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**A SCIENTIFIC AND ETHICAL ARGUMENT AGAINST DEFORESTATION IN
LATIN AMERICA: COSTA RICA AS A CASE STUDY**

**A thesis submitted to
Regis College
The Honors Program
in partial fulfillment of the requirements
for Graduation with Honors**

by

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May 2017

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Introduction

I was first introduced to the rainforests of Costa Rica two years ago as a student in a primate ecology travel learning course. This course took me to La Suerte Biological Field Station in northeastern Costa Rica and began my infatuation with rainforest ecology. In such a complex and beautiful ecosystem, it is hard to ever truly understand how each organism survives and interacts with others and its environment but it is easy to appreciate the beauty of these unknown interactions and to wonder at the sheer amount of life present in such a small space. I began my study to determine how two of the primate species in this forest were sharing their resources by investigating their tree preference as a means of determining differences in habitat use. With the help of grant money from Regis and guidance from Dr. Amy Schreier, I returned the following summer to continue my research in an attempt to learn as much as possible about the interactions of life in the rainforest.

During my two summers in Costa Rica, the extent of deforestation and habitat destruction was very obvious. In some areas of the region, fields of bananas and pineapples stretched out of sight on either side of the road and industrial machinery spit fumes. In other areas, green grass fields dotted with cows accentuated the puzzle-piece strips of rainforest in the distance. Even at La Suerte, the lush beauty of the forest ended all too abruptly at the property fence with fields and palm plantations on the other side. With such an obvious mosaic of destruction, I wondered how my research question fit into the bigger picture of habitat loss in the tropics.

This thesis explores the larger picture of tropical rainforest deforestation from two distinct angles, science and ethics. In the first chapter, I explain the current state of tropical rainforest as we know it. This covers both the natural processes and function of tropical rainforest, but also how and why deforestation is so damaging in the form of both lost habitat as well as compromise to remaining forest fragments like La Suerte. The change of climate and resource conditions to remaining forest fragments after deforestation is an often overlooked but very important aspect of deforestation that deserves careful consideration.

The second and third chapters examine more specifically Latin America and Costa Rica and the unique pressures faced by those areas. Due to the relatively recent colonial history of this part of the world, international influence has a large impact on the state of these rainforests. In fact, international agriculture companies and international investment in cattle are two are the largest causes of rainforest loss in these regions (Bonilla 1985; Rosero-Bixby and Palloni 1996). However, Costa Rica in particular has a number of unique reforestation and conservation efforts. These include a Payment for Environmental Services program (PES) as well as an impressive number of reserves and national parks (Mongabay 2006, Andam et al. 2013). These efforts as well as the still-prominent international agriculture and cattle ranching make the country an incredibly diverse area of study with environments in almost every stage between totally protected and totally deforested.

This is the setting in which I placed my research, an analysis of tree preference in white-faced capuchins and mantled howler monkeys. For one month each summer from 2015-2016 I recorded trees used by these primates for feeding and for resting. I collected data on a total of 183 trees over the course of 54 hours of behavioral data. These data showed a distinct difference in tree use between the two species in number of trees used as well as size and level of trees. This research, when put in the context of a greater body of scientific studies on habitat use of these primates in the tropics, confirms the dietary and activity pattern flexibility of these primates. However, my research also emphasizes an accentuated difference in activity pattern that could be attributed to the limited resources available in the forest fragment in which these primates live. These findings suggest that human alteration of rainforests is forcing changes to the behavioral patterns of primates and shifting their use of their environment. This could have negative long-term effects on the health of rainforest ecosystems.

Despite the knowledge we gain by scientific study, there is no way to understand all of the interactions within the rainforest or how behavioral changes in primates will affect the forest in 10 years. These are some of the shortcomings of science, and why I argue in chapter 4 for the value of ethics in the conversation about deforestation. Whether through a utilitarian concern for protection of resources for our own good or via an argument for the intrinsic value of ecosystems as a whole, we as humans are obligated to fight for conservation of the rainforest. This is a complicated battle in the

face of human poverty and indigenous peoples who all have different moral rights to utilization of the rainforest. However, because we are the dominant reason for loss of environment and loss of non-human life, we have an obligation to limit or stop our species' impact on tropical rainforest.

Through the arguments posed in this thesis, I attempt to convince readers of the importance of tropical rainforests as well as the significance of the damage done by humans. Through proposing different ways of considering this value (i.e., scientific and ethical), I hope to both inform readers and appeal to people by whatever means of consideration is most important to them. Issues of rainforest conservation, as with many matters, are not black and white. While conservation is critically important, so is ensuring that all members of our human community have access to food and water. Due to such conflict, we often cannot remain clearly on one side of the issue. In these cases, it is important to have all the knowledge available through scientific study as well as the clear ethical principles with which we can make decisions. There is no way to protect all tropical rainforest in a virgin state. However, we are responsible for doing the best we can to keep as many ecosystems as possible intact with all of the beautiful life and interactions they contain.

Chapter 1. Tropical Rainforest Dynamics

I. Characteristics, ecosystem services, and biodiversity

Tropical rainforest is a unique habitat located between latitudes 23.5 degrees north and south of the equator. These forests are characterized by year-round high temperatures between 20 and 30 °C and high levels of precipitation between 250 and 450 cm/year (Butler 2006). Many tropical rainforests experience a small amount of seasonality in rainfall due to the seasonal shifting of the Intertropical Convergence Zone (ITCZ), the place at which air masses from the northern and southern hemispheres meet and rise, causing precipitation. The tilt of the equator in relation to the sun causes seasonal differences between the northern and southern hemisphere, moving the ITCZ between 23.5°N and 23.5°S and with it, the bulk of precipitation (NOAA). The degree of seasonality in rainfall varies depending on the distance from the equator. The resulting fluctuation in soil moisture is thought to stimulate cycles in soil nutrient availability by changing the populations of soil microbes responsible for decomposition and nutrient release. This results in nutrient “pulses” throughout the year that, in conjunction with changing soil moisture levels, may even stimulate the uptake of minerals by vegetation in otherwise nutrient-poor soil (Birch 1958; Lodge et al. 1994).

Because of the amount of precipitation tropical rainforests receive, soils are often leached of most nutrients and most are nitrogen and phosphorous deficient (Park 1992). Despite this, there are high levels of vegetation growth, allowing tropical rainforests to harbor the greatest amount of biodiversity in the world (Laurance et al.

2006, 2007). Estimates suggest the rainforest contains half of the world's total biomass, mostly in the form of vegetation (Elsworth 1990). The net primary productivity of rainforests (total amount of biomass produced excluding sugars used for respiration) includes litter, roots, pollen, resins, flowers, and fruit, but the greatest component is tree wood, as trees are the predominant form of vegetation in these habitats (Whitmore 1998). Moreover, large trees are especially important in tropical rainforests. Sist et al. (2014) found that even though large trees (Diameter at Breast Height > 60cm) made up less than 10% of tree density, they contribute almost half of the above-ground carbon mass. Diameter at breast height (DBH) is a common measurement of tree size, calculated from the circumference (cm) at approximately 1.5m above the ground. Larger trees generally correspond to both greater biomass as well as greater productivity (Niklas, 1993; Peters et al., 1988).

In addition to the species richness of trees, diversity and evenness of tree species are also high in rainforests. For example, up to 606 and 609 trees of 300 and 307 different species, respectively, were found in 1 ha plots in Ecuador (Gentry 1988b; Valencia et al. 2004). This abundance of trees allows habitat for climbers and epiphytes and creates a vertically stratified environment in which vegetation is sorted by light availability, with the tallest trees making up a broad canopy receiving most of the sunlight while the lower levels of trees get less light and the shrub undergrowth receives very little light. The traditional representation of this complex three-dimensional

environment includes five layers with the upper 3 layers made up of various trees and the lower two levels representing the undergrowth types (Goudie 1984).

The complex habitats and abundance of plant resources of tropical rainforests are home to birds, reptiles, amphibians, insects, and mammals, many of which are yet to be discovered. The International Union for the Conservation of Nature (IUCN) estimates that 5-30 million species exist on Earth, and that of these, only 1.8 million have been described (IUCN 2008). Tropical rainforests are home to 50-90 percent of these species, including up to 2-3 million species of animals, though the vast majority of these species are invertebrates like insects (Whitmore 1998). The better-studied vertebrate population shows notable differences between the three main tropical areas: Asia, the Americas, and Africa. For example, more species of primates and birds are found in the Americas than Africa or Asia, but the greatest total primate biomass is found in Africa along with a greater number of primate species reliant on leaves instead of fruit (Whitmore 1998).

The incredible species diversity of the tropics is likely due to the fact that the frequency of speciation events in the tropics is significantly higher than those at higher latitudes. Limited seasonality and associated energy fluctuations allow for increased speciation because of the longer reproductive window. Not only do tropical rainforest environments lack the yearly cold temperatures that normally suspend reproductive activities, but they also have nearly constant energy input from the sun, allowing plants and animals to grow and reproduce year-round (Martin and McKay 2004). The result of

this perpetual growing/reproductive season is higher variation in species leading to greater frequency of speciation. Even the most disturbed and fragmented forests have more plant species than would be needed to reach full primary productivity, demonstrating the excess of species present in the rainforest (Ewel and Bigelow 1996). The diversity of tropical rainforests provides a variety of habitats and resources for organisms to use, encouraging symbiotic relationships (Park 1992). These factors combine to allow for greater numbers of species to evolve and survive in these more energy and resource-rich environments than at higher latitudes.

Tropical rainforests also serve important roles in global cycles. Tropical rainforests store large amounts of atmospheric carbon in trees because the activity of heterotrophic organisms in the soil process soil carbon very quickly, preventing significant soil carbon storage (Whitmore 1998). Decomposition in rainforest soils is rapid and increases with moisture, and thus there is a strong seasonality in soil carbon flux with more storage in the dry season than in the wet season. The drying of soils and reduced heterotrophic respiration of soil organisms in the dry season work in conjunction with increased radiation and increasing biomass growth to increase the overall tropical carbon stores (Rowland et al. 2014). Tree density is important for carbon storage, but the presence of large trees plays an even larger role in carbon dynamics because of their above-ground carbon mass. Because very little carbon can be stored in rainforest soils, the above-ground mass is the driver of carbon sequestration,

the removal and storage of carbon from the atmosphere (Rowland et al. 2014; Whitmore 1998).

Rainforests are key players in the global water cycle as well. Water lost to the atmosphere (evapotranspiration) is a combination of evaporation off surfaces and transpiration, water lost through stomatal pores during photosynthesis (Schlesinger and Jasechko 2014). In tropical rainforests, the transpiration to evaporation fraction (T/ET) is as high as 71%, almost 50% higher than dry land habitats (51%) (Schlesinger and Jasechko 2014). This unique balance is responsible for the large amount of water cycled through the rainforest, adding to the high levels of precipitation.

As one of the greatest carbon stores on earth and a key factor in maintenance of the water cycle, tropical rainforests are incredibly valuable. As CO² levels increase in the atmosphere, loss of carbon stores mean loss of places to put excess carbon as well as more carbon in the atmosphere (Sist et al. 2014). Deforestation via logging and clear-cutting directly results in greenhouse gas emissions due to the use of machinery and fire, increasing the negative effects that deforestation has on the carbon cycle. Additionally, though little research has focused on the effect of land use changes on the water cycle, a shift from rainforest to agriculture means a significant reduction in transpiration for an area. Minimizing this important transpiration factor in the T/ET fraction results in loss of humidity in the atmosphere. Additionally, as forests are replaced with crops, more water runs off and is lost with no increase in evaporation to make up for the loss (Salemi et al. 2013). This results in a net loss of water to the

system and a drying of the area as precipitation decreases, creating a positive feedback system making it harder for forests to regenerate, and perpetuating the change in landscape (Betts 2004). This alteration to the water cycle has potentially far-reaching effects as it changes the climate patterns of the region as the climate continues to get drier.

II. Deforestation of tropical rainforests

Loss of tropical rainforests is one of the greatest threats to biodiversity globally (Laurance et al. 2006, 2007). Clearing forests not only causes net loss of habitat for animals, but leaves remaining forests fragmented and climates altered, resulting in both smaller and much changed habitats for the surviving animals (Murica 1995; Fahrig 2003; Santos et al. 2010). Total deforestation as well as selective logging and forest fragmentation compromise animal habitat and resources and negatively impact the amount of carbon storage and the ability to cycle water (Yonekura et al. 2012). Unfortunately, these disturbed forests make up a greater percentage of remaining tropical habitat than ever before.

Deforestation, or loss of forest cover, can happen in a number of ways. In tropical rainforests this can be natural (e.g., caused by disease, insect infestation, or weather), though large-scale tropical deforestation is primarily due to anthropogenic activity (e.g., logging and clear-cutting; Park 1992). Natural forest loss is generally localized, though epidemics like disease and fungus can have far-reaching impacts. In

the tropics, the majority of natural forest loss is due to extreme weather events. In Papua New Guinea, the land is often changing, and forests are affected by landslides, river floods, and volcanic activity (Whitmore 1998). In Peru, regular catastrophic flooding of the Amazonian headwaters wipes out strips of forest annually. In the Brazilian Amazon, wind storms are the cause for large areas of forest loss (Whitmore 1998). After these natural events, regeneration occurs naturally via primary or (more rarely) secondary succession, depending on whether the soil seed bank has been disrupted. This can occur immediately after disturbance, and is an entirely natural process (Park 1992).

Human disturbance is most commonly in the form of selective logging programs, and while they retain some features of the environment, they greatly compromise primary habitat (Park 1992). Selective logging allows more wind and thus dryness to penetrate a rainforest as it lets more air pass through trees, reducing evapotranspiration and vegetation growth. It also increases human access to a rainforest via road building (Reynolds and Peres 2006). This form of logging is meant to be a sustainable form of harvesting natural resources with cutting cycles far enough apart for tree maturation and species logged monitored to foster regrowth. For example, if a shade-tolerant species is being cut, fewer trees will be taken to ensure canopy cover remains intact in order to foster regrowth of this species. However, the potential for profit from logging as well as the lack of research on actual regeneration

times for the trees and impacts of these programs means that selective logging is rarely carried out in a truly sustainable manner (Reynolds and Peres 2006).

Despite negative effects on species diversity, partially disturbed and altered forest environments have been found to support some reptile and amphibian species (albeit in significantly different populations), as long as complete canopy and complex habitats are retained (Gillespie et al. 2015). Similarly, most populations suffer more with full deforestation (i.e, habitat loss) than with only partial disturbance (i.e., habitat degradation), and the presence of nearby contiguous forest helps retain biodiversity (Duraes et al. 2013). Though some species are able to compensate or adapt to survive in selectively logged rainforest environments, many other species do not fare so well. Even those reptile, amphibian, and bird species found to survive do so with altered population dynamics and in smaller groups.

Human-mediated total deforestation used to be localized as small plots were cleared for family agriculture (Park 1992). Today, however, large stands of forest (mostly in the tropics) are cleared for industrial agriculture and cattle ranching. In the 1960s, the conversion of Latin American rainforest to cropland was highly encouraged by governments as a means of claiming territory and reducing demographic pressures in cities (Southgate, 1998). This trend continued through the 1980s, especially in the Amazon even though the lack of success in agriculture was noted in the early 1970s. Archard et al. (2002) estimated that tropical forest was lost at a rate of 8 million ha per year from 1990-2000 and 7.6 million ha per year from 2000 -2010. This rate shows very

little slowing of deforestation in recent years. However, this rate is significantly lower than the estimates of 10 million ha per year loss in the late 1980s (Park 1992).

The largest direct cause of total deforestation is conversion to cropland and pasture (Lindsey 2007). Because of the poor nutrient quality of tropical rainforests, agriculture is not incredibly productive in the tropics. Once a patch is cleared for agriculture, the litter that once was broken down for nutrients is gone, and there is nothing left to replenish the constantly leached soil. Traditionally, slash and burn agriculture provided enough organic material for crops to grow, but farmers had to move every 4-8 years. This was sustainable in a time of fewer people as the plots had time to regrow to mature rainforest within a few years of abandonment and were left alone by other farmers (Goldsmith and Hildyard 1990). The practice of slash and burn, or shifting cultivation degrades large areas of forest and expanded exponentially with recent increases in human population. Furthermore, international interest began to take hold via plantation agriculture, a means to grow tropical crops (bananas, coconuts, pineapple, etc.) in large quantities for export (Park 1992). These exploitative farming practices are encouraged by governments decreasing or subsidizing land prices. When land becomes void of nutrients, it has historically been cheaper to simply buy new land and move on than to regenerate an old plot (Schneider 1995). Similarly, government subsidies on land for industrial purposes make buying large plots of land to use for export crops economically lucrative (Rossero Bixby and Palloni 1996). However, monocrop plantations are often risky in the tropics with poor soils and the prevalence of

disease (Park 1992). Despite these risks, these forms of export-oriented agriculture have been steadily increasing for the past 40 years. Forest plantations covered nearly 28,000ha of the Americas in 2000 and had an estimated annual planting rate of 370ha/yr (FAO).

Cattle-ranching follows a similar trend. As ranching became a lucrative business, governments (almost exclusively in Latin America) provided land subsidies and international investors profited off of exported beef (Elsworth 1990). Similar to agriculture, the poor soil quality in the tropics means that large areas of land are required to support enough primary production to feed cattle after the forest has been cleared and ranching operations generally have to move every 5-8 years (Park 1992). These ranches are logged first and then used to raise cattle for international export. Little of the money from this lucrative business ever benefits the host country. After the land is purchased, land from the sale of meat funds the ranchers, and the profits from logging of said land often goes directly to the investor (Park 1992). This hugely damaging process not only exploits the land, but also the country that allows this degradation.

As agricultural plantations, grazing, and urbanization take over what was once rainforest, habitat loss increasingly threatens resident species (Schroth et al. 2004). Habitat loss is the greatest cause of species extinction (Park 1992, Groom 2006). This means destruction of both the trees and plants that make up that area as well as death of the animals that live there, unless they are able to relocate to another suitable

habitat. Relocated and surviving species are confined to smaller patches of rainforest, increasing competition and extinction risk due to lack of resources (Park 1992). Because of the diversity of species in the rainforest, there are often fewer individuals of a given species and with deforestation, these species are even more sensitive to environmental change and loss. Death of even a few individuals may represent a large percentage of the population, meaning it takes less impact to reach extinction (Goldsmith and Hilyard 1990). Furthermore, small populations are more vulnerable to genetic inbreeding, threatening the population's fitness. Inbreeding often results in decrease in overall fitness because it decreases the adaptability of a population as diversity of traits decreases (Park 1992; Lovejoy 1989).

Forests that remain after deforestation are small, often disconnected fragments. While fragmented forests retain some rainforest area in which animals can live, they differ greatly from continuous forests. Fragmentation reduces the size of forest habitat, and edge effects reaching up to 2km in from the forest boundary leave even less undisturbed forest habitat (Broadbent et al. 2008). Thus, the proportion of edge to interior increases, expanding the amount of forest compromised by edge effects. This corresponds to a decrease in habitat for animals like cats, bears, and primates who often require primary forest habitat (Brodie et al. 2014). These primary forest populations become more densely confined, increasing competition in an already smaller resource bank. Changes in species interactions and survival ability allow a few species to succeed while others suffer (Boyle et al. 2013). Presence of more fragments

or contiguous forest nearby can provide resources and habitat for some animals, effectively reducing competition. It is important to remember, however, that the ability to move between fragments varies greatly between species making these additional resources not equally available for all animals.

Fragmented forests not only have reduced ranging area for species, but also altered resource availability due to edge effects (Broadbent et al. 2008). Edge effects are differences in the forest habitat on the border of a fragment as compared to the interior. This is often manifested in microclimates, humidity, light, and wind differences. Edges will often become drier, lighter, and less humid than the original climate (retained in the interior) as more wind and light can penetrate this region from the open area outside (Broadbent et al. 2008). Additionally, edges are often less dense than the interior, amplifying the effects of this intruding light and wind. Differing edge climate allows different flora and fauna to either succeed or suffer in these edge habitats (Laurance et al. 2002, 2011; Tabarelli et al. 2010; Putz et al. 2011).

As the species composition on the edges of forest fragments change, the interior species face different challenges. Each species occupies a specific niche, or role in the community (Ricklefs 1993). Increased competition in fragments forces species to shift their niches by changing their diet, home range, or activity patterns to better attain limited resources in a smaller, more crowded forest (Magnago et al. 2014; Kulp & Heymann 2015). Niche partitioning, the concept that species adapt in some way to survive in a limited environment with other species who share similar resources, is the

driving force behind specialization in organisms' behavior (Ricklefs 1993). This has been observed in multiple forest fragments. In the Lope Reserve, Gabon, seven primate species were found to offset the decreased food availability of the small fragment by increasing feeding efficiency, changing diet, and shifting social structure (Tutin 1999). Chapman (1987) found a high degree of variability in the diets of three primate species in the forest fragments of Santa Rosa Park, Costa Rica, limiting competition between these species, and thus allowing them to effectively share their habitat. In some less adaptable organisms, like amphibians and reptiles, forest loss leads directly to reduced species richness and diversity as animals are unable to shift their niche or habitat (Russildi et al 2016). Niche partitioning and the ability to adapt are the keys to survival in anthropogenically-altered habitats.

The effects of habitat loss and forest disturbance compound in many high-impact areas (disturbed forest fragments surrounded by mostly deforested area) to reduce populations even more drastically than undisturbed fragments (Duraes et al. 2013). Larger vertebrates and birds require more resources (land area, food, water, etc.) than smaller vertebrates to survive and thus are inherently more threatened by habitat loss compared to smaller animals (Brodie et al. 2014). However, these animals are also more mobile, allowing them to take advantage of neighboring forest fragments (Brodie et al. 2014). Primates are one order greatly affected by forest disturbance, loss, and fragmentation. For example, Costa Rican primates including mantled howler monkeys (*Alouatta palliata*) and white-faced capuchins (*Cebus capucinus*) often live in

highly impacted areas made up of a mosaic of forest fragments surrounded by agriculture and are often found to alter their diets and ranges in an effort to compensate with the disturbed landscape.

One of the most dynamic areas in terms of tropical rainforest alteration is Latin America. Countries in this part of the world have experienced some of the highest rates of deforestation as well as some of the newest reforestation efforts, making it an ideal area to study changes in rainforest habitat and the effects on resident species. In addition to the exploitative farming and cattle ranching taking place in Latin America, certain countries including Costa Rica have taken on ambitious new conservation programs with widely-ranging levels of effectiveness that add an additional layer of interest to these forests.

Chapter 2. Deforestation in Latin America

I. History and Trends in Latin America

Latin American rainforests experience some of the highest forest loss of tropical rainforests worldwide, primarily due to economic expansion activities such as industrial and subsistence agriculture as well as cattle ranching (Schmitz et al. 2015). Subsistence farming has traditionally been prevalent in this part of the world as a primary means of existence. Historically, large patches of seemingly unused rainforest served as fallow land for native populations. These traditional farmers practiced shifting cultivation and allowed their fallow plots to regenerate to secondary forest in between uses (Whitmore 1998). Farmers cared for these secondary forests which served as habitat for animals as well as maintained the biodiversity of the area. The farmers ensured protection from logging and fostered growth of native species. They even cultivated useful species in these plots to enhance and enrich the forest (Whitmore 1998). Unfortunately, shifting cultivation can only support 10-20 persons per km² and local ideas about land ownership proved very different from traditional western ideas (Whitmore 1998). As European influence grew in these traditionally undeveloped areas and populations grew, shifting agriculture became insufficient to provide for the population.

As the “New World” was invaded, colonialism and western exploitation transformed both the image and usage of tropical rainforest. This started relatively harmlessly as trade with local peoples for minor forest products like fruit, spices, and

medicines (Whitmore 1998). Small goods trade quickly evolved into the timber business that soon took over as the primary use of tropical rainforest. The timber industry began in Latin America as early as the 1950s with riparian logging, the cutting of trees along major river channels for easy export to Europe (Southgate 1998), and evolved with new technology in the 1960s to have much further-reaching impacts as roads were built into forests allowing larger trees to be taken from remote rainforest locations (Whitmore 1998). In a trend similar to that of shifting cultivation, forest use intensified and expanded with growing human populations and increasing demand. Specifically in developed countries, demand for tropical hardwood primarily to be used in furniture and construction has multiplied to 15 times that in 1950 (World Wide Fund for Nature 1988; Meyers 1989). This left very few parts (if any) of the Latin American rainforest untouched, and intensified the use of higher impact regions, resulting in nearly unrecognizable environments.

As more of Latin American rainforest was cultivated and logged, the transition to cattle ranching began. In rural areas leached of nutrients, land previously used for agriculture lost its productivity and was left as grassland. Further exploitative culture developed as cattle ranching took over this grazing land that could no longer be cultivated (Fearnside 1983). In uncultivated areas, land was purchased (often by foreign investors) specifically for cattle and these lands were logged for profit before being turned into ranches (Park 1992). Cattle ranching followed logging and agriculture as the

next major source of revenue in developing tropical countries. This uniquely Latin American problem likely originated because of cheap land as well as proximity to the American beef market. Latin American countries (not including Amazonia) export considerably more beef than they consume at half the price of American beef. This encouraged government land subsidies to grow the industry (Park 1992).

Amazonian beef, however, did not pass American meat standards during this period of expansion and was not sold on the American market. Only recently has food trade been opened between the US and Brazil due to bovine spongiform encephalopathy and differing standards for food quality (USDA 2016). Despite this, cattle ranching exploded as a huge industry in Brazil and other northern Amazonian countries. These cattle ranches have historically been subsidized by large international companies like Volkswagen and Armour-Swift, but were more focused on land acquisition and tax exemption than on beef export (Park 1992). This massive push to settle and clear land in Amazonia during the 1960s and 1970s spearheaded the deforestation trend of that time.

Though most of the pressures causing Latin American deforestation (e.g., agriculture, infrastructure) have increased and intensified because of human population growth, some factors proved detrimental to forests regardless of local population pressure. Rosero-Bixby and Palloni (1996) cite banana plantations and cattle ranching as specifically Costa Rican examples of these harmful (primarily international)

influences. While population increases have indirectly driven these industries, it was not local population growth that made them environmentally unsustainable. In most plantation agriculture and cattle ranching, the money from sales as well as the products are exported. The consumer population is not the same population deforesting and operating businesses on the ground. The common trend in most of these deforestation drivers is international exploitation, as the industrial agriculture, cattle ranches, and subsidized land purchases indicate.

II. Costa Rica as a Case Study

Costa Rica is a small Latin American country that epitomizes many of the aforementioned tropical rainforest deforestation trends. The country hosts a number of active volcanoes as well as a central mountain range, dividing the country into a number of diverse life zones. This is the reason Costa Rica has some of the highest biodiversity on the planet (Brown and Bird 2011). Additionally, it is a country with large regions of primary and secondary tropical rainforest, with rainforest making up approximately 50% land cover in this country (Butler 2006). This environmental diversity hosts up to 12,000 species of plants, 838 species of birds, and 232 species of mammals (Butler 2006).

Costa Rica is home to 4 different primate species: Central American squirrel monkeys (*Saimiri oerstedii*), Geoffroy's spider monkeys (*Ateles geoffroyi*), white-faced capuchins (*Cebus capucinus*), and mantled howler monkeys (*Alouatta palliata*). White-faced capuchins and Central-American squirrel monkeys belong to the same family,

Cebidae, while Geoffroy's spider monkeys and mantled howler monkeys belong to the family Atelidae (Jack 2011; Di Fiore et al. 2011). Of these, squirrel monkeys have the smallest geographic range, limited primarily to the central and southern pacific coast, while the other species range over the majority of the forested parts of the country. The smaller capuchin and squirrel monkeys' diets are traditionally categorized as "frugivore-insectivore," though they have some of the most variable diets of the new world monkeys. Capuchins in particular rely mostly on fruit and only eat meat opportunistically, though they are able to hunt and capture decent-sized prey (birds, reptiles, and small mammals in some species). This diet prompts high activity and long periods of foraging (Jack 2011). The Atelidae family is entirely folivorous and frugivorous though these primates also show high dietary flexibility. Howler monkey species are traditionally folivorous and have much lower activity than capuchin species, though they opportunistically eat fruit (Di Fiore et al. 2011).

Despite differences in diet, social structures, and activity patterns, these species share habitat as well as resources in the rainforest (Chapman 1987, 1988). Capuchins have been found to become almost totally folivorous, or totally carnivorous in cases of drastic environmental change or drought (Jack 2011). Similarly, frugivory in howlers may be more or less common depending on the availability of fruit in the ecosystem as well as competition with other animals (Di Fiore et al. 2011). These primate species have faced similar pressures due to deforestation and the expansion of human

populations and agriculture in Costa Rica, and their environments are constantly changing. As previously mentioned, the destruction of rainforest habitat in this part of the world drastically compromises the survival ability of resident species. As forests are removed and habitats are fragmented by plantations and ranches, the decreased availability of resources forces these resident primate species to adapt or go extinct.

After World War II, Costa Rica's human population grew nearly four times its size in two generations from less than 800,000 to more than three million people (Rosero-Bixby and Palloni 1996). During this same time span, nearly 50% of Costa Rican tropical rainforest was lost, primarily through intensified agriculture, plantations, and eventually cattle (Rosero-Bixby and Palloni 1996). There is not much data to suggest direct links between the population explosion of this time and the intense deforestation of this country. Though one likely influenced the other, especially in the original intensification of agriculture, crop plantations and cattle ranching have been principally linked to international influence (Rosero-Bixby and Palloni 1996). International and multinational companies like Del Monte, Dole and Chiquita are controversial not only in their environmental actions, but also in the corporate social responsibility. Investigations into worker rights as well as harmful effects of pesticides have come into public light in recent years, adding insult to injury for these large plantation companies (Prieto-Carron 2006). These activities were prompted by international demand rather than subsistence or profit of the local populations. The greatest increase in Costa Rican deforestation

rates occurred in the 1960s, when cattle ranching and agricultural development dominated the country's economy. By the 1980s, Costa Rica's deforestation rates were some of the highest in the world. These rates have since dropped due to government programs and an international shift in priority towards social and infrastructural development and conservation as evidenced by their increase in the number of national parks and protected areas as well as government incentives for reforestation (Brown and Bird 2011).

The Costa Rican government has implemented one of the most ambitious conservation programs in the tropics with more than 10% of the country designated as protected land in some way (Butler 2006). This is implemented through a number of programs including national parks and reserves, ecotourism, and a payment for environmental services (PES) program. Andam et al. (2013) found Costa Rican protected areas to be more successful in allowing regrowth of deforested areas when compared to regrowth rates in unprotected areas. Conservation of natural places has prompted ecotourism, a tourism industry focused on culture and natural history, which now makes up over a \$1billion industry in Costa Rica (State Department 2013).

The innovative PES program was initiated in 1997 and has had some limited success. The program, funded largely by the national forestry financing fund (FONAFIFO), pays Costa Rican landowners for (a) reforestation, (b) protection of forest, (c) natural forest regeneration, and (d) agroforestry (Daniels et al. 2010). Though,

according to national surveys, this has not reduced overall deforestation rates, it has increased the amount of avoided deforestation (land that would have otherwise been deforested) (Daniels et al. 2010). While success of the PES system is debated, it has played an integral role in bringing conservation to public light and in preserving key forest fragments, especially those that act as corridors between forest islands.

In the midst of the massive amount of change Costa Rican environments have witnessed over the past 60 years, scientific information about these environments is especially valuable. Additionally, the proximity, safety, and economy of this country make it accessible for western scientists and its central location and variety of habitat are perfect for tropical rainforest research. Because the country not only lends itself to tropical rainforest research but also to studies on conservation strategy and effectiveness, Costa Rica serves as an ideal case study. Moreover, the unique status of the country as host to multiple big-name monocrop plantations as well as one of the largest cattle industries contrasts interestingly with the one-of-a-kind conservation programs implemented by the government, from reserves and parks to ecotourism. This dynamic country provides environments in nearly every state between total deforestation and protected primary forest, allowing for direct comparisons between similar environments and a unique perspective on the status of human interaction with tropical rainforests.

Chapter 3. Tree Preference of Two Primate Species at La Suerte Biological Research

Station, Costa Rica

I. Introduction

In Costa Rica's dynamic and varied rainforest, human activity is likely impacting primate species in many different ways. Because Costa Rica is an optimal research site due to its accessibility and focus on conservation, there have been many studies on the shifting of primate niches (Bitetti 2001; Camaratta et al. 2017; Chapman 1988; Chaves and Bicca-Marques 2016). These studies are all conducted via different methods and in different locations to determine dietary overlap, shifts in daily path length, inter-group and inter-species contact. However, there are no studies that look at niche overlap via habitat utilization. The question remains: are primate species differing their use of the environment in an attempt to partition their limited resources? My study, by investigating this issue from this new perspective, provides a novel set of data which provides both confirmation and additional knowledge to the topic of primate niche partitioning.

This study was conducted at La Suerte Biological Research Station, located in a fragmented tropical rainforest in northeastern Costa Rica (10°26'N, 83°46'W) at an altitude of 50m above sea level. The research station was previously a cattle ranch and is now a mixture of primary rainforest, secondary rainforest (both of which were selectively logged in the recent past), swamps, grasslands, and active reforestation

efforts (Bezanson 2009; Garber et al. 2010). Average yearly rainfall is approximately 3800mm at the site with much of the water running off into the Rio La Suerte, which eventually empties into Tortuguero National Park on the Caribbean coast. This area experienced heavy deforestation after the 1970s through the 1990s, like much of Costa Rica, when plantation agriculture expanded into the area as banana and pineapple fields owned by large international companies like Dole and Del Monte (Ploetz 2000). In that time period the Costa Rican government also introduced conservation efforts in the form of national parks, protected areas, and private reserves (Estrada et al. 2006). This move toward protecting natural spaces is what motivated the purchase, reforestation effort, and continued protection of La Suerte by the Molina Family.

At La Suerte there are two primary rainforest patches connected by a corridor, together making up roughly 150 ha of forest. These two patches (referred to as “large forest” and “small forest”) are designated for student research and education. An additional 550 ha of forest is protected but not used for research. These forests are home to three of Costa Rica’s four primate species: white-faced capuchins (*Cebus capucinus*), mantled howler monkeys (*Alouatta palliata*), and Geoffroy’s spider monkeys (*Ateles geoffroyi*). The majority of the primates in the study area have been accustomed to researcher presence as the area has been regularly used by students and researchers since the early 1990s (Garber et al. 2010).

Though white-faced capuchins are considered primarily frugivorous (fruit-eating) and mantled howler monkeys considered primarily folivorous (leaf-eating), the diets of these species occasionally overlap (Chapman 1987, 1988). This may occur more often in smaller habitats, like a forest fragment, because of the reduced quantity of available resources. Both species prefer higher quality foods, which causes niche overlap. Higher quality foods, like fruit and meat, provide more nutrition per unit but may be more difficult to attain. Howler monkeys will eat fruit in addition to leaves when fruit is available (Dunn et al. 2009; Arroyo-Rodriguez & Dias 2010; Asensio et al. 2006), but finding fruit requires traveling further distances in the forest. Similarly, capuchins will supplement their frugivorous diet with insects when possible (Chapman 1987, 1988), but they must expend more energy to catch insects. Some researchers suggest this dietary flexibility is a factor contributing to niche partitioning, allowing the successful coexistence of certain species like capuchins and howler monkeys in forest fragments (Dunn et al. 2009; Chapman 1988).

Diet is also linked to activity budget. Folivorous diets require more thorough digestion than chemically simpler foods (e.g., insects or fruit) because of the toxins that leaves contain as well as the more complex molecules that make up leaves (Milton 1981). They also require folivorous animals to consume more because of the low quality nutrition of leaves in comparison to fruit or meat. Therefore, folivorous species are expected to spend more time eating and more time resting than their frugivorous or insectivorous counterparts (Milton 1981). Though capuchins' diet is of a higher quality

than that of howler monkeys, the patchy distribution of fruit requires more travel than evenly distributed leaves. However, a decreased availability of high quality foods (as in forest fragmentation) and the competition between species results in an even longer daily path length as well as larger home ranges for both species to be able to obtain enough food (Bitetti 2001; Dunn et al. 2009). Despite the fact that these two species occasionally share food sources, the differences in their primary food source corresponds to differences in activity, and thus different ways of using the same environment. When decreased resource availability causes more overlap in food sources, the differences in these activity budgets may be accentuated as a means of sharing these food sources. This would result in a more obvious niche partitioning as the species adapt to alleviate the pressure caused by overlapping food requirements.

In a fragmented and disturbed habitat, the diversity and stratification of the environment (as described in chapter 1) also plays an important role in primate activity. Based on the power function relationship between tree diameter at breast height (DBH) and fruit biomass (Niklas 1993; Peters et al. 1988), correlations may exist between diet and preferred tree size. These different tree sizes as well as tree types are often linked to the division of vegetation by light availability (Goudie 1984). Similarly, vertical stratification of the environment, as described by Goudie (1984), provides differing levels of protection from predation with emergent trees being most exposed to aerial predators, understory trees most vulnerable for terrestrial predators, and canopy trees being most protected. For primates whose activity budgets include more resting for

digestion like the folivorous howler monkeys, tree preference may be linked to this vertical stratification.

The objective of my study at La Suerte was to determine the preferred tree use of mantled howler and capuchin monkeys for both feeding and for resting in a wet tropical rainforest fragment. The small size of this forest fragment relative to the continuous unaltered forest in the area means that fewer resources are available for the resident primate species to use for food and for resting. Comparing the number of trees as well as the number of tree species used for each behavior (i.e., feeding and resting) by each primate species will provide a summary of the way each species uses their shared environment and will accentuate any overlap in usage as well as differences in activity patterns. I also compared the DBH of the trees used by these species and then determined the preferred forest level (emergent, understory, canopy) for each behavior. Because of the difference in diets and activity budgets between mantled howler monkeys and white-faced capuchins, I hypothesized that these species interact in different ways with their environment. In an environment with limited resources, like this forest fragment, differences in activity budget will likely be accentuated in response to indirect competition for food. The same diversity of trees was available to both species, but I predicted the trees would be used differently by the two species depending on nutrition and activity requirements, resulting in a greater number of trees and tree species used by capuchins than howlers because of the more active nature of capuchins. I also predicted that feeding will take place in trees of greater size (i.e.,

higher DBH) than resting will because of the positive relationship between tree size and food production, and that both species will prefer canopy level trees when resting because of the increased protection from predators.

II. Methods

Data Collection

Data were collected at La Suerte Biological Research Station (LSBRS) from June 3 – June 14, 2015 and June 18 – July 17, 2016. The study subjects included groups of roughly 10-15 white-faced capuchins and groups of 10-20 mantled howler monkeys. I collected 25 hours of data in 2015 and tagged 63 trees and collected 29 hours of data and tagged 120 trees in 2016 for a total 54 hours of observational data and 183 tagged trees throughout the course of the study.

I collected both behavioral data and tree measurements to determine tree preferences. Instantaneous scan sampling was used to record the behaviors of both howler monkeys and capuchins at 2-minute intervals for 30-minute sampling periods (Altmann, 1974). The behaviors included feeding, resting, and other (Table 1). I sampled adults and juveniles of both sexes at random, with no individual being sampled more than once per hour, and not more than once per day if possible. An animal was counted as out of view if it was not able to be observed for a period of one minute or greater in each interval. Five intervals (consecutive or nonconsecutive) in a single sampling period of the animal being out of view rendered the data from that period

unusable. If an animal went out of view, a 10-minute period of searching was required before the data were discarded as unusable.

Table 1: Ethogram - definitions of behaviors used for data collection

Feeding(F)	Animal is picking at branches, leaves, fruit, moss, etc. with hands or with mouth and may be followed by placing object in mouth and chewing. The animal may be moving or stationary, sitting, standing or hanging on/from branches or on the ground. In the case that the animal is positioned in one tree but feeding on the parts of another tree/plant, information will be recorded for the tree/plant from which the animal is feeding.
Resting (R)	Animal is sitting, standing, or laying without moving any distance greater than one meter while doing no other activity except self-grooming or scratching. The animal may have eyes open or closed.
Other(O)	Social behavior including grooming, aggression, nursing, etc. Drinking water, looking around, vocalizations and other behaviors irrelevant to immediate study are also included
Out of View (\emptyset)	not currently able to observe animal behavior

For each record of resting and feeding, I recorded the tree in which the behavior occurred. After the 30-minute sampling period, or during the sampling if possible, I tagged each tree with a unique number, the date, and my initials for later identification. I photographed the bark, leaves, and any fruit visible and the numbers of these photographs were recorded on a separate data sheet along with the circumference, the tree level (i.e., understory, canopy, emergent; Table 2) and whether or not a physical sample was obtained. The circumference was later used to calculate DBH ($DBH = \text{circumference}/\pi$) as a means of comparing if tree use was related to plant productivity.

Tree level was recorded to determine whether the behavioral preferences of the animals were related to the height and/or exposure of the trees. I recorded the GPS location of each tagged tree and recorded the primate species using the tree as well as whether it was used for feeding or for resting. In 2015, nearly all of my data were collected from the large forest. In 2016, data were collected across both the large and the small forests. This increased my tree dataset drastically, and it allowed me to maximize the amount of behavioral data collected.

Table 2: definitions of forest level used to classify trees

Canopy (C)	The crown of the tree overlaps with the crowns of at least 2 of the closest 4 trees. Lower branches may overlap with understory, but observations will be recorded based on the top third of the tree branches.
Emergent (E)	The majority of the tree (top two-thirds) is above the crowns of the nearest 4 trees
Understory (U)	The top branches of the tree lie below the top two-thirds of the branches of the nearest 4 trees.

Data Analysis

For all analyses, I averaged the two years data together to limit the effect of this discrepancy. I identified as many of the tagged trees as possible using field books and online plant identification resources. For data analyses, I sorted the behaviors by tree and tree species in which they occurred and compared the frequency of use each tree. I calculated frequency as trees used per hour and species used per hour to correct for an inordinate amount of howler monkey resting data in comparison to other data

categories. I also counted and directly compared the amount of overlap of tree usage for both feeding and resting in each species. I calculated mean DBH of trees used for both feeding and resting. DBH calculations excluded trees for which I was not able to accurately measure circumference but included trees that could be measured and not identified. For forest level quantification, I calculated the percentage of time each species spent feeding and resting in each level (emergent, canopy, understory). Standard T-tests were used to determine the statistical significance of tree use and DBH data ($p < 0.05$).

III. Results

During the 19 hours of focal sampling on capuchins, 296 minutes of feeding and 312 minutes of resting were analyzed after eliminating intervals during which the animals were in an unidentifiable tree or in bamboo, shrubs, or on the ground. Using a similar elimination process, a total of 36 hours of focal sampling on howler monkeys resulted in 484 minutes of feeding and 1512 minutes of resting. The folivorous diet of howler monkeys means that the majority of their time is spent resting in order to digest leave, so although these data seem skewed, they accurately represent the activity patterns of this species.

Tree use

As predicted, capuchins used significantly more trees than howler monkeys ($p=0.0367$).

Capuchins used an average of 12.45 trees per hour (14.05 for feeding and 10.84 for

resting) while howler monkeys used an average of 4.19 trees per hour (4.46 for feeding and 3.91 for resting; Figure 1).

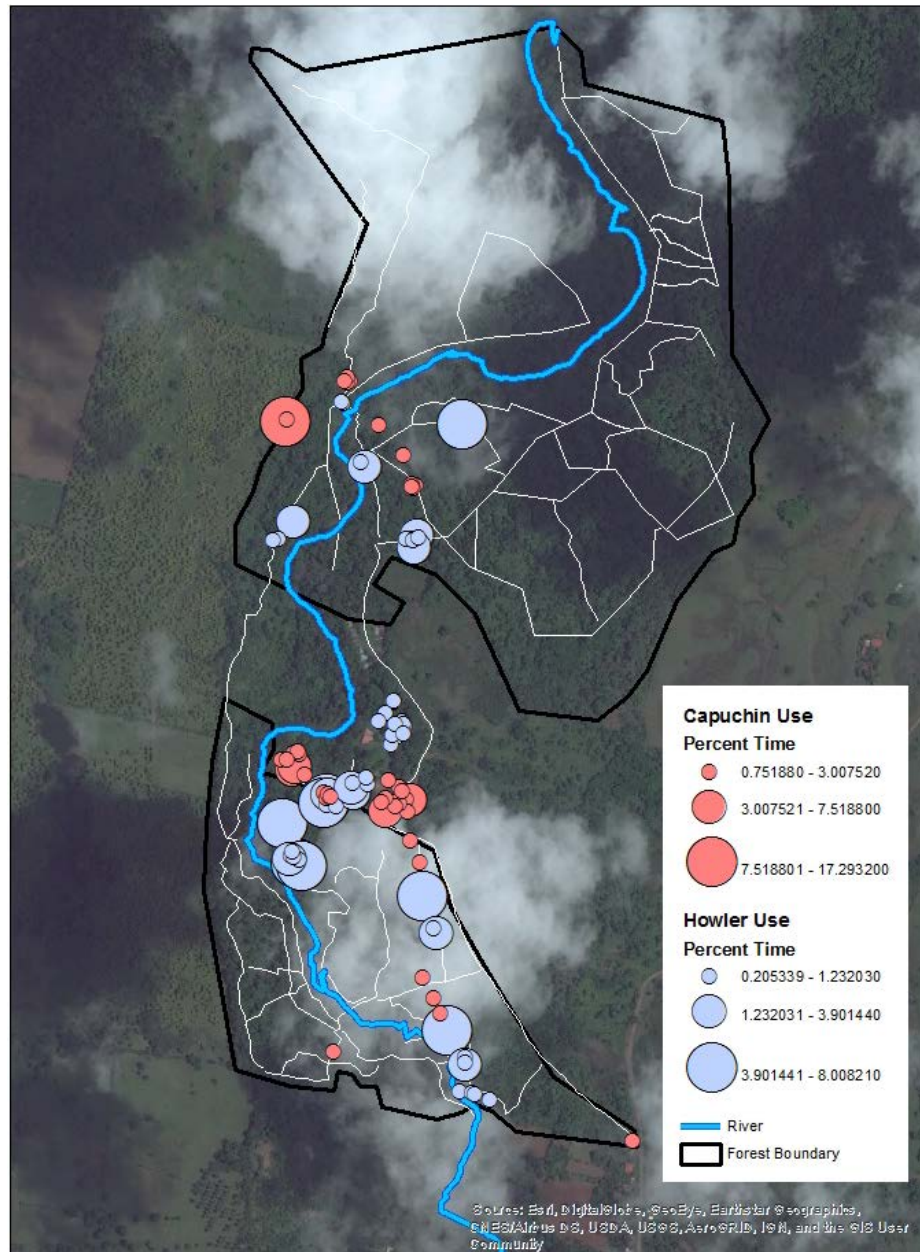


Figure 1: Tree usage by capuchins and howlers was mapped with circle size corresponding to the percentage of time spent in each tree. Capuchins spent less time on average in more different trees while howlers spent longer amounts of time in fewer trees.

Niche overlap

Tree identification data was used at the family level. A niche overlap analysis in EcoSim was used to compare the tree family overlap between the two primate species (Table 3). With 1000 iterations using Pianka values, relaxed niche breadth, and retained zero states, I found significant niche partitioning between howlers and capuchins ($p=0.002$).

Table 3 – Instances of tree family utilization by capuchins and howler monkeys

Family	Capuchin	Howler
Anacardiaceae	0	5
Annonaceae	1	7
Apocynaceae	0	5
Araceae	11	3
Burseraceae	4	0
Cecropiaceae	0	25
Fabaceae	1	98
Mimosoideae	4	56
Melastomataceae	6	13
Moraceae	1	41
Musaceae	14	0
Myrtaceae	0	25
Rubiaceae	4	5

DBH

The results obtained regarding tree DBH did not clearly support predictions. The DBH of trees used by capuchins were smaller on average than those used by howler monkeys, though this difference was only statistically significant for feeding trees ($p=0.024$ for feeding, $p=0.093$ for resting; Figure 3). Fruit productivity was not related to greater large-tree use by capuchins, the primarily frugivorous species.

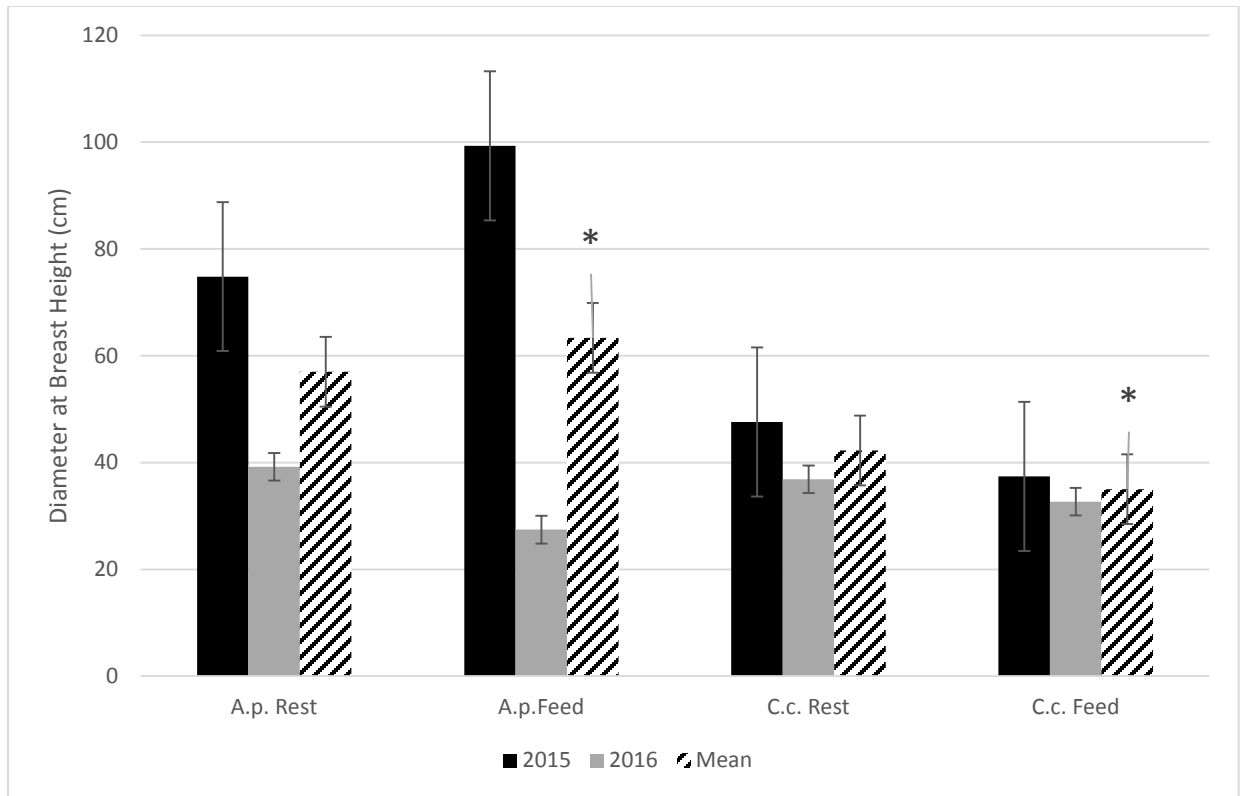


Figure 2: DBH of trees used by howler monkeys and capuchin monkeys in 2015 (black), 2016 (grey), and the mean of both years (striped). Fewer trees were tagged in 2015 in a smaller study area, thus large tree outliers drastically affected the means for that year. Means show a visually distinct increase in mean tree size used by the howler monkeys (A.p) from those used by the capuchins (C.c) but this is only statistically significant (; $p=0.024$) between feeding trees. Standard error bars show overlap between howler and capuchin resting.*

Forest Level

Capuchins spent more total time in the canopy than in other layers of the forest, as predicted, while howler monkeys spent more time in emergent trees, contrary to predictions. Capuchins spent 77% of their resting time and 77% of their feeding time in the canopy while only spending 18% and 10% of their time resting and feeding, respectively, in emergent trees. Howlers spent only 39% of their resting time and 51%

of their feeding time in the canopy while they spent 60% of their resting time and 47% of their feeding time in emergent trees. Time spent in the understory was negligible for both behaviors in both species (Figure 4).

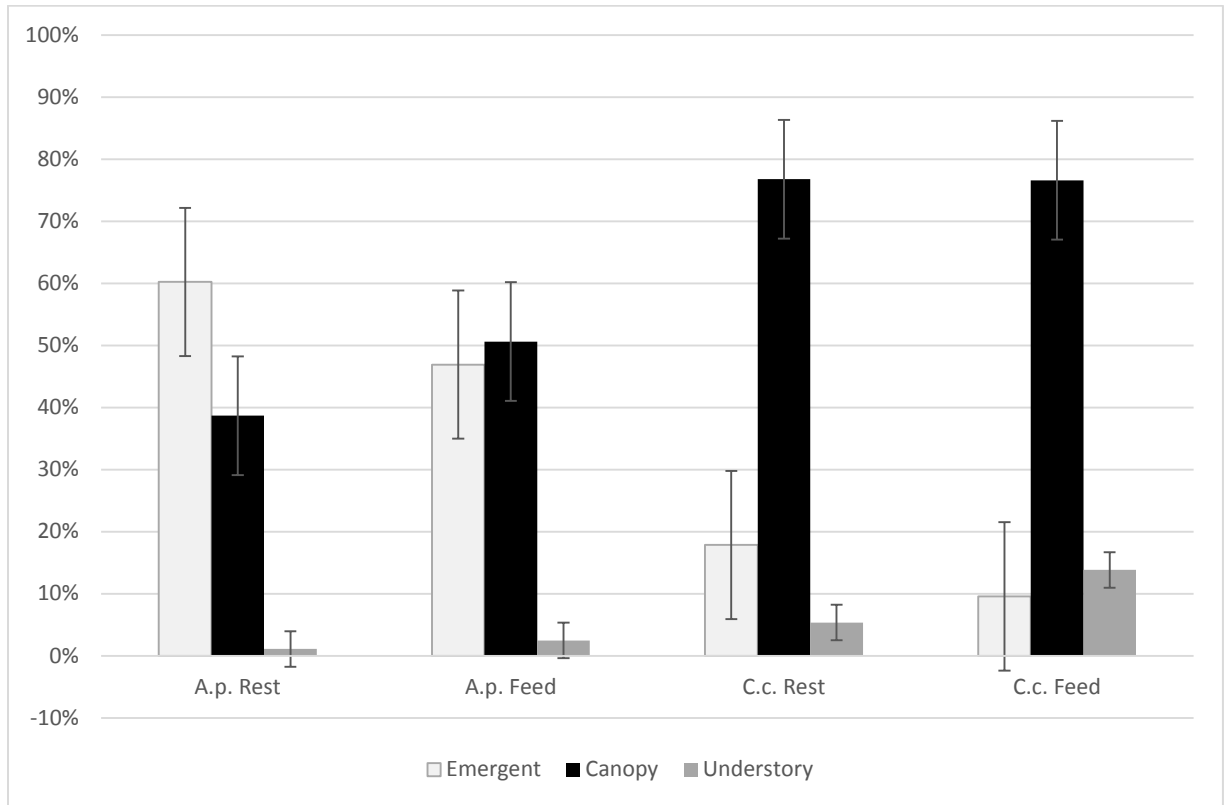


Figure 3: Percentage of time spent in each of the three primary tree layers is reported for each species and each behavior. Howler monkeys (A.p.) spent more time in emergent trees (light grey) than capuchins for both behaviors and neither species spent much time in understory trees (dark grey).

IV. Discussion

My results suggest that white-faced capuchins and mantled howler monkeys use their limited habitat in different ways for feeding and for resting, supporting a potential

system of niche partitioning in this forest fragment. This study shows a considerable amount of overlap in the trees and forest levels used by both species, with distinct patterns of use based on tree use per hour.

In general, capuchins moved much more quickly through the forest, using more trees as well as more different species of trees than howler monkeys. This greater tree use suggests longer daily path lengths which is consistent with the connection made by previous studies regarding food availability and travel patterns (Bitetti 2001; Dunn et al. 2009). The rarity of fruit, the capuchins' primary food source in comparison to leaves, means a longer daily path is required for the group to obtain enough food (Dunn et al. 2009). Decreased availability of fruit due to both opportunistic frugivory by the howler monkeys and forest fragmentation further this effect on the capuchins' tree usage patterns.

In contrast, howler monkeys spent a greater amount of time resting. However, these animals did not necessarily rest in different trees than they fed, as I had predicted. The overlap between feeding and resting trees for howler monkeys is greater than the overlap between feeding and resting trees for capuchins. This behavioral difference might be attributed to the more stationary habits of howler monkeys. Because they travel less on average per day than capuchins (inferred from tree use per hour), howler monkeys may simply prefer to rest near food sources so they can ingest more of their lower quality food. This comparison may also be skewed due to the remarkable

difference in the amount of howler monkey resting data I collected as compared to howler monkey feeding or either feeding or resting in the capuchins.

Despite the connection between tree DBH and fruit production (Niklas 1993; Peters et al. 1988), my results did not clearly support the prediction that capuchins and howler monkeys will feed from larger trees than they rest in. The overlap in usage of trees for both feeding and resting (especially by howler monkeys) could account for the higher DBH values for resting.

Likewise, my prediction of increased canopy use for resting was not supported by these results. Capuchins did rest more in the canopy than in emergent trees or in the understory, but they also fed more in the canopy than in other levels. Howler monkeys spent more time in emergent trees for all recorded behaviors. Though aerial predators including hawks and eagles were seen in the area, howler monkeys did not seem to be threatened by their presence. Preference for emergent trees provides an explanation for the greater average DBH of trees used by howler monkeys for both observed behaviors in comparison to capuchin monkeys. Taller trees will, on average, have a larger trunk than canopy level trees in order to support the greater height (Niklas 1993; Peters et al. 1988). Additionally, howler monkeys are often seen eating *Cecropia* spp. leaves, one of their favorite food sources. These trees are often emergent. This preference for larger trees could also be due to the larger body size of howler monkeys in comparison to capuchins, and the need for larger trees to support their weight.

Capuchins were able to utilize very small branches, even palm fronds to move about the forest, an ability that howler monkeys do not share.

Chapman (1988) described a similar difference in travel patterns that was dependent on food source between capuchins and howler monkeys in Santa Rosa National Park, Costa Rica. While howler monkeys spent longer periods of time in a single area that is known to have food, capuchins tended to merely stop by food trees throughout the course of their daily travel or to visit multiple food trees over the course of a day. This corresponds to both a greater use of habitat by the capuchins as well as the longer daily path length that is dependent on fruit availability (Bitetti, 2001).

Similar trends have been found in other tropical rainforest sites with the same species. The diets of both howler and capuchin monkeys tend to vary with food availability and habitat size (Bitetti 2001; Camaratta et al. 2017; Chapman 1988; Chaves and Bicca-Marques 2016). Though forest fragments have lower overall species richness and diversity than continuous forest, howler monkeys in small forest fragments in Argentina were found to have more varied diets than those in continuous forest, and these monkeys were found to rely much more on young leaves (Chaves and Bicca-Marques 2016). In a limited fragment with multiple groups of monkeys of different species, available fruit would be under much greater demand than in a forest with only one species of primate or than in a continuous forest. This would cause an increase in dietary variability as competition increases and would therefore likely lead to a greater

reliance on leaves. Rano et al. (2016) found a significant relationship between a decrease in daily path length and a similar reliance on leaves in place of fruit in howler monkeys in Argentina. This demonstrates that competition and reduced resource use cause changes in activity patterns based on alterations in food preference.

Based on the observed trends in my research and in published data from numerous sites, not only do these primates' behavioral patterns change with changes in food availability, but also with presence of human development as some primates have been found to actively avoid developed areas while others feed from human waste (Van Hulle and Vaughan 2009; Bitetti 2001; Camaratta et al. 2017; Chapman 1988; Chaves and Bicca-Marques 2016). This demonstrates that human actions (e.g., deforestation, agriculture, ranching, development, etc.) have profound effects on the primate populations in the neighboring remnants of tropical rainforest. Our actions alter their environments and force changes in their activity patterns. While a preference for different trees or an increase in activity may seem like minor changes, they likely have secondary effects that are yet to be studied, including alterations to the ecosystem structure and populations of other plants and animals. If feeding patterns change drastically enough to influence the survival of native plants, then more species of plants and animals could in turn be affected due to chain reactions of population pressure.

Though deforestation has been happening for hundreds of years, and the intensification of such activities started nearly 60 years ago, studies of our effects on the

environment and local animals are still relatively new (30-40 years old). The field of conservation biology is in its infancy and as we learn more about the effects we have on the plants and animals that inhabit the areas we are using, our knowledge of the negative impact we are having as a species increases. In the same way that small changes in forest density can have large consequences on the local climate system through changes in evapotranspiration (Salemi et al. 2013; Schlesinger and Jasechko 2014), small changes in animal behavior and habitat use very well may have large effects on the ecosystem as a whole. Even with our best efforts in science and research, we may never fully understand these systems. Scientific knowledge is perpetually incomplete, but it is crucial to helping us understand how best to protect the environment while we advance our own people.

Chapter 4: The Ethics of Rainforest Conservation

While science reveals the effects our actions as a dominant species have on the environment and its residents, it is also eternally incomplete. Science is always progressing, which is both a blessing and a curse. Increasing scientific knowledge is hugely beneficial to our human population as well as the way we interact with the world, but it also means that the things we know to be true can change, and that we never really have a comprehensive picture of all species, processes, and interactions in an ecosystem. This is not to diminish the value of science and research; without the knowledge we attain from scientific disciplines, we have no tools to repair the problems we create. However, we cannot rely entirely on science. Because of the evolving and dynamic nature of science, facts cannot be the epitome of our worldview. We need context and overarching ethical principles to guide us when facts change.

While people's ethics may have discrepancies depending on culture and background, ethics provides reasoning that both builds on and transcends scientific facts. The field of ethics uses what we know about the world and puts this knowledge in a context of humanity, current events, and culture to provide a sort of norm for acceptable behavior (Resnik 2015). These are all necessary considerations in the complex world in which we live. As scientific knowledge evolves and changes our view of the world, ethics maintains a relatively stable background of ideas and reasoning that we can use to make sense of new and changing information.

The specific field of environmental ethics has origins in a number of people, reaching back even to Charles Darwin who heavily influenced philosophers later in time, including Aldo Leopold. These pioneers in the field are whom my arguments are modeled after and by whom I have been influenced. Ethics and philosophy are ancient practices, but their application to the environment (i.e., to plants, animals and ecosystems) is relatively new (Callicott 2001). Darwin's original concept of ethics, published in 1871, included a strong sense of human community and responsibility to said community. This was based on the supposed origin of ethics in community dynamics as societies grew and people were required to work together to survive. This was expanded upon by Aldo Leopold, who claimed that ecology "simply enlarges the boundaries of the community to include soils, waters, plants, and animals, or collectively: the land" (A Sand County Almanac). Though Darwin very well may have believed in our responsibility to care for nature, it was not explicitly included in his early discussion of ethics (Callicott 2001). However, based on his extensive studies of the natural world (Darwin, 1859), we can assume that the respect he had for nature carried over into his ideas of ethics and that Leopold's expansion of Darwin's original ethical ideas were in line with what both Darwin and other early environmental philosophers believed.

Despite the origin of the field of environmental ethics in community and mutual responsibility, much of the action and motivation in this field is now rooted in human interest (Callicott 2001). While this unfortunately strays from the original focus of

Darwin and Elton (i.e. the environment), human-centered arguments gain the attention and support of many who unfortunately would otherwise be unresponsive and removed from the issues at hand. These anthropogenic arguments span from the potential negative effects of environmental harm to human health, economy and resource base to loss of aesthetic, artistic and cultural value.

The most common human-centered argument for the protection of nature is utilitarian, claiming the need to protect nature for our own good because of the valuable resources it contains (Fisher 2001). We need the lumber, food, water, and medicines harvested in nature, but also the many services provided by natural places (water filtration, climate moderation, nutrient cycling, etc.). Utilitarian conservationists claim that we must protect resources in order to maintain our ability to survive now and in the future, and that this anthropogenic need gives value to the environment. One of the most famous of these utilitarian conservationists, Gifford Pinchot (1905), summarized the gist of this view with the phrase: “the greatest good of the greatest number for the longest time.” We must note that Pinchot’s “greatest number” includes not only humans but plants, animals, and organisms used by humans, despite the fact that protection of non-human elements is necessary only for the ability for sustained human use of these elements. Utilitarianism is not, as some assume, considering solely the good of humanity, but also the long-term survival of everything else in the global community. Unfortunately, the intentions of early utilitarian philosophers (as well as

many today) were not to protect the global community for its own good, but rather for the human good.

Additionally, future generations need to be taken into consideration in the utilitarian effort to protect the environment. The intention to protect nature in order that our grandchildren and great-grandchildren may have access to the same resources that we do is another interpretation of utilitarianism stemming from the desire to protect our progeny. In protecting nature for future generations' material use, we succeed in conserving the environment, but this tends to be justified more by the protection of resources to be used later than by protection of the rights of nature in and of itself. At the very least, in this utilitarian mindset, the intention for protection is not totally self-centered as it is rooted in the desire to serve future generations of humans. However, the intention of use necessarily deals with the environment in such a way that only materially useful resources are the focus and that environmentally compromising activities still occur.

Environmental ethics looks very different when applied to the protection of nature for its own good rather than for the human good. This is Leopold's view and his motive for writing "The Land Ethic" which is now the basis for the environmental ethics field as we know it. Leopold (1949) takes the stance that "a land ethic implies respect for... fellow-members and also for the community as such." Utilitarian arguments may reach so far as to call for respect for fellow (non-human) members of the community

but only insofar as they are valuable to human society. This is not the same respect of which Leopold speaks. Leopold calls for total protection with the justification that each and every part of the environment has a right to survival *in addition to* the survival of the community (i..e, ecosystem/environment) as a whole entity.

In most cases, one part of an ecosystem cannot survive alone, just as many ecosystems will not survive when missing an integral part. In an environment as complicated as a tropical rainforest, science has barely scratched the surface of understanding species interactions. Epiphytes, one of the more obscure organisms in the rainforest, grow in groups specific to host trees and often reliant on the other individuals of the community (Kelly et al., 2004). Similar interspecies interactions are thought to be the reason behind the incredible diversity of the rainforest, as suggested by the Janzen-Connell hypothesis, a detailed series of theories suggesting enemy and ally species killing seedlings in order to promote growth (Janzen 1970; Connell 1971). This complicated theory demonstrates the reliance of organisms on interspecies interactions (Janzen 1970; Connell 1971; Schupp 1992). Protecting singular elements of the environment (such as protecting just the monkeys of the rainforest) is a start, but cannot be our only means of conservation. We must recognize the holistic value of nature and the necessity to protect environments and ecosystems as a whole instead of just in parts.

Unfortunately, there is little or no net material gain for humans in the holistic conservation of the environment, and those motivated solely by material gain rarely support this realm of environmental ethics. Protection of nature for its own good is generally justified by arguments of intrinsic value. These most often utilize the aesthetic value of untouched natural places or the inherent value of the mere existence of untouched or minimally disturbed nature (Fisher 2001). This can be twisted into a utilitarian argument via the ecotourism industry, which provides significant income to many of the undeveloped and poorer parts of the world. In these often rural communities, preservation of an ecosystem as a whole and not merely its components attracts tourists and can be greatly beneficial for populations with little means of income besides subsistence farming. As discussed in chapter 2, the ecotourism industry supports a large section of the Costa Rican people and is utilized as both a means of economic profit as well as for effective environmental conservation. However, there is something to say for protecting environments entirely for their own sake. Recognizing the intrinsic value of ecosystem is to respect the rights to life and reproduction of every living organism.

Many environmental philosophers use the aesthetic value of nature to justify its protection (Fisher 2001). This argument goes far beyond just the idea that we should save the forests “because they are pretty.” The ideas of natural aesthetic include the fact that we have a personal response to nature through what we see and experience. This response may not always be the same between persons or from experience to

experience, but regardless, it is something that we determine based on our knowledge, context, and previous experiences (Tang et al. 2015). Many studies have linked this response to nature to personal health benefits including decreased depression rates and lower risk of cardiovascular disease (Luck et al. 2011). As I mention previously however, the knowledge with which we understand our experience (often scientific knowledge) may change over time. Yet this does not stop us from having an aesthetic experience; it just alters the way we understand what we see, hear, and feel.

Carlson (1979) theorizes that all aesthetic experiences of nature are inherently positive. Accordingly, we as humans experience the beauty of nature differently than we experience that of artwork, for example. The aesthetics of nature do not need the same sort of context and conformation to a category that artwork requires. Others argue that natural aesthetics need not be positive, or that there is a gradation in natural beauty with some things being aesthetically “better” than others (Fisher 2001). These arguments are tossed back and forth depending on opinion and philosophy, but what is important is that these philosophers all believe that there is aesthetic value in nature. Even a negative aesthetic experience is valuable in its distinctiveness from other aesthetic experiences. For these reasons, we should protect the environment and these aesthetic experiences.

In many people’s eyes, nature is worth protecting simply because of the value of wild, untouched, natural places. This inherent value of nature is related to the respect

mentioned by Leopold and the community proposed by Leopold. According to this field of environmental philosophy, wild places have the right to exist and function in their natural state solely because they do exist. It is similar to the humanitarian idea that allows basic rights to survival for every human regardless of background, race, or situation. All of nature, from soil microbes to primates, have a right to their basic needs for survival and to live their natural life. Some even take this philosophy so far as to suggest that the rocks, hills, and shape of the land deserve to exist, save alteration by other natural processes, without human influence simply because that is the natural state of the world (Woods 2001).

Regardless of the rights of nature, need for conservation, and tragedy of deforestation, human needs cannot be ignored. Plenty of humans live in poverty, experience starvation and rely on resources from rainforests or other natural areas to survive. Who are we to deny humans basic human rights in the name of environmental conservation? Most environmental philosophies do not outline rules for these issues, and where our priorities should lie in the case of conflict (Darwin 1871; Callicott 2001). Callicott (2001) has laid out a set of secondary principles to guide these sorts of conflicts. Accordingly, responsibility belongs first and foremost to the most intimate community, or the community to which you most closely belong, and the needs of other communities fall second. This means that the needs of your family supersede the need to save rare species and that our obligation to feed our community comes before the obligation to protect our environment.

This same principle governs the relationship between indigenous peoples and natural resources, especially in communities that have historically used natural resources in a sustainable manner and who are still able to do so. Many populations have grown too large for their traditional practices to be sustainable, and other communities were never sustainably using resources in the first place. Some of these people can be assisted via development or the beginning of industry to replace the reliance on forests and natural places, but others still require the food, shelter, and fuel harvested from the rainforest. In these cases, Callicott's ordering of principles comes into play and thus we cannot fault these people for their use of nature. We can only work to move them out of poverty and into a place economically and socially where conservation of natural resources is possible.

With an environment as diverse and important as the rainforest, we as a species are obligated to protect it. The resources and services of the rainforest are irreplaceable. Activities that destroy or alter the rainforest, including ranching, industrial agriculture, and logging, threaten both the integrity of these environments as well as the life of all the organisms that live there. The fact that forest loss affects not only the deforested land but also the surrounding forest fragments means that human activity has a much larger impact than we see. When forest loss and fragmentation change the availability of resources and the reliant animals are required to adapt, the shifts in diet, behavior, and activity will more than likely affect more than just those

animal species. Overconsumption of plant species and overuse of trees may change the diversity and structure of rainforest patches.

Protection of these environments for both our good and the good of the ecosystem comes in the form of limiting our activities as a species. The protection of nature for our own good or for others is a responsibility, a type of stewardship. Some believe that this is an inherent responsibility of being a human (Fisher 2001; Woods 2001), while others see stewardship as a means of utilitarian ends (Pinchot 1905). Either way, we as a species have such an extensive impact on our environments that blatant disregard of this stewardship is dangerous to all involved. Similarly, ignorance of this can have drastic and lasting effects.

Conclusion

Tropical rainforests are ecosystems critical to our world. They serve important roles in global climate through their integral water and carbon cycling as well as host an incredible amount of the world's biodiversity. More than half of the world's species reside in tropical rainforests, many of them yet to be identified (Whitmore 1998). This biodiversity is valuable to the planet both for the resources it offers humans as well as for its own good. Threatening these ecosystems threatens the lives of all the species of plants, animals, fungi, and microbes in the rainforest as well as the stability of global systems. Additionally, it threatens local human populations who rely on rainforest products and services as well as the greater human population that may benefit from medicines and unique products available only in the rainforest.

The vast majority of deforestation in the tropics is due to anthropogenic activity, most notably logging, agriculture, and cattle ranching. Even selective logging, which does not totally destroy forests but may severely alter them, can be extraordinarily damaging to the ecosystem as it changes climate dynamics and increases human activity in the area. Latin America has historically experienced some of the highest rates of deforestation in the world. Total deforestation in Latin America is primarily caused by agriculture and cattle ranching, often prompted by international influence. Not only do these activities destroy habitat and eliminate natural services in the area being deforested, but they also compromise nearby surviving forest. When areas are

deforested, the fragments left behind suffer from edge effects (altered climatic conditions in the exposed edges). Additionally, loss of neighboring forest constrains surviving animals to a more limited area and thus a more limited resource base. These phenomena have been extensively studied in Costa Rica and are prompting some efforts towards protection and reforestation.

In these forest fragments, like La Suerte, limited resources likely lead to behavioral and activity changes for the resident animals. The niche partitioning I found in howler monkeys and white-faced capuchins took the form of accentuation of differences in activity patterns, though niche partitioning can also occur in dietary shifts, temporal changes in behavior, etc.. We have no idea what the long-term effects of these behavioral changes will be in tropical rainforests.

Though it is important that we learn as much as possible about rainforests, we cannot know everything. Most significantly, we cannot know the future effects of our current actions. Even the things we know now as truth may change. For these reasons, ethical principles are critical to guide our actions as a species. Arguments have been made for utilitarian reasons to protect our environment claiming the need to preserve the resources and services vital to our own species' survival. These arguments emphasize the importance of ecosystems to fulfill our needs as a species as well as for the needs of our future generations. An alternate ethical argument is based on the intrinsic value of the rainforest both for aesthetic purposes as well as for the good of the

ecosystem in and of itself. There is a value to allowing life to survive in its natural state. Though many do not recognize this value because of its non-material nature, others value this above all material reasons.

Both of these ethical views are complicated by the needs of the human community. As important as tropical rainforest conservation is, the survival and nutrition of our fellow humans is equally important, and there are many rural communities who do still rely on rainforests for food, fuel, and shelter. While some communities are able to do this sustainably, others are not. Regardless, we as humans have no right to remove these resources from our own people without adequate replacement.

In the face of all these questions and complications, what are we to do about the rainforest? How ought we to live? First of all, I believe that it is critically important for us to learn as much as possible about our natural world. This can be achieved through scientific research and utilization of the increases in technology. The data collection, analysis, and modeling capabilities of scientists increase exponentially with modern technology and allow us to learn more than ever about ecosystem interactions as well as ways to mitigate our impact on the environment. Data sets can be larger, more specific, and more extensive than ever before thanks to advancements like GPS technology and increased computer processing power, available even to students like myself. The more information we have about the natural world allows us to make

better decisions about how to interact with ecosystems as well as how to protect and save them.

Despite this, we must acknowledge the shortcomings of science. Moreover, we need to have principles to guide both what steps we take based on scientific information as well as what we do in the absence of this knowledge. Individual perspectives and opinions will obviously differ greatly, but we need to determine priorities and values to uphold as a species. This may take many forms. As a country, Costa Rica has recently done an impressive job of upholding high standards for environmental protection in an effort to make up for the great environmental loss of past decades. Though the effectiveness of the Payment for Environmental Services program (PES) has been debated, this program strongly represents steps in the right direction. This program moves to preserve and restore rainforest without ignoring the needs of the human community. By paying landowners for forest protection, the government shows care for both humans and environment. This exemplifies the values that I believe we should hold as both the dominant species as well as stewards of creation.

Admittedly, the money-for-conservation model will not work in every country. If we have learned anything from the history of international development practices, it should be that cultures, histories, and identities are too different for blanket assumptions or implementations. Each country and each community deserves

individual consideration to attend to needs and growth. This applies to both developed and undeveloped countries. In many rural and impoverished areas, infrastructural development as well as the advancement of women, agriculture and industry (when done sustainably) can take place simultaneously with environmental conservation. In more developed countries like Costa Rica or Brazil, education and implementation of government programs or alternate industries (like ecotourism) may work to encourage environmental conservation without compromising the wellbeing of the human population. The only approach that is necessarily applicable across all nations and communities is that of individual consideration.

With an increasing human population on our one Earth, we are becoming resource-limited, much like the primates of a forest fragment. Our advantage as humans is that we have exponentially more ways to alter our activity patterns and lifestyles to make use of our limited environment. Moreover we should be able to do so without compromising the wellbeing of all the other organisms with which we share our world. If our larger brains have enabled us to take over this planet, then they should be able to enable us to preserve it.

References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behavior*, 49, 227-267.
- Andam, K. S., Ferraro, P. J., Hanauer, M. M. (2012). The effects of protected area systems on ecosystem restoration: a quasi-experimental design to estimate the impact of Costa Rica's protected area system on forest regrowth. *Conservation Letters*, 6(5) 317-323.
- Archard, F., Eva, H. D., Stibig, H., Mayaux, P., Gallego, J., Richards, T., & Malingreau, J. (2002). Determination of deforestation rates in the world's humid tropical rainforests. *Science*, 297(5583), 999-1002.
- Arroyo-Rodriguez, V. & Dias, P. A. D. (2010). Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology*, 72, 1-16.
- Asensio, N., Cristobal-Azkarate, J., Dias, P. A., Vea, J. J., Rodriguez-Luna, E. (2006). Foraging habits of *Alouatta palliata mexicana* in three forest fragments. *Folia Primatologica*, 78, 141-153.
- Betts, A. K. (2004) Understanding hydrometeorology using global models. *Bulletin for American Meteorological Society*, 85, 1673-1688.
- Bezanson, M. (2009). Life history and locomotion in *Cebus capucinus* and *Alouatta palliata*. *American Journal of Physical Anthropology*, 140, 508-517.

- Birch, H. F. (1958). The effect of soil drying on humus decomposition and nitrogen availability. *Plant Soil*, 10, 9-13.
- Bitetti, M. S. (2001). Home-range use by the tufted capuchin monkey (*Cebus paella nigrinus*) in a subtropical rainforest of Argentina. *Journal of Zoology London*, 253, 33-45.
- Bonilla, A. (1985). Situacion ambiental de Costa Rica. San Jose, Costa Rica: Ministerio de Cultura, Juventud y Deporte.
- Boyle, S. A., Lenz, B. B., Gilbert, K. A., Sprionello, W. R., Santamaria Gomez, M., Setz, E. Z. F., Marajo dos Reis, A., Ferreira da Silva, O., Keuroghlian, A., Pinto, F. (2013). Primates of the biological dynamics of forest fragments project: a history. In L.K. Marsh & C.A. Chapman (Eds.), *Primates in Fragments*. (57-74). New York: Springer Science+Business Media.
- Broadbent, E.N., Asner, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., Silva, J.N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*, 141, 1745-1757.
- Brodie, J. F., Giordano, A. J., & Ambu, L. (2014). Differential responses of large mammals to logging and edge effects. *Mammalian Biology*, 80, 7-13.
- Brown, J. & Bird, N. (2011). Costa Rica sustainable resource management: Successfully tackling tropical deforestation. Overseas Development Institute.
- Butler, R. A (2006). "Costa Rica." Retrieved 12 March 2017, from *Mongabay.com* / *A Place Out of Time: Tropical Rainforests and the Perils They Face*.

- Callicott, J. B. (2001) *The Land Ethic*. In D. Jamieson (Ed.) *A Companion to Environmental Philosophy*. Malden, MA: Blackwell Publishing.
- Camaratta, D., Chaves, O. M., & Bicca-Marques, J. C. (2016). Fruit availability drives the distribution of a folivorous-frugivorous primate within a large forest remnant. *American Journal of Primatology*, 79, DOI 10.1002/aip.22626
- Carlson, A. (1979). Appreciation and the natural environment. *The Journal of Aesthetics and Art Criticism*, 37, 267-275.
- Chapman, C. (1987). Flexibility in diets of three species of Costa Rican primates. *Folia Primatologica*, 49, 90-105.
- Chapman, C. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29, 177-194.
- Chaves, O. M. & Bicca-Marques, J. C. (2016). Feeding strategies of brown howler monkeys in response to variations in food availability. PLOS One. DOI: 10.1371/journal.pone.0145819.
- Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*, 298, 312.
- Daniels, A. E., Bagstad, K., Esposito, V., Moulaert, A., Rodriguez, C. M. (2010). Understanding the impacts of Costa Rica's PES: Are we asking the right questions? *Ecological Economics*, 69, 2116-2126.
- Darwin, C. R. (1859) *On the Origin of Species*. London: John Murray.

Darwin, C. R. (1871) *The Descent of Man and Selection in Relation to Sex*, 2 vols. Vol. 1.

London: John Murray.

Di Fiore, A., Link, A., & Campbell, C. J. (2011). The Atelines: Behavioral and socioecological diversity in a new world monkey radiation. In C. J. Campbell, A.

Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.) *Primates in Perspective*. Oxford< NY: Oxford University Press.

Dunn, J. C., Cristobal-Azkarate, J., Vea, J. J. (2009). Differences in diet and activity pattern between two groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. *American Journal of Primatology*, 71, 654-992.

Duraes, R., Carrasco, L., Smith, T. B., & Karubian, J. (2013). Effects of forest disturbance and habitat loss on avian communities in a Neotropical biodiversity hotspot. *Biological Conservation*, 166, 203-211.

Elsworth, S. (1990). *A Dictionary of the Environment*. London: Paladin.

Estrada, A., Garber, P.A., Pavelka, M.S.M., Luecke, L. (2006). Overview of the Mesoamerican primate fauna, primate studies, and conservation concerns. In A. Estrada, P.A. Garber, M.S.M. Pavelka, L. Luecke (Eds.), *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation*. (1-22). New York:Springer.

- Ewel, J. J. & Bigelow, S. W. (1996). Plant life-forms and tropical ecosystem functioning. In G. H. Orians, R. Dirzo, J. H. Cushman (Eds.), *Biodiversity and Ecosystem Processes in Tropical Forests* (101-123). Berlin: Springer.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487-515.
- Fearnside, P. M. (1983). Land-use trends in the Brazilian Amazon region as factors in accelerating deforestation. *Environmental Conservation*, 10, 141-147.
- Fisher, J. A. (2001) Aesthetics. In D. Jamieson (Ed.) *A Companion to Environmental Philosophy*. Malden, MA: Blackwell Publishing.
- Garber, P.A., Molina, A., Molina, R.L. (2010). Putting the community back in community ecology and education: the role of field schools and private reserves in the ethical training of primatologists. *American Journal of Primatology*, 72, 785-793.
- Gentry, A. H. (1988). Changes in plant community diversity and floristic composition of environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, 75, 1-34.
- Gillespie, G. R., Howard, S., Stroud, J. T., Ul-Hassanah, A., Campling, M., Lardner, B., ... & Kusriani, M. (2015). Responses of tropical forest herpetofauna to moderate anthropogenic disturbance and effects of natural habitat variation in Sulawesi, Indonesia. *Biological Conservation*, 192, 161-173.

- Goldsmith, E. & Hildyard, N. (1990). *The Earth Report 2*. Mitchell Beasley, London.
- Goudie, A. (1984). *The Human Impact*. Oxford: Blackwell.
- Groom, M. J. (2006). Threats to Biodiversity. In M. J. Groom, G. K. Meffe, & C. R. Carroll (Eds.), *Principles of Conservation Biology, Third Edition*, (63-109). Sunderland, MA: Sinauer Associates, Inc.
- "Illegal Logging." (1988). Retrieved 13 March 2017, from wwf.panda.org.
- Jack, K. M. (2011). The Cebines: Toward an explanation of variable social structure. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.) *Primates in Perspective*. Oxford NY: Oxford University Press.
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104(940), 501-528.
- Kelly, D. L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S. O., & Marciano-Berti, L. (2004). The epiphyte communities of a montane rain forest in the Andes of Venezuela: Patterns in the distribution of the flora. *Journal of Tropical Ecology*, 20(6), 643-666.
- Kulp, J. & Heymann, E.W. (2015). Ranging, activity budget, and diet composition of red titi monkeys (*Callicebus cupreus*) in primary forest and forest edge. *Primates*, 56, 273-278.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002).

Ecosystem decay of Amazonian forest fragments: a 22-year investigation.

Conservation Biology, 16, 605-618.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Fearnside, P.M.,

Ribeiro, J.E.L., & Capretz, R.L., (2006). Rain forest fragmentation and the proliferation of successional trees. *Ecology*, 87, 469-482.

Laurance, W.F., Nascimento, H.E.M., Laurance S.G., Andrade, A., Ewers, R.M., Harms,

K.E., Luizao, R.C.C., Ribeiro J.E. (2007) Habitat fragmentation, variable edge effects, and the landscape-divergence hypothesis. *PLoS ONE* 2, DOI: 10.1371.

Laurance, W.F., Camargo, J.L.C., Luizano, R.C.C., Laurane, S.G., Pim, S.L., Bruna, E.M., *et*

al. (2011). The fate of Amazonian forest fragments: a 32-year investigation.

Biological Conservation, 144, 56- 67.

Leopold, A. (1949). *A Sand County Almanac: And Sketches Here and There*. New York:

Oxford

University Press.

Lindsey, R. (2007). Tropical deforestation. *NASA's Earth Observatory*, 508.

Lindsey, R. & Kennedy, C. (2011). "Annual Migration of Tropical Rain Belt." Retrieved 12

March 2017, from Climate.gov.

Lodge, D. J., McDowell, W. H., & McSweeney, C. P. (1994) The importance of nutrient

pulses in tropical forests. *Trends in Ecology and Evolution*, 9, 384-387.

- Lovejoy, T. E. (1989). Deforestation and the extinction of species. In A. Botkin et al. (Eds.) *Changing the Global Environment*, (91-98). London: Academic Press.
- Luck, G. W., Davidson, P., Boxall, D., & Smallbone, L. (2011). Relations between urban bird and plant communities and human well-Being and Connection to Nature. *Conservation Biology*, 25(4), 816-826.
- Magnago, L.F.S., Edwards, D.P., Edwards, F.A., Magrach, A., Martins, S.V., Laurance, W.F. (2014). Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. *Journal of Ecology*, 102, 475-85.
- Martin, P. R., & McKay, J. K. (2004). *Evolution*, 58(5), 938-945.
- Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*, 117, 496-505.
- Murica, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution*, 10, 58-62.
- Myers, N. (1989). *Deforestation Rates in Tropical Forests and their Climatic Implications*. London: Friends of the Earth.
- Niklas, K. J. (1993). Influence of tissue density-specific mechanical properties on the scaling of plant height. *Annals of Botany*, 72, 173-179
- Park, C. C. (1992). *Tropical Rainforests*. New York, NY: Routledge.
- Peters, C. M., Gentry, A. H., & Mendelsohn, R. O. (1989). Valuation of an Amazonian rainforest. *Nature*, 339, 655-656

- Pinchot, G. (1905). "Letter to 'The Forester.'"
- Ploetz, R.C. (2000). Panama disease: a classic and destructive disease of banana. *Plant Health Progress*. DOI: 10.1094/PHP-2000-1204-01-HM.
- Prieto-Carron, M., Lund-Thomsen, P., Chan, A., Muro, A., & Bhushan, C. (2006). Critical perspectives on CSR and development: What we know, what we don't know, and what we need to know. *International Affairs*, 82(5), 977-987.
- Putz, S., Groeneveld, J., Alves, L.F., Metzger, J.P. & Huth, A. (2011). Fragmentation drives tropical forest fragments to early successional states: a modelling study for Brazilian Atlantic Forests. *Ecological Modelling*, 222, 1986-1997.
- Rano, M., Kowalewski, M. M., Cerezo, A. M., Garber, P. A. (2016). Determinants of daily path length in black and gold howler monkeys (*Alouatta caraya*) in northeastern Argentina. *American Journal of Primatology*, 78, 825-837.
- Resnik, D. B. (2015). "What is ethics in research and why is it important?" National Institute of Environmental Health Sciences.
- Reynolds, J. D. & Peres, C. A. (2006). Overexploitation. In M. J. Groom, G. K. Meffe, & C. R. Carroll (Eds.), *Principles of Conservation Biology*, Third Edition, (253-291). Sunderland, MA: Sinauer Associates, Inc.
- Ricklefs, R. E. (1993). *The Economy of Nature*. New York: W. H. Freeman.
- Rosero-Bixby, L. & Palloni, A. (1996) Population and deforestation in Costa Rica. Paper presented at the annual meeting of the Population Association of America, New Orleans. Retrieved from: <http://www.ssc.wisc.edu/cde/cdewp/96-19.pdf>.

- Rowland, L., Hill, T. C., Stahl, C., Siebicke, L., Burban, B., Zaragoza-Castells, J., ... Williams, M. (2014). Evidence for strong seasonality in the carbon storage and carbon use efficiency of an Amazonian forest. *Global Change Biology*, 20, 979-991.
- Russilidi, G., Arroyo-Rodrigues, V., Hernandez-Ordonez, O., Pineda, E., & Reynoso, V. H. (2016). Species- and community-level responses to habitat and spatial changes in fragmented rainforests: assessing compensatory dynamics in amphibians and reptiles. *Biodiversity Conservation*, 25, 375-392.
- Salemi, L. F., Groppo, J. D., Trevisan, R., de Moraes, J. M., de Barros Ferraz, S. F., Villani, J. P., ... Martinelli, L. A. (2013). *Journal of Hydrology*, 499, 100-109.
- Santos, B.A., Arroyo-Rodriguez, V., Moreno, C.E. & Tabarelli, M. (2010). Edge related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PLoS ONE*, 5, c12625.
- Schlesinger, W. H. & Jasechko, S. (2014). Transpiration in the global water cycle. *Agricultural and Forest Meteorology*, 198-190, 115-117.
- Schmitz, C., Kreidenweis, U., Lotze-Campen, H., Popp, A., Krause, M., Dietrich, J. P., & Muller, C. (2015). Agricultural trade and tropical deforestation: Interactions and related policy options. *Regional Environmental Change*, 15, 1757-1772
- Schneider, R. (1995). Government and the economy of the Amazon frontier. World Bank, Washington D.C.
- Schroth, G., Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L. & Isac, A.M.N. (2004). The role of agroforestry in biodiversity conservation in tropical

- landscapes. In G. Schroth, G.A.B. Fonseca, C.A. Harvey, C. Gascon, H.L. Vasconcelos, & A.M.N. Isac (Eds.), *Agroforestry and Biodiversity Conservation in Tropical Landscapes*. (1-12). Washington D.C.: Island Press.
- Schupp, E. W. (1992). The Janzen-Connell model for tropical tree diversity: Population implications and the importance of spatial scale. *The American Naturalist*, 140(3), 526-530.
- Sist, P., Mazzei, L., Blanc, L., Rutishauser, E. (2014). Large trees as key elements of carbon storage and dynamics after selective logging in the Eastern Amazon. *Forest Ecology and Management*, 318, 103-109.
- Southgate, D. (1998). Tropical forest conservation: An economic assessment of the alternatives in Latin America. Oxford, NY: Oxford University Press.
- “Species Extinction – The Facts.” (2007). International Union for the Conservation of Nature. Retrieved from https://cmsdata.iucn.org/downloads/species_extinction_05_2007.pdf
- Tabarelli, M., Aguiar, A.V., Girao, L.C., Peres, C.A. & Lopes, A.V. (2010). Effects of pioneer tree species hyperabundance on forest fragments in North-eastern Brazil. *Conservation Biology*, 24, 1654-1663.
- Tang, I-Chun, William C. Sullivan, and Chun-Yen Chang. (2015). Perceptual evaluation of natural landscapes: The role of the individual connection to nature. *Environment & Behavior*, 47(6), 595-617.

- Tutin, C.E.G. (1999) Fragmented living: behavioural ecology of primates in a forest fragment in the Lope Reserve, Gabon. *Primates*, 40, 249-265.
- United States Department of Agriculture: Office of Communications. (2016). *USDA Announces Reopening of Brazilian Market to U.S. Beef Exports*. Retrieved from <https://www.usda.gov/media/press-releases/2016/08/01/usda-announces-reopening-brazilian-market-us-beef-exports>
- United States Department of State Bureau of Economic and Business Affairs (2013). 2013 Investment Climate Statement – Costa Rica.
- Valencia, R., Foster, R. B., Villa, G., Condit, R., Svenning, J., Hernandez, C., ... & Balslev, H. (2004). Tree species distributions and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. *Journal of Ecology*, 92, 214-229.
- Van Hulle, M. & Vaughan, C. (2008). The effect of human development on mammal populations of the Punta Leona private wildlife refuge, Costa Rica. *Revista de Biología Tropical*, 57(1-2), 441-449.
- Whitmore, T. C. (1998). *An Introduction to Tropical Rain Forests*. Oxford, New York: Oxford University Press
- Woods, M. (2001) Wilderness. In D. Jamieson (Ed.) *A Companion to Environmental Philosophy*. Malden, MA: Blackwell Publishing.
- Yonekura, Y., Ohta, S., Kiyono, Y., Aksa, D., Morisada, K., Tanaka, N., & Tayasu, I. (2012). Dynamics of soil carbon following destruction of tropical rainforest and the

subsequent establishment of Imperata grassland in Indonesian Borneo using stable carbon isotopes. *Global change biology*, 18(8), 2606-2616.