Characterization of a Tropical Hawkmoth (Family Sphingidae) Community in an Atlantic Lowland Rainforest

by

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Abstract

As conserving biodiversity becomes a global concern, new methods must be developed to ascertain true species richness. Conducting biodiversity surveys may aid conservation groups and governments alike in identifying a conservation priority, or determine proper sizes of national parks to maintain diversity. Fifty percent of the world's biodiversity is concentrated in tropical rainforests (only 5-10% of earth's surface). Insects make up an important, but difficult to measure, component of the world's biodiversity (54%). Quantifying and understanding insect biodiversity is essential if we are to gain an understanding of global biodiversity patterns. New estimators have recently been developed to estimate species richness based on quantitative sampling, and appear to work well with samples containing numerous rare entities, as typical with insects. I conducted a biodiversity survey of the hawkmoths (Family Sphingidae) at Caño Palma Biological Station in the Barra Colorado Wildlife Refuge, about eight kilometers north of the village of Tortuguero and Tortuguero National Park. Sixty-two species and 635 individuals were recording using three sampling methods in June-July 2000. Based on a series of 50 randomized species accumulation curves, estimators Chao1 and Chao2 estimate 74 and 73 species respectively, and Jackknife1 and Jackknife2 estimate 76 and 81 species respectively. Abundance-based and incidence-based estimators (ACE/ICE) estimate 72 and 74 species respectively and Bootstrap estimates 69 species. The Michaelis-Menton fits estimate 68 and 69 species. Most of the estimators consistently estimated 72-76 species and I believe the Choa2 estimator performed best because it rapidly estimated in the range of 72-76 in only 21 samples, and continued to estimate 73 species when all samples were pooled. There was little difference between estimators using abundance-based and incidence-based data, therefore I recommend recording presence or absence of species rather then counting every individual. The estimators are accurate and can possibly be incorporated into a regular regimine of arthropod biodiversity surveys where a large proportion of species are rare. It is important to continue to test the effectively and reliability of the species richness estimators and apply them to conservation management.

Introduction:

A biodiversity survey is the systematic accounting of all species for a given geographic area. It usually includes all relevant plants and animals of a specified area, with either natural (e.g., a forest or a river) or artificial (e.g., a natural park) boundaries. Bacteria, protists, and fungi are often ignored, but there is no question they are integral to the function of any ecosystem surveyed.

The purpose of a biodiversity survey is to generate species lists and estimate true species richness of major taxonomic groups, for example birds or mammals. Surveys range from narrow studies of a specific group, to a collaborative wide-scale "all-taxa" survey. Results from a biodiversity survey relate to three major disciplines: taxonomy, ecology, and conservation biology. Taxonomists discover thousands of new species every year as a result of sampling remote tropical forests or inhospitable places such as thermal springs and deep-sea vents. Diversity inventories generate data on the distribution and abundance of organisms which may enrich ecological understanding. Data may serve as historical records as ecologists or conservationists observe changes over time. Environmental and ecological impacts of human activities may be monitored at the biodiversity level. Conducting assessments of biodiversity at several different localities may help conservation biologists and government officials identify conservation priorities.

Biodiversity inventories are relatively easy to perform for plants, birds, and mammals. The diversity is typically not tremendously high and true species richness can be efficiently recorded in most cases. Arthropods represent a hyperdiverse group and contribute most of the world's biodiversity. Global biodiversity can be summarized as follows: "To a rough approximation… all organisms are insects" (May 1988). Biologists refer to the global number of species as the “grail number” (May 1992), the quest for which will greatly improve our understanding of diversity patterns on earth (Longino 1994). To begin this task, or “quest”, biologists must face the greatest challenge: species are not pennies. A machine can be engineered to count 30 million pennies, but counting 30 million species is different (Longino 1994). Ecosystems are made up of countless individual organisms of an unknown number of species distributed in a variety of ways. In order to count species, individuals must be observed, and for each one the question is asked “Have I seen this species before?”. The human capacity to remember distinct objects, though impressive, is limited (Longino, 1994). The difficulties are apparent in identifying every individual down to species, especially in cases where there is little morphological difference. Measuring the true biodiversity of insects, if not an impossibility, would take far too long to realize the rewards of the effort in terms of both achieving the final list and utilization of a final species list in conservation! It must also be considered that communities are constantly changing and that biodiversity is largely argued to exist in a non-equilibrium state (Connell 1978). Because of the combination of high biodiversity and limited time resources to appropriately sample biodiversity, it would be in the best interest to estimate the true species richness, rather than “get them all” over a very long time period. Since biodiversity does not exist at equilibrium, taking a “snapshot” of the biodiversity would be more advantageous than a long-term study. Besides, as tropical countries increase in population, there will be more pressure to utilize their natural resources, including forests, and biologists must use cost-efficient sampling methods to evaluate the forests. In order to estimate true species richness for a major taxa, quantitative sampling is required (McKamey 1999). The advantage of working with hyperdiverse taxa is that there are many repeated patterns. It may be possible to identify a forest with high biodiversity by sampling a few indicator taxonomic groups. These rapid assessments are already being employed using plants, and are used in assessing conservation priorities.

Knowledge of biodiversity in tropical areas is especially critical, since these regions harbor much of the earth's biodiversity and are undergoing rapid ecological change due to human intervention. In Costa Rica, the demand for biodiversity research is being driven by both ecotourism and conservation concerns, which are not mutually exclusive pursuits. Costa Rica's leading agency conducting biodiversity inventories is INBio, the National Biodiversity Institute. Created in October of 1989, the Institute's ten-year goal was to inventory and catalogue every species of organism within the country's borders (Gamez 1991, Janzen 1991). Currently in their twelfth year, the staff of INBio have realized that a ten-year time-frame has been a serious underestimate. Funding continues and INBio remains a highly successful international project with 23 biodiversity stations scattered in 11 government-designated conservation areas. Their insect collection alone is the largest in the world, containing over 3 million specimens, of which only 24% are identified to the species level. Despite this effort, INBio has yet to conduct a formal entomological inventory in the Tortuguero Conservation Area, which contains *all* of Costa Rica's Atlantic lowland rainforests (Jorge Corrales pers. comm.). Thus, the only conservation area that encompasses the Atlantic lowland forests (and coincidentally is believed to harbor the most biodiversity), is unstudied. Tortuguero potentially could harbor the greatest biodiversity of insects of any eco-region in Costa Rica, since previous studies of plants and mammals report this region as the most speciose (Janzen 1983). The reason for the gap in research is simply the remoteness of this region of the country and the associated costs of transporting supplies and experts. Since an all-taxa biodiversity inventory here would be impractical in terms of both money and time, focusing on a single taxon would be most cost efficient.

Documentation of high species diversity of a focal taxon using cost and time efficient methods is urgently needed for prioritizing conservation managerial decisions and filling the gap in knowledge of Costa Rica's rainforest fauna. Sampling and making collections from specific areas is the first step in developing species lists, assessing rarity of species and species richness, establishing geographic ranges, and describing new species. Scientific collection and preservation (e.g., the deposition of voucher specimens in established museum collections) remains the single most important activity for providing useful information for future conservation decisions (DeVries 1987). Also, results from a biodiversity study can have relevance beyond a focal taxonomic group. Patterns of biodiversity and species richness of one taxon may reflect similar patterns of other taxa in the same eco-region (Colwell and Coddington 1994), thus helping decision makers allocate future resources to more comprehensive biodiversity studies.

In this study I conducted a structured biodiversity inventory of the hawkmoth (Family Sphingidae) community of an Atlantic lowland rainforest at Cano Palma Biological Station on the Caribbean coast of Costa Rica. Hawkmoths are among the best known macrolepidopterans in the world. An efficient inventory of sphingid moths can be achieved because of the relative ease of collection (ultraviolet light and Malaise traps) and because species are readily identifiable. The sphingids are taxonomically well known relative to other Neotropical insect taxa and the biodiversity is not excessively high. A single scientist would be capable of completing a study of sphingid diversity whereas it would take a team of scientists to efficiently measure the biodiversity of nearly any family of Coleopterans (beetles). Finally, since no previous studies have been conducted in this area of the country, surveys in Atlantic lowland forest would represent pioneering work. INBio, the institution responsible for conducting biodiversity surveys, has yet to formally sample the Tortuguero area (Jorge Corrales pers. comm.).

Natural History of Sphinx Moths

Hawkmoths are represented by over 1000 species globally, of which an estimated 150 are known to occur in Costa Rica (Haber 1983). Comparatively, the United States and Canada have 115 species (Hodges 1971). Considering the small size of Costa Rica (50,000 km^2, roughly the size of West Virginia), the pattern of sphingid species richness is weighted heavily towards the tropics, and most particularly Atlantic lowland rainforests.

Sphinx moths are powerful, adroit flyers capable of attaining speeds of 40 km/hr, and can hover, fly backward, or upside down (Haber 1983). Their potential for long distance dispersal is evident from reports of Neotropical species in southern Florida, and formations of subspecies complexes on remote Caribbean and Pacific islands, including the Galapagos archipelago. They are well known as pollinators in the tropics, where they have apparently co-evolved as pollinators of many forest trees, shrubs, and epiphytes. Both sexes sip nectar through a long proboscis (up to 25 cm) during their characteristic hovering flight. Largely nocturnal, they feed on white, tubular night-blooming flowers that typically produce pungent odors. Only six Costa Rican species are known to be diurnal (Haber 1983).

Costa Rica's Geography & Cano Palma Biological Station

Costa Rican geography accounts for a substantial diversity of habitat types and a remarkable range of climate conditions. The most notable feature is the central mountain range than runs northwest to southeast and separates eastern (Caribbean) and western (Pacific) lowlands (Figure 1). The typical climate pattern in Costa Rica reflects stability: a predictable pattern of rain, temperature, and seasonal variation. The Pacific lowlands (with the exception of the Osa Peninsula) are dominated by deciduous trees and have a pronounced dry season lasting up to five months. The local sphingid fauna reflects this seasonality, with species becoming dormant or migrating to wet forest habitat (Janzen 1984). The Atlantic lowlands are evergreen and are believed to have the highest species richness in the country (Haber 1983). Seasonality is not as strongly marked as in their dry forest counterparts, as the species indigenous to wet forests fly year-round (Janzen 1984).

Caño Palma Biological Station is located at 10° 35'62.3" N & 83° 31'68.8" W in the network of canals and rivers in the Barra del Colorado Wildlife Refuge 8 km north of Tortuguero National Park and the village of Tortuguero (Figure 2). The station is administered by COTERC (Canadian Organization for Tropical Education and Rainforest Conservation). Accessible only by boat, the station is situated on a small blackwater canal and protects 40 hectares of primary rainforest. The ecology reflects many typical features of forests found in blackwater river systems (Janzen 1973, Meyer 1990). The annual precipitation usually exceeds 5000 mm, making it the wettest rainforest in Costa Rica. Although the life zone has been described as tropical wet forest (Holdridge *et al.* 1971), the forest surrounding Caño Palma is more properly considered a periodically inundated tropical wet forest. The forest seasonally floods for a few days in the months between November and January, the wettest months, and the forest ecology is intimately dependent on this seasonal flooding.

Collectively, Costa Rica's Tortuguero National Park and Barra del Colorado Wildlife Refuge (green areas on Figure 2), and Nicaragua's southeastern rainforests represent the world's

Figure 1. Topographic map of Costa Rica


Relief map of Costa Rica
NIC
PA
Golfo de Papagayo
Llanura de los Guatusos
Lago Caño Negro
Llanura de San Carlos
Llanura de Tortuguero
Llanura de Santa Clara
Cordillera de Guanacaste
Laguna de Arenal
Cordillera de Tilarán
Cordillera Central
Cordillera de Talamanca
Fila de Matama
Península de Nicoya
Isla Chira
Golfo de Nicoya
Isla San Lucas
Punta Caldera
Isla Negritos
Islas Tortugas
Punta Piedra Amarilla
Punta Coyote
Cabo Blanco
Punta Judas
Punta Quepos
Punta Catedral
Punta Castilla
Isla Machuca
Punta Cahuita
Punta Mona
Valle de La Estrella
Valle de Talamanca
Cerro Chirripó
Punta Dominical
Punta Uvita
Valle de El General
Valle de Coto Brus
Bahía de Coronado
Isla Boca Brava
Isla Zacate
Punta Violín
Bahía Drake
Punta Agujitas
Isla del Caño
Punta Llorona
Península de Osa
Golfo Dulce
Puntarenitas
Valle de Coto Colorado
Punta Salsipuedes
Cabo Matapalo
Bahía de Pavón
Punta Banco
Península de Burica
Punta El Mangle
Punta Burica
Bahía de Charco Azul
Isla del Coco
Isla Manuelita
Cabo Barrera
Punta Ulloa
Cabo Atrevida
Cerro Yglesias
Cabo Lionel
Punta Pacheco
Cabo Dampier
0 20 40 60 km
0 10 20 30 miles

Figure 2. Northeast corner of Costa Rica showing Tortuguero National Park, Barra del Colorado Wildlife Refuge (in green) and neighboring Nicaragua (in purple)


x Caño Palma
x Tortuguero
Punta Castilla
NIC
5
Isla Machura
Isla Calero
Barra del Colorado
Isla Brava
San Juan
Colorado
Chirripó
Trinidad
Sarapiquí
Refugio Nacional de Fauna Silvestre Barra del Colorado
119m Cerro Tortuguero
Zona Protectora Tortuguero
Tortuguero
Llanura de Tortuguero
Sardinal
Boca Río Sucio
4
HEREDIA
Muelle
Puerto Viejo de Sarapiquí
La Selva
Tigre
Zona Protectora La Selva
Sucio
Encina
Suerte
Canta Gallo
Tortuguero
Parque Nacional Tortuguero
San Pedro
Cariari
Esperanza
Sierpe
Griega
Las Horquetas
Rara Avis
Río Frío
Teresa
Zancudo
Jiménez
Rita
Roxana
Villafranca
Llanura de Santa Clara
Río Jiménez
Parque Nacional Braulio Carrillo
3
Santa Clara
Guápiles
Guácimo
Parismina
LIMÓN
Canal de Tortuguero
Jiménez
Pacuare
Pocora
Germania
Manila
Rainforest Aerial Tram
Jardín Botánico Las Cusingas
Zona Protectora Acuíferos Guácimo y Pococí
Cairo
Siquirres
Cuatro Millas
Cordillera Central
2047m Cerro Honduras
Florida
Batán
Matina
Estrada
Reventazón
Zona Protectora Río Pacuare
Barbilla
Bristol
Larga Distancia
Zurquí
Parque Nacional Volcán Irazú
3328m Volcán Turrialba
Stratford
Liverpool
San Isidro
3432m Volcán Irazú
Santa Cruz
Lajas
Peralta
Zona Protectora Barbilla
Río Blanco
Llano Grande
Monumento Nacional Guayabo
1617m
Pacayas

second largest Atlantic lowland rainforest (second only to Brazil). The large area of intact forest supports a wealth of biodiversity and many scientists believe it harbors more species than any other forest type of similar size. Therefore, it is important to conduct biodiversity studies to inventory the myriad species inhabiting the forest.

Inventories of Biodiversity

There are two distinct types of biodiversity surveys. A *strict* inventory aims to obtain an accurate species list for a community, usually of a focal taxon. Specimens are sorted into species because the actual identities of the species are valuable products, while relative abundances may be of minor interest (Longino and Colwell 1997). Strict inventories provide information in the form of locality and collection data, which can be valuable to scientists looking for particular species. A strict inventory is ideal when sampling an area for the first time. While completing an internship at Cano Palma Biological Station from January to May 1999, I conducted a strict inventory of three moth families using mercury-vapor blacklighting: tiger moths (family Arctiidae), giant silk moths (family Saturnidae), and sphinx moths (family Sphingidae) (Wickham 1999 unpublished).

I employed a *structured* inventory to characterize the sphingid community of Caño Palma Biological Station. Goals included assessing species abundance, assessing efficiency of differing sampling techniques, and using species accumulation curves to assess overall completeness of the inventory. Using a data matrix for all species tallied within each individual sample, it was possible to estimate species richness (S_{max}) and compare it to the observed species richness (S_{obs}). A *structured* inventory has characterization of a community as the goal. Such characterization uses structured (more than one) sampling techniques to estimate the distribution and abundance of species, overall species richness, and complementarity with other communities. Several different sampling techniques are employed, and efficiencies of each method can be compared. For example, blacklighting may not attract diurnal moth species, so another method such as Malaise trapping may be employed. Structured inventories enable ecologists to perform analyses which quantitatively compare communities. Applications of this type of inventory include setting conservation priorities (by using various measures of community diversity to rank habitats), and monitoring community changes over time (Longino and Colwell 1997).

Data from structured inventories are an improvement over traditional strict inventories in several respects: (1) progress or completeness of the inventory can be estimated using species accumulation curves, thereby enabling an ecologist to maximize the number of species obtained per unit of sampling; (2) sampling methods can be qualitatively compared to improve efficiency; (3) quantitative data on individual species can improve ecological knowledge of those species (habitat preference, seasonality, etc.); (4) data can be applied to community characterization (Longino and Colwell 1997).

Statistical Approach

The observed number of species in any sample of individuals from a species-rich community inevitably underestimates the true number of species present (Chazdon et al. 1998). In statistical terms the observed species richness, S_{obs}, is a biased estimator of the true richness of the community sampled. A number of species richness estimators have been developed to account for the unknown number of species missed in sampling efforts. The richness estimators are typically illustrated as the total number of species accumulated as a function of some measure of sampling effort. Counting cumulative species as successive samples are pooled can effectively contruct a species accumulation curve.

Ideally, a species richness estimator should be: (1) independent of sample size beyond some minimum threshold, (2) remain stable as sample size increased, (3) when plotted on the same scale as the observed species accumulation curve, it should rapidly increase to S_{max} and remain constant, and most importantly (4) be an accurate estimate of true species richness. It is crucial to evaluate the performance of a species richness estimator and to analyze how the estimator behaves as a function of sample size (Chazdon et al. 1998).

The origins of examining regional species richness date back to MacArthur and Wilson's (1967) theory of island biogeography. These authors noted that species richness increased as a function of the total area sampled, known as the species-area curve (MacArthur and Wilson 1967). Early species richness estimators relied on extrapolation of observed species accumulation curves or species-area curves (Holdridge *et al*. 1971). The curve was usually extrapolated to either an asymptotic level or to sample sizes (or areas) larger than the observed (Chazdon *et al*. 1998).

More complex statistical methods emerged with the use of parametric models. The models fit data on the relative abundance of species in a single sample to a parametric distribution such as log-series, lognormal, and Poisson lognormal (Pielou 1975; Miller and Wiegert 1989). When plotted, some of the distributions resembled species accumulation curves and allowed for estimation of total species richness. Other curves were limited in their predictive powers to only predicting how many species will occur in samples larger than the observed (in area). Since these models heavily relied on fitting data to relative abundance of individual species, they performed poorly for taxonomic groups, such as insects, in which a large proportion of species are rare. These limitations make it impractical to apply parametric models to insects. Numerous rare species are statistically negligible in traditional diversity indexes such as the Simpson's Index and Shannon-Weiner Index.

Another class of estimators is non-parametric and deals better with collections containing numerous rare entities. There are two main groups of non-parametric estimators: those based on incidence (presence or absence) and those based on abundance of species. The only difference between the two groups is the way rare species are tallied. These estimators are more appropriate for the arthropod inventories.

Applications of Biodiversity Inventories to Conservation

Prior to the implementation of the powerful statistical techniques described above, it was extremely difficult to obtain accurate measures of true species richness in diverse habitats such as tropical rainforests. The impetus for saving tropical forests or setting conservation priorities may factor in only a single species or just a handful into the equation. Tortuguero National Park protects mainly the green sea turtle's nesting habitat, but also protects thousands of hectares of forest as well. In the central part of Costa Rica, the golden toad and the quetzal are the "flagship" species to protect in the cloudforests of Monteverde. There is no doubt a great deal of popularity and cooperation when the survival of these beautiful, rare, and unique animals is in question. From a biodiversity perspective, it will be favorable to protect as many species as possible. Conducting biodiversity surveys can aid in ranking habitats that should be set aside for conservation. Habitats with an exceptionally high biodiversity can be identified through the use of inventories, thus identifying a conservation priority.

Systematic reporting of every single organism would be impossible and extremely time consuming. That is where biodiversity surveys can apply. With proper testing of the species richness estimators in the field, scientists in a short period of time can accurately assess the biodiversity. It will be helpful to identify the minimum threshold of sampling effort that will yield accurate estimates of species richness.

Sampling indicator taxonomic groups may reflect the overall pattern of diversity in the forest. Extremely diverse taxa such as the insects typically exhibit similar patterns of diversity among their respective divisions of classification. For example, diversity of ants may be at its peak in a particular forest. The high diversity may reflect similar patterns in the moths, beetles, and bees. Scientists have commonly used species richness of butterflies, birds, and mammals are used demonstrate high species richness of a forest, but unfortunately, they represent less than 1% of the biodiversity.

Currently, an organization called Conservation International has established what are called Rapid Assessment Programs (RAP), where expert biologists do short-duration, but thorough surveys of habitat in order to learn if the area is sufficiently important to be a high priority for preservation (Kricher 1996). Results from RAP have found so much previously unknown biodiversity that decision-makers in many of these countries are using the results to set new conservation priorities and redefine protected areas. Perhaps, as a result of further testing and usage of these species richness estimators, scientists may accurately and rapidly assess true species richness of challengingly diverse taxa such as the arthropods. A variety of insect taxonomic groups can be incorporated into a Rapid Assessment Program instead of being overlooked, and conservation organizations and conservationists alike may be better informed in their decisions.

Methods:

Sampling was conducted nightly over the course of two lunar cycles from new moon to new moon, from 1 June - 31 July 2000. The following weather conditions were monitored: daily high/low temperature and rainfall (mm). In order to provide proper documentation of a species, voucher collections (one individual of each species) were deposited at the National Museum in Costa Rica and the Willard F. Stanley Museum at SUNY College at Fredonia. Species were determined using a photographic guide I had made for the station during 1999 sampling (Wickham 1999 unpublished). Species identifications were also confirmed comparing specimens to identified specimens at INBio, and cross-referencing them using D'Abrera's and Kitching & Cadiou's references (D'Abrera 1986, Kitching and Cadiou 2000). Possible new species were deposited at INBio because their large reference collection would hasten identification.

For the core sampling method, mercury-vapor blacklighting techniques were used (Weiss *et al.* 1941, Hsiao 1972, Heinton 1974). A mercury-vapor light was suspended in front of a white sheet and was run from dusk until dawn. Sphinx moths and many other insects are attracted to the ultraviolet light source and usually alight on the sheet or a nearby surface where they usually remain until morning. Blacklighting is the single-most effective tool for sampling night-flying insects (Janzen 1983). The mercury-vapor light was operated every night, rain or shine, from dusk until dawn, over the course of the sampling period. In the case of a power outage, or while sampling atop Cerro Tortuguero (see below), a lightweight portable generator was used to power the light. Two main sites were employed: (1) the station's boat dock over the canal (Caño Palma) which intercepts a major fly zone used by sphingids, who prefer to fly over the canal rather than navigate the forest. Most sphingids I observed flying over the canal were intercepted by the light; (2) the top of the Cerro Tortuguero. This extinct volcano (119 m) stands alone on the Caribbean coast. Readily accessible from the station, this site provides an ideal location for blacklighting as the light is visible above the forest canopy for kilometers.

Luminescent powder, visible under UV light, was applied to the thorax of individuals captured at lights. Individuals were marked using four different colors (one color for each 2-week period) over the duration of the 8-week investigation. Using this technique may provide insight on the longevity of individuals and increase efficiency of relative abundance determinations by decreasing the likelihood of individuals being counted twice. Live weights of individuals were also recorded to the nearest tenth of a gram, using a hang-scale.

The second sampling technique I employed was the Malaise trap (Malaise 1937). Malaise traps are open-sided tents with a collecting head in which flying arthropods are trapped and accumulate in a container containing 75% ethanol (Matthews and Matthews 1971, Owen 1983, Darling and Packer 1988). The traps were placed in strategic flyways, and with little maintenance can be very effective at catching moths. The Malaise traps were placed in two locations: (1) suspended three-meters over the canal (Cano Palma) tied to overlying trees (six-meter-wide trap); (2) set up in an open area at ground level near a tree-fall on the station's Raphia trail in the rainforest (a two-meter-wide trap). Traps were checked and emptied every two weeks until final takedown on July 31, 2000.

The final sampling technique employed was monitoring trees and shrubs near the station which are commonly visited by sphingids. This technique may obtain species that might otherwise be absent from blacklights or missed by Malaise traps, such as diurnal sphingids. All individuals were captured, marked, and released.

Species Richness Estimators:

The formulas for the various species richness estimators (from Chazdon *et al.* 1998) are listed in this section along with the definitions of the variables used in the equations (Table 1). The true species richness estimators (S_{est}) were calculated using the computer program EstimateS 5.0 (Colwell 1997). In this study, the estimators used presence/absence data (incidence estimators), or relative abundance estimators (Table 1). All these models are non-parametric statistical applications, with the exception of the Michaelis-Menton model which is based simply on the parametric extrapolation of species accumulation curves.

Using the variables below (Table 2, taken from Chazdon *et al.* 1998), Estimates 5.0 calculated S_{est} for each of the estimators, where est is replaced by the name of the estimator. The input data matrix includes the number of individuals of every species (rows) observed within every sample (columns). A sample is defined as a 24-hr period, for the purposes of the program. For example, if a species was represented by a single individual among fifty-nine samples (a singleton), the corresponding species-row in the matrix would be all zeroes except for a single sample-column containing "one". Every species observed in the study is represented in this fashion: number of individuals observed within each sample. For the computation, the computer will select one random sample-day (column in matrix) from all samples pooled, compute S_{est} using a specific species richness estimator formula, and repeats this until 50 random selections are made. Estimated 5.0 terms this 50 randomizations. The mean S_{est} of the 50 randomizations serves as the first datapoint in the species accumulation curve. Next, the computer will select two random samples (from all samples pooled) 50 times, then three, four, … and so on, until all samples are selected at once (the final datapoint, S_{max}). The resulting data-set can be plotted vs. cumulative number of species to generate species accumulations for each richness estimator.

To construct an abundance-rank plot, species (x-axis) is plotted against the number of individuals represented by that species. The species represented by the most individuals is ranked “one”, the second is ranked “two”, and so on. The graph is often plotted logarithmically.

Assessing biological cost requires an examination of how many individuals must be collected in order to add a single species to the inventory. When starting the inventory the biological cost off adding one species to the inventory is one, since the first specimen will represent a new species. Later in the collecting period, drastically more individuals need to be collected in order to add a species to the inventory. This relationship can be represented in an exponential function. Number of individuals required to add a single species to the inventory (x-axis) vs. number of species recorded (y-axis).

Table 1. Estimators used in data analysis

Non-Parametric Estimators		Parametric Estimator
Incidence Estimators	Relative Abundance Estimators	Extrapolation Estimator
Chao 2, Jackknife 1, Jackknife 2, Bootstap, ICE (incidence-based coverage estimator)	Chao 1, ACE (abundance based coverage estimator)	Michaelis-Menton Model

Table 2. Definitions of variables used in the species richness estimators (from Chazdon *et al.* 1998)

S_{max}	Estimated species richness, where max is replaced in the formula by the name of the estimator
S_{obs}	Total number of species observed in all samples pooled
S_{rare}	Number of rare species (each with 10 or fewer individuals) when all samples are pooled
S_{abund}	Number of abundant species (each with more than 10 individuals) when all samples are pooled
S_{infr}	Number of infrequent species (each found in 10 or fewer samples)
S_{freq}	Number of frequent species (each found in more than 10 samples)
M	Total number of samples
m_{infr}	Number of samples that have at least one infrequent species
F_i	Number of species that have exactly i individuals when all samples are pooled (F_1 is the frequency of singletons, F_2 the frequency of doubletons)
Q_j	Number of species that occur in exactly j samples (Q_1 is the frequency of uniques, Q_2 the frequency of duplicates)
P_k	Proportion of samples that contain species k
N_{rare}	Total number of individuals in rare species
N_{infr}	Total number of incidences (occurrences) of infrequent species
C_{ace}	Sample abundance coverage estimator
C_{ice}	Sample incidence coverage estimator
γ^2_{ace}	Estimated coefficient of variation of the F_i's for rare species
γ^2_{ice}	Estimated coefficient of variation of the Q_i's for infrequent species

The estimators (from Chazdon *et al.* 1998)

Chao 1: An abundance-based estimator of species richness (Chao 1984)

$$S_{Chao1} = S_{obs} + \frac{F_1^{\,2}}{2F_2} \;.$$

The variance estimator that EstimateS uses to compute the standard deviation for Chao1 is

$$\mathrm{var}(S_{Chao1}) = F_2\left(\frac{G^4}{4} + G^3 + \frac{G^2}{2}\right)$$

where

$$G = \frac{F_1}{F_2} .$$

Chao 2: An incidence-based estimator of species richness (Chao 1987)

$$S_{Chao2} = S_{obs} + \frac{Q_1^{\,2}}{2Q_2} \;.$$

The variance estimator that EstimateS uses to compute the standard deviation for Chao 1 is the same as for Chao1 (above), but with

$$G = \frac{Q_1}{Q_2} .$$

Jackknife 1: First-order jackknife estimator of species richness (incidence-based) (Burnham and Overton 1978,1979; Heltshe and Forrester 1983)

$$S_{jack1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right) \;.$$

Jackknife 2: Second-order jackknife estimator of species richness (incidence-based) (Smith and van Belle 1984)

$$S_{jack2} = S_{obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right] .$$

Bootstrap: Bootstrap estimator of species richness (incidence-based) (Smith and van Belle 1984)

$$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}} (1-p_k)^m \;.$$

ACE: Abundance-based Coverage Estimator of species richness (Chao and Lee 1992; Chao, Ma, and Yang 1993)

First note that

$$S_{obs} = S_{rare} + S_{abund} \;.$$

The sample coverage estimate based on abundance data is

$$C_{ace} = 1 - F_1 / N_{rare} \ ,$$

where

$$N_{rare} = \sum_{i=1}^{10} iF_i \ .$$

Thus, this sample coverage estimate is the proportion of all individuals in rare species that are not singletons. Then the ACE estimator of species richness is

$$S_{ace} = S_{abund} + \frac{S_{rare}}{C_{ace}} + \frac{F_1}{C_{ace}} \gamma_{ace}^2$$

where γ_{ace}^2, which estimates the coefficient of variation of the F_i's, is

$$\gamma_{ace}^2 = \max\left\{ \frac{S_{rare}}{C_{ace}} \frac{\sum_{i=1}^{10} i(i-1)F_i}{(N_{rare})(N_{rare}-1)} - 1, 0 \right\} \ .$$

ICE: Incidence-based Coverage Estimator of species richness (Lee and Chao 1994)

First note that

$$S_{obs} = S_{infr} + S_{freq} \ .$$

The sample coverage estimate based on incidence data is

$$C_{ice} = 1 - Q_1 / N_{infr} \ ,$$

where

$$N_{infr} = \sum_{j=1}^{10} jQ_j \ .$$

Thus, the sample coverage estimate is the proportion of all individuals in infrequent species that are not uniques. Then the ICE estimator of species richness is

$$S_{ice} = S_{freq} + \frac{S_{infr}}{C_{ice}} + \frac{Q_1}{C_{ice}} \gamma_{ice}^2 \ .$$

where γ_{ice}^2, which estimates the coefficient of variation of the Q_j's, is

$$\gamma_{ice}^2 = \max\left\{ \frac{S_{infr}}{C_{ice}} \frac{m_{infr}}{(m_{infr}-1)} \frac{\sum_{j=1}^{10} j(j-1)Q_j}{(N_{infr})^2} - 1, 0 \right\} .$$

Results:

A total of 62 species and 635 individuals were collected using all methods. Mercury-vapor blacklighting was the most effective method used as every species sampled was collected at least once using the light. Malaise traps had only limited success as only one species was sampled. Hand collection netted two diurnal species of the genus *Aellopos*. Since these latter species were surprisingly observed the blacklight, the blacklighting species accumulation curve equals the combined species accumulation curve for all sampling methods (Figure 3). Twenty-two new species were collected in summer 2000 that were not sampled during my internship from January to May of 1999, when 47 species were collected. Seven species were missing from the 2000 sampling that I collected the previous year. More species were collected in the first month of this project than in the five months combined from 1999. Combining the results from both sampling years yields 69 species. There are confirmed reports of two additional species (one diurnal and one nocturnal,) in the area, so calculated species richness estimations of at least ***71 species*** would appear to be accurate.

The species accumulation curve (also known as a collector's curve) demonstrates a rapid rise in cumulative number of species collected, especially in the first week of the study (Figure 4). During the full moon, there was little species accrual as reflected by the asymptotes. Peak activity was realized at each new moon as the cumulative number of species observed increased at discreet intervals (Figure 4). The accumulation of individuals during the sampling period has many similarities to the observed species accumulation curve (Figure 4). This makes intuitive sense as rapid accumulations of individuals will more likely produce new species records in a biodiversity survey.

Figure 3. Efficacy of Sampling Methods. All of the species sampled in the biodiversity survey had at least one individual present at the Mercury-Vapor blacklight. Maliase traps sampled only one species and hand collection netted 2 diurnal species.

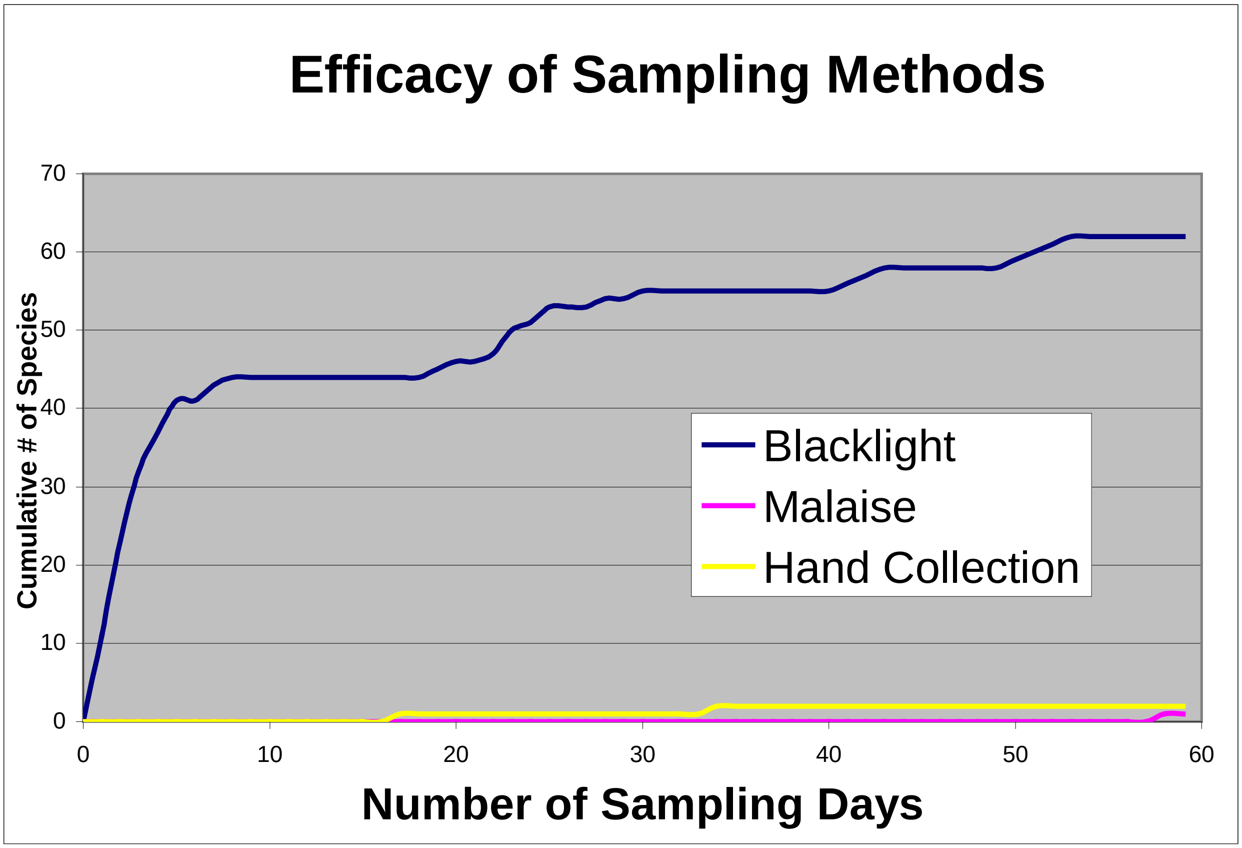
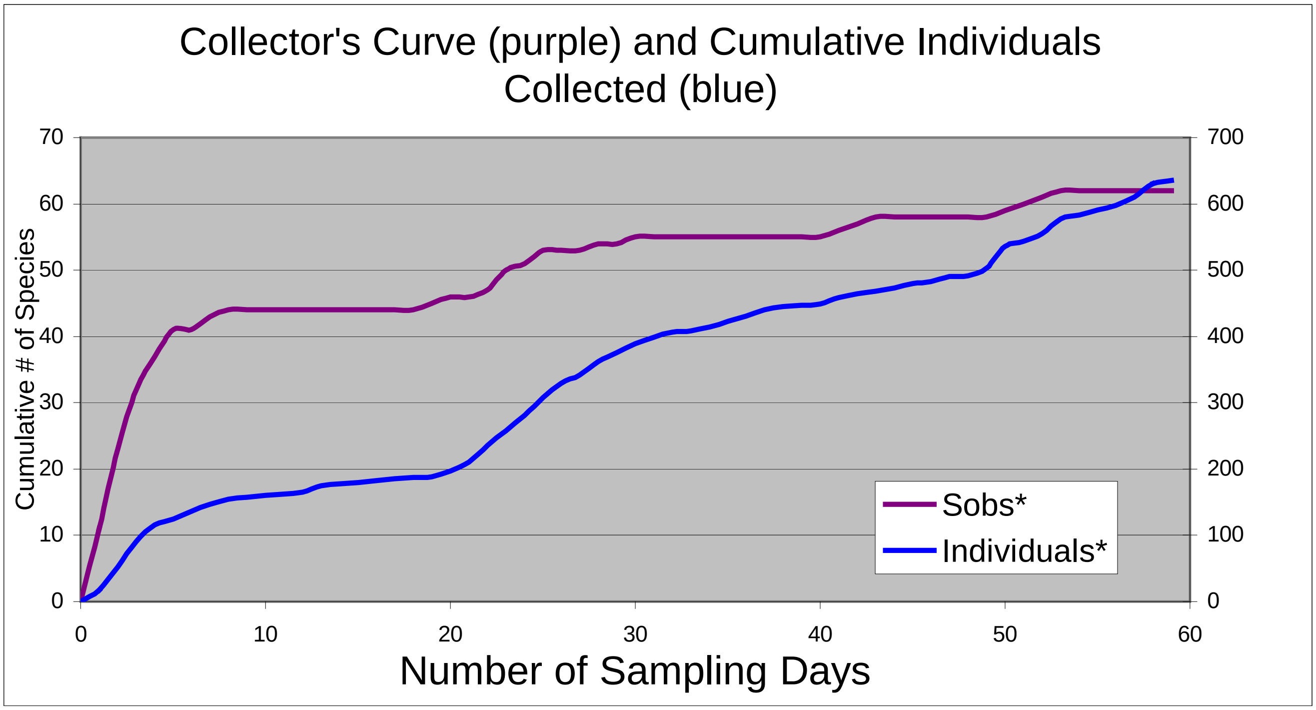

Efficacy of Sampling Methods
Cumulative # of Species
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
Number of Sampling Days
Blacklight
Malaise
Hand Collection

Figure 4. Observed Species Accumulation Curve (in purple) using combined sampling methods. New moon periods are emphasized by rapid accumulations of species and full moon events are represented by asymptotes. Observed accumulation of individuals tallied (in blue, scale on right) using combined sampling methods. The graph is representative of the activity patterns at the light as many individuals were tallied at new moon and very few at full moon. Note the curve is similar in appearance to be species accumulation curve. The graphs are plotted together to illustrate similarities in shape.


Collector's Curve (purple) and Cumulative Individuals Collected (blue)
Cumulative # of Species
70
60
50
40
30
20
10
0
700
600
500
400
300
200
100
0
0
10
20
30
40
50
60
Number of Sampling Days
Sobs*
Individuals*

Biological cost can be determined to analyze how many individuals need to be collected to add a single species to the inventory (Figure 5). Assessing this cost can be useful in determining at what point the survey should be stopped. If too many individuals need to be sacrificed in order to add a single species to the inventory, perhaps it is time to end sampling and rely on the statistical applications to estimate the remaining rare species. Also, it may not be worth the costs of man hours invested.

Constructing a species accumulation curve with random sampling order eliminates the bias of whether sampling starts at a new moon or full moon, and other environmental factors such as weather. A smoother species accumulation curve is demonstrated as the graph S_{obs} was computed by Estimates 5.0 using 50 randomizations, whereas graph S_{obs}* factors sampling in chronological order (Figure 6). The non-randomized curve is more useful at looking at trends in sampling order, where randomized sample order gives a more averaged curve. The two curves often intersected towards the end of lulls associated with full moons (Figure 6), therefore, the averaged curve effectively accounts for the difference for when the sample was taken. As the number of samples plotted increased, the more similar the two curves look in appearance.

The most common species sampled (78 individuals) was *Isognathus scryron*, while over half of the species included in the survey were represented by four individuals or less, as demonstrated in the abundance-rank plot (Figure 7). These rare species serve as the basis of the non-parametric species richness estimators. Ratios of rare species and frequency of occurrence in samples comprise the estimate of species missed in the inventory. The estimate summed with the observed species richness will yield the overall estimate for true species richness.

Figure 5. Biological cost to add a single species to the inventory. The trendline illustrates the exponential function

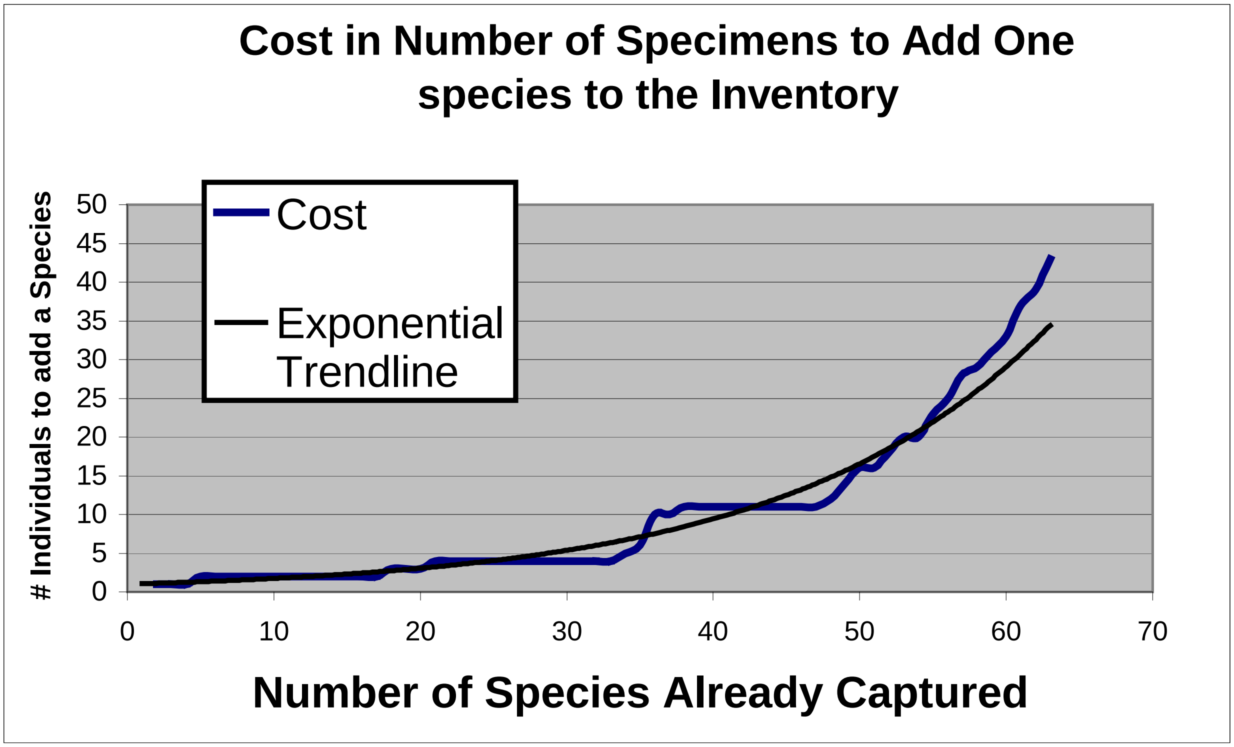

Cost in Number of Specimens to Add One species to the Inventory
Cost
Exponential Trendline
Individuals to add a Species
50
45
40
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
Number of Species Already Captured

Figure 6. Species accumulation curve for randomized sampling order (in blue). Fifty randomizations were made at each data-point. Example: for total samples (3), three samples were randomly selected 50 times (without replacement). S_{obs} was calculated at each randomization and averaged for the data-point.

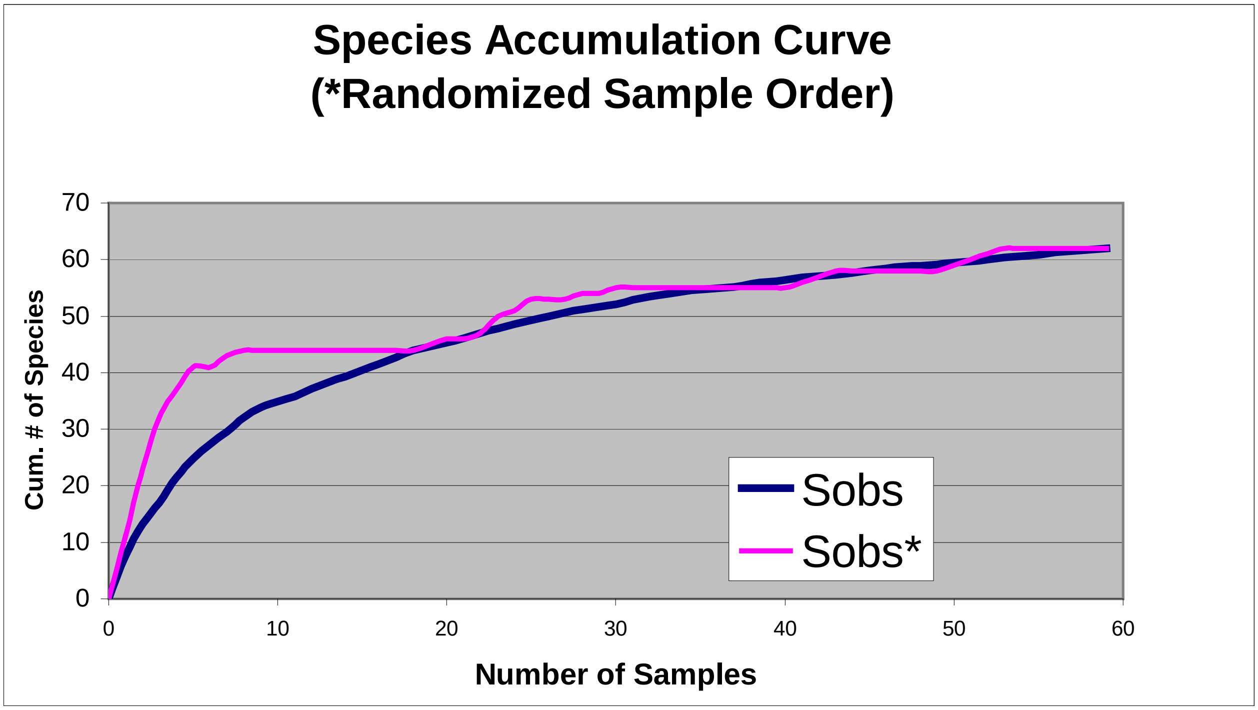
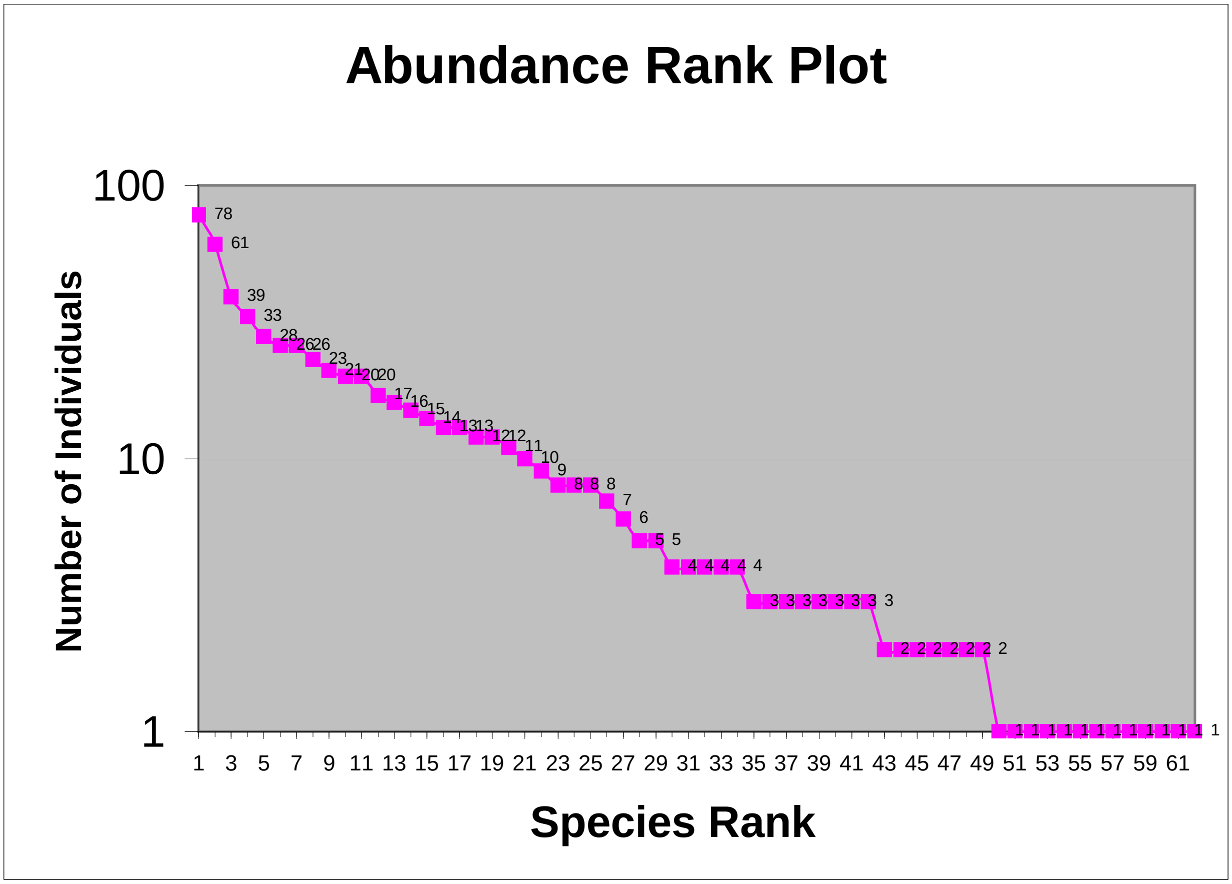

Species Accumulation Curve
(*Randomized Sample Order)
Cum. # of Species
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
Number of Samples
Sobs
Sobs*

Figure 7. Abundance Rank Plot for all species surveyed in the investigation. The most common species is ranked first. Note the logarithmic scale.


Abundance Rank Plot
Number of Individuals
100
10
1
Species Rank
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49 51 53 55 57 59 61
78
61
39
33
28
26 26
23
21
20 20
17
16
15
14
13 13
12 12
11
10
9
8 8 8
7
6
5 5
4 4 4 4 4
3 3 3 3 3 3 3 3
2 2 2 2 2 2 2
1 1 1 1 1 1 1 1 1 1 1 1 1

Results of Species Richness Estimators:

True species richness was estimated using a variety of statistical-based estimators and compared to observed species richness, S_{obs}, when all samples are pooled (Colwell 1997). The first figure compares all the species richness estimators to the observed species accumulation curve (Figure 8). The parametric Michaelis-Menton curves and the Bootstrap curve fail to estimate at least 71 species (Figure 9), the minimum acceptable estimate, since *at least* that number have been recorded from combined 1999 and 2000 sampling. All the non-parametric estimators, with the exception of the Bootstrap method, performed well using the 59 sampling days from summer 2000 data. Estimates range from 72 – 81 species.

The Chao 1 and Chao 2 curves estimate 74 and 73 species respectively (Figure 10a). Chao 1 takes into account abundance data and estimates more species than does Chao 2, which uses incidence (presence/absence of each species) within each sample. Error bars denote +/- 1 standard deviation at each sample size (Fig. 10b). There is significant overlap indicating little difference in using abundance or incidence data to form the curves.

The Jackknife curves use incidence data and estimate 76 (Jackknife 1) and 81 (Jackknife 2) species (Figure 11a). Due to the complexity of the equation for Jackknife 2, the standard deviation cannot be calculated and formulas are not available in the literature. However, +/- 1 standard deviation is shown for Jackknife 1 (Figure 11b).

The abundance-based coverage estimator (ACE) and incidence-based coverage estimator (ICE) estimate 72.29 and 74.06 species respectively (Figure 12a). Note that in this instance the incidence-based estimator estimates more species. Error bars denote 95% confidence intervals for the ICE and +/- 1 standard deviation for ACE (Figure 12b). Final estimates (last datapoint on each graph) are shown in bar graph form for every estimator used (Figure 13).

Figure 8. Results of all true species richness estimators used in the study compared to observed species accumulation curve. Fifty randomizations were made at each sample size.

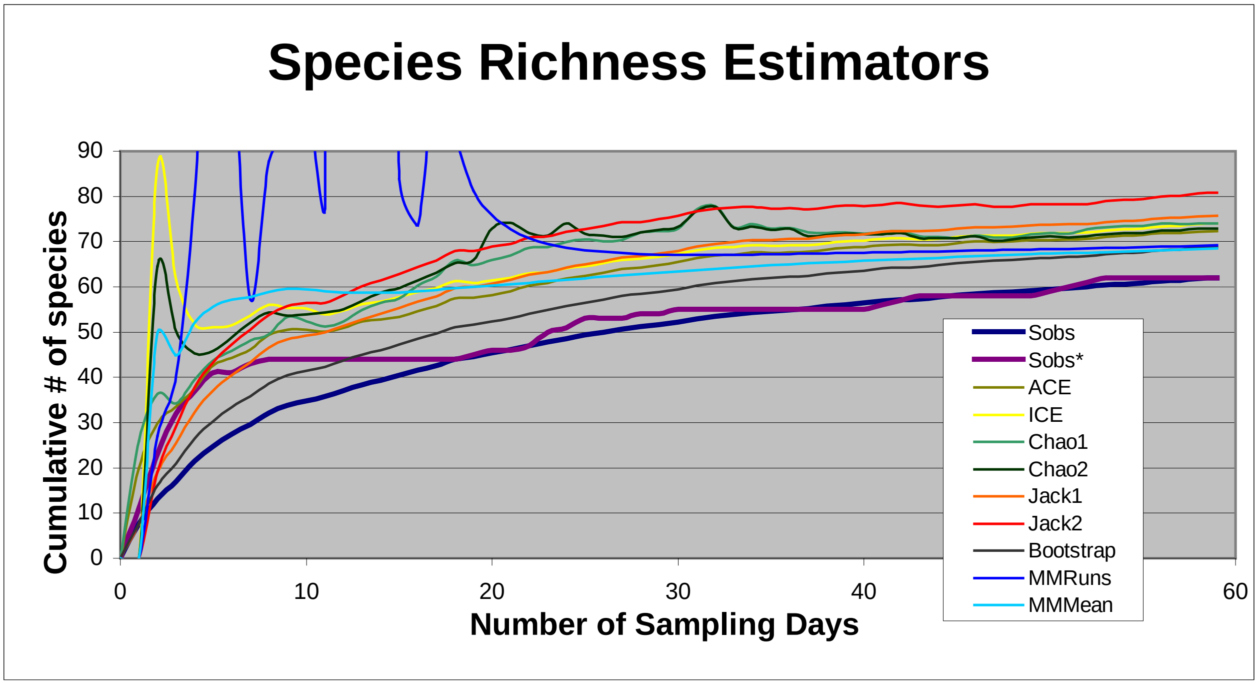
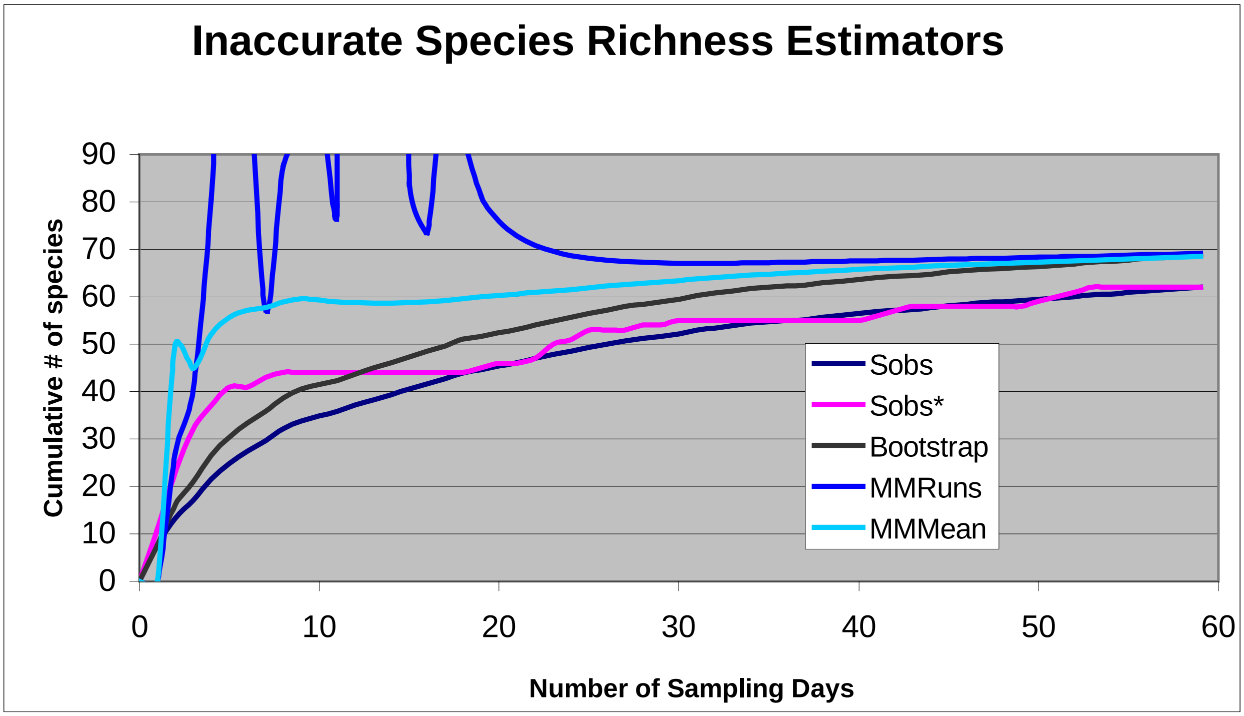
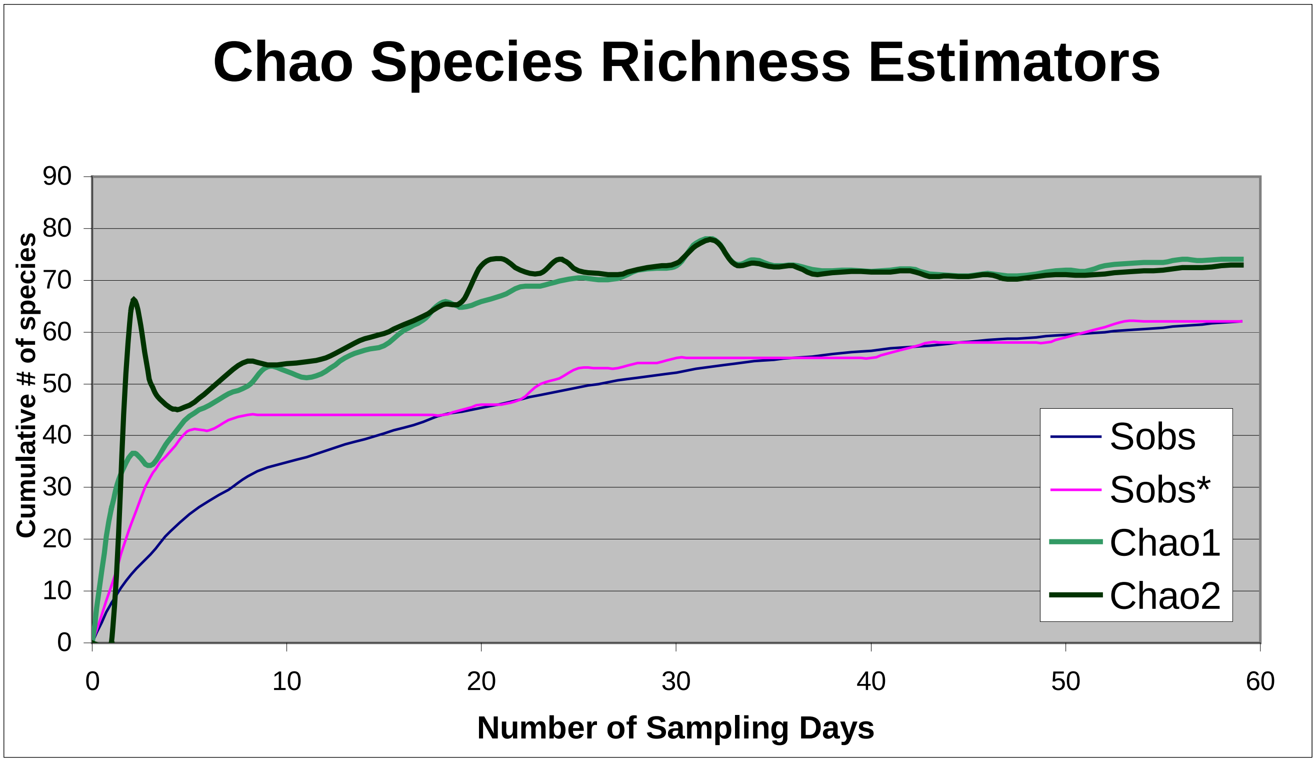
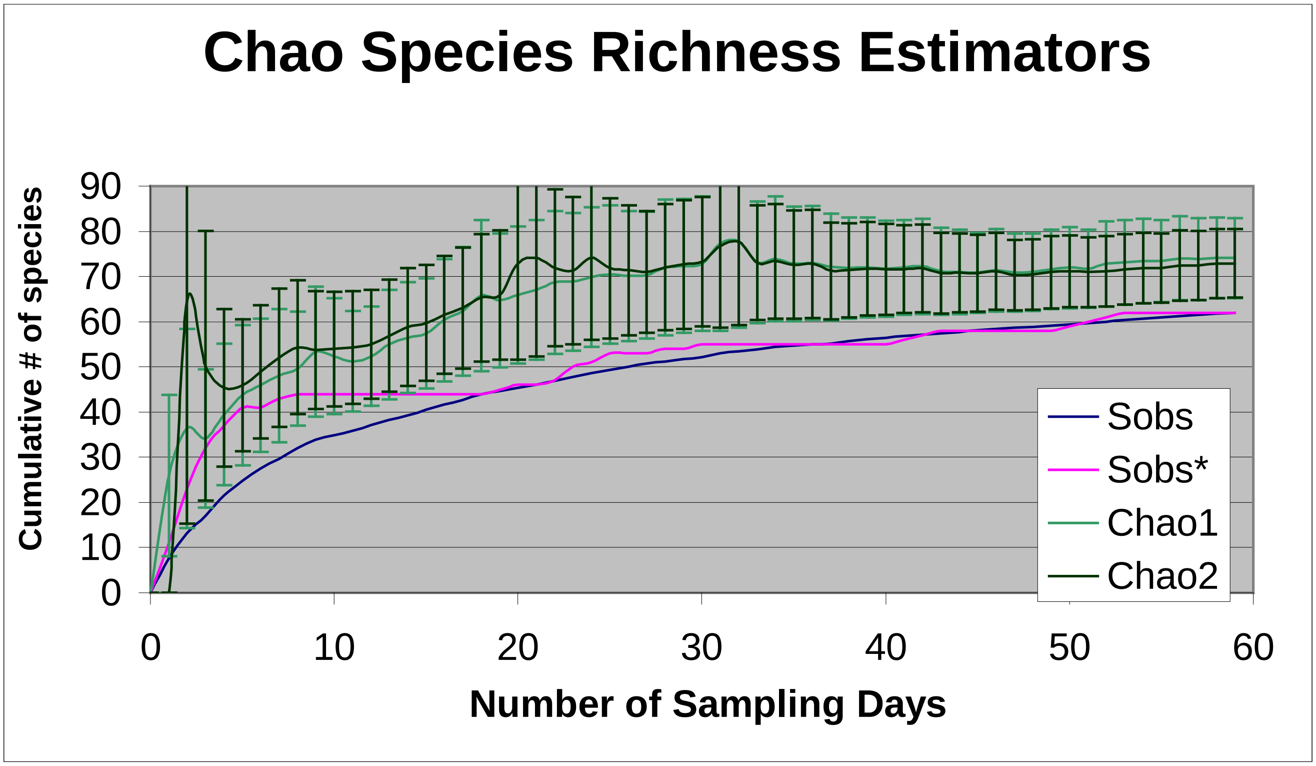

Species Richness Estimators
Cumulative # of species
0
10
20
30
40
50
60
70
80
90
Number of Sampling Days
0
10
20
30
40
60
Sobs
Sobs*
ACE
ICE
Chao1
Chao2
Jack1
Jack2
Bootstrap
MMRuns
MMMean

Figure 9. Species accumulation curves for Michaelis-Menton Means, Michaelis-Menton Runs, and Bootstrap. The Michaelis-Menton curves are parametric estimators and are traditionally inaccurate for arthropod groups. The Bootstrap estimator is the most conservative non-parametric estimator. All estimate less than 70 species. The two species accumulation curves of S_{obs}-randomized sample order and S_{obs}-non-randomized sampling order are included for reference.

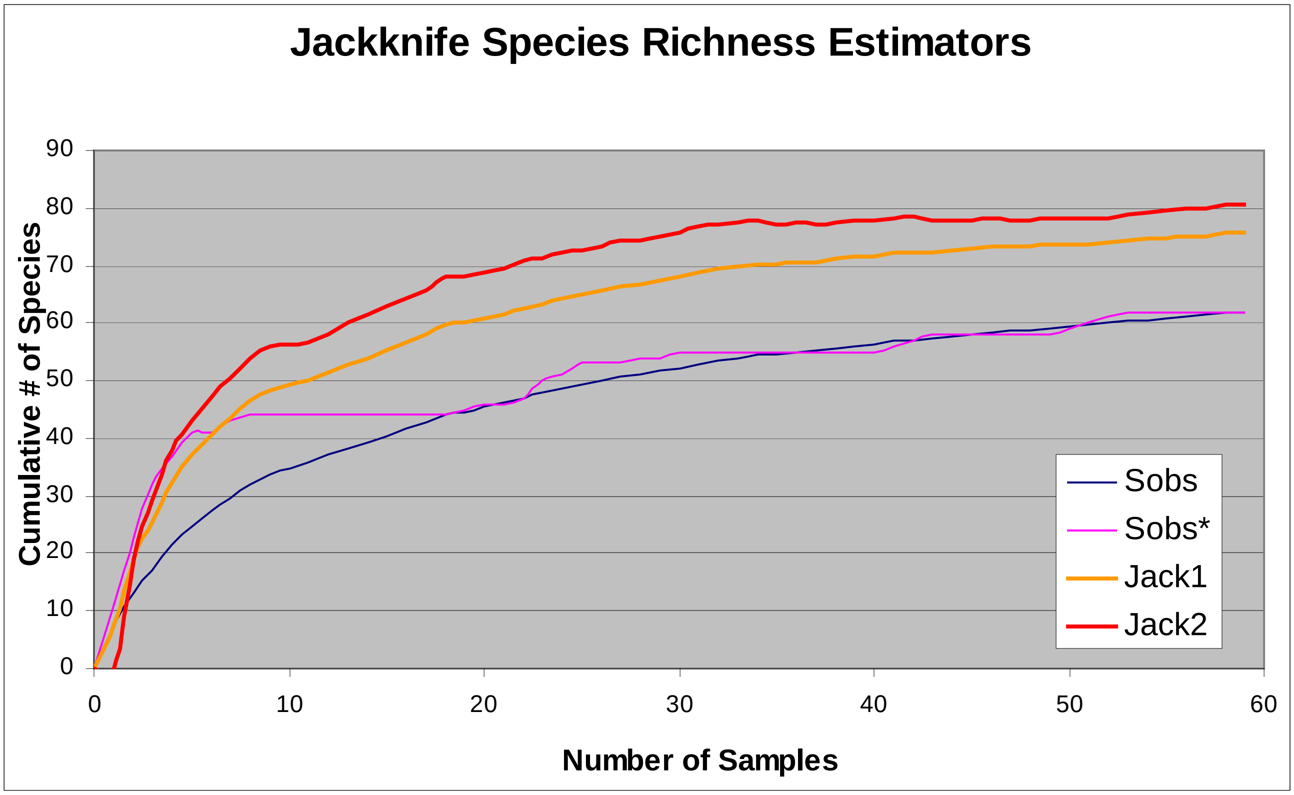

Inaccurate Species Richness Estimators
Cumulative # of species
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
Number of Sampling Days
Sobs
Sobs*
Bootstrap
MMRuns
MMMean

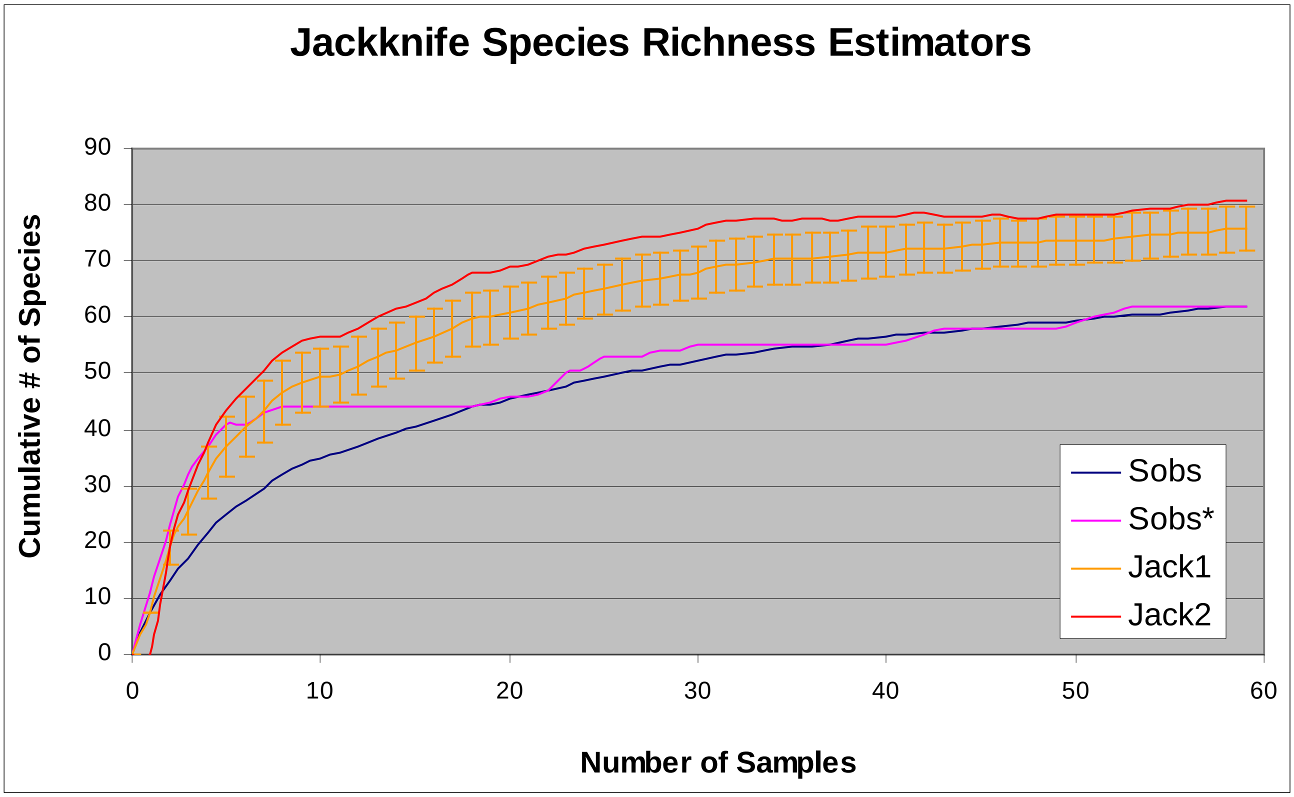
Figures 10a & 10b. Chao 1 & 2 Species accumulation curves. The two species accumulation curves of S_{obs}-randomized sample order and S_{obs}-non-randomized sampling order are included for reference.


Chao Species Richness Estimators
Cumulative # of species
0
10
20
30
40
50
60
70
80
90
Number of Sampling Days
0
10
20
30
40
50
60
Sobs
Sobs*
Chao1
Chao2

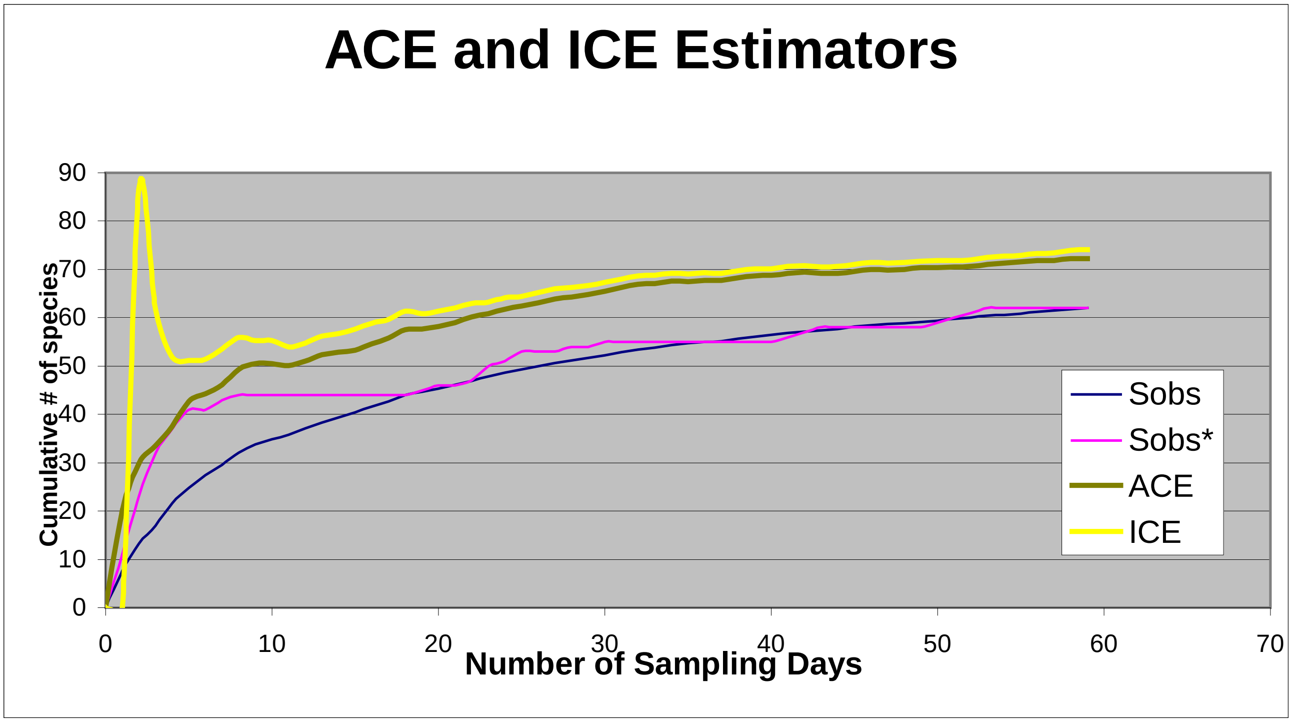

Chao Species Richness Estimators
Cumulative # of species
0
10
20
30
40
50
60
70
80
90
Number of Sampling Days
0
10
20
30
40
50
60
Sobs
Sobs*
Chao1
Chao2

Figures 11a & 11b. Jackknife1 and Jacknife2 species accumulation curves. The two species accumulation curves of S_{obs}-randomized sample order and S_{obs}-non-randomized sampling order are included for reference.


Jackknife Species Richness Estimators
Cumulative # of Species
Number of Samples
0
10
20
30
40
50
60
70
80
90
0
10
20
30
40
50
60
Sobs
Sobs*
Jack1
Jack2


Jackknife Species Richness Estimators
Cumulative # of Species
Number of Samples
0
10
20
30
40
50
60
70
80
90
0
10
20
30
40
50
60
Sobs
Sobs*
Jack1
Jack2

Figures 12a & 12b. ACE and ICE species accumulation curves. The two species accumulation curves of S_{obs}-randomized sample order and S_{obs}-non-randomized sampling order are included for reference. Note: ICE is the only estimator in which the statistics are developed enough to calculate a 95% CI


ACE and ICE Estimators

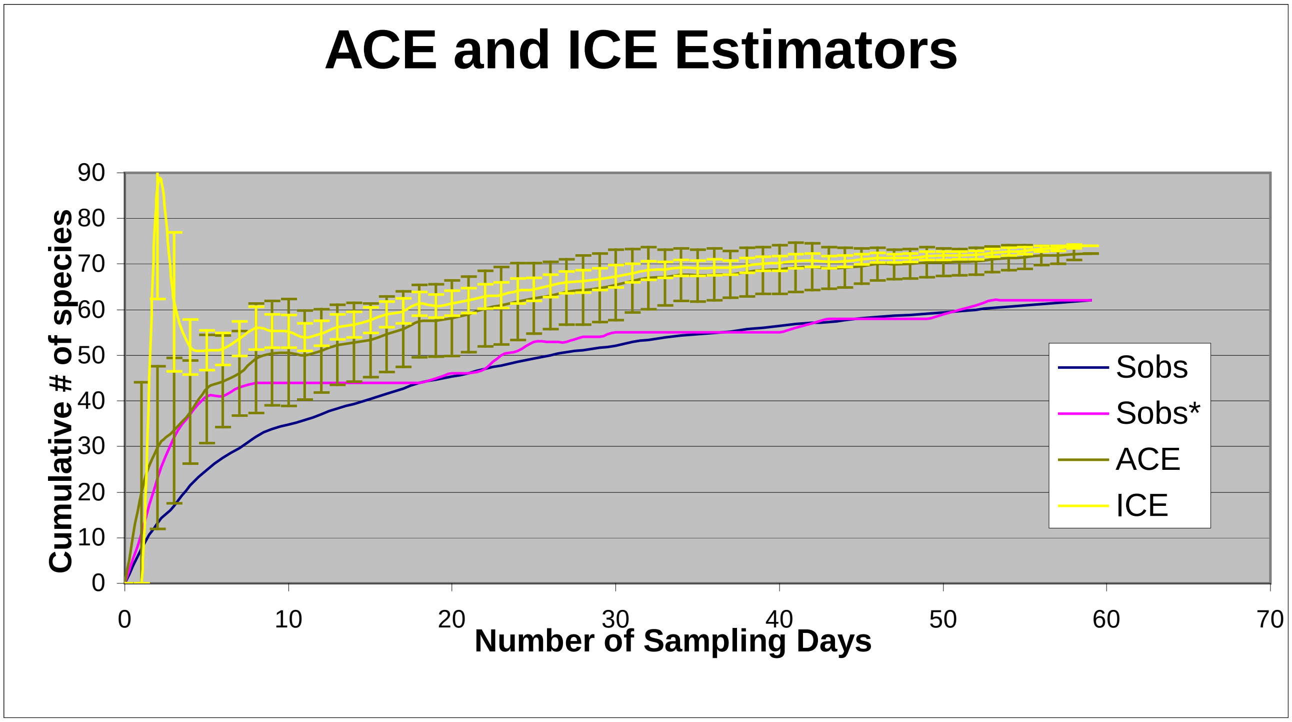
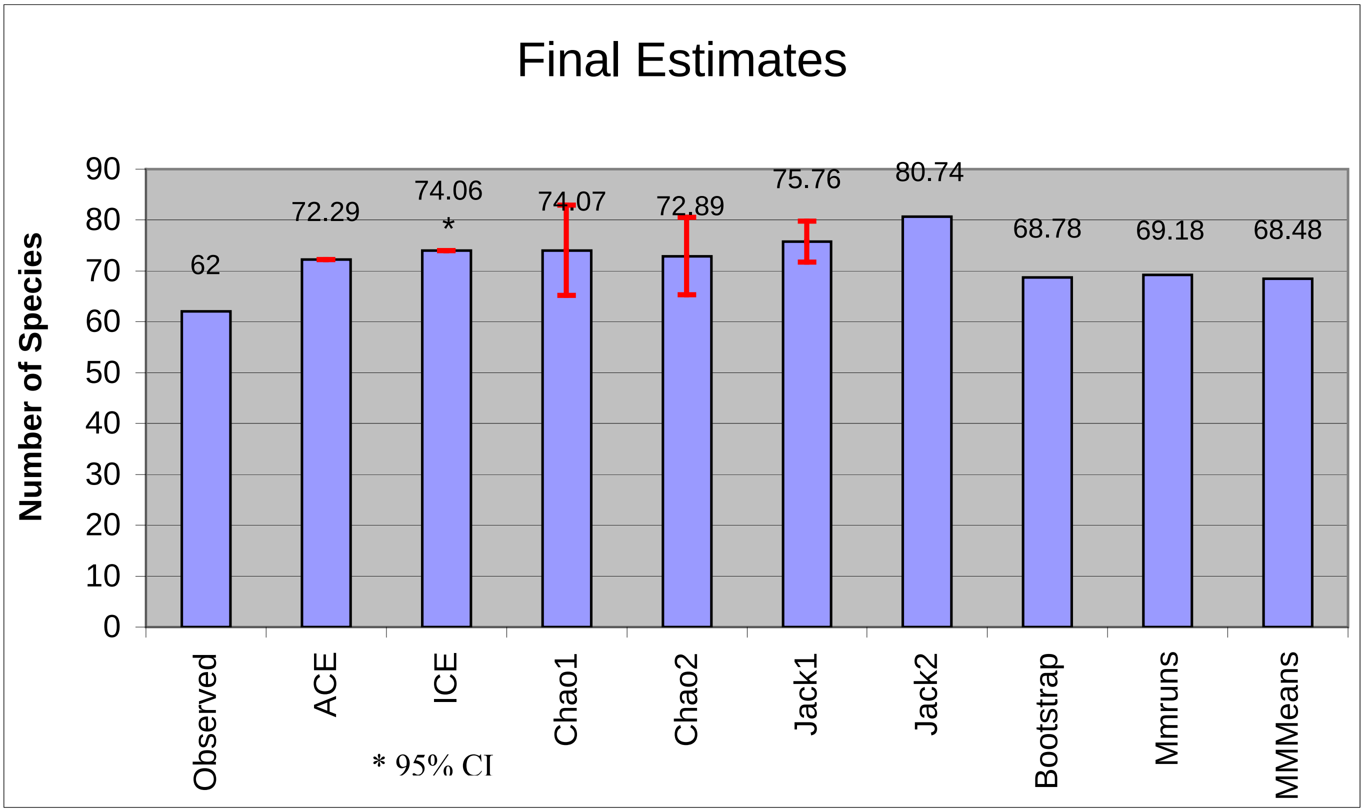

ACE and ICE Estimators

Figure 13. Overall estimates for all estimators used (error bars reflect +/- 1 Standard deviation unless otherwise noted)


Final Estimates
Number of Species
90
80
70
60
50
40
30
20
10
0
62
72.29
74.06
*
74.07
72.89
75.76
80.74
68.78
69.18
68.48
Observed
ACE
ICE
Chao1
Chao2
Jack1
Jack2
Bootstrap
Mmruns
MMMeans
* 95% CI

Discussion:

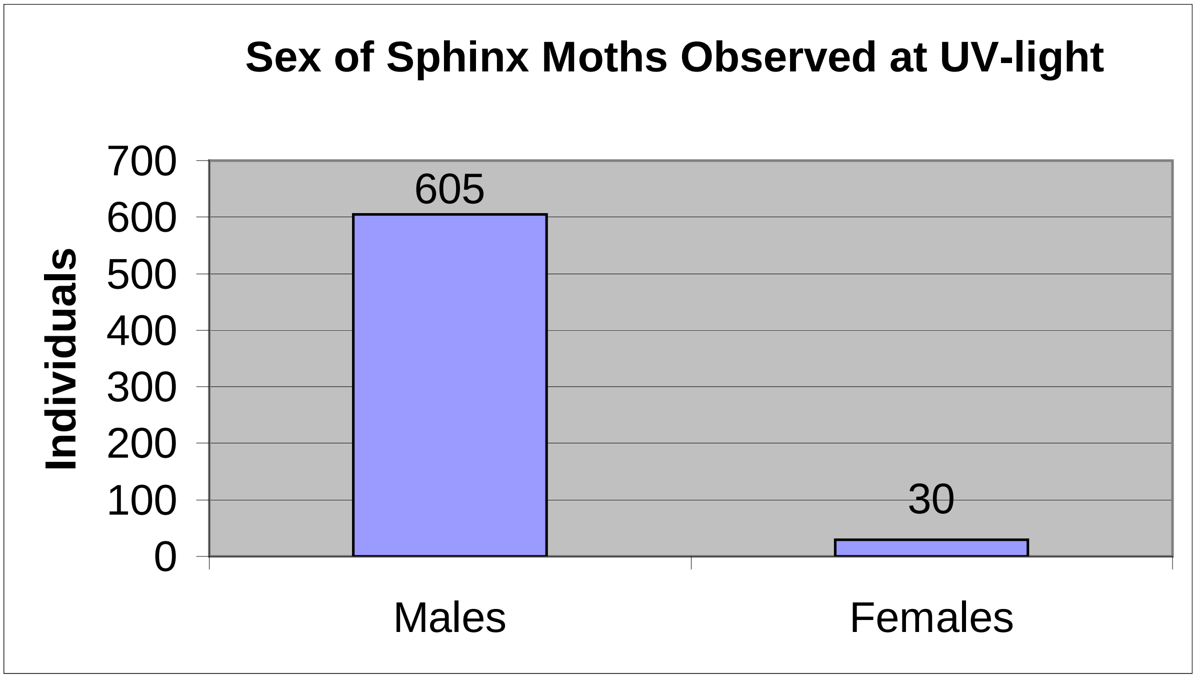
A total of 62 species were observed in this investigation. Based on the sampling data, which takes into account the relative abundance (for abundance-based estimators) or presence/absence (for incidence-based estimators) of each individual species within each sample, most of the species richness estimators estimate the true species richness to be in the range of 72-76 species. The true species richness estimators are strongly supported by the fact that seven species recorded in Jan – May 1999 were not recorded this summer, thereby increasing the observed species richness to 69 species. Two more miscellaneous reports bring the total to 71 species. The absence of these combined nine species from 2000 sampling can be used to examine the reliability of true species richness estimates. Any species estimators that have estimated 71 or more species have made an accurate estimate to account for these species. Only the Bootstrap (69 species) and Michaelis Menton curves (Runs – 69 species, Means – 68 species) estimators fail to estimate at least 71 species. There are probably only a few species (in addition to the nine species) missed by the sampling methods. There is one species (*Amphimoea walkeri*) I confirmed at INBio that is not attracted to UV-light and is indigenous only to the lowland rainforests in Costa Rica (J. Corrales pers. comm). I believe I have seen *Amphimoea walkeri* (wingspan 20 cm, proboscis length 30+ cm) visiting papaya and other long tubular flowers, but I was unable to net it by hand. Diurnal sphinx moths were captured at the UV-light traps, as both *Aellopus titan* and *A. fadus* were collected, a diurnal genus. Ross Ballard, the station's director, captured *Eupyrrhoglossum sagra*, another diurnal species, in December 2000. Based on results from my strict and structured inventories, and the performance of the estimators, I estimate true species richness to be between 72-76 species. According to the scientific literature, most species richness estimators tend to overestimate species richness

(McKamey 1999), and though the reliability for biological data are still being tested (Coddington *et al.* 1996, Silva and Coddington 1996, Chazdon *et al.* 1998), I believe the Chao1, Chao2, Jackknife1, Jackknife2, ACE, and ICE estimators to be accurate as all estimate true species richness to be between 72-76 species.

Of all the estimators, I believe Chao2 performed the best. The species accumulation curve had the most rapid rise to 72-76 species, estimating that in only 21 samples (Figure 10a). According to Chazdon (1998), the ideal species richness estimator should rapidly rise to S_{max}, and remain relatively constant. Chao2 reaches the estimate of about 73 species quickly, and when all 59 samples are included, continues to estimate 73 species.

I expected to be able to estimate population sizes using mark/recapture techniques at lights, but numerous biases were observed which prevented me from doing so. Some species are more prone to attraction to UV-light sources than others. I expected to collect no diurnal species at the blacklight, but both suspected diurnal species appeared on some nights in multiple numbers. Perhaps they are not entirely diurnal. There is also a strong sex-ratio bias with all species observed. More than 90% of the individuals observed at lights were males (Figure 14). Looking into the behavior and natural history of the hawkmoths can provide explanations for these phenomena. Males are likely to be on the wing in search of females to mate with and are more likely to be intercepted by the light. Females, on the other hand are more likely to be in the forest laying eggs, and not in more traditional flyways such as the canals. Equal numbers of males and females are captured using Malaise traps (Owen 1983), but not enough specimens were captured this summer to confirm those findings. There is no sex-ratio bias at UV-lights during migratory events in the mountain passes of Costa Rica at the beginning of the dry season

Figure 14. Sex-ratio bias of Sphinx moths at the blacklight. Males were more prone for attraction to UV-light than females


Sex of Sphinx Moths Observed at UV-light
Individuals
700
600
500
400
300
200
100
0
605
30
Males
Females

for Costa Rica's dry, deciduous forests (Janzen 1983). At this time, entire populations that do not remain dormant in the dry forest will move across the continental divide to preferential habitat in the wet forests. It may be possible to estimate sizes of the moving populations during these migratory events.

Contrary to expectations, peak sphingid activity occurred during unsettled or rainy weather. I propose two explanations for the phenomenon; (1) during rainy weather sphinx moths are less likely to be preyed upon by their chief predator, bats. The rain may hinder the bats' ability to effectively echolocate during moderate-heavy rains (Wickham 2000 unpublished). I witnessed higher activity all summer long during the rains and the moths (surprisingly) had no difficulty navigating the rain. (2) Sphinx moths require a high caloric intake of energy (much like a hummingbird). Rainy weather may decrease the availability of food sources. The rain may change the time at which a night-blooming flower opens. The alteration in the nightly cycle may force moths to forage in haste, or at a time of night they are not accustomed to (most species have a peak activity time each night). The confusion, along with the impending inclement weather, may increase the probability that moths may be intercepted by the light.

Species accumulation curves are a good indicator for assessing the completeness of an inventory. In conservation biology as well as biodiversity surveys, it is important to know when further sampling effort will not yield any more species. Inventories must be conducted in the most cost-efficient manner, both in money and time. Given the deforestation rates, efficient sampling is imperative as many species become extinct before the scientific community discovers them. Achieving the maximum number of species per unit of sampling effort an important objective. During the two months of sampling, there was a rapid rise of species accumulation, followed by a steady decrease in accumulation to an asymptote-like line. Instead of sampling indefinitely to achieve true species richness, the statistical estimators effectively measured richness. In this study, I believe the species richness estimates to be accurate. The experiment could have been continued for another three or four months without any drastic changes in observed species richness. In this case, the species richness estimators served well to estimate the remaining rare species and ultimately true species richness.

The data from this experiment can be used to qualitatively compare species richness in the Atlantic lowland rainforests of Costa Rica to other habitats within the Neotropics. The sampling procedures can also be repeated at the same locality at a future date in order to monitor the community and to assess changes over time. I recommend sampling for two complete lunar cycles in order to generate enough data to perform the statistical measures of S_{max} (true species richness).

Critiquing the estimators, I observed little difference between the performance of the incidence and abundance-based estimators. For example, Chao 1, an abundance-based estimator estimated 74.07 species, while the incidence-based estimator, Chao 2, estimated 72.89 species. The results were almost opposite using the abundance/incidence coverage estimators (ACE/ICE). The incidence-based estimator estimates 74.06 species, while the abundance-based estimator estimates 72.29 species. I expected the abundance-based estimators to be more accurate, but the results are nearly indistinguishable from the incidence-based estimators. In examining the raw data, I discovered a simple explanation for their equatable performance; their respective measures of rarity were almost exactly the same. When all samples are pooled, the abundance-based estimators had 13 singletons (13 species that were represented by only one individual), and seven doubletons (seven species that were represented by only two individuals). Comparably, the incidence estimators had 14 uniques (14 species that occurred in exactly one sample), and nine duplicates (9 species that occurred in exactly two samples). For example, the Chao estimators use calculations of singletons^2/2 x doubletons (abundance-based), and uniques^2/2 x duplicates (incidence-based) to estimate remaining rare species. [$13^2/2$ x 7] and [$14^2/2$ x 9] are 12.07 and 10.89 respectively. This is not a drastic difference, as the difference is approximately one species.

I perceive the equatable performance as an indicator of their reliability as estimators. A common theme in biology is that there are many ways of measuring the same phenomenon, in this case true species richness, and many will produce the same end result. The fact that species richness estimators are producing similar results suggests reliability. The true species richness value is in itself a variable number with the movement of species in space and time. There are indeed many ways to measure the exact same thing and I believe that biologists should not rely on one single estimator. Individual estimators have a unique measure of rarity, and the comparison of their performances is useful. Especially in the sense that these estimators are relatively new in the literature and are still being tested for reliability with biological data. Estimators will continue to be developed and modified to maximize reliability. We can also use some estimators to our advantage. For conservation purposes, it may be in our best interest to use the least conservative species richness estimators, within reasoning of course. It may be unethical to inflate biodiversity numbers.

For future biodiversity inventories, I recommend performing incidence-based methods of recording data. The inventory will be easier to perform, especially since there is no counting of individuals. The biodiversity survey can be continued until (1) species accumulation curves are at near-asymptote levels and (2) the biological cost of adding a single species to the inventory reaches an unreasonable level.

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Appendix A: Species list for Cano Palma Biological Station

Family Sphingidae - 71 species			sampling		
Genus species	Species Rank	Individuals	1999	2000	Other
Adhemarius gannuscus (Stoll, 1790)	4	33	X	X	
Adhemarius ypsilon (Rothschild & Jordan 1903)	14	15	X	X	
Aellopus fadus (Cramer, 1775)	30	4		X	
Aellopus titan (Cramer, 1777)	22	9		X	
Agrius cingulata (Fabricius, 1775)	50	1		X	
Amphimoea walkeri (Boisduval, [1875])	NA	0			X
Callionima denticulata (Shaus, 1895)	NA	0	X		
Callionima falcifera (Gehlen, 1943)	51	1		X	
Callionima nomius (Walker, 1856)	52	1		X	
Callionima parce (Fabricius, 1775)	53	1		X	
Cocytius antaeus (Drury, 1773)	43	2		X	
Cocytius beezlebuth (Boisduval, [1895])	35	3		X	
Cocytius duponchel (Poey, 1832)	15	14	X	X	
Cocytius lucifer Rothschild and Jordan, 1903	44	2	X	X	
Enyo lugubris (Linnaeus, 1771)	36	3	X	X	
Enyo ocypete (Linnaeus, 1758)	6	26	X	X	
Erinnyis alope (Drury, 1773)	31	4	X	X	
Erinnyis crameri (Schaus, 1898)	54	1		X	
Erinnyis ello (Linnaeus, 1758)	37	3	X	X	
Erinnyis oenotrus (Cramer, 1780)	16	13	X	X	
Eumorpha anchemolus (Cramer, 1779)	23	8	X	X	
Eumorpha capronnieri (Boisduval, [1875])	38	3	X	X	
Eumorpha fasciatus (Sulzer, 1776)	NA	0	X		
Eumorpha labruscae (Linnaeus, 1758)	NA	0	X		
Eumorpha megaeacus (Hübner, [1819])	28	5		X	
Eumorpha obliquus (Rothschild and Jordan, 1903)	24	8	X	X	
Eumorpha phorbas (Cramer 1775)	13	16	X	X	
Eumorpha satellita (Linnaeus, 1771)	55	1		X	
Eumorpha vitis (Linnaeus, 1758)	56	1	X	X	
Eupyrrhoglossum sagra (Poey, 1832)	NA	0			X
Hemeroplanes ornatus Rothschild, 1894	26	7	X	X	
Isognathus scyron (Cramer, 1780)	1	78	X	X	
Madoryx plutonius (Hübner, [1819])	39	3	X	X	
Manduca albiplaga (Walker 1856)	57	1	X	X	
Manduca florestan (Stoll, 1782)	7	26	X	X	
Manduca occulta (Rothschild and Jordan, 1903)	NA	0	X		
Manduca pellenia (Herrich-Schäffer, [1854])	10	20	X	X	
Manduca rustica (Fabricius, 1775)	45	2		X	
Manduca sexta (Linnaeus, 1763)	NA	0	X		
Manduca sp. (possible new species)	58	1		X	
Neococytius cluentius (Cramer, 1775)	NA	0	X		
Nyceryx coffeae (Walker, 1856)	59	1		X	
Nyceryx stuarti (Rothschild, 1894)	40	3		X	
Oryba kadeni (Schaufuss, 1870)	41	3		X	

Genus species	Species Rank	Individuals	1999	2000	Other
Pachygonidia drucei (Rothschild & Jordan, 1903)	60	1		X	
Pachylia darceta Druce, 1881	11	20	X	X	
Pachylia ficus (Linnaeus, 1758)	32	4	X	X	
Pachyloides resumens (Walker, 1856)	33	4	X	X	
Perigonia lusca (Fabricius, 1777)	46	2	X	X	
Phryxus caicus (Cramer, 1777)	61	1		X	
Protambulyx eurycles (Herrich-Schäffer, [1854])	21	10	X	X	
Protambulyx strigilus (Linnaeus, 1771)	3	39	X	X	
Pseudosphinx tetrio (Linnaeus, 1771)	62	1	X	X	
Xylophanes amadis (Cramer, 1782)	18	12	X	X	
Xylophanes anubus (Cramer, 1777)	12	17	X	X	
Xylophanes belti (Druce, 1878)	47	2		X	
Xylophanes ceratomioides (Grote and Robinson, 1867)	48	2		X	
Xylophanes chiron nechus (Drury, 1773)	19	12	X	X	
Xylophanes guianensis (Rothschild, 1894)	17	13	X	X	
Xylophanes libya (Druce, 1878)	27	6	X	X	
Xylophanes loelia (Druce, 1878)	2	61	X	X	
Xylophanes neoptolemus (Cramer, 1878)	29	5		X	
Xylophanes pistacina (Boisduval, [1875])	NA	0	X		
Xylophanes pluto (Fabricius, 1777)	34	4	X	X	
Xylophanes porcus (Hübner, [1823])	5	28	X	X	
Xylophanes tersa (Linnaeus, 1771)	8	23	X	X	
Xylophanes thyelia (Linnaeus, 1758)	9	21	X	X	
Xylophanes titana (Druce, 1878)	42	3	X	X	
Xylophanes tyndarus (Boisduval, [1875])	49	2	X	X	
Xylophanes undata Rothschild & Jordan, 1903	20	11	X	X	
Xylophanes zurcheri (Druce, 1894)	25	8		X	

Appendix B: species accounts

The following section is an alphabetized species listing with color pictures, sampling accounts, live weights of individuals recorded at lights, and distribution maps of the individuals species based on specimens in the research collection at INBio collected from 1990-2000.

All maps are courtesy of INBio and can be found on the World Wide Web. All pictures were taken by the author.

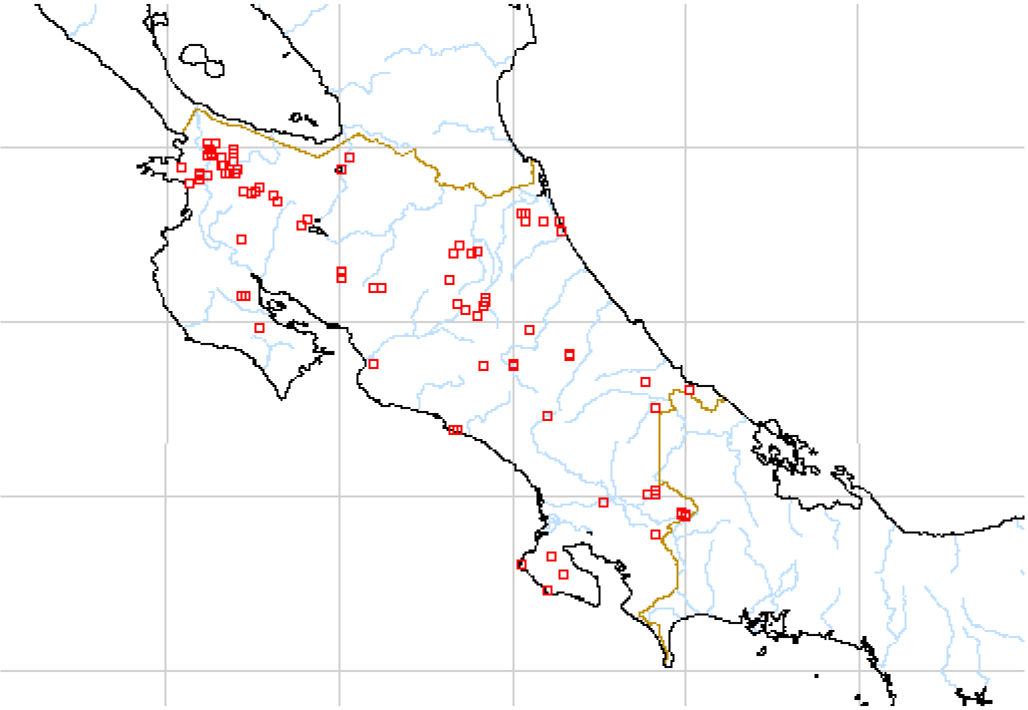
Adhemarius gannuscus
(Stoll, 1790)

Species Rank: 4
Individuals: 33 (1♀)

1999 & 2000 Sampling

Live weights (g) moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.81	0.14	10			



INBio: 614 specimens, 6 from Tortuguero (1♀)

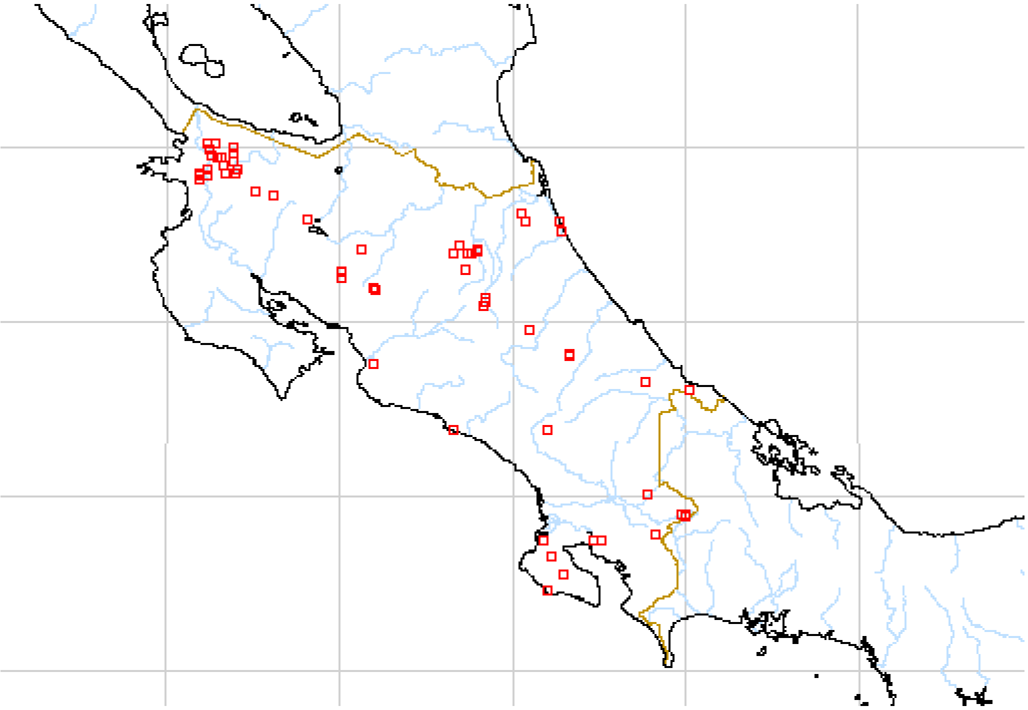
Adhemarius ypsilon
(Rothschild & Jordan, 1903)

Species Rank: 14
Individuals: 15 (1♀)

1999 & 2000 Sampling

Live weights (g) moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.18	0.13	8	1.7		1

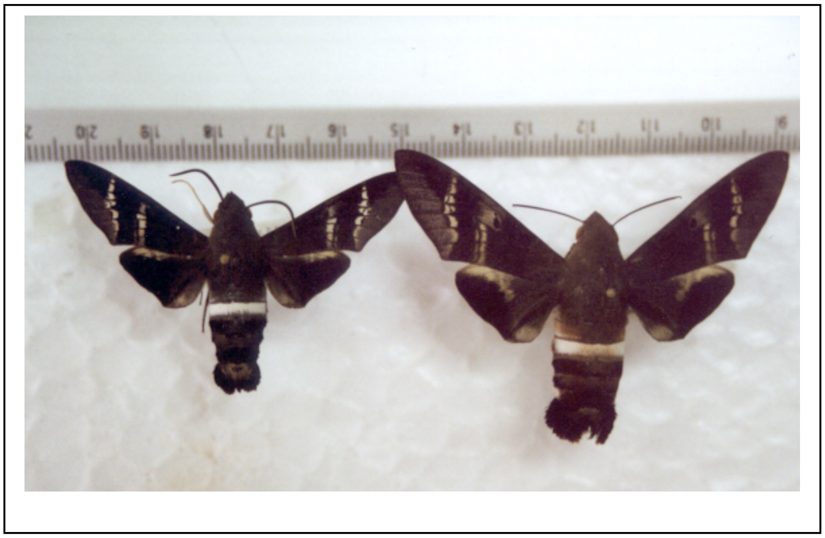


INBio: 312 specimens, 6 from Tortuguero (1♀)

Aellopos fadus
(Cramer, 1775)

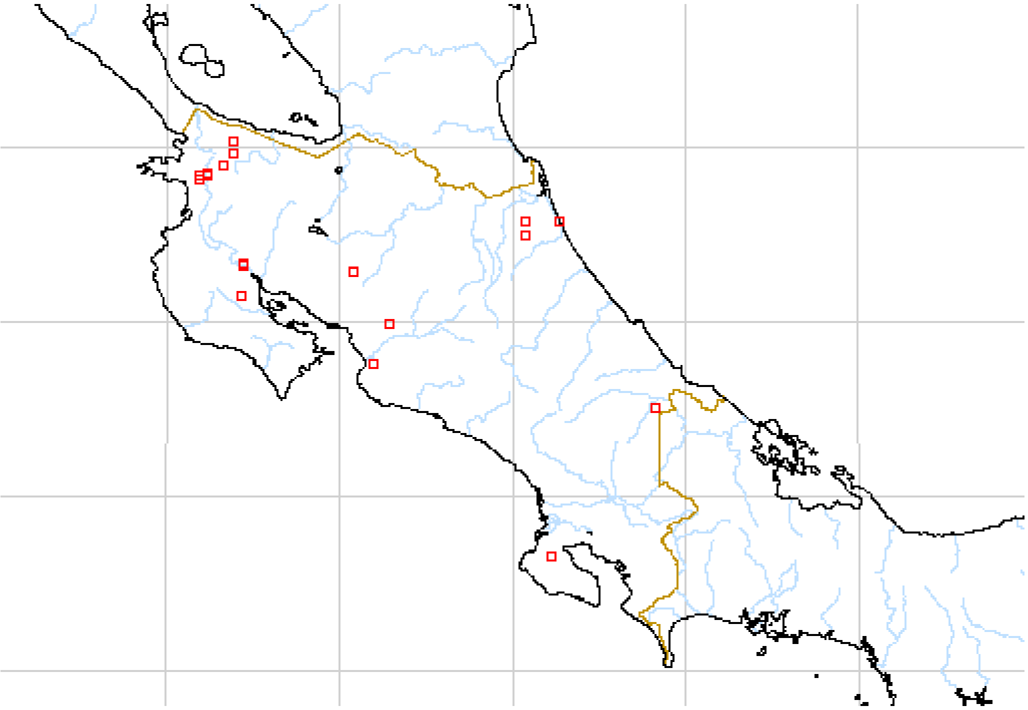
Species Rank: 30
Individuals: 4 (1♀)

2000 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.6		1			



INBio: 43 specimens, 1♀ from Tortuguero

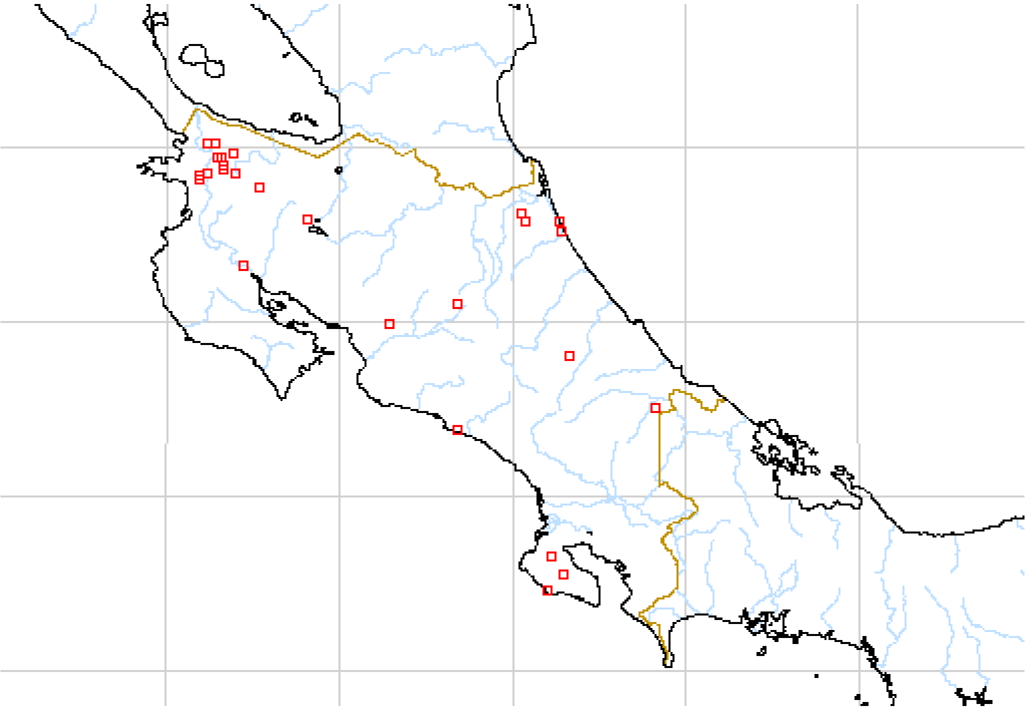
Aellopos titan
(Cramer, 1777)

Species Rank: 22
Individuals: 9 (1♀)

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.71	0.17	7	0.8		1



INBio: 62 specimens, 3 from Tortuguero

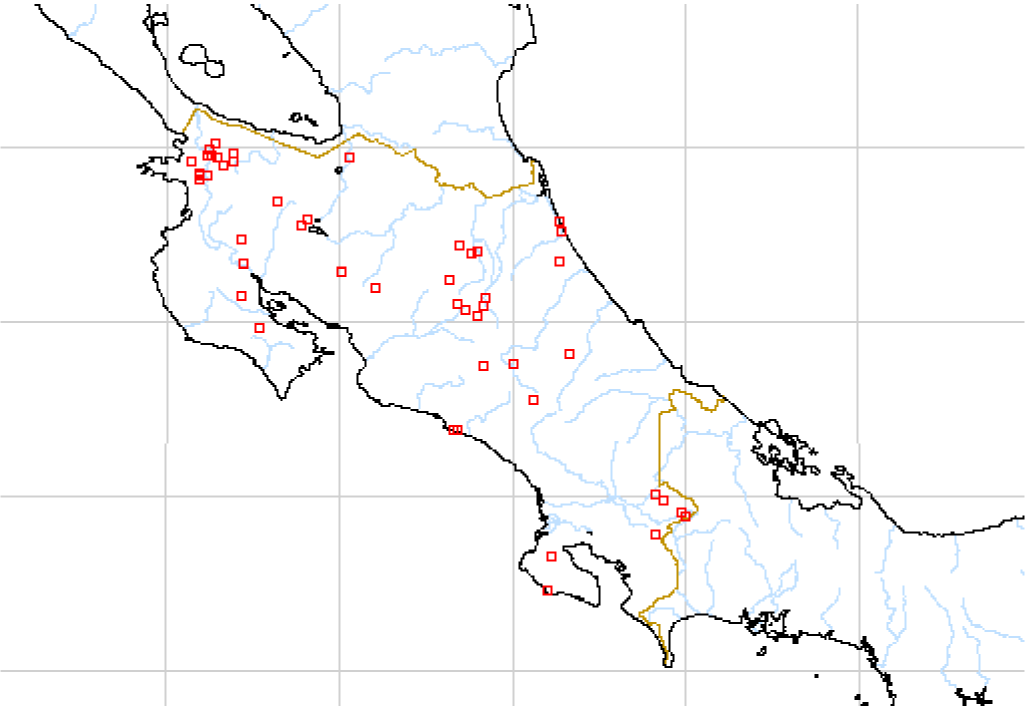
Agrius cingulata
(Fabricius, 1775)

Species Rank: 50
Individuals: 1

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.6		1			



INBio: 247 specimens, 8 from Tortuguero (6♀)

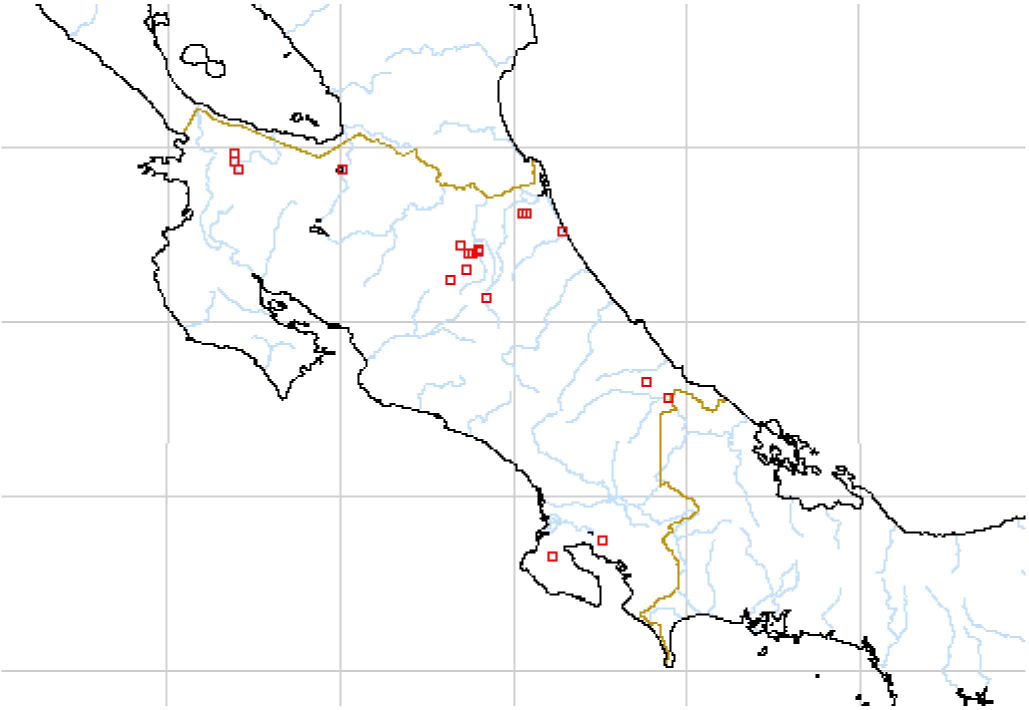
Amphimoea walkeri
(Boisduval, 1875)

Species Rank: NA
Individuals: NA

Spotted at flowers,
but not collected

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 56 speciemans, 1 from Tortuguero

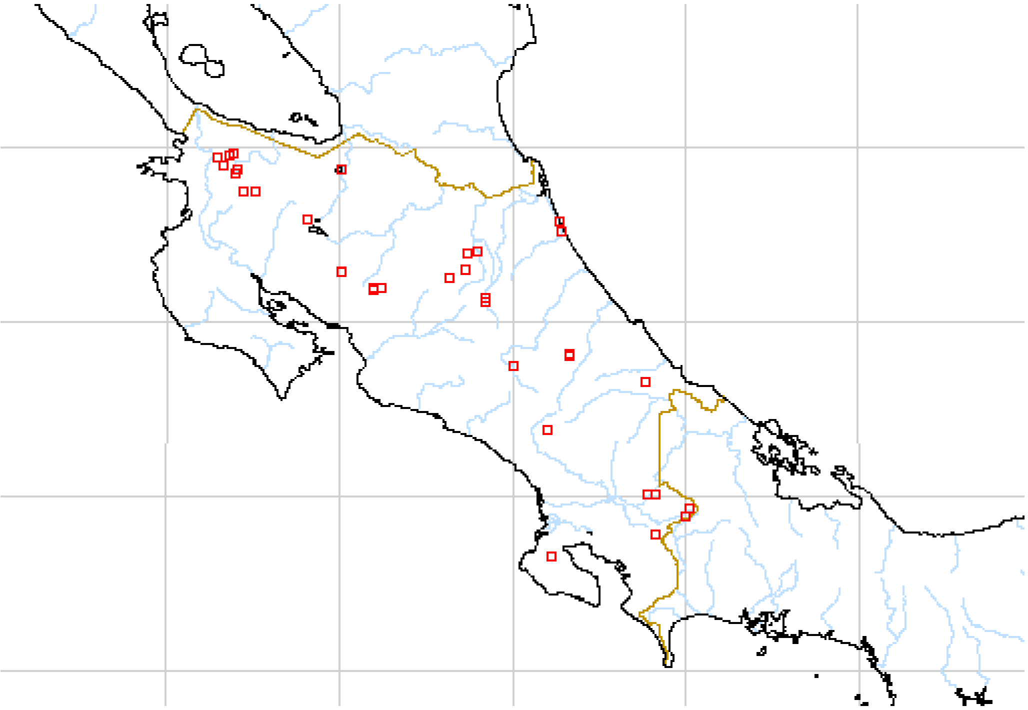
Callionima denticulata
(Shaus, 1895)

Species Rank: NA
Individuals: NA

1999 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n

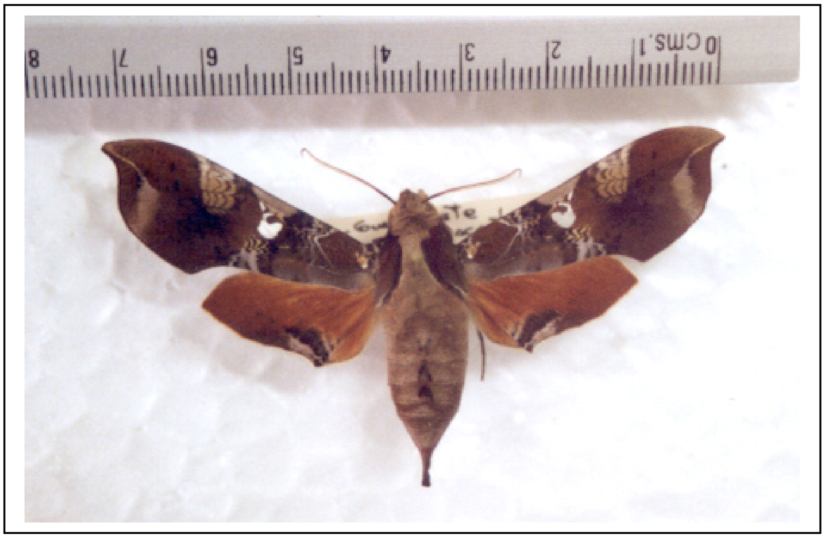


INBio: 130 specimens, 7 from Tortuguero

Callionima falcifera
(Gehlen, 1943)

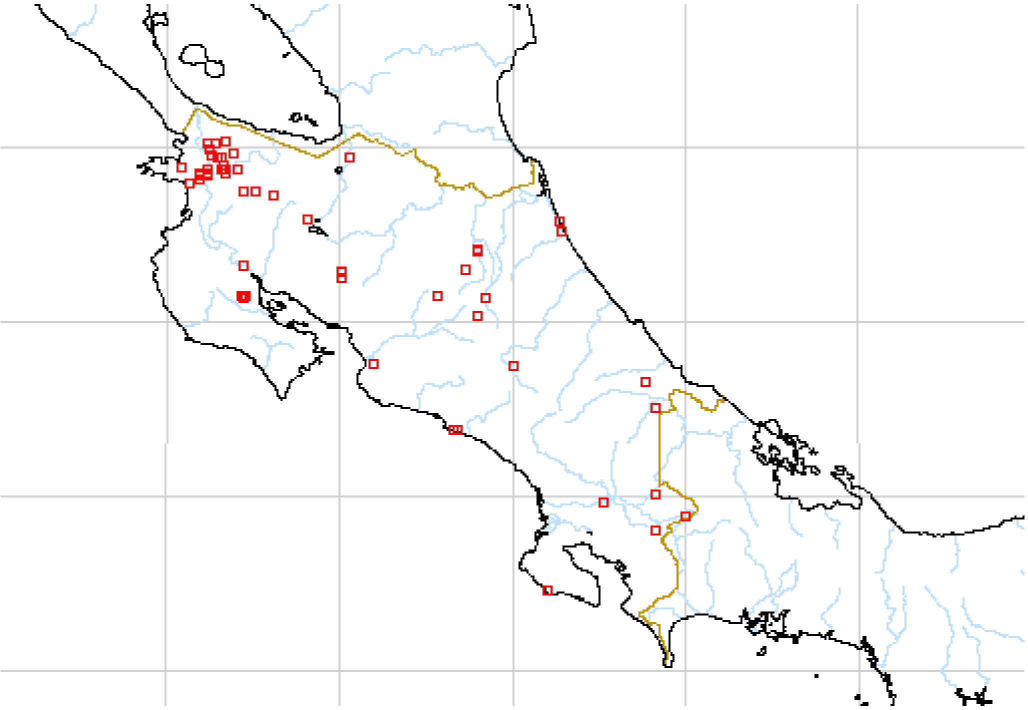
Species Rank: 51
Individuals 1

2000 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.9		1			

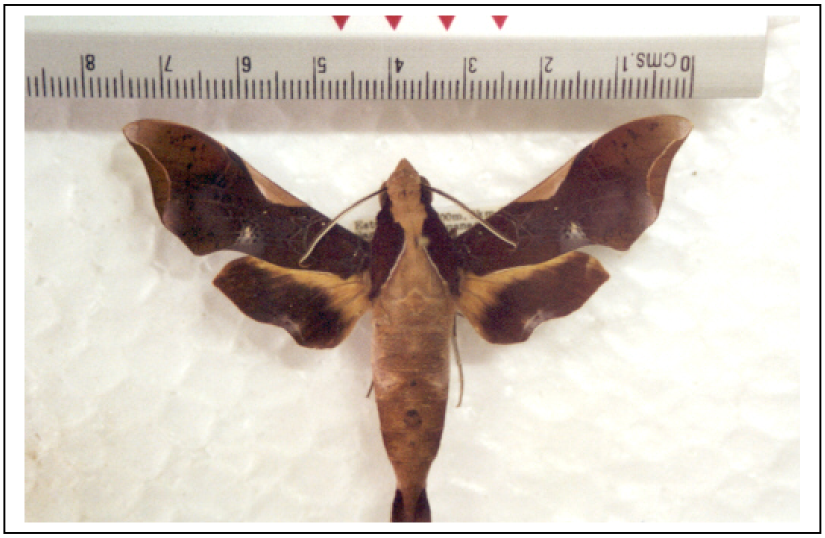


INBio: 323 specimens, 2 from Tortuguero

Callionima nomius
(Walker, 1856)

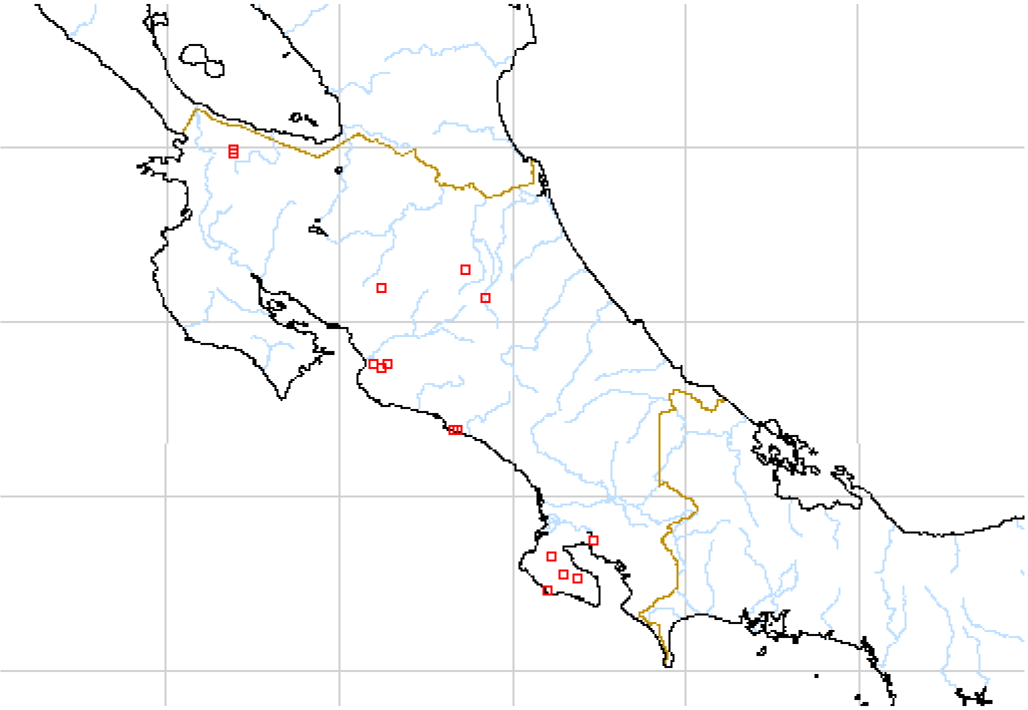
Species Rank: 52
Individuals: 1

2000 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.2		1			



INBio: 81 specimens, 0 from Tortuguero

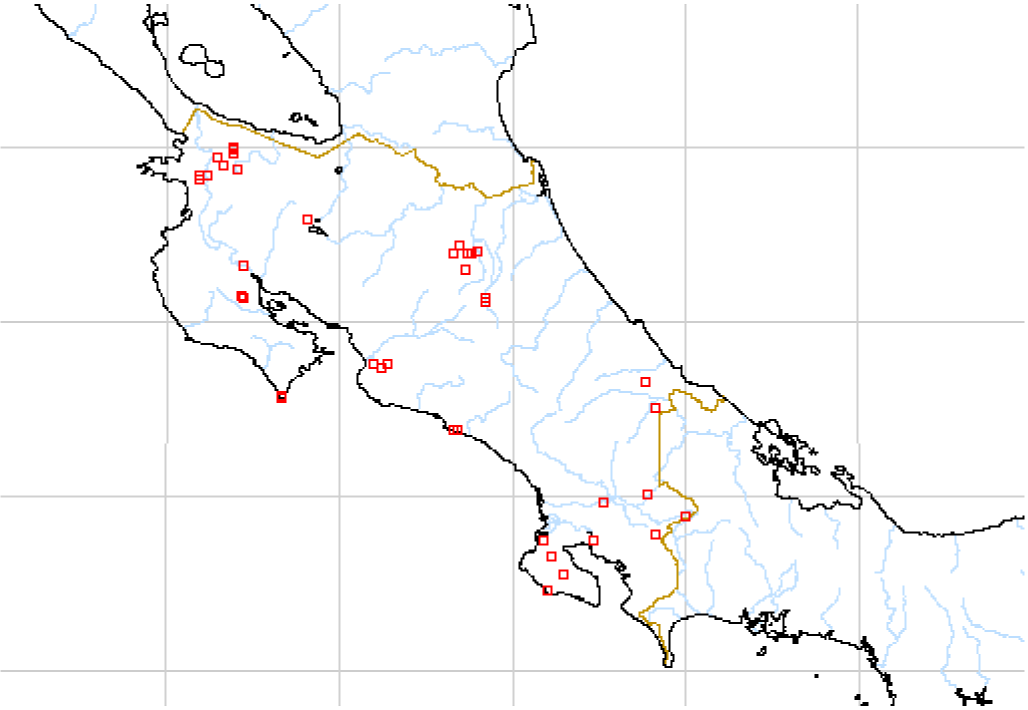
Callionima parce
(Fabricius, 1775)

Species Rank: 53
Individuals: 1

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.2		1			



INBio: 141 specimens, 0 from Tortuguero

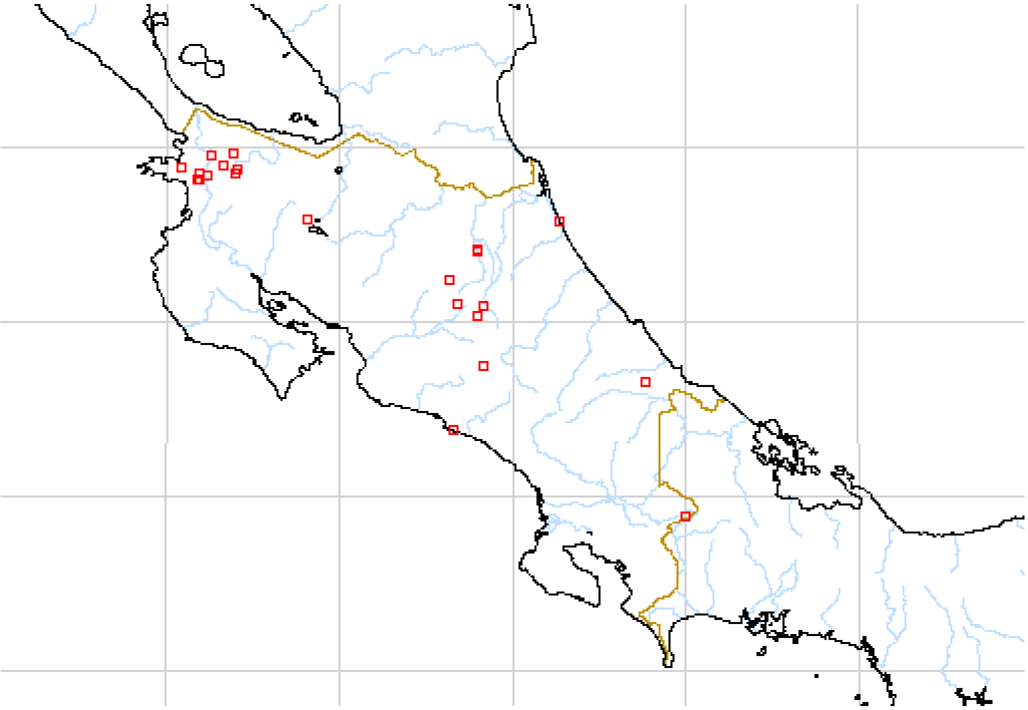
Cocytius antaeus
(Drury, 1773)

Species Rank: 43
Individuals: 2 (2♀)

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
			5.1	0.28	2



INBio: 46 specimens, 1 from Tortuguero

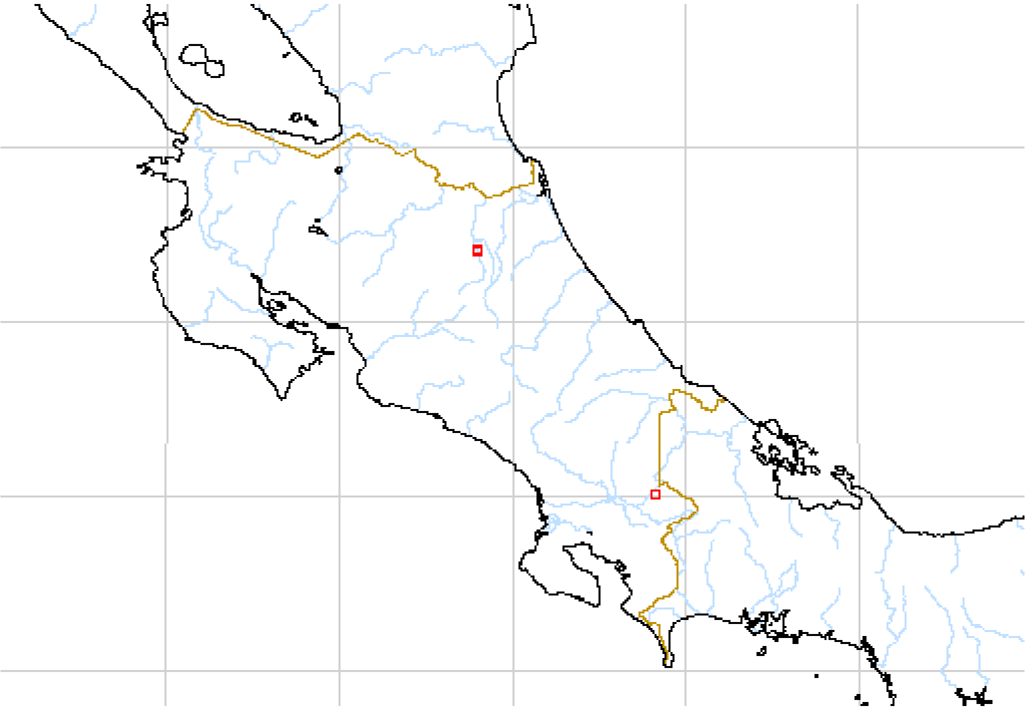
Cocytius beezlebuth
(Boisduval, [1895])

Species Rank: 35
Individuals: 3

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.87	0.35	3			



INBio: 5 specimens, 0 from Tortuguero

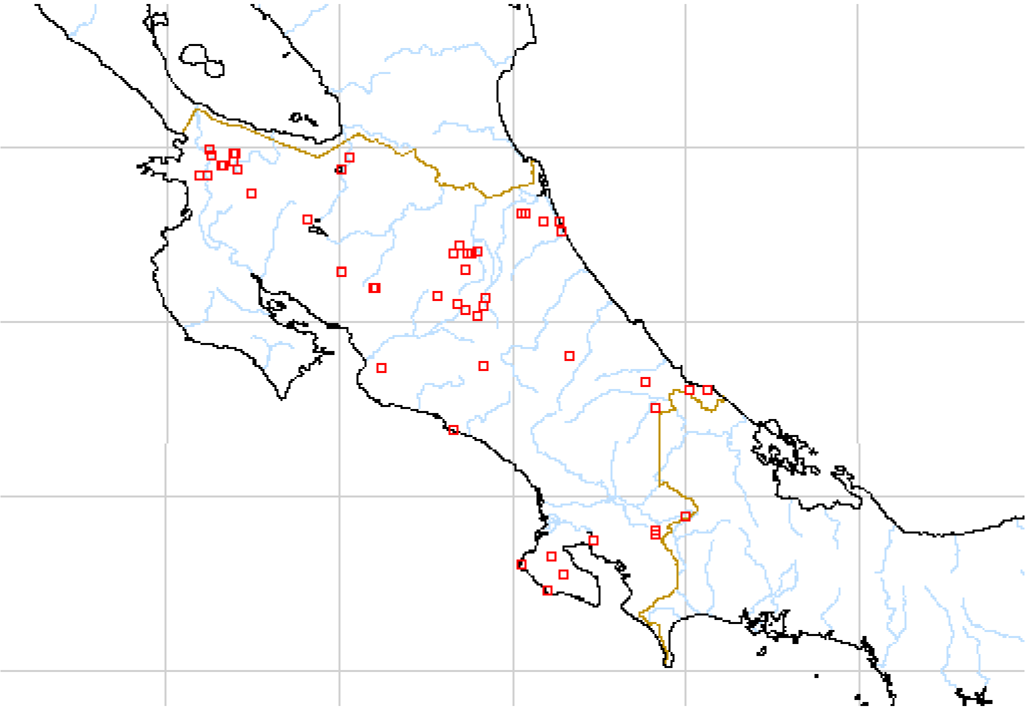
Cocytius duponchel
(Poey, 1832)

Species Rank: 15
Individuals: 14 (2♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
2.4	0.14	6	4.4	0.28	2



INBio: 170 specimens, 8 from Tortuguero (1♀)

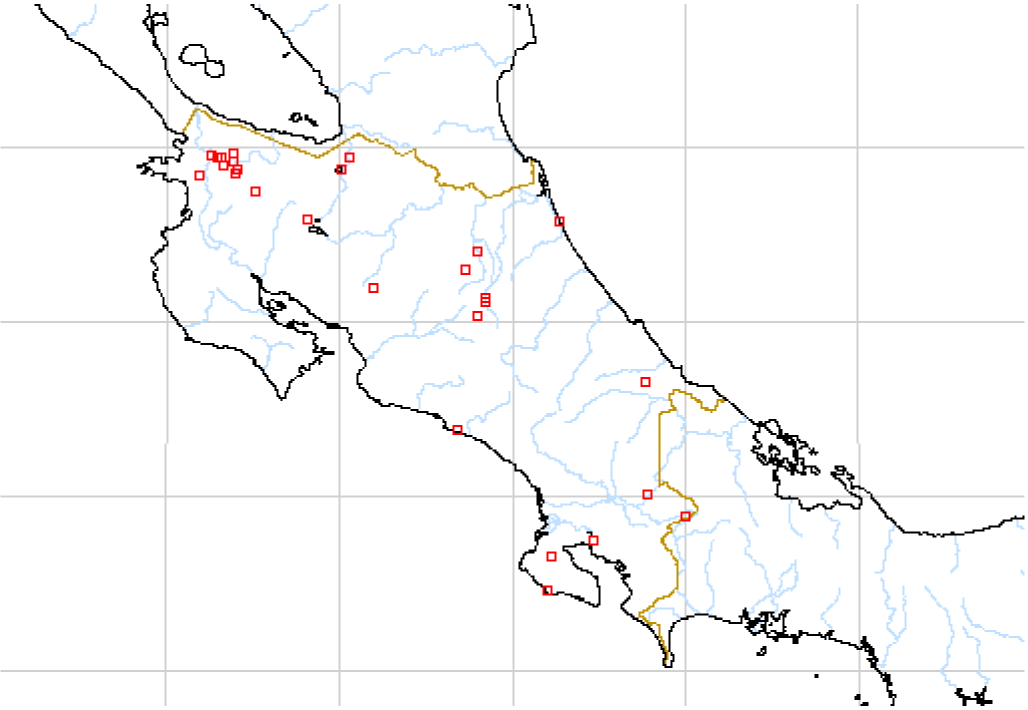
Cocytius lucifer
Rothschild
& Jordan, 1903

Species Rank: 44
Individuals: 2

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
3.1		1			



INBio: 79 specimens, 3 from Tortuguero

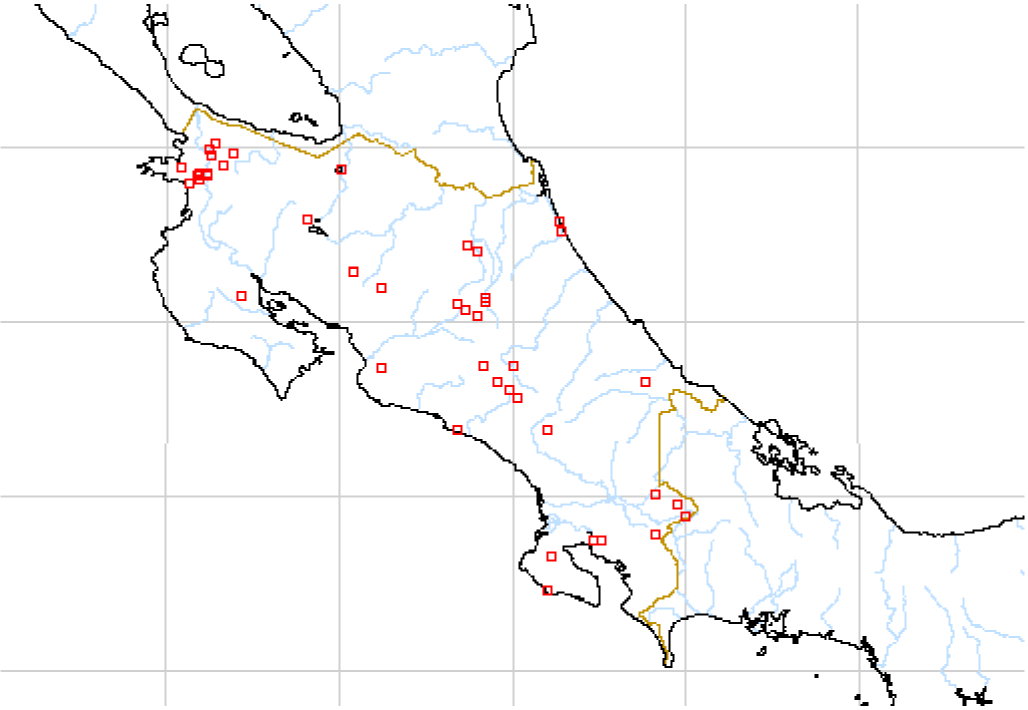
Enyo lugubris
(Linnaeus, 1771)

Species Rank: 36
Individuals: 4 (2♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

	Males			Females	
Mean	S.D.	n	Mean	S.D.	n



INBio: 336 specimens, 17 from Tortuguero (6♀)

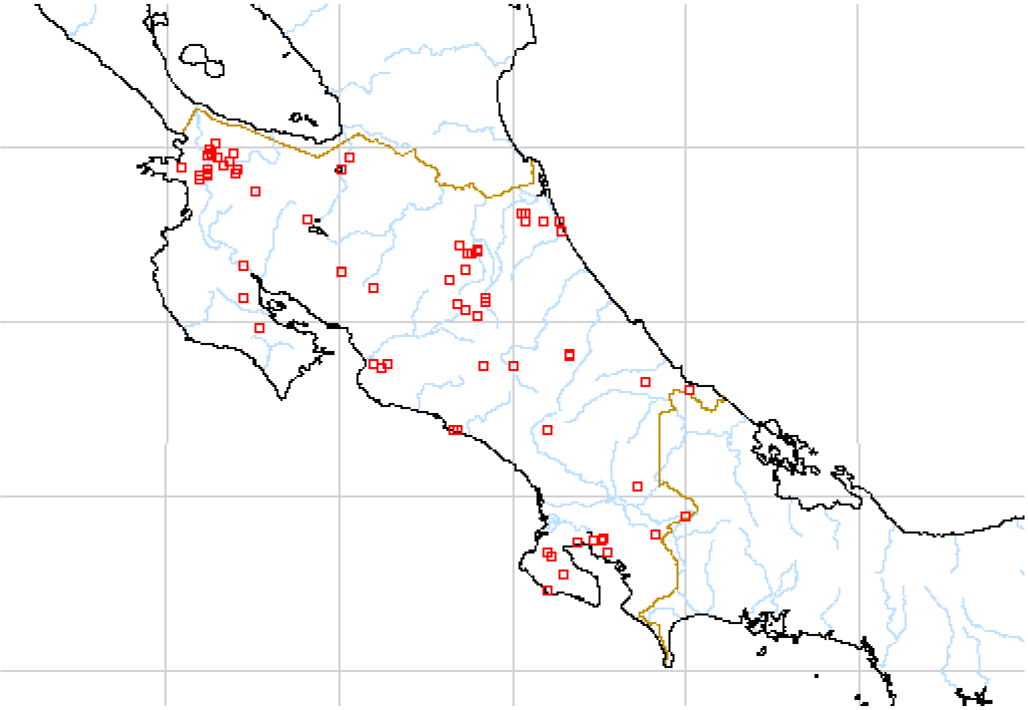
Enyo ocypete
(Linnaeus, 1758)

Species Rank: 6
Individuals: 26 (2♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.63	0.05	10	0.9	0.14	2



INBio: 343 specimens, 8 from Tortuguero (3♀)

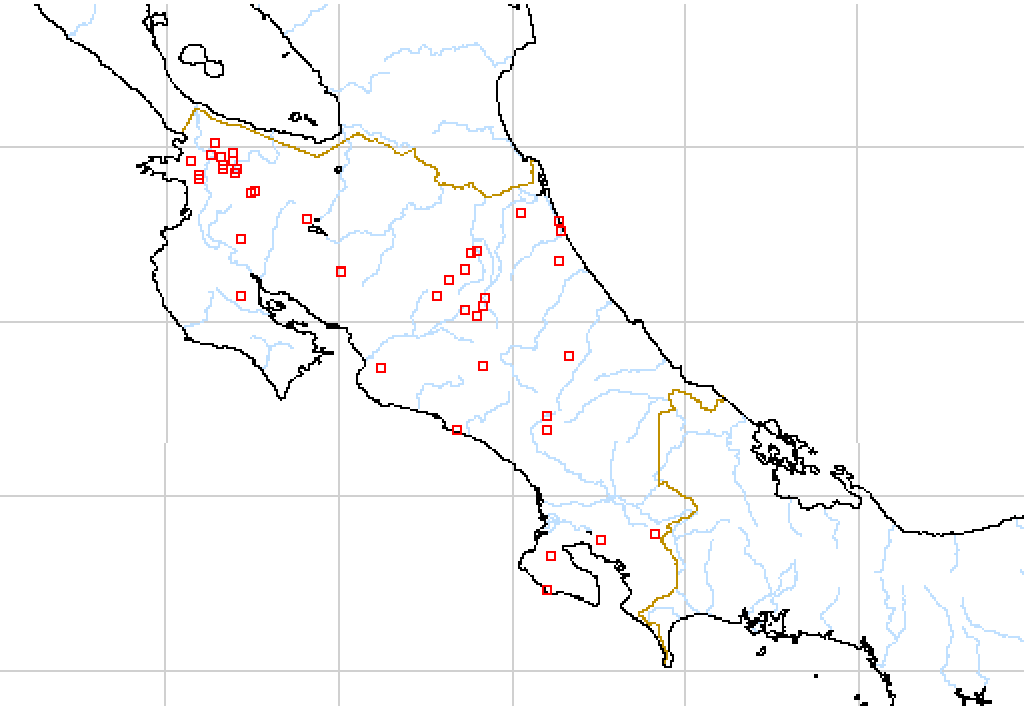
Erinnyis alope
(Drury, 1773)

Species Rank: 31
Individuals: 4

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.35	0.35	2			



INBio: 140 specimens, 33 from Tortuguero

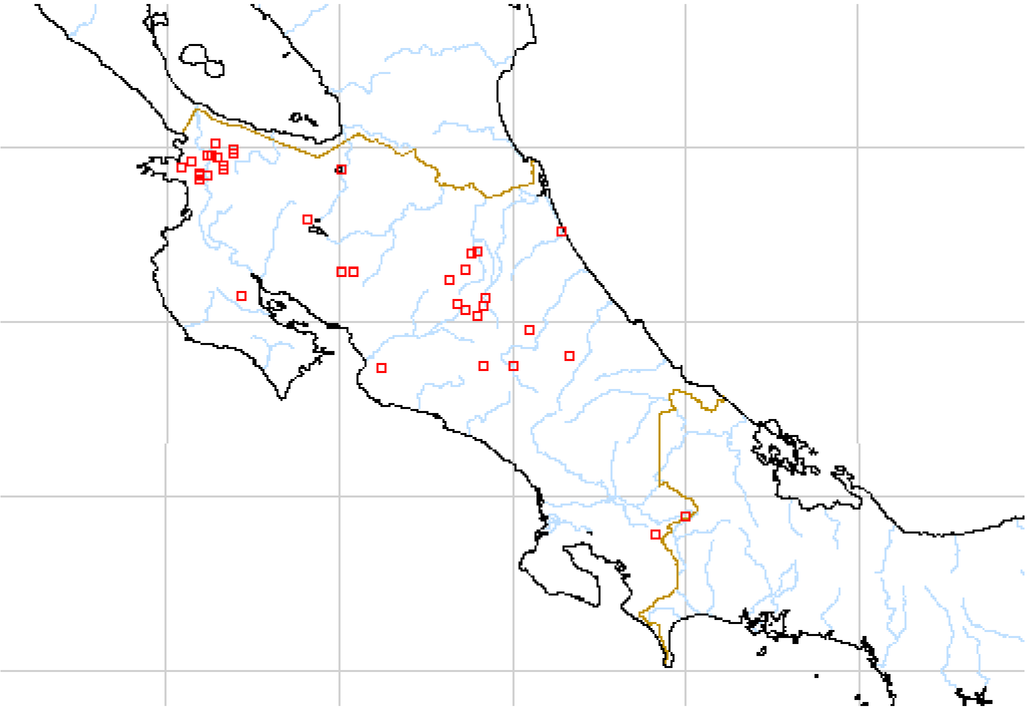
Erinnyis crameri
(Schaus, 1898)

Species Rank: 54
Individuals: 1

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.1		1			



INBio: 116 specimens, 1 from Tortuguero

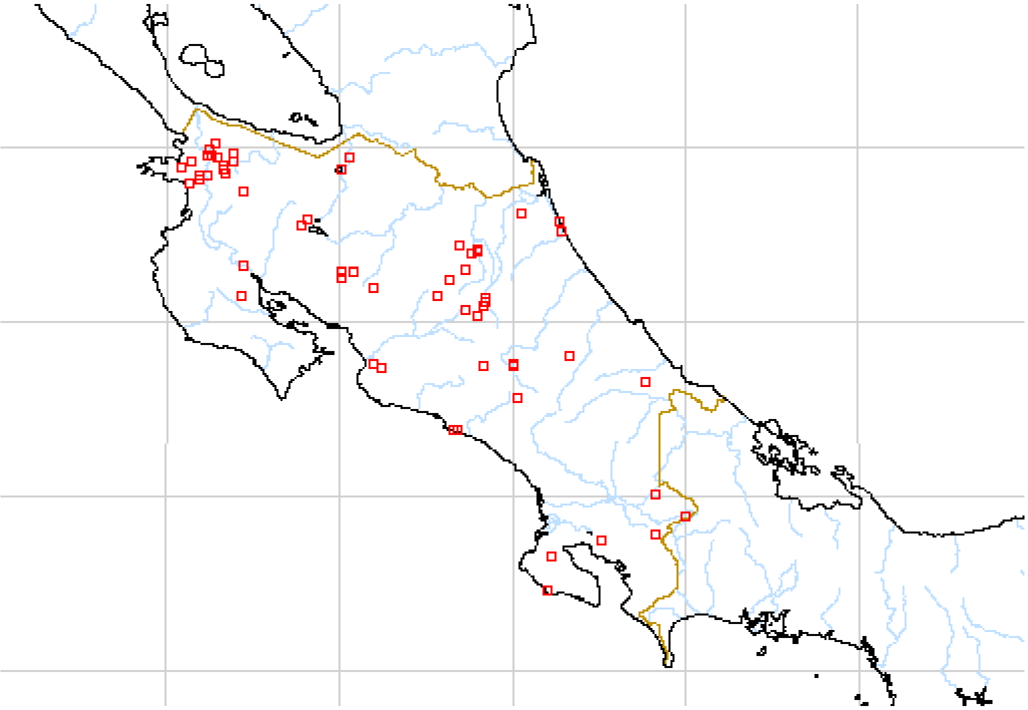
Erinnyis ello
(Linnaeus, 1758)

Species Rank: 37
Individuals: 3

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 386 specimens, 36 from Tortuguero (15♀)

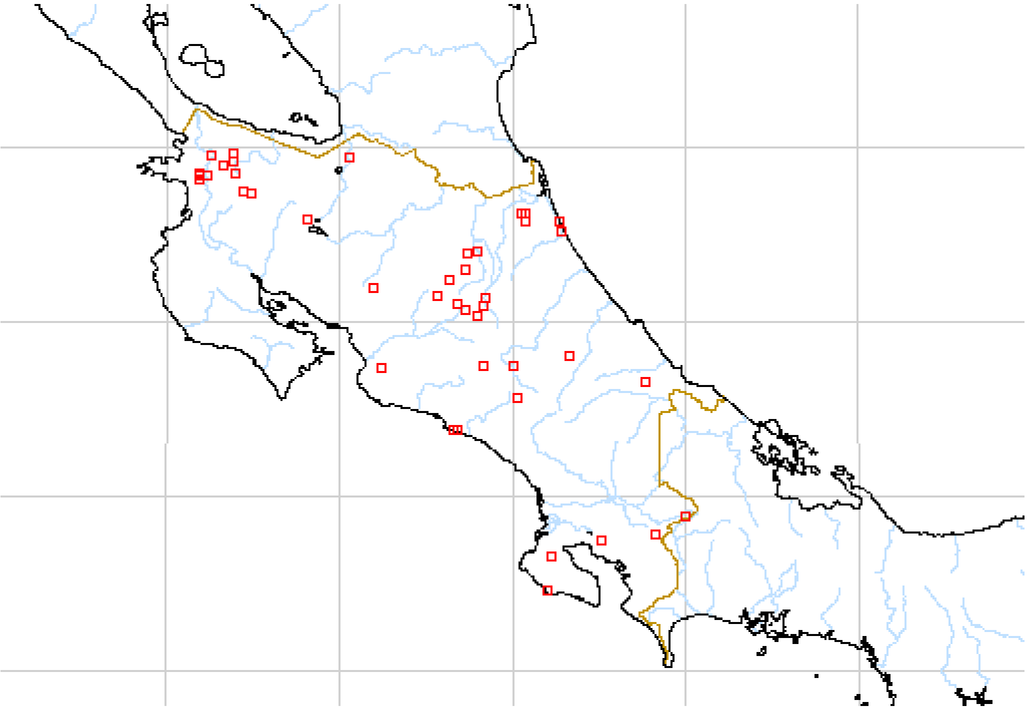
Erinnyis oenotrus
(Cramer, 1780)

Species Rank: 16
Individuals: 13 (6♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.27	0.26	6	1.3	0.23	5



INBio: 231 specimens, 23 from Tortuguero (11♀)

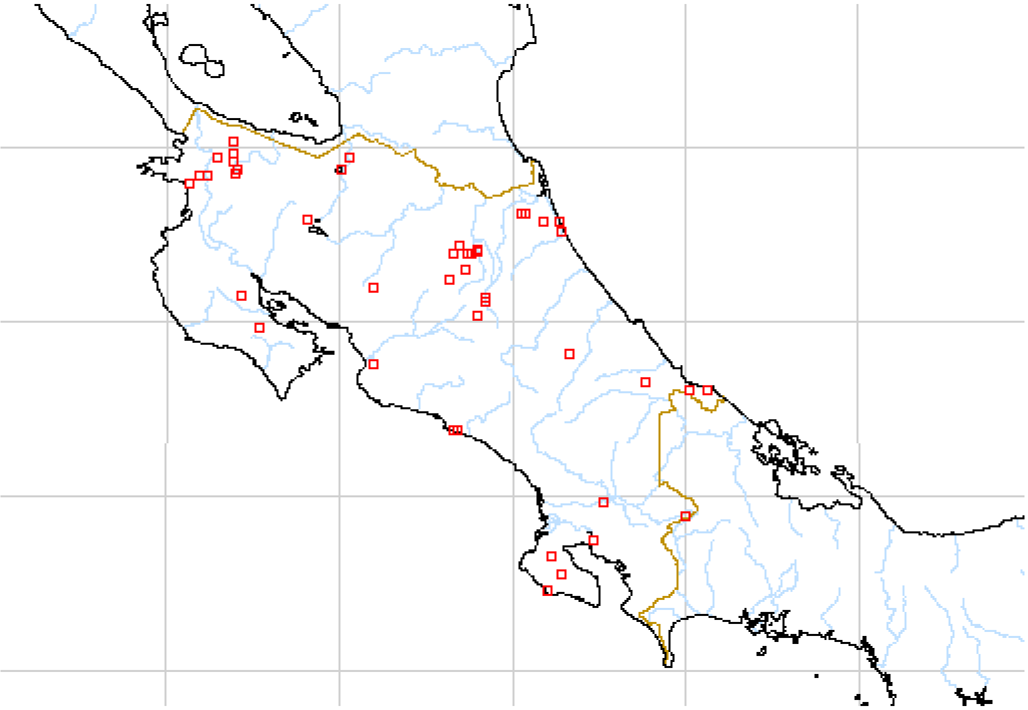
Eumorpha anchemolus
(Cramer, 1779)

Species Rank: 23
Individuals: 8

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
3.63	0.50	4			



INBio: 132 specimens, 12 from Tortuguero (1♀)

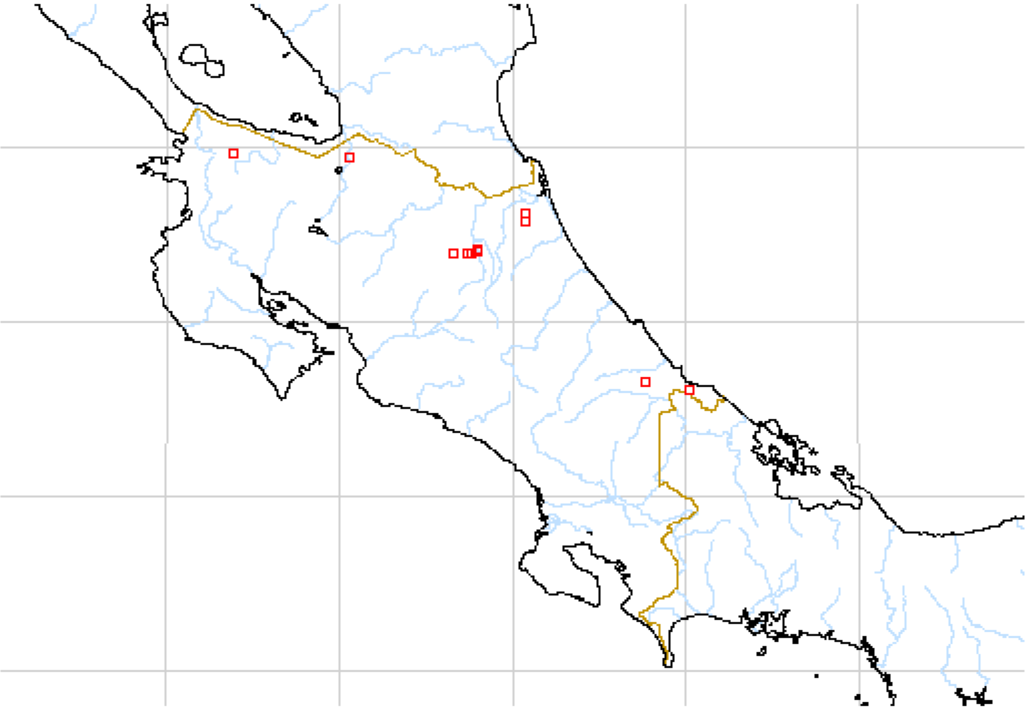
Eumorpha capronnieri
(Boisduval, [1875])

Species Rank: 38
Individuals: 3 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.6	0.14	4	2.2		1

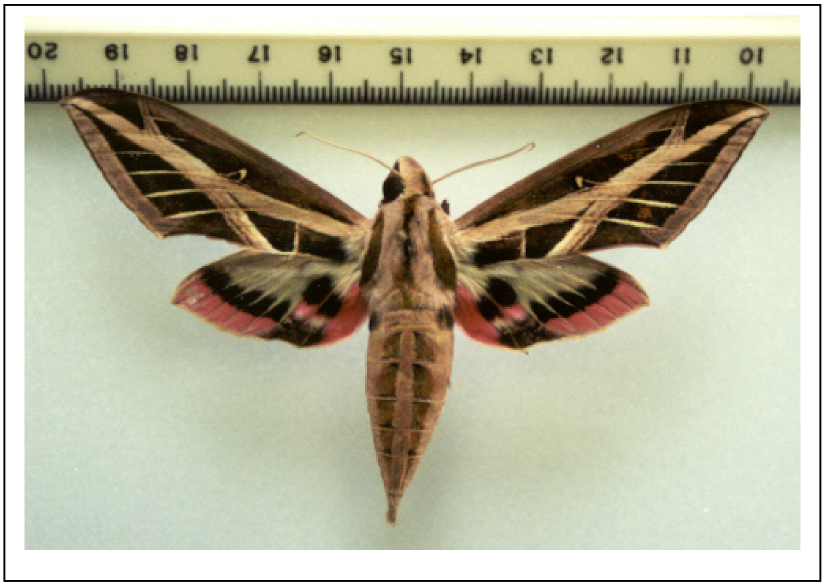


INBio: 38 specimens, 0 from Tortuguero

Eumorpha fasciatus
(Sulzer, 1776)

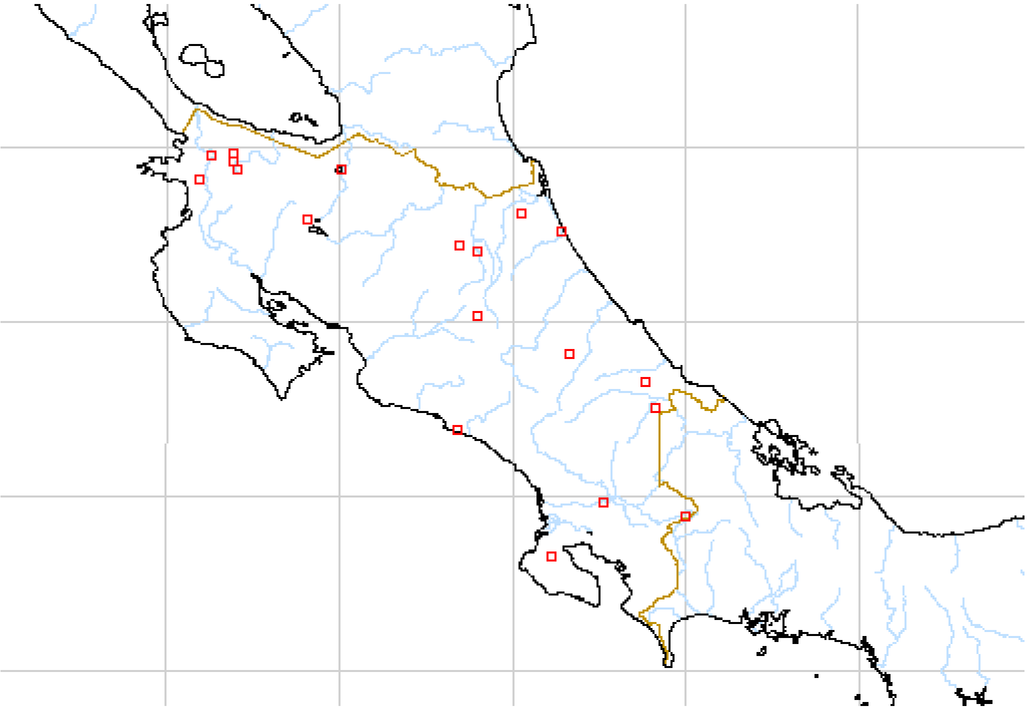
Species Rank: NA
Individuals: NA

1999 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 49 specimens, 1♀ from Tortuguero

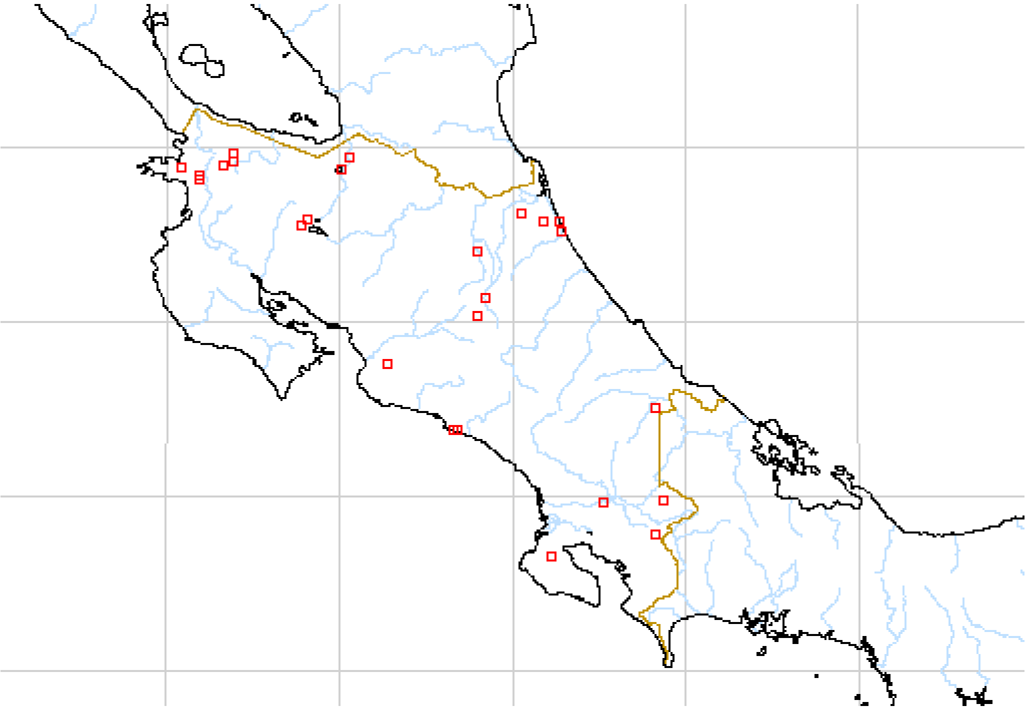
Eumorpha labruscae
(Linnaeus, 1758)

Species Rank: NA
Individuals: NA

1999 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 47 specimens, 5 from Tortuguero (1♀)

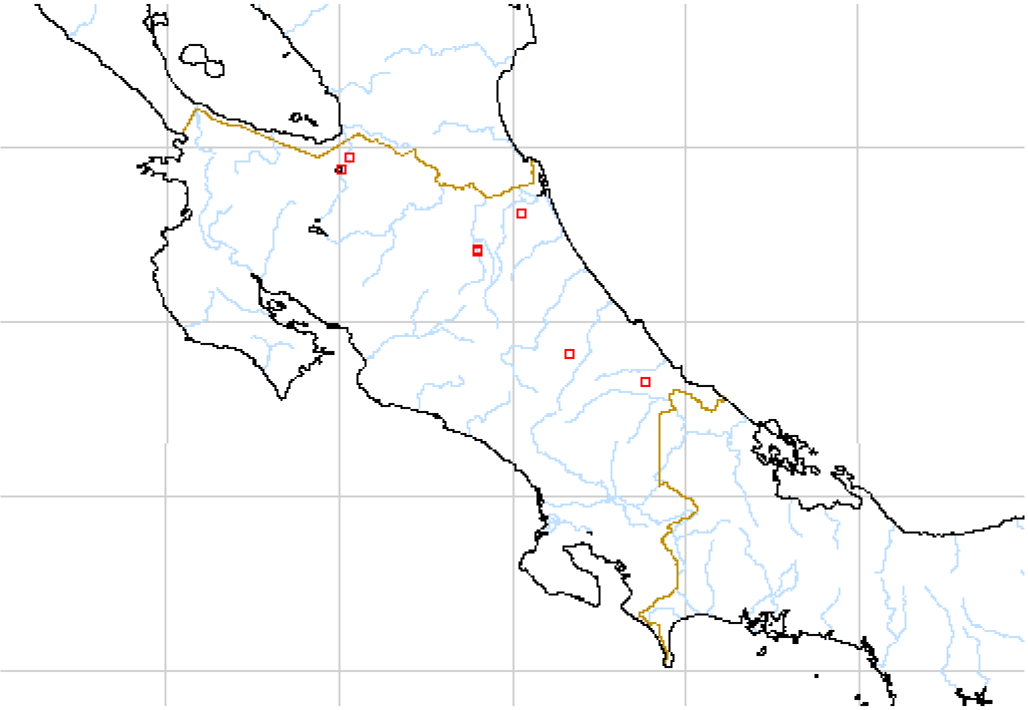
Eumorpha megaeucus
(Hübner, [1819])

Species Rank: 28
Individuals: 5 (1♀)

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.55	0.36	2			



INBio: 13 specimens, 0 from Tortuguero

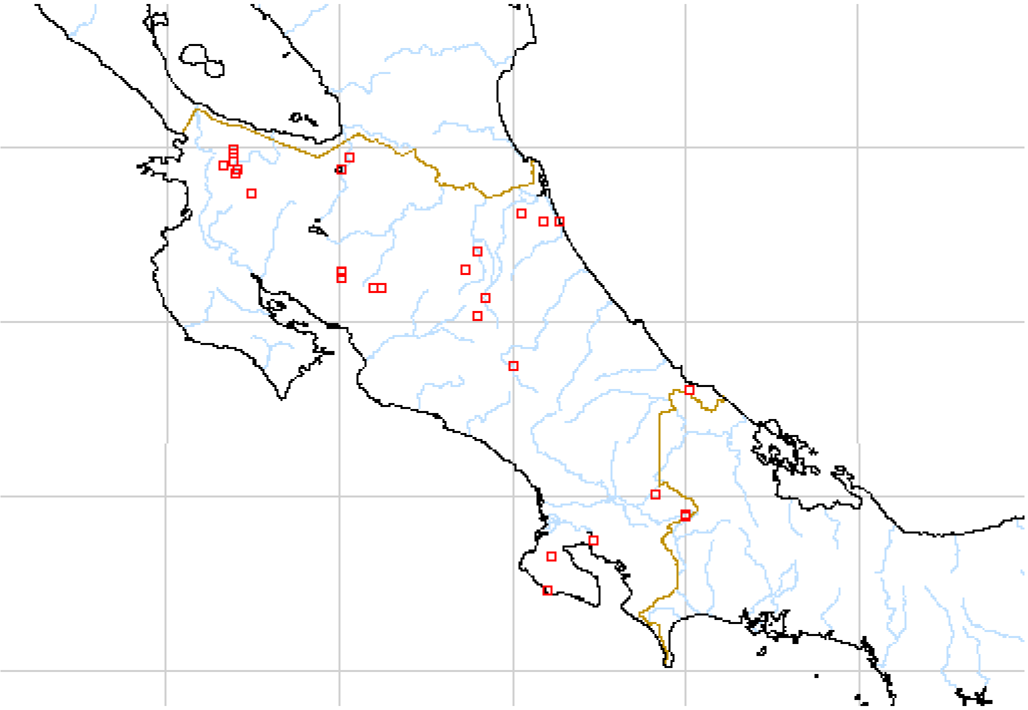
Eumorpha obliquus
(Rothschild & Jordan, 1903)

Species Rank: 24
Individuals: 8 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
3.1	0.71	2	5.0		1



INBio: 79 specimens, 7 from Tortguero (2♀)

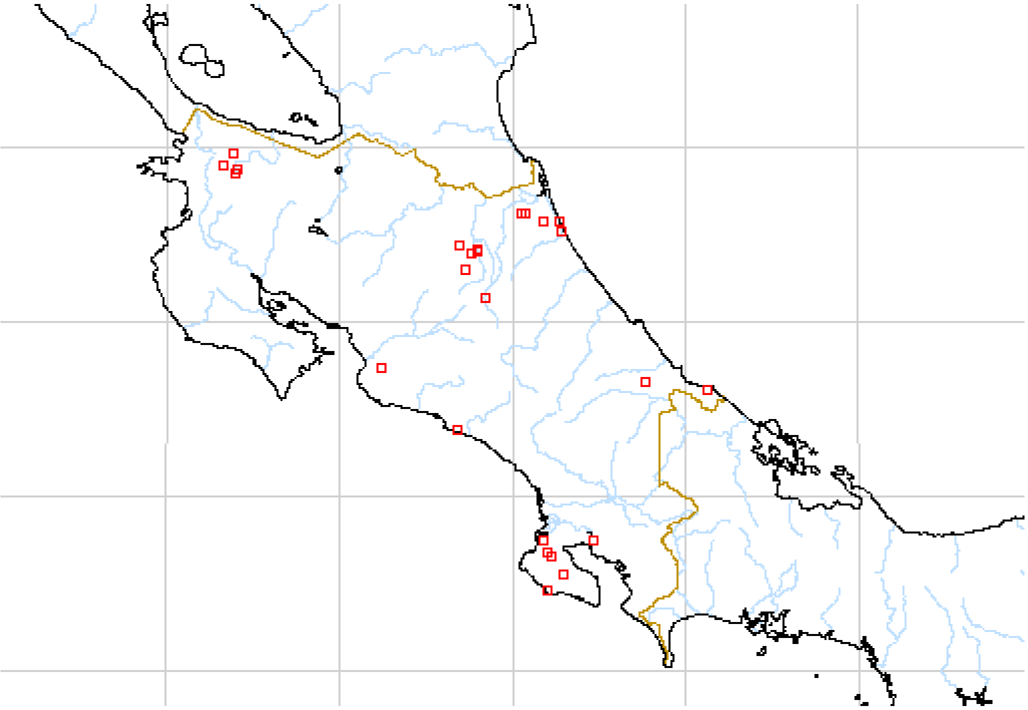
Eumorpha phorbas
(Cramer, 1775)

Species Rank: 13
Individuals: 16 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.71	0.53	7	2.5		1



INBio: 147 specimens, 7 from Tortuguero (1♀)

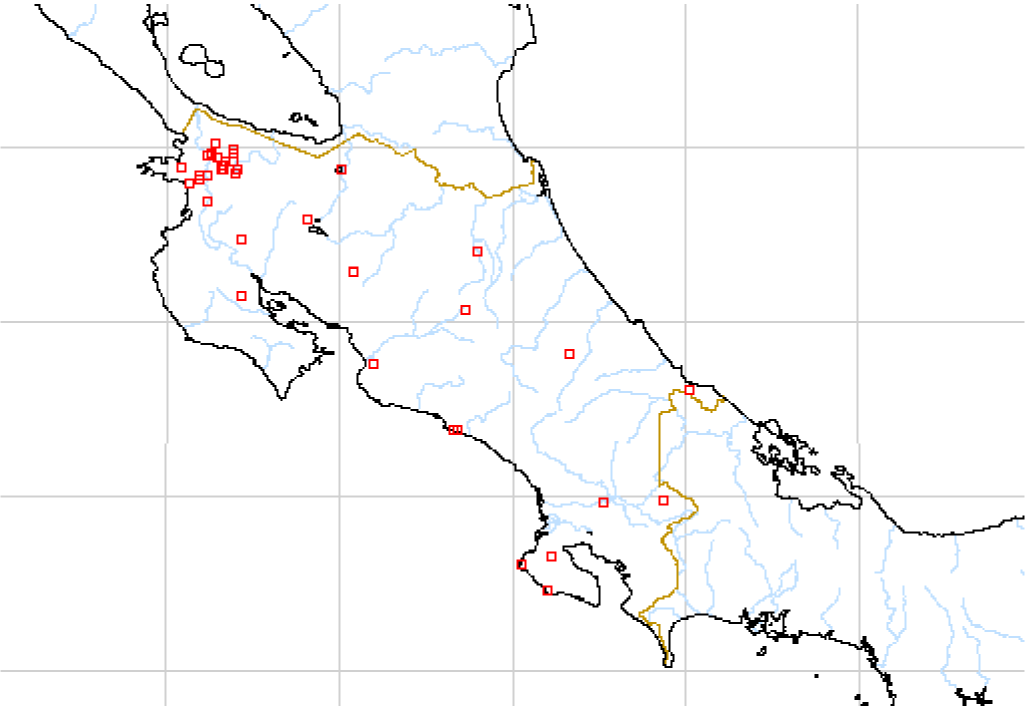
Eumorpha satellita
(Linnaeus, 1771)

Species Rank: 55
Individuals: 1

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.9		1			

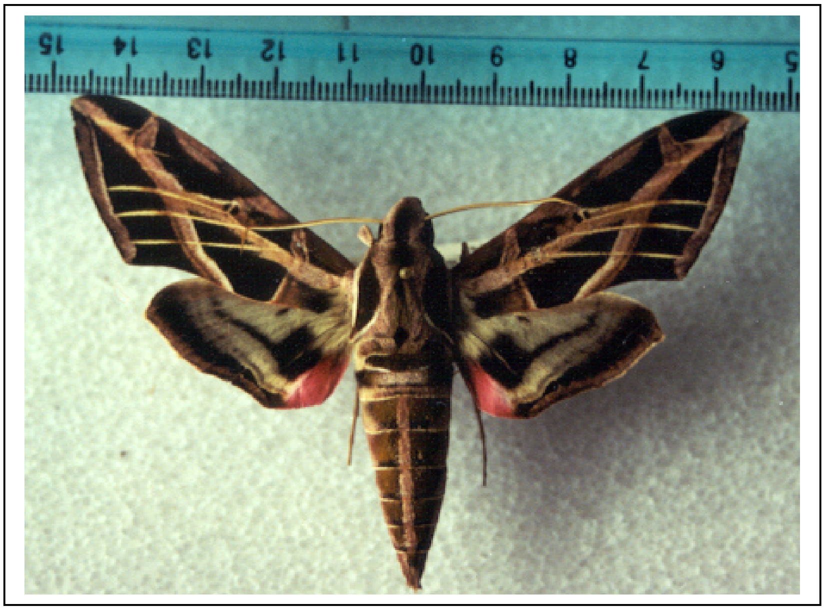


INBio: 181 specimens, 0 from Tortuguero

Eumorpha vitis
(Linnaeus, 1758)

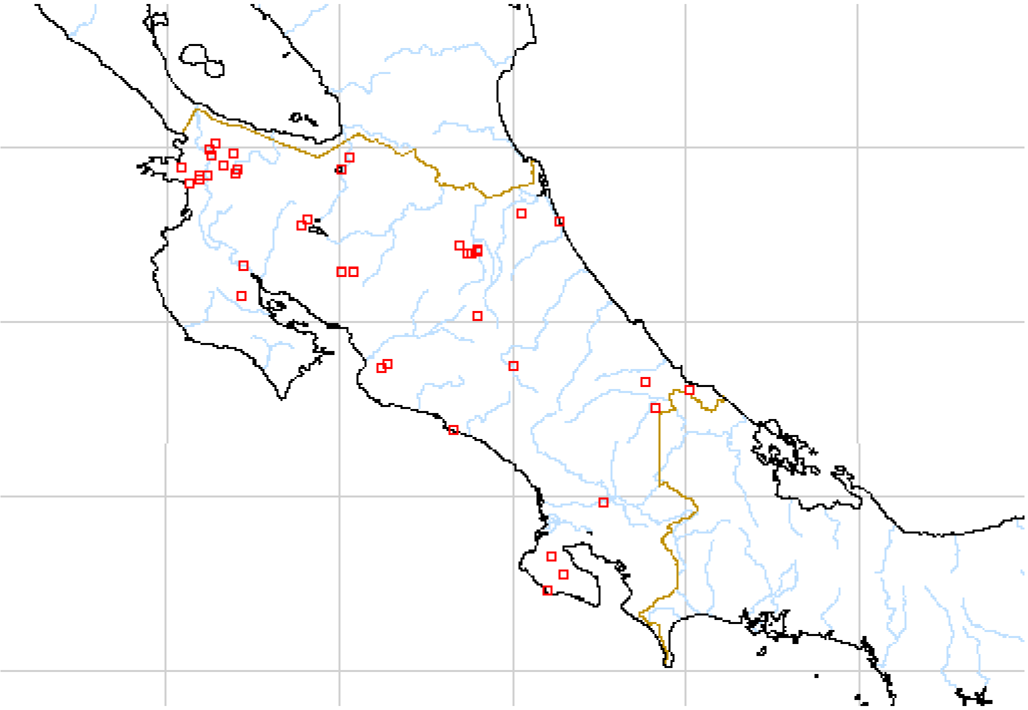
Species Rank: 56
Individuals: 1

1999 & 2000 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.7		1			

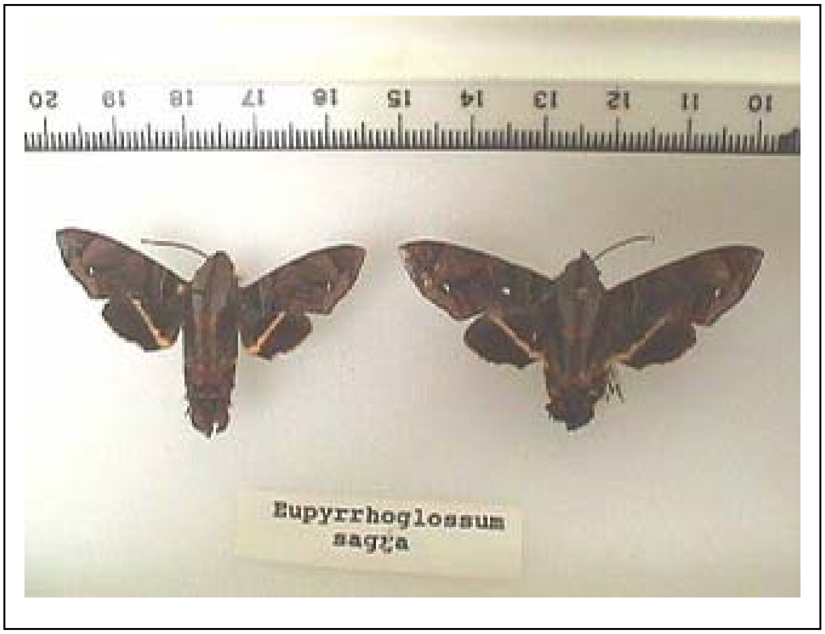


INBio: 157 specimens, 1 from Tortuguero

Eupyrrhoglossum sagra
(Poey, 1832)

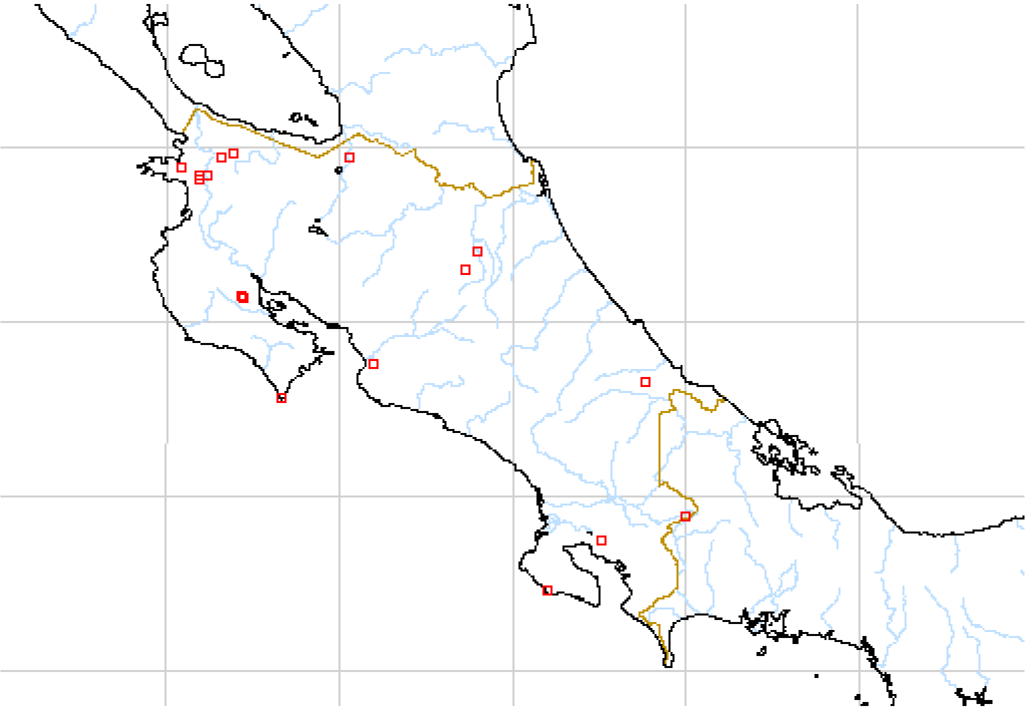
Species Rank: NA
Individuals: NA

Collected by:
R. Ballard, Dec. 2000



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 52 specimens, 0 from Tortuguero

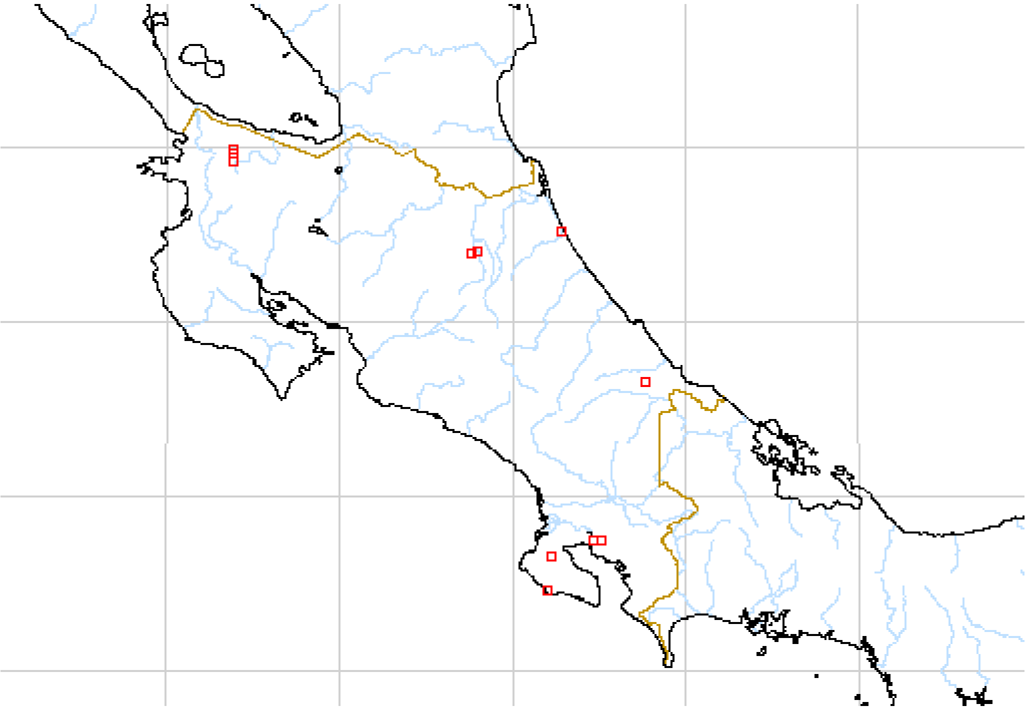
Hemeroplanes ornatus
Rothschild, 1894

Species Rank: 26
Individuals: 7

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.1	0.36	4			



INBio: 26 specimens, 1 from Tortuguero

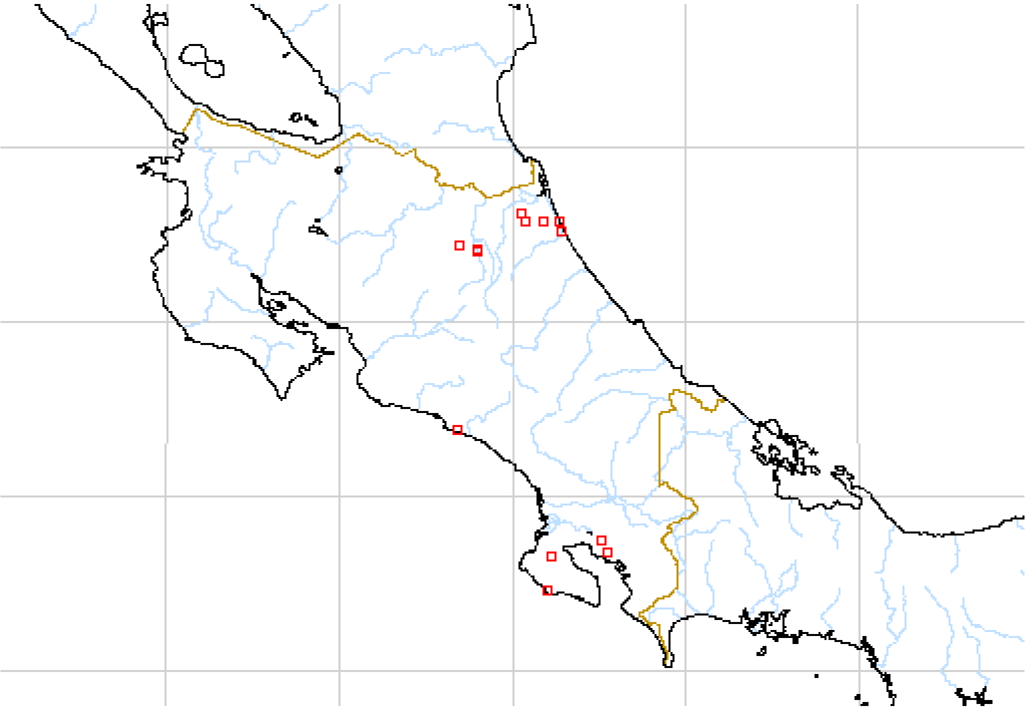
Isognathus scyron
(Cramer, 1780)

Species Rank: 1
Individuals: 78 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.81	0.14	10	1.5		1



INBio: 90 specimens, 24 from Tortuguero (3♀)

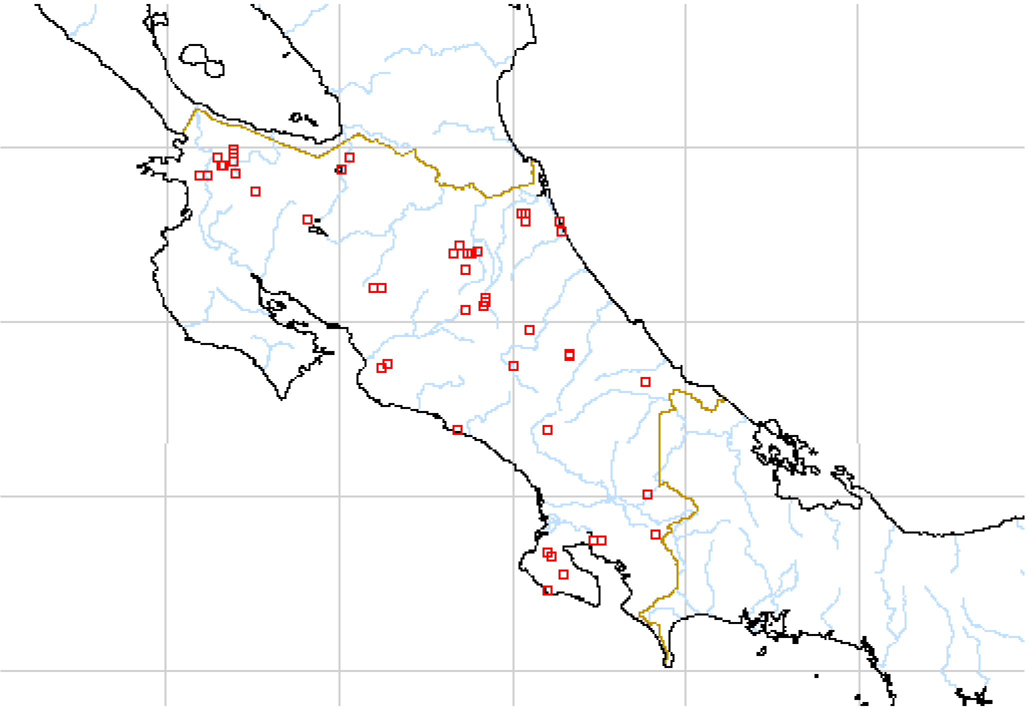
Madoryx plutonius
(Hübner, [1819])

Species Rank: 39
Individuals: 3 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.5		1			



INBio: 204 specimens, 5 from Tortuguero

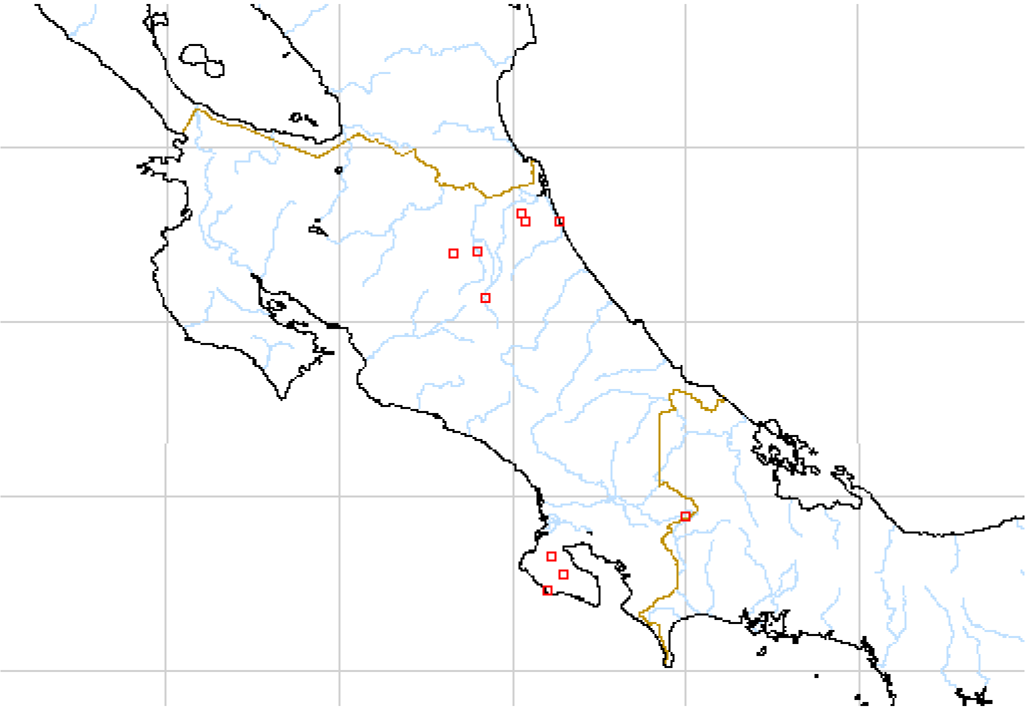
Manduca albiplaga
(Walker, 1856)

Species Rank: 57
Individuals: 1

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
3.4		1			



INBio: 17 specimens, 1 from Tortuguero

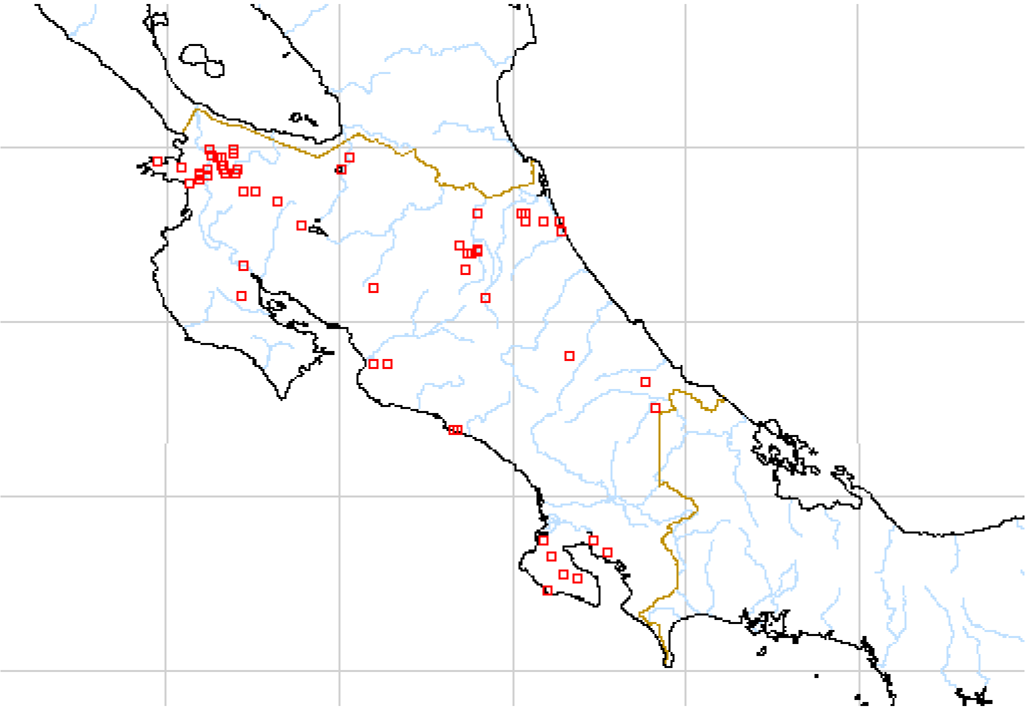
Manduca florestan
(Stoll, 1782)

Species Rank: 7
Individuals: 26 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.64	0.20	10	2.6		1



INBio: 407 specimens, 6 from Tortuguero

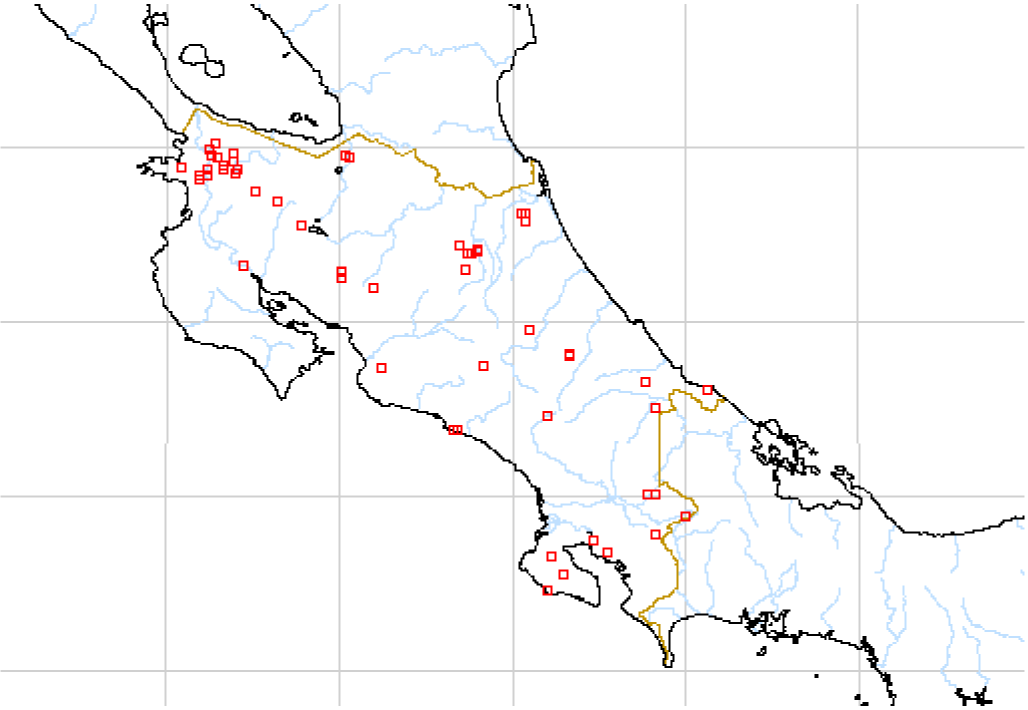
Manduca occulta
(Rothschild & Jordan, 1903)

Species Rank: NA
Individuals: NA

1999 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 210 specimens, 0 from Tortuguero

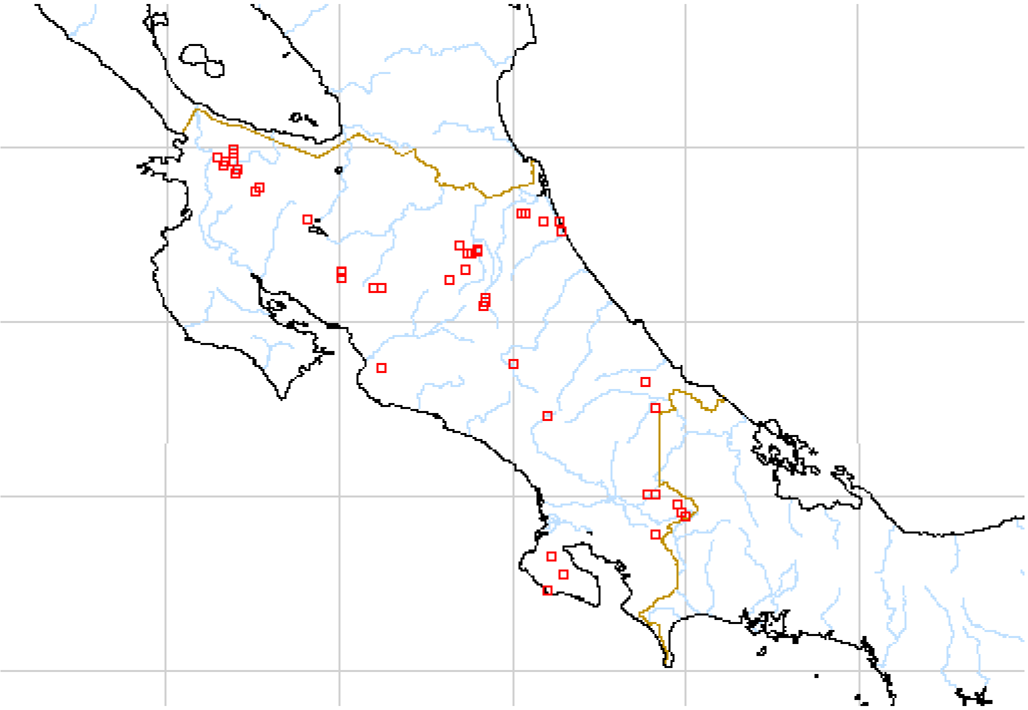
Manduca pellenia
(Herrich-Schäffer, [1854])

Species Rank: 10
Individuals: 20

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.38	0.30	8			



INBio: 182 specimens, 7 from Tortuguero

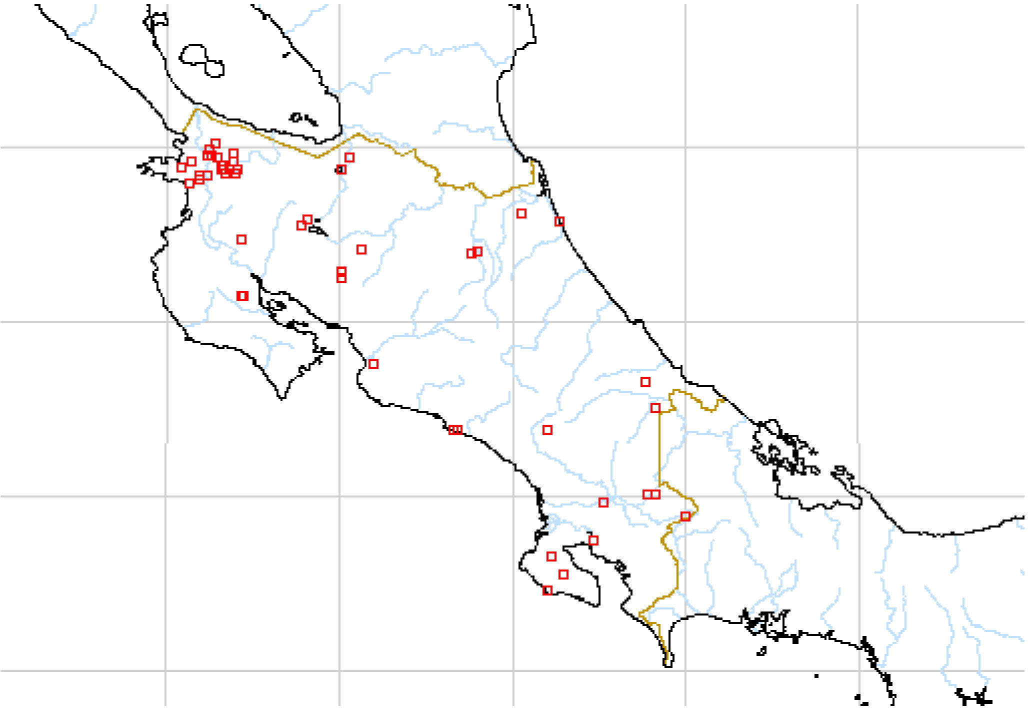
Manduca rustica
(Fabricius, 1775)

Species Rank: 45
Individuals: 2

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
3.15	0.49	2			



INBio: 167 specimens, 2 from Tortuguero

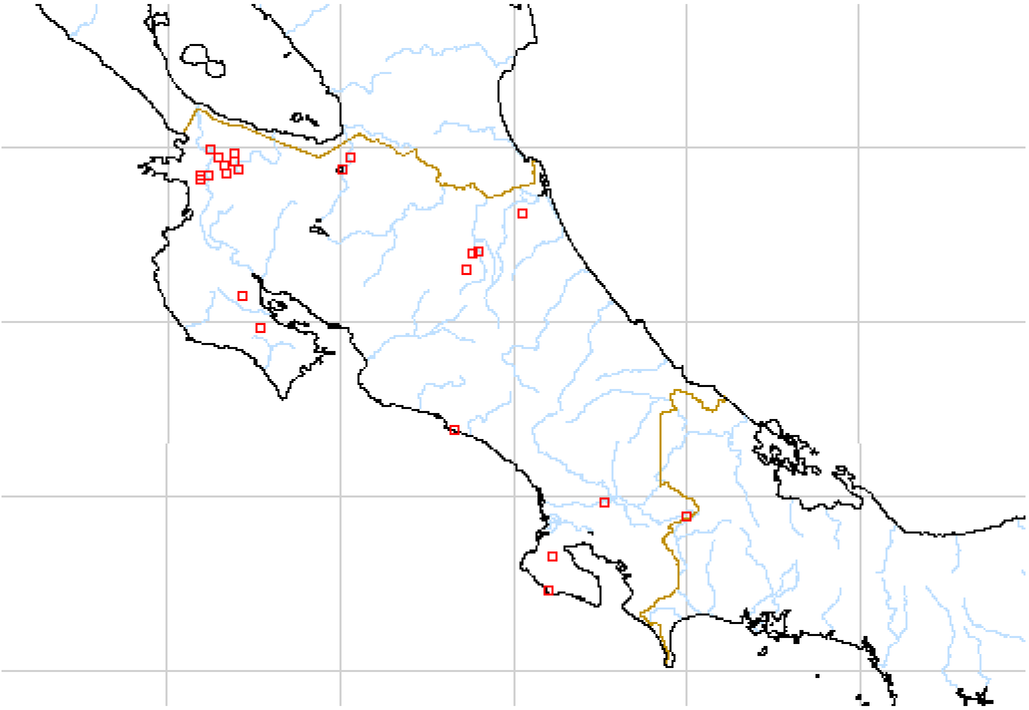
Manduca sexta
(Linnaeus, 1763)

Species Rank: NA
Individuals: NA

1999 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 72 specimens, 0 from Tortuguero

Manduca spp.
(Wickham)

Species Rank: 58
Individuals: 1♀

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
			1.9		1

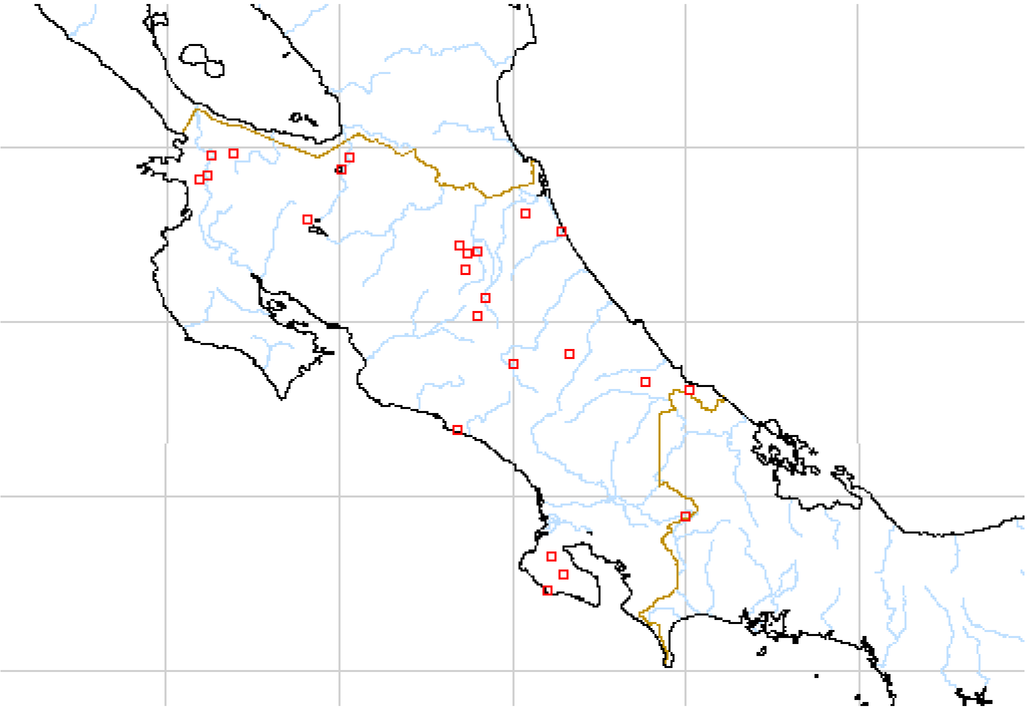
Neococytius cluentius
(Cramer, 1775)

Species Rank: NA
Individuals: NA

1999 Sampling

Live weights (g) of moths taken at lights:

	Males			Females	
Mean	S.D.	n	Mean	S.D.	n



INBio: 44 specimens, 1 from Tortuguero

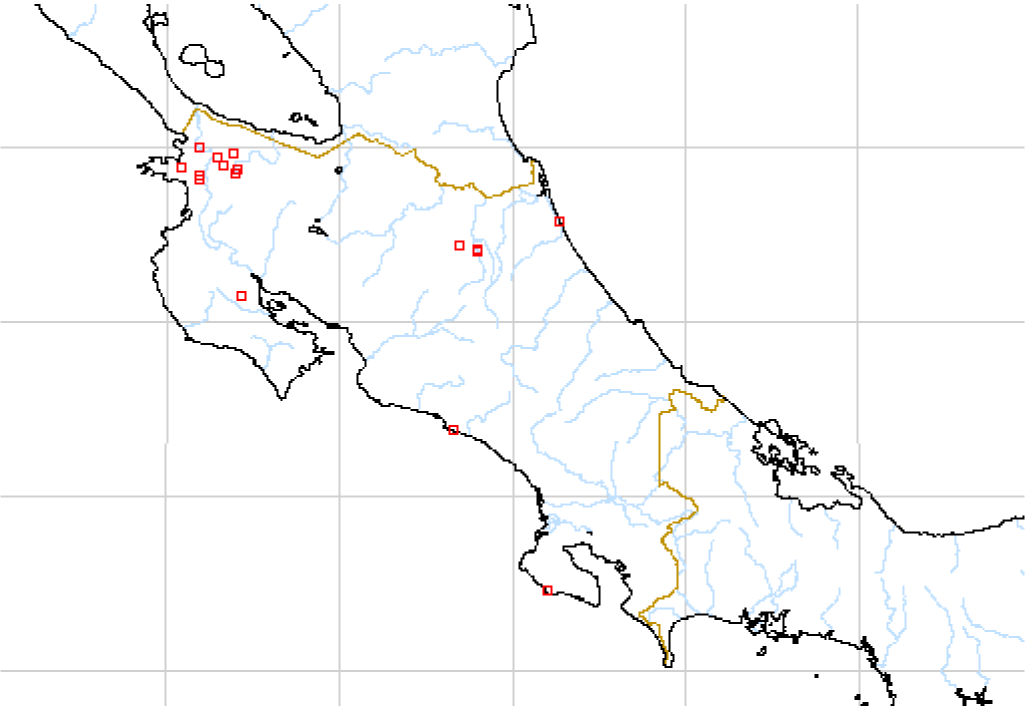
Nyceryx coffeae
(Walker, 1856)

Species Rank: 59
Individuals: 1

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.7		1			



INBio 50 specimens, 1 from Tortuguero

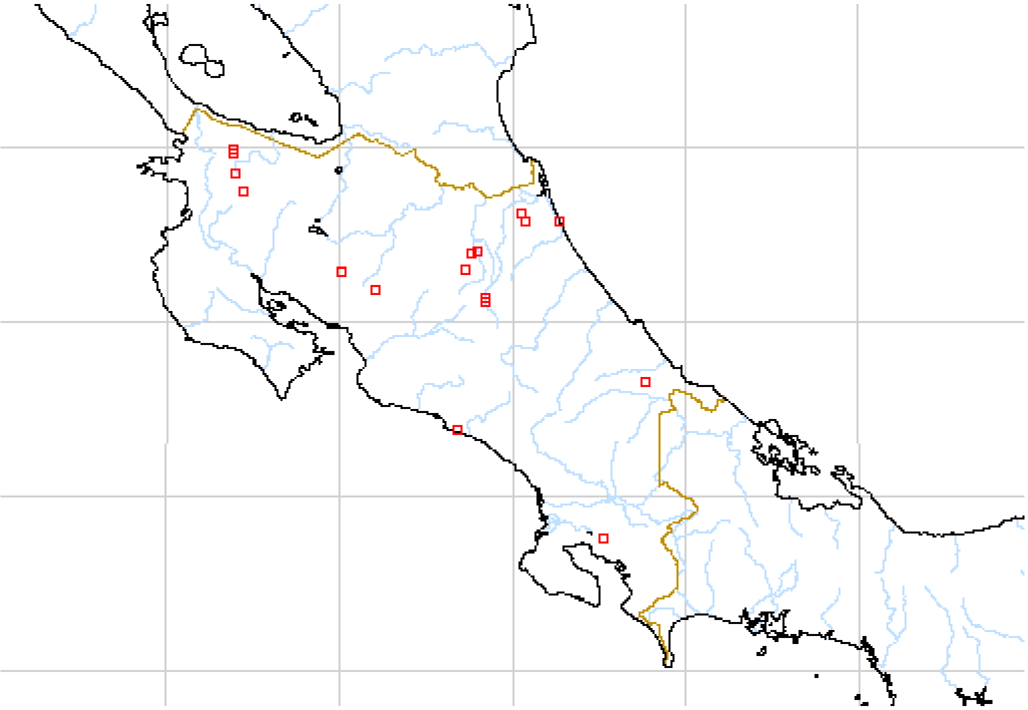
Nyceryx stuarti
(Rothschild, 1894)

Species Rank: 40
Individuals: 3

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.63	0.06	2			



INBio: 40 specimens, 3 from Tortuguero

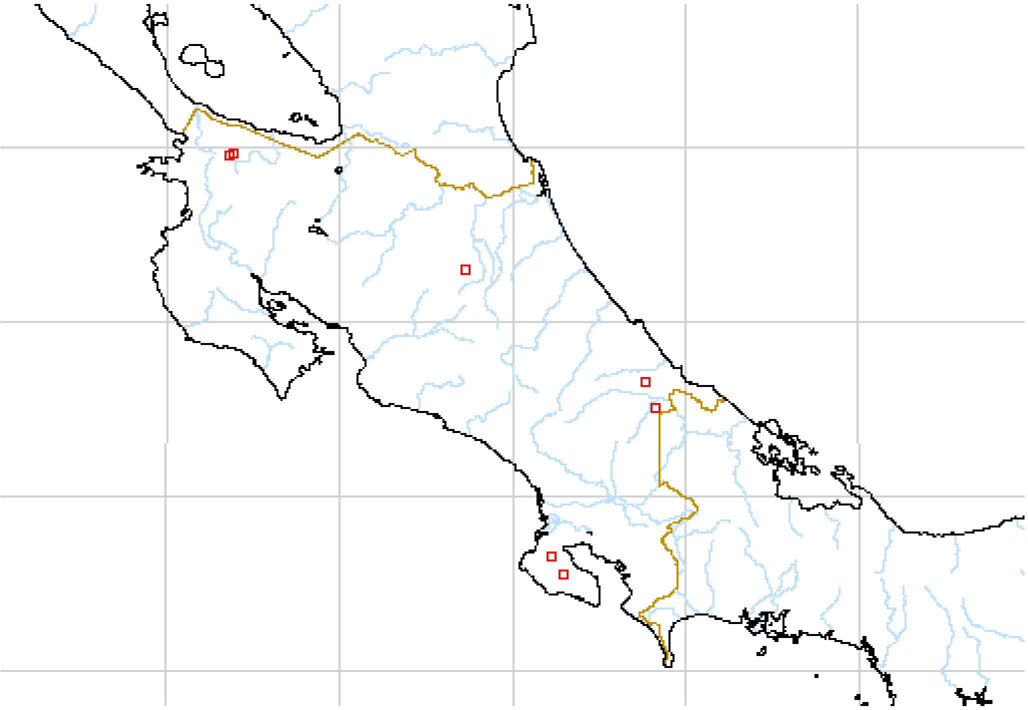
Oryba kadeni
(Schaufuss, 1870)

Species Rank: 41
Individuals: 3

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
2.8	1.15	3			

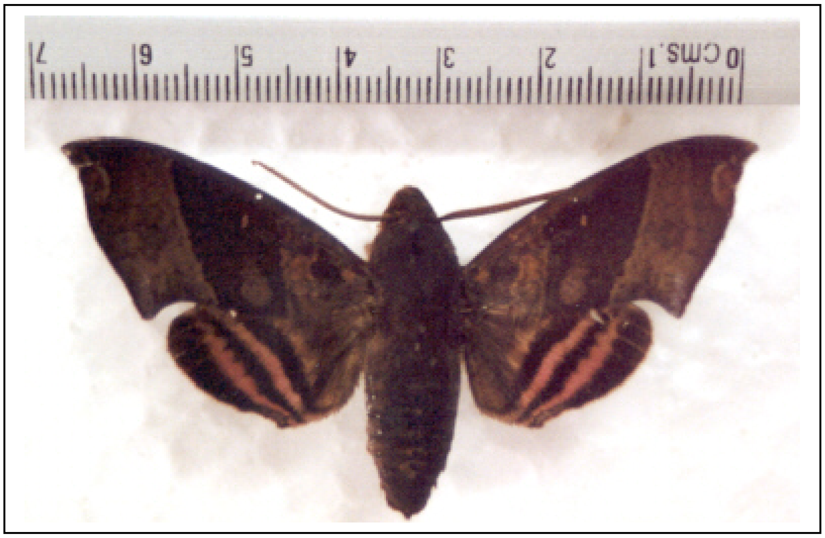


INBio: 28 specimens, 0 from Tortuguero

Pachygonidia drucei
(Rothschild & Jordan, 1903)

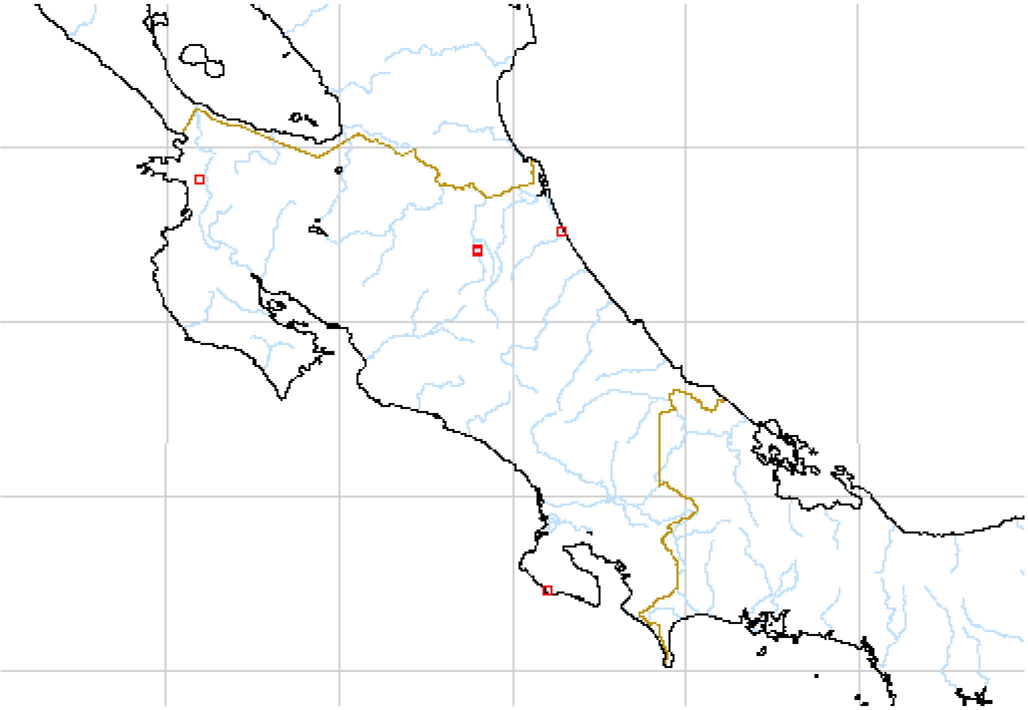
Species Rank: 60
Individuals: 1

2000 Sampling



Live weights (g) of moths taken at lights:

	Males			Females	
Mean	S.D.	n	Mean	S.D.	n



INBio: 7 specimens, 1 from Tortuguero

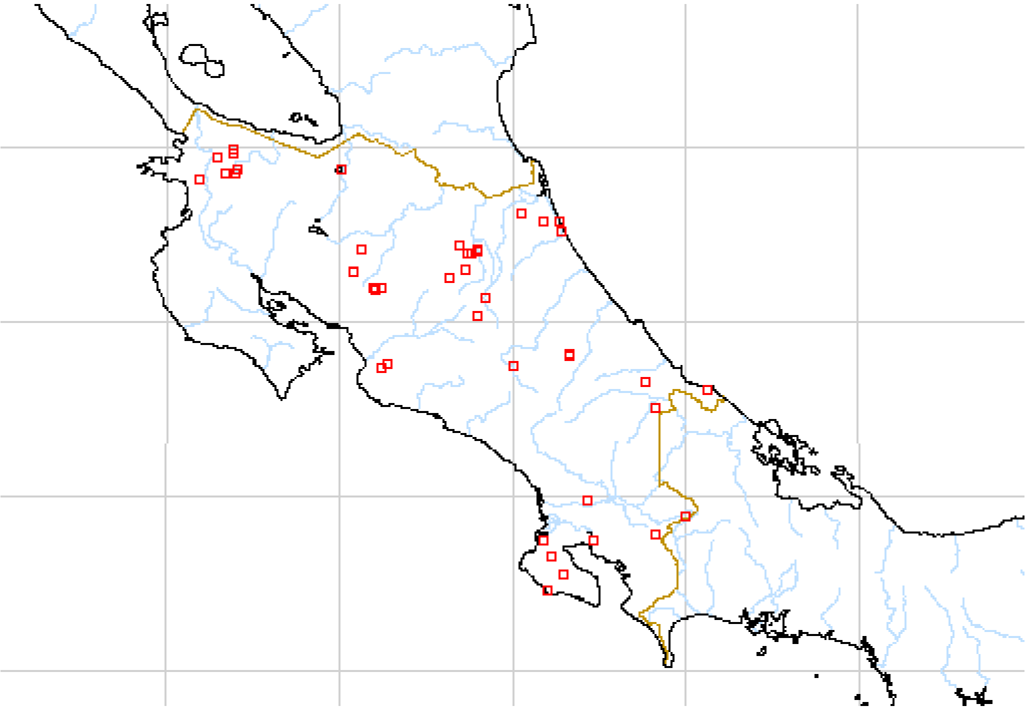
Pachylia darceta
Druce, 1881

Species Rank: 11
Individuals: 20

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.92	0.19	6			



INBio: 178 specimens, 13 from Tortuguero (2♀)

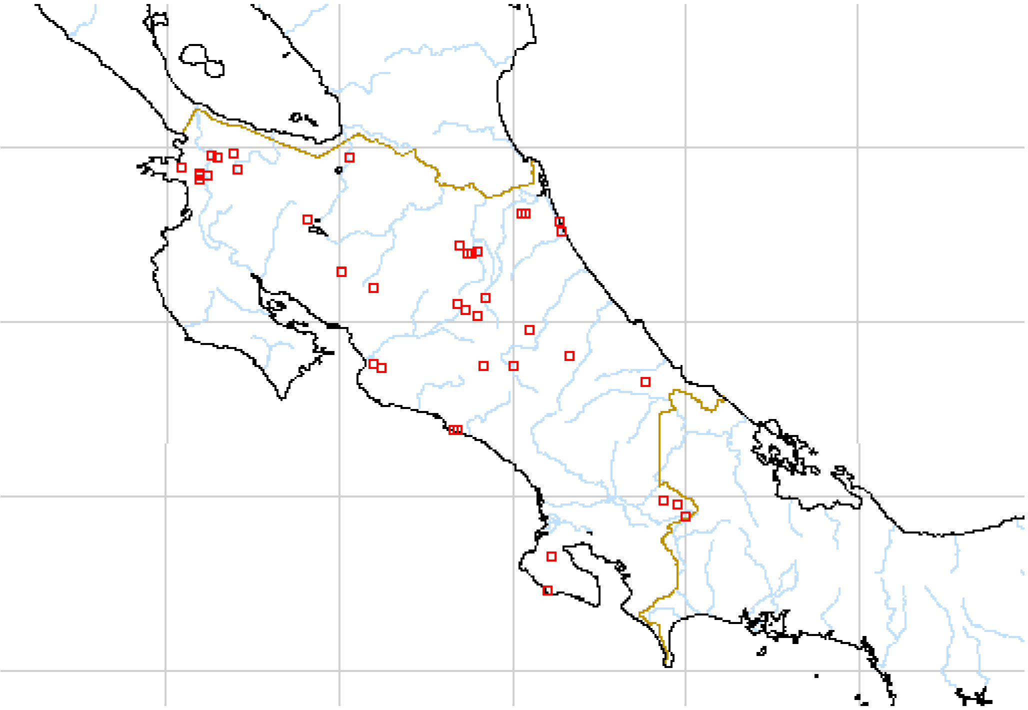
Pachylia ficus
(Linnaeus, 1758)

Species Rank: 32
Individuals: 4

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
2.3		1			



INBio: 135 specimens, 5 from Tortuguero (1♀)

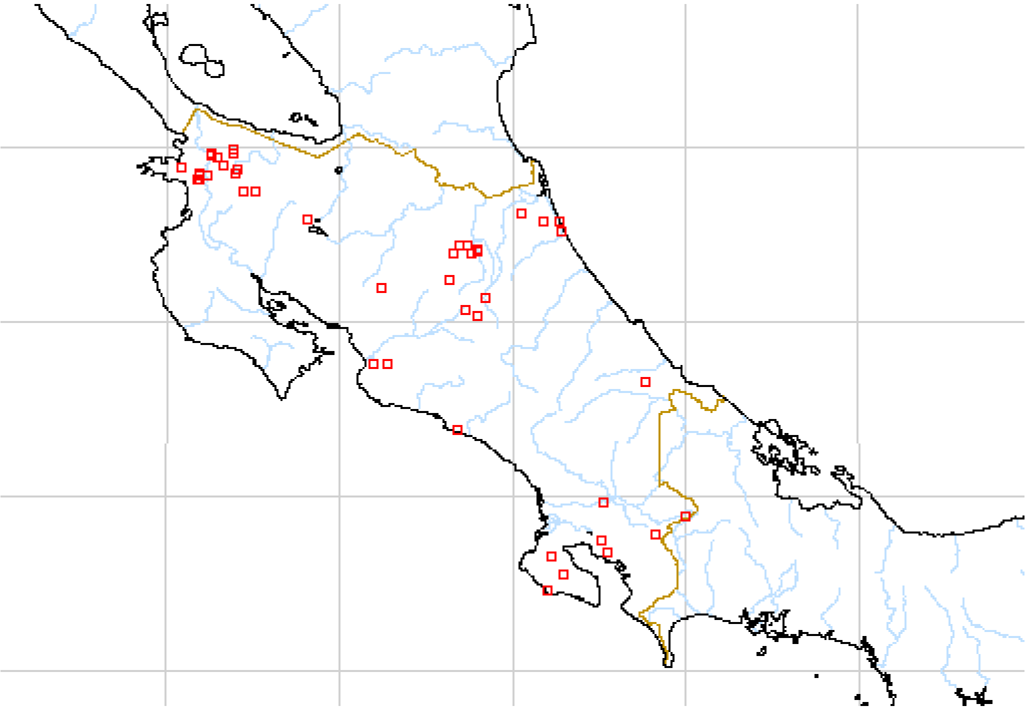
Pachyloides resumens
(Walker, 1856)

Species Rank: 33
Individuals: 4

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
2.1		1			



INBio: 132 specimens, 5 from Tortuguero (1♀)

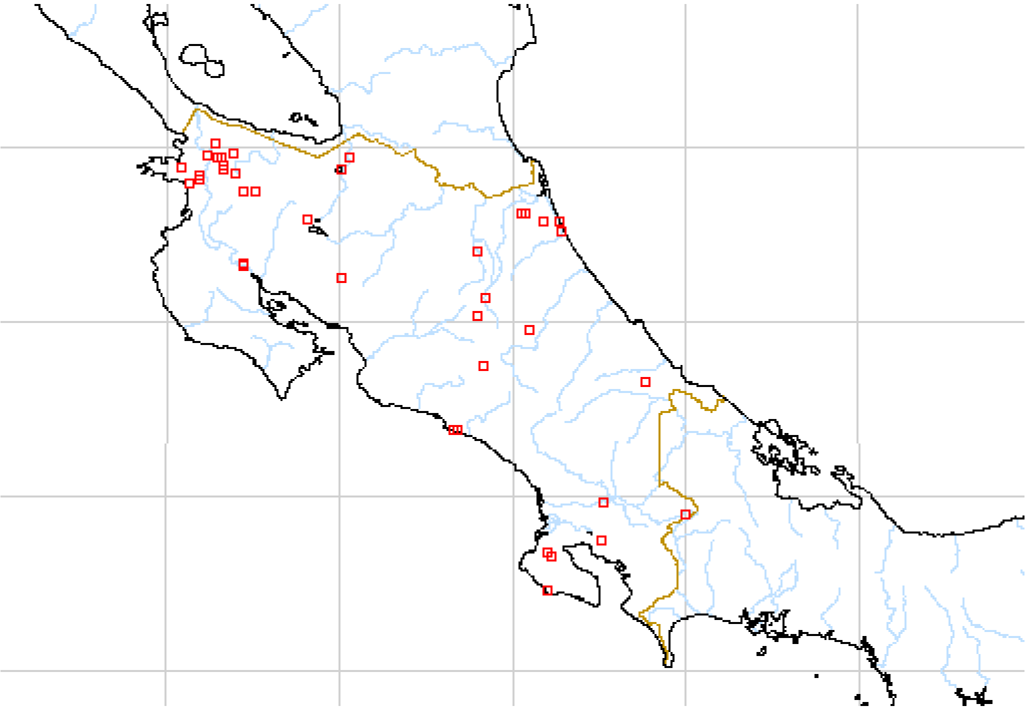
Perigonia lusca
(Fabricius, 1777)

Species Rank: 46
Individuals: 2

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.8	0	2			



INBio: 182 specimens, 3 from Tortuguero (1♀)

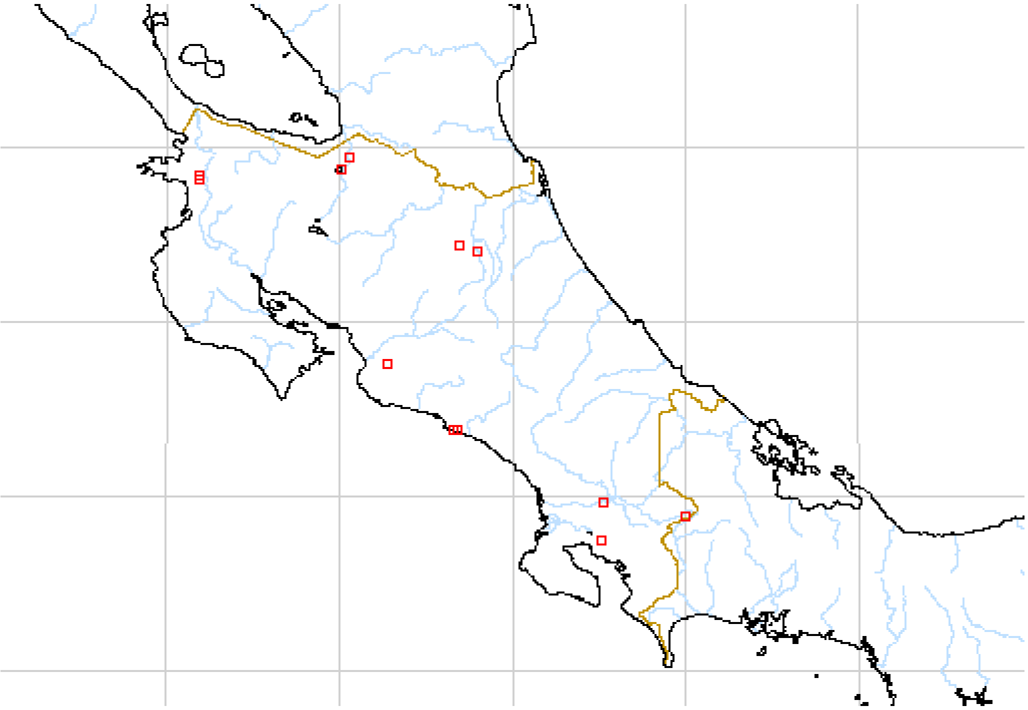
Phryxus caicus
(Cramer, 1777)

Species Rank: 61
Individuals: 1

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.7		1			



INBio: 23 specimens, 0 from Tortuguero

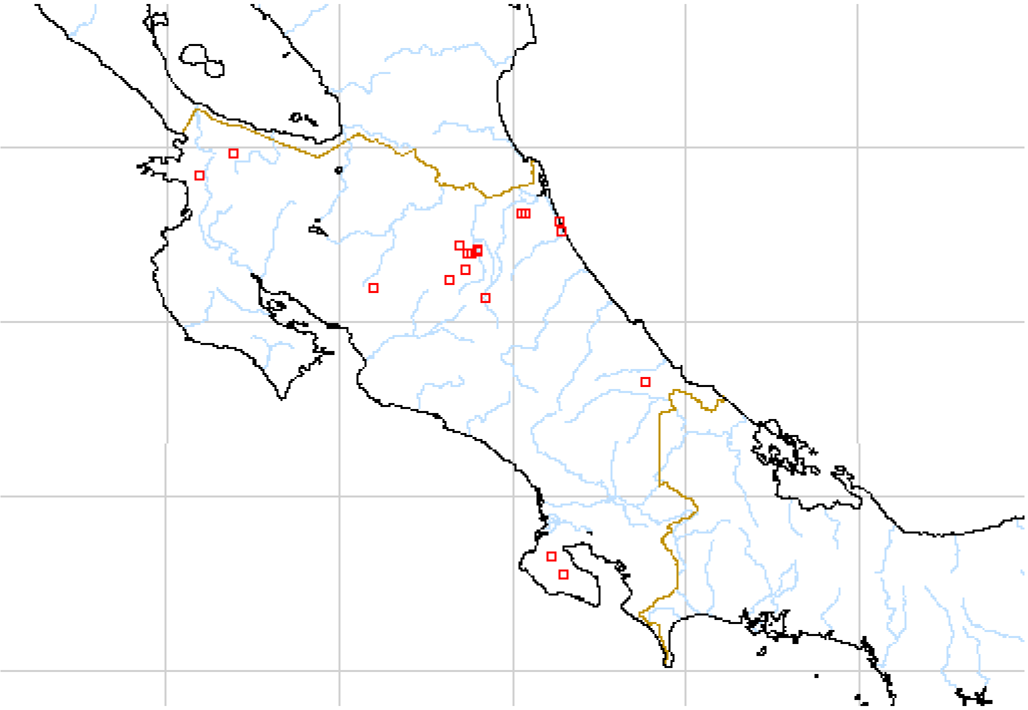
Protambulyx eurycles
(Herrich-Schäffer, [1854])

Species Rank: 21
Individuals: 10 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.33	0.13	7	1.2		1



INBio: 112 specimens, 4 from Tortuguero

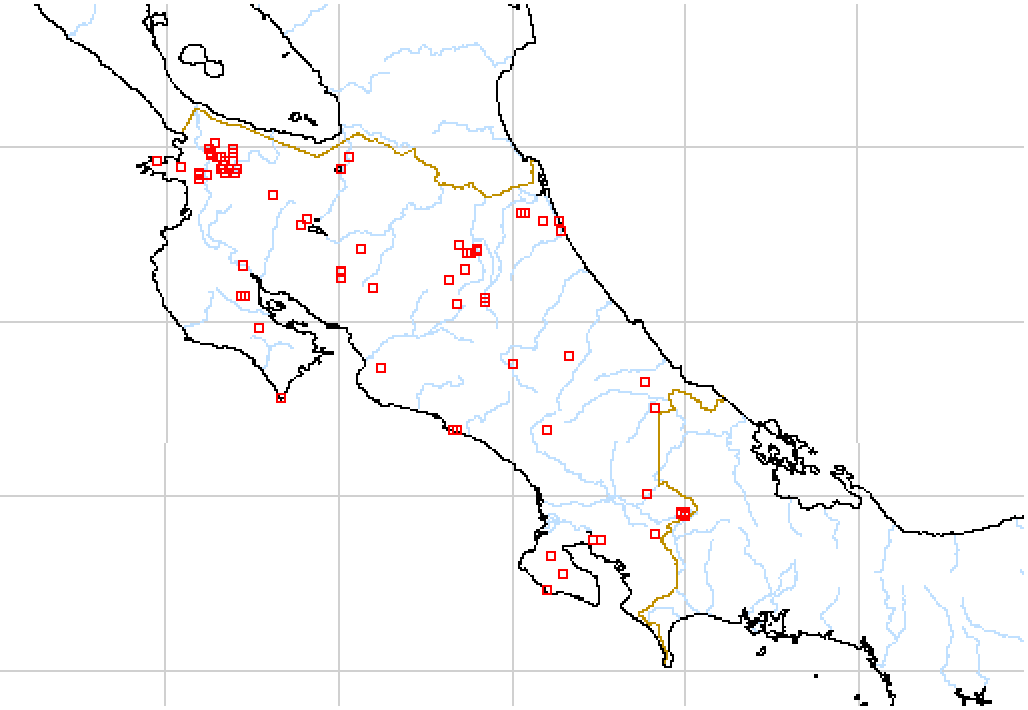
Protambulyx strigilus
(Linnaeus, 1771)

Species Rank: 3
Individuals: 39 (1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.97	0.16	10	1.5		1



INBio: 381 specimens, 26 from Tortuguero (3♀)

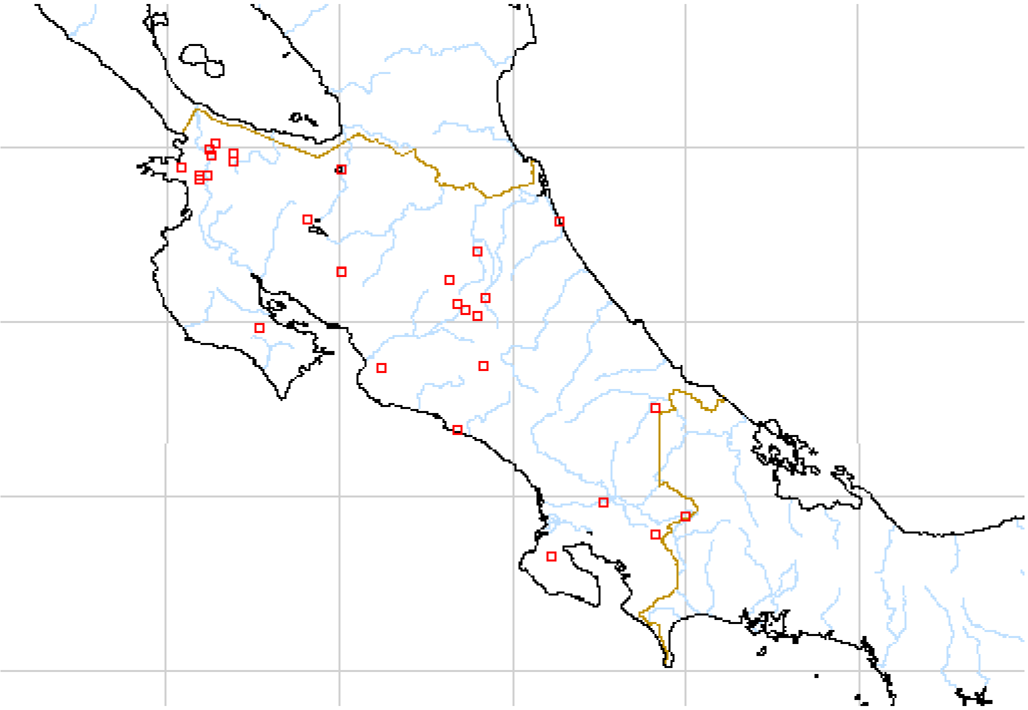
Pseudosphinx tetrio
(Linnaeus, 1771)

Species Rank: 62
Individuals: 1♀

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
			5.4		1



INBio: 82 specimens, 2 from Tortuguero (1♀)

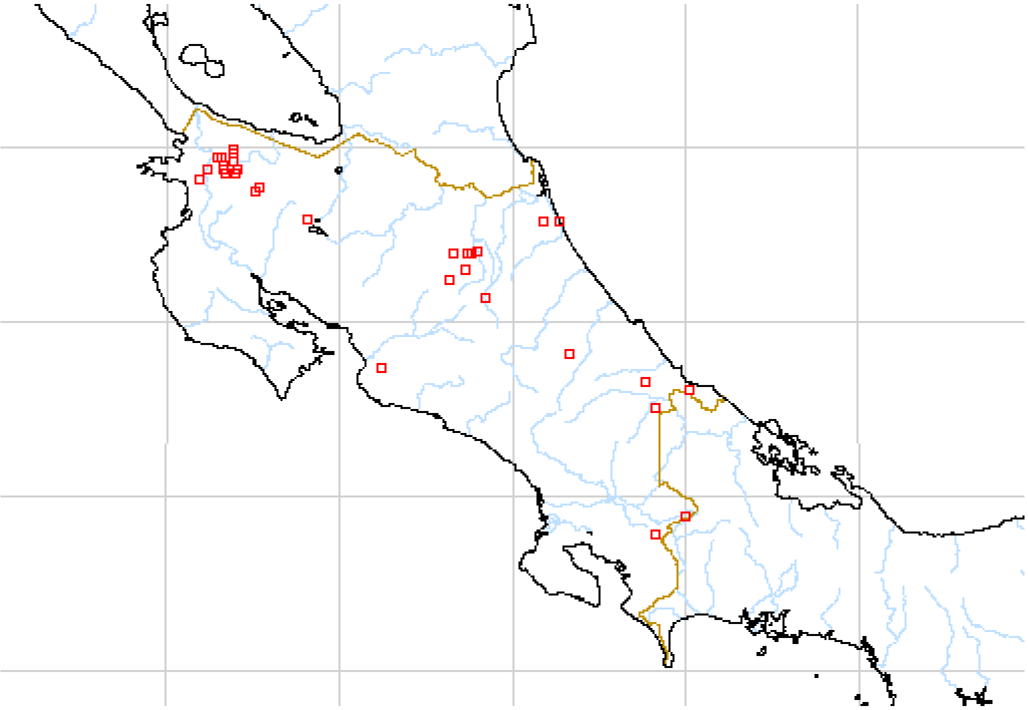
Xylophanes amadis
(Cramer, 1782)

Species Rank: 18
Individuals: 12

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

	Males			Females	
Mean	S.D.	n	Mean	S.D.	n
0.88	0.33	8			



INBio: 197 specimans, 2 from Tortuguero (1♀)

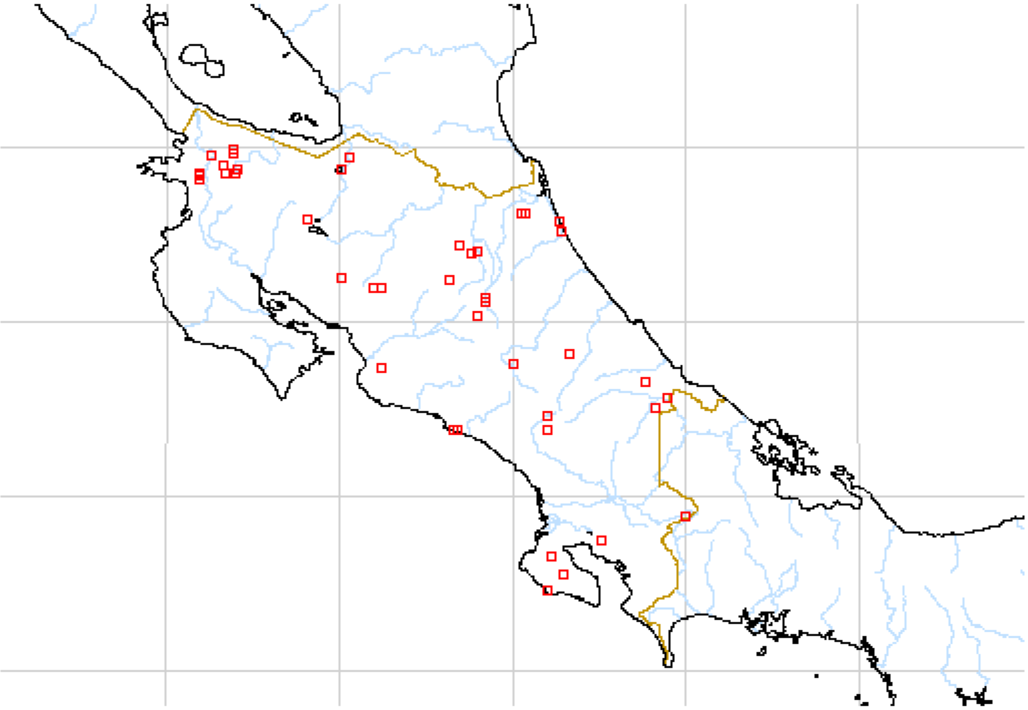
Xylophanes anubus
(Cramer, 1777)

Species Rank: 12
Individuals: 17

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.0	0.27	8			



INBio: 122 specimens, 4 from Tortuguero

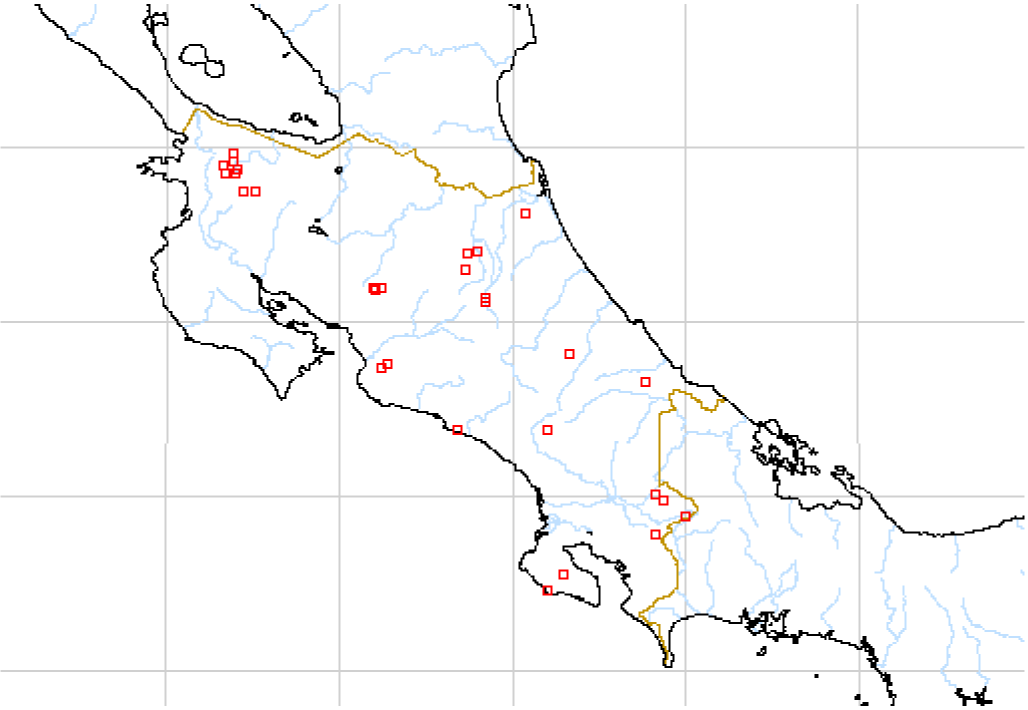
Xylophanes belti
(Druce, 1878)

Species Rank: 47
Individuals: 2

2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.9	0.42	2			

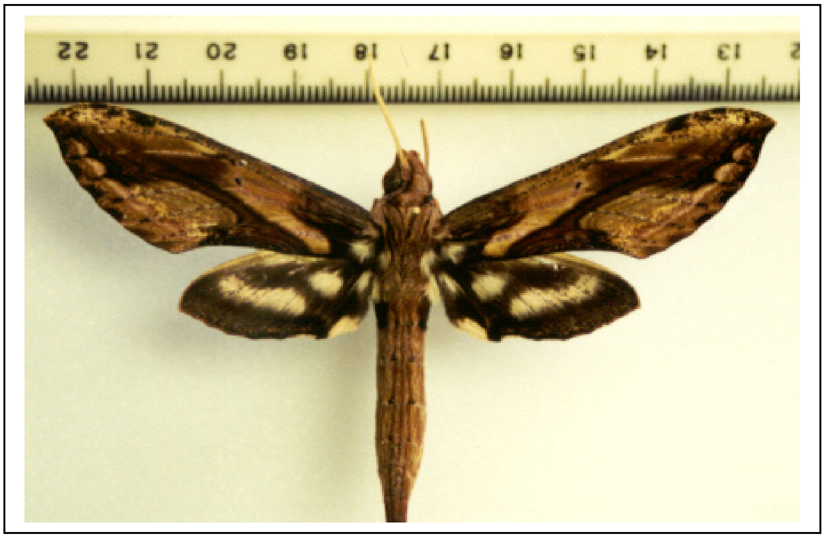


INBio: 101 specimens, 0 from Tortuguero

Xylophanes ceratamioides
(Grote & Robinson, 1867)

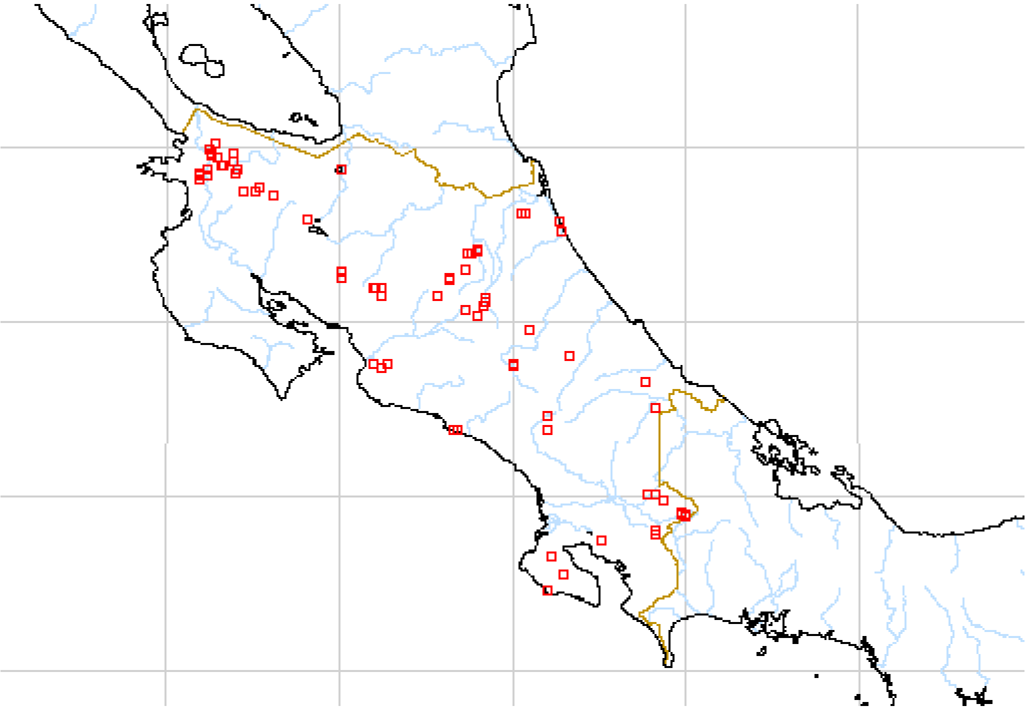
Species Rank: 48
Individuals: 2

2000 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.0	0.14	2			



INBio: 333 specimens, 8 from Tortuguero

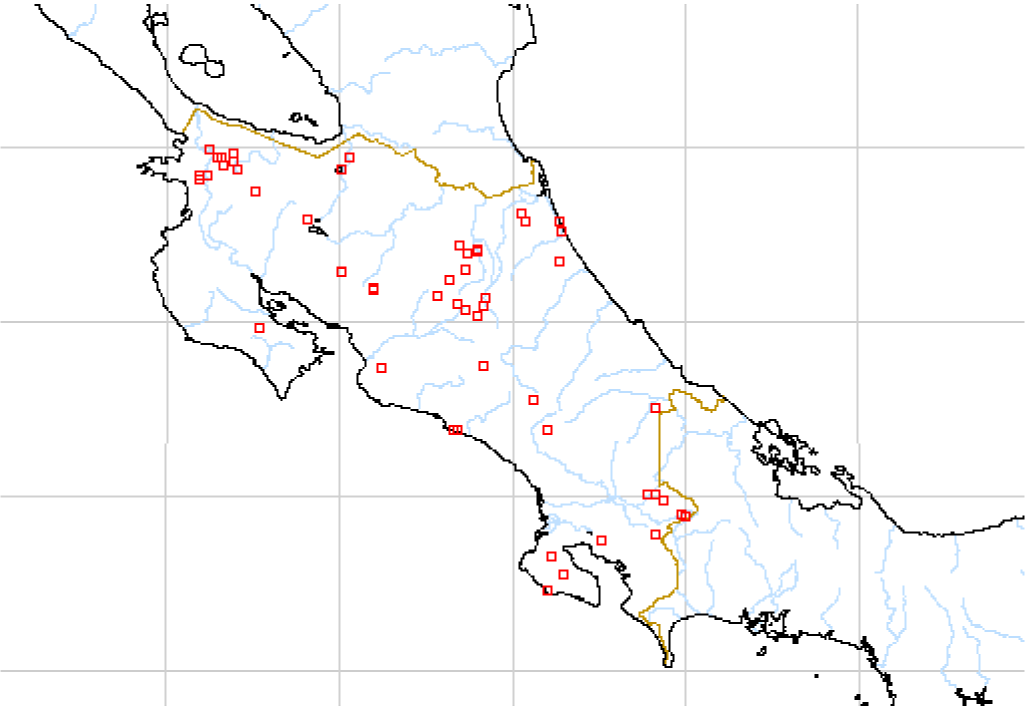
Xylophanes Chiron nechus
(Drury, 1773)

Species Rank: 19
Individuals: 12

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.97	0.06	3			



INBio: 350 specimens, 26 from Tortuguero (5♀)

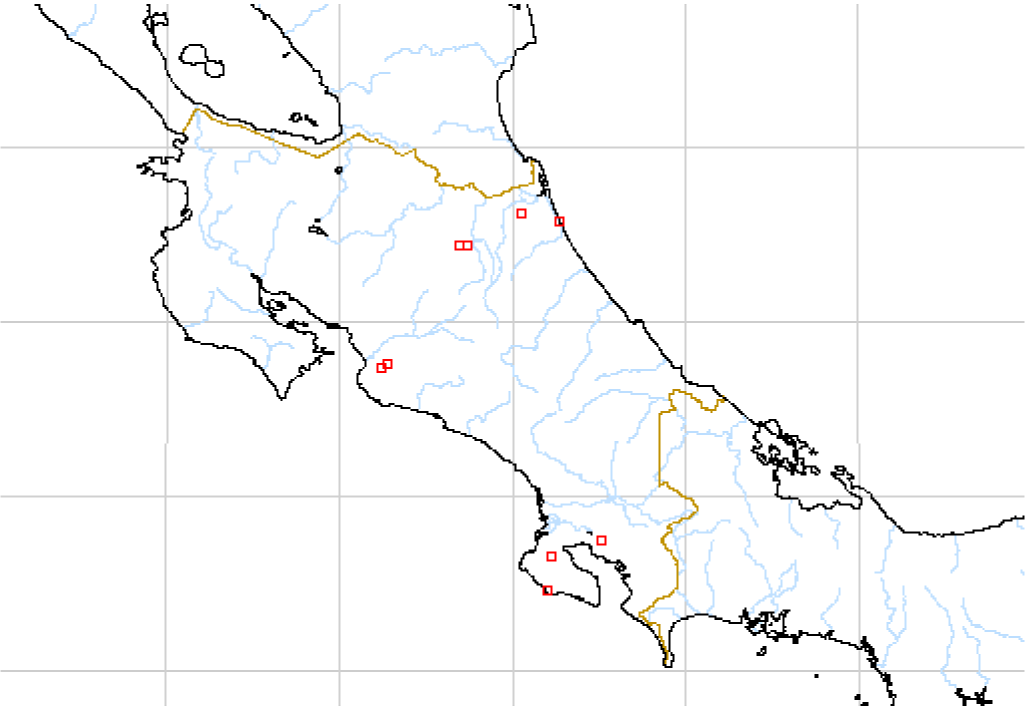
Xylophanes guianensis
(Rothscild, 1894)

Species Rank: 17
Individuals: 13

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.95	0.15	6			



INBio: 12 specimens, 1 from Tortuguero

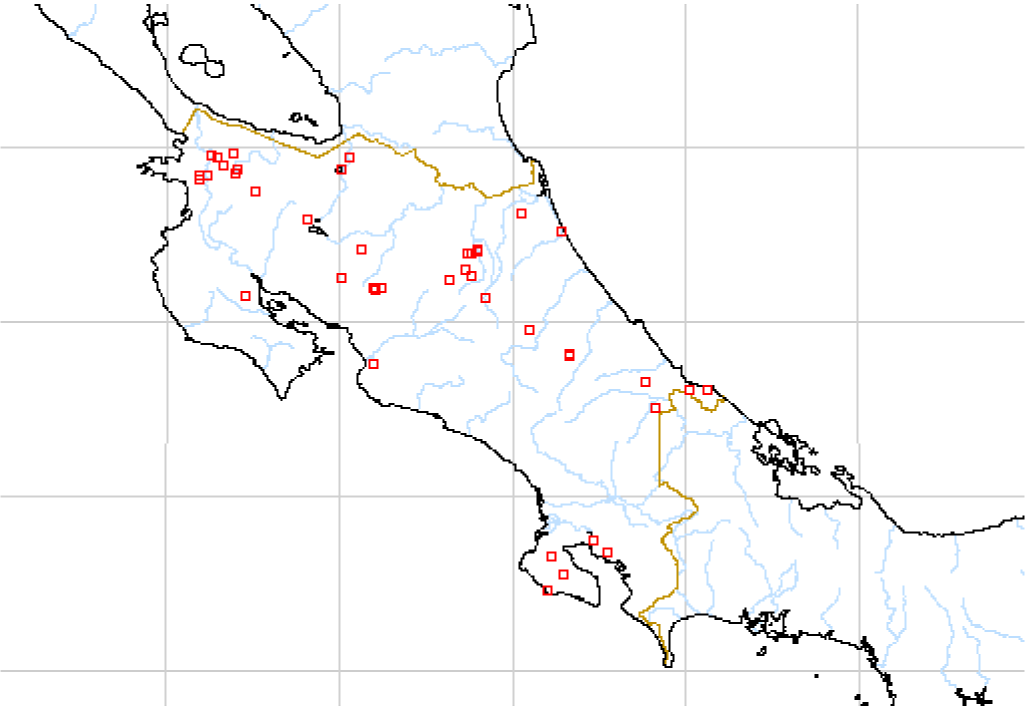
Xylophanes libya
(Druce, 1878)

Species Rank: 27
Individuals: 6

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.53	0.05	4			



INBio: 144 specimens, 1 from Tortuguero

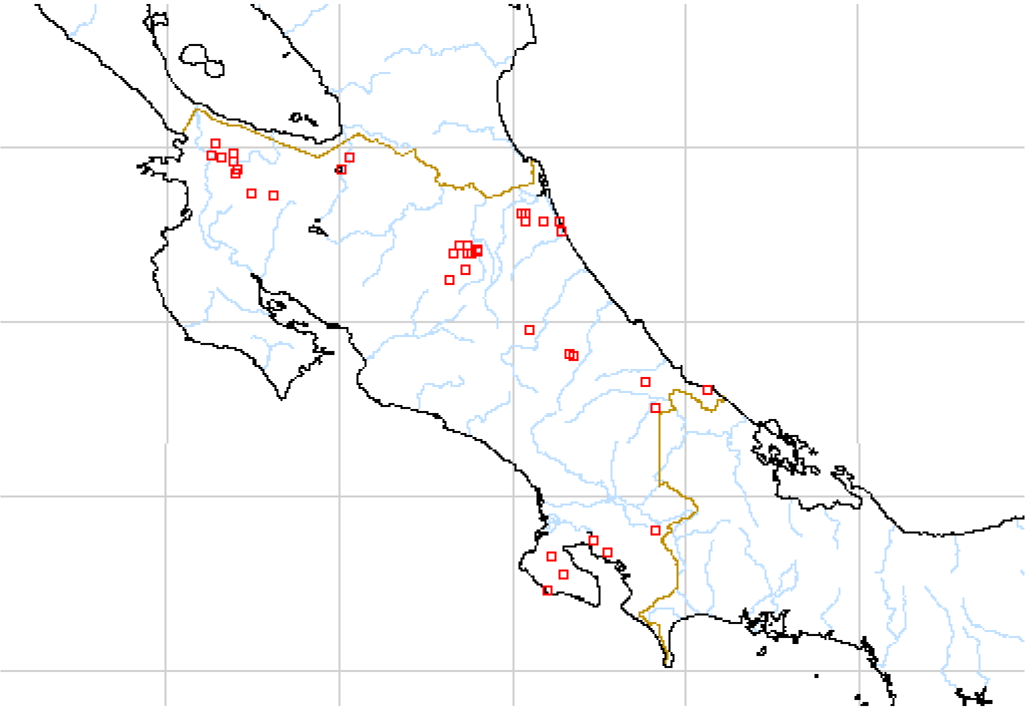
Xylophanes loelia
(Druce, 1878)

Species Rank: 2
Individuals: 61

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.55	0.08	10			

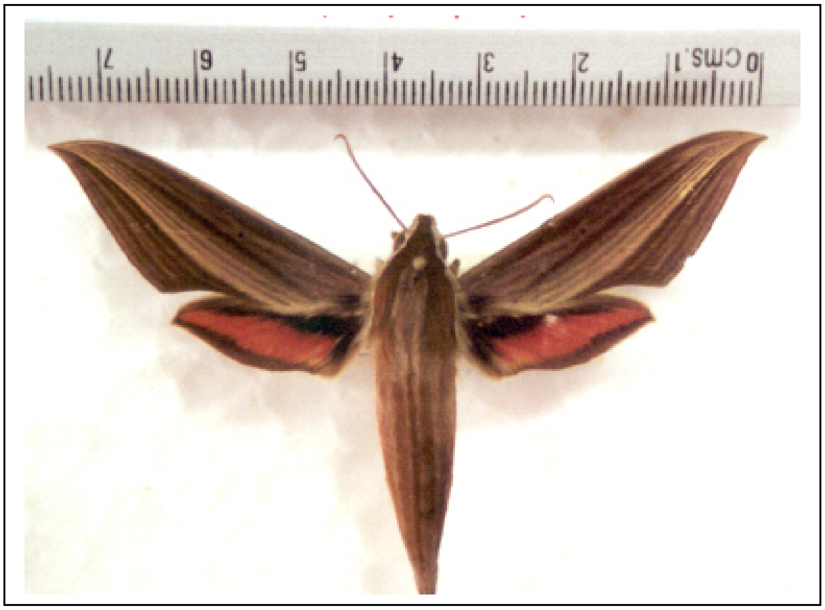


INBio: 330 specimens, 8 from Tortuguero (1♀)

Xylophanes neoptolemus
(Cramer, 1878)

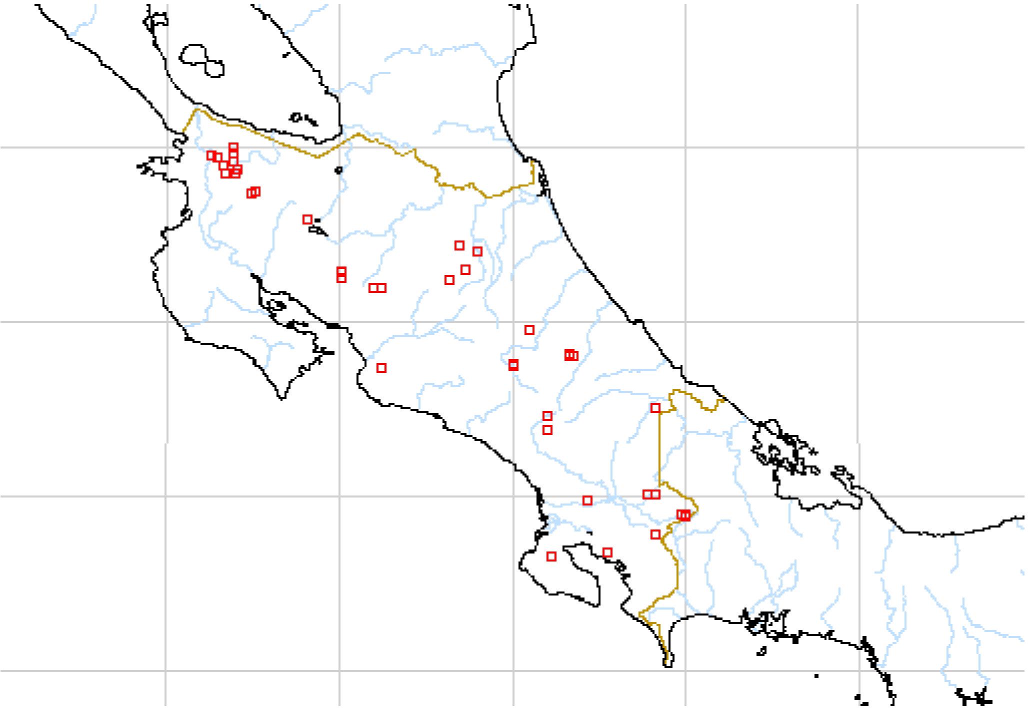
Species Rank: 29
Individuals: 5

2000 Sampling



Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.62	0.15	6			



INBio: 198 specimens, 0 from Tortuguero

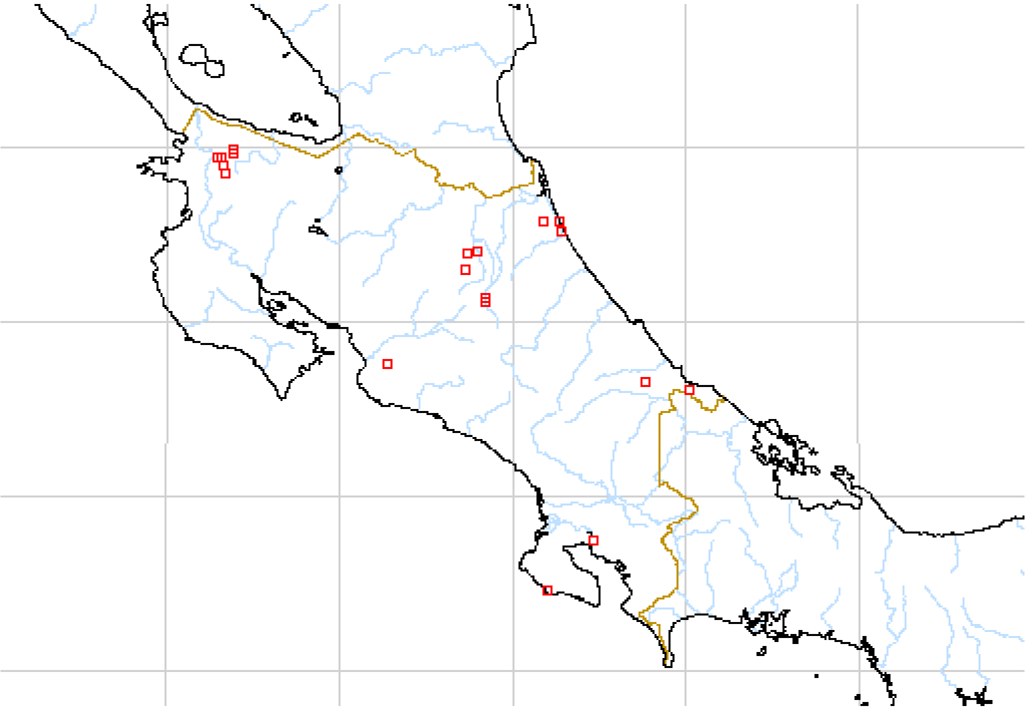
Xylophanes pistacina
(Boisduval, [1875])

Species Rank: NA
Individuals: NA

1999 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 53 specimens, 4 from Tortuguero

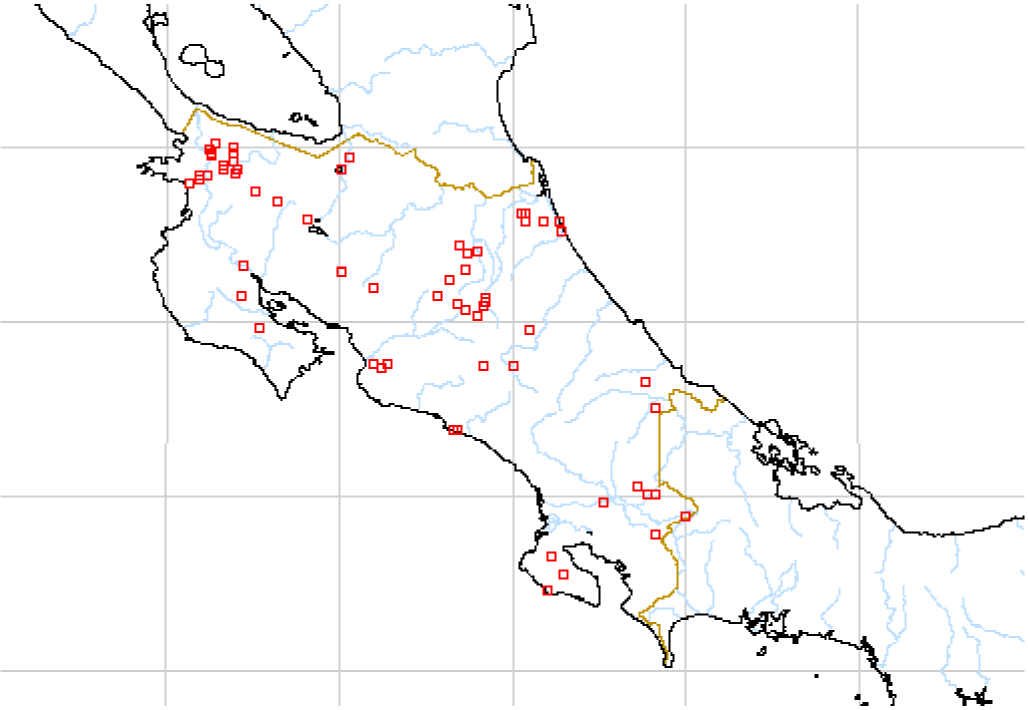
Xylophanes pluto
(Fabricius, 1777)

Species Rank: 34
Individuals: 4

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n



INBio: 407 specimens, 17 from Tortuguero (2♀)

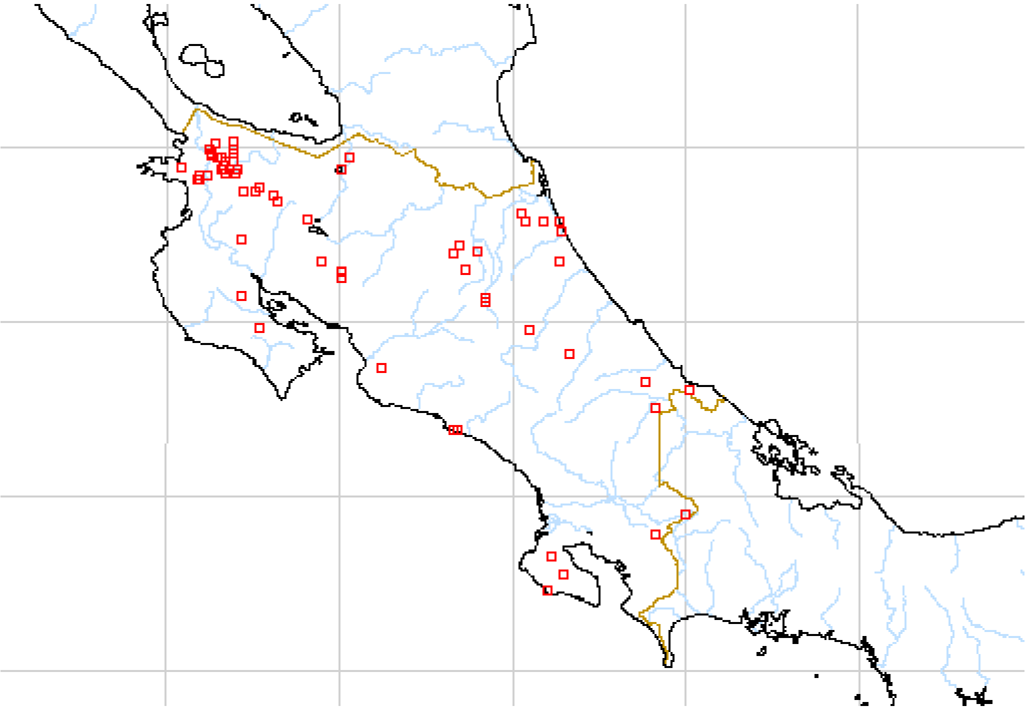
Xylophanes porcus
(Hübner, [1823])

Species Rank: 5
Individuals: 28(1♀)

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.72	0.13	5	0.8		1



INBio: 313 specimens, 31 from Tortuguero (1♀)

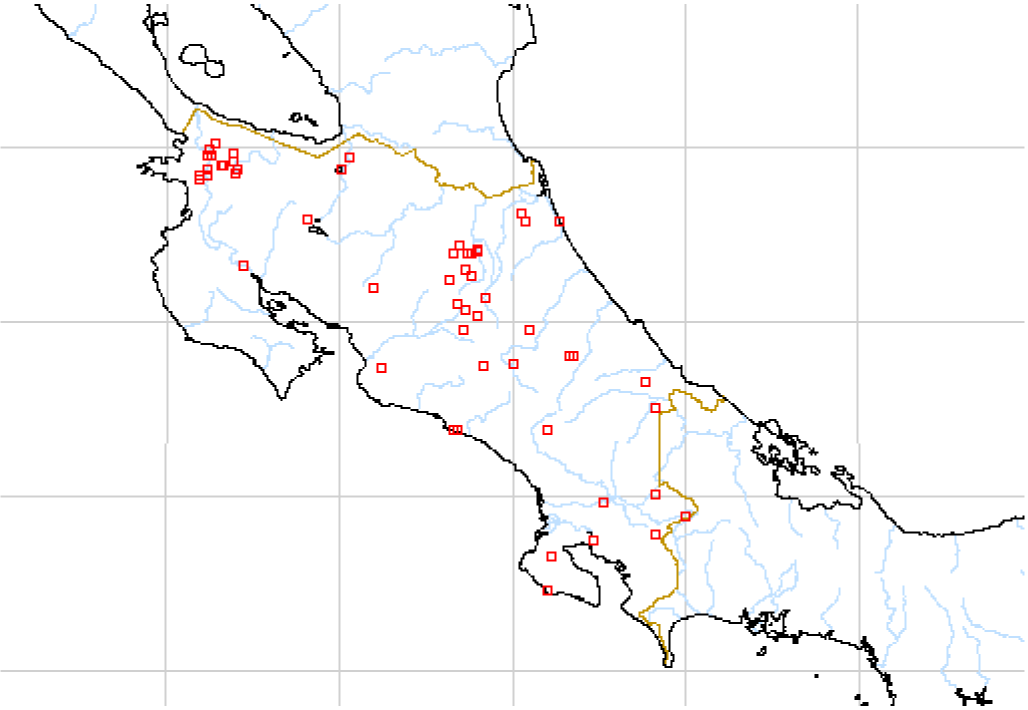
Xylophanes tersa
(Linnaeus, 1771)

Species Rank: 8
Individuals: 23

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.58	0.20	10			



INBio: 399 specimens, 4 from Tortuguero

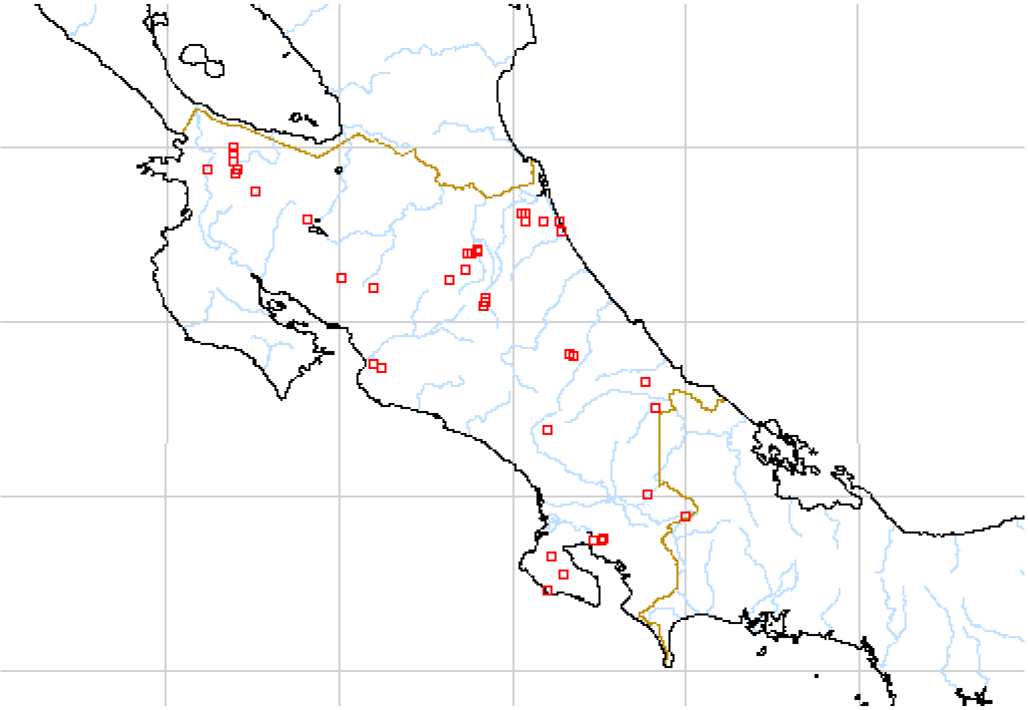
Xylophanes thyelia
(Linnaeus, 1758)

Species Rank: 9
Individuals: 21

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.33	0.02	10			



INBio: 283 specimens, 23 from Tortuguero

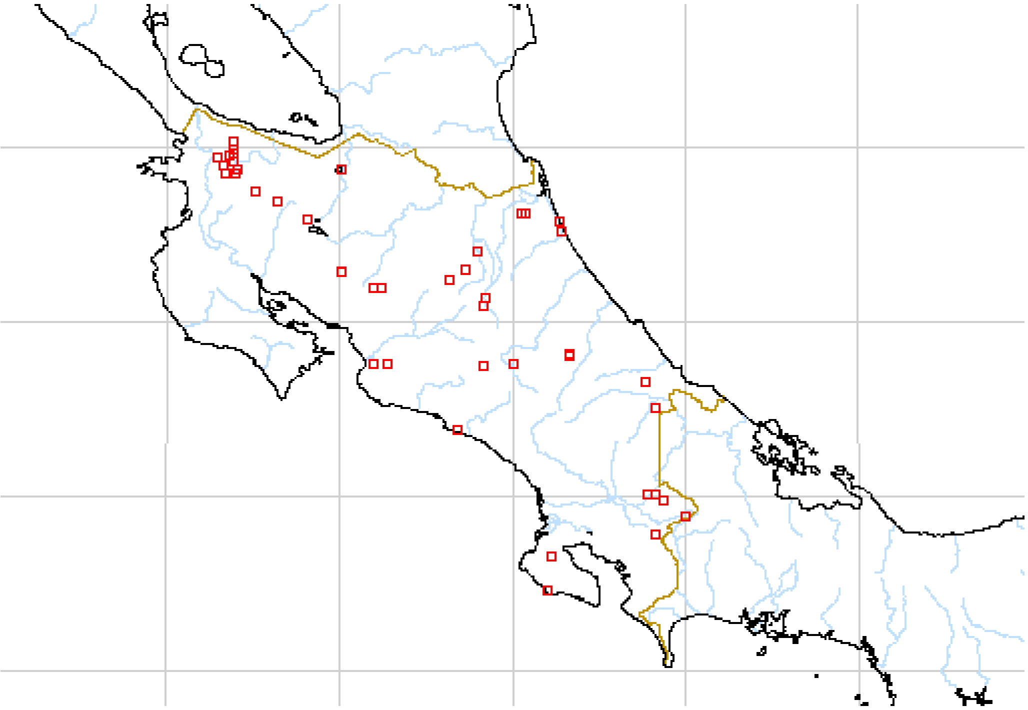
Xylophanes titana
(Druce, 1878)

Species Rank: 42
Individuals: 3

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.7	0.28	2			



INBio: 179 specimens, 6 from Tortuguero

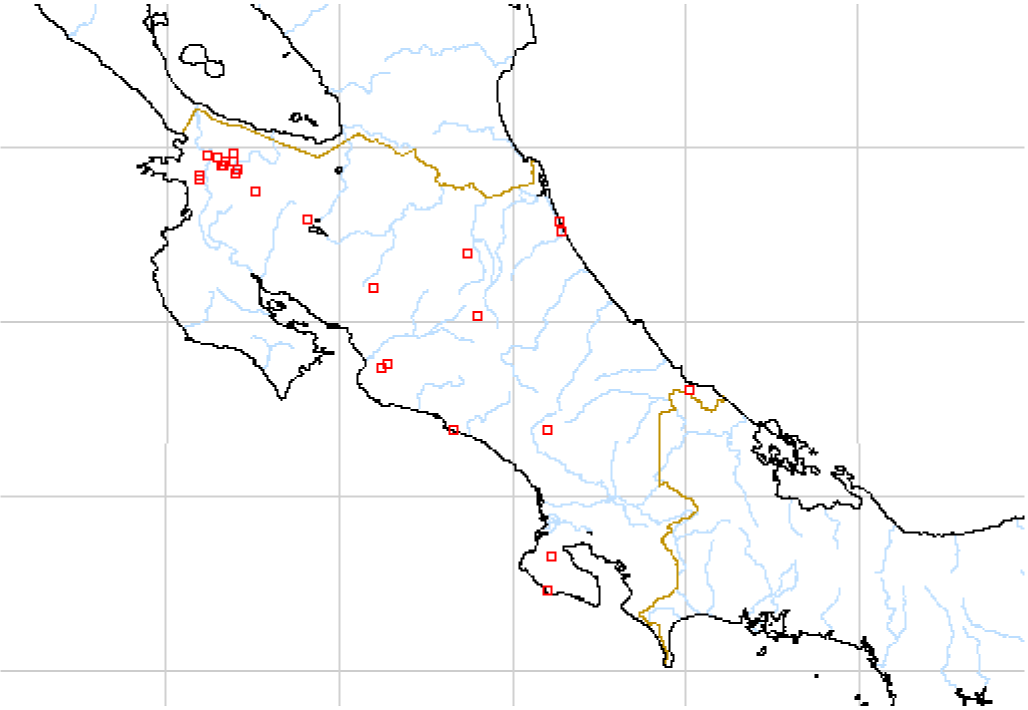
Xylophanes tyndarus
(Boisduval, [1875])

Species Rank: 49
Individuals: 2

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
1.6		1			



INBio: 73 specimens, 4 from Tortuguero

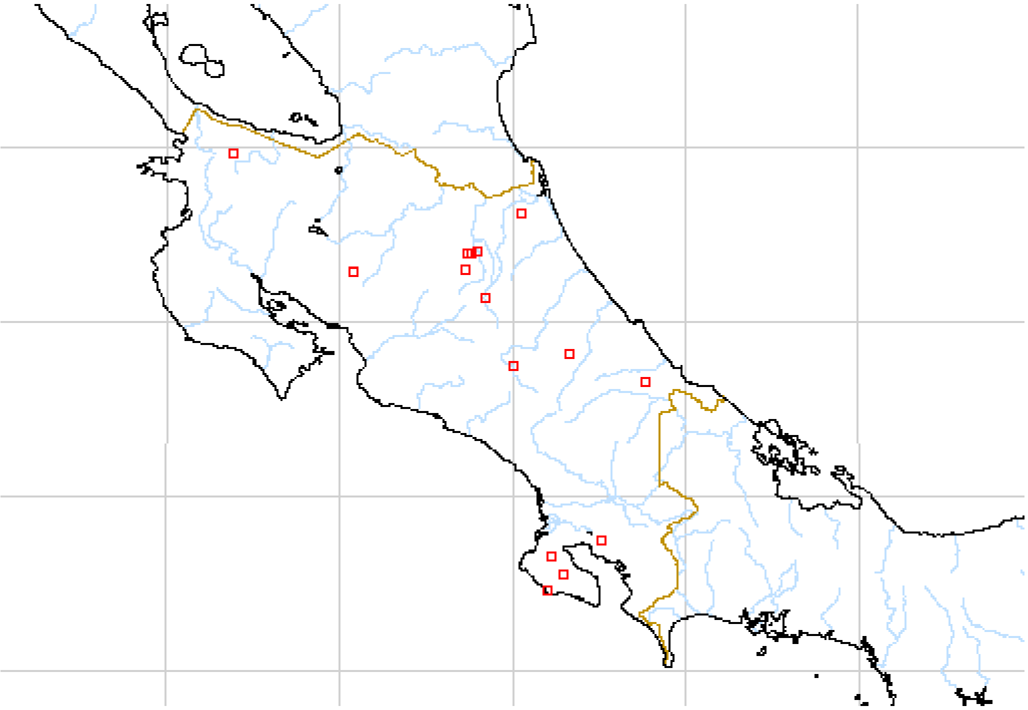
Xylophanes undata
Rothschild & Jordan, 1903

Species Rank: 20
Individuals: 11

1999 & 2000 Sampling

Live weights (g) of moths taken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.67	0.18	6			



INBio: 46 specimens, 0 from Tortuguero

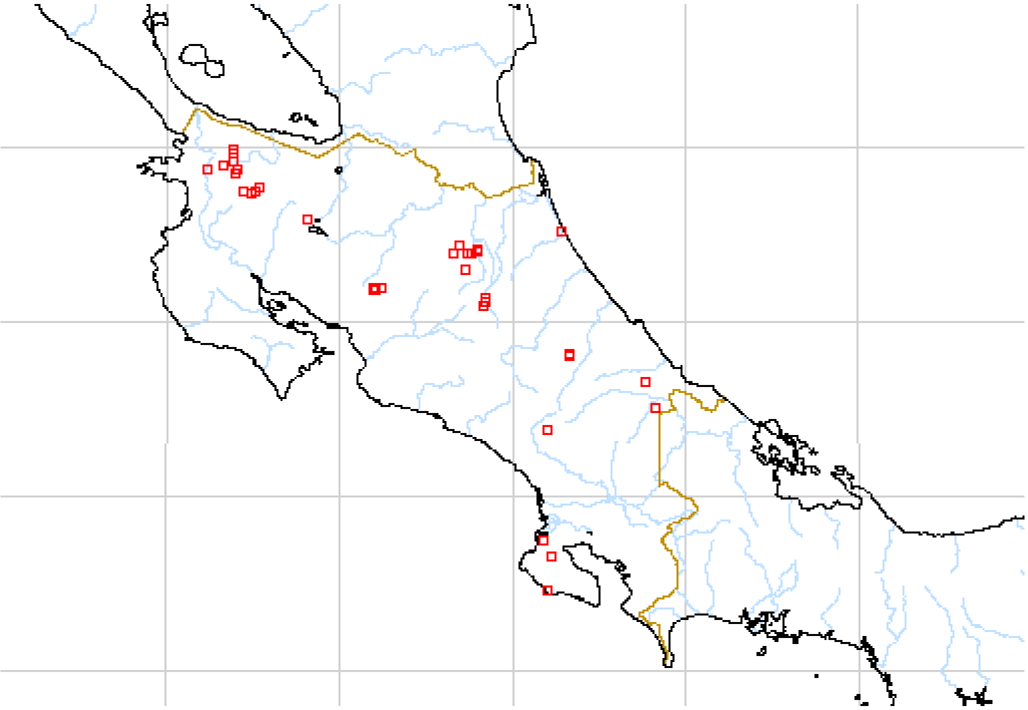
Xylophanes zurcheri
(Druce, 1894)

Species Rank: 25
Individuals: 8

2000 Sampling

Live weights (g) of mothstaken at lights:

Males			Females		
Mean	S.D.	n	Mean	S.D.	n
0.8	0.10	3			



INBio: 187 specimens, 4 from Tortuguero