



Terrestrial mammal communities in Tropical rainforests of Ecuador

A thesis submitted to the University of Manchester

for the degree of Master in Philosophy

in the Faculty of Life Sciences

2016

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INDEX OF CONTENTS

	Page
Abstract	1
Declaration	2
Copyright Statement	3
Acknowledgements	4
Dedication	5
1. General Introduction	6
1.1. Conservation of the Neotropical natural capital	7
1.2. Study area background	10
1.3. Camera trapping systems	12
1.4. Location and target species	14
1.5. Cited literature	17
2. Study1: <i>“Terrestrial mammal community structure: insights from a survey in a portion of the Sumaco Biosphere Reserve (Ecuador)”</i>	27
2.0. Abstract	28
2.1. Introduction	29
2.2. Methodology	32
2.3. Results	36
2.4. Discussion	46
2.5. Conclusions	50
2.6. Cited Literature	52
3. Study 2: <i>“Human disturbance effects on terrestrial mammal communities. A comparison between Sumaco National Park and Yasuní Biosphere Reserve (Ecuador)”</i>	62
3.0. Abstract	63
3.1. Introduction	64
3.2. Methodology	67
3.3. Results	74
3.4. Discussion	83
3.5. Conclusions	90
3.6. Cited Literature	92

4. General Conclusions	102
4.1. Conclusions and considerations	103
4.2. Cited literature	108
5. Appendices	118
5.1. Appendices study 1	119
5.2. Appendices study 2	123

LIST OF TABLES

	Page
Table 1.1 IUCN status and information provided by the Red List	16
Table 3.1 Comparison between Tiputini and Payamino surveys	75
Table 3.2 Species relative abundances observed at both locations	79

LIST OF FIGURES

Figure 2.1 Map of relative position of the surveyed area (Payamino)	34
Figure 2.2 Rarefaction curves of predicted and observed diversity levels	38
Figure 2.3 Camera trap pictures of terrestrial mammals	39
Figure 2.4 Absolute abundances of captured species on cameras	40
Figure 2.5 Activity patterns of nocturnal species	42
Figure 2.6 Activity patterns of diurnal species	43
Figure 2.7 Activity patterns of cathemeral species	44
Figure 2.8 Species activity patterns related to moon phases	45
Figure 3.1 Maps of surveyed areas with their relative position in Ecuador	68
Figure 3.2 Rarefaction curves for Tiputini and Payamino locations	76
Figure 3.3 NMDS plot based on animal occurrences per camera	77
Figure 3.4 Summary plots with activity patterns of all groups together	80
Figure 3.5 Comparison of activity patterns of functional groups by location	81
Figure 3.6 Activity patterns of hunted species across the day	82

Abstract

This is the first study focused on terrestrial mammal community structure carried out in the San José de Payamino community in the Sumaco National Park (Ecuador). This Amazonian Kichwa community at San José de Payamino has a low population density and they have been extracting resources since they settled in the area almost forty years ago. Over time, hunting and timber extraction techniques and equipment have developed, increasing land transformation and fragmentation from intact mature rainforest towards the production of crops (or *chakras*). In addition, recent oil prospecting activities using explosives have been conducted across the entire community lands, which may have influenced natural communities.

In order to describe the local terrestrial mammal community, a survey was conducted using both a camera trapping system (1777 trapping nights) and line transects between March – June 2015. A portion of the collected data was used to compare Payamino to one of the most biodiverse terrestrial regions in the World, the Yasuní National Park. This region is located just 125km away from the sampled area and although it currently remains an intact area, recent oil extractions supported by the national government potentially caused terrible damage to the native species. A study undertaken by Blake et al. (2012) allowed me to compare both regions in order to: 1) quantify how disturbed the terrestrial mammal community in San José de Payamino might be; and, 2) give an idea of the importance of maintaining Yasuní National Park unaltered in the face of continued pressure for development.

First chapter, although it showed similar biodiversity levels among camera trap records (suggesting a lack of human disturbance), many species presented alterations on their abundances. Results in the second chapter, based on a comparison between Payamino and Tiputini, show species richness and relative abundances differed significantly, with Tiputini sustaining a more diverse and homogenously distributed community than Payamino. These evident differences in community structure (abundances and composition) were most probably driven by the lack of top-predators in Payamino, rather than by a direct effect of the hunting pressure. I also found a clear shift in animal activity patterns in Payamino towards more nocturnal behaviour (most probably to avoid human presence) and lower relative abundances within predator-guild species. These results suggest that we may be seeing the beginning of a *Mesopredator Release Effect* in Payamino.

The author concluded continuous human disturbances (oil explorations, hunting pressure and land conversion) must have an effect in Payamino terrestrial community. Although wild populations suffer from temporal natural fluctuations (in abundance and diversity), the fact that both locations have similar environmental conditions suggests terrestrial mammal communities should be more similar than they are. Therefore, long-term studies are needed to exclude possible alterations produced by seasonal variations in community structure. At the same time, it will assure a more detailed quantification of human disturbance effects.

Key Words: terrestrial mammal, population structure, Neotropical rainforest, camera trap, conservation.

DECLARATION

I, Daniel López Martínez, declare that no portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

The first study, “Terrestrial mammal community structure: insights from a survey in a portion of the Sumaco Biosphere Reserve (Ecuador)”, is the result of my own research in San José de Payamino and I was the lead for all stages of this project from design through to writing. The second study, “Human disturbance effects on terrestrial mammal communities. A comparison between Sumaco National Park and Yasuní Biosphere Reserve (Ecuador)”, contains both data collected by me and data provided by D. Mosquera and J. Blake who graciously allowed me to use a small portion of their raw data collected in Yasuní National Park. I explicitly mentioned which dataset corresponds to each author in the second study (section 3.2.2 Camera positioning). I was the lead for design, analysis and writing for the second study.

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AKNOWLEDGEMENTS

First of all, I would like to thank to Jennifer Rowntree (Lecturer in Ecological Genetics), co-supervisor of the thesis, who, even hardly knowing me, saw my potential and gave me the chance to be a member of the University of Manchester in first place. Without her, nothing of this would have been real.

Secondly, I would like to equally give my most sincere gratitude to both my co-supervisors, Richard Preziosi and J. Rowntree, not only because few months later I was designated as research coordinator at the TimburiCocha Research Station (in Ecuador) allowing me to discover the Neotropical rainforest and its people from the inside and, after a while, proposing me to start a master in philosophy programme which I am presenting its results now; but also because without all their sympathy, solidarity and care, this thesis would have not been possible at all. Once again, thank you very much to both of you.

I would like to thank to J. Blake and D. Mosquera for sharing their valuable data without any hesitation. Show my gratitude to Aalborg Zoo (Denmark) for the financing of half of the camera traps used in this study. And I would also like to extend my gratitude to all San José de Payamino community members to allow me to conduct this study on their lands. Finally, thank to all those gave me support and motivation to conduct this study, family and friends.

To you, Marc

1. GENERAL INTRODUCTION:

1.1. CONSERVATION OF THE NEOTROPICAL NATURAL CAPITAL

The term ***nature conservation*** is defined as the “*preservation, protection and restoration of the natural environment and of wildlife*”(Oxford English Dictionary, 2004). Conservation aims to reduce the decline of biodiversity at its different levels caused by human development. At present, seven billion people inhabit the Earth and there are around 50 billion breeding livestock (including chickens, ducks, pigs, cows, sheep)(Tellería, 2012). Since the discovery of the agriculture and the domestication of livestock in the prehistoric era, humans have engaged in a continuous transformation of the land and this process has grown exponentially throughout the last centuries. During the 19th century, our species started an invasive stage. Human lifespan doubled with environmental and nutritional improvements (Finch, 2010), we began to monopolize resources and ecosystems (Tellería, 2012),resulting in a homogenization around the globe.

In 1968, Hardin wrote the controversial article “Tragedy of the commons” about the problems arising from the expansion of the human population and its selfishness and greed towards natural goods. A few years later, Galeano (1979) wrote another controversial article comparing the old exploitations, lead mainly by the Spaniards and the Portuguese when Europe discovered the Americas. It criticized neo-colonialist politics that the Northern countries were taking towards South American countries and the massive exploitation of their resources: petrol companies (e.g. Repsol-YPF, Shell, BP), palm oil producers (e.g. Nestlé) and soya beans (e.g. Monsanto). In the present day, the main *public* threat (i.e. lead by local governments) to the conservation in the Amazon rainforest is the construction of dams, road openings and gas and oil extractions (e.g. Suárez et al., 2009; Finer & Jenkins, 2012; FAO, 2015). Finer and Jenkins (2012) published a study about the potential effects of the planned construction of 150 dams in the Andean Amazon. They concluded that 60% of the dams will affect the connectivity between Andean and Amazonian rivers, and 80% of them will lead to deforestation due to floods and road works. Finally, but not less important, the mining, oil and gas extractions: “may not reach the geographic scale of logging and mass agriculture, but the effects of these activities in the Amazon can be felt in a range of ways that are just as problematic” (WWF, 2015).

Currently, most South American countries depend on the exportation of natural resources (e.g. Argentina with soya beans (IPS, 2015); Ecuador with petrol (Fontaine, 2003); Bolivia with minerals (Ströbele-Gregor, 2012)) as the main source of income. This is the current situation of Ecuador, whose economy depends on its oil reservoirs, which represent 55% of national exports and 15% of the country's GDP (El Universo Press, 2015). In order to support this, the current national government, run by the socialist Correa, has approved the concession of oil blocks around the Ecuadorian Amazon including in both National Parks where this study is based. This situation is aggravated by the actual price decrease of the oil barrel. Previous similar experiences in Ecuador have already led to substantial localised loss of biodiversity. For example, Wunder (1997) described how macroeconomics is counter-productive for conservation and described the example of what he called the "Ecuadorian Dutch Disease" (1974-1982). During this period, the government invested oil revenue in expanding agriculture (by subsidizing cattle ranching) and infrastructure (by building new roads), which exacerbated the situation after the extractions. A few years earlier in 1964, the government gave a land concession for 28 years to Texaco Oil Company (now Chevron) in the Ecuadorian Amazon, known as the "*Oriente*". The company carved out 350 oil wells and left behind 1,000 open toxic waste pits and billions of highly saline "formation waters" (oil wastes). Those leaked into rivers and lakes, which affected not only biodiversity but also the indigenous communities' health and stability for generations (Amazon Watch, 2015). This case was named as the "Rainforest Chernobyl". Legislation in Ecuador has evolved since then, but, oil spills continue to happen around the globe and there is a potential risk of them occurring in the present study areas if extractions expand (Wunder, 1997; Finer & Jenkins, 2012).

South American rainforests have been suffering a **biodiversity loss** for the last half-century, especially due to the progressive standardization of ecosystems through changes in land cover (Pringle, 1976; Mares, 1986; Achard et al., 2002). According to the last Living Planet Report (WWF, 2014), "population sizes of vertebrate species—mammals, birds, reptiles, amphibians, and fish—have declined by 52 percent over the last 40 years". This same report agrees with other studies (e.g. Brooks et al., 2002; Di Marco et al., 2014) in concluding that the global population decline of mammals and birds is concentrated mainly in the tropics. There are three main causes:

low-income countries do not invest enough in their biodiversity conservation programs (see Adams et al., 2004); there is much less definitive research focused on conservation in the tropics (Pearman, 1995; Van Noorden, 2014) because of the high complexity levels in tropical ecosystems (Mares, 1986; Wilson et al., 2007); and national and international governments designate limited money to conservational science and finally, the scientific community and stakeholders lack the necessary training and equipment to undertake research (Pearman, 1995).

The “Earth Summit”, as the United Nations Conference on Environmental and Development in Rio de Janeiro (1992) was named, was an international convention to prevent the decline of global biodiversity and it resulted in the creation of the Agenda 21: an action plan to be followed by governments in order to both preserve the natural environment and improve social *sustainable development*. Two points of the conference concerning the present study are: 1) the inclusion of local inhabitants in the process of negotiations, since their lives will be the ones affected by the results of the exploitation and, 2) to encourage local governments and communities to work together for the monitoring of the action plans established to ensure a sustainable and long-lasting development (Flores & Los, 2006). The creation of *strategic monitoring plans* is a key factor in order to achieve better land management (Tellería, 2012). Ecology books define this methodology as **Adaptive Management** and it has been applied to different contexts and purposes. Tellería (2012) defined two major problems in establishing adaptive management strategies: 1) the lack of basic information and implementation of descriptive studies in the regions of interest (i.e. where there is no information it is difficult to plan the best strategy and it is impossible to undertake comparisons with other regions); 2) the lack of holistic management of species (i.e. collecting not only abundance data as a sign of conservation status but also studying mortality rates, reproductive success, body condition, migrations, etc.).

Therefore, in light of all of these factors and in order to reduce species’ extinction rates, more effort is needed to plan better strategies that consider local institutions in order to instigate the correct management of natural resources in tropical areas.

1.2. STUDY AREA BACKGROUND

Before the European discovery of America, the Kichwa ethnic group was one of the strongest indigenous communities in the west coast of South America. Although many different ethnic groups coexisted by that time, the **Kichwa culture**, spread also by the Inca Empire, colonized the Andean Range from Chile and Argentina to Colombia and, nowadays is one of the more numerous indigenous ethnic groups of South America (Peoples of the World Fundation, 2014). Previous to the Spanish colonization, Kichwa people diversified and some of the groups migrated to the Amazon looking for more fertile lands (Irvine, 1987). These groups descended the Andes and spread along the main rivers and established on the river-banks, adapting all their habits and traditions to these new conditions. These communities were nomads and had always been gathering and hunting as a method of subsistence. When the Spaniards colonized South America, a great number of indigenous people were killed, raped and forced to work to death (Galeano, 1979; Sanchez-Albornoz, 2012). Europeans also transformed native societies through violence, social disruption and depopulation through disease (Irvine, 1987). At the same time, other social changes started to act, including Christianization by missionaries (16th-18th century) and the introduction of capitalism and the agricultural transformation (19th century)(Irvine, 1987).

Particular to this study, the Kichwa community of San José de Payamino became established nearby the Payamino River in Orellana, an Ecuadorian province at the Upper Ecuadorian Amazon. Amazonian Kichwas colonized this area thousands of years ago (like the Chilean case described by Rothhammer et al., 2009) where other indigenous people (the Cofan and Houaranis) previously lived. This region has always been an area of low human density due to the harsh natural conditions (e.g. low nutrient soil, seasonal floods, dispersed faunal resources, uneven terrain) and the community had to adapt to these conditions by improving their fishing techniques; cultivating manioc, plantains and palm fruits and changing their hunting techniques from "deep forest" to "garden/fallow" species (mod. from Irvine, 1987).

By the 1980's and due to a governmental ordinance, the community had to define boundaries and create a communal centre in order to obtain ownership of their lands. Since then, the community centre became an important meeting spot, not only for the communal people, but

also for the neighbouring communities. A few years later, the first road connecting to a local town was built (previously, they had to travel for two days down river by canoe and back). Since then, the influence of the external Ecuadorian society is evident and the community has changed considerably. For example, the community was suddenly incorporated to the national park system with the creation of the Sumaco Napo Galeras National Park (Sumaco National Park from now on) in 1994.

The community, which lies in the buffer zone of the park, owns 15.000ha of mostly primary but also altered forest and has a current population of almost 500 inhabitants (2014 census, including children and woman). Pristine conditions and high biodiversity levels in the region are the main causes of the increase of preservation efforts in this portion of the Andean Range and its foothills. Despite this, in recent times, the national government has started to thoroughly explore the Amazon looking for oil and gas reservoirs. All of the *Oriente* is divided into oil blocks and a portion of the Sumaco Biosphere Reserve is included on the oil Block number 20, for which the Canadian company 'Ivanhoe' holds the exploitation permits. In 2010, the company started exploratory and seismic oil studies in the Pungarayacu camp. Heavy oil extractions like this one produce many residues (e.g. contaminated water or sulphur and nitrogen oxides) affecting water and land resources and causing acid rains and (Amazon Watch, 2012). Payamino River itself lies on Block 7 and many different exploratory studies have been carried out by the national oil company PetroAmazonas and other subcontracted companies. In the San José de Payamino community there have been many oil explorations already, the latest one carried out in 2015 just before this study began. In this same period, a few miles downriver in San Luis de Armenia community, an oil spill occurred. In order to carry out seismic explorations, long distance paths were cut to reach inaccessible areas and consecutive ground perforations with dynamite were used to determine the existence of oil reservoirs. However, Payamino presents oil of too poor quality for the extractions to continue at present.

Although the Payamino community has always hunted, gardened and extracted timber in low quantities and purely as a method of subsistence (Irvine, 1987; Pers. Obs.. 2015), there is an effect of the local community on wildlife populations. The number of motorized boats has tripled in the last year and the use of dynamite for fishing has affected the riparian fauna. In addition,

the number of gardens (or *chakras*) has increased in size and number due to the introduction of chainsaws into the community. All these effects, added to an increasing human population in the community, are a threat to the natural capital in this biodiversity hotspot defined by Myers et al., (2000) as the "Tropical Andes" in the Western Amazon.

1.3. CAMERA TRAPPING SYSTEMS

Camera trapping as an activity started when Prof. G. Fritsch, a German explorer, reported South African wildlife with his camera during the 19th century. During the following century, cameras became more advanced and the purposes of wildlife photography changed into more professional uses. In 1927, Frank M. Chapman undertook the first "census of the living" on Panama wildlife in a purely scientific context. During twelve years, he became established in the then-recently discovered research island of Barro Colorado and successfully photographed birds, peccaries, ocelots, tapirs, coatis, etc (Vuilleumier, 2005). Then throughout the 20th Century, technology advances made cameras more accessible and useful for different purposes and situations. Finally with the digital era, data storage of pictures, shooter sensitivity and image quality have all improved substantially (for more detailed information in (O'Connell et al., 2011) allowing researchers and stakeholders to obtain valuable data with little effort and training.

Camera trapping is an observational method that allows the surveying of small to large sized animals within a population or a geographical area. Camera traps provide data on presence (and absence) of species, although modern camera systems also record the time and date of the capture, temperature and humidity in the field and moon phase, among other useful parameters. For that reason, camera trapping systems have become a great tool for ecologists not only for the study of species' activity patterns, habitat use and reproductive information throughout space and time (Silveira et al., 2003; Silver et al., 2004; Ripple & Beschta, 2008; Cueva et al., 2010; Majumder et al., 2011), but also to create animal inventories (Lee et al., 2004; Azlan & Sharma, 2006; Rowcliffe et al., 2008; De la Torre et al., 2012) and to estimate population densities (Noss et al., 2003; Medri & Mourao, 2005; Rueda et al., 2013a). When surveying animals with elusive and secretive behaviour, and also those only present at low densities,

camera surveys have great advantages over other traditional methodologies: they are a passive and direct technique with high efficiency and success collecting information about individuals without disturbing them (Trolle & Kéry, 2005; Maffei & Noss, 2008; Di Bitetti et al., 2010). In comparison with other field sampling methods, camera traps are well suited to standardization, as human sampling error is reduced to placement and maintenance of the traps and identification of the photographs (Silveira et al., 2003; Lucherini et al., 2009; Ahumada et al., 2011). Combining camera trapping with capture-recapture techniques has become the most efficient methodology for population density surveys (e.g. Noss et al., 2003; Jackson et al., 2006; Gupta et al., 2009). Currently, the most commonly used software for abundance estimations through pictures is CAPTURE (Otis et al., 1978)(O'Connell et al., 2011). The software estimates population size based on the number of identified individuals and the proportion of recaptures. The mathematical *Mark-Release-Recapture* (MRR) models used consider variation explained by the capture probability of the species, variation among individuals (e.g. sex, age, ranging patterns, dominance, activity, health conditions), variation over time, behavioral responses to having been captured, and combinations of these factors(see more detailed information in (O'Connell et al., 2011)). Another important factor when studying populations is the *population density*, understood as abundance of individuals per unit area. Thus, the total area of the survey is a crucial parameter for obtaining a good approximation of real density values. Over the years, different approaches have been developed for this purpose based on individual animal daily ranges, for example the mean maximum distance moved (MMDM) and half of the mean maximum distance moved (HMMDM), for medium to large and small animals respectively (Wilson & Anderson, 1985). Another methodology for estimating animal densities is the hierarchical models presented by Royle & Young (2008). These consider variables such as temporary migrations and daily movement patterns and utilize Bayesian analysis methods (e.g. Gardner et al., 2009).

While there are many advantages of using camera traps, a few issues remain that can limit their usefulness. Firstly, camera traps are particularly sensitive to high humidity as this can damage electronic circuits, and may cause the loss of information before it can be downloaded from the camera memory. Secondly, species inventories based on camera trap data are biased towards

animals whose behaviour facilitates picture capture. For example, the fast movement of a target species across the *active field* of the camera will result in blurry pictures, arboreal species are rarely reported, reduced-size or cold-blooded animals hardly ever trigger the camera. In addition to these limitations, camera trap data must be carefully analyzed to avoid misinterpretations. Identification of individuals must be carefully conducted especially for species with high similarity among individuals, thus these methods are not valid for species like the Amazonian tapirs that have few individually identifiable markings (R. Wallace pers. comment. (2014)). When estimating animal densities and populations, not all species follow the same patterns (even within the same species there is individual variation as mentioned above) and underestimating (or overestimating) population numbers can have serious consequences in conservation.

Despite these disadvantages, three factors were crucial in deciding on the use of a camera trapping system in the present study: 1) the local conditions make it difficult to explore and to move about the rainforest, 2) the elusive behaviour of the target species (i.e. many of them were thought to be crepuscular or nocturnal) and, 3) the author's lack of experience and training in detecting mammals directly (or from their tracks on the leaf litter).

1.4. LOCATION AND TARGET SPECIES

Timburi Cocha Research Station (TCRS) was established through the efforts of both the University of Manchester and the University of Glasgow. Nowadays, it is run by the Universidad Estatal Amazónica (Ecuador) in conjunction with the University of Manchester and welcomes students and researchers from all over the World. The station's location is unique thanks to the proximity of both the Andean Range and the Amazon Basin. The low-density human population, plus the lack of valuable minerals (i.e. gold and oil) are the key reasons for the good preservation of the biota (Irvine, 1987; Pers. Obs., 2015). In addition, the region has been almost inaccessible to people outside of the community until recently, when the national government built a road. Thanks to the isolation and low human impact (i.e. sustainable use of resources) San José de Payamino is a good place to undertake research. The present study is one of the first full descriptive studies focusing on mammals using a non-invasive methodology in the area.

Compared to other countries in South America, Ecuador has a lack of both published scientific and research studies and registration of patents (see Van Noorden, 2014). This dearth of information is more evident in intact and more inaccessible areas, and there is an urgency to redress this imbalance (Suárez et al., 2009; Cueva et al., 2010). Some regions of Ecuador, such as the Yasuní National Park, have been better studied, mainly thanks to creation of the Tiputini Research Station (run by the Universidad San Francisco de Quito of Ecuador) in 1994. As an example of this patchy information, in a recent check on the Felidae family represented in the IUCN Red List (IUCN, 2015), the conservation status of this group is fairly well known in Ecuador (see TABLE 1). However, there is an evident lack of information related to its distribution and abundance in Ecuador.

The present study aims to describe, through the use of a camera trapping system, the conservation status of medium to large-sized terrestrial forest mammal communities around the San José de Payamino community centre in the buffer zone of the Sumaco National Park. Terrestrial mammals play important roles in tropical rainforests. Seed dispersal is a common role due to the huge amount of fruit they consume and the resilience of these seeds when passing through the mammalian gut. Forest maintenance is another role caused by consumption of certain species (allowing others to be more competitive), soil disturbance and excavation of burrows enhancing seed germination, regulation of the undergrowth plant and tree diversity and animal path maintenance. Food web regulation may also be driven by the consumption of lower trophic levels (such as insectivores, herbivores, predators)(Rainforest Conservation Fund, 2016). For these reasons, studies providing information about the conservation status of medium to large mammals are essential in areas with an evident lack of data and for setting a baseline for further analysis in the years to come.

Chapter one provides information on the composition and behaviour of the mammal community in this area. In Chapter two, the data collected from the TCRS is compared with similar data collected at one of the most well-preserved and highest-biodiverse regions in Ecuador; the area around the Tiputini Research Station in the Yasuní National Park. Although population density around the TCRS is low, it represents an area where human activities and oil prospecting might have influenced wildlife communities. In contrast, Tiputini is currently a pristine area within the

Yasuní National Park, albeit an area where the government will start oil prospections in the upcoming months. Therefore, this comparative study could provide important information on how such activities may influence the non-flying mammal community structure.

Species Name	IUCN Status	Native ¹	Home Range ²	Population abundance ³	Conservation Efforts ^{4*}
<i>Leopardus wiedii</i> - Margay	NT	V	X	X	X
<i>Leopardus tigrinus</i> - Oncilla	VU	V	X	X	X
<i>Leopardus pardalis</i> - Ocelot	LC	V	X	X	X
<i>Panthera onca</i> - Jaguar	NT	V	X	X	X
<i>Puma yagouaroundi</i> - Jaguorandi	LC	V	X	X	X
<i>Puma concolor</i> - Puma	LC	V	X	X	X

Table 1.1 IUCN status and information provided by the Red List. “V” means positive and “X” means negative. (1) indicates if species are native from Ecuador and (2,3,4) are referred to the existence of studies elaborated in Ecuador which are documented by the IUCN. (*) is referred to the conservation actions the Ecuadorian government has on these species (as all the species are included in the CITES appendices). The National Constitution of Ecuador comprises the “Pachamama” (the “Nature” as a whole) as an entity, which has to be respectful and the duty to protect it (Visited on 7/22/2015).

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2. STUDY 1:

**TERRESTRIAL MAMMAL COMMUNITY STRUCTURE: INSIGHTS FROM A SURVEY
IN A PORTION OF THE SUMACO NATIONAL PARK (ECUADOR)**

2.0. ABSTRACT

This is the first study on non-flying mammal community structure carried out in the Sumaco Napo Galeras National Park (Ecuador); more precisely, in the buffer area around the Sumaco Biosphere Reserve and in the *Kichwa* indigenous community of San José de Payamino. “Sustainable” extractive activities during the last 30 years and recent oil prospecting in the area may have influenced natural mammal communities. This survey was conducted in a portion of the lowland rainforest using both a camera trapping system, with a total sampling effort of 1777 camera trapping nights, and line transects during the rainy season (March – June of 2015). Rarefaction curves started to level off after 30 cameras were deployed with a biodiversity richness of 25 species (including 19 mammals, 5 birds and one lizard). The absence of *P. onca*(jaguar) may have opened new ecological niches to other carnivores such as *P. concolor*(puma) and other mesocarnivores (whose relative abundances had seen increased) altering herbivores population structure. Compared to pristine regions, many species presented alterations in their activity patterns and the relative abundances indices showed higher abundances for *D. novemcinctus*, *M. americana*, *D. fuliginosa* and *T. terrestris*. Considering all these species are under hunting pressure in the community and they all are documented jaguar prey species, human disturbance may have altered species composition most probably due to a direct effect on carnivore populations rather than by the hunting pressure of herbivores. ADONIS test corroborated the absence of hunting pressure in Payamino showing no relation between the species composition observed among cameras in relation to the distance from the community centre ($F_1= 1.2414$, $R^2=0.044$ $p=0.165$). The author presumes that the lack of top-predators will lead to a *mesopredator release effect* in the future causing both a niche overlapping in carnivores’ intraguild and niche segregation among herbivores. Long-term studies are necessary to better understand the undergoing processes associated to human disturbance and wild population fluctuations in Payamino.

KEY WORDS: terrestrial mammal, camera trapping, population structure, activity patterns, Sumaco, mesopredator release effect

2.1. INTRODUCTION

Since the time of Darwin and the first biological world expeditions, biologists have been interested in how biodiversity concentrates at the tropics and decreases towards the poles (Hillebrand, 2004). Indeed, tropical forests comprise 50-75% of the planet's species of plants and animals, but represent a mere 6% of the world's surface (Rainforest Conservation Foundation, 2015). Different explanatory models for this gradient have been suggested: the old age of the tropical biome has enabled more species to evolve (Rainforest Conservation Foundation, 2015); the stability and benign environmental conditions of the tropics decreases generation times and increases mutational rates (Cardillo, 1999); the vast area occupied by the tropics as well as high productivity and energy levels ensures species survival by reducing the intra guild competition by space and/or resources (mod. from Currie *et al.*, (1999); Losos & Schluter, (2000)) or, the high number of ecological interactions has increased species' efforts to adapt, resulting in the creation of a complex mosaic of species (Pianka, 1966).

More recent paleogeographic studies (e.g. Joly (2008); Hoorn *et al.*, (2010); Rull, (2011)) agree that the Neocene geographic reorganizations (23-2.58Mya) were the most important events that enabled the creation of one of the most species-biodiversity ecosystems in the world: the Amazon rainforest. Firstly, the Andean uplift (20Mya) influenced both rainfall and drainage patterns, completely changing the climate and weather conditions and creating the origin of what we now know as the Amazon Forest (Rull, 2011). Later on, the creation of the Isthmus of Panama (3-2Mya) provided the first contact between South America and another landmass since its separation from Africa (130Mya). The land bridge produced what is known as the Greater American Interchange of species, when many North American terrestrial species successfully became established in the south (much more so than in the opposite direction). As described in Eisenberg & Redford (1999), there was a reduction in the number of competitors of the northern carnivores (Order Carnivora) as they moved south, and they easily diversified and colonized the rainforests. A good example is the diversification of the Felidae family, nowadays still present, in South America. The Felidae family has 37 species around the globe and ten of these are only in South America (Brien & Johnson, 2007). Other carnivores like Canidae, Procyonidae and Mustelidae families also diversified (generally also increasing their body size) and colonized the whole continent (Eisenberg & Redford, 1999).

Since the late Pleistocene glaciations, which wiped out 75% of the *megafauna* in tropical South America, large terrestrial carnivores have generally declined (Webb & Rancy, 1996). According to Sandom *et al.* (2014), species decline in South America was higher compared to other climate-similar regions, such as sub-Saharan Africa, because its fauna has only coexisted with modern humans rather than old hominids. In addition, during the last half century, tropical rainforests around the world have been suffering a human caused biodiversity loss, mainly due to changes in land cover (Pringle, 1976; Achard *et al.*, 2002; WWF, 2014) and habitat fragmentation (Skole & Tucker, 1993). This has led to a decline of wild populations of large carnivores (Laliberte & Ripple, 2004; Ripple & Beschta, 2008; Prugh *et al.*, 2009). Previous studies have demonstrated how the absence of large top-predators can result in increase in the species richness and abundance of lower trophic level species, not only of herbivores but also carnivores, due to the opening of new niches in the community (Walters, 1997; V. R. Moreno *et al.*, 2006; Vance-Chalcraft *et al.*, 2007; Ritchie & Johnson, 2009; Di Bitetti *et al.*, 2010). This concept was first defined by Soulé *et al.* (1988) as the “Mesopredator Release Effect”.

According to the work of Albuja (2011), a total of 19 species of carnivorous predators comprised within the Procyonidae, Canidae, Mustellidae and Felidae families are present in the Ecuadorian rainforest, which represents a mere 1.6% of the Amazon Basin surface. All families are predators but the largest obligate carnivores are the jaguar (*Panthera onca*) and the puma (*Puma concolor*). Both species are considered as top-predators exerting influence on intraguild species and also lower trophic levels. However, studies with sympatric *P. onca* and *P. concolor* species observed a differentiation on prey species selection between these two species (Harmsen *et al.*, 2011). The rest of the felids and the other families are considered as mesocarnivores (medium sized predators \approx 15kg) with more diverse diets, more versatile activity patterns and *less* sensitivity to human disturbances (Roemer *et al.*, 2009; Prugh *et al.*, 2009; Monterroso *et al.*, 2014). Studying terrestrial mammal species' composition and abundance will provide new information for the Payamino area and it will be useful to compare to other Neotropical regions.

The most common methods used to estimate population sizes for mammals are line transects, identifications of tracks and faeces and direct observations (Karanth & Nichols, 1998; Tobler *et al.*, 2008; Abreu *et al.*, 2008). Camera trapping systems are already recognized as one of the best sampling

methodologies for medium to large sized animals (Srbek-Araujo & Chiarello, 2005), having many advantages over more traditional methodologies. They are a non-invasive technique, which can provide multiple forms of information such as activity patterns, habitat use and reproductive information throughout space and time (Silveira et al., 2003; Silver et al., 2004; Cueva et al., 2010). Camera traps are also useful to create animal inventories (Lee et al., 2004; Trolle & Kéry, 2005; Azlan & Sharma, 2006; Rowcliffe et al., 2008; De la Torre et al., 2012) and to estimate population densities (Noss et al., 2003; Silver et al., 2004; Medri & Mourao, 2005; Jackson et al., 2006; Rueda et al., 2013a).

The aim of this study was to determine the structure and composition of the medium and large mammals and other associated species in the territory of the community of San José de Payamino, an area that covers a portion of the buffer zone of the Sumaco National Park (Ecuador). In order to achieve this, the author conducted a camera trap survey between March-June 2015 and also noted any other signs of the species present (observing tracks, diggings, faeces and burrows). Although, the chosen method biases the results to species that are able to be captured by camera traps and identified from tracks, they do provide a baseline study of animal diversity in the area. Descriptive studies such as this one are necessary to reduce the notable dearth of information for this area and thus, promote the conservation of the Ecuadorian Amazon. A preliminary survey in the same area conducted by O'Reilly-Berkeley (2013) analysed the human impact on the mammal community. With almost 600 camera-trapping nights, that study showed that, based on mammal occurrences, both primary and secondary forests were in a good condition. Our study doubles the sampling effort of this previous survey (measured as number of camera trap days) and was undertaken following recent prospecting work by oil companies that may have influenced natural species' presence and activity.

2.2. METHODOLOGY

2.2.1 STUDY AREA

This study was conducted at *Timburi Cocha Research Station* (0°28'S, 77°17'W; 298m.a.s.l.) within the *Kichwa* community of San José de Payamino, located in the buffer zone of the Sumaco Napo Galeras National Park (Orellana, Ecuador). The national park was established in 1994 and declared by UNESCO as a Biosphere Reserve in 2000 in order to protect the region from mining and timber exploitation. Recently, the devaluation of the oil prices has pushed the Ecuadorian government to initiate a high number of oil prospections around the country, including the area of this study.

The surveyed area (27km²) is located mainly in primary rainforest but also in selectively logged rainforest next to the small *Kichwa* community of San José de Payamino (hereafter Payamino). Human density is very low (300pers./15.000ha) and mainly concentrated in the community centre. Due to its proximity to the Andean Range, the region is a heterogeneous forest with hilly terrain and rugged geography. The vegetation community in the area is defined by Sierra et al. (1999) as “Evergreen Forest of Amazonian Lowland” or *tierra firme*, with a daily mean temperature value of 23.1 °C degrees, relative humidity of 99.9%, a heat stress of 25.2 °C, a dew point of 23.1°C (Pers. Obs. 2015) and precipitation between 4000-6000mm (Irvine, 1987; MAE, 2013).

2.2.2 DATA COLLECTION

A total of 23 digital scouting cameras (Bushnell Trophy Cam HD, USA) were used during the rainy season, between March and June of 2015. These cameras are triggered by activation of a Passive Infra-Red (PIR) motion sensor (Bushnell, 2009). All cameras were deployed at 0.3-1 m from the ground, with a mean distance of 500m apart (SD=+/- 140m). Cameras were placed along old and new trails around the community and were positioned where animal paths and tracks were found. Junctions of animal paths were preferential sites due to the higher probability of observations.

Cameras were set to trigger 24 hours per day between 15th March and 13th June of 2015 resulting in a total sampling effort of 1413 camera trap days. A second study undertaken in the previous months

(August 2014 - March 2015) for different purposes, but also using a camera trap system, was added to the dataset of the present study. This survey added 364 camera trap days giving a total of 1777 trapping nights for the full study presented here.

Due to extreme climate conditions in the rainforest during the rainy season, camera settings were adjusted for optimal recording as follows: High sensibility trigger (high temperature environments); night vision at medium intensity and LED sensor medium/high depending on the distance to the path. In order to ensure samples were independent, each animal record was defined by a minimum of a 30 minute time-gap between animal events on the same camera (Vanderhoff et al., 2011; Blake et al., 2012). Cameras were checked every 10-20 days to obtain camera information, verify status and replace batteries and SD cards when necessary. A few cameras (n=7) were relocated during the study because low levels of animal activity were detected (less than 4 occurrences within 14 days)(Srbek-Araujo & Chiarello, 2005; Downey et al., 2007), thus increasing the total area surveyed by 5km² approximately. Location and altitude of the cameras were mapped with a GPS unit (Garmin Etrex 20, USA) and a number of abiotic factors (humidity, stress heat index, daily temperature and dew point) were recorded with a portable weather station (KESTREL Unit D2, USA). For each picture taken, camera id, temperature, time, date and moon phase were noted and animals were identified down to species level when possible. Identification was assisted by members of the local community. All camera records will be uploaded to the Global Biodiversity Information Facility (GBIF).

During the deployment and checking of cameras, many animal tracks were sighted along transects and trails and their GPS location noted. Animal records observed on these transects (97 events) were included in the biodiversity indices (e.g. Shannon, Berger-Parker and Chao1). However, due to consistent differences on camera trap and transect methodologies when collecting data, transect observations were removed from any further analyses (e.g. abundances, activity patterns; see also chapter 2). Along transects, tracks of species that were difficult to identify down to species level (e.g. peccary and deer species) were counted as a part of the *Peccary* and *Mazama complex* respectively (i.e. "Peccary complex" includes *Pecari tajacu* and *Tayassu pecari*; and "Mazama complex" comprises *M. Americana* and *M. gouazoubira*). In order to ensure the independence of the samples, multiple

tracks of the same species were only included when a minimum of 10 days had passed between observations and they were greater than 300m apart from each other.

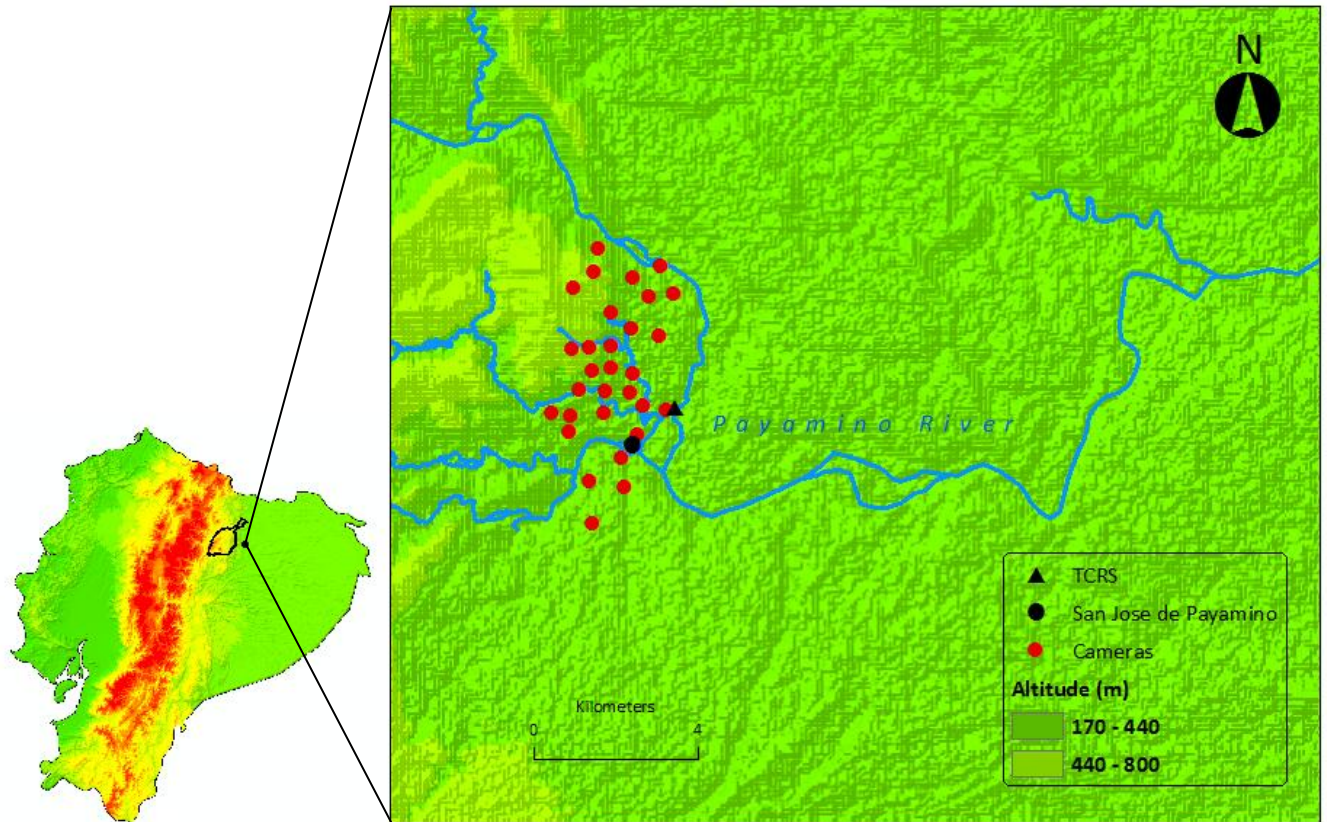


Figure 2.1 –Relative position of the surveyed area in continental Ecuador next to the Sumaco Biosphere Reserve (black polygon). Detailed map represents GPS positions for Timburi Cocha Research Station (▲), San José de Payamino community’s centre (●) and camera traps (●).

2.2.3 COMMUNITY ASSESSMENT

2.2.3.1. Community structure

α -diversity indices (Shannon, Berger-Parker and Chao1) were calculated using the combined camera and transect data with *Estimates* software using 10,000 permutations (Colwell, 2013). Following Robert MacArthur (1965), the Shannon index allow us to compare communities by their diversity of “processes” rather than population diversity; it is a function of the population proportions of the several species (Pielou 1966) and increases as both the richness and the evenness of the community increase. On the other hand, the Berger-Parker Index is useful to compare locations (surveyed with the same sampling effort) by the abundance of most common species (as seen in Ahumada et al., 2011); high values of this index correspond to lower species richness. For example, when there is a super dominant species at the surveyed area, less niches are left to other species and therefore the total number of species is reduced. Chao *et al.* (2004) described *Chao1* richness estimator as a simple calculation of diversity considering species abundances and, especially, rare species (i.e. singletons and doubletons).

Sampling effort was evaluated with rarefaction curves (species accumulation/sampling effort). Relative abundance index (RAI) was calculated per individual species as a proportion of animal occurrences per 100 camera trapping nights (following Azlan & Sharma, 2006; Vanderhoff et al., 2011; Blake et al., 2012).

The majority of local people live in the community centre and human pressure is more evident around the centre than in areas further away (Pers. Obs.). Principal human activities in the area are extraction of timber for cooking and house construction, land cover transformation (e.g. creation of new gardens or *chakras*, building roads and houses), loud human noise (e.g. use of generators, music, cars and motorized boats) and hunting. In order to estimate if there was an impact of human activity on the animal population, geographic distances between each camera and the community centre were calculated.

Species observation data were then analysed with an ADONIS permutation test to see if there was a relationship between diversity of observed species on cameras and distance to centre. Prior to

analysis, data were transformed using the Wisconsin square root transformation, the dissimilarity matrix was constructed using the Jaccard distance equation and a total of 10,000 permutations were undertaken to obtain more robust results (Oksanen et al., 2015). ADONIS tests were calculated with *vegan* package (Oksanen et al., 2015) in R (R Core Team, 2014).

2.2.3.2. Activity patterns

Species' activity patterns were determined by the number of observations per hour throughout the day. As there were limited data on many of the species, only those with at least 11 independent samples were considered for this and further analyses (Monroy-vilchis et al., 2011). Individual species patterns were plotted as relative abundances (i.e. number of observations per hour/total number of observations) using *ggplot2* (Wickham & Chang, 2015).

In order to determine if there was an effect of moon-light on species' activity patterns (*sensu* Harmsen et al., 2011), strict-nocturnal species were plotted by the moon phase on the day of the observations (selected species: *Cuniculus paca*, *Dasyus novemcinctus* and *Tapirus terrestris*).

2.3. RESULTS

2.3.1. COMMUNITY STRUCTURE

The cameras produced a total of 603 animal occurrences (3015 files including pictures and videos). Transect observations produced a total of 93 additional occurrences (for a full list of species observed see Appendix 1.1), representing 13.5% of the total (696 obs.). These were generally biased to larger species, as their tracks were easier to observe. One species (*Priodontes maximus*) was observed in transect surveys but was not captured on the cameras and two species complexes (Mazama and Peccary complex) were added to the list due to difficulties in identifying tracks from the separate species. Sixty-two camera trap events were excluded from this study (8.1% of the total) as the identification of those animals was not clear. A total of 25 species were identified: 19 species of mammals, five birds and one lizard and the most abundant families captured by the cameras were the

Dasypodidae, Dasyproctidae and Cervidae. A total of 43 human occurrences were also recorded on cameras but were not included in any analysis.

Camera traps provided an efficient method of sampling the surveyed area as the number of total species observed began to level off in the rarefaction curves (Fig. 2.2). Looking in more detail at the rarefaction curves, the data set obtained with ten cameras already represents 68% (n=17sp) of the total number of species observed. Doubling the sampling effort to 20 cameras added five new species (88% of the total). Finally the *Observed* curve stabilized when sampling effort reached 32 cameras. The last ten cameras of the figure (cameras 32-42) corresponded to the survey conducted on the previous months before this study was elaborated (see methodology details) and these did not add any new species to the list. The *Chao1* estimator is a mathematical model, which computes the potential number of species capable of being observed in the surveyed area based on the relationship between sampling effort and diversity levels. This estimator predicted almost the same diversity levels as the *observed* data, suggesting that a reasonable sampling effort was carried out. Other species diversity indices for the whole community were as follows: Shannon $H=2.64$ and, Berger-Parker $d=0.15$ (see full table of predicted diversity indices in Appendix 1.2).

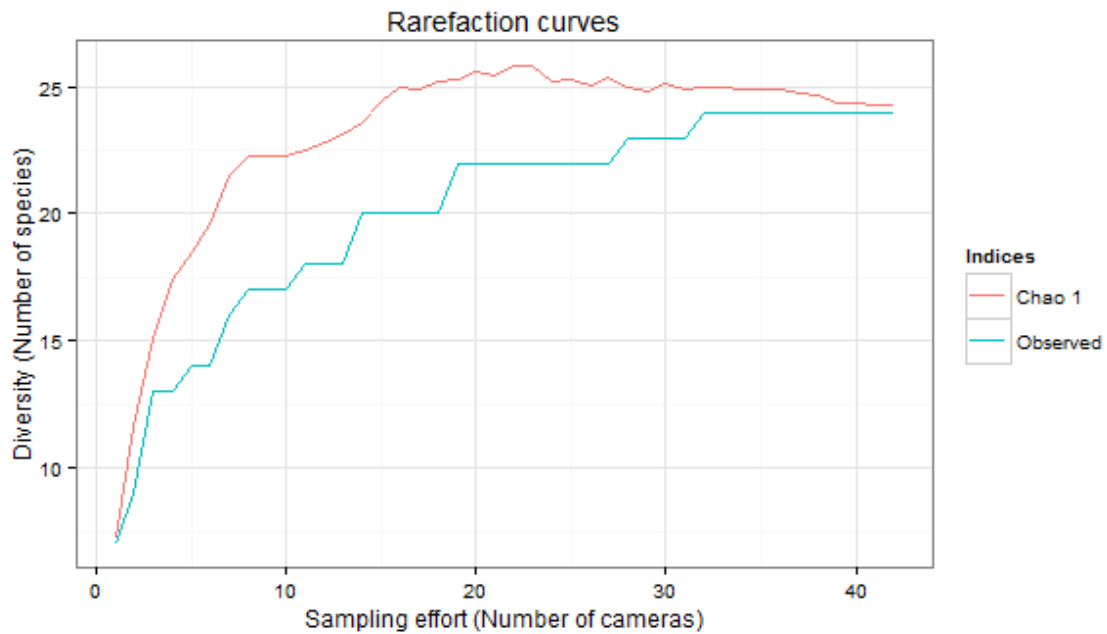


Figure 2.2 - Rarefaction curves of predicted and observed diversity levels. Diversity levels increased with sampling effort (measured in number of camera traps) and increased until both curves reached a maximum and stabilized.

Study1: Terrestrial Mammal Community Structure: Insights from a Survey in a portion of the Sumaco National Park (Ecuador)



Figure 2.3 – Camera trap pictures of terrestrial mammals. **A.** *Mazama americana* **B.** *Tajacu pecari* group **C.** *Myrmecophaga tridactyla* with a juvenile **D.** *Dasyprocta fuliginosa* **E.** *Puma concolor* marking territory **F.** *Tapirus terrestris* diurnal capture.

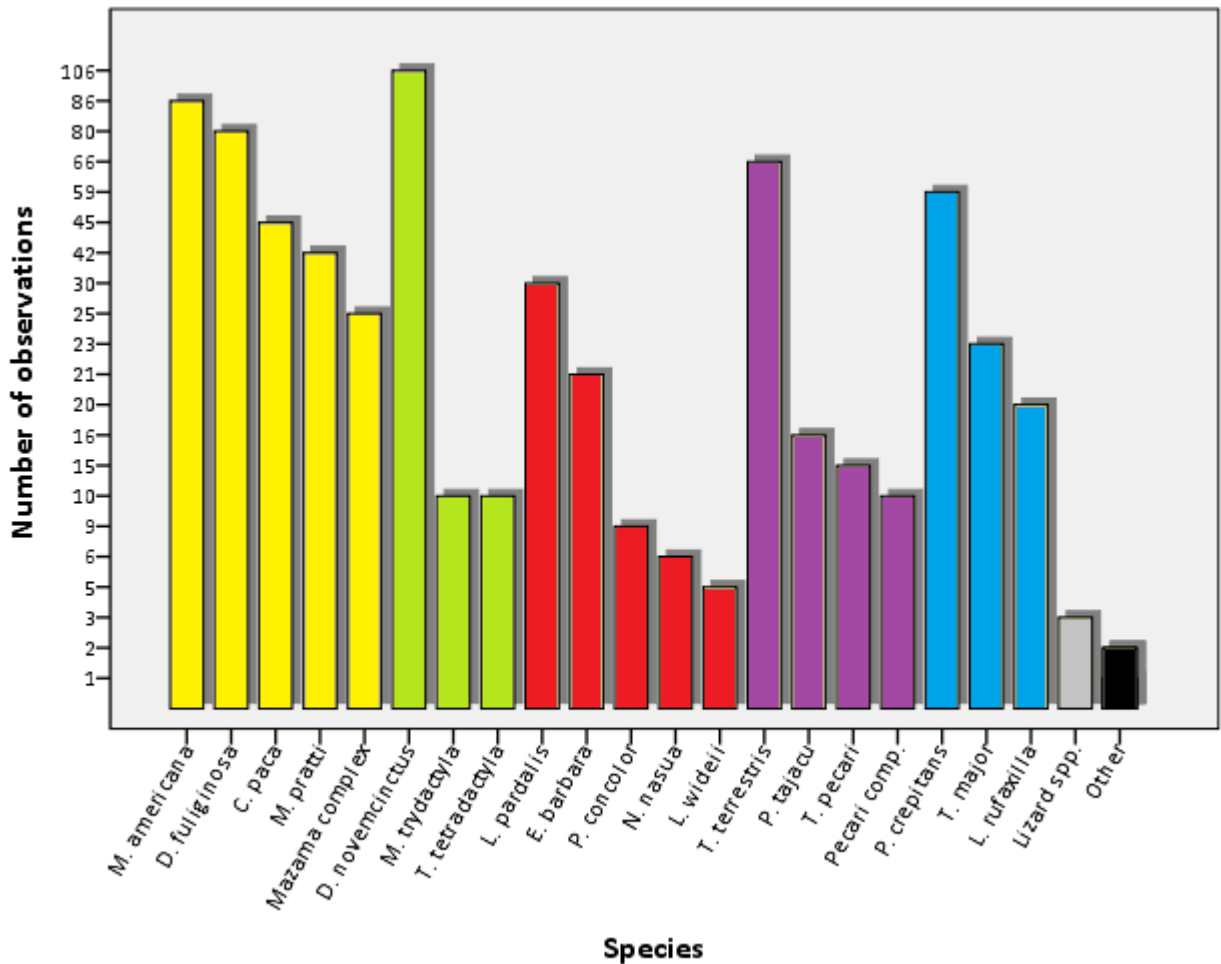


Figure 2.4 - Absolute abundances for the different species captured on the cameras. Each colour represents a functional group (Yellow: *Herbivores*, Green: *Insectivores*, Red: *Carnivores*, Purple: *Omnivores*, B: *Birds*, Gr: *Lizard sp.*, Bl: *Others*). Bars correspond to species events registered on both camera surveys and transect. Species full names can be found in Appendix 1.1.

The absolute number of occurrences observed by the camera traps deployed is summarized in figure 2.4. Surprisingly, the top four most abundant species (*D. novemcinctus*, *M. americana*, *Dasyprocta fuliginosa* and *T. terrestris*) are species under hunting pressure (Pers. Obs.) and are also all jaguar (*Panthera onca*) prey species (except *D. fuliginosa*) (Harmsen et al., 2011). The fifth most abundant species is a bird (*Psophia crepitans*), which moves around in flocks, therefore enhancing the absolute number of records. The sixth and seventh most abundant species are two additional species (*C. paca*

and *Myoprocta pratti*) under human pressure. The most abundant carnivore is *Leopardus pardalis* in 8th position. Four out of the five functional groups are represented in the top ten most abundant species. The first *insectivore* is located in 16th position (*Myrmecophaga tridactyla* and *Tamandua tetradactyla*, with the same number of occurrences n=10).

When studying the effect of “distance to community centre” as an indicator of human pressure, the ADONIS test showed no significant effect of human disturbance on species composition ($F_1= 1.2414$, $R^2=0.044$ $p=0.165$). However, although it is not statistically significant, the resulting model showed that the variable “Distance to the centre” explains the 4.4% of the variation in the camera data.

2.3.2. ACTIVITY PATTERNS

Species showed different behavioural patterns and were categorized as nocturnal, diurnal or cathemeral depending on their daily mean activity time. Nocturnal species (Fig. 1.5) were the most abundant group with activity peaks at dusk and a general decrease of activity levels across the night (21:00h to 05:00h). Although being nocturnal species, few observations were noted at daytime (i.e. noon). Diurnal species (Fig. 1.6) were defined as those species with main activity peaks between 06:00h and 18:00h. This group is represented by *carnivores* (*Eira barbara*), *omnivores* (*P. tajacu*), *herbivores* (*M. pratti*) and *birds* (*Leptotila rufaxilla*, *P. crepitans* and *Timus major*). *E. barbara* was the only carnivore with strict diurnal activity patterns. *P. tajacu* and *M. pratti* presented different times for their activity peaks, although at dusk, both species coincided. *Birds* showed three activity peaks; early in the morning; at noon and at dusk. Curiously, *T. major* also presented two unusual observations after midnight. Cathemeral species (Fig 1.7) presented two different models: *M. americana* and *L. pardalis* showed a preference for night time activity with reduced activity throughout the day. *Dasyppus fuliginosa* and *T. pecari* showed a preference for day time, with an activity peak at dusk. Larger mammals (i.e. *T. terrestris* and the Mazama complex) are mostly nocturnal while the smaller *P. tajacu* was mostly diurnal. Both small rodents (*M. pratti* and *D. fuliginosa*) also showed similar diurnal patterns with reduced activity at night time.

Study1: Terrestrial Mammal Community Structure: Insights from a Survey in a portion of the Sumaco National Park (Ecuador)

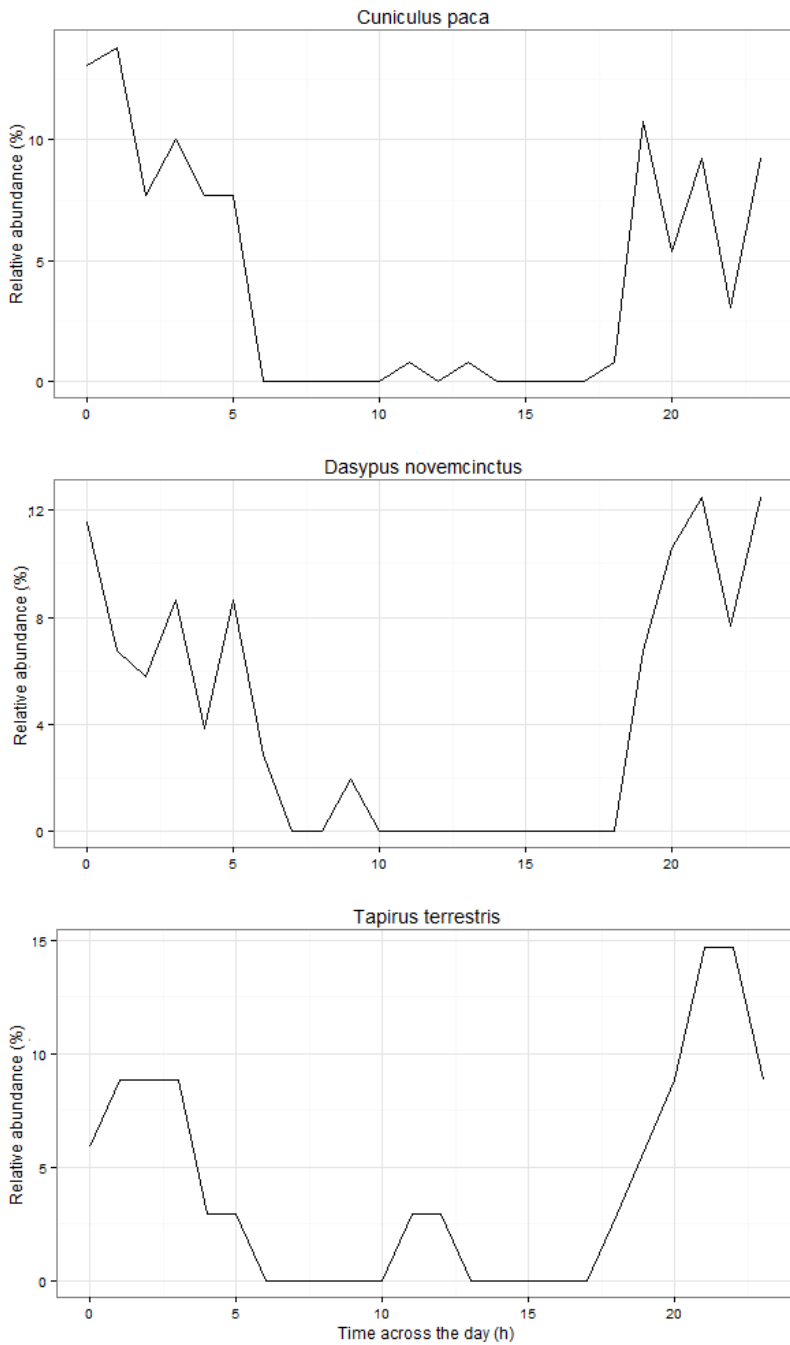


Figure 2.5 - Activity patterns of nocturnal species. Each graph represents the relative abundance of a species across the day (hours). The top activity pattern is for an herbivore (*C. paca*) and the middle and bottom activity patterns (*D. novemcinctus* and *T. terrestris*) are omnivores.

Study1: Terrestrial Mammal Community Structure: Insights from a Survey
in a portion of the Sumaco National Park (Ecuador)

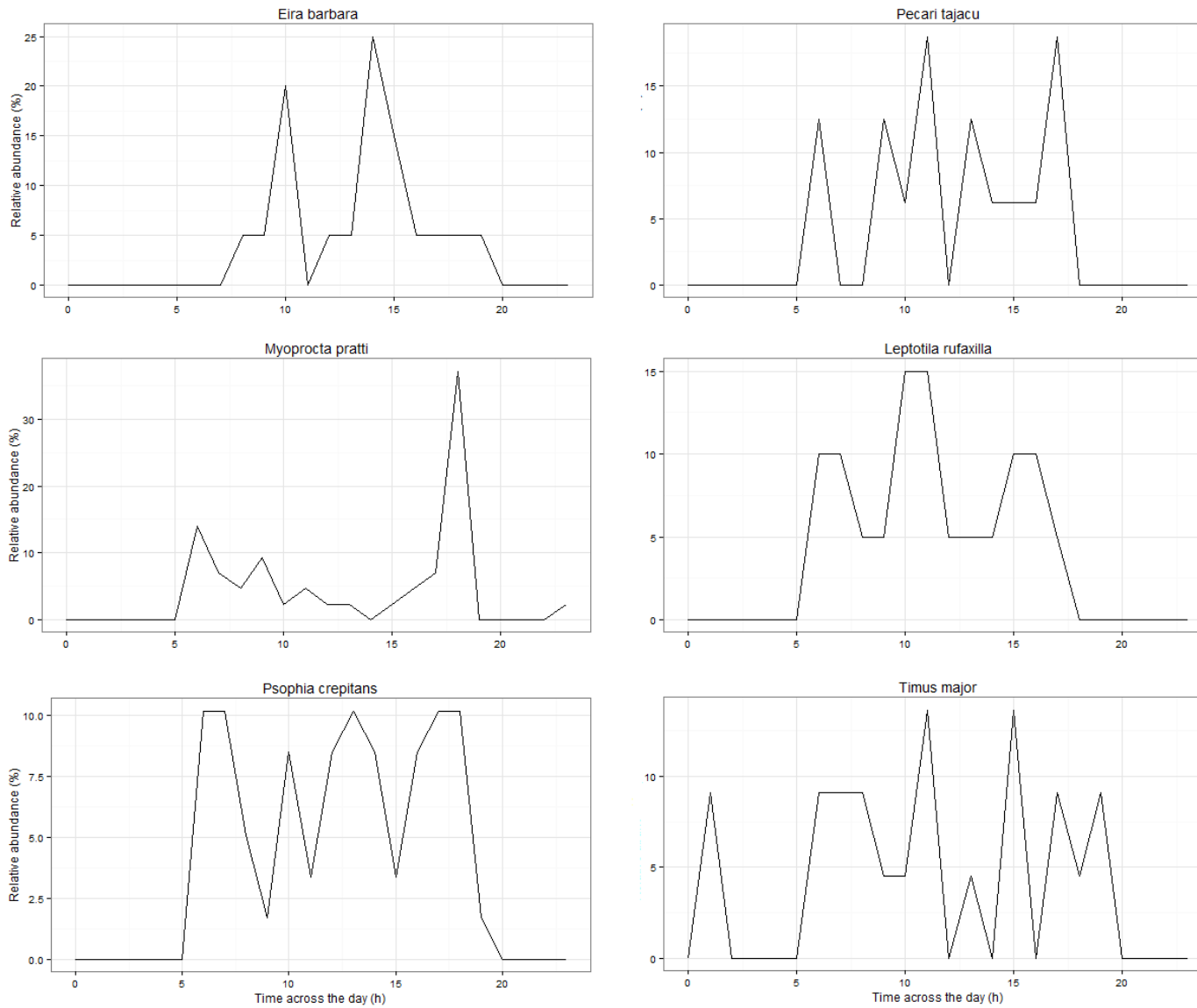


Figure 2.6 - Activity patterns of diurnal species. Each graph represents the relative abundance of a species across the day (hours).

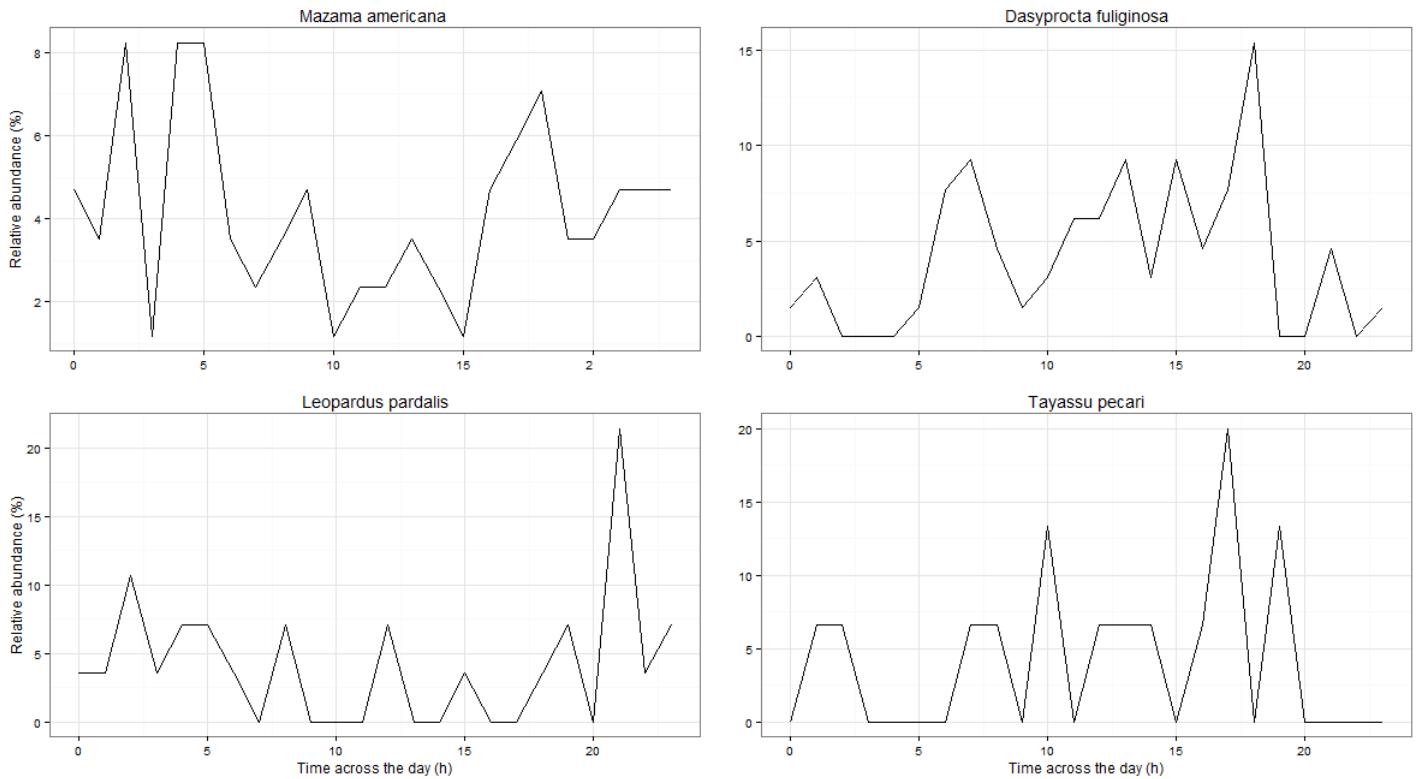


Figure 2.7 - Activity patterns of catemeral species. Each graph represents the relative abundance of a species across the day (hours).

When the three strict nocturnal species were considered in order to determine a relationship between daily activity patterns and moon phases, only two species showed a clear pattern (see fig. 1.8). The monthly activity pattern of *C. paca* (top panel) has a clear relationship between reduced moon phases and activity peaks. It is the clearest example of moon related patterns because confidence intervals between maximum and minimum activity peaks never overlap. Although *D. novemcinctus* (middle panel) also showed a relation between lighter and darker moon phases, activity levels did not fall in such a pronounced way as for *C. paca* and, therefore, confidence intervals overlapped across the month. Finally, *T. terrestris* monthly activity pattern (bottom panel) did not present such a marked pattern related to the moon phases as confidence intervals overlapped, however there was an indication that maximum activity levels were at full moon stages.

Study1: Terrestrial Mammal Community Structure: Insights from a Survey in a portion of the Sumaco National Park (Ecuador)

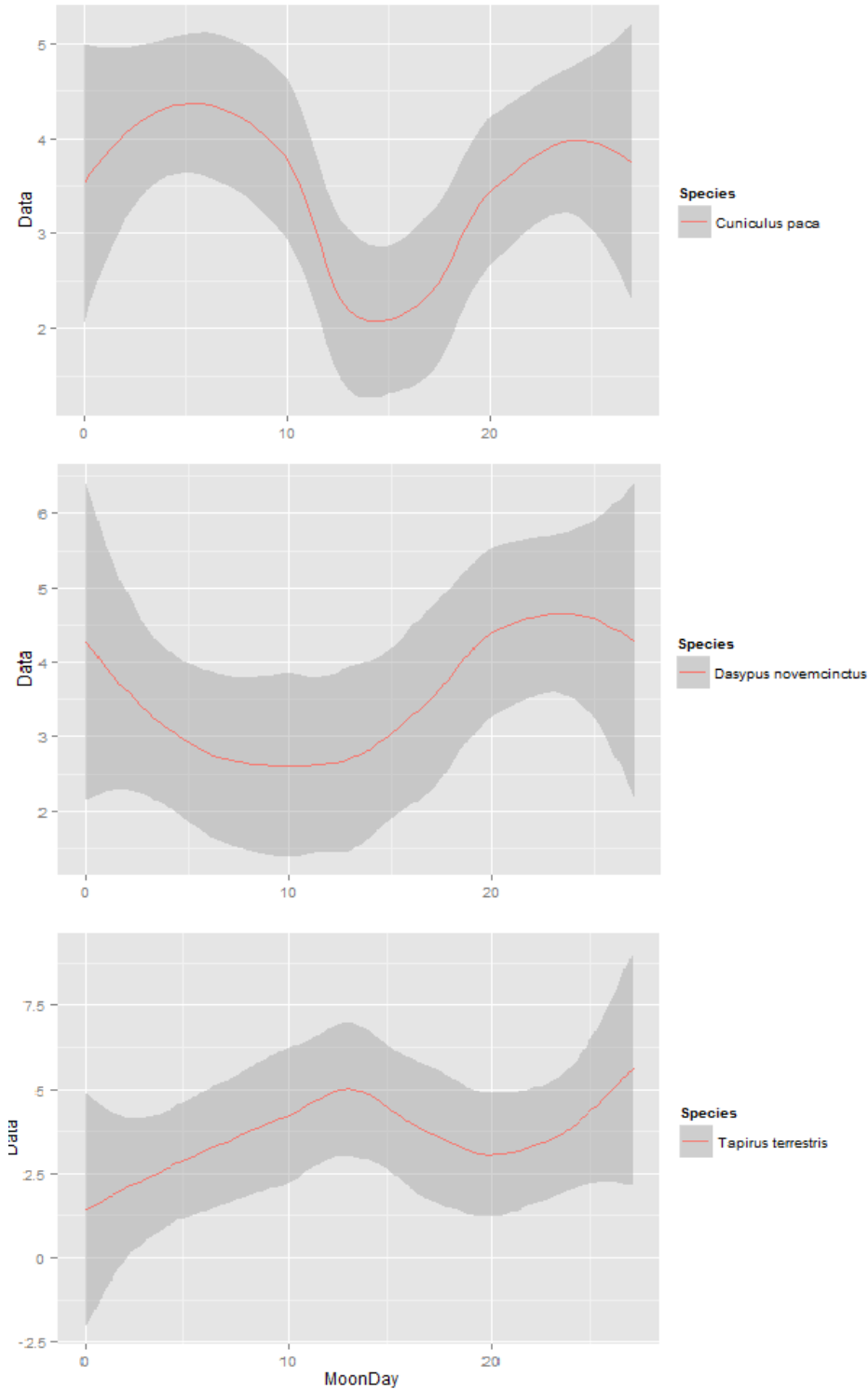


Figure 2.8 – Species activity patterns related to moon phases. Coloured lines show species relative abundance with 95% confidence intervals (darkened areas) across the month. Day 0 represents the new moon. Light then increases until day 15, which represents full moon, after which it decreases until new moon again.

2.4. DISCUSSION

The surveyed portion of the buffer zone of the Sumaco Biosphere Reserve contains nearly all mammal species observed in previous studies (O'Reilly- Berkeley et al., 2013). Four species, which are known to inhabit the area surrounding Timburi Cocha Research Station were not captured (i.e. *Galictis vittata*, *Sylvilagus brasiliensis*, *Atelopus microtis* and *Panthera onca*)(O'Reilly-Berkeley et al., 2013), but this survey added a total of six new records to the area: *Leopardus wiedii* (Margay), *Puma concolor* (Puma), *Puma yagouaroundi* (Yagouaroundi), *P. maximus* (Giant Armadillo), *Sciurus ignitus* (Northern Amazonian Red Squirrel) and *T. tetradactyla* (Southern Tamandua). Relative abundance curves demonstrated that the cameras captured the majority of species present, although transect data added one more species (*Priodontes maximus*). A number of species showed clear activity patterns and could be classified into nocturnal, diurnal and cathemeral species. Two species, *C. paca* and *D. novemcinctus* showed clear activity patterns related to moon phases with avoidance of days around the full moon.

2.4.1. METHODOLOGY

Community studies are complex due to the difficulties in controlling multiple variables in the field. When designing a study, it is important to understand that multiple underlying factors determine community structure (species composition and abundance)(e.g. Dickie et al., 1987; Fox, 1990; Pardini, 2004). For example, seasonal fluctuations in populations, climatic variation, changes in trail preferences and human activity can all alter species distribution. In addition, consideration must be made as to how the chosen methodology can influence the results.

We used a mixture of transects and camera traps in this study. Although transects are very useful, they have the disadvantage that observers must be highly trained to spot living animals (especially, rainforest mammals). The use of camera traps instead had great advantages as low training is required and more accuracy can be gained in identifying species as well as their age and gender. However, species with both elusive behaviour and reduced abundance are usually easier to identify by their tracks (i.e. faeces, scats, holes) than by direct observations or camera traps (e.g. Silveira et al., 2003; Tellería, 2012). Thus, using a combination of both camera traps and transects has proved to be

effective previously. In the present study, transects added a new species record (*P. maximus*) and it considerably increased the absolute number of species records as well (by 13.5%). In addition, when counting animal records on camera traps, those with multiple individuals in a single capture (e.g. herd of peccaries or flock of *P. crepitans*) were considered as a single record for that species.

This survey was designed to estimate community conditions within a restricted three-month period. Although this provides only a snap shot in time, this is the maximum time required to validate the assumption of a closed population of medium to big sized mammals (as seen in Trolle & Kéry, 2005; Mosquera, 2011; Salvador, 2014). Closed populations are understood as a hypothetical condition where species abundances are not altered (e.g. death rate = birth rate, migration rate = immigration rate). In order to obtain the sampling effort used in previous studies (around 1500 camera trapping nights), we planned to deploy a total of 25 camera traps distanced 500 meters from each other depending on the availability of trails and rivers around the community. The total area surveyed by the camera traps (27km²) and the sampling effort carried out did appear to be sufficient, as in the rarefaction curves the *observed* number of species reached similar levels (around 30 species) to those predicted by the estimators (e.g. *Chao 1*). However, according to a previous study in the area (O'Reilly-Berkeley et al., 2013) five additional species were observed which were not detected in the present survey.

2.4.2. COMMUNITY STRUCTURE

2.4.2.1. Species diversity

Two statistics were computed to estimate the total diversity of the area (Shannon and Berger-Parker indices). When compared to another camera trap study undertaken by Ahumada *et al.* (2011), Payamino presented similar values for both of these indices. In that study, authors compared the biodiversity captured by camera traps in six different tropical regions around the world (including South America, Africa and South East Asia). The Shannon index depends on each sampled community and therefore it is not the best index to compare diversity among studies *sensu stricto*. It showed similar biodiversity values to the survey carried out in Manaus, in the Brazilian deep Amazon, although

Berger-Parker species dominance index was higher in Payamino. Most probably due to the unusual overpopulation of *D. novemcinctus* (nine-banded armadillo) observed in Payamino. It is important to mention that the closest peak to the community and to Timburi Cocha Research Station is named *Armadillo hill* (423m.a.s.l.) and, therefore, a higher than usual number of armadillos was expected. This result can be the first indicator of community dynamics alteration at Payamino rainforest.

2.4.2.2. Composition

Considering the location of Payamino in the Western Amazonian rainforest and according to the studies of Zapata (2000), Albuja (2011) and Tirira (2013), the Procyonidae, Echimyidae and Canidae families were potentially underrepresented groups. However, a previous study undertaken in 2013 in Payamino (O'Reilly- Berkeley et al., 2013) did capture all of these groups, as well as *P. onca* (jaguar), the top-predator in the rainforest. In that study, O'Reilly-Berkeley (2013) observed a pregnant jaguar, which is signal of healthy and actively reproductive population. It is important to mention that in the current study, numerous records (n=9) of *P. concolor* (puma) were obtained within two km from the community centre, suggesting a great adaptability of pumas to human presence. While it is possible that *P. onca* is still present in Payamino at low densities, as it has a large home range (e.g. between 11-40 km² per individual – see Silver et al. 2004), it may also be the case that the large predators in Payamino are undergoing a transition from jaguars to pumas as top predators. If this is the case, it could be due to increased human disturbance during harvesting periods, hunting and gardening activities or due to the recent oil prospecting within the community boundaries.

Other studies with sympatric jaguars and pumas (e.g. Gentry, 1993; Taber et al., 1997; Foster et al., 2010) found that the diets of the two species were different when resources were abundant. Pumas had a preference for smaller species like rodents, deer, monkeys and peccaries (between 1-15kg); and, jaguars for bigger prey like tapirs, smaller predators, turtles and caimans (heavier than 15kg)(as seen in Scognamillo et al., 2003; Cascelli & Murray, 2007). Following these assumptions and considering the observed abundance of prey species in the present study (four out of the top six most abundant species - *D. novemcinctus*, *M. americana*, *C. paca* and *T. terrestris*- are potential prey species for jaguars) the Payamino community would appear to be lacking in its top predators. While no effect of

distance to the community could be found on the community composition there do appear to be suggestions that the predator community could be changing.

Mesopredators observed in Payamino are mostly represented by the Felidae family (*L. pardalis*, *L. wiedii* and *P. yagouaroundi*), while Canidae and Procyonidae families both presented lower species richness. Although, two new species of mesocarnivores were recorded (*L. wiedii* and *P. yagouaroundi*), both species had low relative abundances. Despite the observed depletion of mesocarnivores and the high abundances of herbivores previously commented on, it is too early to report the existence of a *mesopredator's release effect* in Payamino (as seen in Ritchie & Johnson, 2009). However, it may be worth considering, this is a potential future situation where human presence is still evident and jaguars are no longer present.

2.4.2.3. Abundance and activity patterns

Species activity patterns in Payamino showed higher abundances of nocturnal species than diurnal species overall (Herbivores: 63%, Insectivores: 89%, Omnivores: 55%, Carnivores: 51%, Birds: 13%). Carnivore species showed both diurnal and cathemeral activity patterns. *Birds* were strictly diurnal (except for rare observations of *T. major* during the night) while herbivores and omnivores presented all three behavioural patterns (i.e. strict nocturnal, diurnal or cathemeral). The cathemeral carnivore *L. pardalis* (ocelot) was active when its favourite prey were also active: the cathemeral black agouties (*D. fuliginosa*); the diurnal green agouti (*M. pratti*) and the nocturnal nine-banded armadillos (*D. novemcinctus*)(as seen in Abreu et al. 2008; Santos-Moreno & Pérez-Irineo, 2013), but it was not possible to test this relationship with our data.

A comparison with other studies would suggest that there is some consistency in large species' activity patterns. For example, when compared to Harmsen et al. (2011), who undertook a study in Belize, our study showed similar behaviours to those that they observed for all species (*D. novemcinctus*, *C. paca*, *L. pardalis*, *Mazama* complex and *T. pecari*) except for *T. terrestris*, which in Payamino, was also active during the day time. When compared to Blake et al. (2012), who undertook a study in Ecuadorian Amazon, all Payamino activity patterns coincided except for *T. pecari* and *D. fuliginosa*, which were only observed during the day time despite being spotted in Payamino during the night.

Cloud cover varied between and within nights affecting light levels on a daily basis in the forest. Despite this, the three nocturnal species with sufficient data showed different patterns with respect to lunar cycles. *C. paca* showed a strict pattern with the least activity on days of full moon phases, most probably due to a higher predation pressure. *D. novemcinctus* presented a similar pattern but was also observed on full moon periods. Finally, *T. terrestris* did not show any clear pattern; perhaps due to the absence of their main predator (*P. onca*). Unfortunately, the low number of records obtained in Payamino prevented a more in depth analysis of prey-predator relationships.

2.5. CONCLUSIONS

The buffer zone of the Sumaco Biosphere Reserve is a portion of the natural park where few human activities are allowed and they are regulated. Indigenous communities are allowed to harvest, fish and hunt for their subsistence and also to extract timber for construction. As far as the authors know, San José de Payamino community decided to not commercialize these resources in order to keep wild animal populations for the upcoming generations. But over the last few years, national and local governments have persuaded the community members to allow oil explorations (and further extractions) in the area. This is the first study in this area since these explorations have taken place.

In general, the region contains high levels of biodiversity similar to other pristine regions on the planet and the forest community contains moderate to high levels of carnivorous and herbivorous species, indicating equilibrium in the food webs. There does not appear to be an effect of disturbance from the local indigenous community although there is some indication of a change occurring in the composition of the predator community. Lack of top-predators increased herbivores abundances and different mesopredators were observed compared to previous studies in Payamino. Species activity patterns also got altered with a tendency towards nocturnal habits.

In order to better understand the ongoing processes in the community structure, further research is needed to analyse yearly animal fluctuations. In addition, it is important to compare these results with other ecologically similar regions in the Amazon with diverse levels of human disturbance. Thus, helping to create a record on how Neotropical rainforest communities are altered by human pressure.

*Study1: Terrestrial Mammal Community Structure: Insights from a Survey
in a portion of the Sumaco National Park (Ecuador)*

This is especially important in such countries where there are many oil reservoirs under the Amazon, whose exploitation could put thousands of species at risk.

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3. STUDY 2:

**HUMAN DISTURBANCE EFFECTS ON TERRESTRIAL MAMMAL
COMMUNITIES. A COMPARISON BETWEEN SUMACO NATIONAL PARK
AND YASUNÍ BIOSPHERE RESERVE (ECUADOR)**

3.0. ABSTRACT

The aim of this study was to compare two surveys of the terrestrial mammal communities of the Ecuadorian Amazon. The surveys were carried out at locations with different levels of disturbance; the first study area, San José de Payamino, has moderate levels of human disturbance and, seismic oil prospecting has recently been undertaken in the vicinity. The second study area, Tiputini Research Station, is located in the most biodiverse hotspot on Earth, the Yasuni National Park (YNP), where human disturbance is currently minimal, but where oil extractions are likely to occur in the future. Both studies used similar camera trapping methodology and sampling effort over the same seasonal period to determine the diversity and structure of the terrestrial mammal communities, although data was collected during different years. As expected, species richness and relative abundances differed significantly between locations, with Tiputini sustaining a more diverse and homogeneously distributed community than Payamino. Activity patterns of individual species and functional groups also differed, with Tiputini presenting higher levels of activity across the day while in Payamino species were more active at night. Species known to be hunted by the local community in Payamino showed a significantly greater difference in abundances between locations than non-hunted species, suggesting that a hunting pressure effect is present in Payamino. There was a lower relative abundance of mesopredators and higher relative abundance of small prey species (i.e. rodents) in Tiputini. Thus, it seems likely that human pressure, presumably through hunting activities but also possibly due to the recent oil exploration activities, has affected the species diversity and activity patterns of the mammal community in Payamino. This study also shows how top-predators appear to regulate the trophic webs in Tiputini and, that the lack of them can potentially alter the equilibrium of community structure. Our results suggest that increasing disturbance in Tiputini could have wide ranging effects on the structure and function of the terrestrial mammal community.

KEY WORDS: community structure, terrestrial mammal, camera trap, Yasuni, human disturbance.

3.1. INTRODUCTION

Neotropical rainforests have been suffering a loss of biodiversity for the last half century, especially due to changes in land cover (Pringle, 1976; Achard et al., 2002; WWF, 2014). Extensive monocultures (e.g. oil palm trees, soya) and oil exploration are the main threats to this rich and complex ecosystem and yet, these activities are also the main source of income for most tropical countries (Azlan & Sharma, 2006; Joly, 2008; Nepstad et al., 2008; Boucher et al., 2011). Such a conflict is present in Ecuador, where the entire Amazon region has been divided into oil blocks. The most famous is block 31 or the *ITT* oil block (i.e. ITT- Ishpingo, Tambococha and Tiputini regions), which is located within the Yasuní Biosphere Reserve, and in which the government has granted oil extraction rights, despite social pressure and resistance. Thorough studies documenting the region's ecological value and mapping relative biodiversity levels are vital in order to estimate how future oil prospecting or other increases in human disturbance might alter wild communities in Tiputini.

When wild mammal communities have contact with human settlements, alterations in their activity patterns and abundances are to be expected (Skole & Tucker, 1993; Whittaker & Knight, 1998; Pardini, 2004). Depending on the degree of the disturbance and the community structure present at the time, species absolute and relative abundance can fluctuate, leading to irreversible changes. Generally, larger mammal species are the most sensitive to human disturbance, especially low density predators (see Jackson et al. 2006; Prugh et al., 2009). Large predators play an important role in trophic webs and can determine both the community structure (e.g. predator-prey cycles, intra-guild competition, adaptive genetic changes in prey and predators) and ecosystem function (e.g. seed dispersal, pest control, cycling of nutrients)(Ripple & Beschta, 2004; Ray et al., 2005; Roemer et al., 2009). In the last century, however, anthropogenic pressure and habitat fragmentation have led to a decline of wild populations of large carnivores around the world (Laliberte & Ripple, 2004; Ripple & Beschta, 2008; Prugh et al., 2009). This decline not only affects prey species, but also can result in an increase in diversity and abundance of lower trophic level carnivores (non-top predators). Disappearance of top-carnivores opens new ecological niches in the community and mesocarnivores are the most likely species to take

advantage of this thanks to their versatile behaviour and higher resilience to disturbance. This situation is known as the *mesopredators release effect* (Soulé et al., 1988).

Although mammals have lower levels of biodiversity and absolute abundance compared to other groups (e.g. birds, arthropods, bats), baseline studies of mammal communities, including species' composition, abundance and behaviour, are crucial for understanding alterations in community structure caused by human impact. The aim of this study was to determine how human disturbance affected non-flying mammal communities by comparing camera trap data from two Neotropical rainforests with different levels of human disturbance.

Camera traps have been recognized as powerful tools for studies of biodiversity (O'Connell et al., 2011). Camera surveys have major advantages over traditional survey methods, especially when surveying low density species with elusive and secretive behaviour (Wallace et al., 2003; Trolle & Kéry, 2005; Maffei & Noss, 2008) because species are not disturbed while being recorded. This methodology can provide useful information on community structure, population densities, species activity patterns, habitat use and reproductive information throughout space and time (Silveira et al., 2003; Silver et al., 2004; Rowcliffe et al., 2008; Cueva et al., 2010; Rueda et al., 2013b). Although many single species surveys have previously been undertaken using remote camera systems (e.g. González-Maya et al., 2012; Kolowski and Alonso 2010; Mosquera 2011; Wang and Macdonald 2009), community structure studies are needed to fully understand how species behave and populations fluctuate over different conditions (Gómez et al., 2005; Tobler et al., 2008; Blake et al., 2012). Camera traps are biased to medium and large sized animals due to their IR sensor system being most responsive to those species, although other animals might also be (Bushnell, 2009). Consequently, they are an excellent tool with which to study the non-flying mammal community.

One of the study sites (San José de Payamino) is located within the buffer zone of the Sumaco Biosphere Reserve, and is inhabited by an indigenous community of *Kichwa* people. The *Kichwas* have been living off the same forest for more than 30 years: extracting timber, picking fruit and seeds, carrying out small scale agriculture, fishing and hunting (Irvine 1987; Pers. Obs., 2015). Moreover, during the last decades two oil companies have undertaken

Study 2: Human Disturbance on Terrestrial Mammal Communities. A Comparison between Sumaco National Park and Yasuní Biosphere Reserve (Ecuador)

explorations, which have involved the daily usage of dynamite for periods of many months at a time. The latest oil survey in this area was undertaken three months prior to the start of this survey. Therefore in this area, the terrestrial mammal community is expected to be under stress caused by the recent human disturbance.

In contrast the second study site, Tiputini Biodiversity Station is located in the Yasuní Biosphere Reserve, one of the richest biodiversity hotspots in the world. Its isolated location has been the key for the preservation of a rich ecosystem removed from human development. By comparing these two sites, we were able to analyse how wild populations of mammals behave and coexist in natural conditions with populations where there is some, but relatively low, human impact (since there is no permanent activity). The present study aims to elucidate if the mammal community in Payamino has been altered by recent human activity. Or whether the indigenous *modus vivendi* and recent oil prospecting had no observable effect on wild populations.

South American rainforests contain megadiverse ecosystems with intricate ecological interactions (Mares, 1986; Myers et al., 2000). Neotropical forests have such complex habitats that there is an evident dearth of information on species relations and all ecological processes (Kolowski & Alonso, 2010; WWF, 2014). More research is needed to understand these areas in natural conditions, which will be especially useful for conservation purposes if an agent of disturbance appears. By comparing one of the best preserved areas in the world, Yasuní Biosphere Reserve, and a small indigenous community in the buffer zone of Sumaco Biosphere Reserve, the present study aims to understand how low levels of human disturbance can alter the structure and composition of the terrestrial mammal's community.

3.2. METHODOLOGY

3.2.1. STUDY AREA

·Sumaco National Park –Timburi Cocha Research Station (Payamino site)

The Sumaco National Park is located in the transitional area between the Andean range and the Ecuadorian Amazon Basin. It was formally established in 1994 and named a UNESCO Biosphere Reserve in 2000. In its entirety, it comprises a wide altitude range (3,732 – 300m.a.s.l.), but the current study site was situated in the lower altitudinal ranges. Timburi Cocha Research Station (TCRS) is located in a *Kichwa* indigenous community within the buffer zone of the Sumaco Biosphere Reserve (0°28'S, 77°17'W; 298 m.a.s.l.)(Orellana province, Ecuador).

For the full site description, see Study 1.

·Yasuní National Park - Tiputini Biodiversity Station (Tiputini site)

The Yasuní National Park was created in 1979 and, due to its great natural value it was named a UNESCO Biosphere Reserve in 1989. Tiputini Biodiversity Station (TBS) is located in this world's biodiversity hotspot surrounded by *tierra firme* rainforest in the deep Amazon basin (0° 37' S, 76° 10'W; 190-270 m.a.s.l.)(Orellana province, Ecuador). The station site is 650 ha and, in contrast with TCRS, there is no hunting or any other human pressure in the area.

The surveyed area (8.64 km²) is also dominated by the “Evergreen Forest of Amazonian Lowland” defined by Sierra et al. (1999). It contains *varzea* forest, palm swamps and various successional habitats. Although annual precipitation values are similar (aprox. 3000mm), the region is flatter than Payamino. Therefore, the rivers are calmer and, during rainy season (April-June), its orography creates greater lakes and big swampy areas.

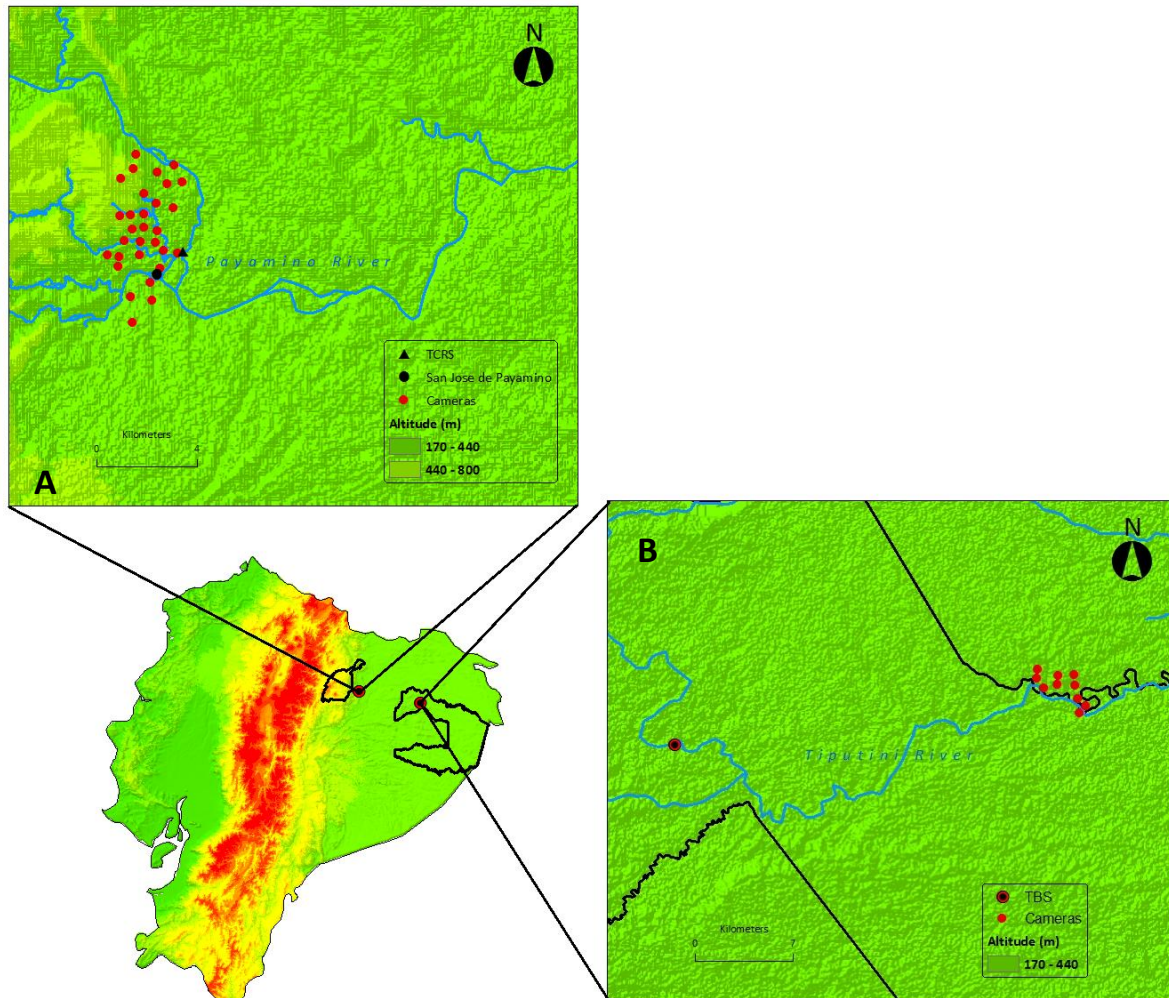


Figure 3.1 - Maps of the surveyed areas with their relative position in continental Ecuador. Top left map (A) represents Sumaco National Park (Payamino survey) and right bottom map (B) represents Yasuní Biosphere Reserve (Tiputini survey). Specific location of camera traps and research stations (TCRS- Timburi Cocha Research Station; TBS – Tiputini Biodiversity Station) are represented on both detailed maps.

3.2.2. CAMERA TRAPS

Camera traps are a non-invasive technique widely used for population surveys (see Jackson & Conservancy, 1995; Di Bitetti et al., 2010; Monroy-vilchis et al., 2011). Cameras are triggered by the activation of their Passive Infra-Red (PIR) motion sensor (Bushnell, 2009). All cameras were deployed at 0.3-1 m from the ground along trails and were positioned

where animal paths and tracks were found. Junctions of animal paths were preferential sites due to the higher probability of captures. Cameras were set to capture data over the entire 24h of each day for a total period of three months. For medium and large mammals, this time window is short enough to consider this a closed population (i.e. number of individuals stable: born/death and migrations rates equalized)(Karanth, 1995; Karanth & Nichols, 1998; Silver et al., 2004; Trolle & Kéry, 2005; Maffei & Noss, 2008).

In order to minimize recaptures of the same animal in an area, captures of the same species on a single camera were defined as a recapture (and not an independent capture of another individual) unless there was a minimum of a 30 minute time-gap between the two capture events (Tobler et al., 2008; Blake et al., 2012). Cameras were checked every 10-20 days to obtain camera information, verify status and replace batteries and SD cards when necessary. Location and altitude of the cameras were mapped with a GPS unit (Garmin Etrex 20, USA) and a number of abiotic factors (humidity, Stress Heat Index, daily temperature and dew point) were recorded for traps sites in Payamino using a portable weather station (KESTREL Unit D2, USA). For each picture taken, camera id and position, temperature, time, date and moon phase were recorded and animals were identified down to species level when possible. Identification was assisted by local guides. All camera records will be uploaded to the Global Biodiversity Information Facility (GBIF).

3.2.2.1. Camera positioning:

Although both surveys had similar objectives, different approaches were used when setting up the cameras.

·Payamino (Sumaco National Park):

Twenty-three cameras (Trophy Cam HD, Bushnell, USA) were deployed between 15th March and 15th June of 2015 resulting in a total sampling effort of 1413 camera trapping days. Cameras were separated by a mean distance of 500m apart. For cameras where low levels of animal activity were detected (less than 4 occurrences within 14 days, n= 7 cameras), these cameras were moved to a new location following the approach of Srbek-Araujo and Chiarello (2005) and Downey et al. (2007). Hence, when the cameras were moved to further

positions, the survey area in Payamino increased and data from a total of 32 camera stations were finally analysed.

Tiputini (Yasuní National Park):

For this study, a subset of data obtained from a longer survey carried out by Blake et al. (2012) was used to define Tiputini community. In that study, eleven cameras (Capture 1125, Cuddeback, USA) were deployed separated by a minimum distance of 1000m for two successive years (Feb 2010 to Jan 2012) for a long-term community study. In order to compare both locations, similar sampling efforts were necessary. For that reason, we have used a dataset corresponding to the same time window as for Payamino (March to June), but with two consecutive years of records. Thus, the total resulting sampling effort for Tiputini was 1565 camera trapping nights: 777 in 2010 and 788 in 2011.

As no differences were found between data from the two years at Tiputini (Wilcoxon-Signed-Rank-Test, normal approximation, $z = 1.48$, $P = 0.14$) and capture rates showed strong correlations between years (Spearman rank correlation - $r = 0.84$, $P < 0.001$), the datasets for both years were considered as independent captures. For that reason, authors of both surveys agreed in using it as a single and independent dataset with sufficient statistical power to be compared to the Payamino survey.

3.2.2.2. Methodology similarities and differences between sites

Both studies followed standard camera-trapping depletion methodologies (O'Connell et al., 2011). However, the main difference between the two studies was in the distance between cameras. In Tiputini, the cameras were located with a mean distance of 1 km between sites, while in Payamino the cameras were placed a mean distance of 500 m apart. The authors considered the different distances among cameras to have little effect in comparison to the distance between the two locations (125km). Even though the distance between the cameras in Tiputini was double that in Payamino, a greater number of cameras were deployed in Payamino (Tiputini $n=11$; Payamino $n=32$) and thus, the total area surveyed in Payamino was three times greater than in Tiputini.

Another difference between the methodologies followed during both surveys is the repositioning of the cameras. In Payamino, seven cameras were moved to new positions after low activity levels were observed, while in Tiputini no camera was moved during the survey. The authors considered this alteration of minimum impact on the study results because the comparison was based on number of camera trapping days (as study effort) and not the total surveyed area.

For studies on large mammal population densities (i.e. nº individuals/area), most authors calculate the surveyed areas using the Mean Maximum Distance Moved (MMDM), which depends on the target species home ranges. Since the present study is not focused on any specific population density, the total area surveyed was calculated as the addition of all areas comprised in circle with a 500m radius around each camera station. This calculation was made with digital cartography ArcMap 10 software (ESRI, USA).

Finally but no less important, species records were defined following the same time window after each of the observations. The minimum gap time between animal occurrences was defined as a 30 minutes period after the first detection, as it was in Blake et al. (2012), standardizing the rawdata. Animal occurrences are the main comparisons considered here, where animal activity patterns mostly likely reflect the effect of human disturbance. Animal density (number of individuals/area) is also important when defining the community *status quo* but, as these studies were carried out at different time periods, they cannot be used for further comparisons.

3.2.3 COMMUNITY ASSESSMENT

2.3.1. Community structure

α -Diversity indices (Shannon and Berger-Parker) were calculated at each location individually using the *Estimates* software (Colwell, 2013)(number permutations=10000). The Shannon index is an estimator of community complexity depending on the ecological processes taking place in each ecosystem (MacArthur, 1965) and, although it gives a rough idea about the community status, it varies both regional and temporarily and therefore is

not frequently used for comparing locations (Hurlbert, 1971). The Berger-Parker dominance index measures the relationship between the most common species and the total number of animal observed (May, 1975). Lower values of the Berger-Parker index correspond to a lower dominance of that species and thus, higher α -diversity levels within the community. It is commonly used as an approximation for population diversity in comparisons among sites.

Sampling effort was evaluated by comparing rarefaction curves (i.e. species accumulation/sampling effort) between the *Observed* data and *Predicted* as calculated using the *Chao1* biodiversity index (as seen in Ahumada et al. 2011). Chao et al. (2004) described the *Chao1* richness estimator as a simple calculation of diversity considering species abundances and, especially, rare species (i.e. singletons and doubletons). The relative abundance index (RAI) was calculated per individual species as a proportion of animal occurrences per 100 camera trapping nights (following Azlan and Sharma 2006; Blake et al., 2012; Vanderhoff et al., 2011).

In order to graphically represent differences in community structure between locations, a Non-metric Multidimensional Scaling (NMDS) ordination was constructed from all recorded species using the *vegan* package (Oksanen et al., 2015) and plotted with the *ggplot2* package (Wickham & Chang, 2015) using *R* (R-Core Team, 2014). Dissimilarity matrices (Jaccard distance) were calculated as the difference in species composition (camera records were previously transformed by a Wisconsin transformation) between each camera. When creating the NMDS, stress values below 0.2 were considered valid as a signal of a good fit of the NMDS model to the data (Oksanen et al., 2015). To determine whether species composition differed between TBS and TCRS, an ADONIS permutation test was run (method: Jaccard, permutations= 10,000) on the distance matrix where location was included as an explanatory factor.

3.2.3.2. Human pressure

The analysis for the existence of human pressure at Payamino consisted of a comparison of species' presence and their relative abundance between the two locations. Considering that there is not any kind of hunting activity (nor human presence) in Tiputini, species with a

minimum of eleven records (considering both sites) were grouped depending on whether they were *Hunted* or *Non-hunted* by local people in Payamino (i.e. community members were questioned and bird species were excluded on this analysis to reduce variability). All species that were an important source of protein for the local people were grouped as *hunted*, including *Cuniculus paca*, *Dasyprocta fuliginosa*, *Dasyprocta novemcinctus*, *Mazama* complex (i.e. *M. americana* and *M. gouazoubira*), *Myoprocta pratti*, *Pecari tajacu*, *Tayassu pecari* and *Tapirus terrestris*. The *Non-hunted* group comprised *Eira barbara*, *Tamandua tetradactyla*, *Myrmecophaga tridactyla*, *Panthera onca*, *Puma concolor*, *Priodontes maximus*, *Leopardus pardalis*, *Leopardus wiedii*, *Puma yagouaroundi*, *Hydrochaeris hydrochaeris*, *Nasua nasua* and *Scirius ignitus*. Cameras without any occurrences of the mentioned species were excluded for this analysis due to incompatibility when computing tests (a total of twelve camera datasets were excluded: *Hunted*- 6 cameras; *Non-hunted*- 6 cameras).

Once both groups were defined, and in order to determine if there was an effect on community structure lead by hunting activities in Payamino, two ADONIS tests were run to observe if there were differences within groups' structure (*hunted* and *non-hunted*) between locations. ADONIS permutation test was run following parameters previously mentioned (method: Jaccard, permutations= 10,000). NMDS and ADONIS tests were run with *vegan* package (Oksanen et al., 2015) and plotted with *ggplot2* package (Wickham & Chang, 2015) also in *R* (R-Core Team, 2014).

3.2.3.3. Activity patterns

Activity patterns of the different species were determined where possible. These were defined using the times from the cameras when the pictures were captured. Daytime in Ecuador (i.e. period of light) ranges from 6:30am to 6:30pm, and species that were active only during this periods were defined as diurnal; species active during the other half of the day were considered as nocturnal; and, species present all day around were defined as cathemeral. Only species with a minimum of 11 occurrences were considered as a representative model of the species' behaviour (Monroy-Vilchis et al., 2011).

Three different approaches were undertaken to observe differences in species activity patterns. Firstly, in order to observe if there were changes in species under human pressure, the *hunted* species were plotted for both locations. Secondly, all species present in each location were plotted together to observe general activity levels for both areas. Thirdly, species present at both locations were plotted on the same graph in order to better compare individual species' behaviour.

All species activity patterns were plotted in R with the *ggplot2* package (Wickham & Chang, 2015) and analysed to observe if there existed human pressure and thus, differences in levels of activity across the day existed between locations.

3.3. RESULTS

3.3.1. COMMUNITY STRUCTURES

Although both sites are located in the Ecuadorian Neotropical rainforest, weather conditions are similar between sites and they are relatively close to each other (only 125km apart in relation to the total extent of the Amazon), distinct results were obtained at both locations:

Payamino (Sumaco National Park):

Camera traps in Payamino resulted in a total of 453 animal records (377 mammals - plus seven human captures- and 76 birds) from a total of 1413 camera-trapping nights. A total of 23 different species were observed (one single species not present in Tiputini: *H. hydrochaeris*, n=1) and the most abundant species were *D. novemcinctus* (Dasypodidae fam., n=73), *M. Americana* (Cervidae fam., n=69), *D. fuliginosa* (Dasyproctidae fam., n=55) and *P. crepitans* (Psophiidae fam., n=51). Species RAI were individually calculated and Rodentia, Cingulata and Artiodactyla were the most abundant orders (see full details in Appendix 2.1).

Tiputini (Yasuní National Park):

The Tiputini survey recorded 67% more animal occurrences than the survey in Payamino. There were a total of 685 animal events (559 mammals and 126 birds) within 777 and 788 camera-trapping nights in 2010 and 2011, respectively. A total of 33 species were identified, ten records more than observed in Payamino, including: singletons for three small-medium size mammals (i.e. *Speothos venaticus*, *Sylvilagus brasiliensis* and *Cebus albifrons*) and a bird (i.e. *Timus major*); a doubleton for *Proechimys echinothrix*; three events for *Atelocynus microtis*, *Proechimys canicollis* and *Didelphis marsupialis*; four events of *Priodontes maximus* and *P. onca* (n=15). The most abundant species were *P. crepitans* (Psophiidae fam., n= 107), *M. pratti* (Dasyproctidae fam., n=105), *D. fuliginosa* (Dasyproctidae fam., n=70) and *T. pecari* (Tayassuidae fam., n=55). Species RAI were individually calculated and Gruiformes, Rodentia and Artyodactyla orders were the most abundant (see full details in Appendix 2.1).

	Region	Dates	Cameras	Stations	Trapping nights	Surveyed area(km ²)	Animal events	Effectivity (#pics/day)	Total spp	Unique spp
Tiputini	Yasuní	March - June 2010	11	11	777					
	National	March - June 2011	11	11	788					
	Park	Total			1565	8.64	685	0.43	33	10
Payamino	Sumaco	March - June 2015	25	32	1413	25.13	453	0.32	23	1

Table 3.1 - A comparison between the Tiputini and Payamino surveys.

Although sampling effort was similar for both surveys (measured in camera trapping nights), biodiversity levels were not equal at the two locations. The Shannon index was higher in Tiputini ($H_{TIP}=2.7$ versus $H_{PAY}=2.64$), although the Berger-Parker dominance index was higher in Payamino ($d_{PAY}=0.161$ versus $d_{TIP}=0.153$). The most abundant species differed between locations: in Payamino *D. novemcinctus* was the dominant species; while in Tiputini

the dominant species was *M. pratti*. Rarefaction curves by survey area also showed distinct patterns (see fig. 2.3).

Although in Tiputini the observed number of species was considerably lower than predicted by estimators (Chao 1), rarefactions curves showed how Tiputini had higher absolute levels of diversity (i.e. α -diversity) than in Payamino despite the total surveyed area being a third of the size of the Payamino site. Top levels of observed biodiversity did not reached estimated levels by a long margin in Tiputini (Chao1 predicted a 30% more of species $n'=41$), indicating that a greater sampling effort is needed in order to record all present species. In contrast, the Payamino survey found both lower overall predicted and observed levels of biodiversity suggesting a sufficient sampling effort was carried out with almost all species present at this site recorded.

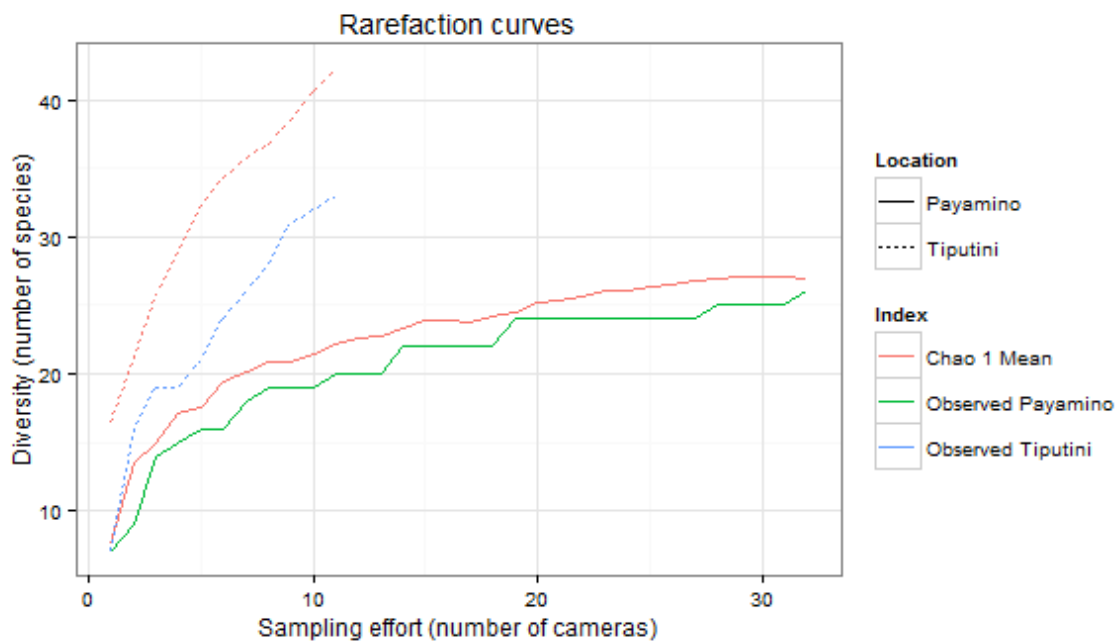


Figure 3.2- Rarefaction curves for both locations (Tiputini and Payamino).The number of detected species increased when both the number of cameras (sampling effort) and the surveyed area increased. Dotted lines correspond to Tiputini survey and solid lines are for Payamino. Chao 1 diversity index was estimated for both locations.

Using the full list of species, NMDS showed a clear difference between locations (see below Fig. 2.3; best solution stress value: 0.204). The ordination showed that cameras in Tiputini captured more similar communities suggesting a higher homogeneity at this site. In contrast, Payamino showed higher values of β -diversity where some cameras captured completely different species observations. The ADONIS test corroborated statistically the observed differences between locations ($F_1= 3.176$, $R^2=0.07532$, $p= 9.999e^{-5}$), with 7.5% of the variation in the data explained by differences in location.

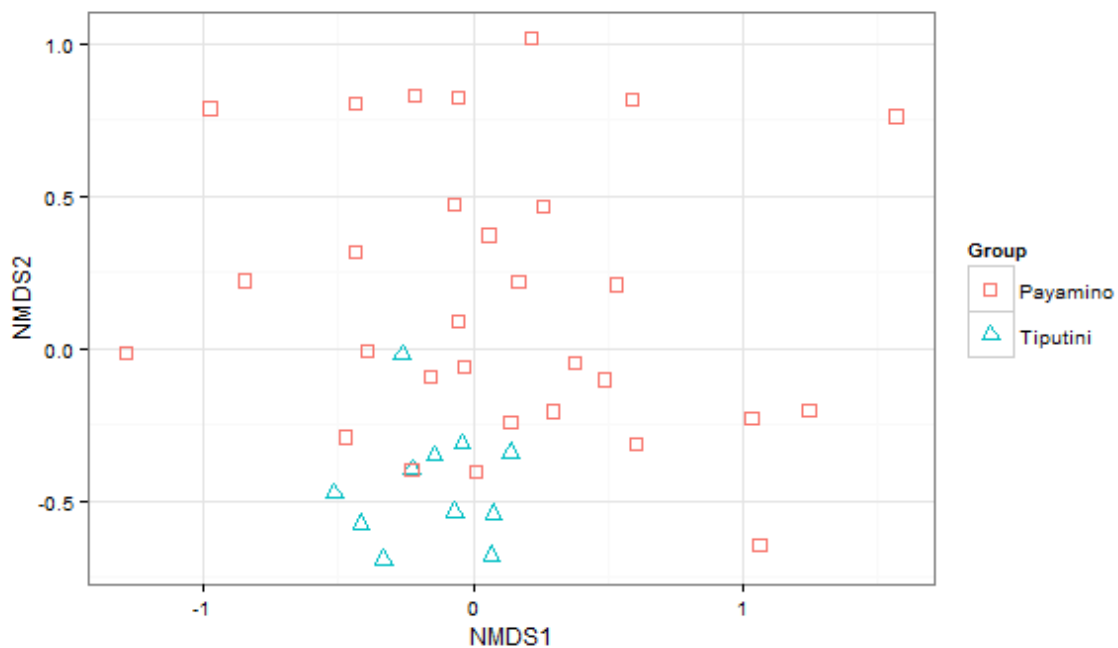


Figure 3.3 - NMDS plot based on animal occurrences per camera (by location). Each value corresponds to a camera dataset for one of the two locations (\square - Payamino, \triangle - Tiputini). Points that are far apart from each other on the graph show cameras that captured different communities of animals to each other, while points that are closer together show cameras with more similar observations to each other. Tiputini showed higher levels of community homogeneity among cameras than Payamino (i.e. β -diversity was higher in Payamino).

3.3.2. HUMAN PRESSURE

The ADONIS test using only those species designated as *hunted* species in Payamino showed significant differences in their community assemblage between the two locations ($F_1= 3.094$, $R^2= 0.08123$, $p\text{-value}= 0.0007$). Similarly, *non-hunted* species also differed significantly between locations ($F_1= 2.512$, $R^2=0.06695$, $p\text{-value}=0.0114$).

When comparing species' relative abundances (see table 3.2 below), Tiputini presented higher values for most of the predators (*P. onca*, *P. concolor* and *L. pardalis*), rodent species (*C. paca*, *D. fuliginosa* and *M. pratti*) and also the larger species such as *T. terrestris* and both peccary species (*P. tajacu* and *T. pecari*). In contrast, *M. americana* and *D. novemcinctus* presented higher abundances in Payamino despite these two species being under hunting pressure. Medium-sized carnivores (*E. barbara*, *N. nasua* and *Leopardus sp.*) also presented higher relative abundances in Payamino, although differences were not that great as the groups previously mentioned. The Myrmecophagidae family (*T. tetradactyla* and *M. tridactyla*) also notably presented more records in Payamino than in Tiputini.

<u>SPECIES RELATIVE ABUNDANCES</u>			
Group		Tiputini	Payamino
Herbivores	<i>C. paca</i>	2.62 [^]	2.12
	<i>M. pratti</i>	6.71 ^{^^^}	2.48
	<i>D. fuliginosa</i>	4.47	3.89
	<i>H. hydrochaeris</i>	NA	0.07
	<i>S. ignitus</i>	0.90 ^{^^^}	0.14
	<i>M. americana</i>	2.75	4.88 ^{^^}
	<i>M. gouazoubira</i>	0.26	NA
Omnivores	<i>T. terrestris</i>	3.32 ^{^^^}	1.49
	<i>P. tajacu</i>	2.24 ^{^^^}	0.92
	<i>T. pecari</i>	3.51 ^{^^^}	0.57
Insectivores	<i>P. maximus</i>	0.26	NA
	<i>D. novemcinctus</i>	2.11	5.17 ^{^^^}
	<i>T. tetradactyla</i>	0.06	0.57 ^{^^^}
	<i>M. tridactyla</i>	0.19	0.57 ^{^^^}
Carnivores	<i>P. onca</i>	0.96	NA
	<i>P. concolor</i>	0.70 ^{^^}	0.43
	<i>L. pardalis</i>	2.94 ^{^^}	1.63
	<i>L. wiedii</i>	0.06	0.28 ^{^^^}
	<i>P. yagouaroundi</i>	0.06	0.07
	<i>E. barbara</i>	0.45	1.06 ^{^^^}
	<i>N. nasua</i>	0.26	0.35 [^]

Table 3.2 - Species relative abundances at both locations calculated as the relationship between the numbers of observations of a determinate species within a time window of 100 camera trapping nights. *Hunted* species are in bold and *NA* means species without records. Species relative abundances with notable increment (+25%; +50%; >100%) when comparing the two locations were marked as [^], ^{^^} and ^{^^^} respectively.

3.3.3. ACTIVITY PATTERNS

All species patterns were plotted together (see fig. 2.4) to observe activity levels per hour at both localities. Wildlife in Tiputini is mainly active during the morning while the wildlife at Payamino is mainly active at night. The maximum activity peak hour in Payamino (21h) almost coincides with the minimum activity level recorded in Tiputini (at 20h). The opposite observation can be found just before dawn (4am). Curiously, both localities presented a relative high activity peak at dusk (17-18h). Another important observation is the irregular pattern recorded across the night in Tiputini, with a drastic reduction of activity just after dusk. In contrast, Payamino showed progressive changes in activity across the day.

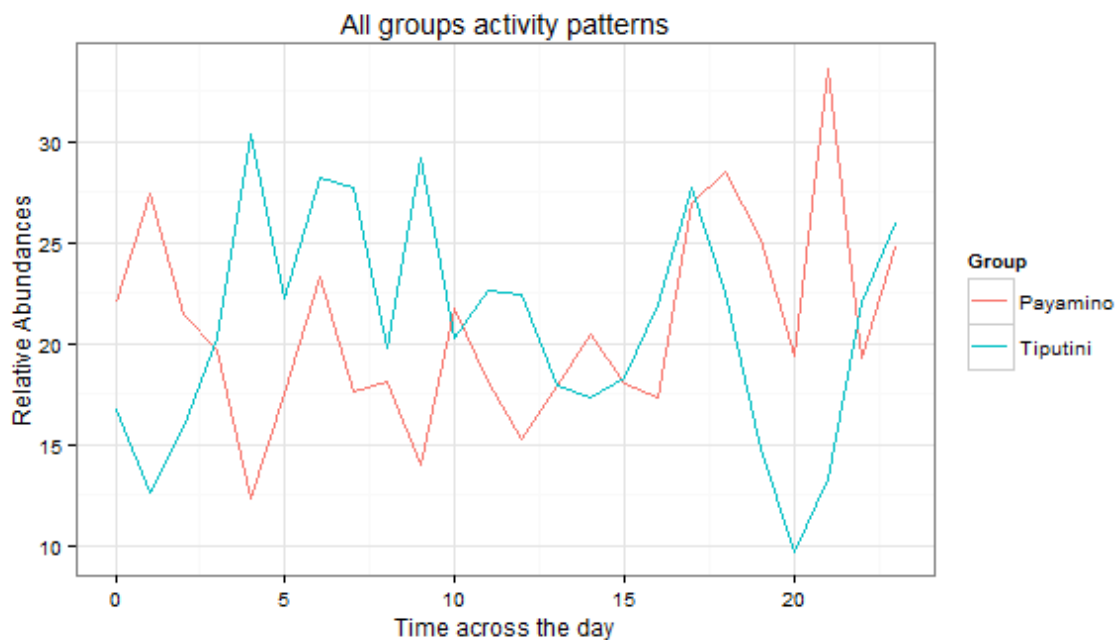


Figure 3.4 - Summary plot with activity patterns of all groups together. Tiputini shows high activity levels during the morning, with a peak before dusk. In Payamino, activity levels increase from dawn until the afternoon with an activity peak early at night and then a decrease in activity across the night.

Activity patterns of functional groups were also plotted for both locations (see below fig. 2.5) and demonstrated clear differences in species' behaviour between the study areas. Following the observations for the full species list (fig. 2.4), Tiputini groups had higher values

of activity during the morning and few hours before dawn. In contrast, in Payamino the peak activity hour for all four groups was after dusk.

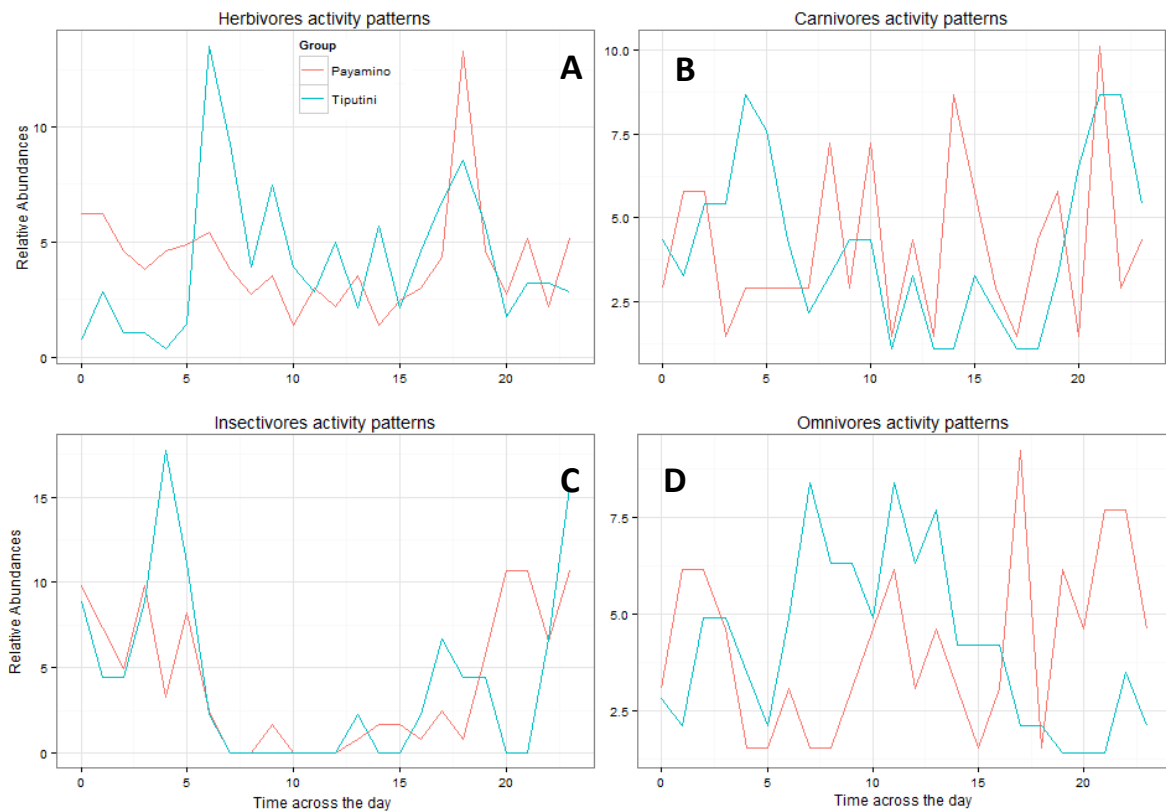


Figure 3.5 - Comparison of activity patterns of functional groups by location. Relative abundances of each functional group across the day (hours) are represented on each graph. **A:** Herbivores, **B:** Carnivores, **C:** Insectivores and, **D:** Omnivores.

Functional group activity patterns (see fig. 2.5) presented differences depending on the group. While *insectivores* presented similar activity patterns at the two locations (but differences for peak hours), *herbivores*, *carnivores* and *omnivores* (graph A, B and D) presented opposing patterns with mostly diurnal activity in Tiputini and mostly nocturnal activity in Payamino (not so evident for the carnivores). Looking at graphs A and B for Payamino, it is possible to observe a direct relation between activity peaks of herbivores and carnivores at dusk. However, this same relation can be observed at dawn time in Tiputini, although they are not completely overlapping. *Carnivores* at Payamino also coincided after dusk (21h) with *insectivores* (Graph C) and *omnivores* (Graph D) maximum activity peaks; preferred time for *D. novemcinctus* (by far the most common insectivore and

potential prey for felids). On the other hand, *carnivores* in Tiputini showed also activity patterns that overlapped with *herbivores* and *insectivores* at dawn time. *Birds* (not represented) had the same diurnal pattern at both locations.

A comparison of the activity patterns of the hunted species showed the clearest change inactivity between the localities (fig. 2.6) coinciding with the observed patterns when grouping by functional groups (see above fig. 2.5). In general, the animals in Tiputini showed higher levels of activity during the day, with the highest levels of activity around 11h. In Payamino the animals preferred to be active at dusk and during the night with peak activity peak at dusk (17-18h).

Individual species activity patterns were also plotted and attached on Appendix 2.2.

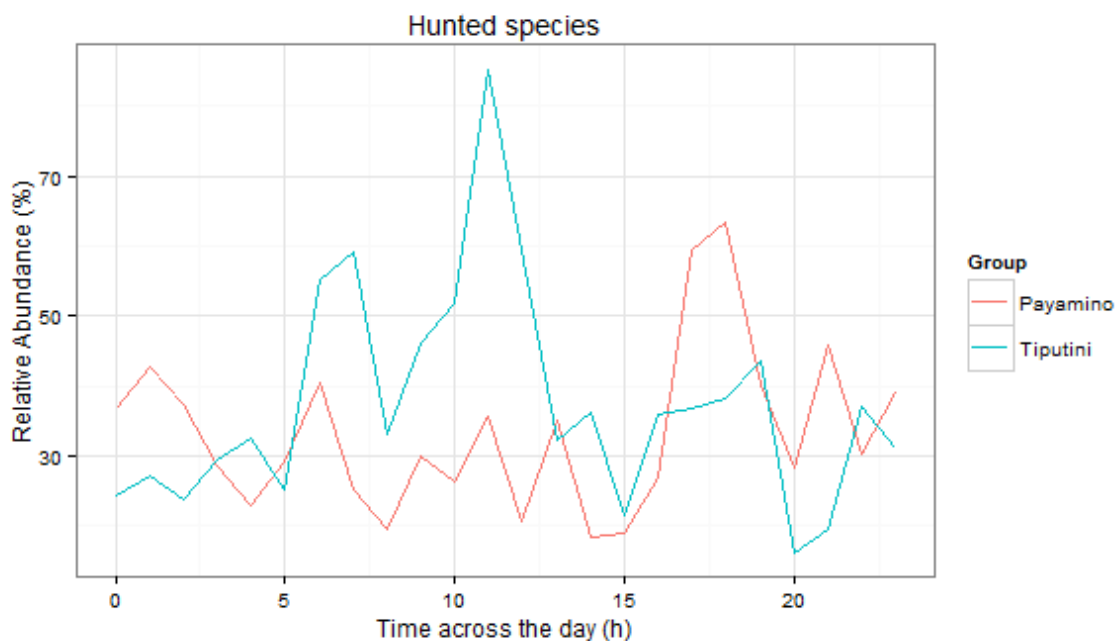


Figure 3.6 - Activity patterns of *hunted* species with relative number of observations according to the hour of the day. Both locations are represented with different colours (Payamino = red; Tiputini = blue).

3.4. DISCUSSION

Results showed high levels of species homogeneity among cameras in Tiputini, a sign of a healthy community. Data from Payamino instead presented higher β -diversity values among cameras, likely due to its heterogeneous territory (primary and secondary forests and disturbed areas). Therefore it seems possible that human activity may have had an effect on the ecosystem due to land conversion and community alteration (as seen in Pardini, 2004; Corlett, 2007; Urquiza-Haas et al., 2009) causing the reduction of absolute levels of biodiversity of terrestrial mammals.

The study of species' activity patterns and their relative abundances also demonstrated differences between the two communities. The most affected species were those with activity peaks at dawn and across the day. The reduced activity just before the dawn in Payamino is evident for most species (i.e. *herbivores*, *carnivores* and *insectivores* functional groups) indicating that human disturbance likely had an impact early in the morning. Relative abundances also diverged between study sites, especially in medium-large sized species (e.g. *T. terrestris*, *M. americana*, *M. tridactyla*) but also in small-sized mammals (e.g. *M. pratti*, *D. novemcinctus*). The absence of the top-predator in Payamino, the jaguar (*P. onca*), might be an indicator of the start of a *mesopredator release effect* with the puma (*P. concolor*) replacing the jaguar as the new top-predator. The authors considered that oil exploration activities carried out for the last months and indigenous extractive activities are a potential cause of the observed differences between Payamino and Tiputini. However, these population fluctuations could also have been produced by imbalances on the trophic network due to the lack of top-predators, suggesting the system is regulated from the top-down.

3.4.1. METHODOLOGY

The methodology used at both locations slightly differed. Both surveys were conducted in the rainy season (March to June) of different years and, although different camera models were used, the authors followed similar camera settings for rainforest conditions and

located the cameras in similar relative positions. Therefore, all animals had the same probabilities of being observed at both locations. Both studies delimited all animal events by a 30minute period between occurrences to preserve the assumption of sampling independence. We note that the total number of cameras differed between locations as did the total surveyed area. However, because we were not estimating densities or occupancy models, but rather defining their community structure, we do not believe these differences were important drivers of the effects we documented.

3.4.2. COMMUNITY STRUCTURE

Although being located in the same ecosystem (*tierra firme*), both study areas contained distinct communities of terrestrial mammals (i.e. richness and abundances). Several factors may have contributed to these differences. Payamino is located closer to the Andean Range and the terrain is not as flat as in Tiputini and, although rainy seasons are similar in length and in amount of rain, Tiputini has larger and longer seasonal floods than those observed in Payamino. As a result of this, Tiputini contains abundant populations of the palm tree *Mauritania flexuosa*, which is only present in swampy areas and whose seeds are an important source of nutrients for tapirs and many other species (Palacios et al., 1999). Another important consideration is the greater effects of human disturbance in Payamino. Firstly, all community members have been living off rainforest resources (i.e. collecting, fishing, hunting and gardening) since their settlement in the early 80's (Irvine, 1987) and they are adapting to the use of new technologies (i.e. motorized boats, chainsaws, sound systems); and secondly, recent oil prospecting has caused short term but intense disturbance, including the use of dynamite.

Tiputini is probably one of the most well preserved tropical rainforests in the world and it has great levels of biodiversity and non-flying mammals are not an exemption. Ahumada et al. (2011) did a comparison among tropical biodiversity hotspots and the richest location (Central Suriname Nature Reserve) presented a lower number of species than found in Tiputini although the survey was conducted in a greater area and for a longer time window.

The Tiputini survey presented notably higher numbers of animal records than Payamino (Tiputini had 685 occurrences vs. 460 in Payamino), representing an increase of 48%. Contrary to the results from Payamino, the *observed* species rarefaction curve for Tiputini (fig. 2.2) did not level off to an asymptote. This is a signal of both a highly preserved and biodiverse region, but also indicates that a greater sampling effort is required in order to observe maximum levels of expected biodiversity. Even though the surveyed area in Tiputini was a third of the one carried out in Payamino, higher α -diversity values were obtained (+43.5%). This is due to its pristine conditions and a great homogeneity in the distribution of mammals around the rainforest (see fig. 2.3).

In contrast, Payamino showed a high heterogeneity among cameras (β -diversity) suggesting that species are not equally distributed in the area. Indeed, the survey in Payamino was conducted in a fragmented landscape, where cameras occasionally were deployed relatively close to *chakras* (garden patches), big trails and human settlements. Even though rarefaction curves almost levelled off meaning that the non-flying mammal community surrounding Payamino community was well sampled.

In addition to the differences in species abundances and species richness, there was also a clear difference in the community structure in a multivariate sense. Overall, 7.5% of the variation in community structure was due to location. This may be partly explained by the fact that human disturbance may reduce the abundance of more sensitive species (e.g. *P. onca*, Peccary complex, *T. terrestris*, *S. venaticus*) while more versatile species like *L. pardalis*, *L. wiedii*, *P. concolor*, Mazama complex or *E. barbara* may have adapted to human presence (most of these carnivores also hunt livestock – Pers. Obs..) and have increased in the presence of human disturbance. Surprisingly, *P. concolor* were found in cameras extremely close to human settlements (around 1km- Pers. Obs..) despite of being described as a species sensitive to disturbance (Brien & Johnson, 2007). In Tiputini instead, presence of top predators produced a different community structure with lower abundances of mesopredators and a higher number of both omnivores and small herbivores. Therefore, the present study might be an example of a top-down trophic cascade from *P. onca* down to *M. pratti*.

3.4.3. HUMAN PRESSURE AND ACTIVITY PATTERNS

When plotting all species behaviour together (fig. 2.4), Tiputini presented an activity peak before dawn and higher activity levels during the morning, while Payamino presented an increase of activity across the afternoon and an activity peak at early night. In general, this is a pattern repeated by functional groups (fig. 2.5) or *hunted* species (fig. 2.6) or when comparing individual species activity patterns between sites (see Appendix 2.2).

The *Kichwa* community is most active in both the community centre and the *chakras* (*Kichwa* gardens) and the oil workers were most active in the forest from early morning until early afternoon (5am-16pm). Results showed a shift in species abundances and activity patterns most probably lead by these daily human activities. *Omnivores* (Peccary complex and *T. terrestris*) were the most affected functional group, with a considerable reduction in their abundances, possibly caused by direct hunting pressure. When looking at the occurrences of *herbivores* and *carnivores*, each presented different patterns for each location. In Payamino, the presence of *herbivores* was reduced across the day and increased throughout the night, a completely opposite pattern to that observed in Tiputini. Payamino *carnivores* instead, presented moderately higher activity during the day than at night, but again the pattern was opposite to that in Tiputini. This is partially explained by differences on species relative abundances, with diurnal species more abundant in Payamino than in Tiputini. In fact, Payamino mesocarnivores with diurnal activity patterns (e.g. *E. barbara*, *Leopardus sp.* and *N. nasua*) are restricted to a reduced number of diurnal prey species, such as small rodents. These results suggest diurnal *carnivores* may have increased their hunting efforts (despite a higher human pressure) due to the reduced number of diurnal *herbivores* in Payamino. Despite of these observed prey-predator relationships, these short-term studies cannot provide enough information to ensure a clear correlation between them and recent human disturbances. This study is a description of a momentary situation in which many other factors are affecting the community structure.

When analyzing species diversity, *herbivores* presented similar levels of richness at both locations. Although abundances and activity patterns differed for a few species, observed differences in *herbivores* structure cannot only be explained by direct hunting pressure. I suggest that these results may also be a product of human pressure on carnivores causing

an indirect effect on the herbivores. Considering the vulnerability of large carnivores to anthropogenic disturbance (Brien & Johnson, 2007) and the increasing human presence around the community's adjacent forest, these circumstances may have led to a change in the carnivores' guild structure. For example, the absence or reduced presence of large top-predators (*P. onca* and *P. concolor*, respectively) can result in an increase in the number and abundance of lower trophic level carnivores as new niches open up in the community (R. S. Moreno et al., 2006; Vance-Chalcraft et al., 2007; Ritchie & Johnson, 2009; Di Bitetti et al., 2010). This concept was defined by Soule et al. (1988) as the *mesopredator release effect* and, Payamino could be suffering from such effect, since the relative abundance of the medium sized carnivores (*E. barbara*, *N. nasua*, *L. wiedii*) doubled or even tripled, except for *L. pardalis*, which presented lower abundance and altered activity pattern in Payamino. This same effect can be understood for *P. onca* where the absence in Payamino leads to new predators as *P. concolor*.

Previous studies have shown how the reduction of big predators can cause many effects on population structures and the present study partially reflects those. Firstly, the loss of big predators can cause changes to occur in the prey species populations (Scognamillo et al., 2003; Novack et al., 2005; R. S. Moreno et al., 2006; Di Bitetti et al., 2010). In Payamino, we observed that numbers of individuals in the Mazama complex and *D. novemcinctus* were unusually high. This is possibly due to a reduction of their main predator *P. onca* (as seen in Harmsen et al., 2011; Moreno, Kays, and Samudio 2006; Santos-Moreno and Pérez-Irineo 2013). Secondly, species activity patterns can be altered by the loss of big predators (see Switalsky 2003). In Payamino: the "early morning effect" on carnivores, herbivores and insectivores can also be partially explained by this lack; and, both small *herbivores* (e.g. *M. pratti*) and diurnal *carnivores* also showed an evident shift in their activity patterns compared to Tiputini. Finally, the loss of top predators can cause an increase in carnivore intraguild competition within the community, which is also known as the *mesocarnivores release effect* (e.g. Allen et al., 2014; Moreno, Kays, and Samudio 2006; Vance-Chalcraft et al., 2007). Although the absolute diversity of carnivores was lower in Payamino than in Tiputini, relative abundances of most of the mesocarnivores (e.g. *E. barbara*, *N. nasua*, *L. wiedii*) were higher in Payamino. In addition, as commented in Chapter 1, two of these

mesopredators are new records for the area, which could be understood as a sign of colonization of new available ecological niches in the forest.

With regard to the nocturnal *carnivores* (Felidae family), these showed two activity peaks in Tiputini (after dusk and before dawn), while in Payamino they showed just a single peak after dusk. This also supports the idea that human activity disturbed early morning carnivores and their preys. In any case, this group had many other nocturnal prey species available (i.e. *herbivores* and, specially, *insectivores*, whose nocturnal behaviour coincide with *carnivores* at both locations) minimizing their competition with diurnal carnivores. With respect to *omnivores* (a heterogeneous group), these presented both nocturnal and diurnal species (i.e. *T. terrestris* are mostly nocturnal and Peccary complex are mostly diurnal). However, individual activity patterns for *T. terrestris* (Appendix 2.2) also demonstrated this repeated *early morning effect* differentiating the two locations.

When comparing the study sites, location explained more variation in the data for the *hunted* species rather than *non-hunted* species (8.1% $p=0.001$ and 6.7% $p=0.011$, respectively). *Non-hunted* group presented lower variation even though many species were only present in a single location (rare and low density species like *P. maximus*, *P. onca* and *H. hydrochaeris*). On the other hand, all *hunted* species were present at both locations and presented a greater amount of variation than *non-hunted* species (+1.4%). Considering both statements, such a difference between a reduced number of *hunted* species ($n=8$) may partially be explained by the effect of human pressure is having on mammal community structure.

The *hunted* species group not only differed in relative abundance at each location, but also in their activity patterns. Among all *hunted* species, Peccary and Mazama complexes are the most coveted hunting game in Payamino (Pers. Obs.) and both groups differed between locations in abundances and activity patterns. The Peccary complex (diurnal) showed a considerable reduction in relative abundances in Payamino, but the Mazama complex (mostly nocturnal) presented a larger population (compared to Tiputini). In the case of strict nocturnal *hunted* species, like *C. paca* and *D. novemcinctus*, only a few animal events were tracked around noon in Payamino. Although differences were not that evident, these behavioural changes implicate important alterations on individual's physiology.

Consequently, human pressure might be affecting not only diurnal species (especially peccaries which move around in packs and are easily observable) but also nocturnal species.

In addition to the hunting disturbance and human pressure in the daytime on wild populations, another possible explanation for these differences in community structure is seasonal or geographical variations. Blake et al. (2012) studied regional and seasonal changes in species activity patterns in the Ecuadorian Amazon and in other Neotropical regions. Firstly regarding the geographical changes, previous studies observed differences in populations from different countries within the Neotropics but, such distances are much greater than the geographical distance between Payamino and Tiputini. Thus, I do not consider there is an effect produced by regional variations between our study areas. Secondly, the same study showed monthly activity variations for *M. americana*, *T. terrestris*, *D. fuliginosa* and *T. pecari* following intricate behavioural changes at Tiputini Research Station, perhaps related to changes in rainfall patterns and habitat uses. Although the present study was performed using the data within the same time window (March-June), the fact they were conducted in different years (2010-11 and 2015), means that we must consider that climatic conditions might have affected wild population structures. It could partially explain low abundances of *hunted* species like the Peccary and Mazama complexes. Hence, we suggest that long-term surveys are needed to better understand non-flying rainforest mammals' biology.

Considering these results and the collected information for such a short period of time, it is difficult to state that community structure divergences between both locations was only a product of direct human pressure (i.e. hunting, resources extractions or fragmentation). Fluctuations on *hunted* species populations are also conditioned by temporal variations of *carnivores'* densities and activity patterns (also seen in Corlett 2007; Novack et al., 2005). Therefore, the possibility still exists that *hunted* species are indirectly affected by an alteration on the *carnivores* community that is in turn caused by human disturbance.

3.5. CONCLUSIONS

It is difficult to assess the effects of human pressure on wild populations (Urquiza-Haas et al., 2009). The lack of previous information on altered ecosystems is a handicap to better understand the ongoing community processes, especially in complex ecosystems like Neotropical rainforests (Ritchie & Johnson, 2009). The present study aims to shed light and partially resolve the unknown effects of oil explorations and human disturbance in general, comparing mammal community structures between disturbed and undisturbed locations. And at the same time, this study can be useful to warn the authorities about the possible consequences when drilling the Yasuni Biosphere Reserve for the upcoming years.

This study partially demonstrated how human disturbance affected terrestrial mammal communities and how Payamino might be under the process of a mesopredators release effect. Roemer et al. (2009) defined three especially dangerous scenarios where ecosystems under this phenomenon can be at risk: total absence of top predators, low biodiversity levels and alien species in the system. Although none of them is currently happening in Payamino, these scenarios are also often produced by alterations on the preferences of carnivores' prey species (see Foster et al., 2010; Moreno, Kays, and Samudio 2006). Unluckily, low relative abundances of carnivores in camera traps data did not allow us to extract clearer results on activity patterns and, therefore on prey-predator relationships. In order to better understand community structure and the possible correlations between carnivores and other species, an analysis of stomach contents would be ideal to determine which species are the main preys and then correlate species presences and abundances. For this purpose, greater survey efforts are needed to obtain samples without disturbing species behaviour. For example, highly trained personnel to spot animal faeces on the super leaf-littered rainforest ground level and increase transect surveys frequency since dung beetles and heavy rains wipe out all kind of faeces and tracks.

Considering that Tiputini has pristine conditions for the natural development of species, its data has reflected what it must be considered the natural behaviour of a wild community in the Neotropical rainforest. On the other hand, Payamino is a special case where an indigenous community has recently had contact with Western society and national government has been carrying out oil prospections for the last decade. Luckily, Payamino

Study 2: Human Disturbance on Terrestrial Mammal Communities. A Comparison between Sumaco National Park and Yasuní Biosphere Reserve (Ecuador)

does not have good quality oil and therefore, its remaining main source of disturbance and management is the indigenous community itself. Not only government authorities but also the scientific community must inform the community and stakeholders about the importance of future decisions and the possible consequences they might have.

In order to fully report how human disturbance can alter terrestrial mammal communities on Neotropical rainforests, a third location with higher anthropogenic disturbance levels and close to both surveyed areas would be ideal to complete the analysis. With this study, the authors wanted to report and make the public aware about the dangers and possible consequences of the oil explorations in the Yasuní-ITT oil block, without considering the alarming outcome of the resulting oil extractions for the biodiversity in one of the world's hotspot.

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4. GENERAL CONCLUSIONS:

4.1. CONCLUSIONS AND CONSIDERATIONS

The present thesis is the outcome of a camera trap study carried out around the *Kichwa* community of San José de Payamino (Orellana, Ecuador) over a three-month period (March-June 2015) in order to study terrestrial mammal populations. The main aim was to undertake the first descriptive study of the mammal community in an area with an evident lack of published information and, afterwards, compare it to another Amazonian rainforest but with comparatively little human disturbance: the Tiputini Biodiversity Station within the Yasuní National Park.

Neotropical rainforests are complex ecosystems where not much is known about the mammal community structure (Lacker and Mares, 1986). For the last half century, humans have been colonizing deep Amazonian areas looking for natural resources (e.g. oil or timber) or planting extensive crops (e.g. oil palm trees or soya)(Pardini, 2004; Nepstad et al., 2008; Suárez et al., 2009; Kissinger et al., 2012). The community of San José de Payamino is enclosed in a special location considered as a world's biodiversity hotspot, the Tropical Andes (def. by Myers et al., 2000). It is located where the Andean range meets the Amazonian rainforest, which starts and expands towards the Atlantic west coast in Brazil. The *Kichwa* community was firmly established along the Payamino River by the 1980's in what is now the buffer area of the Sumaco National Park. In 2013, the community signed a contract with oil companies to start an exploration process throughout the whole community rainforest. Human population density is extremely low (350ha/person, approximately) and they only extract resources for their subsistence, although the author observed a lack of management of their game species. Community members do not demarcate hunting seasons (even if they must know when to hunt each species) and the park authorities do not have any control over the hunting activities of the community because it is not the core area of the National Park. Hunters have preferences over determinate species, such as deer, peccary or tapir; but, all traps and hunting expeditions are based on opportunistic hunting rather than on focusing on these mammal species. There is an evident lack of hunted **species management**, which can alter mammal community structure. Therefore, the question remains as to whether human disturbance is having an effect on wild mammal populations.

Previous studies have suggested that human impact is low in Payamino (Irvine, 1987; O'Reilly-Berkeley et al., 2013; Oldekop et al., 2013) although it is potentially increasing as the population becomes more connected and used to modern technologies. In order to obtain valuable data on how human disturbance may have altered mammal populations in Payamino (i.e. since local community has been extracting natural resources from the forest and fragmenting the landscape with extensive crops plus recent oil explorations), it was compared to one of the most preserved and studied Neotropical forests in Ecuador, the Yasuní National Park.

Tiputini Research Station is located 125km east of Payamino, deeper in the Amazon forest, with difficult access and without any human disturbance except from the research studies carried out in the area. The author took the Tiputini terrestrial mammal community as a reference model of what *natural* species composition and abundance should be in Payamino even though there are seasonal fluctuations in both species abundance and activity patterns (Novack et al., 2005; Harmsen et al., 2011). Previous work of Blake et al. (2012) helped to elaborate this comparative analysis considering the same sampling effort for both surveys.

The main considerations for this work are assuming firstly, that both localities presented similar environmental conditions and secondly, that all species should be represented equally at both locations. However, with the current data available for Sumaco National Park, it is not possible to guarantee these assumptions. Lack of environmental data and information on vegetation composition and river hydrodynamics made it impossible to have a complete description of the natural habitats around Payamino. Although both locations are not so far from each other, and continuous rainforest connects them, increasing human disturbance might have an effect on species natural distributions. Therefore, the results presented here need careful interpretation.

The first chapter consists of a survey conducted using camera traps and transects within the main study area (Payamino). The maximum number of species observed was 25 and there was no direct evidence of a hunting pressure on herbivores (measured as a distance from the community centre). However, these and other species showed differences in both behaviour and abundances when compared to other regions of the Neotropics. For that reason, I considered it possible that these behaviour changes (nocturnal tendency) could be potentially explained by

changes in the populations of carnivores rather than by a direct hunting effect on them. Lack of top-predators was also associated with some herbivores and mesopredators species increasing both their abundance and diversity. In addition to hunting pressure, recent seismic oil explorations (based on the use of explosives) throughout the community might also have altered species occurrences.

In order to shed light on this problem, a comparison was made between Payamino and Tiputini. The results showed how species composition was different between the two locations with Tiputini being a more diverse and homogeneously distributed community than Payamino. When comparing the activity patterns of individual species and functional groups, Payamino species were more active at night while Tiputini presented higher levels of activity across the day. Hunted species showed a significantly greater difference in abundance between locations than non-hunted species, as did their general activity patterns. The study also showed how top-predators seemed to regulate trophic webs in Tiputini and how their absence can alter the community equilibrium. I suggest the possibility that the **Mesopredator Release Effect** is currently starting (or undergoing) around the Payamino community. These results likely suggest, contrary to the findings in chapter one and previous studies in the area, that a human pressure effect is currently affecting the terrestrial mammal community in Payamino.

The Payamino study showed high heterogeneity in species composition most probably as a result of both direct and indirect human disturbance. Possible explanations to this effect are: 1) the *Landscape matrix* is comprised of a mosaic containing a mix of primary and secondary forests, chakras and fallows creating a fragmented habitat where species are geographically segregated; 2) *Human presence*, whether it is by hunting pressure or by oil explorations, is impacting on species abundances and activity patterns.

As Paracelsus (1538) said: “the dose makes the poison”. The main problem with the human pressure (i.e. fragmentation, hunting effect or oil explorations) is the recovery time once the threshold is crossed. Whereas human hunting pressure can temporary alter species presences and it can be mitigated with a hunting management program (with the collaboration of local people), habitat fragmentation or oil extraction activities are potentially longer-term

disturbances, much more destructive and difficult to revert (Laliberte & Ripple, 2004; Nepstad et al., 2008; Boucher et al., 2011; WWF, 2014). Land conversion is the main threat to every ecosystem around the world and the Neotropical Rainforests are not an exception. Previous studies (see Turner, 1996; Cuaron, 2000; Chazdon, 2003) demonstrated how susceptible evergreen rainforest ecosystems are to human disturbance, especially local species when aboveground vegetation is altered.

In reality, San José de Payamino is a small community where mechanical agricultural tools (e.g. chainsaws, tilling machines) have only *recently* been accessible and, while the young generation have become interested in these powerful tools, the older generation mostly prefers to use traditional hunting and farming methods. The lack of knowledge transfer between the older and younger generations is part of the problem and it will be interesting to see their response to how other communities who have, and are currently, suffering the consequences of a massive fragmentation of the ecosystem (i.e. the construction of oil extraction complexes, timber exploitation and extensive crops) have dealt with these issues. However, as is true in all societies, it is difficult to realize the inner problems from which they are suffering until it is too late. As a conservationist, I have the role of giving advice and providing solutions for the problem I think I can help with (for example, it will be interesting to propose the creation of a chart of hunting seasons done by the most experienced hunters of the community or a co-regulation schedule with the park guards); but, as I personally saw, it is difficult to be heard when oil companies are promising them money and construction facilities for the community *ipso facto*. In these cases, long-term projects must be developed in the community and must be supported by government organizations and NGOs. Experience of working in Payamino suggests that conservation ideals imposed from outside parts do not ever really take hold. Therefore, programs must come from the community members and promoted by these organizations. San José de Payamino is in a reversible stage, but the community should redirect their efforts away from increasing their crop's area towards improving the production rates or the fishing extraction techniques and focus on other activities that would give them economic benefits without the loss of the natural capital.

Unluckily, due to the economic recession and against the public will, the Ecuadorian national government has decided to exploit Yasuní National Park: one of the richest areas around the globe for both species biodiversity levels and oil reservoirs abundance. Such big oil extractions can irreversibly alter the ecosystem with serious outcomes not only for the species communities (i.e. fungi, animal and vegetal), but also for human indigenous settlements, and the effects can last for generations. Our study indicates that even low levels of disturbance have the potential to dramatically alter species relative abundances and activity patterns. If the government finally decides to extract all the oil present in the ITT-block, grave consequences can occur at local, national and international levels.

A literature review presented by Turner (1996) found that birds were the most studied animal group in tropical rainforests. Generally, mammals have elusive behaviours and are more difficult to spot, for these and other reasons, there is an evident dearth of information about mammal populations in Ecuador. This study is very important since it is the first elaborated with these purposes in the Sumaco National Park and, probably, one of the first mammal surveys conducted in Ecuador in an active oil prospection area (as far as the authors know). It has provided baseline information on how medium-sized terrestrial mammal populations are locally structured with the presence and absence of humans in the Ecuadorian Amazon. Nevertheless, Neotropical rainforests are complex ecosystems with intricate species interactions and still unknown lots of undergoing factors associated and, these sorts of studies must be taken carefully because from the same results different conclusions can be drawn. For these reasons, further studies are needed and must consider increasing the sampling periods in order to better understand seasonal population fluctuations. Furthermore, in the case of Payamino a new deep social study (as the one carried out by Irvine, 1987) would be interesting to identify changes in community habits such as natural resources extraction, hunting and fishing pressure or crops abundance. These studies would provide us with a better idea about how the community has been altering the biodiversity, where this disturbance is leading to and how this can be solved encouraging the community and getting new generations actively involved.

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5. APPENDICES:

5.1. APPENDICES STUDY 1

Appendix 1.1. Table of animal occurrences observed in San José de Payamino.

	Order	Family	Common name	Species name	Functional Group	Animal Events	RAI	Behaviour	
Mammals	Artyodactyla	Cervidae	Red brocket deer	<i>Mazama americana</i>	Herbivores	86	4.84	Cathemeral	
				Mazama complex (trans.)	-	25	-	-	
		Tayassuidae	White-lipped peccary	<i>Pecari tajacu</i>	Omnivores	16	0.90	Diurnal	
				Collared peccary	<i>Tayassu pecari</i>	Omnivores	15	0.84	Cathemeral
				Peccary complex (trans.)	-	10	-	-	
	Carnivora	Felidae	Puma	<i>Puma concolor</i>	Carnivores	9	0.51	-	
				Ocelot	<i>Leopardus pardalis</i>	Carnivores	30	1.63	Cathemeral
			Margay	<i>Leopardus wiedii</i>	Carnivores	5	0.23	-	
			Jaguarondi	<i>Puma yaguaroundi</i>	Carnivores	1	0.06	-	
			Tayra	<i>Eira Barbara</i>	Carnivores	21	1.18	Diurnal	
			South American coati	<i>Nasua nasua</i>	Carnivores	6	0.34	-	
			Cingulata	Dasypodidae	Giant armadillo	<i>Priodontes maximus</i> (trans.)	-	1	-
	Nine-banded armadillo	<i>Dasypus novemcinctus</i>			Insectivores	106 (3)	5.80	Nocturnal	
	Perissodactyla	Tapiridae	Lowland tapir	<i>Tapirus terrestris</i>	Omnivores	66 (32)	1.91	Nocturnal	
	Pilosa	Myrmecophagidae	Southern tamandua	<i>Tamandua tetradactyla</i>	Insectivores	10	0.56	-	
			Giant anteater	<i>Myrmecophaga tridactyla</i>	Insectivores	10 (2)	0.45	-	

	Primates	Hominidae	Human	<i>Homo sapiens</i>	-	43	2.42	-
	Rodentia	Caviidae	Capybara	<i>Hydrochaeris hydrochaeris</i>	Herbivores	1	0.06	-
		Cuniculidae	Paca	<i>Cuniculus paca</i>	Herbivores	45 (3)	2.36	Nocturnal
		Dasyproctidae	Green acouti	<i>Myoprocta pratti</i>	Herbivores	42	2.36	Diurnal
			Black agouti	<i>Dasyprocta fuliginosa</i>	Herbivores	80 (15)	3.66	Cathemeral
		Sciuridade	Bolivian squirrel	<i>Scirius ignitus</i>	Herbivores	2	0.11	-
Birds	Columbiformes	Columbidae	Grey-fronted dove	<i>Leptotila rufaxilla</i>	Birds	20	1.13	Diurnal
	Gruiformes	Psophiidae	Grey-winged trumpeter	<i>Psophia crepitans</i>	Birds	59	3.32	Diurnal
	Galliformes	Cracidae	Spix's guan	<i>Penelope jacquacu</i>	Birds	2	0.11	-
			Nocturnal curassow	<i>Nothocrax urumutum</i>	Birds	2	0.11	-
	Tinamiformes	Tinamidae	Great tinamou	<i>Timus major</i>	Birds	23	1.29	Diurnal
Reptile	Squamata	Unknown	Unknown	Lizard sp.	-	3	0.17	-

Taxonomic classification of all observed species down to species level (when possible). Giant armadillo and both Peccary and Mazama complex have only data observed by transects (trans. – grey highlight). Total occurrences contains the number of animal events recorded by transects between brackets. **RAI** represents the number of occurrences within a total of 100 camera trapping nights. Species behaviours were defined by the time of most of the occurrences were observed.

Appendix 1.2. Estimators and observed species information related to sampling effort (num. of cameras)

Survey	Cameras	Chao 1	Shannon Mean	Observed
CAMERA TRAPPING SYSTEM (MARCH-JUNE 2015)	1	7.26	1.22	7
	2	11.63	1.74	9
	3	15.08	2.03	13
	4	17.39	2.22	13
	5	18.49	2.29	14
	6	19.54	2.36	14
	7	21.54	2.41	16
	8	22.25	2.44	17
	9	22.29	2.48	17
	10	22.27	2.5	17
	11	22.51	2.52	18
	12	22.79	2.53	18
	13	23.14	2.54	18
	14	23.58	2.55	20
	15	24.46	2.56	20
	16	24.96	2.57	20
	17	24.88	2.57	20
	18	25.22	2.58	20
	19	25.3	2.58	22
	20	25.59	2.58	22
	21	25.4	2.59	22
TRANSECTS	22	25.83	2.6	22
	23	25.86	2.6	22
	24	25.19	2.6	22
	25	25.28	2.6	22
	26	25.08	2.61	22
	27	25.39	2.61	22
	28	24.98	2.61	23
	29	24.83	2.62	23
	30	25.1	2.62	23

	31	24.88	2.62	23
PREVIOUS CAMERA-TRAP SURVEY (AUG 14 – FEB 15)	32	24.95	2.63	24
	33	24.94	2.63	24
	34	24.9	2.63	24
	35	24.89	2.63	24
	36	24.86	2.63	24
	37	24.76	2.63	24
	38	24.69	2.63	24
	39	24.35	2.64	24
	40	24.39	2.64	24
	41	24.3	2.64	24
	42	24.25	2.64	24

5.2. APPENDICES STUDY 2

Appendix 2.1 – Full detailed list of species names, occurrences number, relative abundances indices (RAI) and behaviour at both locations:

	Order	Family	Common name	Species name	TIPUTINI			PAYAMINO		
					Indiv. Obs.	RAI	Behaviour	Indiv. Obs.	RAI	Behaviour
Mammals	Artyodactyla	Cervidae	Red brocket deer	<i>Mazama americana</i>	43	2.75	N	69	4.88	MN
			Gray brocket	<i>Mazama gouazoubira</i>	4	0.26	-	?	?	-
	Carnivora	Tayassuidae	White-lipped peccary	<i>Pecari tajacu</i>	35	2.24	D	13	0.92	D
			Collared peccary	<i>Tayassu pecari</i>	55	3.51	C	8	0.57	C
		Canidae	Bush dog	<i>Speothos venaticus</i>	1	0.06	-	0	0.00	-
			Short-eared dog	<i>Atelocynus microtis</i>	3	0.19	-	0	0.00	-
	Felidae	Jaguar	<i>Panthera onca</i>	15	0.96	N	0	0.00	N	
		Puma	<i>Puma concolor</i>	11	0.70	N	6	0.42	N	
		Ocelot	<i>Leopardus pardalis</i>	46	2.94	N	23	1.63	MN	
		Margay	<i>Leopardus wideii</i>	1	0.06	-	4	0.28	N	
		Jaguarondi	<i>Puma yaguarondi</i>	1	0.06	-	1	0.07	-	
		Tayra	<i>Eira barbara</i>	7	0.45	-	15	1.06	D	
		South American coati	<i>Nasua nasua</i>	4	0.26	-	5	0.35	-	
	Cingulata	Dasypodidae	Giant armadillo	<i>Priodontes maximus</i>	4	0.26	-	0	0.00	-
			Nine-banded armadillo	<i>Dasypus novemcinctus</i>	33	2.11	N	73	5.17	N
Didelphimorphia	Didelphidae	Common opossum	<i>Didelphis marsupialis</i>	3	0.19	-	0	0.00	-	

	Lagomorpha	Leporidae	Tapeti	<i>Sylvilagus brasiliensis</i>	1	0.06	-	0	0.00		
	Perissodactyla	Tapiridae	Lowland tapir	<i>Tapirus terrestris</i>	52	3.32	N	21	1.49	N	
	Pilosa	Myrmecophagidae	Southern tamandua	<i>Tamandua tetradactyla</i>	1	0.06	-	8	0.57	-	
			Giant anteater	<i>Myrmecophaga tridactyla</i>	3	0.19	-	8	0.57	-	
	Primates	Cebidae	White-fronted capuchin	<i>Cebus albifrons</i>	1	0.06	-	0	0.00	-	
	Rodentia	Caviidae	Capybara	<i>Hydrochaeris hydrochaeris</i>	0	0.00	-	1	0.07	-	
		Cuniculidae	Paca	<i>Cuniculus paca</i>	41	2.62	N	30	2.12	N	
		Dasyproctidae		Green acouti	<i>Myoprocta pratti</i>	105	6.71	D	35	2.48	D
				Black agouti	<i>Dasyprocta fuliginosa</i>	70	4.47	D	55	3.89	D
		Echimyidae		Colombian spiny rat	<i>Proechimys canicollis</i>	3	0.19	-	0	0.00	-
				Stiff-spine spiny rat	<i>Proechmys echinothrix</i>	2	0.13	-	0	0.00	-
		Sciuridae		Bolivian squirrel	<i>Sciurus ignitus</i>	14	0.89	D	2	0.14	-
		Birds	Columbiformes	Columbidae	Grey-fronted dove	<i>Leptotila rufaxilla</i>	1	0.06	D	12	0.85
	Galliformes		Cracidae	Salvin's curassow	<i>Mitris salvini</i>	12	0.77	D	0	0.00	-
Spix's guan				<i>Penelope jacquacu</i>	3	0.19	-	1	0.07	-	
Nocturnal curassow				<i>Nothocrax urumutum</i>	2	0.13	-	1	0.07	-	
Gruiformes	Psophiidae		Grey-winged trumpeter	<i>Psophia crepitans</i>	107	6.84	D	51	3.61	D	
Tinamiformes	Tinamidae		Great tinamou	<i>Timus major</i>	1	0.06	-	11	0.78	D	

Animal events were identified down to species level and calculated the number of observations registered by camera traps. Relative Abundance Index (**RAI**) corresponds to number of occurrences/100 camera trap nights. Behaviour was defined depending on sights timing (**C**:Cathemeral; **D**:Diurnal; **N**:Nocturnal;**MN**:Mostly Nocturnal).

Summary table of total number of animal events at both locations:

Group	Tiputini Events	Payamino Events
Mammals	559	377
Birds	126	76
Total	685	453

Appendix 2.2 Pair wise comparisons of single species activity patterns present in Payamino (red) and Tiputini (blue). Relative abundances were plotted across the day (in hours).

