (approximately from the 1600's onward). Fossil records are limited, only showing the portion of the historic fauna that was preserved; this provides a limited scope for accurate measure (Regan et al. 2001). Current knowledge of extinction rates comes primarily from plant and animal extinctions of the past 400 hundred years. May and colleagues (1995) estimated that since 1600 A.D. that there have been 490 animal and 580 plant extinctions globally. The historic and current data point towards a 0.5 to 5 species per year background rate (IUCN 2006).

The contemporary global extinction rate is much higher for certain taxa, with tens of species lost per year, several fold over historic values. In amphibians alone, the current extinction rate may be up to 211 times greater than historically (McCallum 2007). This level of damage is comparable to a million years of normal species loss. This increased background extinction rate and species already known to be lost paint a grim picture (Pimm et al. 1995). Many taxa are currently so depleted in terms of species numbers that it will take centuries to recover.

One major driving factor of extinction is of the loss of endemics from the world's biodiversity hotspots (Mittermeier 2004, Fonseca 2009). There is a constant struggle to preserve these localities to slow the bleeding of biodiversity. The importance of endemics is tied to the interdependence of species (Regan et al. 2000). The loss of a single species may have great impacts, as complex interactions are altered in trophic cascades. Stochastic events and anthropogenic pressures may also have a cascade effect, wiping out entire genera or families owing to phylogenetic relatedness or ecological similarity causing swaths of related taxa to die out.

As a consequence of this battle to prevent biodiversity loss, many scientists have called for increased support for systematics and higher rates of species description by taxonomists. While every taxonomist would prefer to be more productive, the actual limiting factor is the number of taxonomists, which is known as the "taxonomic impediment" (Systematics Agenda 2000, 1994). Funding for taxonomy, as well as new taxonomists, has not met the needs for description of the world's biota or kept pace with some predictions of extinction rates (Gaston and May 1992, Simpson and Cracraft 1995).

What then lends hyperdiverse regions, and specifically the New World Tropics, the breadth of diversity seen? The latitudinal gradient hypothesis states that diversity increases toward the equator; this has received much support and is broad enough to encompass multiple reasons for why the tropics support high diversity (Weins et al. 2008, Arita and Vazquez-Dominguez 2008). The latitudinal gradient is also one of the most conspicuous patterns to arise from the tropics (Arita and

Vazquez-Dominguez 2008). Three main factors have been advanced as causes of the present diversity with respect to latitudinal gradients: speciation, extinction, and biogeographic dispersal (Mittelbach et al. 2007, Wiens et al. 2008). Other hypotheses include: Climatic stability, energy input, increased evolutionary rates, diversity refuges, physical environments, and biodiversity epicenters (Mittenbach et al. 2007, Powell 2007, Arita and Vazquez-Dominguez 2008, Valentine et al. 2008). Testing these theories is difficult without historic data on diversity but the trend is robust, and generally supports an "Out of the Tropics" origin for the latitudinal gradient observed today (Wiens et al. 2009 Valentine et al. 2008). This distance from the equator is still tied to decreases in species diversity, an increase in species range overlap, and an introduction of climatic extremes (Brehm et al. 2003).

As mentioned previously, few animal groups in the tropics have been completely catalogued. Large charismatic fauna such as Aves and Mammalia are relatively complete in their inventories. Insects on the whole have failed to reach similar levels of survey and documentation. The superfamily Fulgoroidea in the Neotropics has yet to receive a comprehensive review or checklist of their diversity. There are an estimated 2,333 species in 470 genera in the Neotropics according to unpublished checklists complied by Lois O'Brien. This means that one sixth of the world's fauna of the known 11,837 planthopper species reside in the Neotropics (Flow Website, accessed April 2011). Despite this, the most comprehensively studied area for Fulgoroidea is central Europe (Holzinger et al. 2003).

The higher classification of Fulgoroidea also is contentious. Debate regarding the phylogeny of planthopper families questions family-level placement of several taxa, with the suggestion that some families (e.g., the Ricaniidae), once properly defined, are not included in Neotropical taxa. Broader definitions of certain families may also influence diversity categorization in the tropics (Issidae, certain tribes of Acanaloniidae, and Nogodinidae) (Personal Communication Dr. Charles Bartlett, March 2011).

Accuracy issues arise with respect to collecting methods. Traditional methods dating back to early European explorers mainly focused on ground dwelling insects and those attracted to lights as current methods were unavailable. While any method will be efficient on a certain portion of the insect fauna, in tropical rainforests the majority of life dwells in the canopy layer presenting a challenge to the traditional methods. In the past 30 years improved efforts have been made to accessing the canopy, the “Last Biotic Frontier” on land (Erwin 1983a).

Many tools have been applied to sampling in the tropics, but do not obtain a full three-dimensional sample of the canopy, often multiple techniques need to be employed (Barker and Pinard 2001). Cranes and walkways have been used to for long-term study of forests canopies, but are expensive and limited in scope. Walkways, while offering excellent vision and vantage, take extensive effort to erect. Cranes, are mobile, but generally limited by terrain, roads, and forest density. These techniques also have limited use as they cannot easily reach remote locations where many biodiversity projects are focused (Lowman and Wittman 1996, Barker and Pinard 2001, Stork 2001). Helicopters and aerial canopies have been explored, but these methods are prohibitively expensive and usually only allow shallow top down sampling and surveys of the canopy. Arboreal scaling and climbing can be used to target individual trees, but the diversity of the tropical forests means that this requires extensive training experience and limits productivity. The need for a large scale sampling method made canopy fogging an appropriate tool in the tropics.

Canopy fogging using insecticides has become an invaluable sampling method due to its thoroughness and limited impact on the forest canopy. Fogging allows for minimal damage to the specimens collected and the canopy is left undamaged and habitable after it has been sampled (Erwin 1983b, Lawton et al. 1998). Harmful residues with most products used will breakdown under ultraviolet exposure leaving the tree ready for colonization almost immediately (Stork and Hammond 1997, Erwin et al. 2005). Recolonization is rapid and resampling within a few months is plausible and effective. Canopy sampling also allows for a snapshot of the fauna present on the surface of leaves, branches, and fruit (Stork and Hammond 1997).

A benefit of fogging is that it eliminates several biases other methods present. No attractants are used, and it does not it rely on any specific activity or behavior of the arthropod, e.g. malaise traps and flight interception traps (Basset et al. 1997). Sticky traps can cause damage to specimens making identification and preservation for collections difficult. Other passive methods of collection may be subject to predation or decay before collection and require considerable monitoring effort. Lastly, time of collection is unimportant as the knockdown factor allows for collection day or night. The largest limiting factors are lack of sampling organisms that dwell inside plant tissue and weather.

Canopy fogging as a practice consists of selecting a tract of trees or a single tree and placing a collecting apparatus below (Erwin et al. 2005). Typical devices include sheets, funnels, or tarps. By quantifying the target plant(s), their size, diversity, and structural character, among others measures, quantitative collections are viable. Canopy fogging provides accurate surveys of ecologically important and critically threatened habitats. The need for accurate records of diversity is of great need to conservation professionals and policy makers. Arguments can be made to craft policies and pass laws to preserve species, but these are most effective when backed with supported by data. By documenting diversity, well informed and well-planned decisions can be made regarding preserving a multitude of taxa.

Alpha and beta diversity surveys can also highlight areas that are of the greatest concern and that are limited in knowledge. These regions are typically hard to reach or so diverse that multiple surveys are needed for reliable results. By identifying regions of high endemic diversity, taxonomists can focus on regions of highest priority and restoration efforts can be focused and targeted for the maximum payoff. This groundwork can also increase our knowledge of the interactions of plants and insects in the tropics.

Information on insect host plants for planthoppers in the tropics is sparse and not always reliable. The breadth of diversity of plant hosts alone makes for confident identifications without a trained botanist unlikely and the host plant to be an undescribed species. A best case scenario may specific as “feeds on x species during the period of time from y to z”. Typically more general information as “may be found on grasses in marsh or forest” is reported. Many studies done in tropical environments (New and Old World) are geared towards surveying richness rather than identifying relationships between insects and hosts (Basset and Novotny 1999, Novotny and Basset 2005). Estimates of host specificity can play an important role in discussions of global richness and diversity stability (Erwin 1982). Plant-phytophage interactions can account for upwards of 40% of food webs globally (Price 2002). The levels of specificity and food web importance can clarify the diversity of the tropics. This makes understanding host plants and their interactions vitally important to future directions of tropical studies. Plant records are progressing steadily with entire regions now possessing near complete surveys and guides (Godfray et al. 1999). Plant inventories of some portions of the tropics are now completed for some regions (Panama, Manuas, Rio de Janeiro) (Morawetz and Raedig 2007).

These data are limited with regard to the ability of future researchers to replicate records and verify host plants. It is also hobbled by incomplete sampling across the tropics (Morawetz and Raedig 2007). Remote regions and “unpopular” taxa leave records of endemism and distribution records incomplete. The range of many endemics may appear narrower than they truly are. Locating host plants in supposed home ranges may be difficult or fruitless efforts limiting the effective of limited sampling efforts available.

Questionable host record localities aside direct observations of plant feeding are even sparser. Most generalized collection methods either do not document host plants or make sweeping generalizations as to hosts e.g., found on bark, in clumps of grass. Collectors may also not interested in obtaining host information or feel they are unable to learn or identify the host plant (not possessing the botanical skills necessary to navigate the tropics). Further compounding this problem are taxa that live in inaccessible places such as underground, remote regions, or in the canopies of trees. Canopies and their arthropod communities though have steadily gained interest as a region of exploration due to their uniqueness and collecting techniques increasing their accessibility (Basset 1992).

Arthropod communities in the canopies have received a variety of treatments relating to their richness and abundance (e.g. Erwin 1983a, Stork 1991) and their seasonality (e.g. Novotny and Basset 1999). Species interaction (e.g. Basset 1992) and community diversity (e.g. Kitching et al. 2001) and their spatial attributes have also been investigated (e.g. Lucky et al. 2002). Predictions for arthropod habitats and predictive techniques have also been explored (Basset 1982).

In addition to the canopies' diverse assemblage, seasonality in the tropics is also unique when compared to the temperate systems. While there are seasons there are no climatic patterns where most insects disappear (e.g. winter or dry periods). While life cycles and developmental stages can be tied to seasonality features in temperate regions (e.g., sunlight hours, temperate) insects in the tropics may adopt year round strategies including polyvoltine breeding. Host switching may also be a common occurrence as host quality may also have cyclical components. Flowering and fruiting plants will be sequestering more energy and nutrients into limbs than at other times.

Host switching in the tropics may then be linked to the rainfall and indirectly plant growth and reproduction. Typically a species of tree in the forest will not fruit year round, but rather have a synchronous time of pollination and reproduction to increase chances of fertilization and overcome predators of progeny (Whitmore 1997). This in turn would lead to unequal nutrient movement throughout the plant to tissues increasing food quality in the plants tissues. Planthoppers as phloem feeders typically an increase in nutrients through a plant's vascular system would be greatly beneficial in terms of both growth and development and for reproduction.

Here I present my findings on the diversity of the superfamily Fulgoroidea in the Eastern forests of Ecuador in the Amazon Basin. The purpose of this research is twofold: 1. to investigate alpha and beta diversity of canopy planthoppers and to quantify seasonal abundance patterns and, 2. explore the host preferences of the selected morphospecies. Basic life history patterns, population demographics, and the prevalence of parasitism will also be investigated. This work highlights the complexity of assessing canopy insects for a phytophagous group. This research is part of a larger project that aims to evaluate and describe biodiversity of a multitude of insect faunas from the canopies of Ecuador, to investigate possible host relationship patterns, explore seasonal patterns of host use, and illuminate the complexity of canopy insect and their interactions with their hosts.

1.2 Methods and Materials

1.2.1 Study location

Two sites in Ecuador were studied, the Tiputini Biodiversity station (00° 39' 25" S, 076° 27' 10" W) in the Yasuni National Forest, and Reserva Etnica Waorani (Onkone Gare Station) (00° 39' 10" S, 076° 26' 00" W) near the Piraña field station (Figure 1). The sites are 35 kilometers apart.

The following description of the region is abridged from Pittman (2000).

The sample sites 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 percent of the region. The canopy is a multi-tiered collection of trees, treelets, lianas, and shrubs with an underdeveloped epiphytic community. Important woody families in the tropics are the same as seen in Yasuni. The canopy generally reaches 30 m in height and emergent trees can reach up to 50 m. An extrapolation of an inventory of Yasuni's shrubs and trees places approximately 3,100 + species in the park and ethnic reserve.

Climatically, the region is a warm, wet, mild, and homogenous. An average of 3.2 m of precipitation fall a year, and air temperature averages 24 to 27º Celsius. Seasonal variation in rainfall is documented from scattered research stations and universities in Ecuador. No month receives less than 100 mm of rain.

1.2.2 Study Design

The samples for this project came from the canopy fogging materials collected by Dr. Terry Erwin of the National Museum of Natural History and others between 1994 and 2006. A sampling year consisted of a wet season, a dry season, and a transitional season instead of a calendar year. Dry season samples were collected in either January or February (1.34 mm per day in January and 1.26 mm per day in February). The wet season samples were taken in either June or July (14.9 mm per day in June and 14.3 mm per day in July). The transitional season samples were taken September or October (5.93 mm per day in September and 5.75 mm per day in October). Rainfall data were compiled from Tiputini Biodiversity station rainfall data collected by Dr. Jamie Guerra. Data for January and February are from 2002 while the remaining months were collected from 2000.

1.2.3 Collection Methods

Collection methods here are abridged from Erwin and Geraci (2009). At each locality (site) a one kilometer transect was laid out in terre firme forest. Along this transect 10 perpendicular cross transects, 100 m long, are set 100 m apart. Along each of the cross transects, 10 3x3 m nylon sheets were arbitrarily placed. The heterogeneous distribution of tree trunks in the cross transects prevented a systematic, or completely random, layout of sheets. The sheets were placed within 10 m of the center line of the cross transect. The sheets were suspended 1 m above the ground (to limit sample contamination from the forest floor and undergrowth). The suspended sheets were provided with 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 0.9 % of the 1 km transect.

Canopy fogging techniques were used to collect the samples (Erwin 1983b). This technique 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 3 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.

Samples were transferred from the sheet bottles to larger bottles and 4 drams vials where they were stored until sorting. Sorting usually took place in Ecuador using parataxonomists, although some samples were first transported to the US. Sample sorting broke the samples into taxonomic working groups, which were twice counted and checked before they are distributed to other researchers.

Sampling began in 1994 and has continued intermittently as funding and the political climate of Ecuador allow. Three years of sampling were taken for Onkone Gare (900 samples) and two years for Tipituni, though only one of these (300 samples) was available for use in this project, for a potential count of 1200 samples. However, some samples were subsequently lost or dispersed during the intervening 14 years, and only 952 (Onkone Gare 726 and Tiputini 226) were available to be processed in this study. Within these 952 samples, there were 17,951 planthopper recorded specimens.

1.2.4 Tree Survey

Plants associated with sample sites were identified in the Onkone Gare site by N. C. A. Pitman (unpublished). Trees were identified to the lowest taxonomic level possible and at least to the family level. Distinctions were also made to whether a tree was a primary tree or a secondary tree. Primary trees were designated as the tree closest to the sampling sheet, and secondary trees were any trees overlapping the sheet.

Twenty-seven different tree families were identified in the Onkone Gare site (Table 1). Family level distinctions were used in presence for three reasons. It was to ensure that the identifications levels were complete for all trees. Some trees received up to species level identifications, but this was not available for all trees in the survey. Also, by using family level identifications it gives overlap in the number of variables. Using finer distinctions (genera) would yield over 150 taxa rather than 27. Increasing the number of variables would reduce odds of finding significance in analysis.

1.2.5 Focal Study Group

The Fulgoromorpha (planthoppers) constitute a sizable clade of Hemiptera with a worldwide distribution, with most families more diverse in the tropics. Fulgoroids are recognized from other Hemiptera by the absence of hemelytra, the presence of tegulae, antennae setaceous and 2 segmented (plus flagellum) with an enlarged pedicel, saltatorial hind legs, and by elongate mid coxae. They can be further separated from the closely related leafhoppers by their antennae below the compound eye and the absence of rows of spines on the hind legs.

There are ~12,000 species of extant and extinct fulgoroids in ~27 families (FLOW website, accessed April 2011). Of those, 16 families occur in the Neotropics. Generally planthoppers are phytophagous on phloem, with the conspicuous exceptions of fungus in immature Achilidae and Derbidae. Feeding is split unequally between monocots and dicots and varies by family. Life history in the tropics is poorly documented, but in the temperate region planthoppers are univoltine (except multivoltine in Delphacidae), and parthenogenesis is known (den Bieman & de Vrijer 1987), but extremely rare.

1.2.6 Sorting Methods

All adult fulgoroid specimens from the samples were sorted and identified to morphospecies. Immature were not included because they cannot reliably be assigned to adult morphospecies and were not always present in the samples. Specimens were sorted to family primarily using O'Brien and Wilson (1985), to lower taxonomic units as practicable, and finally to morphospecies. Data were compiled into a morphospecies-by-sample abundance matrix. In the results and discussion, all references to planthoppers species observed in the canopy refer to morphospecies. The morphospecies concept was used instead of formal species designations largely because many of the specimens represented undescribed taxa. External features (not genitalic dissections) were used to define morphospecies. It is anticipated that the use of morphospecies will tend to under represent sample diversity, especially if cryptic species occur (particularly in the Cixiidae and Derbidae). Alternatively, sexual dimorphism (as was observed for the derbids) may inflate the number of observed taxa.

Additional reasons to use morphospecies are that there are no geographically appropriate keys to the Neotropical planthopper taxa, and formal species identifications would have required excessive time expenditures to compare specimens from the canopy to authoritatively identified reference specimens and descriptions (which may be in Spanish, French, Latin, Portuguese, German, etc.) or to locate primary type specimens.

Parasitism rates in the samples were also recorded. Counts of parasites were limited to those of external presentation and no internal examinations were performed.

The 952 canopy sample sites produced 17,951 fulgoroid specimens (average 14.96 specimens/sample) (Table 2). Three years of fogging at Onkone produced 12,516 specimens (average 13.97 specimens/sample). Tiputini produced 5,435 fulgoroids (average 18.12 specimens/sample) in one year of sampling.

1.2.7 Analyses

1.2.7.1 Alpha Diversity

Biodiversity estimators are used to predict actual diversity based on observed samples. EstimateS (Version 8.2.0) http://prul.oclc.org/estimates) (Colwell 2005) was used to calculate 7 biodiversity estimators. All 7 estimators were used because there was no clear choice on which estimators are most appropriate for canopy fulgoroids. The diversity indices were ACE mean, ICE mean, Chao 1 mean, Chao 2 mean, Jackknife 1 mean, Jackknife 2 mean, and Bootstrap mean (see Appendix A for descriptions, formulae, and citations). 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 the data and randomizes it before calculating. Averaging the results, coupled with a large randomized sample (>17,000) would produce accurate values with little variation (Colwell and Coddington 1994).

Cumulative observed species and alpha diversity estimators were plotted against samples to make species accumulation curves. This was done to assess whether that the sampling was approaching completion. A second indicator is the numbers of “rare” species, those found only once or twice in the accumulated samples (singletons and doubletons), decline with increased sampling.

1.2.7.2 Beta Diversity

Beta diversity was calculated using the software program Spade (Chao and Shen, 2010) to calculate comparative biodiversity indices. Beta diversity comparisons were made both between sites (Tiputuni and Onkone Gare) and among seasons (wet, dry, and transitional). Three sets of data were examined. Complete data sets for both sites including all rare taxa are in Table 4. Morphopecies that appeared in at least 5% and 10% of the samples respectively are in Tables 5 and 6. The 5% cutoff contained 163 morphospecies and the 10% cutoff contained 93 morphospecies. Indices used were Sørensen's similarity index, Bray-Curtis dissimilarity, and the Jaccard's similarity coefficient (Appendix B). 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.

1.2.8 Presence Materials

The 12,516 planthoppers at Onkone Gare were used solely for habitat modeling. Specimen chosen for analysis was limited to morphospecies that occurred in at least 10% of the 726 samples. Morphospecies that had lower occurrence were not used in this project due to perceived lack of data and too low to expect biologically and statistically significant results. The average occurrence was 21.94% and ranged from 14 to 67% (Table 3).

1.2.9 Presence Analysis Tools

Occupancy and extinction calculations were calculated using Program Presence version 3.1 (Hines 2006). A total of 59 models were created using seasonality and tree family as covariates. Morphospecies were evaluated individually and the system was considered closed. Detection was also held constant through the seasons.

Variables were combined to independently test the effects of tree families, rainfall seasons, and the combination of these variables. Each family of tree was modeled separately and with season as a covariate. A model with all tree families with and without season was also tested. A null model and global model were also tested. Analysis was run using the multiseason analysis option. Immigration and extinction were held constant. The capital 3 or 4 letter abbreviation found coupled with occupancy (psi) and extinction (eps) refer to a family tree presented Table 1. An example model is “psi(FAB),gamma(), eps(FAB),p(Season)”. Season refers to the seasonal rainfall broken into the wet, dry, and transitional seasons.

Seasonality as a variable was coded by assigning a season for collection for each collection point. Morphospecies were collected in either the wet season, dry season, or transitional season.

The following section is a collection of the best models for each selected morphospecies. For each species only the top 5 models are presented. Other than the family designation there are not taxonomic implications to the names given.

The tables are sorted by the lowest Akaike Information Criterion (AIC) to explain occupancy in relation to detection and environmental covariates (Akaike 1974). The covariates for the models are in two forms. The ΔAIC is the difference of that model from the top model. The AIC weight is the relative explanatory power of that model. The -2*Loglike is the difference in likelihood of current model and saturated model. PRESENCE reported covariate parameters as mean ± SE.

1.3 Results

1.3.1 Alpha and Beta Diversity

A total of 638 morphospecies were recognized with 573 from Onkone Gare and 432 morphospecies in Tiputini (Table 2). There were 367 morphospecies shared between the two sites. Of the 367 shared morphospecies, 206 were unique to Onkone Gare (32%) and 65 were unique to Tiputini (10%).

There were 150 morphospecies that were singletons (24%) (represented by one individual in the combined samples) and another 67 morphospecies (10%) were doubletons (represented by 2 individuals). Of 16 families reported in the tropics, 15 were present in the canopy samples and are compared with their known diversity in the Neotropics (Table 7). Missing is Caliscelidae, which are mostly brachypterous grass feeders, most abundant in temperate regions. Most families have comparable diversity and abundance, except Fulgoridae, Dictyopharidae, and Achilidae appeared more diverse than relative specimen abundance would suggest, and Delphacidae appeared less diverse.

Species accumulation curves in all instances failed to reach an asymptote. Final species predictions of total species richness were highest for the combined data (Figure 2, Table 8), with Onkone Gare predicting a higher richness than Tiputini (Figures 3 and 4, Table 8). Of the 3 seasons, the wet season had the highest predicted species richness followed by transitional (Figures 5-7, Table 8). Complementary varied between the two sites based on index used, and variations were more pronounced when individual seasons were compared (Table 4-6).

1.3.2 Family Composition of Canopy Samples

The 15 planthopper families found in the canopy were: Achilidae, Achilixiidae, Cixiidae, Derbidae, Delphacidae, Dictyopharidae, Issidae, Kinnaridae, Tropiduchidae, Flatidae, Acanaloniidae, Ricaniidae, Nogodinidae, Lophopidae, and Fulgoridae. All but one known family from the Neotropics was present (Caliscelidae was absent). For estimated diversity of each family in the Neotropics see Table 9 and Figure 9.

1.3.3 Presence Results

A total of 12 morphospecies were independently examined for occupancy. Analyses were conducted on morphospecies that occurred in at least 10% of the sampling sites of Onkone Gare over 3 years of sampling. Four trends can be seen shared among the morphospecies presence models. First is the null model as the best supported (Tables X, Y, Z). Second was a tree family group among the top models, independent of season (Tables A, B, C). Third is seasonality alone producing the best model (Tables ...). Fourth is a tree family group and a season as the top model (tables....).

1.4 Discussion

1.4.1 Analysis

1.4.1.1 Alpha Diversity

As expected, there were a large number of undescribed planthopper species in the canopy. Species accumulation curves failed to reach asymptotes and seasonal variability was found, as has been found previously in forest habitats (Wolda 1988, Novotny and Basset 1999). Alpha diversity analysis results showed that the Fulgoroids in the canopies are diverse, similar to investigation of other insect communities in the canopy (Novotny and Basset 1999, Lucky et al. 2002, Erwin and Geraci 2009).

The failure for any of the estimators to reach an asymptote indicates that additional samples will be needed to accurately assess canopy planthopper diversity. The high percentage of rare taxa (the singletons and doubletons) is an indicator that the canopy planthoppers remain incompletely sampled, since the percentage of rare taxa should decline as sampling became more complete (Colwell & Coddington 1995, Longino et al. 2002).

When examined separately Onkone Gare was the more diverse of the two sites. This was expected as Onkone Gare had 3 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. The much lower predicted value of Tiputini was likely a derivative of the smaller sampling pool and not a lower endemic diversity. Coupled with the smaller data pool Tiputini actually benefitted in the species per sample average for the two sites.

Onkone Gare had a lower average (13.97) compared to Tiputini (18.12), and this is most likely due to the higher percentage of missing or damaged vials for Onkone Gare and a more even data set to draw from.

Tiputini presents an interesting case as the plot was established to document the impacts of a road installed for oil exploration. Currently oil exploration has been suspended in the park. While no correlation or causation will be directly attributed to the presence of the nearby road, it is worth noting that there have been effects from the nearby traffic. The indigenous population has also accumulated along the road from dispersed habitats in the forest, increasing local pressures and traffic on the surrounding woods (Personal Communication T. Erwin 2010). It can be assumed that any disturbance to an environment, tropical or otherwise, would have an impact on an area's fauna.

With respect to seasonality, the wet season was predictably the most diverse of the seasons, with 504 observed and 669 predicted (Table 22). The next most diverse season was the transitional season with 459 observed and 568 predicted. Last was the dry season with 445 observed and 593 predicted. The dry season's higher predicted total compared to transitional was counterintuitive, as the transitional season receives more rainfall, and would be expected to have been richer.

Our alpha diversity findings are consistent with work conducted in Papua New Guinea by Novotny and Basset (1999). In that work they examined the richness of insect herbivores on 15 species of *Ficus* 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 failed to reach an asymptote.

The variation seen in the seasonal data are also consistent with many other tropical insect groups (Wolda 1988). Wolda demonstrated that most (>80%) of insects have a seasonal component to their appearance at Barro Colorado Island (Panama). Less than half of insects (39%) sampled appear year round in tropical climates. Seasonal peaks for different insect groups also appear year round, rather than in temperate climates where the most taxa are restricted to the "warm" season. There is some evidence of a planthopper having a non seasonal distribution, *Saccharosydne sacchrivora* (Westwood) in Jamaica, but examples like this remain the exception.

The unique distribution of the canopy assemblage also differs widely from what traditional ground based collection methods produce. In series of collection events, 4 days and 5 nights, Dr. Charles Bartlett, Nate Nazdrowicz and Dawn Chang collected planthoppers in Yasuni National Park (April 25-29, 2005), in the same habitat as the Tiputini site. In their expedition they collected 1021 individuals and 194 morphospecies in 11 families (Table 23). In their collection the makeup of the families and richness differed greatly from those found in the canopy. The families - Acanaloniidae, Ricaniidae, Lophopidae, and Achilixiidae were not observed. These families were not a substantive part of the canopy samples either, but did provide 28 morphospecies.

Groups such as Nogodinidae, Kinnaridae, Tropiduchidae, Issidae, Derbidae, and Fulgoridae all produced markedly lower diversity at ground level collection. Dictyopharidae, Cixiidae, Flatidae, and Achilidae produced comparable levels of diversity while only Delphacidae exceeded canopy diversity. The high Delphacidae diversity is expected as Delphacidae are primarily grass and sedge feeders.

This informal collection event highlights the overlooked diversity that resides out of reach of traditional methods of collection. The inability of these techniques with multiple collectors to produce comparable diversity, sans Delphacidae, reinforces that tropical forest canopies are untapped sources of species currently unknown to science. Even light trapping, whose reach can extend into the bottom layers of the canopy appeared ineffective.

1.4.1.2 Beta Diversity

Beta diversity analysis was conducted using metrics that took both incidence and abundance into account (Table 4, 5, and 6, Appendix A). Due to the nature of the data, with a high number of rare taxa, on occasion gave conflicting views on the diversity of the two sites and their comparative overlap.

When the full collections from the two sites (726 samples and 226 samples) are compared, the species overlap is highest. 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.

The wet season was the most diverse of the seasons (Table 4). For the wet seasons Onkone Gare and Tiputini had similar numbers of morphospecies (406 and 361 respectively), and shared 263 morphospecies, the most for an individual season. The incidence based estimators produced similar results to the all season comparisons (Table 4). The abundance estimator, Bray Curtis, indicate the assemblages are less similar seasonally than the combined canopy.

The dry season saw a reduction in the morphospecies diversity of Tiputini in relation to Onkone Gare with 185 to 420 respectively with 160 of those being shared (leaving Tiputini with 25 unique morphospecies). The incidence estimators (Table 4) decreased suggesting low similarity between the sites. The Bray Curtis index however 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 ½ similarity and the Bray Curtis was slightly higher at 3/5 similarity.

When the data is restricted to morphospecies that appear in at least 5% of the samples a shift is seen in the disparity of the data (Table 5). The beta diversity indices have a narrower spread in all settings. The 10% threshold also had a similar effect on the spread of the beta indices (Table 6). This limiting of rare or possibly transient taxa may produce a more realistic comparison of the canopies.

Overall, the beta diversity analysis for the seasonal breakdowns showed varying levels of consensus. All the estimators are sensitive to a high number of rare taxa, making for comparisons between them difficult. In comparisons where there were large differences in morphospecies (i.e. transitional season) beta diversity estimators were more susceptible to conflicting results. Overall, the varying levels of similarity (or dissimilarity) are expected in an under sampled community. By limiting the data tested with thresholds greater consensus can be reached.

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 (which will be explored in chapter 2). During the wet season, which exhibits the highest diversity, it is possible that there are more specialists or generalists. Tiputini also had a skew towards the wet season in terms of total abundance with over 3000 individuals compared to 2200 in the dry and transitional combined. The large difference in abundance 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 and their sparse disparity 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 pattern.

1.4.1.3 Family Composition of Canopy Samples

ACANALONIIDAE (Figure 11C). Acanaloniids currently are a mostly New World group with a few taxa in Africa and some island taxa (Metcalf 1954, 1958; Emeljanov 1999). The acanaloniids are a species poor group in the Neotropics, with most New World taxa in the southwestern United States. In the canopy, there were 2 observed species, within which 20 of 23 individuals represent one species. This is less than a 1/3 of one percent of the total planthopper species richness. Nymphs and adults of *Acanalonia* feed above ground, primarily on dicots (Wilson & McPherson 1981, Wilson et al. 1994).

ACHILIDAE (Figure 9E). The achilids were the 2nd largest group with 11.53% of the total individuals and 17.71% of the total diversity. The achilids are known for their diversity and vivid patterning in the tropics. Within the morphospecies there were several possible cryptic taxa and the species count may under represent their true diversity. Genitalic dissections or DNA analysis are likely to needed to parse out several groups. Host preferences for adults are more strongly skewed towards gymnosperms and dicots, making them unusual for fulgoroids, although most host records are from the temperate region (Wilson et al.1994). Gymnosperms make up 34% of host records, and cycads a likely host in the tropics.

ACHILIXIIDAE (Figure 9D). The Achilixiidae are a small group with their greatest diversity in the Old World Tropics. They are morphologically unique with a series of lateral abdominal pits on raised structures, with an analogue in Cixiidae (Cixiinae: Bennini). In the New world there are 2 described genera, one of which, *Bebaiotes*, is recorded from Ecuador. In the canopy, 10 morphospecies of *Bebaiotes* were recognized. This group makes up just over 1% of the sample and of species richness.

CIXIIDAE (Figure 9A-B). The Cixiidae are a temperate and tropical group, in both the New and Old world tropics (Wilson et al. 1994). The Cixiidae diversity and abundance are both roughly one sixth of the total, making them the 4th most abundant and species rich.

The morphospecies definitions of this group are troublesome as cixiids are very cryptic in their forms. Species recognition of Cixiidae is mostly by male genitalia. It is likely that more detailed examinations and dissections of the males will yield more morphospecies than currently recognized.

DELPHACIDAE (Figure 9F). The delphacids, a cosmopolitan group, present an oddity in terms of their abundance. Delphacids are almost strict grass feeders, with some groups feeding on sedges and rushes (Wilson et al. 1994; Urban et al. 2010). In the canopy, almost a fifth of the total specimens (3,186, 17.75%) were delphacids, 2nd largest overall. Epiphytic plants may be hosts for the canopy delphcids.

In contrast, the 3,186 specimens yielded only 8 morphospecies (3rd lowest), making it one of the least diverse families. Nearly 3000 of the 3186 individuals are represented by one species in the genus *Tetrasteira vulgaris* (Barringer and Bartlett in review). The other genus present was *Ugyops*.

DERBIDAE (Figure 10A-B). Derbidae are the most abundant group in the canopy, both in numbers and diversity. Over a quarter of the samples (26.8%) and 22.4% of the richness are accounted for by this fragile group. This is an expected result as the Derbidae reach their peak abundance in the New World tropics. Their high numbers and presence in the canopy is also consistent with their behavior of resting on foliage as adults (O'Brien 1982).

Derbids often exhibit sexual dimorphism (e.g., *Patara*), and some taxa have highly cryptic species that can be recognized only by male genitalia (e.g., *Cedusa*). The external morphology of the derbids as a whole varies greatly in size, color, and gross morphology. Notable variations were seen in body size and this in turn meant the derbid morphospecies sorting was less strict with respect to body size than other taxa. The strong sexual dimorphism did not appear to raise the richness artificially. Special note was taken of the sex during sorting and no discernable patterns emerged linking morphospecies to sex. No morphospecies was biased to all male or all female.

DICTYOPHARIDAE (Figure 11B). The Dictyopharidae diversity in the canopy is highest among *Hyalodictyon*, *Lappida* and *Paralappida*. The group had 34 morphospecies (roughly 5%), many matching already described species (Donovall 2008) and represent just over 2% of species abundance. The dictyopharids, owing to their shape, were occasionally damaged on the frons which presented some difficulty in placing them in morphospecies.

FLATIDAE (Figure 11D). The flatids are a mostly pantropical Old World Group, which reaches into the temperate North (Wilson et al. 1994). They posed some difficulty in assigning morphospecies. While only a small group in the canopy samples, only 22 morphospecies (3%) and 422 individuals (2%), determinations for this group were hard to confirm without dissection since they preserve poorly in alcohol. Storage in ethyl alcohol degrades (washes out) the colors of the wings which can be a strong diagnostic character in this generally colorful family. Despite these limitations the morphospecies were still tractable with a small group. This small number of morphospecies allowed for little reliance on coloration.

FULGORIDAE (Figure 11A). The true fulgorids, commonly referred to as lanternflies, are the largest and showiest planthoppers in the tropics, and are primarily a tropical family (Wilson et al. 1994). The 49 morphospecies (8%) may be an overestimation in the diversity based on external characteristics. Examination of male genitalia may lower the number of observed species. It is unusual that larger fulgoroids (and cicadas) are underrepresented in the canopy fogging samples. The larger Auchenorrhyncha are relatively poorly represented in the canopy fogging samples examined here. Two possible reasons might be that these taxa stay closer to the tree trunk, and do not fall into the collecting sheets. Alternatively, the larger species of insects have a higher vagility (or resistance) to the pesticide and may escape the sampling area.

ISSIDAE (Figure 10C-D). The Issidae have near the 2nd highest abundance to the delphacids, but have significantly more diversity (3rd highest with 16%). The Issidae are a tropical and temperate group in both the New and Old World (Wilson et al. 1994). The Issidae diversity generally is highest in the genus *Thionia*. With nearly 70 described species from the New World the diversity of this is likely underrepresented with 100 *Thionia* morphospecies. It is likely that the canopy samples will greatly increase the size of the genus *Thionia* with a revision of this genus.

KINNARIDAE (Figure 9C). Kinnarids are a relatively small family, primarily found in the Neotropics and Orient (Denno and Perfect 1994). They are represented in the canopy by 18 individuals (0.1%) and 2 species (0.3%*)*. The two species are presumably in the genus *Southia*. Nymphs are presumed root feeders (O'Brien 1991) and adults have been found to associate primarily with dicots with additional records from ferns, gymnosperms, and monocots (Wilson et al.1994).

LOPHOPIDAE (Figure 11E). The lophopids are small group with 7 species (1%) and 0.2% of the diversity for both plots. Their diversity in the canopy fogging samples is restricted to one genus, *Hesticus*. The lophopids are a primarily an Indo-Malayan group with a limited diversity elsewhere (Soulier-Perkins 2000, Soulier-Perkins et al. 2007). In South America they are represented by two genera, but only *Hesticus* occurs in the Ecuador study area. The family status of *Hesticus* is unclear; while it is currently included with the Lophopidae, it was found to not belong to Lophopidae in the phylogenetic treatment of the family by Soulier-Perkins (2000).

NOGODINIDAE (Figure 10F). The nogodinids are a small group with 20 morphospecies (3%) and 1% of the abundance. Very little is known about their biology or hosts for this primarily tropical family (Wilson et al.1994), and it is unclear whether this family is monophyletic (Urban and Cryan 2007).

RICANIIDAE (Figure 10E). The Ricaniidae are a primarily an Old World group with limited New World diversity (Denno and Perfect 1994). The phylogenetic placement of the New World species in Ricaniidae currently remains in doubt (Adam Stroinski, Polish Academy of Science, Personal communication). In the canopy samples, 9 species were observed (1%) and 0.3% of the diversity, most apparently belonging to the genus *Pharsalus* (this genus moved from Issidae to Ricaniidae by Gnezdilov (2009)).

TROPIDUCHIDAE (Figure 9F). The Tropiduchidae are a primarily pantropical group and can range as far North as the Mid-Atlantic states with *Pelitropis rotulata* known as far north as North Carolina (O’Brien 1992, Denno and Perfect 1994). Feeding preference is split with 55% on dicots and 40% on monocots (Wilson et al.1994). With 23 species (4%), morphospecies diversity was highest in the genus *Arenasella*.

1.4.2 Patterns Observed

1.4.2.1 Parasitism in the Canopy

There is currently no known published information on the parasitism of fulgoroids in the canopy. It is the author's personal observation that parasitism of immatures is fairly common. The immature were not documented in this study but were intermittently present when sorting for mounting specimens occurred. The parasite families in adults and immature were Strepsiptera and Dryinidae. This is likely due to the preservation method which made making observation of internal parasites impossible without dissection and even then unlikely.

In adults only 3 families showed signs of external parasitism: Issidae, Cixiidae, and Derbidae. Issidae and Cixiidae each had a lone adult with a strepsipteran parasite and Derbidae had a mixture of Dryinidae and Strepsiptera, with 25 parasitized individuals. No specimen had more than 1 parasite.

1.4.2.2 Brachyptery in the Canopy

Brachyptery was a trait that was not found in the canopy samples in fulgoroids. While brachyptery is common in several families, such as dictyopharids, delphacids, and caliscelids (not present in the canopy samples), no examples were found in the canopy. Brachyptery is even more common in delphacids, especially in North America. With the 3,000 plus specimens from the canopy samples we expected to find brachypterous individuals. The lack therefore points to biological or habitat conditions that are promoting the highly mobile forms seen in the canopy. The high dispersal of host plants, a possible ephemeral host quality, and physical makeup of the canopy might each drive selection for macroptery.

1.4.3 Presence Ovevriew

1.4.3.1 Presence Morphospecies Review

The best occupancy models for the most abundant 12 morphospecies are provided in Table 24.

Flatidae 22

For Flatidae 22 (Table 10, Figure 12A) the family Fabaceae (FAB) coupled with seasonality produced the best model, with seasonality alone as the second best model (AIC 1.84). The wet season had the strongest effect on the appearance of the morphospecies. Two other families, Meliaceae (MLI) and Cercropiaceae (CEC), also produced reasonably strong models. The null model (devoid of any covariates) performed poorly relative to models that included seasonality.

Issidae 18

For Issidae 18 (Table 11, Figure 12B) there are no supported tree families. Seasonality alone gave the best model, with the transitional season having the strongest effect. The null model was next best (AIC 0.83), suggesting that the taxon is not responsive to plant taxa in the analyses. While some *Thionia* are tree feeders (Wheeler and Wilson 1987, 1988; Wheeler 1996) there was no clear tree family. An unmeasured variable such as vines may illuminate the pattern for Issidae

Issidae 60

For Issidae 60 (Table 12, Figure 12C) the tree family Elaeocarpaceae (ELA) was the best fit. This family was also a top model without a seasonal covariate

(AIC 2.12). The null model as the second best model (AIC 1.88) suggests a missing variable may account for Issidae occupancy.

Achilidae 4

For Achilidae 4 (Table 13, Figure 12D) seasonality was not a strong component to morphospecies presence. Only one of the top 6 models contained the seasonality variable, psi(CEC),gamma(),eps(CEC),p(Season) (AIC 1.90). Cecropiaceae (CEC) was the strongest model for occupancy followed by CEC with seasonality (AIC 1.90). Following the CEC models the null model came in third (AIC 1.98). Achilidae 4 makes a good candidate for testing prediction of host preferences in the tropics.

Achilidae 79

For Achilidae 79 (Table 14, Figure 12E) all of the top models lacked a seasonality component. The tree family Elaeocarpaceae (ELA) produced the strongest model without season. The next highest model was the null model (AIC 0.25) followed closely by several tree families: Violaceae (VIO), Fabaceae (FAB), Moraceae (MOR), and Euphorbiaceae (EUP).

This morphospecies had the closest set of models of any of the morphospecies tested. This may result from an unconsidered variable, or Achilidae 79 may be polyphagous.

Cixiidae 9

For Cixiidae 9 (Table 15, Figure 12F) the top model only contained seasonality. The dry season was less influential then the wet and transitional seasons in the model. The seasonality alone as the top model is unique among the analyzed morphospecies. Other tree families that appeared in the top model were Rubiaceae (RUB), with (AIC 0.06) and without (AIC 0.30) a seasonality component, and Myristicaceae (MYRI), and Fabaceae (FAB) with AIC values less than 2.00. Rubiaceae (RUB) makes for the most compelling host plant as it appeared twice with the inclusion of seasonality.

Cixiidae 14

For Cixiidae 14 (Table 16, Figure 13A) seasonality was a strong model component. The null model (AIC 6.18) finished behind every model that included seasonality. The wet and transitional seasons were the most influentially predictive, followed by the dry season. For tree families Cecropiaceae (CEC) (AIC 0.27) was the best predictor, while Elaeocarpaceae (ELA) (AIC 1.42), Bombacaceae (BOM) (AIC 1.48), and Meliacaeae (MLI) (AIC 1.58) were under 2.00 AIC. The strong influence of seasonality in models for this morphospecies suggests that host species may not be a strong predictor of their presence, which is best predicted by the wet season.

Delphacidae 6

For Delphacidae 6 (Table 17, Figure 13C) seasonality was the strongest predictor of presence, similar to Cixiidae 14. Several tree families produced acceptable models under 2.00 AIC. However, delphacids are primarily grass feeders (Wilson et al. 1994), and grass is unusual for forest canopies. It is likely that *Tetrasteira* are feeding on epiphytic vegetation and not directly on trees (Barringer and Bartlett in review). Correlation with tree taxa may be an artifact of the epiphytic communities found associated with the trees.

Delphacidae 6 was also the most common morphospecies present in the canopy with 2,181 individuals and individual samples with 30+ individuals. However, Presence models do not take into account abundance. Other morphospecies had far fewer total individuals (approximately 300).

Derbidae 14

For Derbidae 14 (Table 18, Figure 13D) seasonality is the strongest component is seen in the models with the unusual feature that all seasons had similar strength. Two families stand out as candidate hosts, Rubiaceae (RUB) (AIC 0.96) and Bombacaceae (BOM) (AIC 1.18), coupled with seasonality. The family Arecaceae (ARE) with seasonality (AIC 2.15) and null model (AIC 2.54) were the next best models followed by the rest of the seasonality models excluding host.

Derbidae 35

For Derbidae 35 (Table 19, Figure 13B) the family Cecropiaceae (CEC) with (AIC 0.10) and without (AIC 0.00) seasonality produced the best models. The next two are the null model and the seasonality model alone. This is one of the strongest set of models (in terms of low AIC values) for a single tree family being tied to a morphospecies. Derbidae are noted for their behavior of resting on foliage which may be an important behavior in determining hosts. While feeding or reproductive host relationship cannot be inferred (derbids are fungus feeders as immatures), from these models it is likely that the family Cecropiaceae (CEC) plays an important role.

Interestingly, the family Euphorbiaceae (EUP) also had the 5th and 6th best models (AIC 0.88) excluding tree family. Since models with and without season produced similar model results, host is an important predictor of the presence of this morphospecies.

Derbidae 37

For Derbidae 37 (Table 20, Figure 13E) seasonality did not play a component in any of the top models. The null model was the best predictor followed by the families: Bixaceae (BIX) (AIC 0.12), Cecropiaceae (CEC) (AIC 0.79), Burseraceae (BUR) (AIC 1.35), Elaeocarpaceae, and (ELA) (AIC 1.49). The null model as the best predictor implies that an unmeasured variable is the most important; however, models with the noted tree families had AIC values under 2.00 suggesting that host is an important predictor.

Derbidae 42

For Derbidae 42 (Table 21, Figure 13F) seasonality was the strongest indicator of presence (AIC 0.00), followed closely by Elaeocarpaceae (ELA) (AIC 0.19) with seasonality, ELA without seasonality (AIC 0.19), and the null model (AIC 0.39). The only other model to fall below 2.00 AIC was Bombacaceae (BOM) (AIC 1.79) with seasonality. Elaeocarpaceae did not appear in the top 5 models for any of the other Derbidae examined.

1.4.3.2 Presence Morphospecies Trends

The occupancy models are not definitive accounts of host tree affinities, but instead are hypothesis. Achilixiids and derbids have been documented to feed on fungus and Delphacidae are noted grass and sedge feeders (Wilson et al. 1994). From the models, however, patterns of plant use can be predicted for canopy planthoppers (e.g., feeding, ovipositing, mating sites, and resting places). For the following discussion host usage should be considered in a broader sense then feeding alone.

Four trends can be seen shared among the morphospecies presence models. The first is the null model as the best supported. Three taxa (Issidae 18, Issidae 60, and Derbidae 37) fell into this category. Potential reasons for this pattern are lack of appropriate covariates or polyphagous host usage. The lack of appropriate covariates suggests that there was insufficient data to parse out the factors driving their distribution and more sampling with additional measured variables may be needed.

Derbids are fungus feeders as immature, so ovipositing and feeding are unlikely uses. Epiphytic plants or fungi may be present have not been measured. Resting behavior of adults may be more likely and related to plant morphology or microclimate than plant taxonomy (O'Brien 1982).

Regardless of unknown variables it was anticipated that specialized host use would not be supported for some species, possibly because the planthopper is polyphagous or are not using trees as hosts. Polyphagous species would fit in the null model.

The second trend seen was a tree family group among the top models, independent of season. This suggests that the morphospecies are present year round and the tree family is a strong candidate for a host. This may also be anecdotal evidence of polyvoltism. Conversely, adults of these species may be long lived. Three morphospecies appeared in the top models without a seasonality component: Achilidae 4, Achilidae 79, and Issidae 60. Elaeocarpaceae appeared twice while Cecropiaceae appeared once. That these two tree families occur without seasonality may not be informative, as Elaeocarpaceae and Cecropiaceae are the most common tree family variants in occupancy models for the species examined. This should, however, not completely discount the finding associated with these morphospecies.

The best model for Issidae 60 was the null model. It may be that Issidae 60 is not appropriately handled with the current set of models. Proper observation of feeding habits and life history may be required for *Thionia* (the genus of Issidae 60), one of the most speciose genera in the survey.

The third trend is seasonality alone producing the best model. A possible explanation for this may be that these morphospecies are highly polyphagous and seasonality is driving abundance. These morphospecies, Delphacidae 6, Derbidae 42, and Cixiidae 9, show strong association with rainfall, most typically the wet and transitional seasons.

Alternatively, these species are present year round but use the canopy seasonally, moving up as the rainfall patterns change the environment. If their preferred host is on the ground, moving into the canopies may be an artifact of collection method, i.e., the planthopper moves vertically into the canopy temporarily. However, Delphacidae 6 was likely acting in a peculiar manner using epiphytes instead of trees as hosts (Barringer and Bartlett in press).

The fourth trend is a tree family group and a season as the top model. This suggests that the species presence can be predicted in both time and space. This combination of covariates also suggests that the seasonality is important. The four morphospecies that fell into this category were Flatidae 22, Cixiidae 14, Derbidae 14, and Derbidae 35. These would be the best candidates for further analyses with Presence regarding host use.

The seasonality of host preference suggests canopy quality is not constant year round. The strongest seasonal predictors of presence were the wet and transitional season. The canopy, and specific trees, may not be presenting a constant refuge and food source year round. The lack of brachypterous species would also indicate that mobility is important, especially for location and travel among hosts.

1.4.4 Results Applied

1.4.4.1 Results Applied (Alpha and Beta Diversity)

The total diversity of the planthoppers can be crudely extrapolated from this data set, though the level of confidence of the final prediction can be contested. To set up this extrapolation some basic facts about fulgoroid taxonomy need to be established first. According to FLOW (Fulgoromorpha Lists on the Web, accessed April 2011) there are 11,837 species of described fulgoroids worldwide, and 2,208 species in the Neotropics. An unofficial list of planthoppers (unpublished checklists complied by Lois O’Brien) from Mexico south produces 470 genera and 2,333 species (Table 9). In terms of individual family diversity 3 families were surpassed by Ecuador’s canopy fulgoroids in terms of richness: Lophopidae, Ricaniidae, and Achilidae. This means that as many fulgoriod species were found in the canopy samples as are known currently from all of Central and South America. Here 638 fulgoroid morphospecies were observed and 793 were predicted using the average of seven estimators. This is likely to be below the true value as the species accumulation curve has not yet reached an asymptote, indicating that more samples are needed for good richness estimation.

The predicted total species richness of canopy planthoppers 33% of the estimated Neotropical planthopper fauna (739 predicted/2333 estimated), but was found in only 0.2 square kilometers. This estimate was made from samples that exclude species that may be present in the shrub layer or ground level. Also larger fulgoroids, such as the true Fulgoridae, are poorly represented in the canopy samples. This lack of larger fulgoroids is likely due to the lack of space for larger insects and this space is limited to Tettigoniidae, Phasmatodea, Mantodea, and caterpillars (Pers. Comm. Terry Erwin, 2011). Yet a sampling area of 4.88*10^-8 (or 0.00000004888%) the forest canopy was found to have a diversity of 32% of known planthopper species richness of the entire Amazon basin.

Bartlett and O'Brien, based on preliminary work with the canopy samples, estimated that up to 70% of the fauna in the canopy was undescribed. This implies that the 793 estimated species represents ~6% of the known diversity (793 estimated species/ 11,837 known species worldwide). This also implies that 555 of the estimated 793 morphospecies are undescribed currently.

If Erwin's calculation for diversity from his 1982 paper are used and amended slightly for Fulgoroidea, a broader extrapolation can be done. If there are an estimated 50,000 species of tropical trees in the Neotropics, and a 60-80 percent host affinity in Fulgoroidea, a species richness of 30,000 to 40,000 planthoppers may be found in the Neotropics (50,000 trees species * 0.6 or 0.8 host affinity). These estimates assume that each tree species will have only one specific planthopper species associated with it. This level of monophagy based on primarily temperate records may not be as applicable in the tropics. Work in New Guinea by Novotny et al. (in 2002) argued that monophagous insects are less common in the tropics. They posited that genera are more dispersed and species rich in the tropics. Large genera are phylogentically similar enough to allow herbivores to easily utilize multiple hosts.

Host records for Fulgoroidea for most groups are lacking. At most, 10% of Fulgoroidea have host records, many of which are unconfirmed, and may be over representing monophagy (Personal Communication K. Weglarz 2011). If this overestimation of monophagy is to be believed the estimated number of new fulgoroids in the canopies may be closer to 20,000. Even with this reduced estimation of host monophagy that still places twice as many species in the canopies in the tropics as extant and extinct species known (Flow Website accessed April 2011).

Host preference will be also important for extrapolating host ranges and host loss. The high level of host fidelity increases extinction susceptibility from habitat loss as hosts are lost. It is estimated that many plant have host ranges that are roughly 1% the area of the Neotropics (Morawetz and Raedig 2007). Estimates put 100 plant species being lost each year, each a potential host (Morawetz and Raedig 2007). These pockets of endemism, common in the tropics, can have drastic effects on their dependents survival. The strong host fidelity of certain Fulgoroidea puts them at higher risk for endemic host loss.

Conservation efforts, for better or worse, are tied to species prediction models and estimates. Conservationists are partly limited in some respects that all conservation in the tropics is tied to biodiversity indexes and these “solid truths” biodiversity estimators give us. Mittermeier et al. (2004) is an example of using these metrics to focus attention on these regions identifying 34 hotspots around the world while Myers et al. 2000 identified 24 hotspots. All determination of biodiversity hotspots are subject to the criteria used and their weight so the number of hotspots can vary from authority to authority.

Endemic species and bioindicator species are used as predictors to the threat to biodiversity regions (Fonseca 2009). Tied to this conservation is the knowledge of how vital large masses of protected land are to the retention of endangered species (Chittaro et al. 2010). Logging and other destructive activities can have significant affects on species composition (Zahoor et al. 2003, Willot 2009). Basic alpha taxonomy is a vital tool for conservationists to use for the preservation of the critical habitats of biodiversity. Projects such as these, however, are often daunting to authors (Kitching et al. 2000). They note that his study 100's of morphospecies can be collected from limited hosts (ten trees) and areas (single hectare) and take years sort through. Biodiversity studies in the tropics, as with fulgoroids, are also generally unsatisfactory in terms of taxonomic identifications. Despite the daunting number of morphospecies and specimens that broad tropical studies can produce, these projects often fail to provide the far reaching conclusions that are sought concerning tropical biodiversity.

The problem of protecting regions of high biodiversity is not easily solved. Broad taxonomic surveys should be thought of as a precursor to describing the diversity new to science. Biodiversity metrics now serve more to inform us of the taxonomic short comings of any one group and to possibly give us a metric in which to track the loss of diversity of in these threatened regions.

In many of these diversity hotspots the work done to preserve have been stopgap methods. In rare cases, like the Guyana shield where its remoteness has protected in from human encroachment, most hotspots are enveloped on all sides by human development, management, and manipulations. The protective methods to limit building and logging have defined immediate benefits, but the lingering effects of boundaries, isolated populations, and agricultural and industrial byproducts and pollution still pick at these refugia.

It is plausible that hundreds of species are being lost each year without any kind of documentation. The Atlantic coastal forests of South America likely held a tremendous amount of diversity in its canopies. Sadly, little remains of this habitat and the numerous species lost since the days of Darwin's and others passed by. The momentum of the habitat destructions will be hard to turn back as species are not apt to bounce back (Brook and Bradshaw 2006). Diversity metrics can only serve to tell us that there are fewer morphospecies present, which is far less important than knowing which species went extinct.

Rather than use this information primarily for conservation I posit using this information in trying to spur greater taxonomic research (Kremen et al. 1993). Science is fighting a losing battle in the rate of species description versus species loss at rates of 100 to 1000 times pre human levels (Pimm et al. 1995). Despite the thousands of species named in a year this is not nearly enough to keep pace with the predicted background extinction rate (Reid 1992, Brook and Bradshaw 2006). The rate of loss of species in the tropics over the next 2 to 3 decades ranges from 4 – 15% (Reid 1992). This extinction rate is still increasing as habitats become more fragmented. If climatic predictions also hold true the tropics, as with most ecosystems, will also be assaulted with another grievance, of which will be hard to counter.

The taxonomic disparity is highlighted by that fact that the majority of taxonomists are located in the Europe and North America, and not in the regions where they are needed most. The Neotropics, Africa, and Southern and Southeast Asia are the regions with the largest taxonomic deficits and the greatest disparity in terms of personal and tools. This advantage of biodiversity studies is the ability to highlight precisely where to focus taxonomic efforts and resources both locally and internationally. Focused use of scientific resources in these areas should be elevated to highest priority.

What is done in the next few decades both in terms of conservation and taxonomy will determine the long term future of the tropics and its biodiversity. The diversity of life is one of the world's greatest wonders and there is an inherent responsibility to preserve it.

1.4.4.2 Results Applied (Presence Analysis)

The goal of occupancy modeling was to predict whether a morphospecies was present at a site given imperfect detection. Environmental and collection methodology can have an effect on the detection of a morphospecies in the canopy. Also, only 0.9% of the canopy area was sampled in this study, which makes it highly possible that species were not detected were actually present or could be present at another sampling time.

The best models in most cases were tied to the covariate for seasonality. This indicates that planthopper abundance was tied most strongly to rainfall. Some taxa also had a tree family, coupled with or without seasonality as a top model. This gives the best hypothesis that can be tested with field experiments for a host tree usage by a morphospecies.

1.5 Future Directions

1.5.1 Alpha and Beta Diversity

To improve on this project several component could be expanded upon. The first is to improve is analyses resolution by locating and including any missing samples. While 952 samples is a large data set, the alpha and beta diversity estimators should improve with their inclusion. The additional sampling year from Tiputini would also be beneficial. The third inclusion that would help this project would be a 3^{rd} year of sampling from Tiputini to provide equal data sets. That set of specimens has not yet currently been collected. The equal data would be most beneficial for the beta diversity estimates to more readily compare the sample sites.

A different approach would be a comprehensive set of dissections to improve morphospecies sorting (especially for Cixiidae and Derbidae). Alternatively, the morphospecies sorting would be improved if it was performed by the experts of each taxonomic group. While many of the families will likely be distributed to taxonomists, this will be post hoc and not incorporated into this work. DNA barcoding and genetic analysis may also be useful tools for morphospecies identification, as well as allow for phylogenetic examinations.

1.5.2 Presence Analysis

These results show that Presence, software designed to model bird and mammal occupancy, appears to work for insects collected by canopy fogging. The results are influenced by limited covariate choices and morphospecies selection. Refined covariate choice with specified criteria would produce more specific models as each morphospecies may have a unique life history. Covariates may include epiphyte or vine presence, further refined tree identification, and sunlight exposure.

Study design that also incorporated a more observational approach in the canopy may also improve models, moving from inferred hosts to observed hosts.

The broader application of Presence and similar styles of analysis can allow entomologists interested in ethology and host preference to take data of various qualities and scopes and infer host usage. This can lead to greater accuracy in host preference and identification with limited information. Much host data (at least in Fulgoroidea) is incomplete and Presence or similar tools would allow for the creation of models to filter and sort these sparse host data sets to find hosts.

Figures and Tables

Figure 1. Location of fields sites, Tiputini Biodiversity station and Onkone Gare Station in eastern Ecuador.

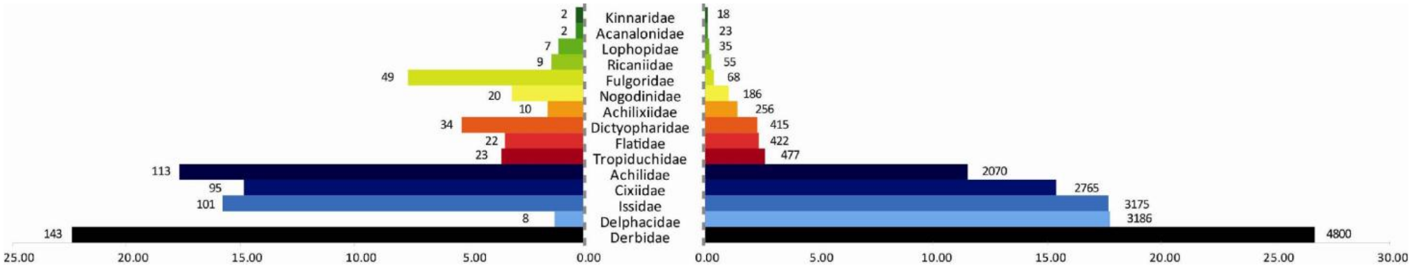

Figure 2. **Combined species discovery curve for 952 planthopper canopy fogging samples (2 sites, 4 collecting years) including select estimators of diversity.** Total observed morphospecies was 638, with 24% represented as singletons. The averaged value of the diversity estimators is 793 species. Curves for species observed and diversity estimators failed to reach an asymptote.

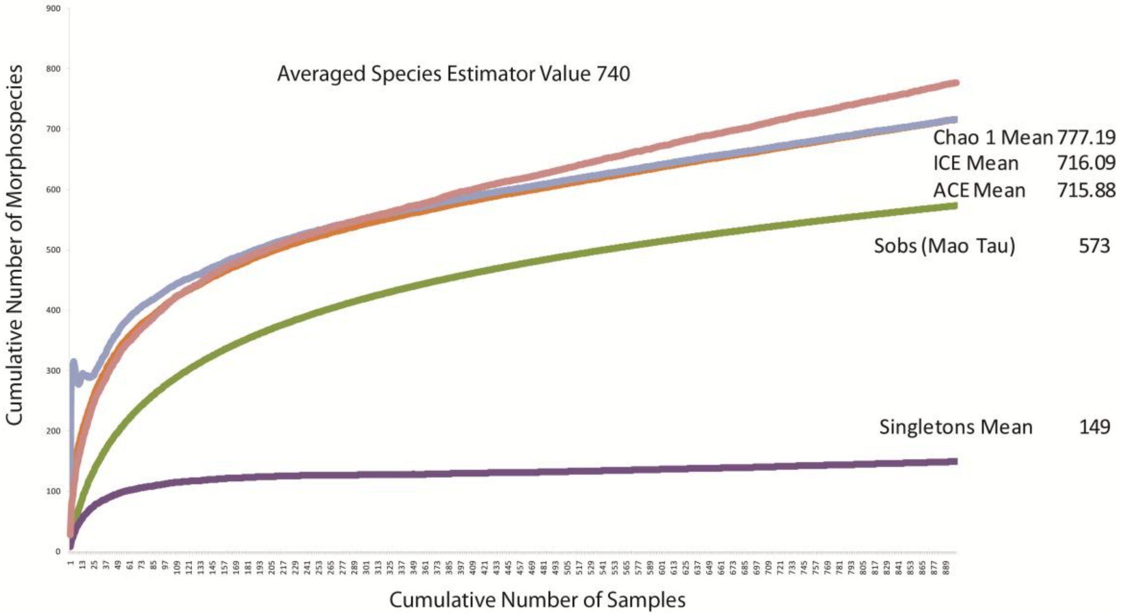

Figure 3. **Combined species discovery curve for 726 planthopper canopy fogging samples from Onkone Gare (3 collecting years) including select estimators of diversity.** Total observed morphospecies was 573, with 26% represented as singletons. The averaged value of the diversity estimators is 740. Curves for species observed and diversity estimators failed to reach an asymptote.

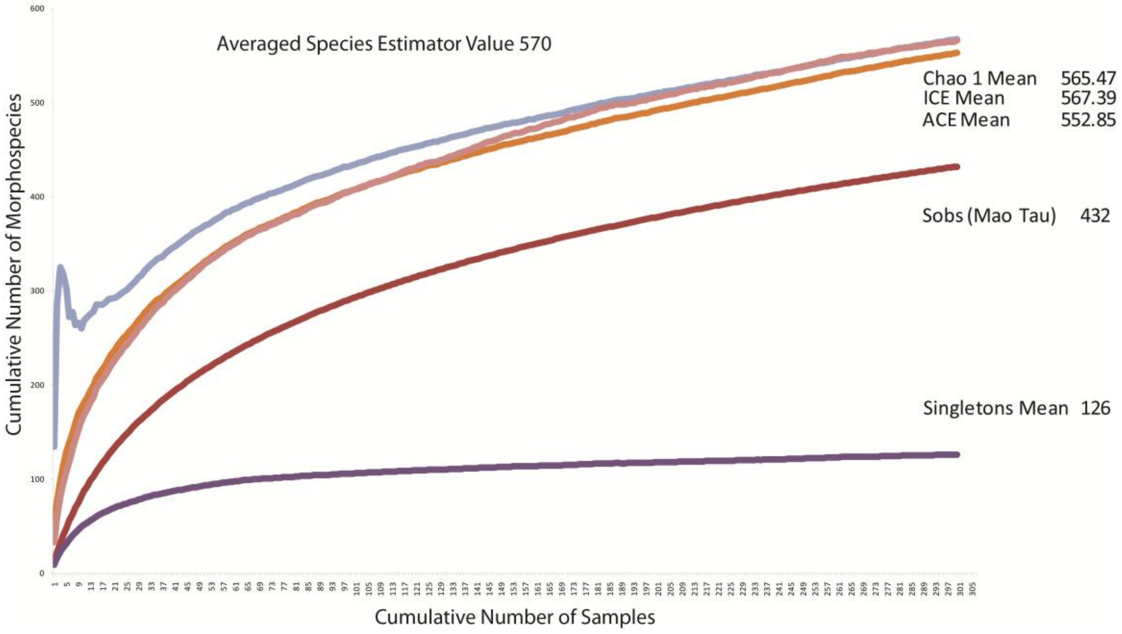

Figure 4. **Combined species discovery curve for 226 planthopper canopy fogging samples from Tiputini (1 collecting year) including select estimators of diversity.** Total observed morphospecies was 432, with 29% represented as singletons. The averaged value of the diversity estimators is 570. Curves for species observed and diversity estimators failed to reach an asymptote.

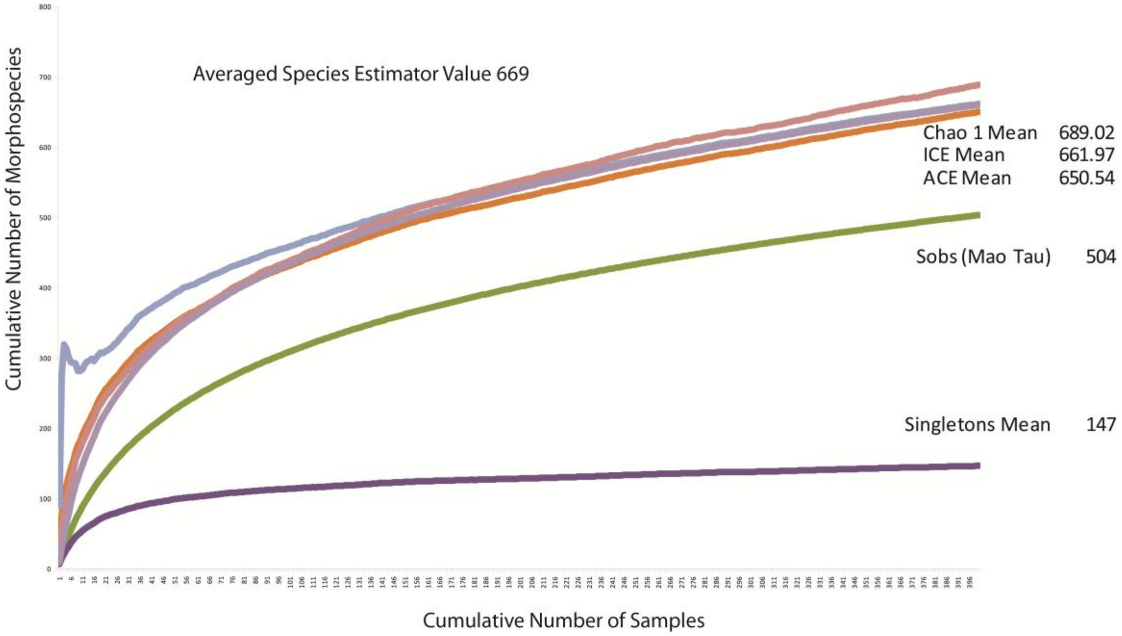

Figure 5. **Combined species discovery curve for 313 planthopper canopy fogging samples from the wet seasons (2 collecting sites, 4 collecting years) including select estimators of diversity.** Total observed morphospecies was 504, with 29% represented as singletons. The averaged value of the diversity estimators is 669. Curves for species observed and diversity estimators failed to reach an asymptote.

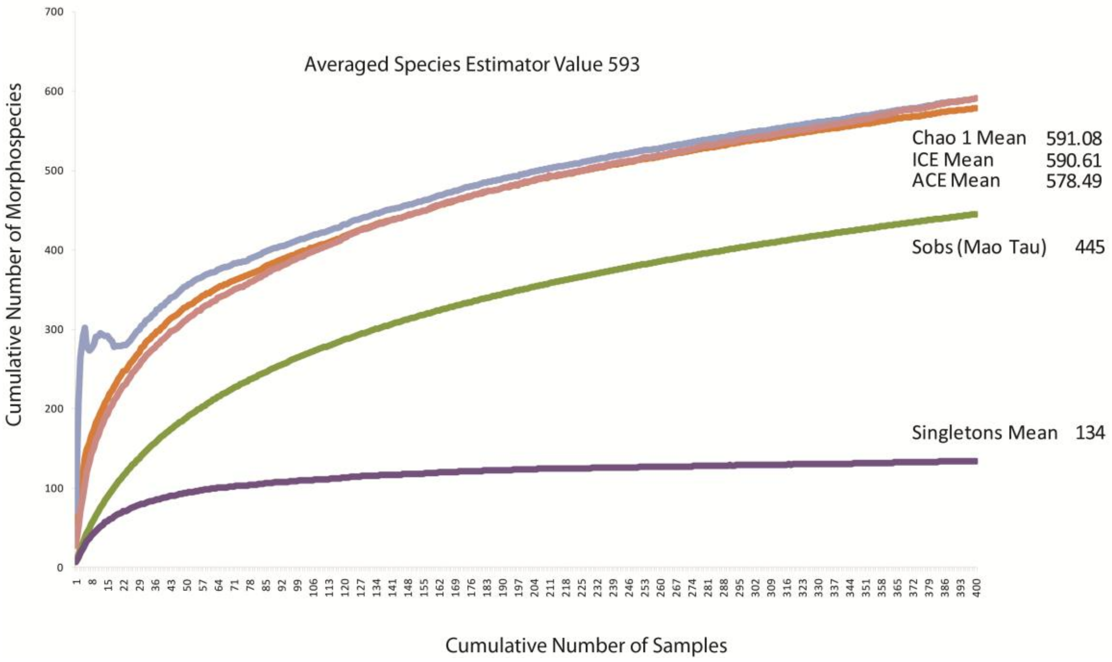

Figure 6. **Combined species discovery curve for 344 planthopper canopy fogging samples from the dry seasons (2 collecting sites, 4 collecting years) including select estimators of diversity.** Total observed morphospecies was 445, with 30% represented as singletons. The averaged value of the diversity estimators is 593. Curves for species observed and diversity estimators failed to reach an asymptote.

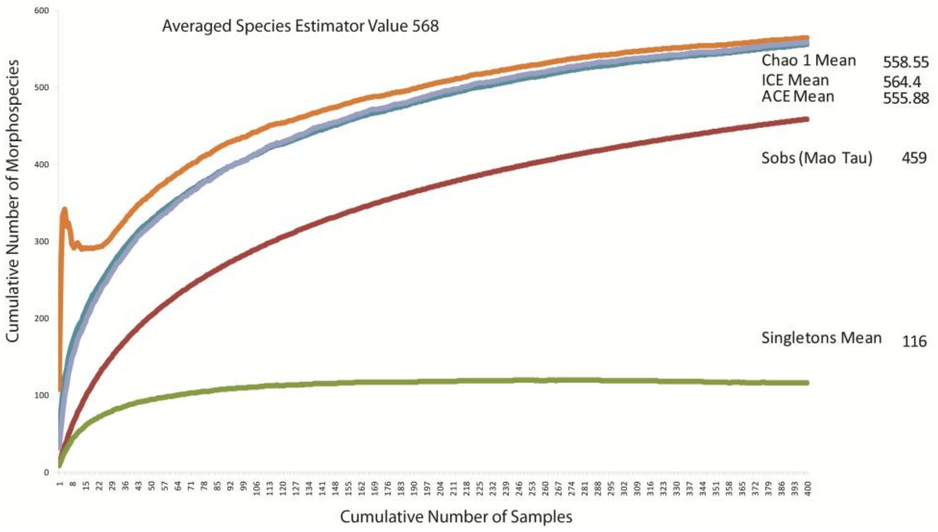

Figure 7. **Combined species discovery curve for 295 planthopper canopy fogging samples from the transitional seasons (2 collecting sites, 4 collecting years) including select estimators of diversity.** Total observed morphospecies was 459, with 25% represented as singletons. The averaged value of the diversity estimators is 568. Curves for species observed and diversity estimators failed to reach an asymptote.

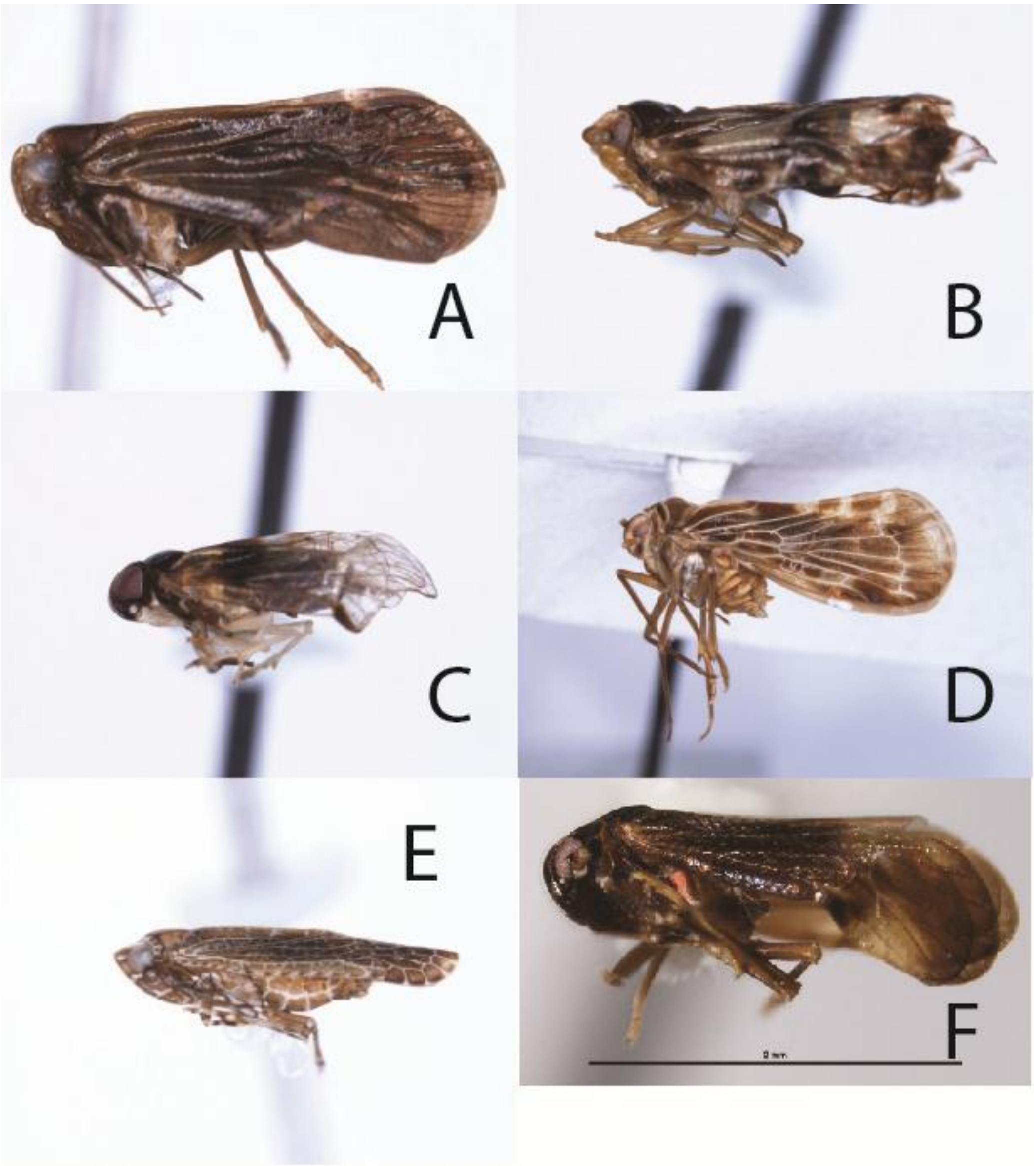

Figure 8 **Selected planthopper morphospecies from the canopy.** A. Cixiidae (*Pintalia*), B. Cixiidae (*Bothricera*), C. Kinnaridae (*Southia*?), D. Achilixiidae (*Bebiaotes*), E. Achlidae (*Opsiplanon*?*)*, F. Delphacidae (*Tetrasteira*).

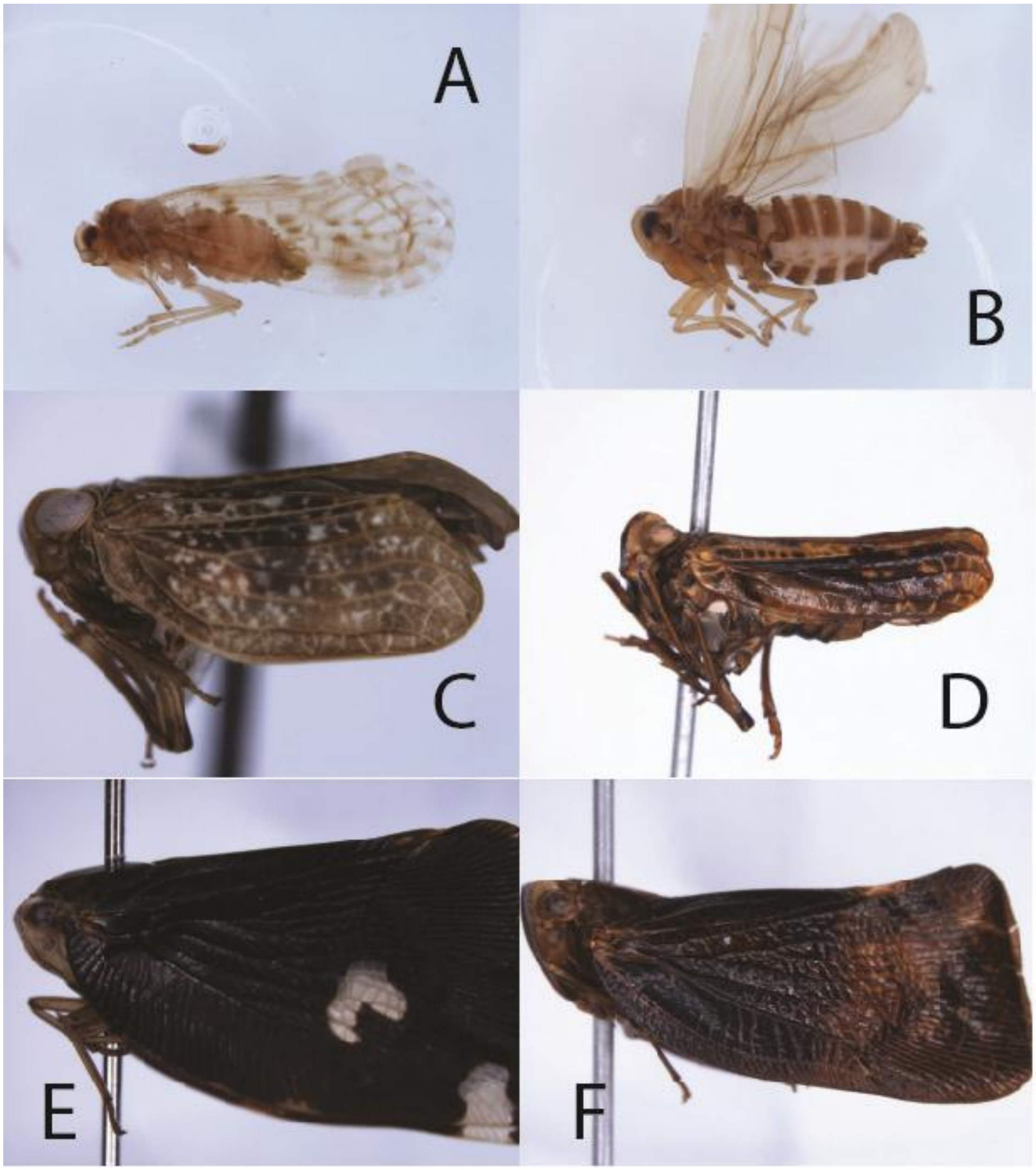

Figure 9. Abundance and diversity of planthoppers by family from 1200 Ecuador canopy fogging samples. Of the 15 represented families, 5 families (Derbidae, Delphacidae, Achilidae, Issidae, and Cixiidae) comprised over 80 percent of the observed specimens; however, the Derbidae are represented by a large number of morphospecies, where as the Delphacidae are represented by few taxa.

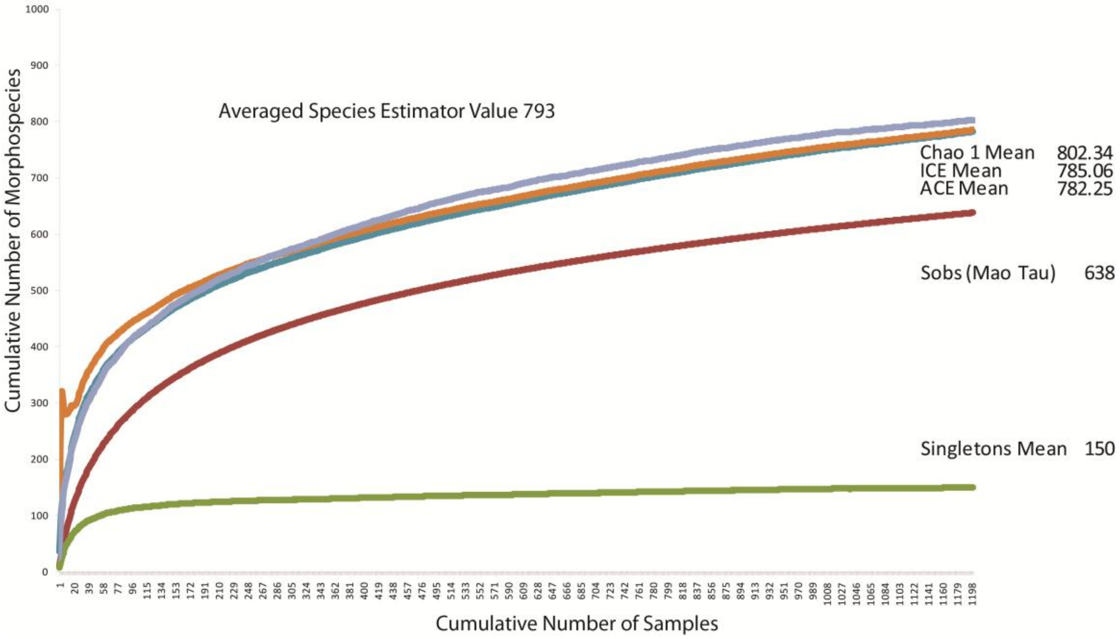

Figure 10. **Selected planthopper morphospecies from the canopy.** A Derbidae (*Dysimia*), B Derbidae (*Cenchrea*), C and D Issidae (*Thionia*), E Ricaniidae (*Vutina*), F Nogodinidae (*Bladina*).

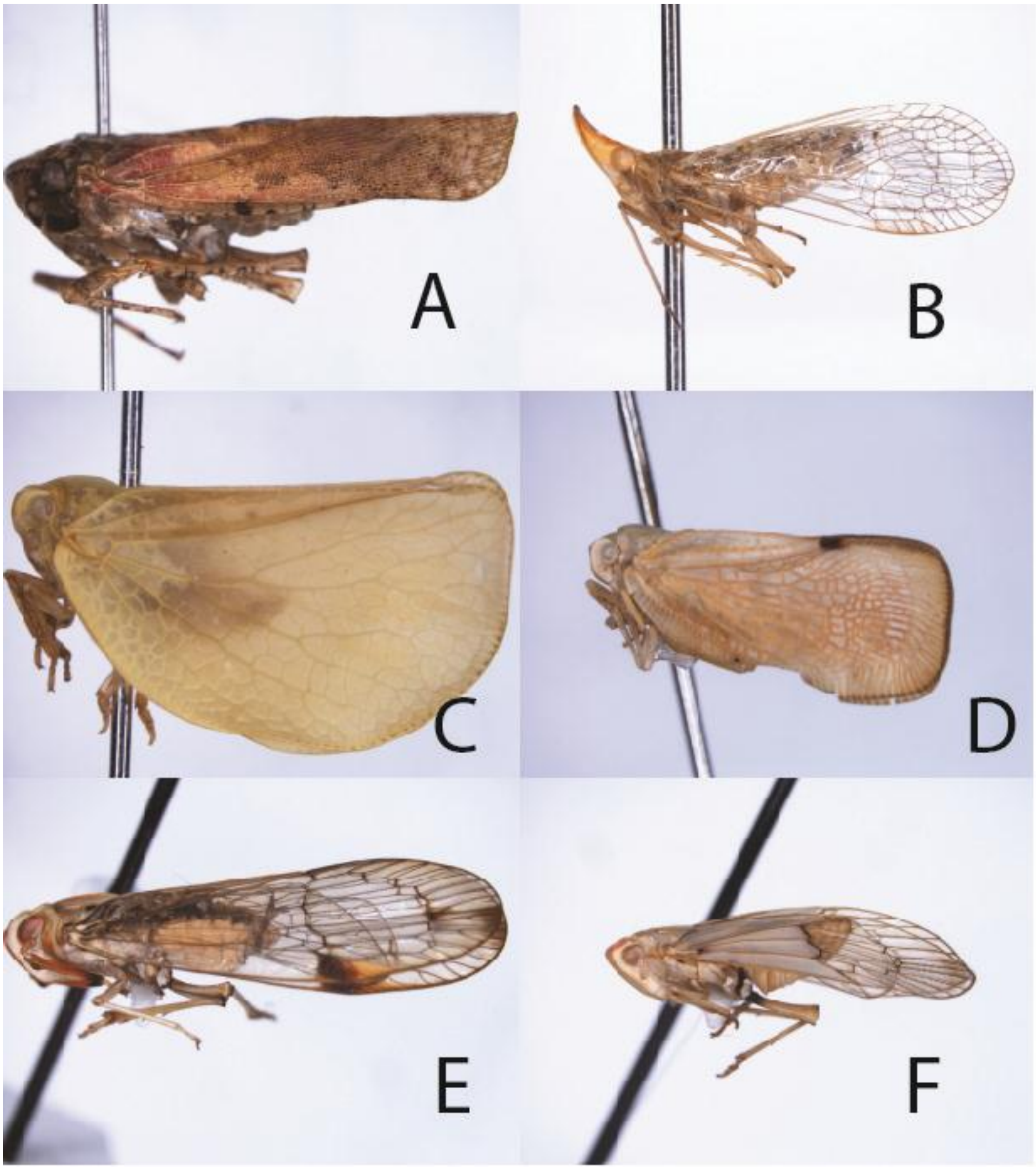

Figure 11. **Selected planthopper morphospecies from the canopy.** A Fulgoroidae (*Calyptoprocus*), B Dictyopharidae (*Mitrops*), C Acanaloniidae(probably *Acanalonia)*, D Flatidae (*Anormenis*), E Lophopidae (*Hesticus*), F Tropiduchidae (*Arenasella*).

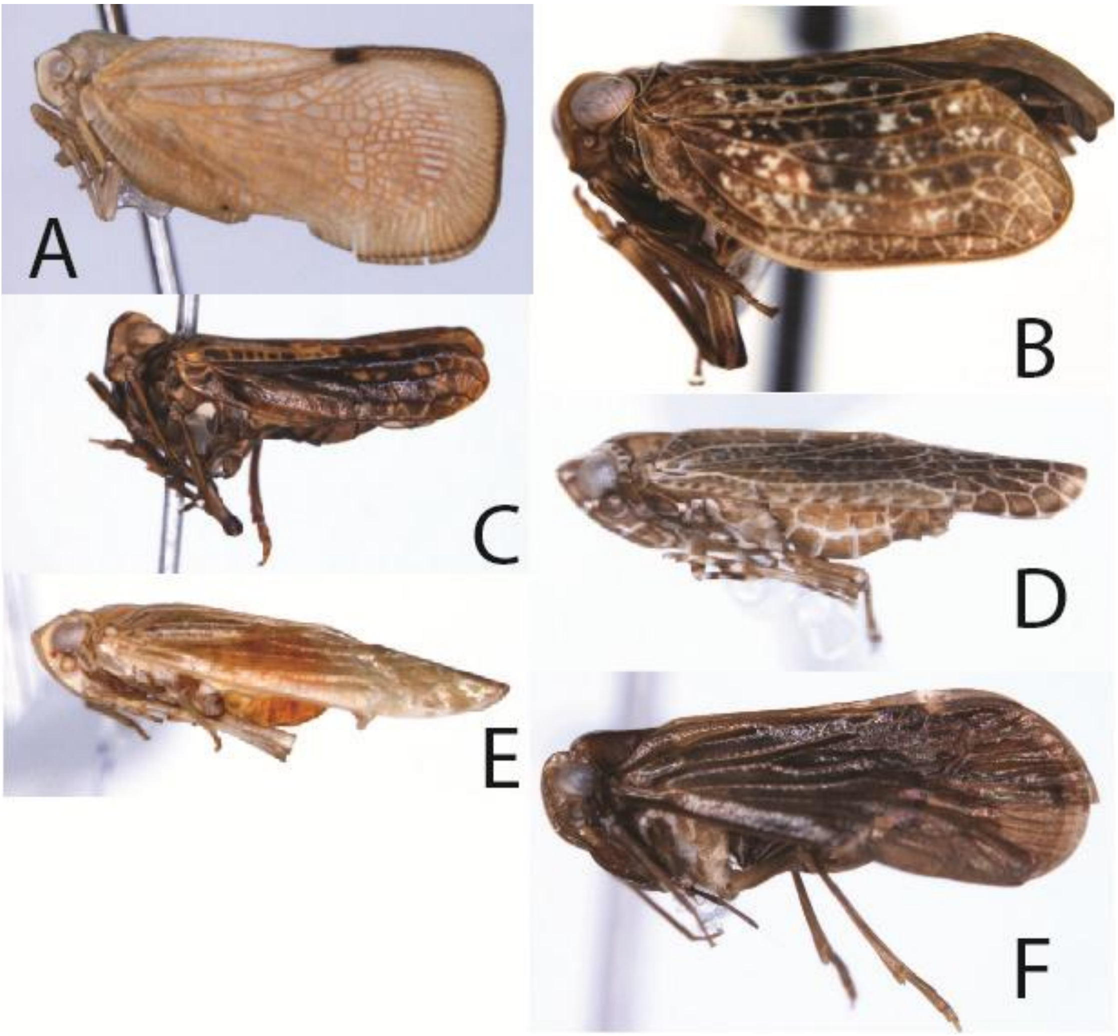

Figure 12. Abundant canopy morphospecies. A Flatidae 22 (*Anormenis*), B Issidae 18 (*Thionia*), C Issidae 60 (*Thionia*), D Achilidae 4 (*Opsiplanan*?), E Achilidae 79 (*Opsiplanon*?), F Cixiidae 9 (*Pintalia*).

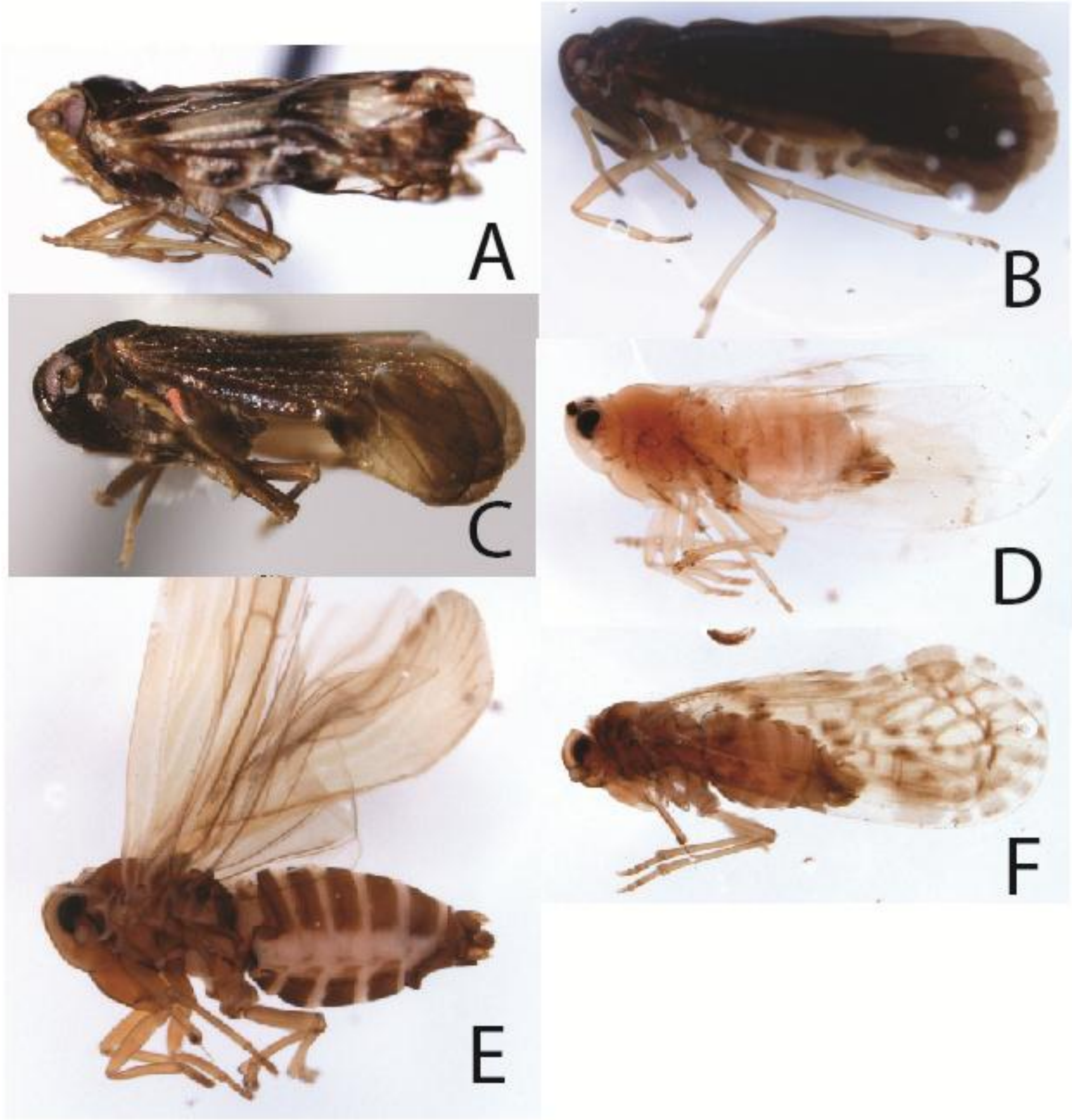

Figure 13. Abundant canopy morphospecies. A Cixiidae 14 (*Bothricera*), B Derbidae 35 (*Neocenchrea?*), C Delphacidae 6 (*Tetrasteira*), D Derbidae 14 (*Cenchrea?*), E Derbidae 37 (*Cenchrea?*), F Derbidae 42 (*Dysimia?*).

Table 1 A list of the families that are primary trees in the Onkone Gare sampling area, their abbreviation used in this paper, and the number of trees present in the transect.

Family Name	Abbreviation	Number of Trees
Apocynaceae	APO	2
Arecaceae	ARE	11
Bixaceae	BIX	2
Bombacaceae	BOM	6
Burseraceae	BUR	5
Cecropiaceae	CEC	8
Clusiaceae	CLU	3
Elaeocarpaceae	ELA	2
Euphorbiaceae	EUP	3
Fabaceae	FAB	9
Flacourtiaceae	FLA	1
Lacistemataceae	LAC	1
Lauraceae	LAU	1
Lecythidaceae	LEC	10
Melastomataceae	MLA	1
Meliaceae	MLI	5
Moraceae	MOR	11
Myristicaceae	MYRI	4
Myrtaceae	MYRT	2
Arecaceae	NYC	1
Polygonaceae	POLN	1
Rubiaceae	RUB	2
Rutaceae	RUT	1
Sapotaceae	SAPO	2
Tiliaceae	TIL	1
Violaceae	VIO	4
Dead	XXX	1

Table 2 Summary statistics for planthoppers in Ecuador canopy fogging samples. Unique morphospecies are taxa found only at that site. The number of singletons and doubletons is the number of taxa at each site that are represented by only 1 individual or 2 individuals respectively.

	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 3 Occurrence data for the 12 most abundant morphospecies.

Morphospecies	Number of Samples Present in (726 Total)	Percentage of Samples Present in
Flatidae 22	125	17.22
Achilidae 4	133	18.32
Achilidae 79	130	17.91
Issidae 18	106	14.60
Issidae 60	120	16.53
Cixiidae 9	175	24.10
Cixiidae 14	104	14.33
Delphacidae 6	493	67.91
Derbidae 14	109	15.01
Derbidae 35	133	18.32
Derbidae 37	124	17.08
Derbidae 42	159	21.90
Average	159.25	21.94

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Table 4 **Beta diversity indices for the four comparisons.** Jaccard's and Sørensen's indices are incidence based estimators and Bray Curtis is an abundance based estimator.

Onkone Gare vs Tiputini		
	Jaccard Incidence	0.5752
	Sørensen Incidence	0.7303
	Bray Curtis	0.5384
Tiputini Wet vs Onkone Gare Wet		
	Jaccard Incidence	0.5218
	Sørensen Incidence	0.6858
	Bray Curtis	0.6190
Tiputini Dry vs Onkone Gare Dry		
	Jaccard Incidence	0.3596
	Sørensen Incidence	0.5289
	Bray Curtis	0.2888
Tiputini Transitional vs Onkone Gare Transitional		
	Jaccard Incidence	0.3747
	Sørensen Incidence	0.5452
	Bray Curtis	0.4174

Table 5 **Beta diversity indices for the four comparisons 5% cutoff.** Jaccard's and Sørenson's indices are incidence based estimators and Bray Curtis is an abundance based estimator. Species examined were restricted to morphospecies that appeared in at least 5% of the samples.

Onkone Gare vs Tiputini		
	Jaccard Incidence	0.4954
	Sørensen Incidence	0.6626
	Bray Curtis	0.5019
Tiputini Wet vs Onkone Gare Wet		
	Jaccard Incidence	0.4038
	Sørensen Incidence	0.5753
	Bray Curtis	0.5838
Tiputini Dry vs Onkone Gare Dry		
	Jaccard Incidence	0.3814
	Sørensen Incidence	0.5522
	Bray Curtis	0.2644

Tiputini Transitional vs Onkone Gare Transitional		
	Jaccard Incidence	0.3889
	Sørensen Incidence	0.5600
	Bray Curtis	0.4020

Table 6 **Beta diversity indices for the four comparisons 10% cutoff.** Jaccard's and Sørenson's indices are incidence based estimators and Bray Curtis is an abundance based estimator. Species examined were restricted to morphospecies that appeared in at least 10% of the samples.

Onkone Gare vs Tiputini		
	Jaccard Incidence	0.4531
	Sørensen Incidence	0.6237
	Bray Curtis	0.5012
Tiputini Wet vs Onkone Gare Wet		
	Jaccard Incidence	0.3457
	Sørensen Incidence	0.5138
	Bray Curtis	0.5640
Tiputini Dry vs Onkone Gare Dry		
	Jaccard Incidence	0.3000
	Sørensen Incidence	0.4615
	Bray Curtis	0.2477
Tiputini Transitional vs Onkone Gare Transitional		
	Jaccard Incidence	0.3378
	Sørensen Incidence	0.5051
	Bray Curtis	0.3886

Table 7 **Morphospecies diversity of the 15 planthopper families found in the Ecuador canopy samples and family diversity of the Netropics (Mexico southwards).** List of unpublished checklists compiled by Lois O'Brien and Charles Bartlett.

Family	Number of Individuals	Number of Morphospecies	Number of Described Species
Kinnaridae	18	2	56
Acanaloniidae	23	2	79
Lophopidae	35	7	7

Ricaniidae	55	9	8
Fulgoridae	68	49	298
Nogodinidae	186	20	38
Achilixiidae	256	10	8
Dictyopharidae	415	35	160
Flatidae	422	22	342
Tropiduchidae	477	23	67
Achilidae	2070	113	100
Cixiidae	2765	95	299
Issidae	3175	101	170
Delphacidae	3186	8	304
Derbidae	4800	143	438
Totals	17,951	638	2333

Table 8 Alpha diversity estimator values for the six sampling categories. Presented are the final values for the alpha diversity estimators, singletons, and doubletons along with ancillary information. The bottom row is the averaged value of all the diversity estimators.

	Combined Data Set	Onkone Gare	Tiputini	Wet Season	Dry Season	Transitional Season
Number of Samples	1200	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

Table 9 **Number of genera and species of Fulgoroidea found in the South and Central America (Mexico and south).** List updated from unpublished checklists compiled by Lois O’Brien and Charles Bartlett.

	Genera	Species
Achilidae	42	100
Cixiidae	36	299
Delphacidae	67	304
Derbidae	42	438
Dictyopharidae	39	160
Flatidae	71	342
Fulgoridae	66	298
Issidae	50	170
Acanaloniidae	4	79
Achilixiidae	1	8
Lophopidae	3	7
Ricaniidae	4	8
Kinnaridae	13	56
Nogodinidae	12	38
Tropiduchidae	20	67
Total	470	2333

Table 10 **Rankings of Flatidae 22 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.**

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Log like
psi(FAB),gamma(), eps(FAB),p(Season)	706.86	0.00	0.2646	1	8	690.86
psi,gamma(), eps(),p(season)	708.70	1.84	0.1055	0.3985	6	696.70

psi(MLI),gamma(), eps(MLI),p(Season)	709.42	2.56	0.0736	0.278	8	693.42
psi(CEC),gamma(), eps(CEC),p(Season)	709.81	2.95	0.0605	0.2288	8	693.81
psi(NYC),gamma(), eps(NYC),p(Season)	711.19	4.33	0.0304	0.1147	8	695.19

Table 11 Rankings of Issidae 18 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi,gamma() ,eps(),p(season)	659.05	0	0.0836	1	6	647.05
psi,gamma(), eps(),p()	659.88	0.83	0.0552	0.6603	4	651.88
psi(ELA),gamma(), eps(ELA),p(Season)	660.79	1.74	0.0350	0.4190	8	644.79
psi(BOM),gamma(), eps(BOM),p(season)	661.11	2.06	0.0299	0.3570	8	645.11
psi(RUB),gamma(), eps(RUB),p(Season)	661.32	2.27	0.0269	0.3214	8	645.32

Table 12 Rankings of Issidae 60 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi(ELA),gamma(), eps(ELA),p()	691.84	0	0.1730	1	6	679.84
psi,gamma(), eps(),p()	693.72	1.88	0.0676	0.3906	4	685.72
psi(ELA),gamma(), eps(ELA),p(Season)	693.96	2.12	0.0599	0.3465	8	677.96
psi(FAB),gamma(), eps(FAB),p()	694.34	2.50	0.0496	0.2865	6	682.34
psi(EUP),gamma(), eps(EUP),p()	694.34	2.50	0.0496	0.2865	6	682.34

Table 13 Rankings of Achilidae 4 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi(CEC),gamma() ,eps(CEC),p()	740.29	0	0.18	1	6	728.29
psi(CEC),gamma(), eps(CEC),p(Season)	742.19	1.90	0.07	0.3867	8	726.19
psi,gamma(),eps(),p()	742.27	1.98	0.07	0.3716	4	734.27
psi(ELA),gamma(), eps(ELA),p()	742.77	2.48	0.05	0.2894	6	730.77
psi(RUB),gamma(), eps(RUB),p()	743.14	2.85	0.04	0.2405	6	731.14

Table 14 Rankings of Achilidae 79 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi(ELA),gamma(), eps(ELA),p()	733.10	0	0.0950	1	6	721.10
psi,gamma(), eps(),p()	733.35	0.25	0.0838	0.8825	4	725.35
psi(VIO),gamma(), eps(VIO),p()	733.61	0.51	0.0736	0.7749	6	721.61
psi(FAB),gamma(), eps(FAB),p()	733.94	0.84	0.0624	0.6570	6	721.94
psi(MOR),gamma(), eps(MOR),p()	734.48	1.38	0.0476	0.5016	6	722.48

Table 15 Rankings of Cixiidae 9 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi,gamma(), eps(),p(season)	866.03	0	0.0803	1	6	854.03
psi(RUB),gamma(), eps(RUB),p(Season)	866.09	0.06	0.0779	0.9704	8	850.09
psi(MYRI),gamma(),	866.33	0.30	0.0691	0.8607	8	850.33

eps(MYRI),p(Season)						
psi(FAB),gamma(), eps(FAB),p(Season)	866.72	0.69	0.0569	0.7082	8	850.72
psi(RUB),gamma(), eps(RUB),p()	867.82	1.79	0.0328	0.4086	6	855.82

Table 16 Rankings of Cixiidae 14 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi(CEC),gamma(), eps(CEC),p(Season)	632.42	0	0.1211	1	8	616.42
psi,gamma(), eps(),p(seasonal)	632.69	0.27	0.1058	0.8737	6	620.69
psi(ELA),gamma(), eps(ELA),p(Season)	633.84	1.42	0.0595	0.4916	8	617.84
psi(BOM),gamma(), eps(BOM),p(season)	633.9	1.48	0.0578	0.4771	8	617.90
psi(MLI),gamma(), eps(MLI),p(Season)	634.0	1.58	0.0550	0.4538	8	618.00

Table 17 Rankings of Delphacidae 6 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi,gamma(),	1195.98	0	0.1241	1	6	1183.98

eps(),p(season)						
psi(BIX),gamma(), eps(BIX),p(Season)	1196.55	0.57	0.0933	0.7520	8	1180.55
psi(APO),gamma(), eps(APO),p(season)	1196.55	0.57	0.0933	0.7520	8	1180.55
psi(RUB),gamma(), eps(RUB),p(Season)	1197.01	1.03	0.0741	0.5975	8	1181.01
psi(BUR),gamma(), eps(BUR),p(Season)	1197.41	1.43	0.0607	0.4892	8	1181.41

Table 18 **Rankings of Derbidae 14 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.**

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi,gamma(), eps(),p(season)	663.94	0	0.1115	1	6	651.94
psi(RUB),gamma(), eps(RUB),p(Season)	664.90	0.96	0.0690	0.6188	8	648.90
psi(BOM),gamma(), eps(BOM),p(season)	665.12	1.18	0.0618	0.5543	8	649.12
psi(ARE),gamma(), eps(ARE),p(Season)	666.09	2.15	0.0380	0.3413	8	650.09
psi,gamma(),eps(),p()	666.48	2.54	0.0313	0.2808	4	658.48

Table 19 Rankings of Derbidae 35 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi(CEC),gamma(), eps(CEC),p()	755.13	0	0.0636	1	6	743.13
psi(CEC),gamma(), eps(CEC),p(Season)	755.23	0.10	0.0605	0.9512	8	739.23
psi,gamma(),eps(),p()	755.41	0.28	0.0553	0.8694	4	747.41
psi,gamma(), eps(),p(season)	755.48	0.35	0.0534	0.8395	6	743.48
psi(EUP),gamma(), eps(EUP),p()	756.01	0.88	0.0410	0.6440	6	744.01

Table 20 Rankings of Derbidae 37 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi,gamma(), eps(),p()	696.23	0	0.0963	1	4	688.23
psi(BIX),gamma(), eps(BIX),p()	696.35	0.12	0.0906	0.9418	6	684.35
psi(CEC),gamma(), eps(CEC),p()	697.02	0.79	0.0648	0.6737	6	685.02
psi(BUR),gamma(), eps(BUR),p()	697.58	1.35	0.0490	0.5092	6	685.58
psi(ELA),gamma(), eps(ELA),p()	697.72	1.49	0.0457	0.4747	6	685.72

Table 21 **Rankings of Derbidae 42 occupancy models based on AIC to explain occupancy. Data were collected in Onkone Gare, Ecuador over 3 years of sampling.**

Model	AIC	ΔAIC	AIC Weights	Likelihood	No. Parameters	-2*Loglike
psi,gamma(), eps(),p(season)	819.71	0	0.0726	1	6	807.71
psi(ELA),gamma(), eps(ELA),p(Season)	819.90	0.19	0.0661	0.9094	8	803.90
psi,gamma(), eps(),p()	820.10	0.39	0.0598	0.8228	4	812.10
psi(ELA),gamma(), eps(ELA),p()	820.32	0.61	0.0535	0.7371	6	808.32
psi(BOM),gamma(), eps(BOM),p(season)	821.50	1.79	0.0297	0.4086	8	805.50

Table 22 **Seasonality results from Onkone Gare and Tiputini.**

	Wet Season	Dry Season	Transitional Season
Number of samples	313	334	295
Individuals	7202	5167	5582
Species Observed	504	445	459
Singletons Mean	147	134	116
Doubletons Mean	57	60	66
Average Estimator Value	669	593	568

Table 23 **Richness data for Yasuni ground based collecting methods.** Specimens were collected over 4 days and 5 nights in Yasuni National Park (April 25-29, 2005) using light trapping, hand collection, and sweep netting targeting fulgoroids. Specimens were collected by Dr. Charles Bartlett, Nate Nadrowicz, and Dawn Chang.

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

Table 24 **Summary of best occupancy model for 12 morphospecies collected in canopy fogging.**

Taxon	Best Model	Best Model Combination
Flatidae 22	psi(FAB),gamma(),eps(FAB),p(Season)	FAB + Season
Issidae 18	psi,gamma(),eps(),p(season)	Season
Issidae 60	psi(ELA),gamma(),eps(ELA),p()	ELA
Achilidae 4	psi(CEC),gamma(),eps(CEC),p()	CEC
Achilidae 79	psi(ELA),gamma(),eps(ELA),p()	ELA
Cixiidae 9	psi,gamma(),eps(),p(season)	Season
Cixiidae 14	psi(CEC),gamma(),eps(CEC),p(Season)	CEC + Season
Delphacidae 6	psi,gamma(),eps(),p(season)	Season

Derbidae 14	psi,gamma(),eps(),p(season)	Season
Derbidae 35	psi(CEC),gamma(),eps(CEC),p()	CEC
Derbidae 37	psi,gamma(),eps(),p()	NULL
Derbidae 42	psi,gamma(),eps(),p(season)	Season

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Appendix

Appendix A

Descriptions, formulae and references for biodiversity estimators.

Test	Description	Citation	Formula
ACE: Abundance-based Coverage Estimator of species richness	Based on the principle that $S_{obs} = S_{rare} + S_{abund}$. The total number of samples is the largest factor in the accuracy of this test. ACE does not work when all the rare specimens are singletons.	Chao and Lee 1992, Chao et al. 1993	$S_{obs} = S_{rare} + S_{abund}$
ICE: Incidence-based Coverage Estimator of species richness	Operates on a division of frequent and infrequent. Infrequent being any species with < 10 samples and frequent > 10 samples.	Chao et al. 2000	$S_{obs} = S_{inf\ r} + S_{freq}$
Chao 1	Uses both singletons and doubletons to calculate species richness. When applied to a single collection is referred to as Chao 1.	Chao 1984	$S_{chao1} = S_{obs} + F_1^2 / 2F_2$
Chao 2	Same principle as Chao 1, except applied to multiple collections. Singletons and doubletons are from the combined collections.	Chao 1984, 1987	$S_{chao2} = S_{obs} + Q_1^2 / 2Q_2$
Jackknife 1	An incidence based estimator that relies on singletons encountered.	Burnham & Overton 1978, 1979	$S_{jack1} = S_{obs} + Q_1(m-1/m)$

Jackknife 2	An incidence based estimator that relies on singletons and doubletons encountered.	Burnham & Overton 1978, 1979	$S_{jack2} = S_{obs} + [(Q_1(2m-3)/ m) - (Q_2(m-2)^2 / m(m-1))]$

Appendix B

Descriptions, formulae and references for beta diversity estimators.

Jaccard's	The long used test for comparing two communities using present/absence data. Assumes that the population has been thoroughly sampled.	Chao et al. 2005	**J (A,B) = $\lvert A \cap B \rvert / \lvert A \cup B \rvert$**
Jaccard's Abundance	A variant of Jaccard's that handles a large number of rare individuals more accurately. Also uses the abundance of the sample to reign in estimates.	Chao et al. 2005	J = A / A + B + C
Sørensen's Similarity Index	Is a statistic used for comparing the similarity between two samples.	Chao et al. 2005	B = 2c / $S_1 + S_2$
Sørensen's Abundance	A variant of Sørensen's that gives weight to the number of samples.	Chao et al. 2005	B = 2A / 2A + B + C
Bray Curtis	Used to examine dissimilarity, as opposed to similarity, between two sites.	Chao et al. 2005	$BC_{ij} = \sum \frac{\lvert n_{ik} - n_{jk} \rvert}{(n_{ik} + n_{jk})}$