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Land use effects on geometrid and arctiine moth assemblages in the tropical lowlands of southwestern Costa Rica

by

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DEDICATION

To my parents, Alicia and Luis, for the unconditional love and support they have always given me. Thank you for your continuous understanding and encouragement.

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BIOGRAPHY

Aura was born in San Juan, Puerto Rico on December 15th of 1987. She studied Biology and Environmental Sciences in the University of Puerto Rico, Río Piedras Campus, and graduated with honors in the year 2011. During her undergraduate studies, she had the opportunity to work in various research projects, primarily in the area of ecology. First, she developed a project on the impact of bamboo invasion on earthworm populations and decomposition of organic matter of a tropical forest in Puerto Rico. She participated in two summer internships; the first was in the Rocky Mountains of Colorado, where she studied the optimal foraging behavior of butterflies, and the second was in La Selva Biological Station in Costa Rica, where she studied the thermal preferences of litter dwelling ants. The project on litter ants was the basis for her undergraduate thesis and was published in an international journal in 2013. Aura started CATIE's Master's degree in Management and Conservation of Tropical Forests and Biodiversity in the year 2012 and graduated with honors in 2014. She plans to continue working in scientific research on conservation biology and ecology of tropical rainforest biodiversity, as well as contributing to sustainable development initiatives throughout Latin America and the Caribbean.

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LIST OF ABBREVIATIONS

ACOSA	Osa Conservation Area
ASADA	Administrative association of rural aqueducts
CATIE	Tropical Agricultural Research and Higher Education Center
DBH	Diameter at breast height
FI	Old-growth forest interior
FM	Old-growth forest margin
GPS	Global positioning system
IDH	Intermediate Disturbance Hypothesis
INBio	National Biodiversity Institute of Costa Rica
OPP	Oil palm plantation
PES	Payment for Environmental Services
RSPO	Roundtable on Sustainable Palm Oil
SINAC	National System of Conservation Areas of Costa Rica
UCR	University of Costa Rica
YSF	Young secondary forest

ABSTRACT

Land use change is one of the greatest threats to biodiversity in tropical human dominated landscapes. Biodiversity assessments provide useful information on the responses of different taxa to these anthropogenic changes, which may be used to develop evidence based conservation strategies to reduce biodiversity loss. Oil palm plantations are currently one of the most rapidly expanding crops throughout the world, yet information on the repercussions to biodiversity have not been assessed in the Neotropics, especially for insect fauna. This thesis project is focused on evaluating geometrid and arctiine moth assemblages in a human dominated landscape of southwestern Costa Rica, where oil palm plantations have become the second most area intensive land cover in the last decade. Moths were sampled during six months (Feb-Jul) with automatic funnel traps in four habitat types (interior and margin of old-growth forests, young secondary forests and oil palm plantations) inside a 30km^2 area. Richness and diversity was severely reduced in oil palm plantations for both groups, while only geometrids show differences in abundance between land use types; catchment of geometrids was highest in old-growth forests and lowest in oil palm plantations. Arctiine abundance did not differ between habitats due to the presence of a few extremely common lichen moths in oil palm plantations. Species composition was distinct in the forest interior and oil palm plantation sites when compared to the other intermediately disturbed habitats. Vegetation structure resulted as the strongest predictor for moth community composition, whereas microclimate had little effect. According to these results, Geometridae is a better indicator of habitat disturbance as they are generally bound to undisturbed forests, while arctiines are more adapted to open habitats. Even though successional forests harbor different species composition than old-growth forests, they may provide alternative habitat for forest species that may ameliorate biodiversity loss in the face of oil palm expansion. The results of this study were shared in several outreach activities in Turrialba and La Gamba, Costa Rica. The collected moths (almost 4,000 individuals) were shown to the public in two exhibitions in Turrialba that were visited by approximately 200 people, both scientists and non-scientists from the area. A talk and workshop was also offered in La Gamba, an activity that counted with the participation of approximately 50 people from the community and diverse local organizations. A moth identification guide for La Gamba was prepared and distributed in the community and several other interested parties. This research project may be used as a baseline for the development of effective monitoring protocols that include moth assemblages as biological indicators of habitat disturbance. Further studies on the possible ecological consequences of oil palm expansion in the Neotropics are needed to better understand how to prevent irreversible losses to biodiversity and ecosystem services that are essential for the sustainable development of rural communities.

Keywords: *Land use change, human dominated landscapes, moth assemblages, oil palm plantations, outreach, La Gamba, Costa Rica*

RESUMEN

El cambio de uso de suelo es una de las mayores amenazas para la biodiversidad en agropaisajes tropicales. Censos de biodiversidad proveen información valiosa sobre las respuestas de diferentes taxones a estos cambios antropogénicos, que puede ser utilizada en estrategias de conservación basadas en evidencia enfocadas en reducir la pérdida de biodiversidad. La palma aceitera es actualmente uno de los cultivos de más rápida expansión en el mundo, pero no se conoce su impacto en la biodiversidad del Neotrópico, en especial para los insectos. Este proyecto de tesis se enfoca en evaluar el ensamblaje de geométridos y ártidos en un agropaisaje tropical del suroeste de Costa Rica, donde durante la última década las plantaciones de palma aceitera se han convertido en el segundo uso de suelo de mayor área. Las mariposas nocturnas fueron colectadas durante seis meses (feb-jul) con trampas de embudo automáticas en cuatro tipos de hábitat (interior y margen de bosque maduro, bosque secundario joven y plantaciones de palma aceitera) dentro de un área de 30km^2. La riqueza y diversidad de estas mariposas fue muy reducida en las plantaciones de palma, pero solo geométridos mostraron diferencias en abundancia entre los hábitats, con mayores capturas en bosque maduro y menores en plantaciones. La abundancia de ártidas no difirió entre hábitats debido a la presencia de algunas mariposas de la tribu Lithosiini, las cuales fueron muy comunes en las plantaciones de palma. La composición de especies fue diferente en el interior del bosque y en las plantaciones de palma, en comparación con los otros hábitats perturbados y sucesionales. La estructura de la vegetación resultó ser el factor más influyente en la composición de especies de mariposas en este paisaje, mientras que el microclima tuvo muy poco efecto. De acuerdo a estos resultados, Geometridae es mejor indicador de perturbación de hábitat ya que están más confinados al bosque maduro, mientras que los ártidos están más adaptados a hábitats perturbados. Aunque los bosques sucesionales albergan una composición de especies diferente a bosques maduros, pueden representar un hábitat alternativo para especies de bosque frente a la expansión de la palma aceitera. Los resultados de este estudio fueron expuestos en varias actividades de difusión en Turrialba y La Gamba, Costa Rica. La colección de mariposas (cerca de 4,000 individuos) fue mostrada en dos exhibiciones en Turrialba, las cuales recibieron visitas de aproximadamente 200 personas, tanto científicos como no científicos de la región. En la Gamba se ofreció una charla y taller, que contó con la participación de casi 50 personas de la comunidad y diversas organizaciones locales. Se preparó una guía de identificación de especies de mariposas nocturnas de la Gamba, la cual fue distribuida en la comunidad y otros interesados. Este proyecto puede usarse como línea base para el desarrollo de protocolos de monitoreo que incluyan a las mariposas nocturnas como bioindicadores de perturbación de hábitat. Se necesitan más estudios sobre las posibles consecuencias ecológicas de la expansión de palma en el Neotrópico para intentar prevenir pérdidas irreversibles de biodiversidad y servicios ecosistémicos que son esenciales para el desarrollo sostenible de comunidades rurales.

Keywords: *Cambio de uso de suelo, agropaisajes tropicales, ensamblaje de mariposas nocturnas, plantaciones de palma aceitera, La Gamba, Costa Rica*

1. INTRODUCTION

Tropical human dominated landscapes have been changing rapidly due mainly to human induced land use change and habitat fragmentation. Conversion of terrestrial ecosystems to livestock farming areas or into monoculture based agricultural lands is amongst the leading causes of these land transformations in the last century (Lambin *et al.* 2003, Grau and Aide 2008). Most tropical landscapes are now comprised of few and often small forest patches surrounded by a matrix of diverse land use types that may offer a variety of differing ecological niches (Ricketts *et al.* 2001). Forest conversion and concomitant native habitat loss may be one of the leading causes of biodiversity loss (Sánchez-Azofeifa *et al.* 2003), since a great variety of plant and animal groups have experienced severe declines in species richness and even local extinctions in these modified landscapes (e.g. Fahrig 2003). Nevertheless, contradictory scientific results have been observed as responses to fragmentation and landscape conversion vary across taxa and local landscape characteristics (Barlow *et al.* 2007a, Jauker *et al.* 2009).

While most studies have concentrated on the implications of land use change for many well-known vertebrate and plant groups, increasing attention has recently been rendered for invertebrates, which are now widely recognized as indicators of environmental quality, conservation monitoring and human land use impacts on the ecosystem (Brown 1997, Andersen *et al.* 2002, Pearce and Venier 2006, Nakamura *et al.* 2006, Fleishman and Murphy 2009). In particular, the Lepidoptera is one of the most studied insect groups and diverse taxa are recognized as biological indicators, but most studies have concentrated on butterflies (Kitching *et al.* 2000, Lomov *et al.* 2006, Bonebrake *et al.* 2010). Less research has been conducted on nocturnal moths, even though they are easily assessed in manual or automatic light traps (Brehm and Axmacher 2006) and carry out a great variety of ecological processes by acting as prey, pollinators and selective herbivores in the ecosystem (New 2004).

Several studies on moth assemblages in fragmented landscapes have shown that responses greatly vary among moth taxa (Summerville and Crist 2004, Schmidt and Roland 2006, Hawes *et al.* 2009). Some groups have shown more vulnerability to land use change, particularly the strongly forest-dependent Geometridae family (Ricketts *et al.* 2001, Hilt *et al.* 2006), while other groups like the tiger moths (Erebidae-Arctiinae) contain many species that seem to thrive in disturbed habitats (Hilt and Fiedler 2005, Nöske *et al.* 2008). Nevertheless, most comparative studies of moths and habitat disturbance have been conducted in temperate regions or in tropical Southeast Asia, which may not illustrate the true vulnerability of Neotropical moth assemblages (New 2004).

The present thesis project aims to characterize moth assemblages throughout a human dominated landscape located in the wet tropical lowlands of Costa Rica, a region that has suffered a marked increase in oil palm expansion in the last decades (Höbinger *et al.* 2011). The only study to date that assesses the impact of oil palm plantations on moth assemblages was performed in Borneo, where moth richness and diversity was shown to be severely reduced in this monoculture (Chey 2006), yet this has not been assessed in the Neotropics. For this reason, this study focuses on evaluating geometrid and arctiine moths along four different land use types in the Costa Rican Golfo Dulce region, to ascertain whether these groups differ in their distribution and habitat preferences along the landscape. A series of microclimate and vegetation parameters were recorded to determine their influence on moth composition and diversity. The results of this study serve as a baseline for evidence-based conservation actions to be developed, which take into consideration moth biodiversity as a possible indicator of habitat disturbance.

1.1. Justification and Importance

Land use intensification and habitat fragmentation are currently the major threats to tropical forests and biodiversity, but their precise effects are unknown for many groups of species. This is especially true for moths, which have received less attention even though they compose the majority of Lepidoptera (Kristensen *et al.* 2007). This research study contributes to the knowledge of land use change dynamics and how it affects moth assemblages, which were chosen as a focal group to assess ecosystem quality in the Golfo Dulce Region of Costa Rica. It helps determine which moth taxa show resilience to habitat changes and are more likely to persist in human dominated landscapes, as well as identifies the most vulnerable moth groups that may need to be the focus of conservation initiatives. This is a necessary step towards understanding the ecological impacts of land use change in this particular landscape and in the wet tropical lowlands in general.

As a highly biodiverse and heterogeneous landscape (Weissenhofer *et al.* 2008), the region around La Gamba community in the Golfo Dulce Region of Costa Rica is an ideal study site to assess faunal distributions throughout a variety of land use types, which include different types of old-growth forest, pastures, secondary forests of various ages, small and large scale agriculture, and urban settlements. Preliminary studies of butterflies in this region show reduced diversity in disturbed habitats (Wiemers and Fiedler 2008), yet moths had never been assessed to determine whether they show the same patterns.

Of the many intensive agricultural practices, oil palm plantations are rapidly expanding in the Golfo Dulce Region and worldwide (Koh and Wilcove 2008), which are known to reduce biodiversity and provoke habitat fragmentation and pollution (Fitzherbert *et al.* 2008). Effective biodiversity assessments and monitoring tools are required to help provide a scientifically sound basis for decisions to be made that stop or control habitat loss, perhaps by the improvement of local land use and agricultural practices. Tropical secondary forests may contribute to the conservation of biodiversity by providing alternative habitats to old-growth forests (Taki *et al.* 2012), which could serve as an additional incentive for local forest restoration and reforestation. Thus, the main purpose of this study was to compare moth assemblages in old-growth forests (interior and edge habitats), secondary forests and oil palm plantations, as a means to understand their dynamics throughout this fragmented landscape.

This study is not only among the few that evaluate the relationship between land use patterns and moth assemblages in the Neotropical lowlands, but also assesses how microclimatic and vegetation characteristics affects their diversity, abundance and composition.

This serves to identify critical habitat characteristics for moth conservation. In addition, due to the lack of methodologies for the use of moths as biological indicators, there is a need to identify practical and effective indicator species among moth species. Thus, the families Geometridae and Erebidae-Arctiinae were chosen specifically in this study since they have shown to be sensitive to land use change (Ricketts *et al.* 2001, Beck *et al.* 2002, Hilt and Fiedler 2005) and thus show higher potential as indicators.

1.2. Objectives

1.2.1. General objective

Contribute to the knowledge of land use impacts on moth assemblages in the humid tropical lowlands.

1.2.2. Specific objectives and study questions

- Characterize species richness, composition and diversity of geometrid and arctiine moths across four different land uses (old-growth forest interior, old-growth forest margin, young secondary forest, and oil palm plantations).
    - Do geometrid and arctiine assemblages differ between habitat types?
    - Are there any moth species that show higher affinity to certain habitat types, which may thus serve as potential biological indicator species?

  Prediction: We predicted that species composition of arctiine and geometrid moths will be markedly different across land use types. The diversity of geometrid moths will be highest in old-growth forests (Ricketts *et al.* 2001, Beck *et al.* 2002), while for arctiines it will be highest in secondary forests (Hilt and Fiedler 2005), and both will show lowest diversity in oil palm plantations (Fitzherbert *et al.* 2008).

- Evaluate the relationship between geometrid and arctiine moth assemblages and the vegetation and microclimate characteristics found in each land use type.
    - Are richness, diversity and composition of moth assemblages affected by microclimate and vegetation characteristics of each land use type?
    - Which habitat variables have a higher effect on moth assemblages?

2. THEORETICAL FRAMEWORK

2.1. Land use change in tropical human dominated landscapes

2.1.1. Land use change and biodiversity

Global population growth in the last century has resulted in an unprecedented increase of natural resource use for the fulfillment of human needs, such as food, fiber, shelter and freshwater (MEA 2005). Although land use change is essential for humanity, it has come at the expense of the degradation of natural habitats and ecosystem services, mainly by unsustainable agricultural expansion (Foley *et al.* 2005). Approximately 38% of terrestrial ecosystems have been converted to croplands, mostly after deforestation of forest habitats, greatly modifying landscape characteristics across the world (Grau and Aide 2008). If the human population reaches its projected 9 billion by 2050, these trends are expected to increase by 30%, owing to higher food and resource demands (Tilman *et al.* 2001, Foley *et al.* 2005).

Human dominated landscapes now cover most of the land area in many parts of the world, especially in the tropics, where land use change has had a very high and rapidly growing impact at the expense of natural ecosystems (MEA 2005). Land use practices in tropical rainforests, the most biologically diverse of all terrestrial biomes, have resulted in highly fragmented landscapes mainly by means of large scale forest conversion and colonization of livestock based agriculture (Lambin *et al.* 2003). Tropical forests are not only threatened by land use change and deforestation, but also by unsustainable hunting and logging activities, forest fires and climate change (Cochrane 2003, Allen *et al.* 2010, Sodhi and Ehrlich 2010).

Tropical landscape fragmentation reduces the total area covered by forests and exposes forest organisms to conditions of a different surrounding habitat (Murcia 1995). These human dominated landscapes are mosaics of land uses, generally made up of isolated forest patches at different stages of succession surrounded by an agricultural matrix that offers differing niche availability for local biota (Gómez *et al.* 2003, Donald and Evans 2006). The variability of land use types may provoke differing ecological responses, depending on the taxonomic group and their ecological attributes (Barlow *et al.* 2007a, Jauker *et al.* 2009, Sodhi and Ehrlich 2010).

Some traditional livelihood practices are often known to conserve biodiversity, by the maintenance of forest patches at different successional stages; each stage or land use type may represent a unique community and contribute to create a dynamic and heterogeneous landscape (Sodhi and Ehrlich 2010). This is also supported by the Intermediate Disturbance Hypothesis (IDH), which predicts that local species diversity will be higher at an intermediate level of disturbance (Connell 1978, Bongers *et al.* 2009). Hence, various studies have concentrated on assessing the conservation value of agricultural systems, secondary forests and tree plantations for biodiversity (Chazdon *et al.* 2009), but there has been a lack of consensus in this regard since the results have not been consistent and depend on the focal taxa (Barlow *et al.* 2007a, Gardner *et al.* 2008, Hawes *et al.* 2009). Some disturbed or heterogeneous landscapes have been shown to possess an unexpected high biodiversity, mainly due to the cultivation of a diversity of crops in the same area via the use of small-scale agroforestry systems that have a low impact on the ecosystem (Tscharntke *et al.* 2005, Sodhi and Ehrlich 2010).

However, for species that once lived in a continuous expanse of forest, the general assumption is that they will not survive in these human dominated habitats (Daily 1999, Tabarelli 2010), especially when the agricultural matrix is particularly hostile due to modern intensive agriculture (Donald and Evans 2006), such as cattle pastures and industrial high-yield monocultures, as well as urban settlements. As a result, land use change and consequent habitat fragmentation are now recognized among the key drivers of global species loss (Foley *et al.* 2005), since multiple studies have demonstrated a negative effect on a variety of plant and animal groups (see Fahrig 2003).

Future land conversion practices are projected to be concentrated on low-income and developing countries, like most in Central America, while industrial countries are experiencing an increase in forest cover due to the abandonment of agricultural lands (MEA 2005). In addition, the tropical rainforests of Central America are already among the most fragmented in the world (Rudel and Roper 1997). Due to this high vulnerability to human activities, Central America and the Neotropics in general hold special conservation priority (Brooks *et al.* 2006), especially since the region supports a higher biodiversity than other parts of the world in most taxonomic groups (Dirzo and Raven 2003). Urgent measures are required to ensure the sustainability of natural resources and ecosystem services for present and future generations. Thus, the quest for balance between production and conservation has become an important and challenging matter for conservation scientists (Garnett *et al.* 2007), as well as the assessment of the political, socioeconomic and ecological factors that shape land use decisions and management actions (Rudel *et al.* 2005).

2.1.2. Land use change in La Gamba, southwestern Costa Rica

Costa Rica is recognized internationally by its efforts in balancing nature conservation and economic development (Sánchez-Azofeifa *et al.* 2001). Even though the country suffered high deforestation from the 1940s to the 1990s and was once known as having one of the world’s highest deforestation rates, deforestation was significantly reduced by the early 2000s thanks to a wide variety of governmental policies and conservation initiatives (Pagiola 2008, FAO 2010). During the last 30 years, the government has set aside more than 25% of terrestrial land for the conservation of biodiversity, natural resources and ecosystem services, under a comprehensive National System of Conservation Areas (SINAC) (MINAE-SINAC 2006). The implementation of strict Forestry Laws that prohibit deforestation, the rise in ecotourism practices and the establishment of an innovative country-wide program of Payments for Environmental Services (PES) (Pfaff and Sánchez-Azofeifa 2004, Pagiola 2008) have also contributed to set an example for sustainable management and conservation of national resources in developing countries.

Despite these noticeable achievements, there has been a noticeable expansion of croplands in areas outside of old-growth forests, as well as an increase in the clearing of native reforestation areas, for the establishment of large-scale and export-oriented plantations such as pineapple (Fagan *et al.* 2013). In the Golfo Dulce Region, which is located on the Pacific side of southern Costa Rica and is part of the Osa Conservation Area (ACOSA), remaining forests are faced with constant pressure due to such unsustainable and intensive agricultural activities. From the 1940s to the 1970s, a large amount of land from this region was seized without regulation for the unplanned expansion of croplands and cattle pastures, especially on flat lands, leaving most ridges and steep slopes undisturbed; much of these practices and the expansion of high-yield monocultures are occurring in the border of small but highly biodiverse protected old-growth and secondary lowland forests, which poses a severe threat to forest dependant biodiversity (Weissenhofer *et al.* 2008).

La Gamba is a small rural village of the Golfo Dulce Region that lies on the eastern edge of the Piedras Blancas National Park. The village is surrounded by farm lands with different land use intensity, mainly cow pastures, rice fields and a growing area of oil palm plantations (Höbinger *et al.* 2011). Forest conversion in La Gamba was also mostly concentrated on flat lands, leaving undisturbed forest habitats on narrow ridges and steep slopes near or inside the National Park. The agricultural mosaic is thus surrounded by old-growth forest and patches of secondary forest in a variety of succession stages (Weissenhofer *et al.* 2008). Land use activities around La Gamba are being closely monitored by the La Gamba Tropical Field Station, an Austrian research station that has established there in the last 20 years to promote ecological investigation, reforestation and conservation of tropical rainforests. Thus, this area presents an ideal opportunity for researchers to assess the effects of land use change on biodiversity and ecological processes. This study focuses specifically on four habitat types found around La Gamba village (old-growth forest interior, old-growth forest edges, young secondary forests and oil palm plantations), which show singular biotic and abiotic characteristics that may thus sustain distinct faunal communities.

2.1.2.1. Old-growth forests

It is common knowledge that the area of undisturbed forest around the world is being continually reduced by the activities of humankind. Over the past three centuries, forest habitats have been reduced to roughly half of their global extent, leaving smaller fragments of the original forest that are being further threatened by natural and anthropogenic drivers (Sodhi and Ehrlich 2010). According to the Millennium Ecosystem Assessment (2005), tropical forests are disappearing at up to 130,000 km^2 a year, which is rather worrisome given that a great number of species are uniquely found in undisturbed old-growth forests and may face local extinction in human dominated habitats (Barlow *et al.* 2007a). In this study, the term old-growth forest is used in reference to forests that are free of significant human disturbance (have not been previously converted to any other non-forest land cover).

Old-growth forests reach a dynamic equilibrium that allows for habitat specialization among forest species, which explains their high species uniqueness when compared to secondary forests or tree plantations (Barlow *et al.* 2007a). They are considered the most biologically diverse habitats in the world, and generally show higher species richness in a great variety of taxonomic groups, such as: trees and lianas, small mammals, bats (Barlow *et al.*

2007a), birds (Barlow *et al.* 2007b), fruit-feeding butterflies (Barlow *et al.* 2007c), amphibians and lizards (Gardner *et al.* 2007), dung beetles (Gardner *et al.* 2008) and epigeic arachnids (Lo-Man-Hung *et al.* 2008). However, this higher species richness pattern does not necessarily hold true for all taxa, as evidenced with moths (Hawes *et al.* 2009), large vertebrates (Parry *et al.* 2007), grasshoppers, scavenger flies and orchid bees (Barlow *et al.* 2007a), which have shown distinct community structures in each habitat type.

The interior of old-growth forests are the least affected by anthropogenic activities, where the forest shows no detectable edge influence and is the most similar to the original habitat (Harper *et al.* 2005); these areas are dominated by native tree species that generally support native fauna (Lugo and Helmer 2004). Yet forest interiors are being increasingly threatened by external pressures due to the reduction of forest patch area in tropical fragmented landscapes. The fate of forest dependent species that require continuous forests remains subject to the maintenance of the original habitat conditions in the interior of these fragments, and may face extinction when exposed to edge influences and habitat degradation.

2.1.2.2. Edge habitats

One of the main consequences of the deforestation and fragmentation of forest habitats is the creation of new ecosystem boundaries or edge habitats, which expose forest organisms to the conditions of the surrounding land uses (Murcia 1995). These edges often posses physical and structural conditions that are characteristic of neither of the adjacent habitats, and give rise to ecological communities that are distinct from forest interiors (Malcolm 1994). As forest fragmentation increases, so does the extent of forest edges, which explains why the ecological dynamics of these habitats have been studied extensively (Fahrig 2003, Ries *et al.* 2004, Harper *et al.* 2005).

Edge effects are changes in the biotic and abiotic conditions that originate in the vicinity of sharp transitions between two adjacent and distinct patches, created by the differences between the adjacent habitats (Kattan 2002). Abiotic edge effects refer to physical changes such as radiation, moisture, temperature, humidity, wind speed and soil nutrients, while biotic edge effects are biological changes and processes such as species composition of fauna and flora, and patterns of competition, predation and parasitism (Fischer and Lindenmayer 2007). The most common characteristics of edge habitats that have been documented are a high structural contrast at the edge, high wind speed, high temperatures and light intensity, reduced humidity, leaf litter accumulation, higher tree mortality and damage, and the presence of exotic, invasive and pioneer taxa (Harper *et al.* 2005).

Even though edge effects are commonly associated with detrimental consequences for biodiversity (Fischer and Lindenmayer 2007), it is difficult to predict and compare the ecological responses to edge effects at different spatial and temporal scales and varying habitat characteristics. Several authors have proposed models and hypothesis which attempt to describe edge effects and dynamics, yet there is little consensus on the development of a clear-cut framework or unifying theory (Malcolm 1994, Ries *et al.* 2004, Harper *et al.* 2005). In general, the magnitude and degree of the impact greatly depends on the community characteristics of the adjacent habitats, as well as local and regional abiotic conditions (Murcia 1995).

2.1.2.3. Secondary forests

The destruction and degradation of old-growth forests worldwide has given rise to increasing interest on the value of secondary forests for the conservation of biodiversity and ecosystem services (Chazdon *et al.* 2009). There have been numerous definitions of the term "secondary forest", based on whether the prior disturbance was human or natural, the intensity of the disturbance, and/or the vegetation development process (Chokkalingam and de Jong 2001). For the purposes of this study, the term secondary forest refers to the product of natural secondary succession on abandoned farmland, where the original forest was totally cleared prior to agricultural use (Wadsworth 2000).

As economic activities intensify around large cities in industrialized and developed countries, deforestation trends are reversed and a slow increase in forest cover takes place after abandonment of an agricultural based economy (Rudel 1998, Lugo and Helmer 2004). This process has been termed "the forest transition" by Alexander Mather (Mather 1992, Rudel *et al.* 2010), and explains why the area covered by secondary forests now covers as much as 60% of remaining tropical forests worldwide (FAO 2006), due to the regeneration of secondary vegetation on previously deforested and degraded lands (Dent and Wright 2009). As deforestation and habitat loss continues, secondary forests could slow climate change by carbon sequestration and provide alternative habitat for many forest taxa (Rudel *et al.* 2002).

There are some key generalities that differentiate secondary from old growth forests; these include the lack of a full canopy, the presence of smaller trees, more light reaching the forest floor which produces a dense understory, and the presence of pioneer and invasive species. Brown and Lugo (1990) estimated it takes approximately 80 years for secondary forests to achieve similar woody plant species richness and vegetation characteristics as seen in old-growth forests. However, it is now well known that there exists great variability in the structural and functional characteristics of a naturally regenerating forest due to regional differences and patterns of disturbance or prior land use (Chokkalingam and de Jong 2001). For this reason, over a period of decades or centuries, these habitats generally have different species assemblages and community structures from those seen in old-growth or undisturbed forests (Finegan 1996, Dent and Wright 2009). Due to these characteristics and new species compositions, secondary forests have also been termed new forests (Lugo and Helmer 2004) or novel ecosystems (Hobbs *et al.* 2006), as an attempt to describe their varying dynamics in different developmental conditions. Despite extensive literature on the potential of secondary forests for the conservation of old-growth forest faunal species, their value and dynamics is poorly understood for many taxa and is still a debated topic (Chazdon *et al.* 2009).

On a broad review of published literature from the last 3 decades on the recovery of tropical faunal species in secondary tropical forests, Dent and Wright (2009) found that many species are able to survive in these habitats and that the similarities between secondary and old-growth forests is higher than previously thought by scientists. The similarity increases with secondary forest age, nearness to old-growth forests and seed sources, as well as when the prior land use was of low intensity (e.g. shifting agriculture and small scale tree plantations). This may be explained by the intermediate disturbance hypothesis, which predicts that species diversity will be higher when disturbance is of intermediate intensity (Connell 1978). Therefore, even though old growth forests are irreplaceable, conservation efforts should also promote the development of structural and functional complexity in tropical secondary forests, for their role in supporting forest species populations in human dominated landscapes (Finegan and Delgado 2000, Dent and Wright 2009).

2.1.2.4. Oil palm plantations

Oil palm is currently recognized as one of the world's most rapidly expanding crops and has widely contributed to tropical forest deforestation (Fitzherbert *et al.* 2008). Plantations of African oil palm (*Elaeis guineensis*) have grown from 10.1 million ha in 2000 to 17.3 million ha in 2012 throughout 44 countries, with a global annual growth rate of more than 8% (FAOSTAT 2013). Currently, around 27% of the total global production of vegetable oil and fat comes from oil palm plantations, placing it as the world's most important oil crop (Turner *et al.* 2008). Is it estimated that oil palm demand will continue to increase rather steeply due to its low production costs, reaching double of what it is today by 2050 (Carter *et al.* 2007, Corley 2009). Thus, there is growing concern on the impacts on this crop on tropical forests and biodiversity (Sandker *et al.* 2007, Koh and Wilcove 2008).

Oil palm plantations are only grown in tropical humid lowland areas, which are naturally occupied by moist tropical forests of high biodiversity. Compared to the original habitat, most palm monocultures are structurally simple, with a uniform tree structure, a low canopy, almost no understory growth and a high degree of human disturbance; in addition, they are clear cut every 25-30 years for rotation of crops (Corley and Tinker 2003). The most comprehensive assessment on the effects of oil palm plantations on biodiversity is a review by Fitzherbert *et al.* (2008), who found that they harbor less species richness than old-growth, secondary forests and other tree crops. According to this review, only 15% of old-growth forest faunal species were also recorded in oil palm plantations, where assemblages are dominated by a few generalists, non-forest, invasive and/or pest species. The forest species that were lost tended to be those of specialized diets, small range sizes and/or an already high conservation concern. Yet most of these studies concentrated on large animals and birds, while little attention has been rendered for insect communities, which are generally better indicators of biodiversity (Turner *et al.* 2008).

It is now widely accepted in literature that oil palm plantations have severe negative effects on biodiversity, since they are unsuitable habitat for most forest species and act as barriers across the landscape (Fitzherbert *et al.* 2008). To reduce these effects, many authors have suggested the use of alternative wildlife-friendly oil palm plantations, which include the protection of remaining natural forests, the use of anthropogenic grasslands for oil palm cultivation, and financial incentives that promote adequate production behavior (Koh 2008, Corley 2009, Wilcove and Koh 2010). This has resulted in initiatives such as the Roundtable on

Sustainable Palm Oil (RSPO) certification program, which was created to protect forest fragments within plantations and avoid further conversion of tropical forests (RSPO 2007). The effectiveness of these and other strategies is still in debate (Edwards *et al.* 2010), and will largely depend on the willingness of governmental and non-governmental organizations of producer countries (Fitzherbert *et al.* 2008).

Most oil palm expansion is taking place in Southeast Asian countries, especially Malaysia and Indonesia with 80% of global oil palm area, mainly at the expense of native forests (Koh and Wilcove 2008). However, this crop has also increased recently in the Neotropics, such as the Amazon and Costa Rica (Butler and Laurance 2009, Höbinger *et al.* 2011). There is now more than 60,000 hectares of oil palm plantations in Costa Rica, of which approximately 64% is concentrated in the southern Pacific region (CANAPALMA 2014). Even though oil palm plantations in this region have shown biodiversity loss for a wide variety of taxonomic groups (Dirzo *et al.* 2013), the majority of the producers do not understand the long-term social and environmental impacts of oil palm production (Beggs and Moore 2013). Thus, studies on ecological impacts of this crop are needed to further develop sustainable management strategies and environmental awareness programs for local oil palm producers.

2.2. Moth assemblages in tropical landscapes

2.2.1. Moth biology and ecological functions

Lepidoptera are one of the largest and most diverse insect groups, with over 160,000 described species in more than 120 families (Gullan and Cranston 2010). Butterflies have become important icons for insect conservation due to their attractive colors and sensitivity to anthropogenic habitat disturbance (Horner-Devine 2003). Much less attention has been given to the less conspicuous moths, even though they are known to comprise more than 90% of the known lepidopteran species and are distributed globally throughout a wide range of habitats (Janzen 1988). It is estimated that moths are spread among 30 superfamilies (compared with 2-3 for butterflies), with some of the largest families (e.g. Noctuidae and Geometridae) comprising more species than the whole of butterflies (New 2004).

Moths are responsible for a great variety of ecological processes and ecosystem functions as pollinators, selective herbivores and prey for migratory passerines (Summerville and Crist 2004, Lomov *et al.* 2006). All of these functions represent ecosystem services that moths provide human beings, especially through pollination, which may be regarded both as a regulating and a supporting service due to its importance for plant reproduction and for the maintenance of other ecosystem services (MEA 2005). Even though moths have been known to visit fewer flower heads than bumblebees, they fly significantly greater distances than other insect pollinators, which aids in plant gene dispersal by expanding the area of plant neighborhoods within a population and increasing individual plant fitness (Schmitt 1980).

Moth survival is highly dependent on effective feeding during the larval stage, yet many species have a specialized host-plant relationship that may greatly restrict their distributions (Vane-Wright and Ackery 1989). Nevertheless, the larval foodplant of many moth species is not yet known (New 2004), which is critical information for the conservation of these species since their survival in disturbed habitats may depend on the availability of host-plants (Summerville and Crist 2004, Nöske *et al.* 2008). Due to this host-plant relationship, moths have been strongly associated with vegetation structure and composition (Lomov *et al.* 2006).

For the aforementioned reasons, moths have been considered as possible indicator taxon for various ecological studies (e.g. environmental quality: Summerville and Crist 2004, restoration monitoring: Lomov *et al.* 2006, environmental change: Hilt *et al.* 2006). Yet moths have also been considered as pests due to their severe depredation on crops, ornamental plants or stored products, which has contributed to reducing their popularity (New 2004). Extensive research has been conducted mainly to develop viable pest management techniques (Baggen and Gurr 1998, Trimble *et al.* 2001, Witzgall *et al.* 2008), which has partially obscured their high ecosystem value and conservation worth when compared to diurnal butterflies. Thus, there is a need for further studies on moth ecology and their response to anthropogenic stressors if the ecosystem services they provide are to be maintained in human dominated landscapes.

2.2.2. Impacts of land use change on moth assemblages

For the purposes of this study, special attention was given to Geometridae and Erebidae-Arctiinae, which are two of the four largest groups of Lepidoptera, with species numbers worldwide in the range of 21,000 and 11,000, respectively (Scoble 1999, Watson and Goodger 1986). These families are particularly species-rich in the Neotropics, where more than half of Arctiinae and more than 6,000 Geometridae species may be found (Watson and Goodger 1986, Brehm 2010). Their high species numbers enables sufficient sampling numbers to achieve significant power in statistical analyses, which may serve to find consistent spatial patterns relative to land use type. In addition, a high proportion may be identified to species and some have well-known host plants (Brehm 2007).

2.2.2.1. Geometrid moth assemblages in human dominated landscapes

Geometrid moths are a common study group among lepidopterists due to their noticeable high biodiversity. They are found in every biogeographical region and generally have well known taxonomy (Scoble 1999), yet their distribution patterns seem to be very specific to the subfamily and the region (Intachat and Holloway 2000, Brehm and Fiedler 2003). Geometrid moths have shown higher richness and diversity in the understory of tropical forests, potentially due to their host plant preferences (Brehm 2007). A consistently high diversity has been recorded along complete elevational gradients, although in Costa Rica they seem to reach peak diversity between 1000 and 2000 m.a.s.l (Brehm *et al.* 2007, Brehm 2010).

Geometridae has served as a focus group in a variety of environmental change and ecological studies as they seem to be relatively habitat-specific (Kitching *et al.* 2000, Beck *et al.* 2002). These sedentary habits may be explained by their generally small size and low mobility (Usher and Keiller 1998), and the fact that their herbivore larvae mainly feed on woody plants and many are host-specific (Scoble 1999, Schmidt and Roland 2006). Intachat *et al.* (2001) demonstrated that geometrid moth abundance is directly dependant on the availability of larval food in the forest, while tree diversity and understory vegetation have been found to be important explanatory variables for observed variations in geometrid diversity (Beck *et al.* 2002, Brehm *et al.* 2003).

The aforementioned characteristics of geometrid moths have been used to explain their tendency to be negatively affected by land use change. Ricketts *et al.* (2001) noted a higher proportion of geometrid moths in closed forest sites compared to agricultural sites. Accordingly, in the montane region of southern Ecuador, Hilt *et al.* (2006) noted higher geometrid species diversity in late successional study sites and old-growth forest, and also a decrease in diversity with increasing distance to natural forest. These patterns have been observed in studies from a variety of other regions (England: Usher and Keiller 1998, Australia: Kitching *et al.* 2001, Borneo: Beck *et al.* 2002, North America: Summerville and Crist 2004, Tanzania: Axmacher and Fiedler 2008), which explains why several authors have suggested this family as potential indicators for forest recovery or environmental change (New 2004, Hilt *et al.* 2006).

Despite these observed patterns of geometrid moths in human dominated landscapes, there are still many inconsistencies. Some publications have shown that a high proportion of species benefit from habitat disturbance (Brehm and Fiedler 2005). Higher richness and densities have been recorded in late succession habitats, especially those close to near-natural forests, but not in old-growth forest interiors (Nöske *et al.* 2008). Nevertheless, this may be due to the presence of extremely common species, as well as tourist species from nearby forest remnants (Brehm and Fiedler 2005, Beck *et al.* 2011). Additional studies have found that the diversity of vascular plants or plant species richness is not positively correlated with geometrid moth diversity (Axmacher *et al.* 2004, Axmacher *et al.* 2009).

In general, it seems true that geometrid moth assemblages are sensitive to land use change, as the degree of habitat disturbance has been recognized as a key variable to explain their composition and spatial structure (Beck and Chey 2007). Due to their variability in terms of habitat preferences, conservation efforts should not only be concentrated on old-growth forests, but also on secondary forests of advanced succession (Brehm and Fiedler 2005). These disturbed habitats have proven to be suitable for many geometrid species, so long as they have undisturbed forest remnants nearby which serve as a source habitat (Beck *et al.* 2011).

2.2.2.2. Arctiine moth assemblages in human dominated landscapes

Among tropical moths, tiger moths (Erebidae-Arctiinae) have received research attention due to their singular behavior, ecology and life history patterns, yet knowledge of this family in Neotropical regions is still rather reduced (Brehm 2009). Nevertheless, this family has relatively well known taxonomy (Hilt and Fiedler 2005), which facilitates their study in tropical landscapes. Contrary to geometrids, arctiine moths may be found both in the understory and the canopy of tropical forests, but have shown higher abundance and diversity in the canopy, perhaps due to higher resource availability (Brehm 2007). Highest diversity has also been reported in the elevational ranges of 215-1000 masl, showing reductions in lower and higher elevations (Brehm 2009).

Some distribution patterns have been documented for arctiine moths in tropical human dominated landscapes. In Ecuador, Hilt and Fiedler (2005) found that highest arctiine abundance and diversity was not found in old-growth forests, but in advanced succession habitats in close proximity to such forest, confirming results found in Costa Rica by Ricketts *et al.* (2001). Meanwhile, in Brazil, Hawes *et al.* (2009) found marginally higher species richness in secondary forests and eucalyptus plantations when compared to primary forests. Additional publications have also demonstrated that arctiine moths are more abundantly found in disturbed habitats when compared to intact forests, indicating that a high portion of tribes benefit from anthropogenic habitat disturbance (Kitching *et al.* 2000, Choi 2008a, Nöske *et al.* 2008). However, there are still some subfamilies that remain constrained to forest patches (Hilt and Fiedler 2006), where a higher number of unique species have been found (Hilt and Fiedler 2005).

Since different land use types harbor distinct arctiine communities, their distribution patterns have been associated to a wide range of life-history strategies in accordance with the life-history hypothesis (Hawes *et al.* 2009); the larvae of many subfamilies feed on a variety of early colonizing plant species, such as grasses and herbs (Kitching *et al.* 2000). The intermediate disturbance hypothesis has also been used to explain these observed patterns, as abundances are higher in early and late succession stages, but not in open vegetation areas or old-growth forests (Hilt and Fiedler 2005, Nöske *et al.* 2008). In addition, they have shown a positive correlation with temperature, openness and sunshine duration (Choi 2008b, Beck *et al.* 2011).

In summary, tiger moths hold substantial recolonization potential, as some of them seem to thrive in secondary forests and other disturbed habitats (Brehm 2009). Nevertheless, it should be noted that the species inhabiting these disturbed sites are generally extremely common species (Beck *et al.* 2011), which highlights the conservation value of remnant native forest patches. Although the potential of disturbed habitats to support arctiine moth species from old-growth forests is still unclear, maintaining a close proximity to forest remnants seems a key conservation strategy in human dominated landscapes (Hilt and Fiedler 2005, Hawes *et al.* 2009).

2.2.2.3. Major response patterns

The response and adaptability of moth assemblages to land use change greatly depends on their distribution capacities, life history characteristics and resource needs (Beck *et al.* 2006, Hawes *et al.* 2009). Therefore, certain families have better capacities of colonizing disturbed habitats, while others may be constrained to forest patches and possess a higher risk of extinction (Franzén and Johannesson 2007). Results also vary according to the geographical region, the sampling method used, as well as the spatial and temporal scale of the study. While tropical moth faunas and their response to disturbance in forest landscapes have been extensively assessed in the South-East Asian tropical forests, less attention has been rendered to the more diverse and species-rich Neotropical realm (New 2004, Hilt and Fiedler 2005, Hilt *et al.* 2006).

General impacts of land use change and anthropogenic habitat disturbance on moth communities are difficult to assess, due to the highly diverse and complex nature of moth assemblages. It has been hypothesized that nocturnal moths have lower extinction risks in fragmented landscapes when compared to butterflies, due to the advantages of nocturnal habits, which may enable individuals to fully utilize fragmented landscapes without being restricted by heterogeneous climatic variables like temperature and solar radiation (Daily and Ehrlich 1996, Franzén and Johannesson 2007). Yet extinctions have been reported for moth species, as demonstrated by a long term study in southern Sweden, where an estimated 20% of moths had gone extinct over a 50 year period (Franzén and Johannesson 2007).

Most studies have demonstrated that moth community structure is significantly different throughout human dominated landscapes (Summerville and Crist 2004, Schmidt and Roland 2006, Hawes *et al.* 2009). Broadly, moth diversity seems to be reduced with agricultural conversion and degradation of natural forests; losses are mainly seen for rainforest specialists, while species replacement by generalists or herb-feeding taxa is common in non forest habitats (Kitching *et al.* 2000, New 2004, Summerville 2004, Winfree *et al.* 2011). Overall diversity seems mostly reduced in cleared pastures and heavily disturbed sites, while late secondary succession stages and mature secondary forests serve to maintain and even increase moth diversity, although lower levels of rare species have been noted (Beck *et al.* 2002, Axmacher *et al.* 2004, Hilt *et al.* 2006, Hawes *et al.* 2009). Habitat restoration and reforestation has thus been given increasing importance in terms of their contribution to moth conservation (Lomov *et al.* 2006, Taki *et al.* 2010).

2.3. Biological indicators for ecological monitoring

Bioindicators are biological tools (species or guilds) that contain appropriate features that allow them to be used in ecological monitoring assessments, to estimate the state of a variety of parameters or processes, which are in general too expensive or difficult to measure directly (Isasi-Catalá 2011). Bioindicators have been suggested to monitor biodiversity (Noss 1990), ecosystem health (Hilty and Merenlender 2000), ecological integrity (Carignan and Villard 2002), habitat disturbance or condition (Summerville *et al.* 2004, Debuse *et al.* 2007), environmental quality (Hodkinson and Jackson 2005), climate change (Nehring 1998), habitat restoration (Lomov *et al.* 2006), among other natural or anthropogenic processes. They have been rendered special attention by conservationists, managers and monitoring agencies (both governmental and non-governmental), since they generally enable the evaluation and monitoring of these processes in a cost and time efficient manner (Carignan and Villard 2002).

Nevertheless, it is very common to find conceptual or methodological errors when using an indicator species, and in many cases, inadequate bioindicators have been chosen to assess a particular process of interest. Hilty and Merenlender (2000) found 100 vertebrate and 32 invertebrate taxa to be documented in published literature as potential or supposed indicators of ecosystem health, and concluded that the great majority of them do not effectively correlate with ecosystem changes and may be inappropriate indicator species. This has brought the question of whether bioindicators can truly serve as a viable tool for ecological monitoring.

Many authors have attempted to highlight key features and characteristics that bioindicators should have, as well as methodologies to ensure their adequate use (Noss 1990, Dale y Beyeler 2001, Niemi and McDonald 2004, Isasi-Catalá 2011). However, sometimes it is difficult or nearly impossible to find species that fill all these requirements, which creates problems in their proper application.

2.3.1. Potential of moths as biological indicators

A great variety of taxonomic groups have been proposed as bioindicator species, including birds, mammals, plants, phytoplankton, corals, mangroves, lichens, amphibians, arthropods, among many others. Of these, aquatic insects and other benthic invertebrates have historically been the most widely used, specifically for biomonitoring of freshwater ecosystems (Bonada *et al.* 2006). The use of invertebrates as bioindicators, especially insects, carries several advantages such as: many groups have relatively well-known taxonomy, are easy to locate and inventory, carry important ecosystem functions, are ecologically well understood, have a short life-cycle and high turnover rates, for which they have low resilience and respond rather quickly to small changes in the ecosystem (Brown 1997, Hodkinson and Jackson 2005). Also, their high species numbers in tropical forest landscapes enable statistical power in habitat comparisons and most sampling methods are standard and easy to use (Kitching *et al.* 2000).

Among insects, butterflies are one of the preferred indicators, as they are one of the most studied groups in terms of their ecology and taxonomy (Bonebrake *et al.* 2010). On the other hand, moths have been generally neglected in environmental monitoring projects, even though they could also be suitable indicators and may serve to understand anthropogenic impacts on natural habitats (Kitching *et al.* 2000, Summerville *et al.* 2004, New 2004). Dr. Holloway was the first to develop moths as an indicator and target group in biodiversity and conservation research in tropical forest biomes (Holloway 1983, Holloway 1984, Holloway 1985). Nevertheless, there is still much uncertainty and variability on observed spatial patterns and responses of moths to habitat disturbance, which is why distinct methodologies for the use of moths as indicators have not been developed.

Of all tropical moth taxa, Geometridae has been widely regarded with the highest potential as viable bioindicators for environmental change and habitat disturbance (Hilt *et al.* 2006). This may be due to their habitat and host plant specificity (many on arboreal vegetation), high fragility and low mobility, which translates to high habitat fidelity (Intachat *et al.* 2001). They are also relatively well-known taxonomically in the Neotropics and have proven to be negatively affected by habitat disturbance (Kitching *et al.* 2001, Brehm and Fiedler 2003, Summerville and Crist 2004, Axmacher and Fiedler 2008). Yet specific guidelines for the use of geometrid species in environmental monitoring studies are yet to be proposed. This may be due to inconsistent results in observed patterns, as they are not always constrained to a certain habitat type or do not fulfill key bioindicator criteria (Hilt and Fiedler 2005, Hilt *et al.* 2006). Further research is needed with this family to ensure their effective and proper use as bioindicators in tropical regions, as they may hold the highest role in overall conservation actions.

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4. RESEARCH ARTICLE

OIL PALM EXPANSION THREATENS TROPICAL MOTH ASSEMBLAGES IN SOUTHWESTERN COSTA RICA

Aura M. Alonso-Rodríguez, Konrad Fiedler and Bryan Finegan

ABSTRACT

Oil palm is currently one of the most rapidly expanding crops throughout the tropics, yet little is known about its impacts on Neotropical biodiversity, especially for insect faunas. Responses of moth assemblages to land use change may substantially vary among taxa, depending on their functional traits and resource needs. In this study, geometrid and arctiine assemblages were surveyed in a tropical human dominated landscape of southwestern Costa Rica, where oil palm plantations have become the second commonest land cover after pastures. Moths were sampled during six months (Feb-Jul) with automatic funnel traps in four habitat types (interior and margin of old-growth forests, young secondary forests and oil palm plantations) inside a 30km^2 area. Geometrid and arctiine richness and diversity was high in the interior of old-growth forests as well as at forest margins and young secondary forests, but was severely reduced in oil palm plantations. Abundance patterns of both groups showed seasonality, with a decrease in abundance towards the wet season. Geometrid numbers were highest in the interior of old-growth forests and lowest in oil palm plantations, while arctiine numbers did not differ between habitats due to the presence of a few extremely common lichen moth species in oil palm plantations. Dominance values were highest in oil palm plantations, where one species of each group accounted for over 40% of total abundance. Species composition was distinct in the forest interior and oil palm plantation sites when compared to the other intermediately disturbed habitats. Vegetation structure was the strongest predictor for moth community composition, whereas microclimatic differences were hardly relevant. The results of this study confirm that tropical forest geometrid moths are more vulnerable to land use change and are more strongly bound to the interior of rain forests, showing higher potential as bioindicator species, while many arctiines are more adapted to thrive in disturbed habitats. Conservation strategies should focus not only on the protection of old-growth forest remnants, but also on the promotion of natural forest re-growth and structural complexity of degraded habitats. Although successional forests harbor different species composition than old-growth forests, they may ameliorate biodiversity loss in the face of continuous oil palm expansion, which may have severe repercussions on the structure of ecological food webs and provisioning of ecosystem services in human dominated landscapes.

Keywords: *Arctiinae, Geometridae, moth assemblages, land use change, oil palm plantations, human dominated landscapes, seasonality, tropics, La Gamba, Costa Rica*

RESUMEN

La palma aceitera es actualmente uno de los cultivos de más rápida expansión en el trópico, pero poco se conoce sobre su impacto en la biodiversidad de la región Neotropical, en especial para los insectos. Las respuestas de mariposas nocturnas al cambio de uso de suelo puede variar sustancialmente entre taxones, dependiendo de sus rasgos funcionales y necesidad de recursos. En este estudio, se evaluó el ensamblaje de Geometridae y Erebidae-Arctiinae en un agropaisaje tropical del suroeste de Costa Rica, donde las plantaciones de palma aceitera se han convertido en el segundo uso de suelo más común luego de las pasturas. Las mariposas nocturnas fueron colectadas con trampas de embudo automáticas durante seis meses (feb-jul) en cuatro tipos de hábitat (interior y margen de bosque maduro, bosque secundario joven y plantaciones de palma aceitera) dentro de un área de 30km^2. La riqueza y diversidad de geométridos y ártidos fue mayor en el interior del bosque, como también en el margen del bosque y bosque secundario joven, y fue marcadamente reducida en las plantaciones de palma. Los patrones de abundancia para ambos grupos de mariposas mostraron diferencias en la estacionalidad, con una reducción en abundancia hacia la época lluviosa. La captura de geométridos fue mayor en el interior del bosque maduro y menor en las plantaciones de palma, mientras que los árctidos no mostraron diferencias entre hábitats debido a la presencia de algunas mariposas de la tribu Lithosiini, las cuales fueron muy comunes en las plantaciones de palma. Los valores de dominancia fueron mayores en las plantaciones, donde una especie de cada grupo representó más del 40% de la abundancia total. La composición de especies fue diferente en el interior del bosque y en las plantaciones de palma, en comparación con los otros hábitats perturbados y sucesionales. La estructura de la vegetación resultó ser el factor más influyente en la composición de especies de mariposas en este paisaje, mientras que el microclima fue poco relevante. Los resultados de este estudio confirman que los geométridos son más vulnerables al cambio de uso de suelo y están más confinados a bosques maduros, por lo que muestran mayor potencial como indicadores biológicos, mientras que muchos ártidos están más adaptados a prosperar en hábitats perturbados. Se recomienda que las estrategias de conservación no se enfoquen únicamente en la protección de bosques maduros, sino también en la promoción de sucesión secundaria y aumento de la complejidad estructural de hábitats perturbados. Aunque los bosques sucesionales albergan una composición de especies diferente a bosques maduros, este hábitat podría reducir la pérdida de biodiversidad ante la acelerada expansión de palma aceitera, la cual puede tener consecuencias graves en la estructura de las cadenas alimenticias y provisión de servicios ecosistémicos en agropaisajes tropicales.

Palabras clave: *Arctinae, Geometridae, ensamblaje de mariposas nocturnas, cambio de uso de suelo, plantaciones de palma aceitera, agropaisajes tropicales, estacionalidad, La Gamba, Costa Rica*

INTRODUCTION

Land use change has long been recognized as one of the leading drivers of biodiversity loss throughout the world (Fahrig 2003, Rands *et al.* 2010, MacDougall *et al.* 2013). Human dominated landscapes in tropical realms, generally made up of isolated old-growth forest remnants surrounded by an agricultural matrix, offer differing ecological niches for local biota (Ricketts *et al.* 2001). The ecological consequences of these land transformations are greatly variable, depending on the group of organisms under consideration as well as the intensity of land use (Jauker *et al.* 2009, Sodhi and Ehrlich 2010). However, for species that once lived in a continuous expanse of forest, the general assumption is that they will not survive in these anthropogenic landscapes (Daily 1999, Tabarelli 2010), especially when the agricultural matrix is particularly hostile due to modern intensive agriculture (Donald and Evans 2006), such as industrial high-yield monocultures like pineapple and oil palm plantations.

Oil palm (*Elaeis guineensis*) in particular is now one of the world's most rapidly expanding crops, with a global annual growth rate of more than 8% (Carter *et al.* 2007). Most oil palm expansion is taking place in Southeast Asian countries, especially Malaysia and Indonesia with 80% of global oil palm area, mainly after deforestation of tropical rainforests (Koh and Wilcove 2008). Yet this crop has also been expanding in the Neotropics (Butler and Laurance 2009), especially in Costa Rica, where plantations of oil palm have grown from 39.8 thousand ha in 2000 to 63.5 thousand ha in 2012 (FAOSTAT 2013). It is estimated that global oil palm demand will continue to increase rather steeply due to its edible and biofuel uses as well as its low production costs, reaching double of what it is today by 2050 (Corley 2009). This potential oil palm expansion represents a huge threat to Neotropical biodiversity, as studies have demonstrated a loss of as much as 85% of old-growth forest species from a wide variety of taxa in oil palm plantations (Fitzherbert *et al.* 2008).

Effective biodiversity assessments are required to help provide a scientifically sound basis for decisions to be made that serve to reduce biodiversity loss in the face of oil palm expansion, perhaps by the improvement of local agricultural practices and the promotion of forest recovery. Tropical secondary forests may contribute to the restoration and conservation of biodiversity by providing alternative habitats to old-growth forest species (Finegan and Delgado 2000, Wright and Muller-Landau 2006, Taki *et al.* 2012). However, there exists great variability in the structural and functional characteristics of a naturally regenerating forest due to regional differences and patterns of disturbance or prior land use (Chokkalingam and de Jong 2001, Norden *et al.* 2009). For this reason, over a period of decades or centuries, these habitats generally have different species assemblage and community structure when compared to old-growth or undisturbed forests (Finegan 1996, Dent and Wright 2009). In general, despite extensive literature on the potential of secondary forests for the conservation of forest species, their value and dynamics is poorly understood for many taxa and is still a debated topic (Chazdon *et al.* 2009).

Most studies on the impact of land use change on biodiversity have typically focused on charismatic and/or well-known vertebrate groups (e.g. Barlow *et al.* 2007a, Barlow *et al.*

2007b, Gardner *et al.* 2007 and Parry *et al.* 2007). Yet increasing attention has recently been given to invertebrates (Hawes *et al.* 2009), which are now widely recognized as indicators of environmental quality, valuable for conservation monitoring of human land use impacts on the ecosystem (Brown 1997, Andersen *et al.* 2002, Pearce and Venier 2006, Nakamura *et al.* 2006, Fleishman and Murphy 2009). Moths in particular are responsible for a great variety of ecological processes and ecosystem functions as prey, pollinators and selective herbivores (Summerville and Crist 2004, Lomov *et al.* 2006). Nevertheless, not many studies have been conducted on Neotropical moth faunas in a land-use framework, even though they are very abundant and species rich in this region and are easily assessed in manual or automatic light traps (Ricketts *et al.* 2001, Hilt and Fiedler 2005, Brehm and Axmacher 2006).

The response and adaptability of moth assemblages to land use change greatly depends on their dispersal capacities, species traits and resource needs (Hawes *et al.* 2009, Slade *et al.* 2013). Some moth families have shown higher vulnerability to land use change, particularly the strongly forest-dependent Geometridae family (Ricketts *et al.* 2001, Hilt *et al.* 2006), which has been considered a potential indicator group to monitor forest recovery or habitat disturbance due to their habitat fidelity (Kitching *et al.* 2000, Beck *et al.* 2002, New 2004). Other groups have shown better capacities of colonizing human dominated habitats, where species replacement by generalists or herb-feeding taxa has been documented (Summerville 2004, Winfree *et al.* 2011). Arctiinae for example, an Erebidae subfamily, contains many species that are effective colonizers of disturbed habitats and may thus benefit from anthropogenic land use change (Summerville and Crist 2004, Hilt and Fiedler 2005, Nöske *et al.* 2008), perhaps due to a wide range of life-history strategies within this group (Hawes *et al.* 2009). Even though moth species respond in different ways to land conversion, the only study to date on moth fauna in oil palm plantations shows a loss of at least 60% of species from various moth families found in pristine Bornean lowland forest (Chey 2006), thus highlighting the importance of assessing the impact of oil palm expansion on moth biodiversity in the Neotropical region (Butler and Laurance 2009).

Geometrid and arctiine moths are ideal focus groups to study the impacts of land use change on biodiversity, as they are particularly species-rich in the Neotropics and a high proportion can be identified to species level (Watson and Goodger 1986, Brehm 2010). The present study aims at understanding, at a small spatial scale, how geometrid and arctiine assemblages respond to local land use practices in the tropical lowlands of southwestern Costa Rica, a region that has suffered a marked increase in oil palm plantations in the last decades (Höbinger *et al.* 2011). Moths were sampled in four habitat types (the interior and margin of old-growth forests, young secondary forests and oil palm plantations) to assess differences in species diversity and community composition along the landscape. Vegetation and microclimate of each sampling site were considered as possible predictors of moth assemblage composition and structure in each habitat (Beck *et al.* 2002, Beck *et al.* 2011). Literature suggests that geometrids will be particularly diverse in the interior of old-growth forests and arctiines in secondary forest sites, while both are expected to suffer severe species losses in oil palm plantations due to reduced resource availability in these monocultures.

METHODOLOGY

Study sites

The study was conducted in the vicinity of La Gamba Tropical Field Station, adjacent to Piedras Blancas National Park in the southwestern lowlands of Costa Rica, in the Golfo Dulce region. This region is particularly rich in biodiversity due to a lowland perhumid climate and a variety of orographic formations (Höbinger *et al.* 2011); its biogeographical situation enables it to function as a bridge between North and South America, which explains its similarities to the flora and fauna of the Amazon (Weissenhofer *et al.* 2008). Therefore, the area is of high importance for the connectivity of plant and animal habitats of southwestern Costa Rica and nearby forest areas.

La Gamba Tropical Station is immersed in an agroforestry mosaic, mainly comprised of old-growth forests, secondary forest patches in different stages of forest regrowth, agricultural lands of intense use and cattle pastures (Weissenhofer *et al.* 2008). Conversion of old-growth forests for agricultural land uses in La Gamba has been concentrated in flat lands, leaving most remaining forests in narrow ridges and steep slopes. As global oil palm cultivation has been increasing, so has this land use risen steadily throughout the years around the La Gamba village, where oil palm plantations are only surpassed by pastures in terms of land cover (Höbinger *et al.* 2011). The average annual temperature in La Gamba is 28.5°C and the average annual precipitation is 6000 mm; the driest months are from January to March, while peak precipitation is reached from August to November (Weissenhofer and Huber 2008, Seaman and Schulze 2010).

In this study, 20 sites were selected to represent four of the most common land use types of the area, with five replicate sites for each habitat type: a) undisturbed old-growth forest interior (FI); b) old-growth forest margin (FM); c) young secondary forests (YSF) with diverse regeneration histories and stages of succession, and d) even-aged oil palm plantations (OPP) of area ≥1ha, with palms of approximately 10m high and lacking any substantial understory vegetation. All sites were separated by a distance of no less than 200m from one another; trap sites in FI and OPP were located at least 200m from the habitat edge, and traps in FM and YSF at least 20m from the edge.

The range of altitude around La Gamba lies between 60 and 345 masl (Höbinger *et al.* 2011). Due to the expansion of cattle pastures and croplands in flatlands (Weissenhofer *et al.* 2008), the selected forest interior sites are in general of steeper slopes and higher altitudes, forests margins are of intermediate altitude, whereas young secondary forests and oil palm plantations possess the lowest altitudes as they were developed mostly in lands that were previously cleared for pastures. Most habitat types are relatively homogeneous, but as is to be expected, secondary forests were quite variable, being found on slopes from 1-22% and with wide variation in vegetation characteristics, probably due to variations in the type and intensity of previous land use, continuing disturbance, and other factors. There are no extensive secondary stands in the study area and the ages of those sampled ranged from three to ten years.

A better description of the 20 sampling sites is provided in Appendix 1. Geographical coordinates and altitude of the sampling sites were measured with a global positioning system (GPS) device (Garmin GPSMAP 60CSx Handheld GPS Navigator, Garmin Instruments Inc., Olathe, KS, USA), while slope was measured with a SUUNTO® clinometer from the highest to the lowest edge of the plot.

Data collection

Moth sampling and identification

Moths were sampled in each site with automatic funnel traps, using an 8-W UV-emitting weak fluorescent light tube (see Brehm and Axmacher 2006 for a detailed description of the trap). Automatic traps collect an incomplete subset of moth diversity; they have a slight bias towards larger bodied moths and also cause some damage to the collected specimens (Axmacher and Fiedler 2004). However, they may be operated during the entire night, which is useful for obtaining all-night moth inventories with minimum manpower, and have proven to reliably describe spatial patterns of tropical moth fauna across heterogeneous landscapes (Brehm and Axmacher 2006). Low-power light sources were deliberately chosen to minimize attraction of stray individuals from the surrounding landscape matrix. Thus, samples reflect moth activity around the trap sites at a very small radius (usually less than 25m) and are not severely biased through long-range attraction from outside of the study habitats (Schulze and Fiedler 2003, Truxa and Fiedler 2012, Merckx and Slade 2014).

Light traps were installed in the understory at a height of 1-2m above ground and were operated during the entire night (19h to 05h) using 12-V lead batteries as power supply. After attraction to the light and collision with a transparent intercept, moths glide down through a funnel and fall into a bucket, where chloroform plus a killing agent (potassium cyanide) was applied. Moth communities at the 20 sites were surveyed once a month from February to July 2013 (for a total of six trap periods/nights per site), and sampling was mostly restricted to five days prior to and after new moon nights to reduce the effect of moonlight on moth catches (Beck *et al.* 2011, Jonason *et al.* 2014). A maximum of four sites, one belonging to each land use type, were sampled on each sampling night according to their locality and transportation logistics, randomizing as much as possible the sampling order of the sites to eliminate any influence of lunar phase and weather. Collected specimens from the families Geometridae and Erebidae-Arctiinae were mounted, sorted to morphospecies level and taxonomically identified as far as possible, by comparing with labeled specimens in the Lepidoptera collection of the National Biodiversity Institute (INBio) of Costa Rica. Further identification was completed by consulting with expert taxonomists and comparing with online plates compiled by Dr. Gunnar Brehm (available at http://www.personal.uni-jena.de/~b6brgu2). Voucher specimens were deposited at the Tropical Agricultural Research and Higher Education Center (CATIE), the National Biodiversity Institute (INBio) of Costa Rica and the Zoological Museum of the University of Costa Rica (UCR).

Vegetation and microclimate of the study sites

The composition and diversity of the vegetation at each sampling site was evaluated in circular plots of 10m radius (plot area = 314m^2), with the trap point at the center of the plot. All trees, lianas, palms, ferns and herbaceous plants ≥2cm in diameter at breast height (DBH) were counted and measured in diameter, as well as identified as far as possible in the field by a trained parataxonomist; further plant identifications were carried out by a taxonomist from the INBio herbarium. Vegetation diversity of each plot was quantified with the Fisher's alpha index. Basal area in m^2 per ha as a measure of above-ground tree biomass was estimated from all individuals ≥10cm DBH in these circular plots (Finegan *et al.* 2004).

Canopy cover above each trap site was estimated with a spherical densiometer; a reading was taken on each of the four cardinal directions, averaged and converted to percent canopy cover (Lemmon 1957). Vertical vegetation structure at each site was measured by standing in the center of each plot and subjectively estimating a percentage range of vegetation cover (0:0%, 1:1-33%, 2:34-66%, 3:67-100%) in 5 vertical strata, from the understory to the upper canopy (0-2m, 2-9m, 10-20m, 20-30m, >30m: Thiollay 1992); the values in each stratum were combined into a measure of vertical complexity per plot, by means of the Shannon entropy index.

In each circular plot, a 5x5m^2 quadrat was placed 5m away from the trap point on each of the four cardinal directions. Within these quadrats, the percentage of undergrowth cover was estimated in the same subjective manner as vertical structure; the mean of the four quadrats per site was calculated and used as a measure of undergrowth cover for each site. All separate plant shoots that were taller than 50cm and <2cm of DBH inside the quadrats were counted and sorted into one of the following categories: trees, herbs, palms, ferns and lianas. The sum of the stem count of separate shoots was used as a measure of understory density per plot (Beck *et al.* 2002). In addition, a measure of understory complexity was calculated with the data on counts of separate shoots per category, by means of the Shannon entropy index.

Data loggers (Lascar EL-USB-2) for the measurement of temperature and relative humidity were placed alongside the light traps (i.e. 1-2m above ground) in each site, to measure these microclimate parameters once every half hour during each sampling night. Data loggers were proven to be equally calibrated, so post calibration of the data was not necessary. For analyses, the mean and coefficient of variance of temperature and relative humidity over all trap nights per site was calculated, as well as maximum, minimum and range of the temperature. In addition, the fraction of the moon illuminated during each trap night was extracted from the United States Naval Observatory (http://aa.usno.navy.mil/data/docs/MoonFraction.php) and used as a measure of moonlight.

Analysis of data

Characterization of moth assemblages

Total species numbers and individual numbers were recorded. It should be noted that these cannot truly describe regional moth assemblages, since the sampling method does not allow a complete moth inventory (Gotelli and Colwell 2001). To correct for possible bias when comparing land use types with different sample sizes, 'true' local richness was estimated by an individual-based rarefaction and extrapolation method (Chao and Jost 2012), extrapolating to 3000 individuals on the family level and to 750 individuals on habitat level, using 100 randomizations in EstimateS 9.1.0 (Colwell 2013). The 95% confidence intervals of each curve were used to assess statistical significance of differences between families and habitat types.

As recommended by Beck and Schwanghart (2010) and Fiedler and Truxa (2012) for the evaluation of diversity in species-rich, incompletely sampled communities of mobile insects, Shannon's bias-corrected exponential diversity was calculated as a measure of 'effective' species numbers, while Fisher's α was used to compare local species diversity between habitats. These indexes were calculated for each moth family on the habitat level (i.e. aggregating all samples from replicate sites and nights) using the software SPADE (Chao and Shen 2010), and compared according to their 95% confidence intervals. Individual trap catches per night and per sampling site were usually too small to allow for meaningful estimates of diversity measures at this local scale.

To evaluate moth activity density (count of individuals per night) with respect to land use types, sampling month and moonlight, a generalized linear mixed model (GLMM) followed by Fisher's LSD post-hoc test with Bonferroni correction was conducted in INFOSTAT (Di Rienzo *et al.* 2013). For this analysis, moth density data was square-root transformed and moonlight data was arcsin of square-root transformed for normalization; temporal correlation structure was modeled with first order autoregression. To assess the dominance structure of the local fauna at the site level, the Berger-Parker index (proportion of the most abundant species) was calculated for each trapping site (May 1975). A one-way Analysis of Variance (ANOVA), followed by Fisher's LSD post-hoc test with Bonferroni correction, was conducted with the software INFOSTAT to evaluate differences in the level of dominance between habitats, after the data was arcsin of square-root transformed for normalization.

To explore the relative position of each sample plot in the multidimensional ecological space spanned by the moth species, samples were ordinated by Non-metric Multidimensional Scaling (NMDS) (Clarke 1993) in the software PC-ORD (McCune and Mefford 2011). Ordination space for both geometrids and arctiines was restricted to two axes. This ordination method has proven to be rather robust even if applied to incomplete inventories of tropical insects (Brehm and Fiedler 2004). Afterwards, the significance of differences in species composition between the pre-defined groups of land use types was assessed by an Analysis of Similarities (ANOSIM) with 9,999 random permutations using the PAST 3.01 software (Hammer *et al.* 2001). Both the NMDS and ANOSIM were based on a standardized Bray-

Curtis dissimilarity matrix of the raw abundances (count of individuals) aggregated per sampling site, separately for each moth family (Clarke and Warwick 2001).

To identify those geometrid and arctiine species that show a significant preference for a certain land use type in the study area, the Indicator Value method proposed by Dufrene and Legendre (1997) was applied. This analysis uses the abundance and frequency of species in each land use type to identify those that mostly contribute to the faunistic uniqueness of each habitat; it gives a value (IV) to each species between 0 (no indicator) and 100 (perfect indicator), and statistical significance is inferred on permutations (McCune and Grace 2002). The analyses were confined to those species with a minimum of five captured individuals in at least one of the habitats, using 1000 random permutations, with the '*indicspecies*' package of the R software (De Caceres and Jansen 2013).

Relationships between habitat variables and moth assemblages

Multiple linear regressions were used to assess possible effects of vegetation and microclimate characteristics of each sampling site on the species richness, activity density and species diversity of geometrid and arctiine moths across the land use types. To reduce the quantity of predictor variables, principal components were extracted to avoid multi-collinearity between vegetation or microclimate variables and enable a more integrated interpretation of the data (Clarke and Warwick 2001). Two PCAs were conducted with the software INFOSTAT (Di Rienzo *et al.* 2013), one for the vegetation data and one for the microclimate data, after normalizing and standardizing the raw variable measurements. The scores of the first two principal components of each PCA, which explained the majority of variance of the data, were selected to represent the vegetation and microclimate components, respectively. These were then used as predictor variables in regression models. Pearson correlation coefficients between the habitat variables and PCA axis scores, also performed in INFOSTAT, were used to better identify the variables that were concentrated at each axis.

The dependent variables used in the multiple linear regressions were observed species richness, activity density (total count of individuals per site), and species diversity (Shannon's bias-corrected exponential diversity) of arctiine and geometrid moths for the 20 sampling sites; all dependent variables were square root transformed for normalization. There was no spatial autocorrelation between sampling sites, which was reviewed by adjusting a polynomial regression model with the geographic coordinates. Regression models were conducted with the '*lm*' function of the R package (R Development Core Team 2011, Version 2.14.1) and retention of predictor variables was performed with an automated forward selection procedure, based on Akaike information criterion (AIC).

Finally, distance-based redundancy analysis (dbRDA) was used to determine the relationship between habitat characteristics (the two vegetation and two microclimate principal components) and the species composition of each moth group at the 20 sampling sites (Legendre and Anderson 1999). These constrained ordination analyses were based on the Bray-Curtis dissimilarity measure using the '*vegan*' library (Oksanen *et al.* 2012) in the R software.

There was no spatial autocorrelation between the community composition and the study sites, which was reviewed by adjusting a polynomial model (dbRDA) with the geographical coordinates. The significance of the overall ordination models, the individual predictor variables and the dbRDA axes was assessed with permutation tests, using 9,999 random permutations. The sampling sites, as well as the more abundant individual species (those with at least 5 individuals in one habitat type) and their relationships to the environmental predictors, were plotted in reduced ordination space according to the first and second dbRDA axes for visual comparison. The moth indicator species identified by the aforementioned Indicator Value method were identified in the plots, to visualize their position in relation to the sampling sites and the environmental variables.

RESULTS

Moth richness and diversity

A total of 3740 moth individuals of the two focal taxa were collected during six months at 20 sites. Of these, 3644 were sorted into 312 morphospecies. A few seriously damaged specimens (2.6% of total catch) were excluded from the analyses. Moths were separated into two taxonomic groups: 1340 Geometridae individuals of 170 morphospecies (115 of these were identified to species), and 2304 Erebidae-Arctiinae individuals of 142 morphospecies (98 of these were identified to species). For a full species list, see Appendix 2.

Individual-based extrapolation/rarefaction of each moth group revealed that the survey was incomplete, as was expected due to the high biodiversity in the tropics (**Fig. 1**). Extrapolation to 3000 individuals was not enough to reach an asymptote in the curves, especially for arctiines, suggesting that the sampling effort should be at least doubled to reach a more complete inventory of the total richness of these moth groups in the region. By comparison of the confidence intervals of each curve in Figure 1, it is clear that species richness of these groups is statistically different, with a higher observed as well as expected richness in Geometridae.

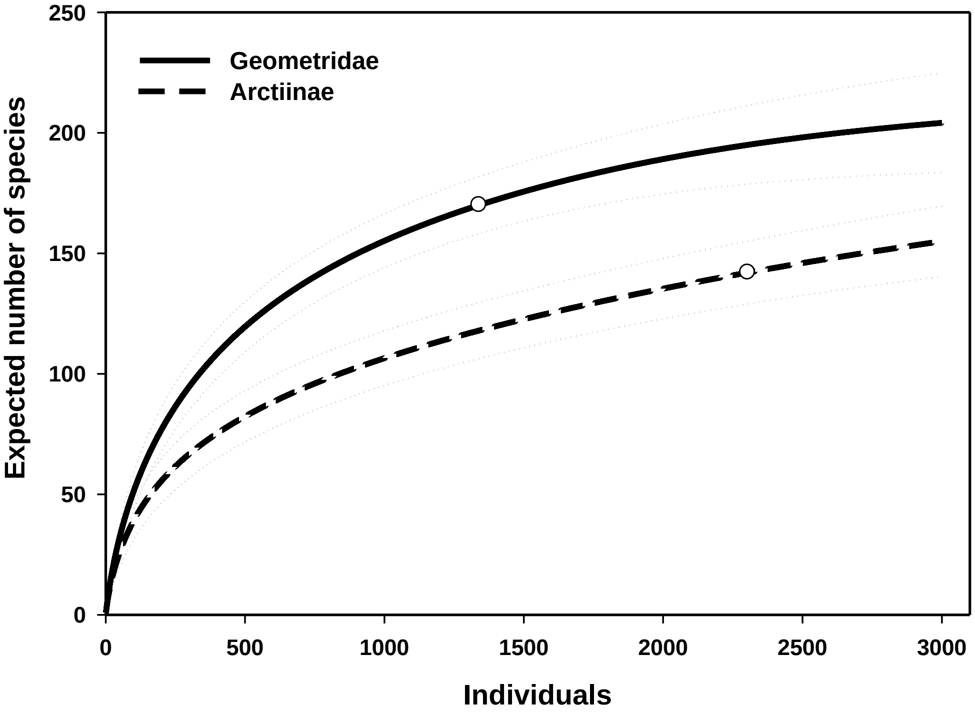


Figure 1. Individual-based rarefaction/extrapolation curves with 95% confidence intervals (dotted curves), comparing overall Geometridae and Arctiinae species richness across the 20 study sites. Observed species richness [S(obs)] is indicated by clear circles.

When repeating this analysis by habitat type, individual-based extrapolation/rarefaction curves of geometrid and arctiid moths showed a significantly lower observed and expected species richness in oil palm plantations, with no clear differences between the other three habitat types for either moth group (**Fig. 2**). Of all the curves in Figure 2, geometrid richness in forest interior sites shows to be consistently increasing, even after extrapolating to 750 individuals, suggesting that the inventory of geometrid moths in this habitat was the least complete of all. The total numbers of geometrids seen in the four main habitat types were: 570 individuals of 113 morphospecies (FI), 321 individuals of 93 morphospecies (FM), 314 individuals of 90 morphospecies (YSF), and 135 individuals of 31 morphospecies (OPP). The total numbers of arctiines in these four habitat types were: 582 individuals of 83 morphospecies (FI), 525 individuals of 77 morphospecies (FM), 668 individuals of 98 morphospecies, and 529 individuals of 35 morphospecies (OPP).

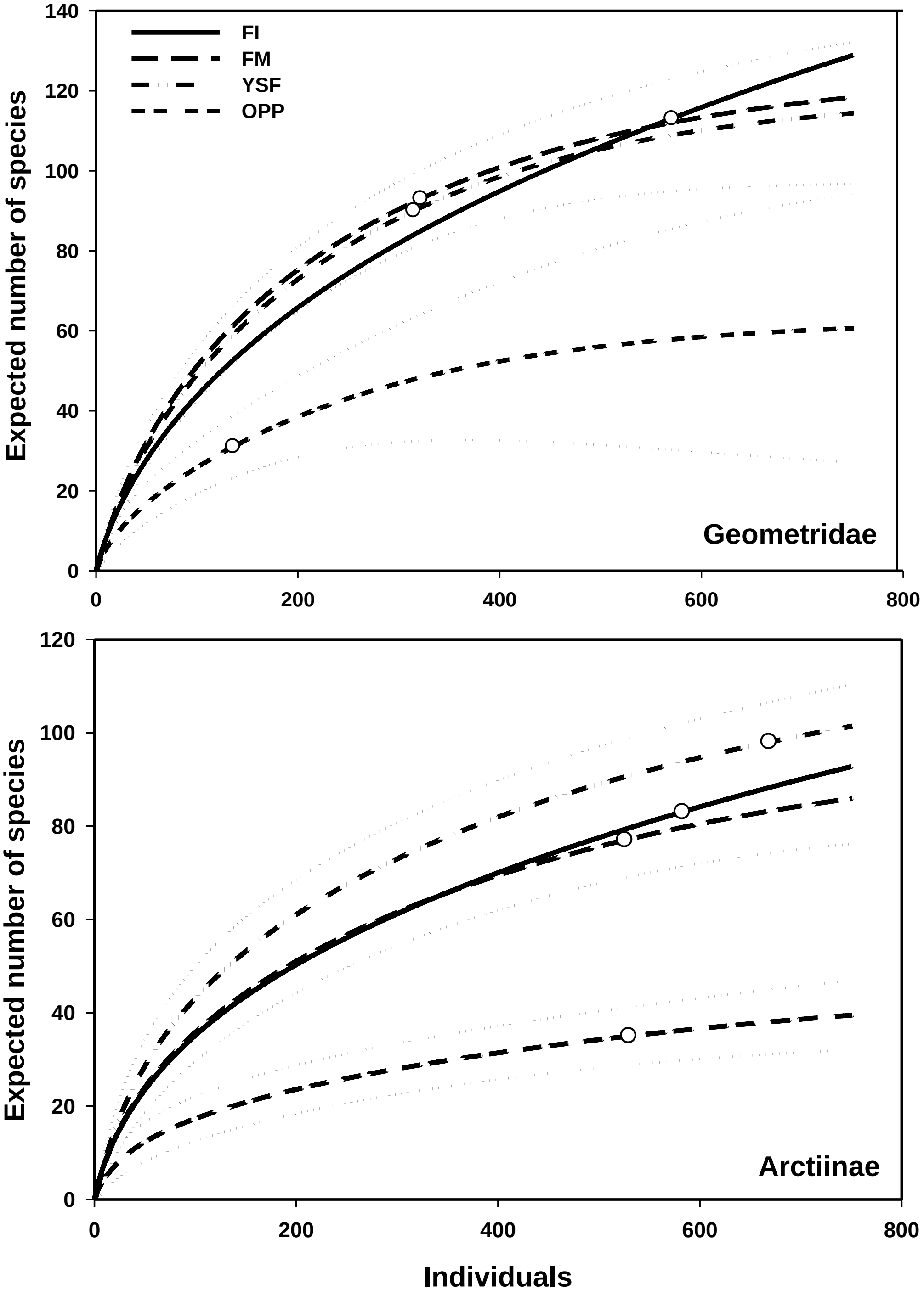


Figure 2. Individual-based rarefaction/extrapolation curves for Geometridae and Arctiinae, sampled at the four habitat types. For visual clarity, only a few key 95% confidence intervals (dotted curves) are shown. Observed species richness [S(obs)] is indicated by clear circles.

Table 1. Results of the GLMM analysis for moth activity density of each family, according to habitat type, sampling month and moonlight. *F* statistics, degrees of freedom (df) and *p* values are shown, with significant results ($\alpha = 0.05$) highlighted in bold.

	Geometridae			Arctiinae		
Tested factors	F	df	*p*	F	df	*p*
Habitat type	3.32	3,72	**0.025**	0.79	3,72	0.501
Month	4.30	5,72	**0.002**	3.43	5,72	**0.008**
Moonlight	0.30	1,72	0.586	0.64	1,72	0.425
Habitat*Month	1.17	15,72	0.317	1.09	15,72	0.380
Habitat*Moonlight	0.60	3,72	0.619	0.27	3,72	0.848
Month*Moonlight	3.60	5,72	**0.006**	3.79	5,72	**0.004**
Habitat*Month*Moonlight	1.27	15,72	0.245	1.03	15,72	0.437

The GLMM for the comparison of moth activity density per night between habitats, sampling months and moonlight revealed that the type of habitat had a significant effect on geometrid activity density (**Table 1**). This was highest in forest interior sites, lowest in oil palm plantations, and intermediate in forest margin and secondary forest sites. No such consistent difference in activity density between habitats was seen for arctiines. For both arctiine and geometrid moths, sampling month showed a strong effect on activity density. Individual moth catches were highest in February and consistently declined towards July, which corresponds to the transition from the dry to the wet season in southwestern Costa Rica. Moth catches during February, April and May depended on moonlight; in April, individual catches of both groups were higher when there was less moonlight, as well as in May for geometrids only, while catches of both moth groups during February showed the opposite pattern. Moonlight by itself did not have an effect on overall moth catches, which suggests that the measures taken to prevent moon bias in the field were largely successful.

Two indexes were used to compare the species diversity of each moth group among habitat types (**Fig. 3**). Both Shannon's bias-corrected exponential diversity (as a measure of 'effective' species numbers) and Fisher's alpha for arctiines and geometrids disclosed a significantly lower diversity in oil palm plantations when compared to all three other habitats. Oil palm plantations show drastic losses in species diversity, with values three or four times lower than all other habitats, which mostly did not differ from each other. An increase in statistical power may be required to record significant pair-wise differences in geometrid Shannon's diversity between interior forests and oil palm plantations, since this lack of significance is attributed to the small sample size of this study.

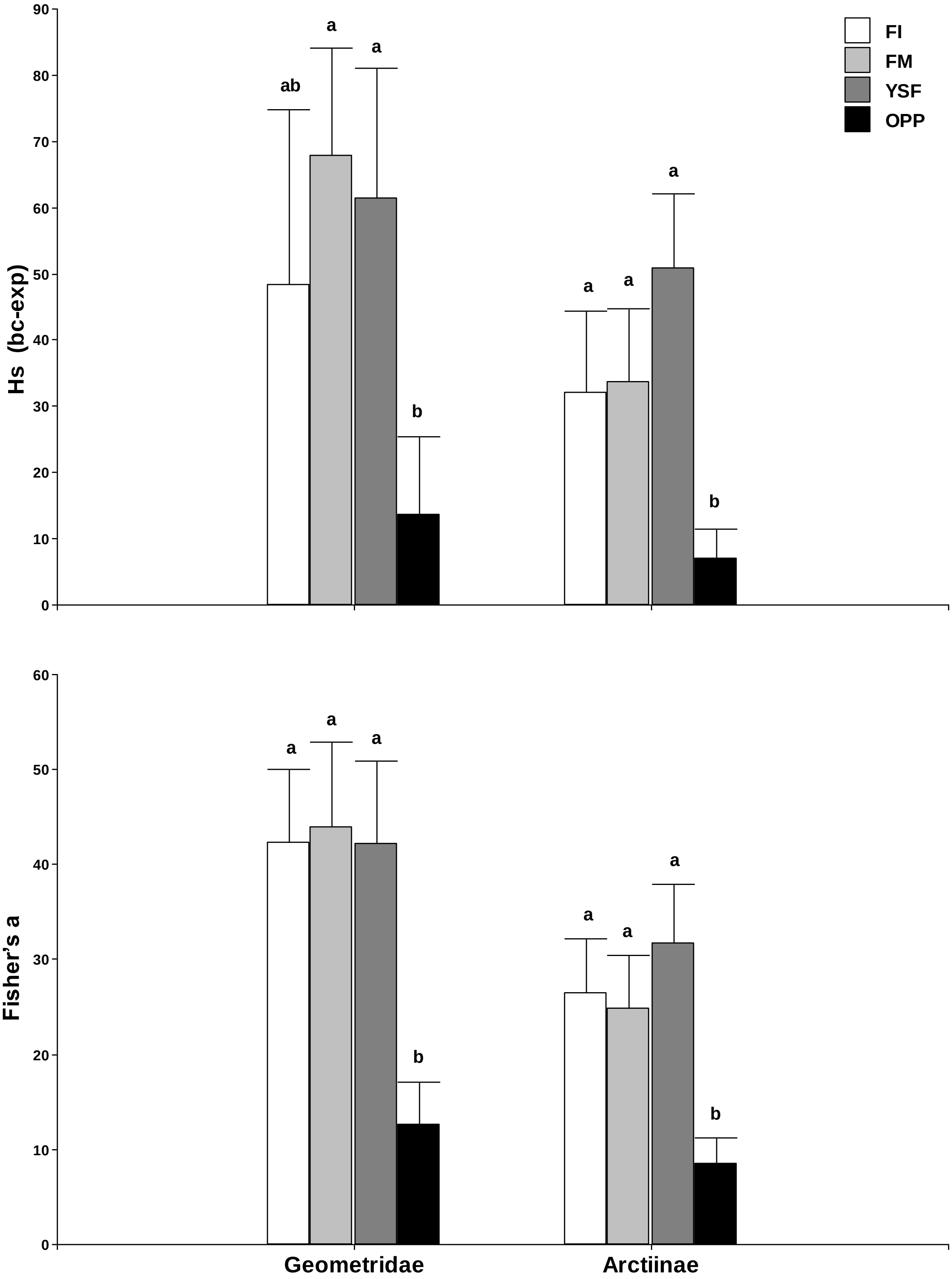


Figure 3. Means per habitat type of Shannon's bias-corrected exponential index [H_S (bc-exp)] and Fisher's α of Geometridae and Erebidae-Arctiinae moths. Error bars indicate the 95% confidence intervals (bars labelled with different letters differ significantly at α = 0.05).

Moth community structure and composition

As a corollary to species diversity, the Berger-Parker dominance index for geometrids showed higher dominance in oil palm plantations than in both forest margin and young secondary forest sites (ANOVA: $F_{3,16} = 8.86$, $p = 0.0011$), with intermediate levels of dominance in forest interior. Amongst arctiines the most abundant species invariably had a much higher share of total catches in oil palm plantations as compared to all three remaining habitat types (ANOVA: $F_{3,16} = 14.98$, $p = 0.0001$) (**Fig. 4**).

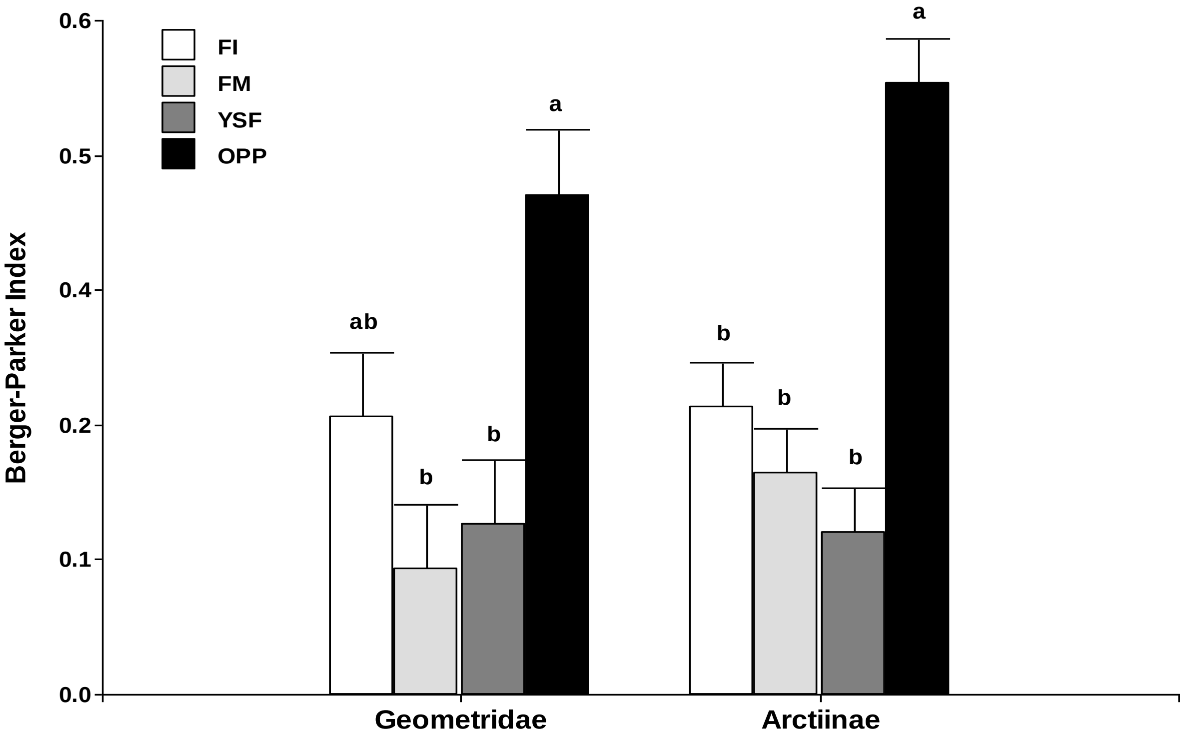
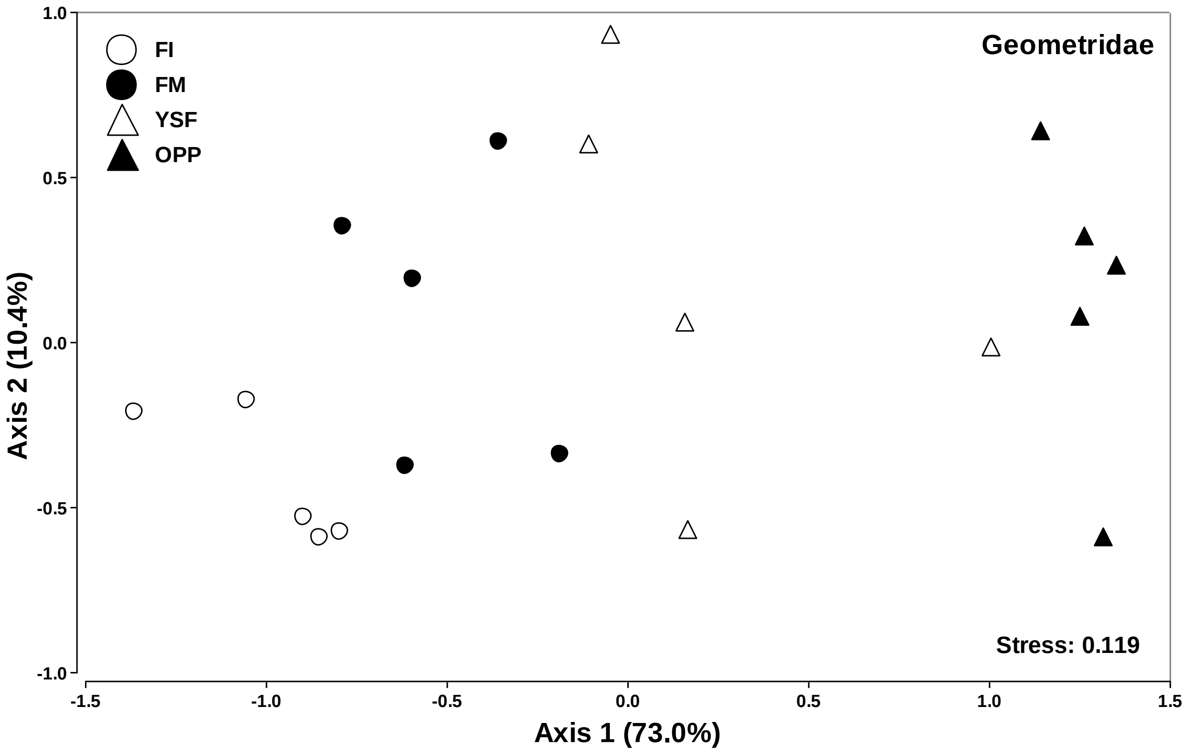


Figure 4. Berger-Parker dominance index (mean ± SE) of Geometridae and Erebidae-Arctiinae moths per habitat type. Different letters denote significant differences at $\alpha = 0.05$ (univariate ANOVA followed by Fisher's LSD test with Bonferroni correction).



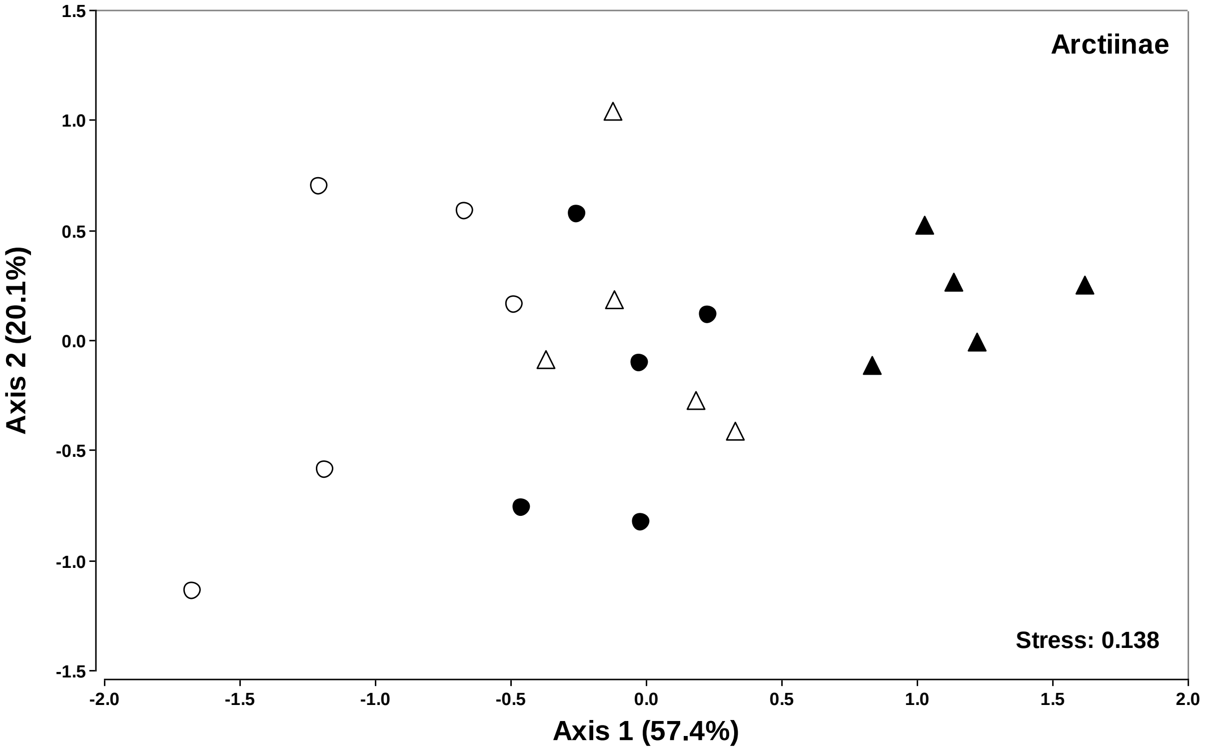


Figure 5. NMDS ordination plots (based on Bray-Curtis similarities) of Geometridae and Erebidae-Arctiinae assemblages for all study sites. The axis percentages indicate the amount of variance that is explained by each ordination axis.

NMDS ordination plots for Geometridae and Erebidae-Arctiinae are shown in **Figure 5**. Both ordinations show a very clear grouping of moth assemblages at the sites according to the four habitat types, although segregation was stronger in Geometridae (Global ANOSIM: R = 0.71, p = 0.001) than in Arctiinae (Global ANOSIM: R = 0.58, p = 0.001). In both ordinations, forest interior and oil palm plantation sites are the most different from each other, with forest margin and young secondary forest sites in an intermediate position. While geometrid assemblages from these two habitat types were rather distinct from another, this was not the case for Arctiinae. Stress values of both ordinations are moderate, which denotes that configurations in reduced ordination space represent the community composition reasonably well (McCune and Grace 2002). The NMDS for Geometridae clearly demonstrates a continuous species composition gradient congruent with the degree of habitat disturbance, starting with forest interior sites and ending with oil palm plantations along the first axis. The only habitats that did not differ significantly in terms of species composition, when doing pairwise comparisons with ANOSIM, were forest margins and young secondary forests (**Table 2**). This result indicates that these two land use types support similar assemblages of arctiine and geometrid moths, while all other pairwise combinations of habitats show distinct communities.

Table 2. Global and pairwise results of Analyses of Similarity (ANOSIM) between the habitat types for Geometridae and Erebidae-Arctiinae. R and p values are shown, with significant results (α = 0.05) highlighted in bold.

	Geometridae		Arctiinae	
Site comparisons	*R*	*p*	*R*	*p*
Global	0.71	**0.0001**	0.58	**0.0001**
FI-FM	0.48	**0.0089**	0.26	**0.0575**
FI-OPP	1.00	**0.0079**	0.89	**0.0079**
FI-YSF	0.81	**0.0083**	0.54	**0.0080**
FM-OPP	1.00	**0.0075**	0.72	**0.0095**
FM-YSF	0.24	0.1029	0.03	0.4024
OPP-YSF	0.53	**0.0087**	0.88	**0.0090**

An indicator species analysis was used to single out those moth species that show a significant preference to one of three habitat types, confirmed by an Indicator Value (IV) higher than 0.7 and $p < 0.05$. Since the results of the ANOSIM showed that forest margins and young secondary forests do not differ substantially in species composition for either moth group, these two habitats were aggregated for this analysis (FM+YSF), to single out indicator species for disturbed forests. The complete list of indicators provided by this analysis is shown in **Table 3**. The outcome is similar for both geometrid and arctiine moths; there are only one or two species characteristic for both oil palm plantations and disturbed forests, respectively. In contrast, there are many species that are highly characteristic for old-growth forest interior sites, especially in Geometridae, which yielded a higher number of indicators overall.

Table 3. Indicator species of Geometridae and Erebidae-Arctiinae identified with the Dufrene-Legendre indicator value (IV) method, sorted in descending order according to their IV values. Only those species with IV > 0.70 and $p < 0.05$ are shown. Habitat type: FI = old-growth forest interior, OPP = oil palm plantation, FM+YSF = disturbed forest.

Geometridae				Arctiinae			
Species	IV	*p*	Habitat type	Species	IV	*p*	Habitat type
Pyrinia sp01	0.99	0.005	FI	*Talara esperanza*	0.97	0.005	OPP
Rhodochlora brunneipalpis	0.93	0.005	FI	*Heliura thysbodes*	0.92	0.005	FI
Leucula festiva	0.93	0.005	FI	Lithosiini 2	0.92	0.005	OPP
Physocleora pauper	0.89	0.005	FI	*Eucereon* sp03	0.87	0.020	FI
Cimicodes albicosta	0.89	0.005	FI	*Episcepsis demonis*	0.85	0.010	FI
Tricentrogyna violescens	0.85	0.015	OPP	*Symphlebia ipsea*	0.85	0.005	FI
Melinodes sp01	0.84	0.005	FM+YSF	*Virbia* sp02	0.84	0.010	FI
Ennominae 1	0.81	0.005	FI	*Aclytia punctata*	0.82	0.010	FI
Nemoria scriptaria	0.80	0.015	FI	*Lophocampa catenulata*	0.79	0.025	FM+YSF
Epimecis subroraria	0.79	0.040	FI	*Agylla* sp02	0.78	0.020	FI
Physocleora plenaria	0.78	0.010	FI	*Delphyre testacea*	0.75	0.010	FI
Cyclophora sp02	0.75	0.035	FI	*Hyalurga sixola*	0.74	0.010	FI
Eusarca minucia	0.75	0.020	FI	*Eucereon* nr. *argutum*	0.74	0.035	FM+YSF
Dyspteris tenuivitta	0.74	0.020	FI				
Tmetomorpha bitias	0.73	0.030	FI				
Hymenomima camerata	0.73	0.040	FI				

Responses of moth assemblages to vegetation characteristics and microclimate

Information on vegetation characteristics of the 20 sites was scored in nine variables (the values for each site are in Appendix 3). Two principal components (referred to as VC1 and VC2) could be extracted that accounted for 80.5% of the total variation in these data (**Fig. 6**). VC1 accounted for most of the variation (62.8%); it was positively correlated with overall vegetation density, plant species richness, plant species diversity, vertical complexity, understory complexity and understory density, and negatively correlated with undergrowth cover. VC2 was positively correlated to canopy cover and tree basal area, accounting for 17.7% of the variation of the data. See Appendix 4 for correlations between the original variables and the extracted components.

The ordination of the sampling sites by their vegetation characteristics in Figure 6 shows a clear cluster of the oil palm plantation sites, which are characterized by dense herbaceous undergrowth cover and very low vegetation diversity and complexity in general.

Forest margin and forest interior sites are similar in their vegetation characteristics, and associated positively with the first vegetation component. Meanwhile, young secondary forests sites do not cluster closely together, mainly because two sites (YSF3 and YSF5) showed higher similarities of their vegetation structure to forest margin and interior sites.

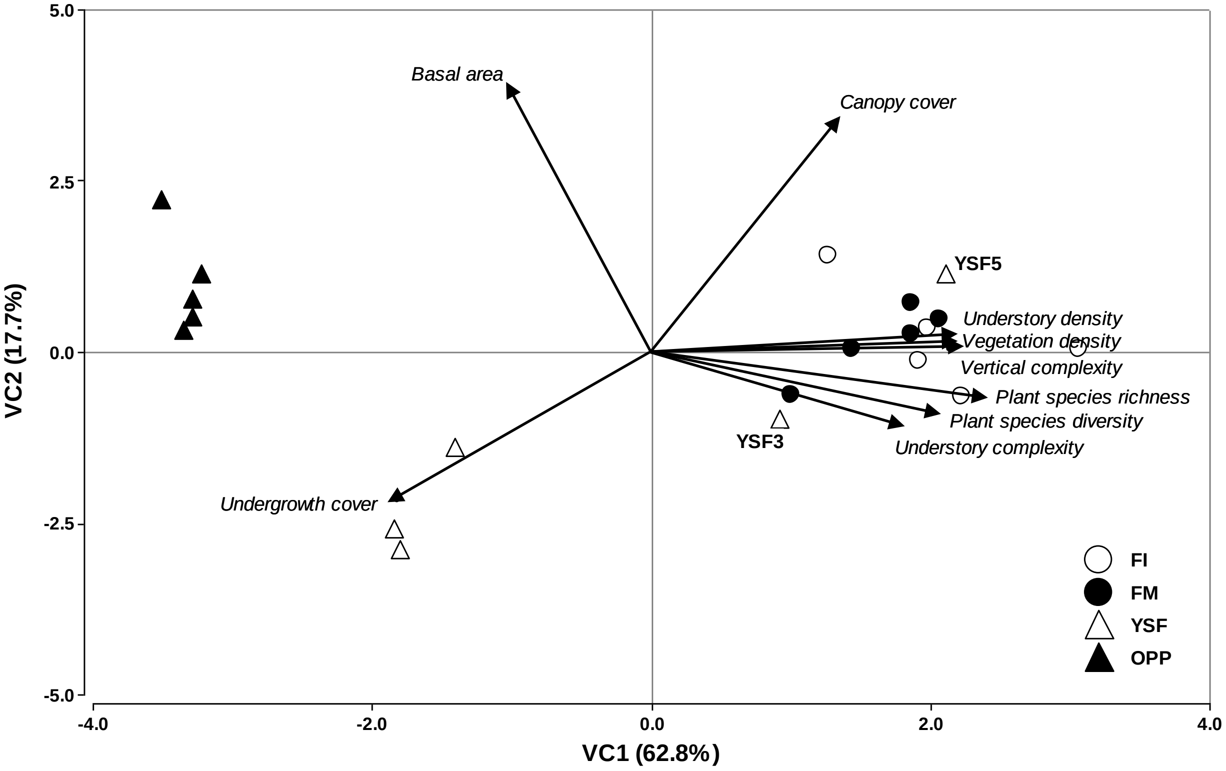


Figure 6. Ordination of the 20 sampling sites using principal component analysis of 9 vegetation variables, based on Euclidean distances. The variables abundance, observed richness and diversity include all trees, ferns, lianas, palms and herbs with a DBH higher than 2 cm.

The microclimate data obtained at each sampling site was summarized in seven climate variables. Two principal components extracted from these (referred to as CC1 and CC2) accounted for 77.4% of the total variation in the data (**Fig. 7**). CC1, which accounted for 52.8% of the variation, was positively associated with the temperature coefficient of variation (T_CV), maximum temperature (Tmax), temperature range (Tmax-min) and mean relative humidity (Hmean), and negatively correlated with the coefficient of variation of relative humidity (H_CV). Meanwhile, CC2 explained 24.6% of the variation and was positively correlated with mean (Tmean) and minimum (Tmin) temperature. In this climate-based ordination, the 20 sites are not clearly clustered by habitat type, which indicated that the microclimate characteristics of each sampling site were not dependant on the type of habitat. See Appendix 5 for correlations between the original variables and the extracted components.

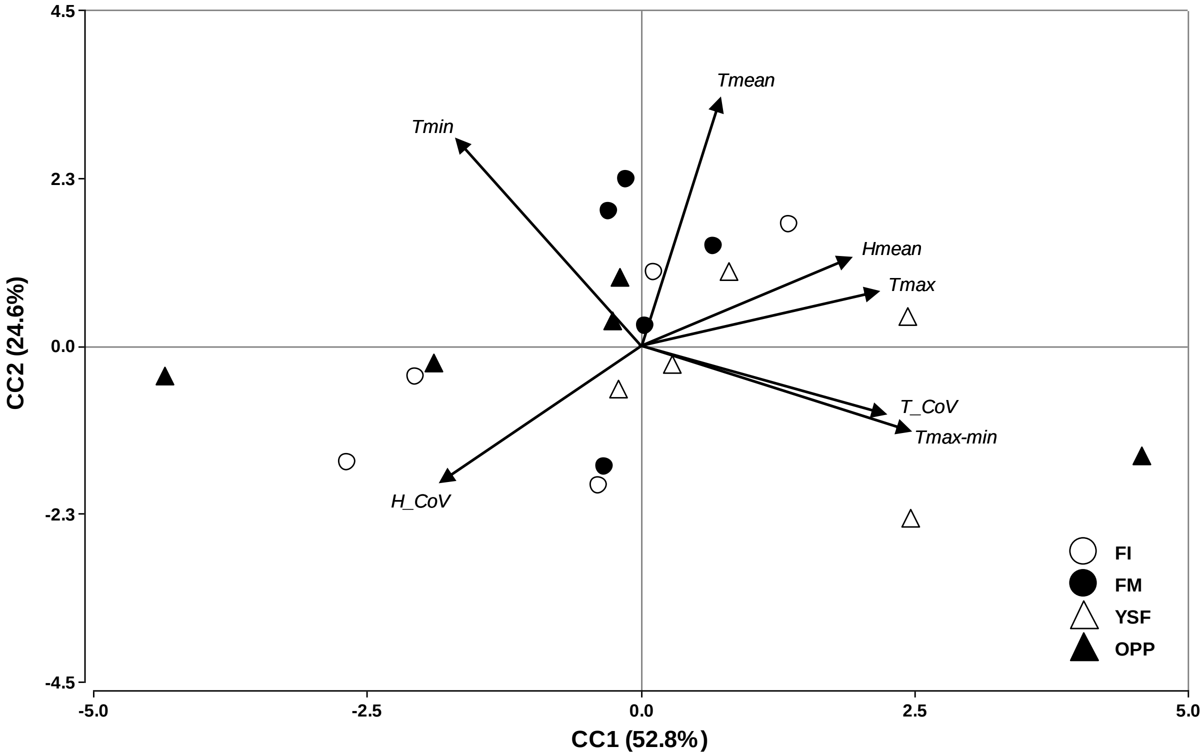


Figure 7. Ordination of the 20 sampling sites using principal component analysis of the microclimate variables, based on Euclidean distances. Abbreviations: Tmean, mean temperature; T_CV, coefficient of variation of temperature; Tmax, maximum temperature; Tmin, minimum temperature; Tmax-min, temperature range; Hmean, mean relative humidity; and H_CV, coefficient of variation of relative humidity.

The site scores from the two vegetation (VC1 and VC2) and two microclimate components (CC1 and CC2) were used in multiple regression analyses to model arctiine and geometrid activity density, richness and diversity (**Table 4)**. These models indicated a significant positive influence of VC1 on geometrid activity density and richness, as well as both arctiine and geometrid diversity; thus, high plant species diversity and pronounced vertical and understory complexity of the vegetation seem to increase the aforementioned dependant variables, while extensive herbaceous undergrowth cover as seen mostly in oil palm plantations, has a negative effect on them. VC2 had a negative effect on arctiine richness and on both arctiine and geometrid diversity, which indicates that they may be reduced by an increase in canopy cover and tree basal area. With regard to microclimate, only CC2 was significantly associated with attributes of moth assemblages, showing that arctiine richness was negatively affected by an increase of mean and minimum local temperature. According to these analyses, vegetation characteristics of the habitat have a strong, and largely concordant, influence on geometrid and arctiid richness and diversity, whereas microclimate only weakly contributes to improving these models.

Table 4. Summary of multiple linear regression models of geometrid and arctiine activity density (N), observed richness [S(obs)] and Shannon's diversity [H_S (bc-exp)] as dependant variables, with plot coordinates on the first two principal components of vegetation (VC1,VC2) and microclimate (CC1,CC2) PCAs as regressor variables. The plus (+) and minus (-) signs indicate a positive or negative relationship of the component with the dependant variable, with *p* values shown in parentheses; significant results ($\alpha = 0.05$) are highlighted in bold. Empty cells indicate that the component was not included in the model. Adjusted R^2, *F* and *p* values of each model are shown.

	VC1	VC2	CC1	CC2	R^2adj	*F*	*p*
Geometridae							
N	**+ (0.010)**		– (0.111)	– (0.136)	0.36	4.6	0.017
S(obs)	**+ (<0.001)**	– (0.227)	– (0.141)	– (0.252)	0.52	6.1	0.004
H_S (bc-exp)	**+ (0.006)**	**– (0.006)**			0.48	9.9	0.001
Arctiinae							
N			– (0.093)	**– (0.031)**	0.26	4.3	0.030
S(obs)	+ (0.077)	**– (0.008)**	– (0.189)	– (0.148)	0.46	5.0	0.009
H_S (bc-exp)	**+ (0.001)**	**– (<0.001)**			0.66	19.70	<0.001

Distance-based redundancy analyses of moth community composition at the sampling sites revealed that the vegetation and microclimate components collectively explained 40.1% of the variance of compositional diversity for geometrids ($F_{4,15} = 2.51$, $p = 0.005$) and 43.8% for arctiines ($F_{4,15} = 2.92$, $p = 0.005$) (**Fig. 8**). In both ordinations, the first axis separated the oil palm plantation sites from all the other habitats, while only in Geometridae there was a clear gradient from interior forest sites to oil palm plantations, as was seen in the NMDS. The second axis mildly separated forest interior sites from forest margin and secondary forest sites, the last being the most similar habitats in vegetation and climate characteristics as well as moth composition.

Permutation tests revealed that VC1 was the only significant predictor variable for geometrid composition ($F_{1,15} = 6.49$, $p = 0.005$, 66.6% of fitted variation), while arctiines were influenced by both the first ($F_{1,15} = 5.88$, $p = 0.005$, 52.8% of fitted variation) and the second ($F_{1,15} = 2.00$, $p = 0.028$, 17.9% of fitted variation) vegetation components; thus, VC1 emerged as the strongest predictor for both geometrid and arctiid assemblage composition. The microclimate principal components did not have a detectable effect on either geometrid or arctiid species composition, which is generally consistent with the results of the previous multiple linear regressions for moth activity density, richness and diversity. As far as the position of the indicator species, it is clear in Figure 8 for both moth groups that forest interior indicators fall in the first quadrant and are positively related to VC1. Oil palm plantation indicators are in the second quadrant and related to VC2, and indicators for disturbed sites (FM+YSF) fall in the fourth quadrant of the ordination plots, positively related to CC2 in geometrids and to CC1 in arctiines.

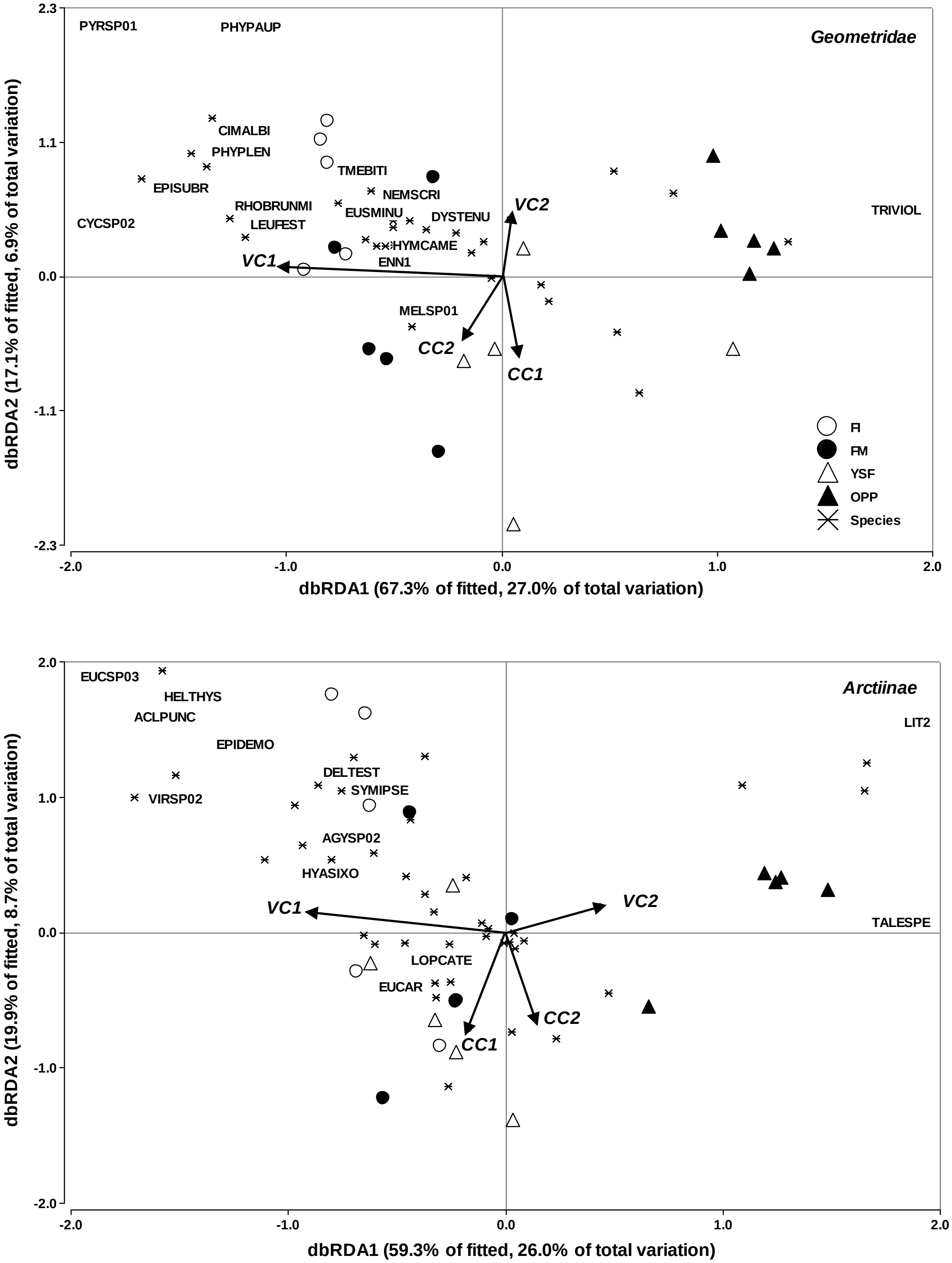


Figure 8. Relationship between the vegetation (VC1,VC2) and climate (CC1,CC2) principal components with the species composition of geometrid and arctiine moth assemblages in each study site, by means of distance-based redundancy analyses (dbRDA). For visual clarity, only species with 5 or more individuals in at least one habitat type are shown in the ordination plot, with indicator species labeled according to the codes in Appendix 2.

DISCUSSION

This is the first study in the Neotropical region to concentrate on the impact of oil palm plantations on moth assemblages. Surveys of geometrid and arctiine moths from La Gamba indicate that oil palm plantations are not a suitable habitat for the majority of species, showing a severely impoverished fauna with very distinct species composition when compared to other less disturbed forest habitats. Meanwhile, the interior of old-growth forest did not show higher richness or diversity of moths when compared to young secondary forest or the margin of old-growth forest, but did possess a distinct community composition. Although both moth groups show similar patterns in their response to habitat disturbance, geometrids revealed a higher dependence on old-growth forests, with many species that are characteristic of this habitat and may potentially serve as bioindicators of habitat disturbance. Finally, the vegetation composition and structure of the habitat, rather than microclimate, was mostly responsible for the observed patterns of moth assemblages in this landscape.

Moth species richness and diversity in the main forest types around La Gamba

A total of 312 moth species were collected during this survey, 142 arctiines and 170 geometrids, in an area of approximately 30km^2 around La Gamba rural community. Sampling coverage was incomplete, as is usual with studies of species rich tropical insect communities (Brehm and Fiedler 2004). Overall moth richness and diversity in La Gamba is similar to, or slightly lower than, what has been documented for other areas of Costa Rica (Ricketts *et al.* 2001, Brehm and Axmacher 2006, Brehm *et al.* 2007). Yet, sampling was restricted to the habitat understory, which can undoubtedly underestimate true regional moth richness. Vertical stratification of arctiines in a Costa Rican lowland rainforest indicated higher richness and diversity in the canopy whereas geometrids were more prevalent in the forest understory (Brehm 2007), so Arctiinae may be especially undersampled in this study. A study from lowland Amazonia also registered similar arctiine richness as recorded around La Gamba with only understory sampling (Hawes *et al.* 2009). However, the results from this study support Brehm (2010) in that regional as well as local moth richness and diversity in the Ecuadorian Andes (Brehm and Fiedler 2005, Hilt and Fiedler 2005, Hilt *et al.* 2006) is much higher than in Costa Rica. Overall, La Gamba can be considered a moderately rich and diverse region for these two moth groups when compared to other Neotropical lowland regions, yet studies on other countries or regions are needed for more valid comparisons.

Tropical forest moth assemblages have proven to be highly sensitive to environmental and land use changes at a surprisingly small scale, which makes them suitable indicators of environmental and habitat disturbance (Fiedler *et al.* 2007). Thus, despite the small spatial scale of this study and the short distances between study sites, which surely are less than the dispersal ability of many moth species (Slade *et al.* 2013), sampling was sufficient to register fine-scaled responses to land use change among the study groups. In this study, Geometridae showed higher species richness and diversity, as they are one of the largest groups of Lepidoptera worldwide (Scoble 1999). Nevertheless, total captures of Arctiinae were higher, which may be explained by the apparent affinity of some Arctiinae species to successional and disturbed habitats (Kitching *et al.* 2000, Nöske *et al.* 2008), while tropical forest geometrids are more bound to intact close canopy habitats (Axmacher and Fiedler 2008, Choi 2008a).

Extrapolation of richness for both arctiines and geometrids showed that the two types of disturbed forest habitats (FM and YSF) did not differ consistently in species richness from old growth forest interior. Various studies have demonstrated that species richness in advanced succession habitats may be even higher than in undisturbed old-growth forests (Hilt and Fiedler 2005, Choi 2008b, Nöske *et al.* 2008), but this result was not expected in early succession habitats such as the young secondary forests sampled in this study, especially for geometrid moths (Hilt *et al.* 2006). However, other studies have noted that differences in moth assemblages after land use change seem more pronounced in terms of community structure and composition and not richness *per se*, as forest dependent species seem to be replaced by edge specialists or widespread species in disturbed habitats (Summerville and Crist 2004, Hawes *et al.* 2009, Tabarelli 2010). Of all sampled habitats, oil palm plantations showed the least arctiid and geometrid richness, at least 2-3 times lower than all other forested habitats.

Even though seasonal changes in the perhumid tropics are less extreme than in temperate zones, it is common knowledge that a wide variety of insect groups show temporal abundance variations due to their life cycles (Wolda 1988). While the abundance of many insect groups (e.g. Isoptera, Hemiptera, Coleoptera and Orthoptera) tends to increase in the beginning and/or during the wet season (Boinski and Scott 1988, Pinheiro *et al.* 2002), seasonal abundance fluctuations among tropical Lepidoptera vary greatly from taxon to taxon (Kitching *et al.* 2000, Hilt *et al.* 2007). Around La Gamba, moth catches of both geometrids and arctiines significantly decreased in the transition from dry to wet season. Precipitation around La Gamba declines significantly from January to March, then rainfall intensity starts increasing until the next pronounced decline in July or August (Weissenhofer and Huber 2008).

Higher moth activity density during the dry season might have several explanations: 1) the effectiveness of the light traps is higher on drier nights than on wet nights (Holyoak *et al.* 1997); 2) high rainfall reduces adult moth movement and flying activity as they may prefer to take refuge (Choi 2008b); 3) rainfall decreases moth survival by increasing larval and pupal mortality due to the presence of pathogens (Intachat *et al.* 2001, Bodner *et al.* 2010). Previous studies have shown dramatic effects of precipitation and seasonality on tropical Geometridae (Intachat *et al.* 2001, Beck and Chey 2007), which seem to decrease in abundance from the dry to the wet season (Hilt *et al.* 2007). While arctiine moths are presumably less affected by seasonality (Kitching *et al.* 2000, Choi 2008b), a recent study of arctiines from the Brazilian Cerrado shows seasonal differences in abundance and species composition, with higher abundance also registered during the dry season (Scherrer *et al.* 2013).

The moth family Geometridae is known for being highly sensitive to land use change and habitat degradation (New 2004). This study supports this premise, as geometrid activity density was significantly affected by habitat type. More individuals were captured in forest interior sites than in all other habitats, as was also found by Ricketts *et al.* (2001) in southern Costa Rica. The larvae of geometrids are often bound to forest woody plants, and very few species use host plants such as grasses that abound in open, disturbed tropical landscapes (Scoble 1999). Thus, less larval resource availability may be a possible reason for their reduced numbers in degraded habitats such as the forest margins and young secondary forests in this study (Hilt *et al.* 2006, Brehm 2007). Nevertheless, alpha diversity did not differ among forested habitats and was only lower in oil palm plantations, suggesting that some disturbed habitats may have potential for conserving geometrid richness and diversity. Similar studies have also found high abundance and diversity of geometrids at tropical forest margins and on late succession habitats, especially when they are near to old growth forests (Beck *et al.* 2002, Brehm and Fiedler 2005, Hilt *et al.* 2006, Nöske *et al.* 2008).

Representatives of various arctiine clades are known to benefit from anthropogenic habitat disturbance, especially those with larvae feeding on grasses or early successional herbs and shrubs (Kitching *et al.* 2000, Choi 2008a, Nöske *et al.* 2008). Choi (2008b) demonstrated that arctiines are positively associated with temperature and sunshine duration, characteristics typically associated with disturbed habitats. Contrary to geometrids, arctiine activity density was not affected by land use change in this study. However, arctiine species diversity was significantly lower in oil palm plantations, because high abundance in oil palm plantations is due to very few, extremely common species (Beck *et al.* 2011). In oil palm plantations around La Gamba, two lichen moth species were the only really abundant representatives of the Arctiinae and accounted for the massive dominance of single species in these habitats. In addition, one *Macroptila* and two *Agylla* species, to other members of the Lithosiini tribe, were also amongst the 10 most abundant species in oil palm plantations; these lichen moths seem to thrive in highly disturbed tropical habitats, as was found in a montane zone in Ecuador by Hilt and Fiedler (2006).

Literature on biodiversity in Southeast Asian oil palm plantations reiterates severe biodiversity losses for all animal groups, where the vast majority of old-growth forest species are presumably absent (Fitzherbert *et al.* 2008). The results of this study provide evidence of similarly severe depauperation of moth fauna in oil palm plantations in the Neotropical region, with response patterns as pronounced as those reported for Asian fauna (Chey 2006, Koh and Wilcove 2008). In the case of Geometridae, activity density and species richness were bot significantly lower in oil palm plantations, which proves that they are more sensitive to land use change when compared to arctiines. At least two thirds of the species that were registered in the other land uses were not recorded in oil palm plantations. This is a cause for concern if oil palm agriculture continues to increase steadily in southern Costa Rica and especially around La Gamba, where it is already the second leading land use type (Höbinger *et al.* 2011). Observed faunal shifts in oil palm plantations may affect the functional roles these moths may play in the ecosystems, since their reduction indicates less food availability for predators such as insectivorous bats and birds (Cooper and Smith 1995, Rydell and Lancaster 2000, Jacobs *et al.* 2008), with unforeseeable further repercussions on the structure of ecological food webs as well as the ecosystem services provided by these vertebrate groups (Kunz *et al.* 2011, Maas *et al.* 2013).

Species composition and community structure after land use change

Of all sampled habitats, oil palm plantations exhibited substantially higher levels of single species dominance. This finding is in concordance with results from Southeast Asian plantations, where assemblages are mostly dominated by a few generalist, non-forest, invasive or pest species (Fitzherbert *et al.* 2008). The most common geometrid species in oil palm plantations was *Tricentrogyna violescens* (Schaus 1901), a member of the Sterrhinae subfamily which accounted for 44% of total geometrid abundance in this habitat. Meanwhile, the most abundant arctiine species in oil palm plantations was an unidentified member of the lichen moth tribe Lithosiini, accounting for 56% of total arctiine abundance. These moths are both very small species, with a wingspan of less than 1.5cm, which may indicate that large-sized moths are not as successful in oil palm plantations. In addition, 74% and 54% of total catch of geometrids and arctiines in oil palm plantations, respectively, consisted of singletons and doubletons, another strong indication that this habitat can hardly support viable moth populations.

The available host plant information on the geometrid species collected in this study indicates that most of them use woody plants (e.g. trees and shrubs) as larval host plants, with very few that feed on herbaceous or cultivated plants (Janzen and Hallwachs 2009). Thus, most geometrids from La Gamba can seldom find larval resources in oil palm plantations and most are dependent on natural forest habitats. In the case of arctiines, the species composition in oil palm plantations was mostly dominated by various species of Lithosiini, whose larvae feed primarily on lichens and have been known to be positively related to habitat disturbance (Hilt and Fiedler 2006, Scott *et al.* 2014); lichens grow as epiphytes in the leaf bases and the surface of palm trunks (Nadarajah and Nawawi 1993), which may explain the high abundance of lichen moths in oil palm plantations, as was found by Chey (2006) in Borneo. Remarkably, colorful arctiine species with aposematic wing patterns were numerous in forest habitats, but rarely found in oil palm plantations. Several of these are members of the Ctenuchini tribe, many of which have host specific larvae and are generally affiliated with forested habitats (Hilt and Fiedler 2006). These observations suggest a shift in functional diversity in oil palm plantations due to the absence of complex, co-evolved mimicry rings, as well as shifts in trophic relationships. A few moths related to weedy herbaceous plants and epiphytes may proliferate, whereas arboreal (and often host specific) herbivores are severely reduced.

There were many more geometrid and arctiine species that proliferate in forest interior sites, and some of these could potentially be used as indicator species for this habitat (Table 4). A species of the genus *Pyrinia* was the most common geometrid in the interior of old-growth forests, an Ennominae moth that tends to be polyphagous on weedy shrubs and woody plants (Janzen and Hallwachs 2009). Meanwhile, the Ctenuchini moth *Heliura thysbodes* was the arctiine most indicative of forest interior sites. Most arctiine moths that thrive in this habitat were from the Ctenuchini and Arctiini tribes, which were fairly absent from oil palm plantations. Species traits such as larval host specificity, mode of adult feeding, length of the flight period and body size could be driving the observed changes in species composition as well as their risk of extinction in oil palm plantations (Mattila *et al.* 2006, Slade *et al.* 2013).

Further research is needed on the life history and morphology of moth species to understand their distribution in human dominated landscapes.

Species composition of geometrids and arctiines was distinct in the interior of old-growth forests and in oil palm plantations, with unique communities in each one of these land use types. However, forest margins and young secondary forests did not differ significantly in species composition for either moth group. Studies from both Ecuador and Borneo have also shown that assemblages of these moth groups do not greatly differ between succession habitats (Beck *et al.* 2002, Hilt and Fiedler 2005, Hilt *et al.* 2006). The geometrid and arctiine communities that survive in these two habitats are presumably species related to forests with intermediate levels of disturbance, and they may also contain a mixture of species from both the old-growth forest and the agricultural matrix. This might explain why forest margins and secondary forests showed lower dominance values when compared to forest interior and oil palm plantation sites, a result also found by Hilt and Fiedler (2006) when comparing arctiines between old-growth forests and succession habitats.

Even though not all habitats contained distinct assemblages, the NMDS plot for geometrids showed a clearer grouping of the land use types that follows a gradient of habitat disturbance. This result was also registered by Beck *et al.* (2002) along two habitat gradients in Borneo. Thus, as sustained by Beck and Chey (2007), geometrid assemblages are more sensitive indicators of land use change, as habitat disturbance seems to serve as a key driver explaining their community structure. Hence, Geometridae may be the most suitable moth family to be used as an indicator group for monitoring human impacts of forest ecosystems, as has been suggested by many authors (Intachat *et al.* 1997, New 2004, Hilt *et al.* 2006). Future research should focus on the development of biomonitoring protocols oriented specifically on evaluating habitat disturbance as indicated by geometrid moths.

Vegetation structure as the main predictor of arctiine and geometrid assemblages

Geometrid and arctiine moths were not affected exactly in the same manner by the measured vegetation parameters, since geometrid assemblages seem more vulnerable to changes in vegetation structure, in agreement with Choi (2008a) and Beck *et al.* (2011). Yet, community structure and composition of both groups were strongly related to structural complexity of their habitats, such as plant species richness and diversity, vegetation density, understory density, understory and vertical complexity. With increasing structural complexity of the habitat, it seems likely there will be more ecological niches for diverse moth guilds to occupy (Ricketts *et al.* 2001). This may be the reason why structurally homogeneous land use types such as oil palm plantations do not support diverse moth assemblages, while secondary forests and edge habitats do sustain diverse populations that, although different from the original forest, may serve to ameliorate biodiversity loss after forest conversion and continued oil palm expansion.

Beck *et al.* (2002) propose three mechanisms that may be responsible for changes in moth assemblages with increasing habitat disturbance: variations in microclimate, predation, or resource availability. In this study, it was vegetation and not microclimate that resulted as the main predictor of variation in moth assemblages. However, since some vegetation parameters were autocorrelated, it is difficult to pinpoint exactly the variable or combination of variables that were mostly responsible for the observed patterns of species richness, diversity and composition. Given that host plant information is not available for the majority of the species collected in this study, it is difficult to determine whether the main driver of moth assemblages in this landscape is vegetation structure in general, or rather the availability of specific host plant resources (Summerville and Crist 2003, Hawes *et al.* 2009). Since the life histories of most species are not known, it is presently not possible to recommend specific measures to maintain individual species. Such would also not be relevant, unless very rare species of high conservation value were concerned.

Implications for conservation

There is still much collaborative work needed to clearly assess the response of moth fauna to land-use change, especially in Neotropical regions, which would permit the implementation of targeted moth conservation strategies. There are still a large number of unknown species, as well as much uncertainty about the life history characteristics, vagility and host-plant relationships for the majority of described species (Kitching *et al.* 2000). Specific knowledge of moth population dynamics and population structures is indeed rare, even for many pest species (New 2004). Thus, community level studies such as this one are essential for the improvement of conservation and landscape management strategies, which may be relevant to a wide range of other arthropod groups in human dominated landscapes.

Community studies have typically concentrated on comparing homogenous agricultural systems with forest remnants, which are bound to show differences in moth communities (Ricketts *et al.* 2001). As expected, this study demonstrates that oil palm monocultures provoke a severe decay in rainforest moth richness and do not sustain diverse populations of moth fauna. However, this study also provides evidence of the value of intermediately disturbed habitats, such as young secondary forests and forest edges, for moth conservation in the face of increasing land use change. Although agroforestry systems have been shown to support a small proportion of mostly widespread and generalist tropical forest butterflies (Schulze *et al.* 2010), it may be possible that sustainable production schemes such as these provide a more structurally complex vegetation which, according to the results of this study, may support higher moth species richness. Further research is needed to test this hypothesis.

Even though most of the study sites were close to remnant forest patches, this study did not evaluate the effects of distance to nearby forest on the other land use types. Nevertheless, old-growth forests in this landscape undoubtedly serve as source habitats essential for recolonization after forest conversion (Beck *et al*. 2002, Hilt and Fiedler 2005, Hawes *et al.* 2009). The most viable alternative for moth conservation seems to be directing efforts towards the overall preservation of natural habitats, especially remnant old-growth forest patches, which have no real substitute when it comes to maintaining biodiversity (Gibson *et al.* 2011). Conservation efforts should also include the promotion of secondary forest re-growth and preservation of landscape heterogeneity as a whole (New 2004). In addition, strategies may be developed to reduce the aggressiveness of oil palm plantations towards biodiversity, such as the maintenance of dense understory thickets and shrubs that may provide shelter and niche availability for more species (Kitching *et al.* 2000). As oil palm plantations continue to expand in the Neotropics, there is a growing need for proof of their severe impacts on biodiversity, which may serve to encourage local farmers and landscape managers to implement evidence based conservation actions to reduce biodiversity loss in human dominated landscapes.

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APPENDIX 1. Brief description of the 20 sampling sites within forest interior (FI), forest margin (FM), young secondary forest (YSF) and oil palm plantation (OPP) as main habitat types

Code	Habitat	Latitude	Longitude	Altitude (m)	Slope (%)
FI1	FI	8° 41' 44.81"	-83° 12' 13.93"	149	35
FI2	FI	8° 40' 16.21"	-83° 11' 55.03"	138	38
FI3	FI	8° 42' 10.04"	-83° 12' 18.29"	111	27
FI4	FI	8° 41' 57.01"	-83° 12' 29.12"	194	22
FI5	FI	8° 42' 15.55"	-83° 12' 12.53"	116	27
FM1	FM	8° 42' 0.22"	-83° 12' 11.02"	100	3
FM2	FM	8° 41' 2.94"	-83° 11' 54.85"	112	20
FM3	FM	8° 41' 23.53"	-83° 10' 50.66"	104	2
FM4	FM	8° 42' 8.82"	-83° 12' 50.29"	134	27
FM5	FM	8° 42' 36.04"	-83° 12' 45.50"	106	28
YSF1	YSF	8° 42' 22.03"	-83° 11' 31.67"	87	16
YSF2	YSF	8° 42' 1.01"	-83° 11' 38.54"	79	1
YSF3	YSF	8° 42' 24.55"	-83° 10' 34.28"	88	1
YSF4	YSF	8° 41' 23.89"	-83° 11' 3.70"	133	22
YSF5	YSF	8° 43' 1.45"	-83° 11' 31.99"	94	1
OPP1	OPP	8° 41' 53.30"	-83° 11' 54.92"	96	1
OPP2	OPP	8° 42' 18.54"	-83° 12' 54.83"	109	1
OPP3	OPP	8° 42' 5.83"	-83° 11' 24.90"	80	1
OPP4	OPP	8° 43' 9.77"	83° 12' 22.93"	103	1
OPP6	OPP	8° 42' 56.59"	83° 10' 18.77"	79	6

APPENDIX 2. Full list of species and abundances of geometrid and arctiine moths from 6 nights of light-trapping at five forest interior (FI), five forest margin (FM), five young secondary forest (YSF) and five oil palm plantation (OPP) sites within the tropical lowlands of southwestern Costa Rica

		Number of individuals				
Code	Species	FI	FM	YSF	OPP	Total
	Geometridae					
BRYSP01	*Bryoptera* sp01	1	3			4
BRYSUBB	*Bryoptera subbrunnea*	1		1		2
CHLSP01OP	*Chloropteryx* sp01 nr. *opalaria*	2				2
CHLSP02	*Chloropteryx* sp02	2	4	2	2	10
CHLSP03	*Chloropteryx* sp03	1	2			3
CIMALBI	*Cimicodes albicosta*	15	7	1		23
CYCMINU	*Cyclomia minuta*	1	2	8	9	20
CYCINSI	*Cyclophora insignata*	5	2	1		8
CYCNIVE	*Cyclophora nivestrota*	2	1			3
CYCNODI	*Cyclophora nodigera*	1	1	1		3
CYCSP01	*Cyclophora* sp01	5	8			13
CYCSP02	*Cyclophora* sp02	23	27	8		58
DICOBLI	*Dichorda obliquata*		1		2	3
DYSTENU	*Dyspteris tenuivitta*	6	1			7
DYSTRIF	*Dyspteris trifilaria*	17	5	3		25
DYSVECI	*Dyspteris vecinaria*	1				1
EOIAPYR	*Eois apyraria*	1				1
EOICEDO	*Eois cedon*				1	1
EOICHAC	*Eois* chacón16	4		1		5
EOICHAC	*Eois* chacón35		1			1
EOICHAC	*Eois* chacónII	1				1
EOICOLO	*Eois coloraria*	1				1
EOISP01	*Eois* sp01	1				1
EOISP02SU	*Eois* sp02 nr. *subtectata*	1				1
EOISP03UN	*Eois* sp03 nr. *undulosata*	2				2
EOISP04PL	*Eois* sp04 nr. *plana*	1				1
EOITEGU	*Eois tegularia*		3	1	1	5
EOIZENO	*Eois zenobia*	4	1			5
EPIMATR	*Epimecis matronaria*			1		1
EPIPATR	*Epimecis patronaria*		4			4
EPISP01	*Epimecis* sp01	1	1			2
EPISUBR	*Epimecis subroraria*	22	8	4		34
ERADECR	*Erastria decrepitaria*			2		2
EUBSP01	*Eubaphe* sp01				1	1
EUPSP01	*Euphyia* sp01	1				1
EUSCAYE	*Eusarca cayennaria*		6	6	3	15
EUSCHAC	*Eusarca* chacón01			2	1	3

EUSCRAM	*Eusarca crameraria*	1		3		4
EUSDIST	*Eusarca distycharia*			1		1
EUSFLEX	*Eusarca flexilis*	1	25	13	4	43
EUSMINU	*Eusarca minucia*	8	4	3		15
EUTARTE	*Eutomopepla artena*			1		1
HEMSUBN	*Hemipterodes subnigrata*	1				1
HERLILA	*Herbita lilacina*	1				1
HERPRAE	*Herbita praeditaria*	2				2
HYDSP01PO	*Hydata* sp01 nr. *povera*	5	3			8
HYDSP02	*Hydata* sp02	1				1
HYDSTIG	*Hydata stigmatica*	4	4	1	1	10
HYMCAME	*Hymenomima camerata*	7	5	2		14
HYMCHAC	*Hymenomima* chacón01	7	2			9
HYMMEMO	*Hymenomima memor*	34	19	16	1	70
HYMUMBE	*Hymenomima umbelularia*				3	3
IDARUBI	*Idaea rubidentata*	5		7	1	22
IDASUBF	*Idaea subfervens*	3	1	1		5
IRIOBER	*Iridopsis oberthuri*			1		1
IRIPAND	*Iridopsis pandrosos*		1			1
ISOSP01	*Isochromodes* sp01	1	2			3
LEPCHAC	*Leptostales* chacón01		2			2
LEPDELI	*Leptostales delila*	1	3	28		32
LEPTERMNU	*Leptostales terminata nursica*			1	2	3
LEUFIMB	*Leuciris fimbriaria*			11	1	12
LEUFEST	*Leucula festiva*	15	5			20
LISMANO	*Lissochlora manostigma*			1		1
LOBSUBC	*Lobocleta subcincta*	14	12	4		30
MACACHE	*Macaria achetata*	1			1	2
MACAPPR	*Macaria approximaria*	2				2
MACBEJU	*Macaria bejucoaria*			1		1
MACCATU	*Macaria catualda*	1	2	3		6
MACGAMB	*Macaria gambarina*	1	2	3		6
MACINFU	*Macaria infusata*	3				3
MELSP01	*Melinodes* sp01		5	1		15
MICRHODRH	*Microgonia rhodaria rhodaria*		1			1
MICRUFA	*Microgonia rufaria*		1			1
NEMAREN	*Nematocampa arenosa*		1	2		3
NEMCOMP	*Nematocampa completa*	1	3	5		9
NEMSP01	*Nematocampa* sp01		1			1
NEMSP02	*Nematocampa* sp02		1			1
NEMSTRA	*Nematocampa straminea*			2		2
NEMADJU	*Nemoria adjunctaria*	4	2	4		10
NEMDEFE	*Nemoria defectiva*	1		1		2
NEMPACI	*Nemoria pacificaria*	4	4	3		11
NEMPUNC	*Nemoria punctilinea*	1				1

NEMSCRI	*Nemoria scriptaria*	8	4			12
NEMSP03	*Nemoria* sp03			1		1
NEPPOLI	*Nepheloleuca politia*			1		1
OOSALBIAL	*Oospila albicoma albicoma*	1				1
OOSALBI	*Oospila albipunctulata*			1		1
OOSATOP	*Oospila atopochlora*			1		1
OOSRUPT	*Oospila ruptimacula*	3	2			5
OPIASOP	*Opisthoxia asopis*		1			1
OPIBELL	*Opisthoxia bella*	1	1			2
OPISP01	*Opisthoxia* sp01	1				1
OXYAPID	*Oxydia apidania*	3				3
PALMICA	*Palyas micacearia*			1		1
PARCRUR	*Paragonia cruraria*	6	2			8
PARTASI	*Paragonia tasima*	1				1
PATAENE	*Patalene aenetusaria*	1	3	2		6
PATFALC	*Patalene falcularia*			1	1	2
PATHAMU	*Patalene hamulata*	1	1	1		3
PATLUCI	*Patalene luciata*			1		1
PERALBI	*Perigramma albivena*	2	3	2		7
PERSIMI	*Pero simila*	1				1
PETSP01	*Petelia* sp01	2				2
PHRALBISI	*Phrudocentra albicoronata sixola*	1	1			2
PHRJANETE	*Phrudocentra janeira tenuis*			1		1
PHRNEISNE	*Phrudocentra neis neis*			2		2
PHRPUPI	*Phrudocentra pupillata*	6	1	3	1	20
PHYSP01	*Phyllodonta* sp01	1				1
PHYPAUP	*Physocleora pauper*	46	18	6		70
PHYPLEN	*Physocleora plenaria*	16	8	2		26
PHYTAEN	*Physocleora taeniata*	2	2			4
PLESP01	*Pleuroprucha* sp01		2	4	1	7
PLESP02	*Pleuroprucha* sp02	1		1		2
POLHEME	*Polla hemeraria*			1		1
PROMARC	*Prochoerodes marciana*	1		1		2
PROMIRI	*Proutoscia mirifica*	1				1
PYRHELV	*Pyrinia helvaria*	1			1	2
PYRRUTI	*Pyrinia rutilaria*	1		6		7
PYRSP01	*Pyrinia* sp01	114	4	2		120
PYRSP02AR	*Pyrinia* sp02 nr. *arxata*		5	2		7
PYRSP03AR	*Pyrinia* sp03 nr. *arxata*		1			1
PYRTRAN	*Pyrinia transitata*	5	1	2		8
PYRRANI	*Pyrochlora ranis*		2	2		4
RHOBRUNMI	*Rhodochlora brunneipalpis minor*	16	5			21
SCOCOMP	*Scopula compensata*	1	3	11	12	27
SCOUMBI	*Scopula umbilicata*		1		1	2
SEMEXQU	*Semaeopus exquisitata*	2	1			3

SEMILLIIL	*Semaeopus illimitata illimitata*	3	1	3		7
SEMMINI	*Semaeopus miniata*	5	2	2		9
SEMNALT	*Semaeopus naltona*	1	1			2
SEMPAPL	*Semaeopus paplamearia*	1	1			2
SEMSP01PA	*Semaeopus* sp01 nr. *paplamearia*	3	1			4
SEMSP02CO	*Semaeopus* sp02 nr. *commaculata*	3				3
SEMSALS	*Semiothisa salsa*	1	1			2
SPHVULN	*Sphacelodes vulneraria*		1	1		2
SYNEXPUAT	*Synchlora expulsata atrapoides*	1		4		5
SYNFRONFR	*Synchlora frondaria frondaria*	1		8		9
SYNGERU	*Synchlora gerularia*			2		2
SYNPULC	*Synchlora pulchrifimbria*	3	1	2		6
SYNTENUTE	*Synchlora tenuimargo tenuimargo*		3	1		4
TACALBI	*Tachyphyle albisparsa*		1			1
TACOLEA	*Tachyphyle oleaster*			3		3
TACSP01	*Tachyphyle* sp01	3		1		4
TETANOP	*Tetragonodes anopsaria*		1	1	1	3
TETSP01	*Tetragonodes* sp01		2	1		3
THYCARF	*Thysanopyga carfinia*	2				2
THYCERM	*Thysanopyga cermala*	2	2	2	1	7
THYGAUL	*Thysanopyga gauldi*	1	2	1		4
THYNIGR	*Thysanopyga nigristicta*	1	2		1	4
THYSP01CE	*Thysanopyga* sp01 nr. *cermala*	4		2		6
TMEBITI	*Tmetomorpha bitias*	9	2			11
TRIGAVI	*Tricentra gavisata*	2			1	3
TRISP01	*Tricentra* sp01	2		1		3
TRISP02	*Tricentra* sp02	4	1			5
TRIUNIM	*Tricentra unimaculata*	1				1
TRISP01	*Tricentrogyna* sp01			1		1
TRISP02	*Tricentrogyna* sp02	1		2	6	9
TRIVIOL	*Tricentrogyna violescens*	2	6	37	6	105
ENN1	Ennominae 01	9	2		1	12
ENN4	Ennominae 04			1		1
ENN5	Ennominae 05	1				1
ENN6	Ennominae 06	1				1
ENN7	Ennominae 07		3	4		7
STE1	Sterrhinae 01		1	2		3
STE5	Sterrhinae 05	1				1
STE6	Sterrhinae 06	1	1	2	2	6
STE7	Sterrhinae 07	2	1			3
STE10	Sterrhinae 10		1	2		3
STE11	Sterrhinae 11				2	2
STE12	Sterrhinae 12		1			1

Erebidae-Arctiinae

ACLALBI	*Aclytia albistriga*	2	1	12		15
ACLPUNC	*Aclytia punctata*	52	13	26	6	97
ACLSP01HE	*Aclytia* sp01 nr. *heber*	1		5	2	8
AGAMINU	*Agaraea minuta*	15	31	21	2	87
AGASEMI	*Agaraea semivitrea*	2	3	3		8
AGYMARG	*Agylla marginata*	11	19	7	2	57
AGYSP01	*Agylla* sp01	14	2	9	12	55
AGYSP02	*Agylla* sp02	7	3	6		16
AMPPRIS	*Amphelarctia priscilla*			2		2
ANASP01	*Anaulosia* sp01	9	4	8	1	22
BALDORS	*Balbura dorsisigna*	14	12	1		36
CERSYLV	*Cercopimorpha sylva*	2		2		4
CISDECO	*Cissura decora*	1				1
CLODIGN	*Cloësia digna*		1			1
CORFULV	*Correbia fulvescens*	6	8	8	1	23
CORSP01AF	*Correbia* sp01 nr. *affinis*		1			1
CORSP02UN	*Correbia* sp02 nr. *undulata*	1	1	5		7
CORSP03	*Correbia* sp03		1			1
CORCOST	*Correbidia costinotata*	1				1
CORELEG	*Correbidia elegans*		1			1
CORSP01GE	*Correbidia* sp01 nr. *germana*	1				1
CORSP02GE	*Correbidia* sp02 nr. *germana*	3	2	2		7
CORSP03ST	*Correbidia* sp03 nr. *striata*	1				1
COSANGU	*Cosmosoma angustimargo*	3				3
COSCAEC	*Cosmosoma caecum*			1		1
COSHECT	*Cosmosoma hector*	4		5	1	10
COSSARO	*Cosmosoma saron*	1				1
COSSEMI	*Cosmosoma semifulva*		2	1	1	4
COSXANT	*Cosmosoma xanthostictum*	2				2
DELTEST	*Delphyre testacea*	13		2		15
DOLFALS	*Dolichesia falsimonia*		3	3		6
DYCVITR	*Dycladia vitrina*		2			2
DYSJANS	*Dysschema jansonis*			4	1	5
DYSPANA	*Dysschema panamensis*			1		1
ECDOBSC	*Ecdemus obscurata*	1				1
ELYDISC	*Elysius discoplaga*		2	2		4
EPAIMPE	*Epanycles imperialis*	1				1
EPELEPH	*Epeiromulona lephina*		6	4		10
EPIOCEO	*Epidesma oceola*	1				1
EPIURSU	*Epidesma ursula*			2		2
EPICAPY	*Episcepsis capysca*			1		1
EPIDEMO	*Episcepsis demonis*	21	3	1		25
EPIHYPO	*Episcepsis hypoleuca*	2		4		6
EPILENA	*Episcepsis lenaeus*	2		1		3

EPISP01	*Episcepsis* sp01	2	1	2		5
EUCATRI	*Eucereon atrigutta*		1	1		2
EUCAURA	*Eucereon aurantiaca*		1	3	1	5
EUCMAIA	*Eucereon maia*		2	18		20
EUCAR	*Eucereon* nr. *argutum*	2	4	14	2	22
EUCPOME	*Eucereon* nr. *pometinum*		1			1
EUCRELE	*Eucereon relegata*			1		1
EUCROSI	*Eucereon rosinum*	1				1
EUCSP01OB	*Eucereon* sp01 nr. *obscurum*			1		1
EUCSP02OB	*Eucereon* sp02 nr. *obscurum*	1		1		2
EUCSP03	*Eucereon* sp03	84	8	3		95
EUCSP04	*Eucereon* sp04			1		1
EUCVARI	*Eucereon varium*	3		2	2	7
EUPINVO	*Eupseudosoma involuta*		5	23		28
EUPAB	*Eupseudosoma* nr. *aberrans*	1				1
EUTSP01	*Euthyone* sp01		2	12	1	15
GYMJANS	*Gymnelia jansonis*			1		1
HALFUMO	*Halysidota fumosa*	4		1		5
HELRHOD	*Heliura rhodophila*	1	1	3		5
HELSP01PH	*Heliura* sp01 nr. *phaeosoma*			1		1
HELTHYS	*Heliura thysbodes*	37	1	3		50
HYASIXO	*Hyalurga sixola*	12	2			14
HYASORA	*Hyalurga sora*			2	1	3
HYPLAGU	*Hyperandra laguerrei*	3				3
HYPSP05	*Hypercompe* sp05	1	2	17	5	25
ICHSP01	*Ichoria* sp01		1			1
IDACRIN	*Idalus crinis*			2		2
IDACRIT	*Idalus critheis*	1				1
IDATYBR	*Idalus tybris*		1			1
ILLCITR	*Illice citrina*	1	1			2
ILLOPUL	*Illice opulentana*		1			1
ILLSP01	*Illice* sp01	3	8	26	5	42
ILLSP02	*Illice* sp02	8	4	15	2	47
ILLSP05	*Illice* sp05		4	9	6	19
ISACRAB	*Isanthrene crabroniformis*			1		1
LAMSP01	*Lamprostola* sp01	1				1
LEUSP01	*Leucanopsis* sp01	3	26	46	19	94
LEUSP03	*Leucanopsis* sp03			1		1
LOPCATE	*Lophocampa catenulata*	1	7	7	2	17
LOPDEBI	*Lophocampa debilis*	1	1	2		4
LOPMARO	*Lophocampa maroniensis*			1		1
LOPMODE	*Lophocampa modesta*	1		1		2
LOPSUBA	*Lophocampa subannula*	1		1		2
LOXPY	*Loxophlebia* nr. *pyrgion*		2			2
LYCSORD	*Lycomorphodes sordida*			1		1

MACCABI	*Macrocneme cabimensis*	1		2	1	4
MACIOLE	*Macrocneme iole*		17	2		37
MACLADE	*Macrocneme lades*			1		1
MACROTU	*Macroptila rotundata*	2	17	3	7	29
MELINCE	*Melese incertus*	9	3	23		35
MELLAOD	*Melese laodamia*	2	2	4		8
MELSIXO	*Melese sixola*	99	85	58	4	246
METSP01	*Metalobosia* sp01		2	2		4
MYDNOTO	*Mydromera notochloris*		4		2	6
NAPLEUC	*Napata leucotelus*			1	1	2
NODHIER	*Nodozana hieroglyphica*	1	1			2
NOTPROX	*Notarctia proxima*		2	9		11
NUDFLAC	*Nudur flactivittarum*	3	3			6
OCHPRON	*Ochrodota pronapides*	6	6	3	1	16
ODOSIXO	*Odozana sixola*	4	2	2		8
ODOSP01	*Odozana* sp01	1		1		2
ORMATAE	*Ormetica ataenia*			7		7
ORMSICI	*Ormetica sicilia*		1	3		4
PARINSU	*Pareuchaetes insulata*			12	3	15
PELARON	*Pelochyta arontes*	1		1		2
PELRUFI	*Pelochyta ruficollis*	1				1
PHAVAMP	*Phaeomolis vampa*			1		1
PHOSANG	*Phoenicoprocta sanguinea*			1		1
POLSP06	*Poliopastea* sp06		1	1		2
POMSP01	*Pompiliodes* sp01		1	2	1	4
PRESP01	*Prepiella* sp01	1	2	1		4
PSEMELA	*Pseudomya melanthoides*			3		3
PSOBASI	*Psoloptera basifulva*	5	2	5		12
PTECAER	*Pterygopterus caeruleus*	1				1
ROBBART	*Robinsonia bartolana*	1		1		2
SAUAFFL	*Saurita afflicta*	1	1	4	2	8
SAUPHOE	*Saurita phoenicosticta*		1	6		7
SAUTIPU	*Saurita tipulina*	5	8	8	3	24
SUTREDU	*Sutonocrea reducta*			2		2
SYMIPSE	*Symphlebia ipsea*	1	2			12
TALESPE	*Talara esperanza*		1	3	29	33
TALSP01MI	*Talara* sp01 nr. *minynthadia*	5	2	2		9
TALSP02	*Talara* sp02	2	4	2		8
THYHAEM	*Thysanoprymna haemorroides*				1	1
TRIANDR	*Trichromia androconiata*	1				1
TRICARD	*Trichromia cardinalis*		1			1
TRILOPH	*Trichromia lophosticta*	1				1
TRISP02	*Trichromia* sp02	1				1
TRISP01	*Trichura* sp01	1				1
TRIIMPE	*Tricypha imperialis*	2	1			3

VIRSP01ME	*Virbia* sp01 nr. *medarda*	8	62	64	49	183
VIRSP02	*Virbia* sp02	18	13	2		33
VIRSP03	*Virbia* sp03		1			1
VIVSALM	*Viviennea salma*			1		1
WATREIM	*Watsonidia reimona*	1				1
LIT1	Lithosiini 01		1			1
LIT2	Lithosiini 02	2	41	26	296	383
ARC1	Arctiinae 01	1				1
	Total	1125	810	946	547	3644

APPENDIX 3. Main vegetation descriptors for the 20 sampling sites

Code	Habitat	Plant species richness ≥ 2cm DBH (S'/314m²)	Vegetation density ≥ 2cm DBH (N/314m²)	Plant species diversity (Fisher's α/314m²)	Understory density < 2cm DBH and ≥ 50cm height (N/100m²)	Understory complexity (Shannon)	Undergrowth cover*	Vertical complexity (Shannon)	Canopy cover (%)	Tree basal area ≥ 10cm DBH (m²/ha)
FI1	FI	34	45	63.36	132	1.21	2	1.28	81.3	12.47
FI2	FI	22	52	14.39	128	1.19	0	1.37	84.9	10.19
FI3	FI	16	34	11.80	135	0.77	0	1.52	87.0	27.16
FI4	FI	31	51	33.52	124	0.73	0	1.33	75.8	8.61
FI5	FI	35	46	66.82	187	1.25	0	1.55	77.4	20.09
FM1	FM	27	64	17.60	190	0.86	0	1.35	71.7	19.01
FM2	FM	19	48	11.62	132	1.12	2	1.28	73.0	11.01
FM3	FM	27	51	23.26	172	0.68	1	1.49	67.8	23.20
FM4	FM	25	86	11.84	149	1.37	0	1.08	81.0	19.28
FM5	FM	25	47	21.68	114	1.14	0	1.52	78.7	28.67
YSF1	YSF	6	9	7.87	29	0.81	3	1.04	30.9	5.15
YSF2	YSF	8	21	4.72	25	0.78	3	0.69	35.4	0.60
YSF3	YSF	26	71	14.61	149	0.83	3	1.1	72.7	8.12
YSF4	YSF	10	20	7.96	48	0.45	3	0.69	63.3	3.13
YSF5	YSF	20	140	6.39	196	0.84	0	1.31	84.4	22.31
OPP1	OPP	1	4	0.43	7	1.08	3	0	70.1	40.92
OPP2	OPP	1	5	0.38	66	0.27	3	0.56	64.6	65.44
OPP3	OPP	1	4	0.43	0	0	1	0.56	78.2	60.36
OPP4	OPP	1	4	0.43	51	0.22	3	0.56	61.8	42.15
OPP6	OPP	1	4	0.43	25	0.44	3	0.56	65.7	50.24

* 0:0%, 1:1-33%, 2:34-66%, 3:67-100%

APPENDIX 4. Pearson correlations of the original vegetation variables with the extracted principal components (VC1 and VC2)

Variable	VC1	VC2
Plant species richness	0.97***	–0.15
Vegetation density	0.89***	0.01
Plant species diversity	0.84***	–0.2
Understory density	0.9***	0.05
Understory complexity	0.72***	–0.24
Undergrowth cover	–0.75***	–0.48*
Vertical complexity	0.91***	0.01
Canopy cover	0.55*	0.73***
Tree basal area	–0.42	0.84***

*$p < 0.05$, **$p < 0.01$, ***$p < 0.005$.

APPENDIX 5. Pearson correlations of the original climate variables with the extracted principal components (CC1 and CC2)

Variable	CC1	CC2
Tmean	0.28	0.85***
T CoV	0.85***	-0.24
Tmax	0.81***	0.18
Tmin	-0.63***	0.71***
Tmax-min	0.92***	-0.3
Hmean	0.73***	0.29
H CoV	-0.68***	-0.47*

*$p < 0.05$, **$p < 0.01$, ***$p < 0.005$.

5. COMPLEMENTARY CHAPTER: PUBLIC OUTREACH ACTIVITIES

An essential part of this thesis project was to share with others the ecological importance and richness of moth fauna in Costa Rica and the threats that oil palm expansion may pose on local moth biodiversity. Thus, several outreach activities were conducted to create ecological awareness and promote sustainable land use practices both in Turrialba and La Gamba, Costa Rica. The purpose of this complementary chapter is to document the outcomes of these activities and how they will eventually aid in biological conservation and sustainable development.

5.1. Moth exhibitions in Turrialba

Despite the small scale of this study, the high biodiversity of the study area and the effectiveness of the sampling technique that was used enabled the preparation of a moth collection of approximately 4,000 individuals. Most of the species were geometrid and arctiine moths, but the collection also included several hundred individuals from other families. As an attempt to share this collection with the community around the university, this collection was exhibited in CATIE and in the Jorge de Bravo School in Turrialba (**Fig. 9**). The exhibition in CATIE was offered for two whole business days, during which at least 100 people from the university (including students, staff members and professors) visited the collection. Meanwhile, the collection was exhibited for half a day during the annual field day of the Jorge de Bravo School, and was attended by approximately 100 elementary and high school students, their relatives and teachers. See Appendix 1 for the complete list of visitors to both exhibitions.

Figure 9. Exhibitions of the La Gamba moth collection that were offered in CATIE (a) and in the Jorge de Bravo School (b) in Turrialba.

Information on moth biology and ecological functions as well as details about the development of the study was also offered during the course of the exhibitions. They were written in several cards that were distributed among the moth drawers, to guide visitors throughout the exhibition. There was also a slideshow of photographs that included images of the methodology that was used for moth collection, as well as images of how some of the moth species that were collected look like alive. The principal investigator of this study was available for questions and walkthroughs of the exhibition during both activities.

The exhibitions were highly effective in raising the curiosity of visitors in terms of the incredible moth biodiversity found in Costa Rica. Many of them had never seen moths like the ones included in the exhibition and did not believe they could have so many interesting colors and strange morphological characteristics. The activities served to educate children, scientists and non-scientists on the enormous value of moth biodiversity for the ecosystem, which will hopefully promote more research and awareness on this relatively unnoticed insect group.

CATIE published a short note about the activity and the project on their Facebook page and official website (http://catie.ac.cr/es/noticias-catie/entry/innovadora-investigacion-de-mariposas-en-el-catie). The results of the project also appeared in a Costa Rican online newspaper (http://www.crhoy.com/cultivos-de-palma-africana-amenazan-vida-de-mariposas-nocturnas-u1n5n6x/) and a science and technology website from the University of Salamanca (http://www.dicyt.com/noticias/estudian-la-diversidad-de-las-mariposas-nocturnas-de-costa-rica). This moth collection was donated to several national institutions, including CATIE, INBio and UCR, to continue contributing to tropical moth research in Costa Rica and Central America.

5.2. Awareness and information sharing in La Gamba

Biological indicators are useful tools that may be used to monitor the ecological consequences of anthropogenic land use change. Even though butterflies are one of the most commonly used bioindicators, moths also carry high potential as indicator groups, yet distinct methodologies for the use of moths as indicators have not been developed. This study was designed as a baseline for the development of such methodologies for the Costa Rican Golfo Dulce Region, since the first step towards this goal is learning as much as possible about these species and their ecological responses to habitat disturbance and degradation.

The results of this study served to identify 16 geometrid and 13 arctiine species of high indicator value; the majority are indicators for old-growth forests, but there are also one or two indicators for disturbed habitats and for oil palm plantations. Although a test for the validity of these indicators for actual ecological monitoring was not conducted in this study due to time constraints, these species were included in a moth identification guide for La Gamba (see Appendix 3 for an image of the guide). The guide includes all of the species of indicator value that were preserved enough to enable a good photograph, as well as other species that were very common in the area. It includes color photographs of 20 geometrid and 20 arctiine species, and indicates their scientific name, average wingspan and habitat preference. Three hundred exemplars of this moth guide were printed with the financial aid of the Rufford Foundation and distributed in La Gamba and other governmental and non-governmental organizations.

On April 12th of this year, a talk and workshop was offered in La Gamba, where the landowners and members of the community were invited (**Fig. 10**). Approximately fifty people attended the activity, mostly leaders and members of several local organizations, such as the oil palm farmers, the Church, the elementary school, the aqueduct association (ASADA), the police, the La Gamba Tropical Station and park rangers from the Osa Conservation Area (ACOSA); see Appendix 2 for the complete list of participants. The talk included general information about moth biodiversity, land use change, oil palm plantations and the importance of biological conservation and environmental awareness; it also included the objectives, methodology and general results and conservation implications of the study. The power point presentation was filled with photographs of moths that were found in the area, to show the people how much biodiversity exists around them. Each person received a moth species guide to take home, and after the talk, there was a dynamic where they studied the guide in detail to identify the species they had seen before and the ones they liked the best.

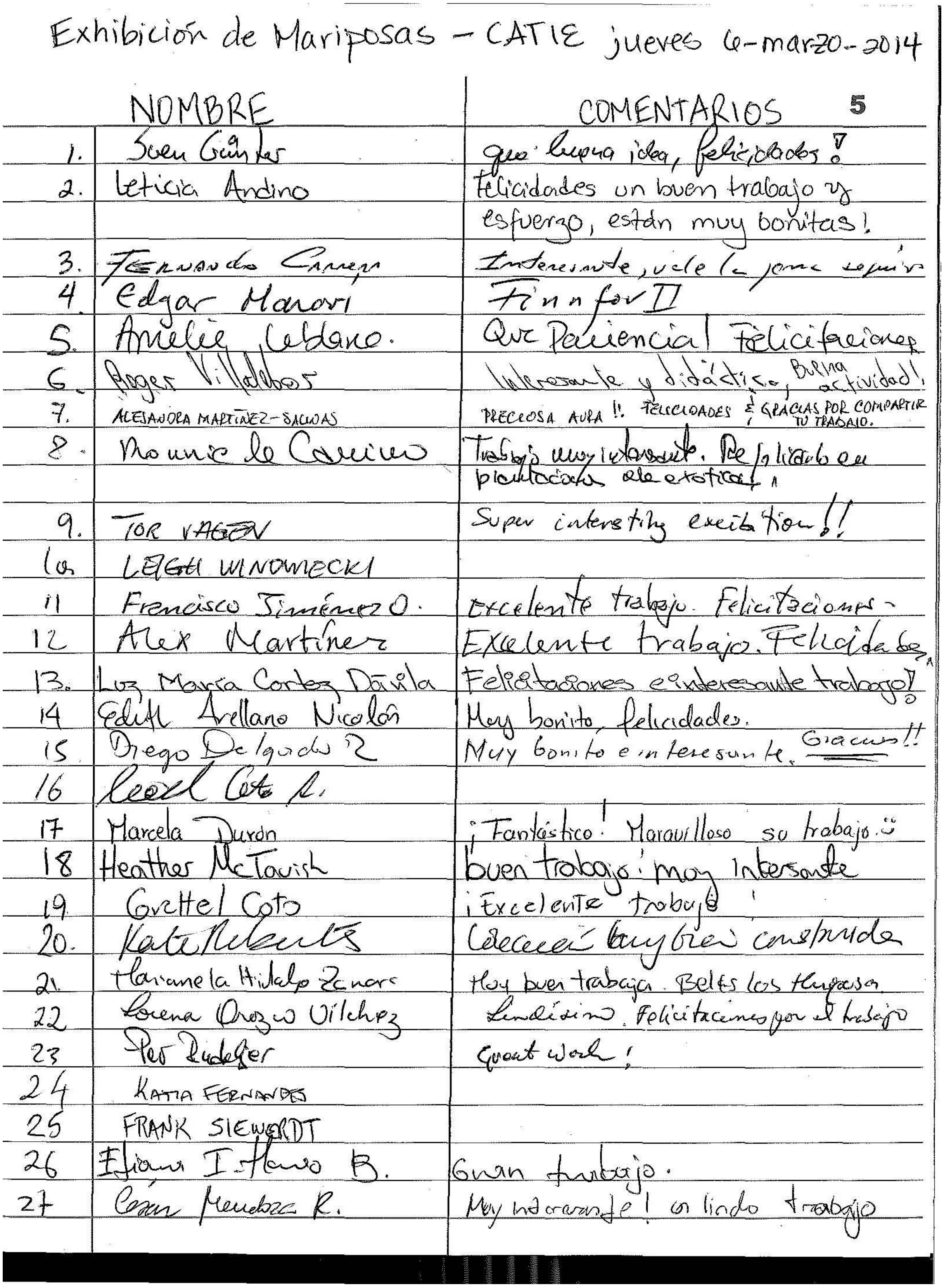
Figure 10. Public outreach activity in La Gamba Tropical Station with the participation of community members and oil palm plantation owners.

The response of the community to the activity was very positive and encouraging. They were surprised that moths were of the same order as butterflies, with the only difference of their nocturnal habits. They were eager to learn about their life cycle, reproduction and ecological functions and services, such as pollination. Most of them were unaware that moths came from larvae they have encountered frequently in the field and in their backyards. School teachers wanted to learn more so they could teach their students in the elementary school, and oil palm farmers wanted to learn which species inhabited the oil palm plantations. Farmers were also interested in learning more on the activities they could adopt to reduce their negative impacts on biodiversity and contribute to sustainable development of the community. They all acknowledged the importance of these types of studies and were very impressed and appreciative of the information given. The main comment amongst the participants was the usefulness of spreading the outcomes of studies conducted by foreigners in La Gamba Tropical Station, since most students and researchers have not shared their results with the community.

One of the most lucrative activities in La Gamba is oil palm farming, and many members of the community are changing their crops to oil palm due to its high demand, financial rewards and easy care. The community is also benefited by ecological tourism, mainly of Austrians and Germans who come to stay at the research station or the Esquinas Rainforest Lodge. Even though the community is still surrounded by relatively undisturbed tropical rainforest and Costa Rican law prohibits deforestation of these forests, flat agricultural lands keep being converted to high intensity oil palm monocultures that represent hostile barriers across the landscape, which reduces habitat connectivity. Thus, studies such as this one are essential to maintain tourism activity by reducing the severe consequences to biodiversity that have been documented in Southeast Asian oil palm plantations.

Although it might be impossible to prevent oil palm expansion in La Gamba and the Golfo Dulce Region, this public outreach activity served create environmental awareness amongst farmers and community members. Hopefully, they will now take into consideration their impact on biodiversity when making land use decisions and will have a higher appreciation of moth fauna in general. According to their participation and comments on the activity, the community is definitely interested in contributing to conservation and sustainable development. Activities such as this one should keep being offered in this community, to enhance their knowledge and capabilities on conservation actions and promote sustainable development.

APPENDIX 1. Attendance to moth exhibitions at CATIE and at the Jorge de Bravo School in Turrialba, in the order of the date of the activity



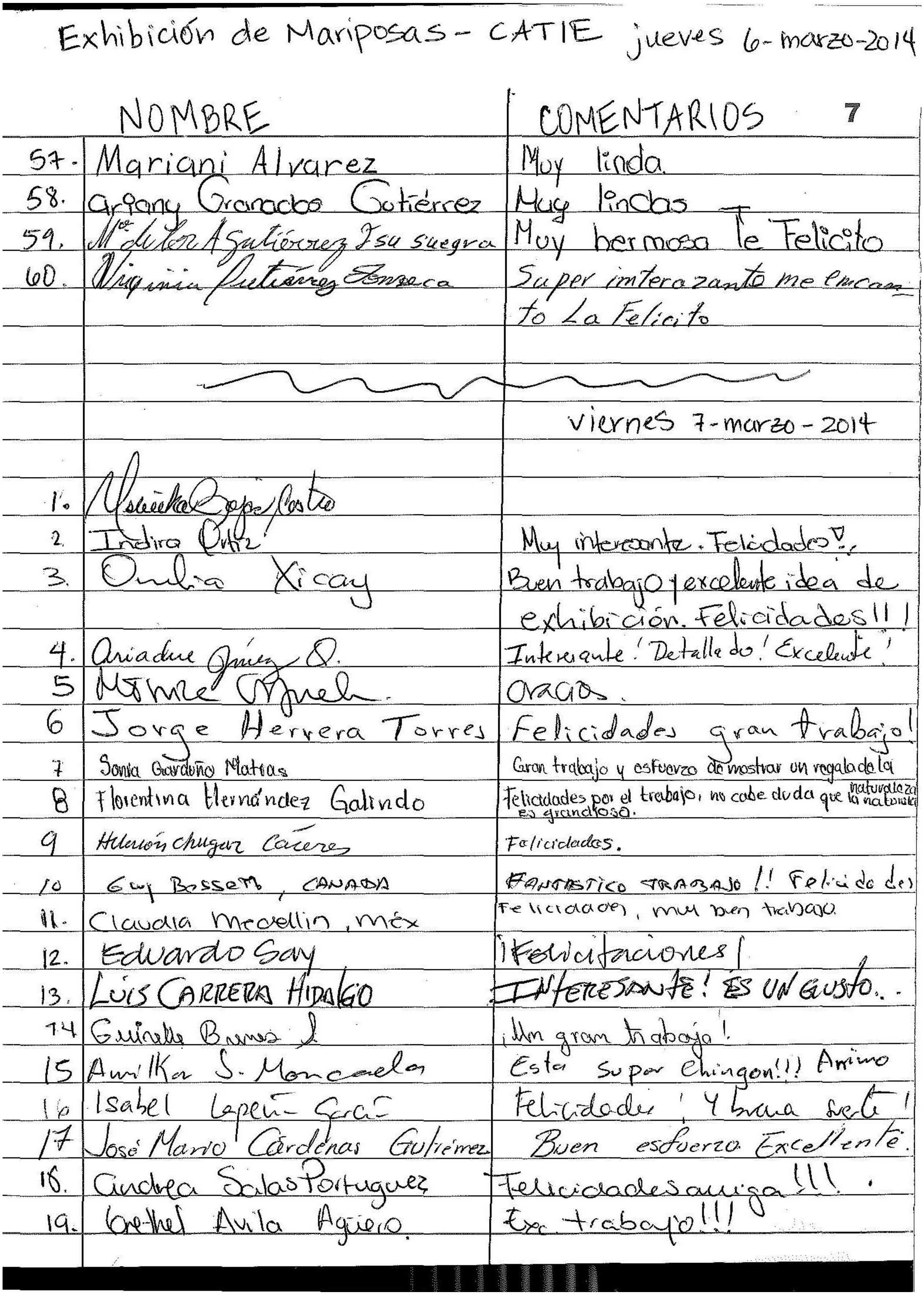
Exhibición de Mariposas – CATIE jueves 6-marzo-2014

5

	NOMBRE	COMENTARIOS
1.	Sven Günter	que buena idea, felicidades!
2.	Leticia Andino	Felicidades un buen trabajo y esfuerzo, están muy bonitas!
3.	Fernando Carrera	Interesante, vale la pena seguir
4.	Edgar Marovi	Finn for II
5.	Amelie Celdano.	Que Paciencia! Felicitaciones
6.	Roger Villalobos	Interesante y didáctico, Buena actividad!
7.	ALEJANDRA MARTÍNEZ-SALINAS	PRECIOSA AURA!! FELICIDADES Y GRACIAS POR COMPARTIR TU TRABAJO.
8.	Monique le Carrion	Trabajo muy interesante. Refleja el trabajo en plantación de estética!
9.	TOR VAGEN	Super interesting exibition!!
10.	LEIGH WINOWECKI	
11	Francisco Jiménez O.	Excelente trabajo. Felicitaciones.
12	Alex Martínez	Excelente trabajo. Felicidades.
13.	Luz María Cortez Dávila	Felicitaciones e interesante trabajo!
14	Edith Arellano Nicolás	Muy bonito, felicidades.
15	Diego Delgado R	Muy bonito e interesante. Gracias!!
16	[illegible] Coto A.	
17	Marcela Durón	¡Fantástico! Maravilloso su trabajo :)
18	Heather McTavish	buen trabajo! muy Interesante
19.	Grettel Coto	¡Excelente trabajo!
20.	Kate Roberts	Colección muy bien construida
21.	Marianela Hidalgo Zamora	Muy buen trabajo. Bellas las mariposas.
22	Lorena Orozco Vilchez	Lindísimo. Felicitaciones por el trabajo
23	Per Rudiger	Great work!
24	KATIA FERNANDES	
25	FRANK SIEWERDT	
26	[illegible] B.	Gran trabajo.
27	César Mendoza R.	Muy interesante! un lindo trabajo

Exhibición de Mariposas - CATIE jueves 6-marzo-2014

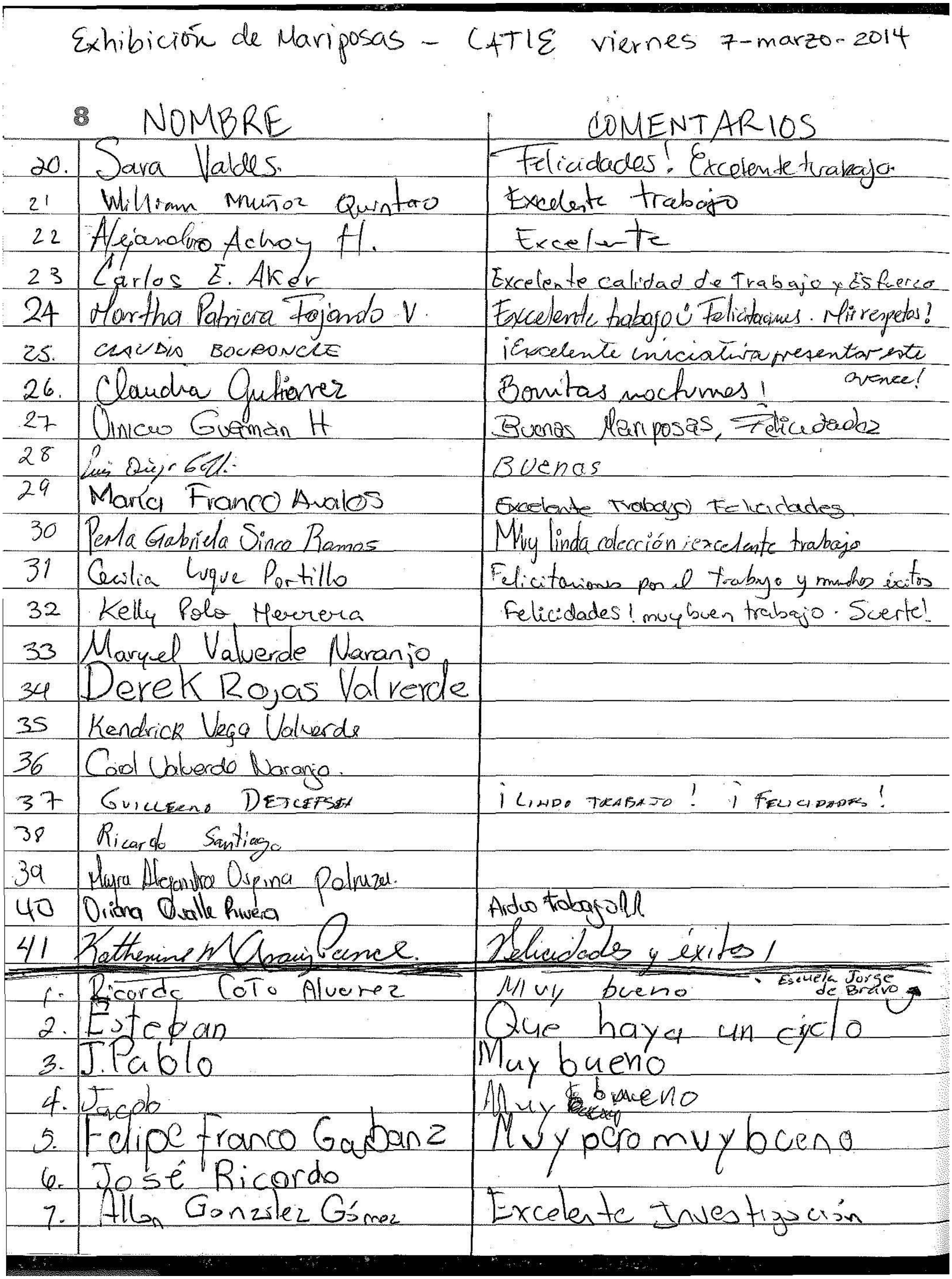
6	NOMBRE	COMENTARIOS
28.	Marilyn Marrow Villalobos	Muy interesante y excelente trabajo!
29.	Tabaré Capitán	
30	Sergio Vilchez	[illegible]
31	Marco Ortega Gutierrez	Seguir con este tipo de eventos
32	Julio H. Eguigurens E.	Interesante!
33	Julia Faro	Me encantó el trabajo y el cuido
34	Luis Calderón	Muy interesante y un gran trabajo
35	Virgiles Johnier	Muy interesante y mucho trabajo
36	Rebecca Rivera	Lindo muy Lindo! Buen trabajo!
37	Adolfo Artavia	Se nota el esfuerzo y dedicación!
38	DENIS SONWA	Congratulation to making the Collection
39	Irina Narváez.	Gran Trabajo y dedicación
40	Sandra Escobar	Excelente trabajo, felicitaciones!
41	Maria Cristina Coelho	Muito interessante
42	Vanessa [illegible]	
43.	Erra [illegible]	
44.	Arlen & Lana Etling	Beautiful
45	Mariela Ory	Interesante Proyecto! Felicidades
46.	Lilliana Correa Alfaro.	Muy interesante.
47.	Maria Fernanda Robles Correa	Muy lindo y buen trabajo
48.	Gabriela Robles Correa	Me encantaron.
49.	Jose Tomas piedra carranza	Muy interensantes
50.	Gladdys mariapiedra carranza	Me gusto mucho
51.	Josue David Mollinedo	estuvo muy bonito
52.	Gabriel Robles	estu interesante felicitaciones!
53.	ASTRID GÓMEZ	FELICIDADES, muy interesante. Bendiciones.
54	Magaly Gutiérrez Fonseca	Muy interezante y bella
55	Silvia Gutiérrez Fonseca	Presioso te Felicito.
56.	Sebastián Gonzalez	Muy bonita.



Exhibición de Mariposas - CATIE jueves 6-marzo-2014

7

	NOMBRE	COMENTARIOS
57.	Mariani Alvarez	Muy linda.
58.	Ariany Granados Gutiérrez	Muy lindas
59.	Mª [illegible] A Gutiérrez y su suegra	Muy hermosa Te Felicito
60.	Virginia Gutiérrez Fonseca	Super interazanto me encanto La Felicito
		viernes 7-marzo-2014
1.	[illegible] Castro	
2.	Indira Ortiz	Muy interesante. Felicidades♡.
3.	Onelia Xicay	Buen trabajo y excelente idea de exhibición. Felicidades!!!
4.	Ariadne Jiménez Q.	Interesante! Detallado! Excelente!
5	[illegible]	Gracias.
6	Jorge Herrera Torres	Felicidades gran trabajo!
7	Sonia Gardoño Matias	Gran trabajo y esfuerzo de mostrar un regalo de la naturaleza
8	Florentina Hernández Galindo	Felicidades por el trabajo, no cabe duda que la naturaleza es grandiosa.
9	Hilarión Chuguer Cáceres	Felicidades.
10	Guy Bossem, CANADA	FANTASTICO TRABAJO !! Felicidades
11.	Claudia Medellin, méx	Felicidades, muy bien trabajo.
12.	Eduardo Say	¡Felicitaciones!
13.	LUIS CARRERA HIDALGO	INTERESANTE! ES UN GUSTO..
14	Guiselle Barrios S.	¡Un gran trabajo!
15	Anilka S. Moncada	Esta super chingon!!! Animo
16	Isabel López García	Felicidades! Y buena suerte!
17	José Mario Cárdenas Gutiérrez	Buen esfuerzo Excellente.
18.	Andrea Salas Portuguez	Felicidades amiga!!!
19.	Grethel Avila Agüero.	Exc. trabajo!!!



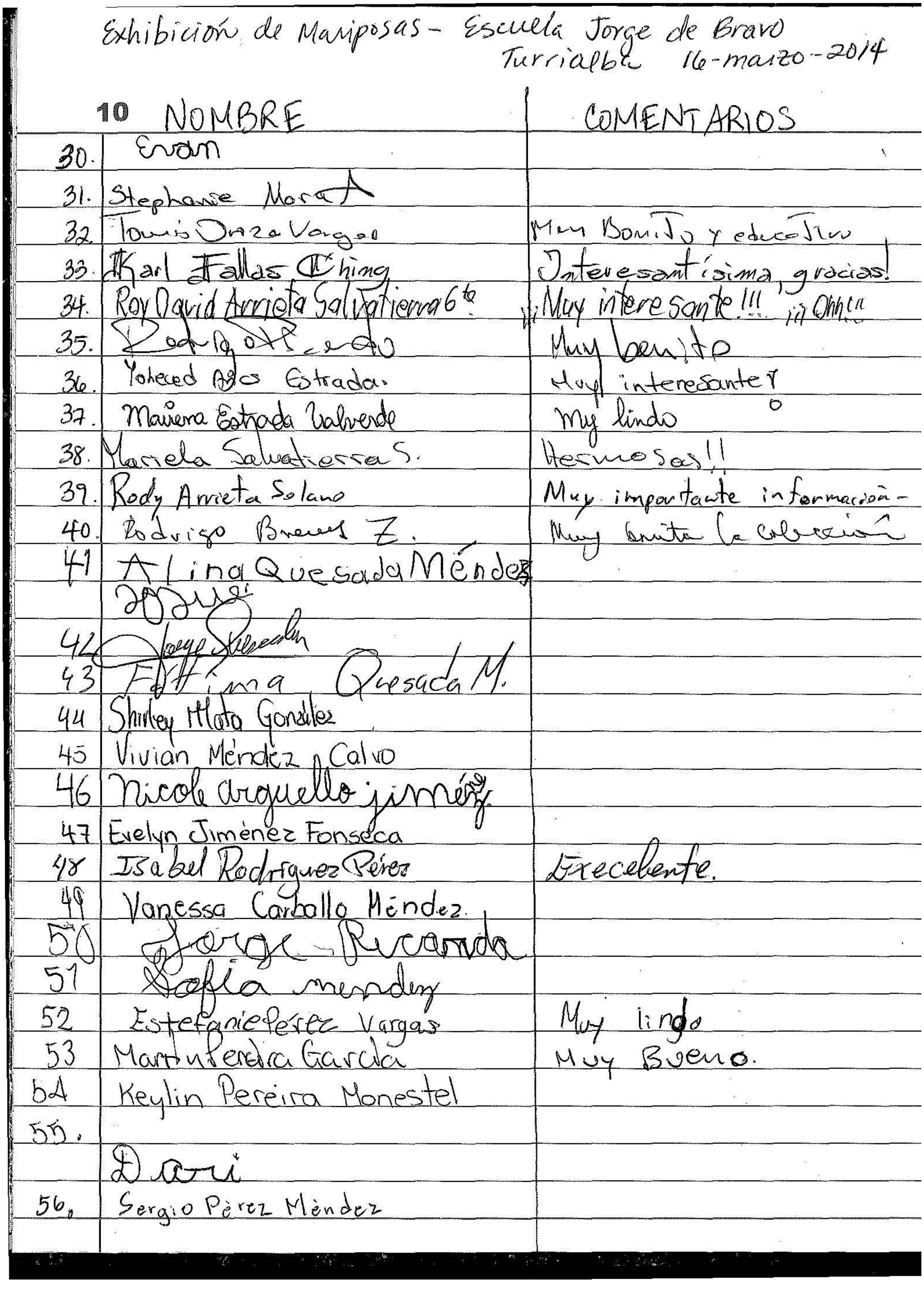
Exhibición de Mariposas - CATIE viernes 7-marzo-2014

8	NOMBRE	COMENTARIOS
20.	Sara Valdes.	Felicidades! Excelente trabajo.
21	William Muñoz Quintero	Excelente trabajo
22	Alejandro Achoy H.	Excelente
23	Carlos E. Aker	Excelente calidad de Trabajo y Esfuerzo
24	Martha Patricia Fajardo V.	Excelente trabajo ¡Felicitaciones. Mis respetos!
25.	CLAUDIO BOURONCLE	¡Excelente iniciativa presentar este avance!
26.	Claudia Gutiérrez	Bonitas nocturnas!
27	Vinicio Guzmán H	Buenas Mariposas, Felicidades
28	Luis [illegible]	Buenas
29	María Franco Avalos	Excelente trabajo Felicidades.
30	Perla Gabriela Sinco Ramos	Muy linda colección ¡excelente trabajo
31	Cecilia Luque Portillo	Felicitaciones por el trabajo y muchos éxitos
32	Kelly Polo Herrera	Felicidades! muy buen trabajo · Suerte!
33	Maryel Valverde Naranjo	
34	Derek Rojas Valverde	
35	Kendrick Vega Valverde	
36	Carol Valverde Naranjo.	
37	GUILLERMO DETLEFSEN	¡LINDO TRABAJO! ¡FELICIDADES!
38	Ricardo Santiago	
39	Mayra Alejandra Ospina Palruza.	
40	Oriana Ovalle Rivera	Arduo trabajo!!!
41	Katherine M. Araujo Ponce.	Felicidades y éxitos!
1.	Ricardo Coto Alvarez	Muy bueno · Escuela Jorge de Bravo
2.	Esteban	Que haya un ciclo
3.	J. Pablo	Muy bueno
4.	Jacob	Muy bueno
5.	Felipe Franco Garbanz	Muy pero muy bueno
6.	José Ricardo	
7.	Allan Gonzalez Gómez	Excelente Investigación

Exhibición de Mariposas - Escuela Jorge de Bravo
Turrialba 16-marzo-2014

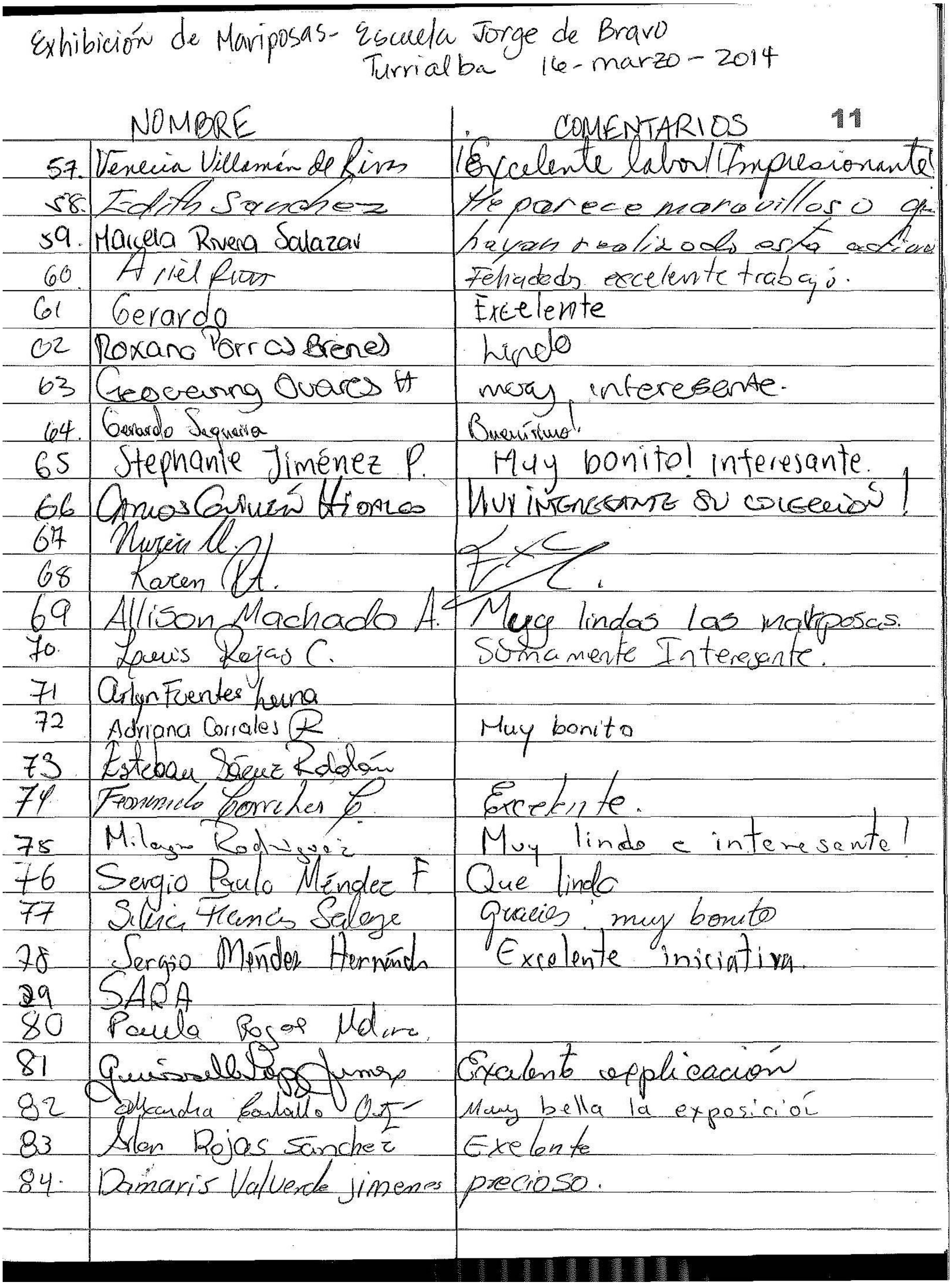
9

	NOMBRE	COMENTARIOS
8.	Oscar Rodriguez Vindas	Muy interesante y una forma de interesar a los niños en la naturaleza local
9.	Mayra Solano Loaiza	Excelente proyecto, felicidades, muy bonito.
10.	Maria Paola	~~Muy~~ Muy lindo
11.	Natalia Leiva Bustamante.	Muy bonito e interesante.
12.	Kattia Martínez Leiva	Bonitos.
13.	Sandra Segura y Saulo Loaiza	Muy bonitas!!
14.	José B. Carballo Espinoza	Excelente trabajo
15	Meredith Porras	Muy buena variedad
16	Lorena Chacón Rosales	muy linda los felicitos.
17	Vivian Acuña Rosales	Muy interesante.
18	Jennifer Vargas Acuña	Muy lindas
19.	José Rodolfo Bogarín Nájera	Muy interesante e importante para la conservación. ¡Suerte!
20.	Cinthya Aguilar Aguilar	Exc!
21.	Raúl Aguilar Aguilar	
22.	Ariana Reid Aguilar	muy lindo
23.	Camila Cruz A.	
24.	[illegible] Solano Nova..	
25.	Evan	
26.		muy interesante la felicito por tan bello exposision
27	Ingrid Marín N.	
28.	Ian Stewart	
29.	Evan Campos.	



Exhibición de Mariposas - Escuela Jorge de Bravo
Turrialba 16-marzo-2014

10	NOMBRE	COMENTARIOS
30.	Evan	
31.	Stephanie Mora	
32.	Tomás Oraza Vargas	Muy Bonito y educativo
33.	Karl Fallas Ching	Interesantísima, gracias!
34.	Roy David Arrieta Salvatierra 6to	¡¡Muy interesante!!! ¡¡¡Ohh!!
35.	[illegible]	Muy bonito
36.	Yohaced Arias Estrada.	Muy interesante y
37.	Mariena Estrada Valverde	Muy lindo
38.	Marcela Salvatierra S.	Hermosas!!
39.	Rody Arrieta Solano	Muy importante información-
40.	Rodrigo Brenes Z.	Muy bonita la colección
41	Alina Quesada Méndez	
	Josué	
42	Jorge Quesada	
43	Fátima Quesada M.	
44	Shirley Mata González	
45	Vivian Méndez Calvo	
46	Nicole arguello jiménez	
47	Evelyn Jiménez Fonseca	
48	Isabel Rodríguez Pérez	Excelente.
49	Vanessa Carballo Méndez.	
50	Jorge Ricardo	
51	Sofía méndez	
52	Estefanie Pérez Vargas	Muy lindo
53	Martin Pereira García	Muy Bueno.
54	Keylin Pereira Monestel	
55.		
	Dari	
56.	Sergio Pèrez Mèndez	



Exhibición de Mariposas- Escuela Jorge de Bravo
Turrialba 16-marzo-2014

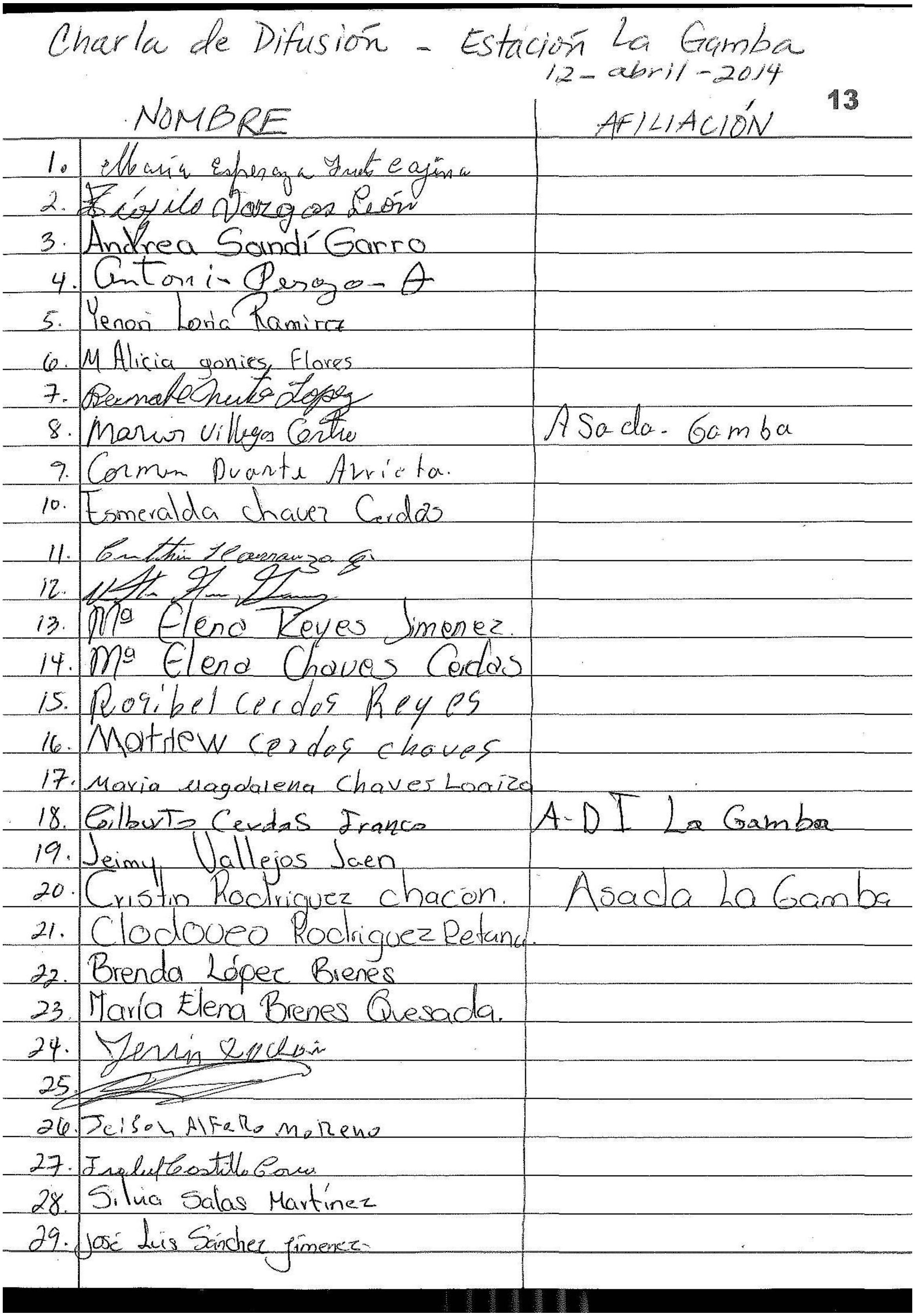
11

	NOMBRE	COMENTARIOS
57.	Venecia Villamán de Rivas	¡Excelente labor! ¡Impresionante!
58.	Edith Sanchez	Me parece maravilloso q
59.	Marcela Rivera Salazar	hayan realizado esta acti
60.	Ariel Rivas	Felicidades excelente trabajo.
61	Gerardo	Excelente
62	Roxana Porras Brenes	Lindo
63	Geovanny Ovares H	muy interesante.
64.	Gerardo Sequeira	Buenísimo!
65	Stephanie Jiménez P.	Muy bonito! interesante.
66	Carlos Carrión Herrera	MUY INTERESANTE SU COLECCIÓN!
67	Nuria U.	
68	Karen U.	
69	Allison Machado A.	Muy lindas las mariposas.
70.	Laura Rojas C.	Sumamente Interesante.
71	Arlyn Fuentes Luna	
72	Adriana Corrales R	Muy bonito
73	Esteban Sáenz Roldán	
74	Fernando Sánchez G.	Excelente.
75	Milagro Rodríguez	Muy lindo e interesante!
76	Sergio Paulo Méndez F	Que lindo
77	Silvia Flores Salazar	Gracias! muy bonito
78	Sergio Méndez Hernández	Excelente iniciativa.
79	SARA	
80	Paula Rojas Molina.	
81	Guiselle Rojas Jimenez	Excelente aplicación
82	Alejandra Carballo Ortiz	Muy bella la exposición
83	Alan Rojas Sanchez	Exelente
84.	Damaris Valverde jimenez	precioso.

Exhibición de Mariposas - Escuela Jorge de Bravo
Turrialba 16-marzo-2014

12	NOMBRE	COMENTARIOS
85.	Ale Calde Figueroa	
86.	Begoña Agrela Jardón	Bello !!
87.	Sofia	¡Lindo!
88.	Matias	¡Lindo¡
89.	Ariana	¡Lindo¡
90	Javier Rojas Saiz Zar	
91	Elizabet	¡Lindo
		¡Lindo
92	Gabriela	¡Muy bonitas!
93	Emmy	Interesante!!
94	Horacia Rodríguez	ADMIRABLE LA DEDICACIÓN MUCHAS
95	Yeimi Jiménez	Muy interesante
96	Ronald Calderón	Excelente
97	Harel Méndez Calvo	Lindo !!!
98	Alexander Núñez Rojas	Increíble
99	Varren Coto Vega	Exc. Iniciativa!

APPENDIX 2. Attendance to the talk and workshop in La Gamba on April 12th, 2014



Charla de Difusión - Estación La Gamba
12 - abril - 2014

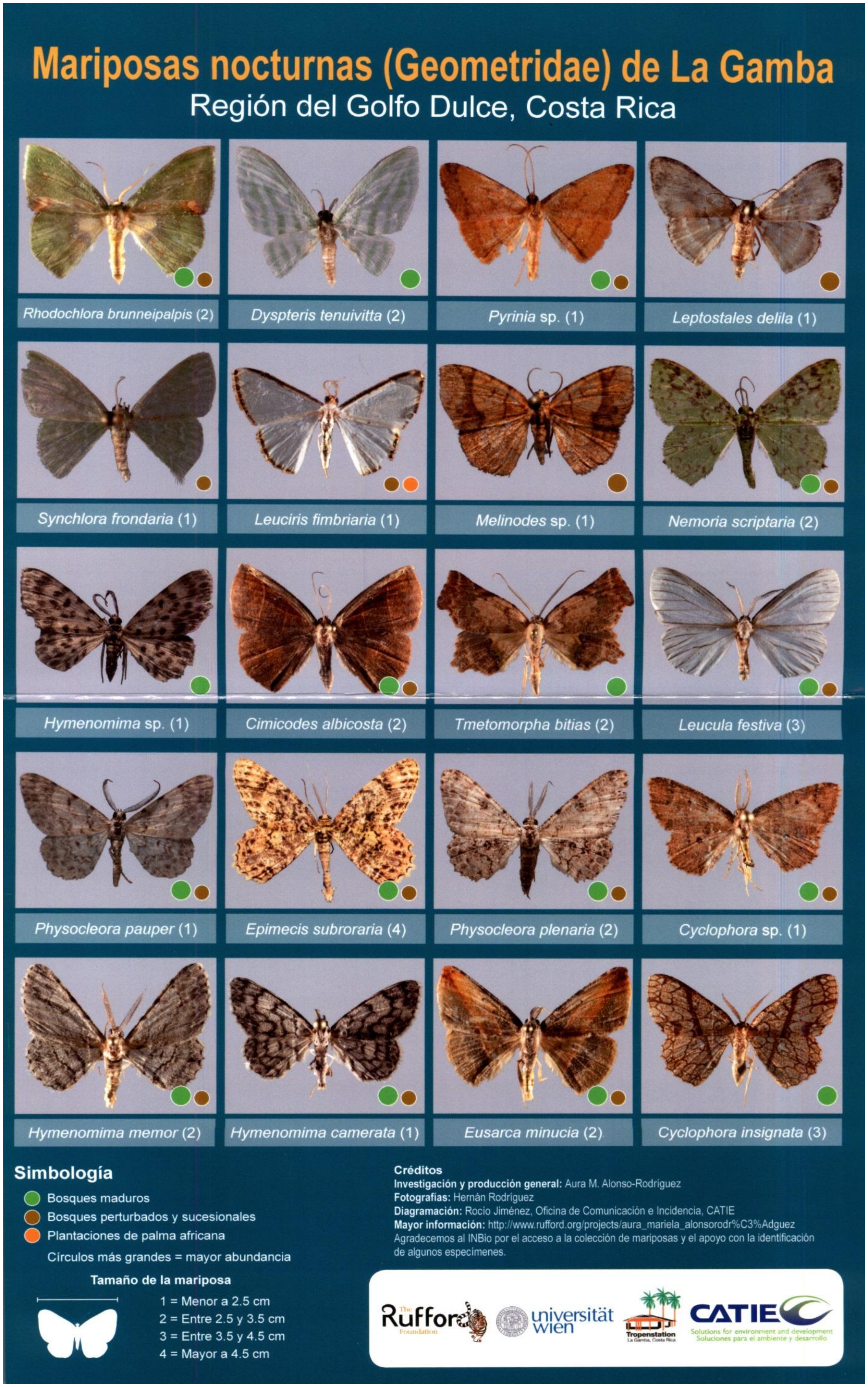
13

	NOMBRE	AFILIACIÓN
1.	María Esperanza [illegible] Cajina	
2.	Teófilo Vargas León	
3.	Andrea Sandí Garro	
4.	Antoni- Perozo- A	
5.	Yenori Loria Ramirez	
6.	M Alicia gomes, Flores	
7.	[illegible] López	
8.	Marvin Villegas Castro	ASada. Gamba
9.	Carmen Duarte Arrieta.	
10.	Esmeralda chaver Cerdas	
11.	Cinthia Carranza G.	
12.		
13.	Mª Elena Reyes Jimenez.	
14.	Mª Elena Chaves Cerdas	
15.	Rosibel Cerdas Reyes	
16.	Mathew cerdas chaves	
17.	Maria Magdalena Chaves Loaiza	
18.	Gilberto Cerdas Franco	A-D I La Gamba
19.	Jeimy Vallejos Jaen	
20.	Cristin Rodriguez chacon.	Asada La Gamba
21.	Clodoveo Rodriguez Retana.	
22.	Brenda López Brenes	
23.	María Elena Brenes Quesada.	
24.	[illegible]	
25.		
26.	Jeison Alfaro moreno	
27.	Isabel Castillo Corea	
28.	Silvia Salas Martínez	
29.	José Luis Sánchez Jimenez	

Charla de Difusión - Estación La Gamba : 12-abril-2014

14	NOMBRE	AFILIACIÓN
30	Leticia Moya Castillo.	
31.	Maria Luisa Sanchez P.	Estación tropical
32.	Olivier Chacón Elizondo	
33.	Orlando Bravo Padilla	ACOSA - La Gamba
34.	Brayan Jimenez Carmona	Fuerza Publica La Gamba
35.	Henar Bogantes Rojas	Fuerza Publica/a Gamba
36.	Alondra Chacon Sanchez	La Gamba.
37.	Maritza Sanchez Porras	La Gamba
38.	Octavio toro pinedo.	la gamba
39.	[illegible]	la gamba
40.	[illegible]	LA GAMBA
41.	Jose peña S.	La gamba
42.	Vannesa Chacon S.	La gamba
43.	Roybin Sánchez Jiménez	Rio bonito
44.	Byron Miranda Chacon	La gamba.
45.	[illegible] M.	
46.	Rodolfo Fernández Durán	Km 37
47.	Daniel Jenking Aguilera	La Gamba
48.	Thomas Witzenader	Austria/Linz
49.	Eduardo Gerardo Arauz Suárez	Costa Rica

APPENDIX 3. Identification guide for geometrid and arctiine moths of La Gamba



Mariposas nocturnas (Geometridae) de La Gamba

Región del Golfo Dulce, Costa Rica

Rhodochlora brunneipalpis (2) 🟢🟤
Dyspteris tenuivitta (2) 🟢
Pyrinia sp. (1) 🟢🟤
Leptostales delila (1) 🟤
Synchlora frondaria (1) 🟤
Leuciris fimbriaria (1) 🟤🟠
Melinodes sp. (1) 🟤
Nemoria scriptaria (2) 🟢🟤
Hymenomima sp. (1) 🟢
Cimicodes albicosta (2) 🟢🟤
Tmetomorpha bitias (2) 🟢
Leucula festiva (3) 🟢🟤
Physocleora pauper (1) 🟢🟤
Epimecis subroraria (4) 🟢🟤
Physocleora plenaria (2) 🟢🟤
Cyclophora sp. (1) 🟢🟤
Hymenomima memor (2) 🟢🟤
Hymenomima camerata (1) 🟢🟤
Eusarca minucia (2) 🟢🟤
Cyclophora insignata (3) 🟢

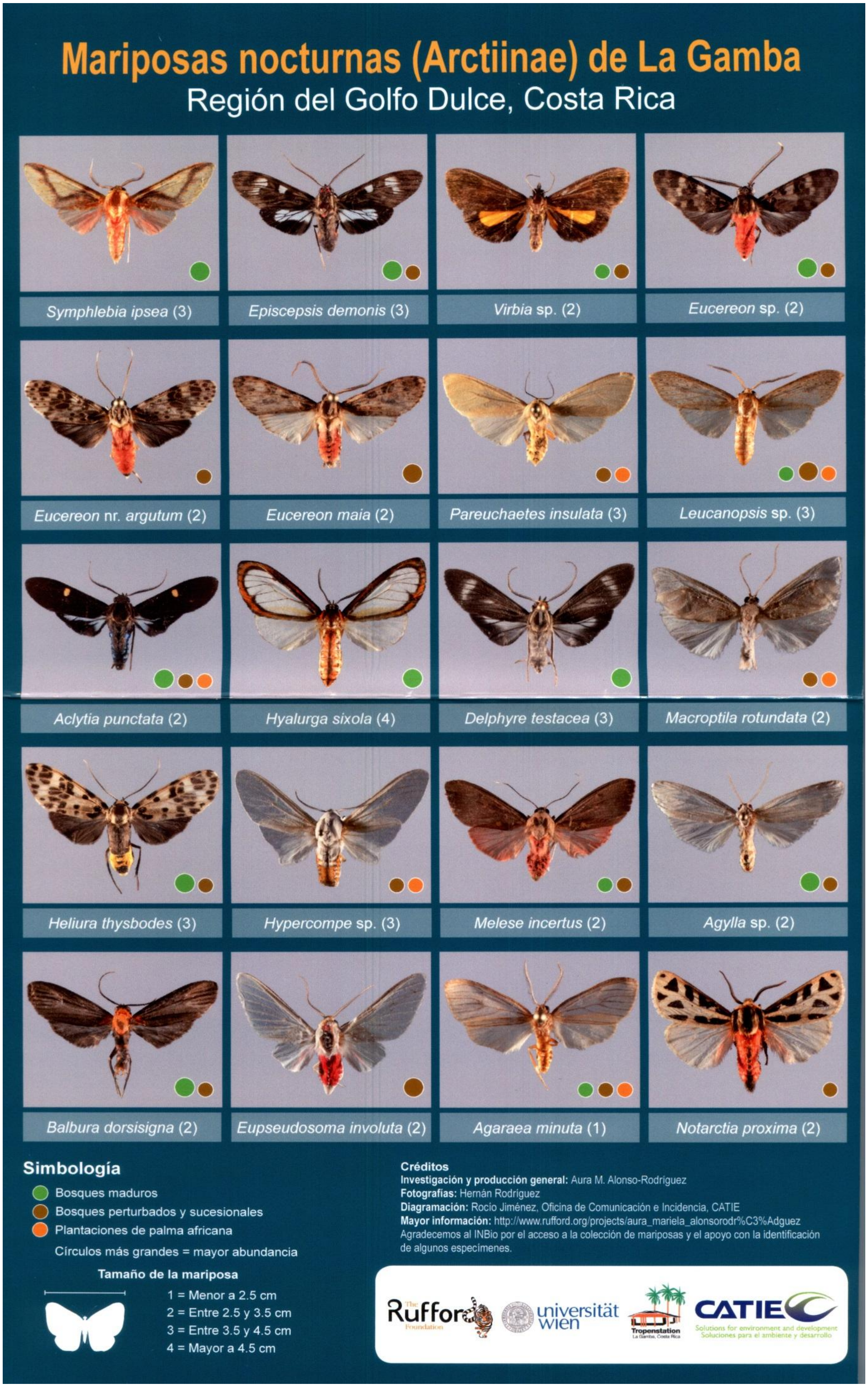
Simbología

🟢 Bosques maduros
🟤 Bosques perturbados y sucesionales
🟠 Plantaciones de palma africana
Círculos más grandes = mayor abundancia

Tamaño de la mariposa

1 = Menor a 2.5 cm
2 = Entre 2.5 y 3.5 cm
3 = Entre 3.5 y 4.5 cm
4 = Mayor a 4.5 cm

Créditos
Investigación y producción general: Aura M. Alonso-Rodríguez
Fotografías: Hernán Rodríguez
Diagramación: Rocío Jiménez, Oficina de Comunicación e Incidencia, CATIE
Mayor información: http://www.rufford.org/projects/aura_mariela_alonsorodr%C3%Adguez
Agradecemos al INBio por el acceso a la colección de mariposas y el apoyo con la identificación de algunos especímenes.



Mariposas nocturnas (Arctiinae) de La Gamba

Región del Golfo Dulce, Costa Rica

Symphlebia ipsea (3) 🟢

Episcepsis demonis (3) 🟢🟤

Virbia sp. (2) 🟢🟤

Eucereon sp. (2) 🟢🟤

Eucereon nr. *argutum* (2) 🟤

Eucereon maia (2) 🟤

Pareuchaetes insulata (3) 🟤🟠

Leucanopsis sp. (3) 🟢🟤🟠

Aclytia punctata (2) 🟢🟤🟠

Hyalurga sixola (4) 🟢

Delphyre testacea (3) 🟢

Macroptila rotundata (2) 🟤🟠

Heliura thysbodes (3) 🟢🟤

Hypercompe sp. (3) 🟤🟠

Melese incertus (2) 🟢🟤

Agylla sp. (2) 🟢🟤

Balbura dorsisigna (2) 🟢🟤

Eupseudosoma involuta (2) 🟤

Agaraea minuta (1) 🟢🟤🟠

Notarctia proxima (2) 🟤

Simbología

- 🟢 Bosques maduros
- 🟤 Bosques perturbados y sucesionales
- 🟠 Plantaciones de palma africana

Círculos más grandes = mayor abundancia

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Tropenstation La Gamba, Costa Rica
CATIE Solutions for environment and development
Soluciones para el ambiente y desarrollo