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Lepidopteran diversity and abundance across five different indigenously managed land use zones in the Naso-Teribe Territory, Bocas del Toro Province, Panama

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Abstract

Lepidopterans, the order that includes both moths and butterflies, are among the best-known insects taxonomically and ecologically due to the relative ease of monitoring them in comparison to other groups of insects. Their distribution follows that of other insects and forms of life, as around 90% of species have a tropical distribution. This incredibly speciose group of animals fills many vital roles in the ecosystems they inhabit, including herbivores in their larval stages, prey for a variety of predators in all life stages, and pollinators for many plant species as adults. In some circumstances, certain species may also serve as accurate indicators, which can be used to predict the biodiversity of other groups of animals and assess the health of ecosystems. As a result of all these important features, the conservation of Lepidopterans in the age of the Anthropocene is of high priority. Within conservation biology, an ideological debate on the ideal way to maximize both biodiversity conservation and agricultural production has arisen. Currently it appears that in the tropical regions of the world, the 'land sharing' approach which encourages the enhancement of habitat across the landscape, including in agricultural zones, is superior to the 'land sparing' approach that emphasizes the importance of protected areas. In this study, the effect of indigenous land-management in 5 different land-use zones on Lepidopteran communities in the Naso-Teribe Territory of Panama is investigated. The hypothesis was that areas such as pastures and agroecological crop fields will be able to support similar levels of biodiversity as primary forests. While the forest was found to be the most biodiverse area with high levels of endemism, the pasture and agroecological zones were also found to harbor high levels of species richness and important populations of Lepidopterans.

Resumen

Los lepidópteranos, el orden que incluye las polillas y las mariposas, se encuentran entre los insectos más conocidos taxonómicamente y ecológicamente debido a la relativa facilidad de monitorarlos en comparación con otros grupos de insectos. Su distribución sigue la de otros insectos y formas de vida, ya que alrededor del 90% de las especies tienen una distribución tropical. Este grupo increíblemente específico de animales llena muchos papeles vitales en los ecosistemas que habitan, incluyendo herbívoros en sus etapas larvales, presa de una variedad de depredadores en todas las etapas de la vida, y polinizadores para muchas especies de plantas como adultos. En algunas circunstancias, ciertas especies también pueden servir como indicadores precisos, que pueden utilizarse para predecir la biodiversidad de otros grupos de animales y evaluar la salud de los ecosistemas. Como resultado de todas estas características importantes, la conservación de los Lepidópteranos en la edad del Antropoceno es de alta prioridad. Dentro de la biología de la conservación, ha surgido un debate ideológico sobre la forma ideal de maximizar la conservación de la biodiversidad y la producción agrícola. En la actualidad parece que en las regiones tropicales del mundo, el enfoque de "compartir la tierra" que fomenta la mejora del hábitat en todo el paisaje, incluso en las zonas agrícolas, es superior al enfoque de "preservación de tierras" que enfatiza la importancia de las áreas protegidas. En este estudio, se investiga el efecto de la ordenación de la tierra indígena en 5 zonas diferentes de uso de la tierra en las comunidades de Lepidópteran en el territorio de naso-Teribe de Panamá. La hipótesis era que áreas como pastos y campos de cultivo agroecológicos podrán apoyar niveles similares de biodiversidad como los bosques primarios. Mientras que el bosque fue encontrado para ser la zona más biodiversa con altos niveles de endemismo, las zonas de pastos y agroecológicos también se encontraron para albergar altos niveles de riqueza de especies y poblaciones importantes de Lepidópteranos.

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1. Introduction

1.1 Lepidopteran Biology

Within the vast cornucopia that is insect life on planet earth, some of the most aesthetically appealing and biologically significant species can be found in the order Lepidoptera. Encompassing both moths and butterflies, Lepidopterans have fascinated human beings for millennia with their iridescent colors and intricate patterns, exerting such a powerful influence that they serve as recurrent motifs in art and spirituality in many human cultures (Hogue 2009). In part due to this allure, Lepidopterans are among the best-known insects in terms of taxonomy and ecology; over 157,000 species are currently recognized, with around 800 new species being described each year (Kristensen et al. 2006; Mitter et al. 2017). Moths compose the majority of this order, as there are between 18,000 and 20,000 described species of butterflies (Kristensen et al. 2006). However, moths are a more vexing subject of study due to their speciosity and primarily nocturnal nature. Butterfly biology has made substantial contributions to general scientific understanding of ecological principles, speciation and evolution, and conservation, but the Lepidopteran fauna of temperate regions are much more well-known than their tropical counterparts (Bonebrake et al. 2010; Devries et al. 2011). In addition, the looming threats of deforestation and habitat destruction that jeopardize the populations of many animals continue to thwart conservation efforts in the tropics (Lele et al. 2010). Thus, a research imperative exists to further explore the diversity, abundance, and distribution of tropical Lepidopterans.

Aggregate insect biodiversity peaks in tropical forests and dwindles as latitude increases and, accordingly, around 90% of butterfly species have a tropical distribution (Bonebrake et al. 2010). In addition, within the world's tropical areas (defined as land between the tropics of Cancer and Capricorn) forests are the predominant component of the landscape, though deforestation is a looming threat (FAO 2015). The distribution of Lepidopteran communities within these vast tracts of forest is determined by a number of factors. Tropical butterflies can be divided into two guilds based on the food resources utilized by adults: those that feed primarily on flower nectar, and those that obtain nutrition from rotting fruits or plant sap (Riberio et al. 2012). The floristic composition and physical structure of sylvan environments can be highly variable at small scales, and thus the distribution of butterflies often reflects that of the resources used by that species in the larval and adult stages rather than being random (Ribeiro et al. 2012). In addition, most butterflies are specialists on one or a few closely related species of plant. Less than 10% of all butterfly species are polyphagous, eating more than three families of plants (Friberg et al. 2008). Butterflies that are specialists on just a few plant species will accordingly be more spatially restricted than generalists. This high degree of reliance on particular plant species illustrates how complex and interconnected trophic interactions in robust ecosystems can be, and emphasizes the role that floral community composition plays in the species assemblages of all other organisms.

 Within undisturbed tropical forest environments, the different resources and microhabitats produced by each level of the canopy also results in a vertical stratification of butterfly diversity (Devries et al. 2011). For fruit feeding butterflies in the Neotropics, nearly half of species diversity has been found to be in the canopy layer (Molleman et al. 2006). Dispersal capability, a function of both morphology and behavior, is highly variable among tropical butterflies. Some

species, such as those in the genus *Heliconius*, exhibit remarkable home range behaviors, returning daily to the same roosting site (Mallet 1986). Alternately, although the climatic extremes of winter and summer that dictate life in temperate zones are absent from the tropics, seasonality in the form of wet and dry periods still prompts Neotropical butterfly populations to disperse or migrate sizeable distances. One common strategy utilized is a contraction of habitat during inhospitable dry periods, as individuals take refuge in riparian or moist areas, and then subsequent expansion during favorable conditions (Bonebrake et al. 2010). All of these factors that contribute to butterfly distribution and species assemblages across spatial and temporal scales have important implications for conservation, an increasingly important discipline in the age of the Anthropocene. A recent paper reports that 53% of global Lepidopteran species are declining in number and 34% are threatened, according to IUCN criteria (Sanchez-Bayo and Wyckhuys 2019). What consequences does this striking deterioration have in store for terrestrial ecosystems?

      1.2 Importance of Lepidopterans for Ecosystems

Caterpillars, the larval stages of a Lepidopterans' life cycle, constitute a vital part of many forest food webs. In many regions, they consume more plant leaves than all other animals combined (Janzen 1988; Endara et al. 2017). Scientists have characterized the relationship between plants and their associated herbivores as a co-evolutionary arms race due to the defense chemicals that plants produce as secondary metabolites, which repel herbivores by being toxic, anti-digestive, or anti-nutritive (Kessler and Kalske 2018). In response, when Lepidopterans sense these chemical cues, they will search for a more suitable host plant, which may be in a different stage of life and thus more palatable, or may be a different species entirely (Ehrlich and Raven 1964; Kessler and Kalske 2018). This coevolutionary model of escalating plant evasion and subsequent insect adaptation to enable consumption has been posited to account for the astounding diversity of both insects and their plant hosts in the tropical regions of the world (Marquis et al. 2016; Endara et al. 2017). However, Endara et al. (2017) found evidence of an evolutionary asymmetry in the interaction of the Amazonian tree genus *Inga* and its lepidopteran herbivores. They propose that the herbivores are not demonstrating coevolutionary adaptations, but engaging in resource tracking by chasing certain plants with similar defense systems. Thus, the exact mechanisms driving speciation in tropical insects and their host plants have not been completely elucidated, yet the capacity of Lepidopteran larvae to affect floral evolution via herbivory is clear. A significant reduction in caterpillar populations could thus have profound consequences for the genetic posterity and vitality of an ecosystem.

Caterpillars also serve as an integral trophic link in food webs; as primary consumers, they procure energy and resources from plants and make them available to secondary consumers, or predators. In tropical ecosystems a wide variety of animals, from monkeys and mice to a myriad of bird species, rely on caterpillars for sustenance (Janzen 1988). Larvae are thus a critical component of the food base. Another foundational interspecific interaction that Lepidopterans engage in is pollination, a process that takes on an increased importance in the tropics for several reasons. First, a well-documented feature of tropical forests is the extremely low densities of many tree species, with conspecifics often being isolated and self-incompatible (Bawa 1990). In addition, the hyper-competitive tropical environment, fraught with predators, pathogens, and

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other antagonistic plants, places a premium on the genetic recombination made possible by pollinators (Bawa 1990). Both of these factors demonstrate how reliant tropical angiosperms are on other organisms for their reproduction, and there is evidence in the literature that Lepidopterans are second only to bees in terms of the number of plant species pollinated (Bawa et al. 1985). Highly specialized pollination systems that work in conjunction with just a few Lepidopteran species are also common in plant families such as Rubiacea (Bawa 1990). A dearth of these Lepidopteran pollinators would thus be catastrophic for the reproduction of many tropical plant species.

1.3 Lepidopterans as Indicators and Their Response to Disturbance

The incredible fecundity of tropical ecosystems across all forms of life presents scientists with a dilemma: with limited time and resources, how can biodiversity be suitably catalogued and changes to the community monitored? One potential solution is the concept of an indicator species. Among insect orders, butterflies have been identified as the most suitable candidates for indicator species (Thomas 2005; Bonebrake et al. 2010). This is due to their sensitivity to environmental change, short generation time, and relatively resolved systematics (Bonebrake et al. 2010). In one study, Fleishman et al. (2005) found that certain butterfly species were reliable indicators not only for the butterfly community but also across taxonomic groups. In particular, butterfly species in the Neotropical sub-family Ithomiinae have been identified as especially good predictors of total lowland forest butterfly species richness due to their sensitivity to anthropogenic effects (Uehara-Prado and Freitas 2009). However, while some species may be uniquely suited to respond to the degradation of their habitat, the utility and accuracy of Lepidopteran indicators has been questioned in some circumstances.

This is due to the fact that the responses of butterfly communities as a whole to habitat loss or degradation such as would occur after conversion to agricultural land are still enigmatic. For example, a particularly sensitive indicator species may be absent from an ecosystem, but the Lepidopteran community as a whole may not necessarily be reduced in diversity or size. Bonebrake et al. (2010) included 40 studies examining the effect of land use change on tropical butterflies in their review, and found 13 studies which showed decreased diversity in anthropogenically disturbed sites as compared to protected forests. Intriguingly, they also found 13 studies that showed the opposite trend, while the rest of the studies were equivocal. The response of each individual butterfly species to anthropogenic disturbance depends on its life history and the resources it utilizes. Thus, one of the consistent patterns found in these studies is that rare and endemic species with small ranges or specialized niches are the most vulnerable to habitat loss, and usually require natural forest to persist (Horner-Devine et al. 2003). Another factor that determines how robust a community is after disturbance is the nature of the disturbance and the quality of the resulting habitat, in addition to its proximity to natural forests (Horner-Devine et al. 2003). The exact response of each Lepidopteran community will be highly dependent upon local circumstances, and more research is needed to expand scientific knowledge on the subject before broad conclusions can be reached. Regardless, though their utility and accuracy as indicators of disruption or degradation is problematic in some instances, the relative ease of monitoring butterflies compared with other insects cements their status as a valuable tool for conservation and habitat monitoring.

1.4 Conservation Paradigms and their Implications for Lepidopterans

 In the context of the present uncertainty about the response of not only moths and butterflies, but also many other orders of animals to habitat disturbance, the problem of how best to conserve populations and species arises. In human terms, the tropics today are a region of burgeoning populations and imminent demographic and economic transition, a milieu highly conducive to changing land use patterns. According to the United Nations' Global Forest Resource Assessment (2015), there was a global net loss of some 129 million ha of forest between 1990 and 2015, representing an annual net loss rate of 0.13 percent with most of that loss occurring in the tropics. The same report asserts that the rate of loss decreased substantially in recent years, and that 'planted forest' area has increased by over 105 million ha since 1990. This report relies on data that countries self-report, and has caused controversy due to conflicting results obtained in other studies. For example, Kim et al. (2015) reported a 62% acceleration of net forest loss over the humid tropics from the 1990's to the 2000's, and then a slight deceleration of 7.2% in the following decade. Regardless of the exact rates and fluctuations of forest coverage, the pivotal issue at the core of these statistics is that land use decisions determine both levels of human well-being and levels of biodiversity. Agriculture, which in various forms is the leading cause of tropical deforestation, is also the primary means by which people in non-urban areas earn a living (Houghton 2012). A pivotal debate on the optimal way to maximize both agricultural production and biodiversity has thus emerged within the conservation biology discipline (Tscharntke et al. 2012).

In temperate, economically developed countries such as those in Europe, the United States, and Japan, the conversion of forests to agriculture was a phenomenon of the past. After the 1950's, these countries underwent a forest transition in which the land area devoted to agriculture declined and the forest area increased (Wright and Samaniego 2008). Agricultural intensification was then ramped up to continue producing sufficient amounts of food, and industrial systems of agriculture characterized by monoculture, copious chemical inputs, and genetically modified crops was created (Tscharntke et al. 2012). This is still the dominant agricultural paradigm in the United States, which boasts some of the highest crop yields in the world while also facing increasing environmental degradation due to the intensive practices (Macdonald et al. 2012). Under this model of 'land sparing', a certain amount of space is reserved for nature and enclaves such as national parks are established in which human interaction with the landscape is limited to create space for other species. The ideology behind this form of conservation is largely based on theories of island biogeography that were extrapolated to these mainland 'islands' of habitat (Mendenhall et al. 2014). This extension of island biogeography developed into the associated concept of metapopulation theory, which views the areas outside of protected enclaves as a 'matrix' (Donald & Evans 2006). In land sparing, the various matrices of a landscape are inhospitable to most species of animals, so islands of habitat must be linked via the conservation mechanism of wildlife corridors to ensure gene flow among populations.

An alternate vision of landscape management is the 'land sharing' model, which suggests that partitioning the landscape into strict human and non-human zones is not the most effective way to provide habitat for other species. Instead, agroecological approaches that can sustain high levels of biodiversity while still producing sufficient food could provide a viable alternative

(Mendenhall 2014). In practice, an agroecological approach involves principles such as a reduction of chemical inputs, crop rotation, a diversity of crop species in the same field, and the cultivation of non-productive spaces such as hedgerows and buffer strips. This model of fostering a fertile matrix seems to be more amenable to the wide diversity of land use decisions present in the tropics, as it is far from clear that developing countries will or should follow a similar path of landscape transition seen in countries such as the United States (Wright and Samaniego 2008). The determining factors for the ideal system of land management will vary widely by the specific biome and locality, but generalities about the merits of both of these paradigms can be discussed.

 In recent years significant evidence has accumulated suggesting that the theories of island biogeography and metapopulation theory, so adept at predicting species distribution and loss on islands, don't translate accurately to mainland areas (Mendenhall et al. 2014). One primary reason for this inaccuracy is that these theories assume that the matrix outside of protected areas is barren, like the ocean surrounding an island, and unable to provide habitat for species that in fact often venture out into the landscape. There is also evidence that corridors, which often come with a high price tag, do not increase the functional connectivity of ecosystems as they are meant to do (Donald and Evans 2006). In certain systems, the transition from low intensity to high intensity production has been shown to have a more severe impact on biodiversity than the conversion of pristine habitats to low intensity agricultural systems (Donald and Evans 2006). With biodiversity conservation under the land sparing model failing to meet goals, an approach that considers the geographic distribution of diversity across an entire landscape is needed. Distinct communities may contribute differentially to total diversity. While the refuge provided by protected areas is vital for many species, the quality of the novel biotic assemblages that will develop in the intermittent matrices will constitute an increasingly important part of tropical gamma diversity in a future where human hegemony over the landscape only promises to increase. Thus, in terms of biodiversity conservation a land sharing approach appears to be more sustainable in the long term (Perfecto and Vandermeer 2010).

Yet the food production aspect of the problem is equally as important to consider. The applicability of intensive agriculture as a means of subsistence for the small scale, often impoverished agriculturists who will ultimately make the final land use decisions in many areas of the tropics has been questioned, as facets of the agroecological approach such as reduced chemical inputs and crop diversity are often more appealing (Perfecto and Vandermeer 2010). However, it has been projected that in order to meet a rapidly expanding population's demand for food, by 2050 the area of agriculture in developing countries may have to increase by more than 30% (Donald and Evans 2006). Authors such as Laurance et al. (2014) have asserted that even in the tropics, industrial agriculture can likely produce more food while using land, water, chemicals, and energy much more efficiently than other forms of agriculture. This claim is disputed by a number of authors, who cite concepts such as the 'paradox of the scale' or the 'inverse farm-size productivity relationship' and examples where agroecological systems produce as much, if not more, than conventional systems (Tscharntke et al. 2012; Perfecto and Vandermeer 2010). In a veritable indictment of the land sparing model, the IAASTD, an intergovernmental assessment process that involved 3 years of research and 400 experts from all

over the world, concluded that conventional/industrial agriculture is not a rational option for alleviating poverty and ending hunger and malnutrition nor for sustainable development (McIntyre et al. 2009). With these facts in consideration, it seems the land sharing model also offers more potential for the amelioration of human problems. Variations of the agroecological system that defines the land sharing model are many, and the unifying principles underlying this model that encourage non-domesticated forms of life to flourish have been present in agriculture in some areas for many years.

1.5 Applications of Indigenous Knowledge for Conservation

Science is the creed of modernity, responsible for the astounding technological advances evident in much of the developed world. However, science often brings with it pernicious externalities or side effects, especially when dealing with a natural world that often doesn't reflect rigid models or mechanistic ways of thinking. On the other hand, the rich body of knowledge possessed by many indigenous groups regarding land management in their environment is often accumulated through trial and error for generations. Though not un-scientific in nature, this wealth of information has often been ignored by scientists, to the detriment of both groups (Toledo et al. 2003). An example of the discord that exists today is the land-tenure battles that many indigenous groups find themselves fighting, which are often a result of the land sparing or colonial conservation approach to conservation; this approach dictates that all human occupants are forcibly expelled from protected areas (Schmidt and Peterson 2009).

Conservation efforts in the future will depend on a successful syncretism of science and indigenous experience, because over 85% of the world's protected areas are inhabited by indigenous peoples (Schmidt and Peterson 2009). Indigenous communities have already proven helpful in meeting conservation objectives in a variety of ways, including prevention of illegal logging, mining, and deforestation, suppression of land speculation, and protection of communal resources like fisheries (Peres 2011). This is due to their occupation of the land in addition to the unique relationship between the natural and supernatural world found in the cosmology of many of these societies that often regulates the use of land (Davis and Wali 1994). In addition, the ecological knowledge possessed by indigenous groups can offer new models for development and land usage that are ecologically and socially sound (Posey 1985; Toledo et al. 2003).

The focal area of this study is a nexus of all these previously discussed concepts, a not yet officially recognized indigenous territory that has been inhabited for generations and thus reflects the collective land-management decisions of the Naso people. Physically it is a mosaic of different environments, a lush mélange consisting of primary and secondary forest interspersed with cultivated areas and homesteads. The purpose of this investigation is to first catalogue the Lepidopteran community extant in the study area, which is little-studied and very remote. In pursuit of this objective, a comparison of the diversity and abundance of the Lepidopteran communities present in five land-use zones, all under the management or control of the Naso, will be executed. This will be an attempt to gather data on the response of a Lepidopteran community to disturbance and to determine if anthropogenically disturbed areas are capable of hosting similar levels of biodiversity as the pristine tropical forests that are known to be so diverse. In the context of the land sparing vs. land sharing debate, data on butterfly communities

may be able to offer insights into the ideal ways to maximize the equally important criteria of food production for humans and habitat conservation for plants and animals.

2. Research Question

How does the diversity and abundance of the Lepidopteran community differ across five different indigenously managed land use zones in the Naso-Teribe Territory, Panama?

3. Methods and Materials

3.1.1 Study Site-Overview

This investigation was conducted from April 13-April 19, 2019 in and around the community of Sieykin, Naso-Teribe, Panama. Composed entirely of Naso people, an indigenous group that has lived along the Teribe or Tjerdi river for generations, Sieykin is located in the Bocas del Toro province in the Northwest part of Panama, on the Caribbean slopes of the Talamanca Mountain range (Figure 1). Within Panama, autonomously managed and owned indigenous territories are called Comarcas. The Naso are one of only two indigenous groups currently without a Comarca of their own, and have been requesting that their right to and presence on the land be recognized by the Panamanian government in the form of a Comarca for at least 40 years (Rainforest Foundation, Sanchez 2019). In October 2018, the Panamanian congress approved Law 656, which grants the Naso people control over 160,000 hectares of their ancestral land, but it has not yet traversed all the levels of bureaucracy or come into effect and doubts remain as to whether it
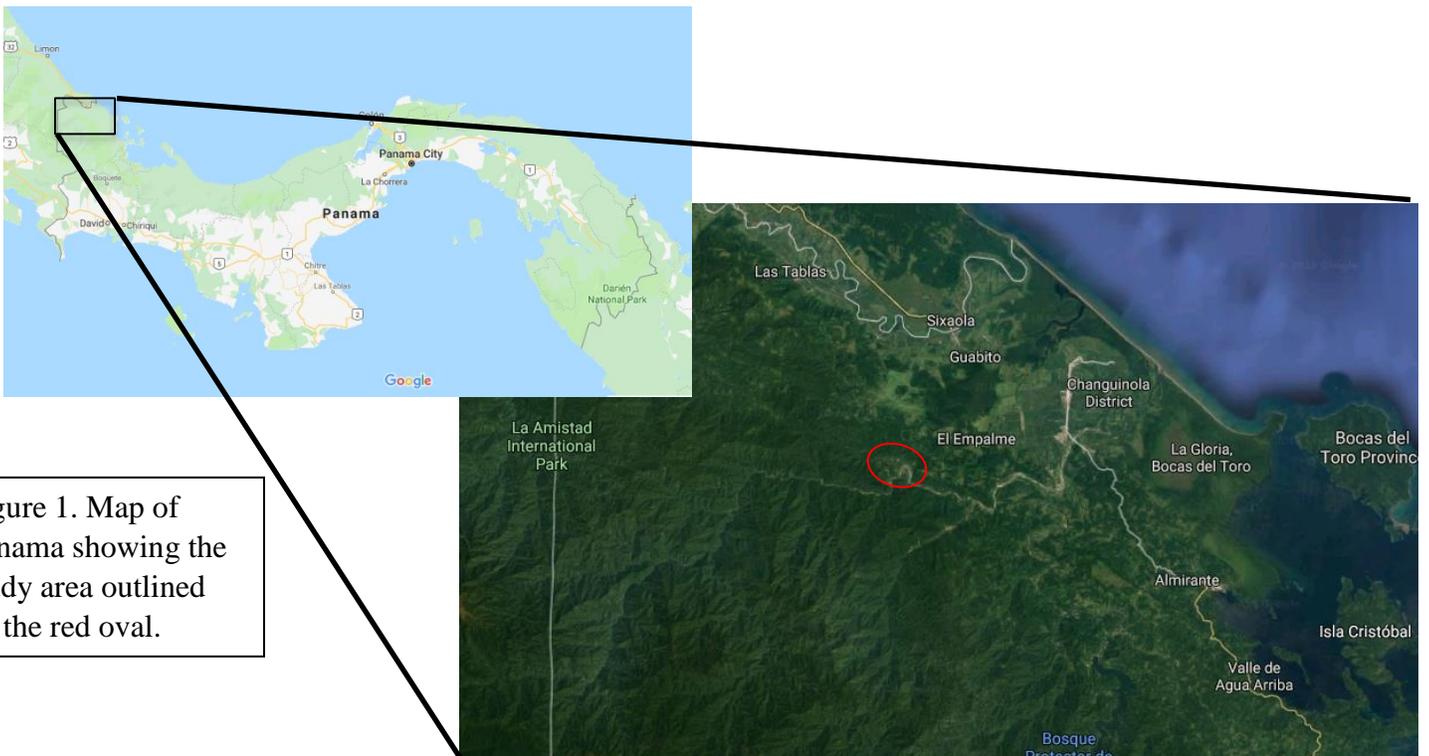

Figure 1. Map of Panama showing the study area outlined by the red oval.

Figure 2. Large scale map of the study area with the ancestral territory of the Naso outlined in green (Rainforest Foundation).

Figure 3. Large scale map of the study area with ancestral territory of Naso outlined in green and contiguous protected areas such as Parque Internacional La Amistad and Palo Seco Protected Forest in purple (Rainforest Foundation).

will become a reality (See Figure 2) (Panama Today 2019; Sanchez 2019). The Naso, who number around 5,000 people, currently live on a very small percentage, estimated at only around 6,000 hectares, of the proposed 160,000-hectare Comarca (Sanchez 2019). The rest of the land is composed of mountainous primary and secondary forest that is included in both Palo Seco Protected Forest and the UNESCO biosphere reserve Parque Internacional La Amistad (PILA) (See Figure 3). Over 125,000 hectares of the proposed Comarca overlaps with PILA, which is the largest biological reserve in Central America and hosts thousands of species of plants and animals with high rates of endemism (Panama Today 2019; UNESCO.org). Previous research in the area has been scarce, as the most extensive and recent scientific expedition into PILA occurred in 2006 (Darwin Initiative).

3.1.2   Study Site-Transects

Within the study area, three transects to observe and collect butterflies were established in each of five different zones, described in depth in Appendix A. The sites form a gradient of anthropogenic disturbance, with the highest amounts present in the Homestead site and descending amounts present in the Pasture, Agroecological Field, River, and Primary Forest sites. Components of this parameter of human disturbance include land management practices such as cutting down the majority of trees in an area as occurred in the Pasture and Homestead, trimming of undesirable plants as in the Agroecological zone, and the continual presence of humans or livestock as occurred in all zones except the Forest. All of this information was obtained from an interview conducted with Edwin Sanchez (Appendix D).

It is important to note that exact delineations of the landscape into each land-use zone are not possible in this study site. The environment that has developed over decades of land-use decisions in the Naso territory is extremely heterogenous and best defined as a mosaic. Homesteads as described in Appendix A are spread out around the central community zone of Sieykin that includes a school, general store, community building, health care center, and large open field for activities such as soccer. Outside of this area, patches of secondary forest are interspersed with pastures and agroecological zones of a wide variety, with primary forest prevailing as one travels further up the Teribe river or deeper into the Talamanca range.

3.2 Observation and Collection of Specimens

The principle methodology utilized in this study was a modified form of the Pollard walk, a hallmark of butterfly studies for over 40 years (Pollard 1977). In a Pollard walk, transects of a standard length are established and the observer walks the transects at a slow but steady pace. A zone of observation is imagined to surround the observer; in this study the size was three meters on either side, in front of, and above the observer. Transects were 100 meters long, as measured by a handheld GPS, for a total of 600 m^2 sampled per transect. In order to produce standardized, replicable results a Pollard walk must occur within a strict range of conditions including the time of day, temperature, wind speed, and cloud cover. However, the method was originally developed in England, and thus the exact parameters must be revised for individual study sites. In this study, each transect took place between 9:30 AM and 3:30 PM, with the majority occurring during peak butterfly activity hours of 11 AM- 1 PM. Other environmental conditions are listed in Table 1. Though conditions were not always ideal for a Pollard walk throughout the duration of this study, the limited time available required that I proceed whenever possible; the only time walks were not performed was if rain was falling. Three unique transects were performed in each of the land use zones. For the river and primary forest sites, conditions were sufficiently poor that an additional transect was performed at each site in an attempt to attain samples of similar quality from each site, so there were 17 total transects performed.

When the Lepidopteran fauna of a region are unfamiliar to the observer or difficult to identify in the field, the Pollard walk can also be altered to include the collection of specimens for later identification, which is what I did in this study (Caldas et al., 2003; Sparrow et al., 1994). If a butterfly flew into the imaginary zone that I could not visually identify, I attempted to catch the specimen with a butterfly net. If it was a new specimen, the butterfly was placed into a killing jar and subsequently a labeled paper bag for later identification. If it was actually an already seen specimen, it was recorded and quickly released. If the specimen was not able to be captured, a brief description was recorded. Full record of individuals observed and captured by transect is listed in Appendix B.

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Table 1. Averages are listed for environmental conditions during each of the transects performed at each land-use zones.

Transect	Elevation (M)	Temperature	Cloud Cover
Homestead	121	30.8 C	76%
Pasture	143.8	29.6 C	40 %
Agroecological field	267.8	30.3 C	66 %
River	129.2	29.4 C	76 %
Primary Forest	373.8	26.1 C	85 %

3.3 Specimen Identification

Captured butterflies were later identified in the lab by utilizing the online resources listed in Appendix C. Physical appearance, size, and any habitat or behavior descriptions listed were all taken into account, and identification to the species level was verified by cross referencing the species name on other sites.

3.4 Interview

In order to obtain information regarding the current and historic agricultural practices and land use decisions in the study sites, one interview was conducted with Edwin Sanchez, a Naso individual who kindly allowed me to stay with his family and perform my study on his land. The interview was conducted with Edwin in Spanish, and consisted of the questions listed in Appendix D.

3.5 Statistical Analysis

All statistical analysis and graphs were performed in Microsoft excel. After the data was entered and compiled, relevant graphs were constructed to display totals of individuals and species present in each land-use zone.

To quantify the Lepidopteran biodiversity, the Shannon diversity index for each individual zone as well as the butterfly community as a whole was calculated with the following formula:

$$(H) = - \Sigma \, p_i \, (\ln p_i)$$

Simpson's diversity index, which represents the probability that two individuals randomly selected from a sample will belong to different species, was calculated with the following formula:

$$D = \Sigma \, (n \, / \, N)2 \, , \, Simpsons = 1\text{-}D$$

Simpson's evenness index was calculated with the equation

$$D = 1/ \sum p_i{}^2, \; E = D/D_{max}$$

To display the richness and evenness of the community graphically, a rank abundance chart was generated. Species were assigned a rank based on the number of individuals that were observed, and this rank was placed on the x axis, while the number of individuals was graphed on the y axis.

Single factor ANOVA tests were performed using the number of species and number of individuals data from each land-use zone to determine if statistically significant differences existed in the data. When there were differences present, t-tests were performed to further elucidate between which groups the differences existed.

3.6 Ethics

Implicit in this research was the fact that live insects native to this area were killed and their bodies collected. This is a particularly intrusive method for collecting data, but one that is common in entomology and indeed the only way that identification of the specimens can be achieved due to the diminutive and elusive nature of the insects being studied. I faced this dilemma this past year in an entomology class in college, and though I did feel remorse at killing these beautiful creatures and removing them from their native ecosystem, I believe the benefits to be gained from their capture in this study outweigh the negative consequences. The number of specimens killed was kept to a minimum by only collecting one of each species observed. Also, due to the incredible fecundity of insects in tropical ecosystems, a large and thorough sample size can be obtained from a relatively small area, which should limit the impact of my research on the ecosystem.

Throughout the duration of the study, I did my best to remain cognizant of the cultural lens that has been imparted on my worldview and how this might impact my experience with the Naso and their various mores and norms. I did my best to respect the wishes of my hosts and the participant in the study. Prior to my arrival in Sieykin, I submitted an Application for Human Subjects Review to the Local Review Board in Panama. This was a form that asked for a brief summary of the proposed project in addition to several questions on the purpose of any human subjects included in the study and how the information these subjects provided would be utilized. This process helped me to consider aspects of my research that I had not anticipated, such as the consequences that any power differential between me and the human subjects would have on my study, and it forced me to be more mindful of the human dimensions of both this study and my time with the Naso people. I also submitted the questions I would be asking in the interview to the Review Board.

4. Results

4.1 Community Overview

Throughout the duration of the study, 197 individuals were observed from an estimated 63 different Lepidopteran species. In total, 44 specimens were collected. Of these, 6 were not able to be identified, 3 were identified only to family, and the other 35 were identified to species. Thus, out of the 63 total species, 44 were collected and 19 were only observed in the field. These 19 were not able to be captured and were assigned colloquial names for data collection purposes. Of the 35 species identified, 6 were moth species and 29 were butterflies. A complete list of all the species identified and how many were observed can be found in Appendix E. Of the specimens collected, 9 families were represented with 3 being moth families and 6 being butterfly families. The community was dominated by the family Nymphalidae, which is the largest butterfly family in the world. Hesperiidae was the only other family with more than 2 specimens collected (Figure 4). For the individuals observed, Nymphalidae was also the most common family, followed by unknown Lepidopterans and then Hesperiidae (Figure 5). Of the five most common species, four were Nymphalidae and one was Hesperiidae (Figures 6-10). A total of 10,200 m^2 of space was sampled throughout almost 10 person-hours of sampling. With 197 specimens and 63 species, there was a density of 1 Lepidopteran per 51.7 m^2 and 6.3 species per person-hour found for the study area as a whole.
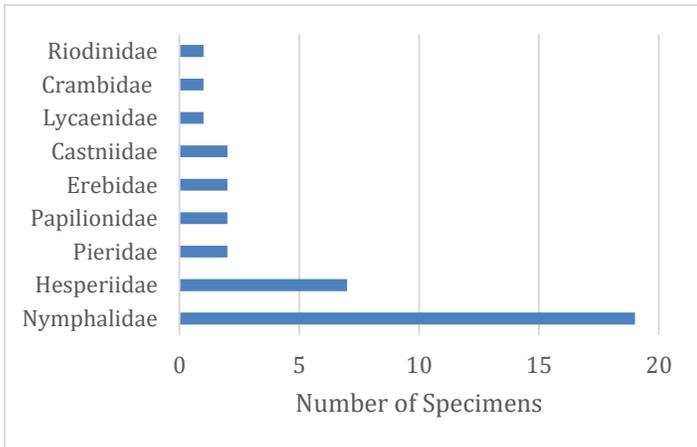

Figure 4. Number of specimens collected by Lepidopteran family. The community is dominated by Nymphalidae, which constituted exactly half of the specimens collected.
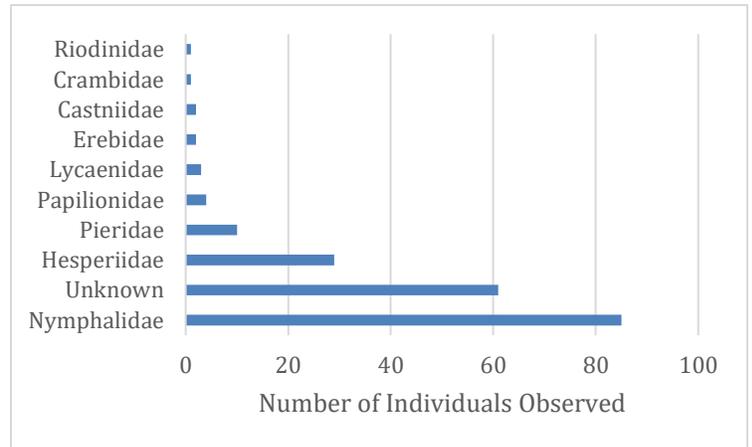

Figure 5. Number of individuals observed by Lepidopteran family. The community is also dominated by Nymphalidae, of which 85 individuals were observed.

Figure 5. Hermeuptychia intricate. Most common (15 individuals).

Figure 6. Anartia Fatima. 2nd most common (13 individuals)

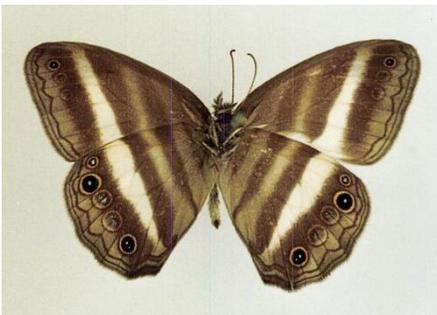Figure 7. Anartia jatrophae. 3rd most common (12 individuals)

Figure 8. Pareuptychia summandosa. 4th most common (10 individuals)

Figure 9. Bolla atahuallpai. 5th most common (10 individuals). Hesperiidae.

The Shannon diversity index for the entire Lepidopteran community was calculated to be 3.74, and the Simpson index was 0.966 (Table 2). These values were also calculated by land-use zone. In addition, the Simpson index of evenness was calculated to be 0.473 for the whole community and is also listed by land use zone in Table 2. Figure 11 shows a rank abundance graph that was generated to display the richness and evenness of the aggregate community in a different manner. Species were assigned a numerical rank based on how many individuals of that species were observed, and this rank is plotted on the x axis. On the y axis is the number of individuals. A line of best fit is also included on the graph along with its equation. The slope of this line illustrates the species evenness of the ecosystem, as a graph with a steep slope signals a more uneven community than a graph with a relatively flat slope.

Table 2. Diversity indices by land-use zone, arranged in ascending order by value.

Land-use Zone	Shannon Diversity	Simpson's index (1-D)	Simpson's Evenness (1/D)/Dmax
Homestead	2.26	0.859	0.508
Ag Eco	2.79	0.925	0.665
River	2.82	0.926	0.672
Pasture	2.99	0.934	0.584
Forest	3.05	0.950	0.916
Overall	3.74	0.966	0.473
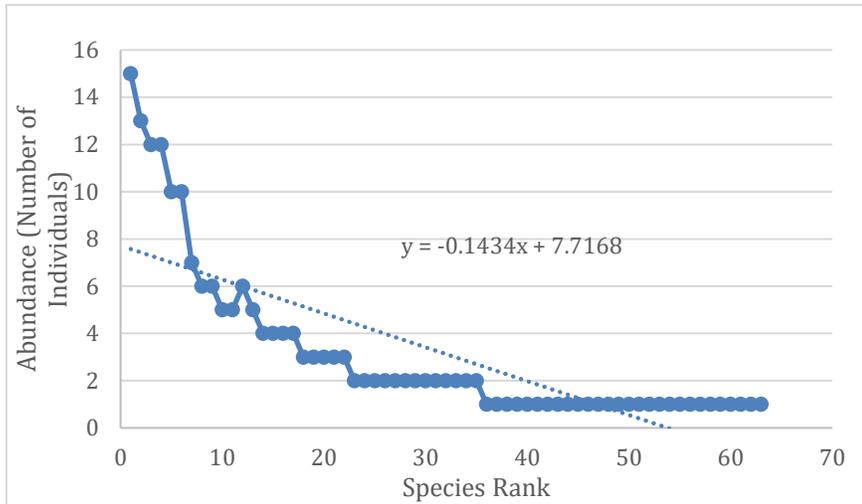
Figure 11. Rank abundance graph for the entire Lepidopteran community surveyed in this study.

4.2 Results by Transect

Figure 12 displays the species richness and evenness of the Lepidopteran community in the study area. Total numbers of species and individuals observed are compiled by land-use zone. The butterfly community in the Pastures proved to be the most species rich and had the most individuals, while the Forest had the least individuals and the Homestead was the least speciose. Results from the forest are intriguing because a high number of species was recorded, but a low number of individuals. An ANOVA test revealed that there were no statistically significant differences among the number of individuals across land-use zones (P-value 0.0584), but there was a statistically significant difference among the number of species across land-use zones (P-value 0.0297). T-tests were then performed to elucidate these differences. There were significant differences present between the number of species in the Pasture and in the River and Forest land-use zones (Table 3).

Figure 12. Total number of species and individuals of Lepidopterans observed throughout transects in each land use zone. Bars represent standard error.

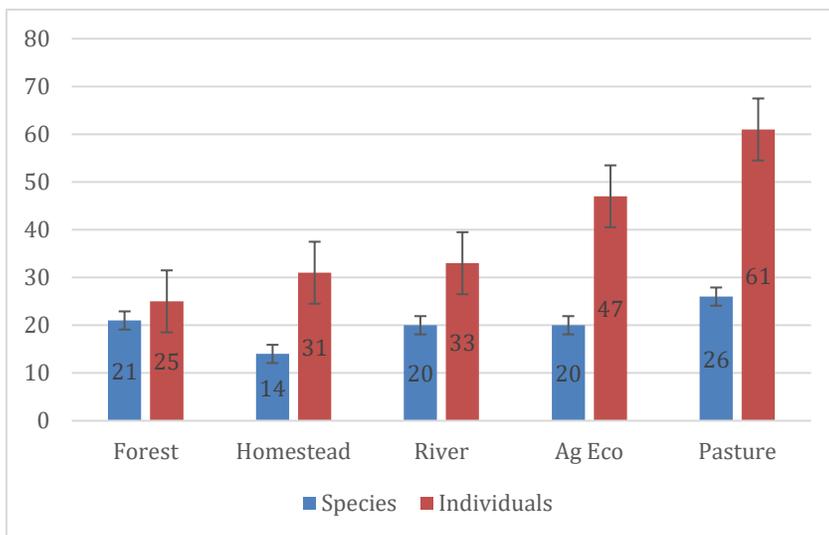Table 3. Relevant statistics are given for t-tests performed on species data for land-use zones.

Test Group	T-stat	T-critical Two tail	Conclusion
Pasture-River	2.969	2.571	Significant
Pasture-Forest	3.938	2.776	Significant

Another relevant aspect of the data collected is the degree to which each land-use zone fostered endemic or unique species, defined as those that were only observed in one transect. These species would presumably be those that depended on resources present exclusively or mainly in the zone they were found in. Figure 13 displays the percentages of endemic species found in each land-use zone. Transects in the Forest zone found the most endemic species (11), as over half of the individuals in this zone were found nowhere else. The homestead contained the least endemic species (3), at just over 20%.
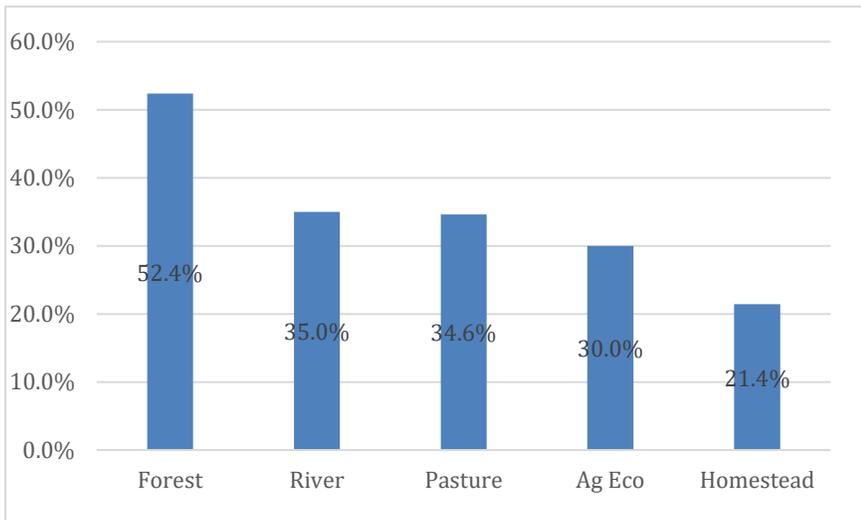
Figure 14. Rates of endemism, or unique species that were only observed in that transect, expressed as a percentage of the total number of species found at that site.

Species accumulation curves can be used to estimate the number of species in an area by extrapolating from the number of species found in the survey. They also display how well a community was sampled given the sampling effort, which can be a helpful measure when comparing the biodiversity of different areas. If the curve begins to level off by the end, that is a sign that the community was sufficiently sampled to capture the biodiversity present. If the slope of the graph remains high and sharp throughout, that is a signal that more sampling needs to occur. The species accumulation curves for each land-use zone exhibited a wide variety of shapes. The curve for the river zone (Figure 15) exhibits the flattest curve at the end, indicating that sampling was the most representative of the whole community in this zone. The curve for the Agroecological zone (Figure 16) also appears to be levelling off towards the end. The curves for the rest of the graphs (Figures 17-19) all appear to be increasing sharply at the end of the graphs, which indicates that more sampling is necessary to capture the full range of species.

Figure 15. Species accumulation curve for the River zone.

Figure 16. Species accumulation curve for Agroecological zone

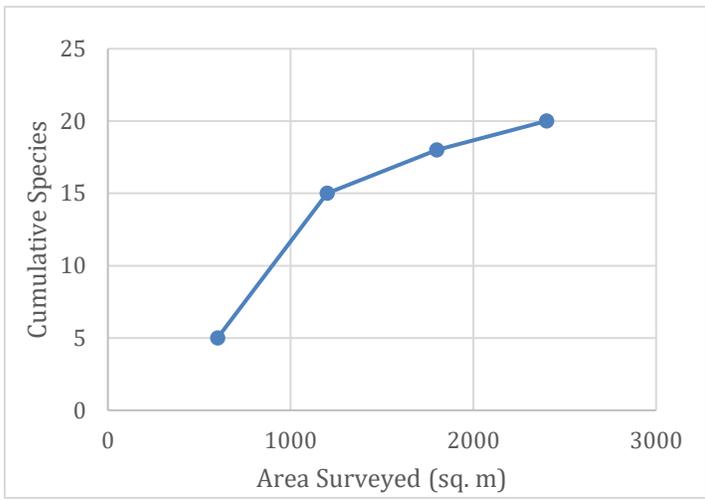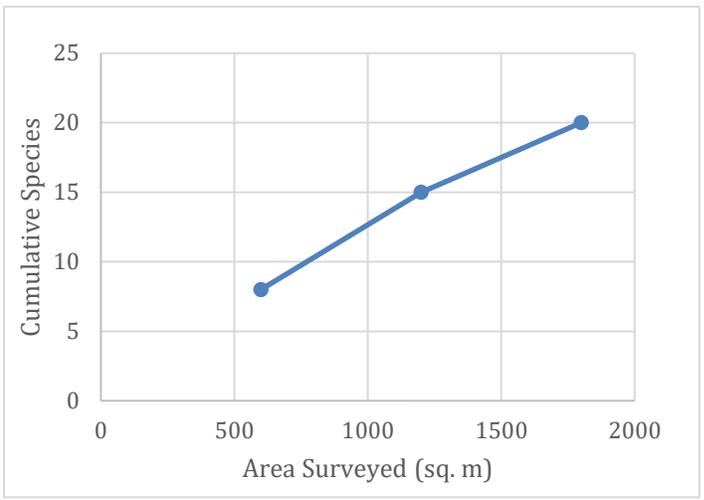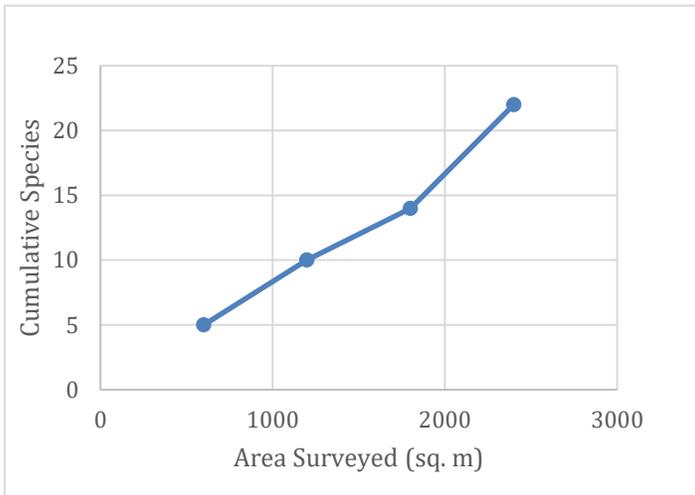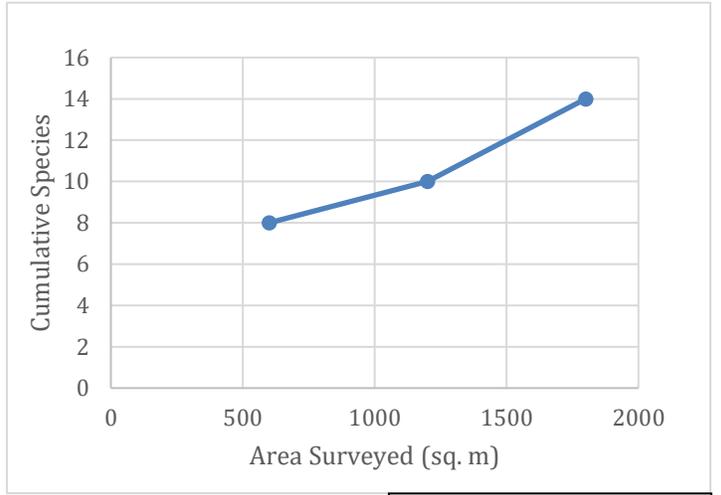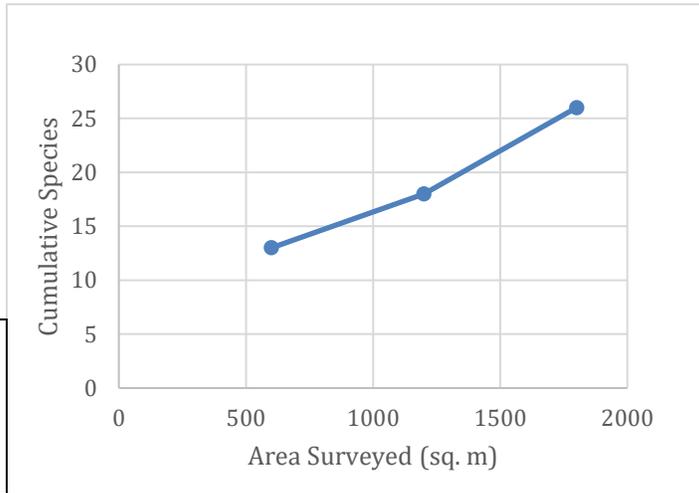Figure 17. Species accumulation curve for Forest zone.

Figure 18. Species accumulation curve for the Homestead zone.

Figure 19. Species accumulation curve for Pasture zone.

5. Discussion

5.1 Analysis of Results

One objective of this study was to characterize the Lepidopteran community in the little-studied Talamanca Mountains of Panama, specifically in the Naso-Teribe Territory, and analyze its abundance and species richness. In total, just under 10 person-hours were spent collecting data in this study, which covered an area slightly larger than 1 hectare (10,200 m^2). Across all zones, 197 individuals from 63 species were observed and the Shannon Diversity Index was calculated to be 3.74. To contextualize these results, a comparison with other studies utilizing similar methods in different locations was performed. Caldas & Robbins (2003) employed undergraduate students and modified Pollard walks in two national parks in southeastern Brazil. They found 189 species in 43.5 person-hours at one park and 170 species in 46.5 person-hours at the other. The species found per person-hour was thus 4.3 and 3.6, respectively. Artusi (2014) used both transects and fruit traps to survey the butterflies of the La Hesperia Reserve in Ecuador, where 113 species and a Shannon Diversity Index of 3.78 were recorded. The species found per person-hour was thus 6.27, although butterflies sampled using both of the methods are included in this value. The rank abundance curve constructed for this community had a slope of -0.166. In this study the species found per person-hour was 6.3 and the slope of the rank abundance curve was -0.143, values that cannot be exactly compared with the studies above due to the inclusion of moths in this study. However, only 6 moth species were recorded and the methods in this study were primarily targeted towards butterflies, as transects occurred during daylight hours. Thus, the Lepidopteran community observed in the study area harbors an impressive amount of biodiversity, similar to if not richer than the biodiversity present in other tropical environments that have been surveyed.

Another main objective of this study was to determine how the Lepidopteran community varied across five land-use zones. Two biodiversity indices-Shannon and Simpson-were utilized to enable a comparison of the biodiversity in each zone. Both measurements were in agreement about the order of the gradient of biodiversity among the sites. In each index the Homestead was the least biodiverse, followed by the Agroecological field and then the River and Pasture, with the Forests containing the most biodiversity. The values for the Shannon index ranged from 2.26 in the Homestead to 3.05 in the Forest (Table 2). In the Simpson index, values ranged from 0.859 to 0.950. The fact that both indices ranked each zone in the same spot on the gradient of biodiversity is evidence that this gradient reflects the reality of biodiversity in the study area. It also provides evidence that the zone with least human disturbance, the Forest, was the most biodiverse zone while the zone with the most human disturbance, the Homestead, was the least biodiverse zone. However, each index takes into account both species richness and species evenness, and these results cannot be accepted without considering both parameters individually.

First, species richness is a critical component of biodiversity. The most species rich zone was the Pastures, followed by the Forest, while the least species rich zone was the Homestead. An ANOVA test was performed on the species data for each transect to determine variance of means. There were only significant differences observed among the number of species present between the Pasture site and the River, and the Pasture site and the Forest (Table 3). At first the

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difference between the Pasture and the Forest may seem odd because these were the two most species rich zones. However, four transects were conducted in the Forest due to environmental conditions, while only three occurred in the Pasture. This lowered the average mean in the Forest zone, giving rise to the variance. Four transects also occurred in the River zone, which led to the same phenomenon. Ideally the same number of transects would have been performed in each land-use zone, but environmental conditions on the days that the Forests and Rivers were sampled were very poor. High percentages of cloud coverage and precipitation preceding or directly following the sampling events were common, so an extra transect was performed in both of these areas in an attempt to attain the same quality of sample in each land-use area. These extra transects certainly contributed to the biodiversity values obtained for each site, but are valuable for the increased sample size they provide. With these facts in mind, the validity of the conclusion of a statistically significant difference between the species richness of the Pasture and these two other sites is significantly weakened, and other sources of data should be considered to determine which zone is the most biodiverse.

The other parameter integral to the calculation of biodiversity, species evenness, considers the relative abundances of the different species observed. The relative abundance of each species indicates the degree to which one species dominates the community, and is expressed in the Simpson evenness index (Table 2). The value for the Pasture was the second lowest of all land-use zones at 0.584, which demonstrates that though being the most speciose zone, the Pastures were dominated by just a few species of Lepidopterans. The evenness value for the Forest was the highest at 0.916, which demonstrates that the Lepidopteran community in this land-use zone was composed of a more equal distribution of species. Despite the high number of species found in the Pasture zone, the degree of evenness exhibited in the Forest led to its classification as the more biodiverse zone. This indicates that although species richness is often prioritized or emphasized in conservation, the evenness of a community of organisms makes an important contribution to overall biodiversity.

Abundance is another useful criterion to examine because it shows the number of Lepidopterans in a given zone, demonstrating how well-populated the zone is and what kind of population densities it can host. Abundance of individuals was the highest in the Pasture zone (61), followed by the Agroecological zone (47), the River (33), Homestead (31), and Forest (25). On the gradient of human disturbance used to categorize these zones, the Pasture and Agroecological fields were both on the higher end, while the Forest was the zone with the least amount of human disturbance. This result suggests that areas subject to human disturbance are capable of harboring larger populations of Lepidopterans than pristine areas. However, according to an ANOVA test performed, there was no significant difference among the numbers of individuals across land-use zones (P-value 0.0584). Thus, it cannot be concluded that the land-use zone a transect occurred in determined the number of Lepidopterans observed. In addition, the abundance of Lepidopterans in the Forest and Agroecological zones could've been affected by the elevation that these transects occurred at, which is known to have limiting effects on Lepidopteran populations (Artusi 2014). The average elevation in the Forest zone was 373.8 meters, and in the Agroecological zone the average was 267.8 meters. Each of these values is almost twice as high

as the elevations of the transects in the other zones, and could explain the relative dearth of Lepidopterans observed in these areas.

Another facet that should be considered when assessing the capability of each land-use zone to support Lepidopteran communities is the number of endemic species each area contained. An ecosystem may support high population densities and levels of diversity, yet if it has few endemic species its contribution to landscape diversity may be limited. In this study endemic species were defined as those that were only observed within one transect. The Forest zone had the most endemic species (11), followed by the Pasture (9), River (7), Agroecological field (6), and finally the Homestead (3). To better visualize the role of these endemic species in the Lepidopteran communities of each land-use zone, Figure 14 displays these numbers as a percentage of the total number of species found in the zone. The results show that the Forest harbors a wealth of rare species that constitute a large proportion of that community and also contribute significantly to the overall species richness of the study area.

The strength of any conclusions drawn from these results is tempered by the species accumulation curves (Figures 15-19). Though two of the graphs level off towards the end, the other three still exhibit sharp increases. This leaves little doubt that additional transects are needed in each land-use zone to properly determine the biodiversity in each area. This in turn will allow a better analysis of the effect of land-use decisions on Lepidopteran communities. In addition the nature of ecological field work, observational by definition due to the inability to isolate variables or control experiments, means that data will be correlational and not causational. None of the conclusions drawn from this study are able to be proven beyond doubt, the results merely indicate that certain phenomena may be occurring. With that being said, the data collected in this study do allow for an examination of the effects of land-usage on Lepidopteran communities.

The metrics compiled thus far outline the details of the Lepidopteran communities found in each land-use zone. The Forest proved to be the most biodiverse zone and had high rates of endemism despite occurring at the highest elevations, all of which illustrates the importance of this zone in gamma diversity. On the other end of the spectrum, the Homestead was the least biodiverse zone with the lowest species richness and rates of endemism. However, the picture that emerges from the data is not simply one of a gradient of biodiversity that mirrors a gradient of human disturbance, with the least disturbed site hosting the most biodiversity and vice versa. Though not statistically significant, the results on the abundance of individuals have important implications. The Pasture zone specifically contained more individual Lepidopterans than any of the other sites, and also had the highest species richness and second highest amount of unique species. The Agroecological zone was also notable for having the second-highest number of individuals observed despite transects occurring at the second highest elevation.

Based on the statistical analysis, the composition of the butterfly community does undergo changes in response to alterations in the physical environment that are the result of habitat fragmentation and degradation from the conversion of forest to agricultural land. The main example of these alterations in the study area is a change in the floral composition and physical structure of the environment as a result of timber harvesting or tree clearing to create space for

pasture or crops. As for the butterfly community, the main shift that was revealed in the data is a decrease in the endemic or rare species in areas where disturbance occurs. This was evidenced by the high rates of endemism in the Forest and also the River zone, which were the least exposed to human disturbance. These rare species likely have limited ranges and are dependent on resources that are only offered in areas where human activity does not alter the composition of the ecosystem, a conclusion also reached by a study in Costa Rica (Horner-Devine et al. 2003). However, statistically significant differences in the species richness and population sizes of Lepidopterans in different zones were not found in this study. In addition, the Pasture and Agroecological zones hosted the largest populations of Lepidopterans. These facts are important because they suggest that areas such as pastures and crop fields that do not militantly discourage non-productive plants, a practice characteristic of the agroecological approach employed by the Naso, can be important sustainers of biodiversity. Though some of the rare, endemic species will always require tracts of forest, these other environments can be utilized by a wide variety of other Lepidopteran species and may even prove to be more productive in terms of carrying capacities. Thus, the results of this study tacitly endorse the conclusions of the land sharing model, as the areas that existed outside of the pristine primary forest were important habitats for Lepidopteran populations.

Without a non-indigenously managed site for comparison, it is impossible to determine whether the land-use practices that have developed in the Naso territory contribute in any special manner to the fostering of biodiversity. It is possible that the mosaic landscape that results from the Naso's lifestyle and characterizes the study area connects the various zones of the environment such as forest and agricultural land so intimately that animal orders such as Lepidopterans are able to access all the resources the landscape has to offer. It is also possible that the sprawling manner of agriculture practiced in the Naso, which is low in intensity and often results in leaving areas unmanaged for months at a time, is inefficient to the point that more area than is needed is transformed from forest into fields. However, based on the high levels of species richness found in this study in comparison to the others previously described, it seems likely that the presence of the Naso and the ways they shape their physical environment are not overly antagonistic to many of the species that also inhabit their territory.

5.2 Limitations

The original intention of this ISP was to study pollinator populations of all insect varieties in primary forest compared to in an agroecological field using water and soap-based traps deployed in transects. After the first day of sampling, I realized this method would not work, and had to adjust. If I had known that my study would revolve only around Lepidopterans, I could've refined my methods and brought better supplies to execute this study, as there was no internet access when I lived with the Naso or access to a store that would sell relevant supplies. In particular a killing jar would've been helpful, as I had to construct one out of a water bottle and tape, as well as an identification book to the Lepidopterans of this region.

Although the results of this study are significant, there are several sources of error that need to be considered and their effects evaluated. With regards to data collection, there were several possible sources of error. As previously noted sampling conditions were not always ideal during

the transects. Environmental conditions, especially sunlight, often determine the movement of Lepidopterans throughout the day, so transects completed during unideal conditions could distort the data. Due to the conditions, more transects were performed in two of the land-use zones in an attempt to attain a similar quality sample from each site. Ideally each zone would have the same number of transects. It would also be ideal to have each transect be in a unique location with a new orientation, which was not possible for the Homestead location. The fact that each transect in the Homestead was identical could've influenced the results in this zone. Based on the results, especially the species accumulation curves, it seems that more transects in each zone would also be ideal to ensure thorough sampling. In hindsight, I also do not think it was necessary to include the River as one of the land-use zones. Lastly, it would have been ideal to have each transect occur at the same or a similar elevation, which is known to affect the diversity of the Lepidopteran community (Artusi 2014). Primary forest are usually only extant in the study area above a certain elevation, and it was not possible to find areas in each land-use zone that were at the same elevation.

On the transects themselves, error could've been introduced as a result of the method. It is possible that while walking the transects my perception wasn't sharp enough to see all of the Lepidopterans present. It is also possible that of the Lepidopterans that I saw, but did not capture or collect, the species assigned to them could be incorrect. There was also several times when I was unable to capture an individual, which would've allowed a proper identification and greater degree of specificity instead of having to use colloquial names. However, I had previous experience with Pollard walks as a part of my job as a biology intern at the Neal Smith National Wildlife Refuge in Iowa during the summer of 2018. I underwent training for a monarch monitoring program that was federally funded, a part of which was to complete Pollard walks and observe monarch populations. For this reason I believe I was competent and consistent in my use of this method.

The method chosen to execute in this study was also clearly biased to observe and collect butterflies rather than moths. Though the number of moths collected was few, I chose to include them in the study and focus my literature review on all Lepidopterans, rather than just butterflies, because of how important and under-studied moths appear to be in tropical ecosystems. If I had known that my study would revolve only around Lepidopterans, I could've researched and designed a component of the methods to more thoroughly sample moths as well. It is also possible that Pollard walks are inherently biased in their sampling of butterfly families, as Caldas & Robbins (2003) reported that in their study the families of Papilionidae, Pieridae, and Nymphalidae were oversampled while the families of Lycaenidae, Riodinidae, and Hesperiidae were under-sampled.

5.3 Future Research

The first project that could be undertaken in the future as a corollary to this one is a full species inventory of the moths and butterflies of this region. The insect species of lowland forests remain much more well known than montane species in tropical regions, mainly due to the inaccessibility of mountainous regions. The ecosystems in the study area are also under-studied, as most of the research in Panama on insects thus far has occurred in Barro Colorado. A full

species inventory would doubtless reveal species never yet described, and would also provide a comparison with some of the thoroughly sampled sites in South America. Depending on the results, such an inventory would also provide further justification for Parque Internacional La Amistad, the expansive biological reserve that is currently in danger of losing its designation as a UNESCO biosphere/heritage site due to environmental degradation.

It would also be beneficial to replicate this study or one similar to it focusing on the Lepidopteran communities present in different land-use zones on a larger scale or at a different time. While I believe that I collected high quality and significant data in this study, a larger sample size via more transects under better conditions would allow for stronger conclusions with regards to the effects of the Naso's land-use decisions on moth and butterfly populations. The focus of the study could also be broadened to include other orders of insects or even other types of animals such as birds to get a clearer picture of how the entire ecosystem changes during and after various types of disturbance. It would also be interesting to replicate this study in a similar environment that was managed by farmers who were not part of an indigenous group. This would test the ability of other agroecological systems to sustain high levels of biodiversity, and also indicate if there are special characteristics present in indigenous techniques or ways of thinking that are beneficial for conservation and should thus be investigated further.

6. Conclusion

The first conclusion that can be confidently drawn from this study is that the Lepidopteran community present in the focal area of the Naso-Teribe Territory is highly diverse. When compared with other studies utilizing similar methods, this study found species at a faster rate and had more biodiversity, and species accumulation curves indicate that the wealth of the Lepidopteran community sampled is just a fraction of what the total may be. Further research in this pristine and remote region of the world would be beneficial for the expansion of scientific knowledge on tropical ecosystems. The second conclusion drawn from this study is that the zone with the least amount of human disturbance, the Forest, was the most biodiverse of all the zones sampled. This was due to the high rates of species richness and especially evenness, both which contributed to the high Shannon Diversity index score, in addition to high rates of endemism. The third conclusion is that although the Forest was indispensable for a certain segment of the moth and butterfly community, two of the other zones that were subject to higher levels of human disturbance, the Pasture and the Agroecological field, were also important contributors to the species richness and population levels of Lepidopterans. Despite the presence of humans and livestock and the alteration of the floral structures of these environments, these were the two zones with the highest numbers of Lepidopterans observed. Though no bona fide conclusion could be reached about the effect that indigenous management played in the Lepidopteran communities of each zone, it seems likely that the presence of the Naso and the ways they shape their physical environment are not overly antagonistic to many of the species that also inhabit their territory.

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8. Appendices

8.1 Appendix A-Description of land-use zones

Homestead: This was the only site where the location of each transect was identical due to the fact that permission to collect specimens was only obtained for land owned by the Sanchez family. This site consisted of three Naso houses, raised on stilts around 2 meters high, a lawn area in which most trees had been chopped down to create grazing space for horses and chickens, and various ornamental, medicinal, and edible plants in clusters. The homestead area was slightly longer than 100 meters long and was about 30 meters wide on average. It was located on a flat area on the slope of a hill situated between two tributaries of the Teribe river, the Rio Sieykin and the Rio Shlobin. This was the site with the highest amount of anthropogenic impact and disturbance due to the dwellings and the constant presence of humans and livestock.

Pasture: All three transects in this zone were conducted in the same pasture, once again due to the restrictions placed on collecting. The pasture was located next to the homestead of another member of the Sanchez family on steep slopes that were surrounded by forest. It was around 5 or 6 hectares in size and had been converted from forest to pasture about a decade ago. Currently there are 7 cows, 7 goats, and 1 sheep that roam freely throughout the paddocks of the pasture. This site was considered to have the second highest amount of anthropogenic disturbance due to the considerable alteration undergone by the landscape, as the majority trees in the area were cut down to facilitate the cultivation of grass.

Agroecological Field: All three transects in this zone were conducted in separate locations, but all were considered to be agroecological systems by Edwin Sanchez. Management practices in this zone depended on the distance of the field from the homestead, with the closest site receiving attention each month or month and a half, the most distant site receiving visits only once or twice a year, and the mid-distance site receiving visits around 8-10 times per year. The primary management practice utilized is a clearing of the small plants encroaching on crops on the forest floor with machetes as well as any overhanging trees. Sometimes fields further from the homestead would be left to fallow for a year to allow nutrients to return, but sites closer to the homestead are under continuous cultivation. At the closest site (Transect 4), the primary crops were bananas, plantains, sugar cane, and yuca. At the mid site (Transect 10), primary crops included banana, plantains, and wood for construction materials. The furthest site (Transect 11) was a corn field with intermittent banana plants.

River: Although the Naso occasionally use parts of the river as walking trails, anthropogenic disturbance was largely absent from these sites. In terms of size and water flow all sites were very similar, but the middle transect (#7) was much more open than the other transects, which were characterized by dense vegetation right next to the water. Each river was around 3-5 meters wide, and the imaginary zone surrounding the observer started right at the edge of the water. This meant that the zones in the river transects were slightly wider than in other areas, but this extra

space consisted of fast flowing water that has no use for Lepidopteran species except as a means of transport, as some species use the rivers as highways.

Primary Forest: Each transect in this zone was executed along a trail called Sendero Loma Gallote, one among the network of trails the Naso maintain to enable movement within the dense primary forest. Anthropogenic disturbance was minimal in this zone, as the trail was accessed by hiking about an hour out from the settlements that make up the town of Sieykin; Edwin informed me that this was pristine forest untouched by human activities. Throughout my stay with the Naso, I was able to get a sense of their environmental ethic by observing their behavior and asking questions about their beliefs, as well as viewing evidence of their stewardship every day in the landscape around me. They consider themselves to be the guardians of this ecosystem, demonstrated by the health of the forests that have been in inhabited by Naso people for generations. The ecosystem in the study area has been characterized as tropical rainforest, montane at higher elevations and lowland in lower areas.

8.2 Appendix B-Data for each transect

Transect #	Location	Date	# Species	# Individuals	Time	Temp. (C)	Cloud Cover	Direction
1	Pasture	4/14	13	22	1:30 PM	32	20-30%	S-SE
2	River	4/15	5	6	9:30 AM	27.2	60-70%	N
3	Homestead	4/15	8	15	10:30 AM	33.4	40%	W-NW
4	Ag Eco	4/15	8	23	2:30 PM	28.4	60%	W-NW
5	Homestead	4/15	4	7	3:30 PM	29.1	90%	W-NW
6	Pasture	4/16	9	12	11:30 AM	29.2	20%	N-NE
7	River	4/16	10	20	2:00 PM	34.6	60-70%	N-NW
8	Forest	4/17	5	6	9:30 AM	25.3	80%	W
9	Forest	4/17	5	7	11:15 AM	25.1	70-80%	SW
10	Ag Eco	4/17	9	13	12:00 PM	34.8	50%	W
11	Ag Eco	4/18	7	11	11:30 AM	27.7	100%	S-SW
12	River	4/18	3	3	12:15 PM	26.6	100%	NW
13	River	4/18	4	4	1:50 PM	27.5	100%	NW
14	Forest	4/18	4	4	2:30 PM	27.9	100%	E
15	Pasture	4/19	12	27	9:30 AM	27.8	60-70%	N-NE
16	Homestead	4/19	8	9	11:00 AM	30	100%	W-NW
17	Forest	4/19	8	8	2:00 PM	27.5	60%	E

8.3 Appendix C-Sources used in the identification of specimens

- Panama Insects.org, https://www.panamainsects.org/
- Neotropical butterflies, http://sandianet.com/neotropic/hesperiidae.htm
- Learn about butterflies.com, http://www.learnaboutbutterflies.com/Amazon%20-%20Parelbella%20ahira.htm
- Butterflies of America, http://www.butterfliesofamerica.com/L/Neotropical.htm

8.4 Appendix D-Interview questions

- How long has this specific plot been farmed for?
  - Durante cuanto tiempo ha trabajado esta finca?
- What crops are produced on this plot? Has this crop always been grown here?
  - Que produce en su finca?
- Do you consider this plot to provide anything else besides food/money (depending on the crop) to you?
  - Su finca produce algo mas que comida y dinero? (por ejemplo medicina, penca para techo, postes para cerca, alimentos para animales u otra cosa)
- What are the yields like? Do they stay constant? Where are the products sold/consumed?
  - Como es la produccion de la finca? Es constante?

Every Lepidopteran species that was able to be identified to family or species and the number of individuals observed throughout all transects.

Adelpha Cytherea	4
Aeria eurimedia	2
Anartia Fatima	13
Anartia jatrophae	12
Astraptes fulgerator	2
Autochton neis	1
Bolla atahuallpai	10
Castniomera atymnius	1
Cissia proba	7
Cithaerias pireta	3
Dryas iulia	5
Eueides aliphera	2
Eurema albula	4
Haetera macleannania	2
Heliconius cydno	1
Heliconius erato	2
Heliconius hecale	1
Heliconius hecalesia formosus	3
Heliopetes arsalte	1
Hermeuptychia intricata	15
Herminiinae sp 2	1
Herminiinae sp. 1	1
Morpho peleides	2
Palpita flegia	1
Papilio cresphontes	1

Pareuptychia	summandosa	10
Parides iphidamas		3
Phoebis argante		6
Pierella helvina		1
Pyrginae sp.		4
Pyrgus orcus		6
Strymon melinus		3
Urbanus procne		5
Xanthocastnia evalthe		1