

**A STUDY OF EDGE EFFECTS ON TREE  
SPECIES DISTRIBUTION AND COMPOSITION  
ALONG THE PARQUE NATURAL  
METROPOLITANO'S SENDERO PANAMÁ**

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# of equivalent full days spent on project in Panama: 22

# of equivalent full days spent on project in the field: 3

Panama Field Study Semester

ENVR 451: Research in Panama

Thursday, April 14<sup>th</sup>, 2016

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## HOST INSTITUTION

The Parque Natural Metropolitano is located in the heart of Panama City in the Ancon district right between the Curundu River and Amistad Road. Though it was officially created on June 5<sup>th</sup> 1988, World Environment Day, the idea of delimiting a protected area originated in 1974 with the Soil Management Plan for the Panama Canal Area. Originally, the area where the park lies today was dedicated to agricultural and pastoral activities before the United States declared it part of the Canal Zone in 1903 so as to build barracks to house canal workers. Indeed, the 1903 Hay-Bunau Varilla Treaty allocated five miles of land on both side of the interoceanic canal to the American government for them to construct, manage, protect and operate the aquatic highway. When the canal construction was completed in 1914, the forest was allowed to start regenerating which is why the park today is a secondary forest of relatively low canopy. Nonetheless, other activities kept taking place on park grounds with the aforementioned barracks being used to house military personnel receiving training from the “Fuerza de Defensa de Panama” (FFDD). Nowadays, the park covers 232 hectares and is the only wildlife refuge contained within city limits in all of Central America. It is mainly composed of a humid tropical forest and it houses an impressively high biodiversity of faunal and floral life: 284 tree species, 45 mammal species and 254 bird, reptilian and amphibian species. As part of the Panama Canal Biological Corridor, it fulfills a very important role in permitting connectivity between protected areas of the region. On a more local scale, the park contributes to the conservation of fauna and flora while providing urban dwellers with a green area for outdoor recreation. This increases overall life quality in the city as well as contributing to maintaining good air quality in an urban setting; this is why the park is also known as the “lungs of the city”. Similarly, the extensive

rainforest along the waterway that the park is part of participates in protecting the Panama Canal watershed from erosion and reduction of water flow. In that sense, because Canal activities require large amounts of water, the park also plays an economic role by ensuring efficiency of the Canal. Moreover, the Parque Natural Metropolitano's activities have numerous objectives that go beyond pure environmental conservation. Their mission as environmental educators consists of providing infrastructures and activities for raising the awareness of youth and citizens around the importance of conserving local ecosystems and natural resources. The park offers infrastructures and personnel for environmental education, environmental interpretation, guided recreation, ecological research and related cultural-scientific activities. More broadly speaking, they strive to reinforce the educational curriculum in Panama by identifying needs of the formal education system. In conclusion, the park is an important member of the community in Panama City for the numerous reasons cited above and the present research paper fits in the scientific and educational themes of Parque Natural Metropolitano's mission.

## OUR RESEARCH PROJECTS

Our internship at the Parque Natural Metropolitano allowed us to participate in two distinct projects. Firstly, the park administration expressed their interest in receiving a proposal for the creation of an arboretum. We came to understand that the project is still tentative because the budget required for it has not yet been allocated. They plan to open this arboretum along and around the *Sendero Panamá*, a trail that had been closed for around 6 years. Being an important physical and conceptual link between urban dwellers of Panama City and nature, the park hopes to eventually use this arboretum as another teaching tool within their environmental education mission. More specifically, the park is concerned that with the rapid urbanization and rural exodus that Panama is experiencing, there is an increasing number of people who live disconnected from the land. Such a reality seriously threatens the survival of knowledge surrounding traditional and folkloric uses of Panamanian forest products. With this in mind, we conducted a census of tree species that presently exist along the *Sendero Panamá* and produced a design proposal containing a list of tree species to include in the arboretum. The list contains a high species diversity which responds to both the educational aim of the project and to the need for coexistence of diverse fauna and flora life forms; something necessary to the health and survival of the future arboretum. The proposal document also includes tips and suggestions as to where, when and how to plant different seedlings. Additionally, we created an educative pamphlet containing pictures and interesting facts about certain trees or plants that could be found within the future arboretum. If they desire to, we hope the park can use this product as a brochure to hand out to visitors. The arboretum design proposal and informative pamphlet were submitted to our host institution, but since they are not directly related to the present research paper, they were not included in this document.

Secondly, we designed a scientific research to verify the “edge effect” hypothesis, a theory in ecology that refers to the changes occurring in population dynamics and composition at the boundary of two habitats. According to this theory, the creation of edges can affect biodiversity within fragments because edges create new microclimates at a local scale: air temperature, soil moisture, levels of photosynthetically active radiation and vapour pressure deficit are all different in edge environments. Certain anthropogenic activities such as road construction and land clearing for agriculture are responsible for the creation of ecosystem edges around the world. Given the interest there is in studying the dynamics linked to habitat fragmentation, we designed a research project through which we tested the edge effect hypothesis along the *Sendero Panamá* in Parque Natural Metropolitano. The present document is the final report we have produced for this project.

## **INTRODUCTION AND LITERATURE REVIEW**

### Biodiversity In The Tropical Forest

The diversity of life forms encountered in tropical forests around the world is astonishing: some tropical forests can support more tree species in a 0.5 km<sup>2</sup> parcel than all of North America or Europe (Burslem et al, 2001). Biologists and ecologists still engage in some debating when trying to explain this, but such high tropical forest diversity is thought to be maintained by at least four different factors: niche differentiation, natural enemies, seed dispersal limitations and competitive equivalence (Burslem et al, 2001). On top of being home to an enormous number of plant and animal species, tropical forests play a central role in the global carbon cycle, which means that any alterations to these ecosystems can be expected to affect global climate (Cramer et al, 2004). Though they only cover 7 to 10% of the Earth's land surface, tropical forests store 25% of all global carbon and harbour up to an estimated 53,000 species (Slik et al. 2015), corresponding to 96% of all tree species in the world. Conserving these ecosystems therefore offers us the possibility of creating a win-win situation where biodiversity is safeguarded whilst simultaneously achieving carbon storage. Additionally, protecting biodiversity might actually enhance carbon sequestration and storage in tropical forests by increasing its productivity. There is a growing amount of scientific literature highlighting the role of biodiversity in ecosystem services, processes and properties; and the argument promoting conservation of biodiversity simply for the sake of biodiversity is being replaced by a more complete understanding of how species richness can positively affect the productivity and health of an ecosystem (Poorter et al, 2015). Species richness is thought to increase productivity through: (1) niche complementarity, where species live in different niches with different resource requirements, allowing them to facilitate each other and hence increase overall productivity

(Tilman et al, 2001); (2) the selection effect, where simply by having more species in the community there is a higher chance to harbour a very productive species (Loreau & Hector, 2001); and (3) the insurance effect, according to which if one species contributes less to ecosystem productivity in a given year, another species can compensate in another year and vice versa (Isbell et al, 2011). Since productivity is defined by how quickly biomass is accumulated, the above hypotheses directly link forest species richness to carbon sequestration and storage capacity. For example, Poorter and colleagues (2015) found that tree species richness had an independent positive effect on above ground biomass accumulation. In other words, it is not only the sheer extent and size of tropical forests that holds importance, but the diversity they harbour is also fundamental to safeguarding the present structure and functions of these ecosystems. Unfortunately, the environmental costs of deforestation extend beyond the simple loss of forest cover: scientific evidence has found that deforesting one area can affect the structure and composition of other adjacent forested areas (Murcia, 1995).

### Habitat Fragmentation

Considering that agriculture, road construction, settlement development and both legal and illegal logging are currently causing extensive deforestation in many tropical countries, there is great urgency in understanding the dynamics triggered by the above anthropogenic activities. Indeed, the state of tropical forests is alarming, even more so when we realise that there is much uncertainty surrounding how animal and plant communities will react to the modified landscapes humans are creating (Murcia, 1995). More specifically within this context, habitat fragmentation is one of the most pervasive forms of anthropogenic disturbances because it encompasses both

deforestation and the patch-forest dynamics that it triggers. Local extinction, invasion of plant species, lower seedling abundance and lower species richness are expected to occur following habitat fragmentation, especially within the smallest fragments (Benitez-Malvido, 1998; Leigh et al. 1993). The main issue with fragmentation for plant communities is that it decreases propagule sources and interrupts their fluxes (Benitez-Malvido and Martinez-Ramos, 2003). Yet, in tropical rain forests, propagule fluxes are needed for new habitats to be colonized, seedling banks to be renewed, and understorey plant diversity to be maintained (Benitez-Malvido et al. 2003). Additionally, a decline in seed fluxes means a greater incidence of rare or non-abundant seedling species. These rare species are more prone to extinction because their low abundances make them quite vulnerable to random fluctuations in population size (Scariot, 1999). Alarming, the loss of certain seedling species may eventually affect other species' recruitment to later life stages, jeopardizing future forest regeneration and the maintenance of high species richness (Benitez-Malvido, 1998). It is therefore clear that fragmentation contributes to making ecosystems very vulnerable to environmental change at the individual level by rendering tree species inside the fragments more susceptible to extinction.

The genetic dimension of the fragmentation issue is also a serious one. Habel and Zachos (2012) define fragmentation as “the breaking up of a formerly (more) connected habitat resulting in an increased mean isolation of habitat patches dispersed within an unfavourable matrix, with the main result being an impediment to migration among these patches and thus to gene flow”. This can be explained by the fact that fragmentation disrupts the connectivity that exists in continuous forests by creating a landscape of disconnected patches of forest. Breaking down natural corridors that otherwise permit exchanges between communities and ecosystems may affect species already at risk and hence contribute to reducing biodiversity. Species that are part

of interconnected population networks have the possibility to maintain a high proportion of genetic diversity, whereas a sudden rupture of gene flow brought about by fragmentation can severely affect genetic diversity, something very detrimental to the persistence and fitness of species (Habel and Zachos, 2012). Ultimately, fragmenting naturally interconnected habitats not only reduces species diversity, but also intraspecific diversity and overall viability through increased homozygosity (Habel and Zachos, 2012).

### Edge Effects

Habitat fragmentation can promote rapid shifts in the composition and structure of ecosystems due to habitat loss, rupture of connectivity, isolation of populations, proliferation of invasive species and the creation of forest edges (Fahrig, 2003). Indeed, habitat edges strongly affect many forest species and ecological processes such as forest regeneration, litter production, and biotic interactions (Murcia, 1995). A good understanding of the dynamics regime triggered by the creation of these artificial edges can provide useful knowledge on forest regeneration because seed dispersal into disturbed areas is usually highest at the fringe of the forest (Holl et al. 1997).

In general, abiotic factors are modified near the edges as opposed to the forest interior: differences in incident light, soil and air humidity, temperature, wind and frequency of fires can affect the recruitment and the composition of plant species within the edge zone (Benitez-Malvido and Martinez-Ramos, 2003). A hotter and drier environment than continuous forests, edges are not always suitable for the germination and establishment of certain tree species (Bruna, 2002). Therefore, the success of seedling establishment directly depends on a species'

ability to cope with harsh environmental conditions (Kapos, 1989). In addition, isolated forest fragments are disconnected and do not have the opportunity to be colonized or recruit from nearby forests. (Primack, 1992). Such recruitment limitation is exacerbated near the forest edges where increased tree mortality also causes a decrease in local seed production (Lewis, 1998). Accordingly, a study by Benítez-Malvido and Martínez-Ramos (2003) found that in a given fragment, the number of tree seedling species recruited varied inversely with the number of edges where adverse conditions cause higher seed and seedling mortality. In other words, the greater the number of edges in a forest fragment, the lower the number of seedling species recruited. With isolation impeding on colonization and edges reducing seed production through increased tree mortality, habitat fragmentation and its edge effects are a real threat to biodiversity as they tend to homogenize the species composition in a given area (Holl et al. 1997).

Edge effects are that much more pervasive because they do not limit themselves to the boundary of forest fragments: sometimes they propagate as deeply as several hundred meters into the forest interior (Benítez-Malvido and Martínez-Ramos, 2003). Though forest centers harbour higher species richness than fragments exposed to edges, edge effects can reach the interior and significantly impact forest structure (Laurance et al. 1997), diminish seedling recruitment and facilitate arrival of invasive species (Curran et al. 1999). Ultimately, the extent to which edge effects will penetrate and affect the forest interior depends on the change of canopy structure at the edge itself (Didham and Lawton, 1999). Much empirical and theoretical evidence has been accumulated on the subject, and it is argued that edge effects launch a series of processes that ultimately drive tropical forest fragments into a permanent early-successional system (Tabarelli et al 2008).

## Early-Successional Systems

In a continuous tropical forest, shade-tolerant trees and high-climbing liana species predominantly compose what is known as the regeneration guild (Tabarelli et al. 2008). Consequently, these woody plants can be expected to dominantly guide habitat structure and resource availability for the other plant, vertebrate and invertebrate species of the ecosystem in old growth forests. However, when fragments are created, a quick spread of short-lived pioneer species along the edges can significantly alter the structure, functionality and composition of the forest (Laurance et al. 2006). Following a disturbance, the pioneer species proliferation is triggered by augmented light availability, but as these trees reach maturity and form an even canopy layer, abundant seed production and other edge-induced microclimatic factors contribute to guarantee the persistence of appropriate conditions for pioneer recruitment and for cycles of pioneer self-replacement (Tabarelli et al. 2008). Tree species that are common and/or abundant in mature forests may be much less abundant or even absent in the early-successional forests that disturbances (such as edges) create (Capers et al. 2005). Indeed, quick proliferation of pioneer species happens at the detriment of old-growth, large-seeded and shade-tolerant species which are not as quick to reproduce and colonize: this drives them to rarity and sometimes even extinction at the landscape scale (Cramer et al. 2007). In addition, the majority of pioneer species are soft-wooded canopy species; hence their propagation at the expense of old-growth trees exacerbates the reduction of forest biomass that was initially caused by increased tree mortality in edges (Nascimento et al. 2005).

Despite gap disturbance theory predicting that pioneer species should eventually get outcompeted and replaced by shade-tolerant trees as disturbed areas age, edge-affected fragments contradict this by maintaining environmental conditions that are not suitable for the recruitment

and growth of longer-lived tree species (Tabarelli et al. 2004). As a matter of fact, the persistent recruitment of pioneer seedlings, even along old edges of hyper-fragmented landscapes, is defending the hypothesis that pioneer-dominated communities might actually be reaching equilibrium as a permanent rather than a transient successional stage (Oliveira et al. 2004). In other words, the pioneer-dominated ecosystem can persist because the maintained edge (ex: a road) redundantly favours light-intensive plants at the expense of a more diverse old-growth floral community (Tabarelli et al. 2008). This has serious implications for the composition of tropical forests, especially when considering that edge effects can penetrate inside the forest interior. Indeed, the simplification of tree assemblages that accompanies early-successional systems simply translates to the elimination or rarefaction of many large-seeded, old-growth tree species (Santos et al. 2008). Consequently, the rapid spread of pioneer trees rearranges the species composition of fragments and leads to a reduction in alpha (within a fragment) and beta (between fragments) diversities (Oliveira et al. 2004). The risk of such a rearrangement in favour of pioneer species in tropical forests is an alarming possibility: shade-tolerant tree species are responsible for the large majority of the diversity in morphological and life-history traits observed in tropical trees – including root systems, crown architecture, seed-dispersal systems and anti-herbivory defense systems (Turner, 2001). Driving to extinction these tree species is also eliminating centuries of ecological evolution.

In sum, the creation of forest edges through fragmentation significantly affects a tropical forest's capacity to harbour high tree diversity and retain biomass and nutrients (Tabarelli et al. 2008). Nonetheless, an understanding of how forest fragmentation reverses successional processes (turning a mature forest into a persistent early-successional system) allows scientists and land managers to better predict the ecosystem changes that occur with fragmentation.

Ultimately, such knowledge is essential in assessing the potential that human-modified landscapes offer for biodiversity conservation and retention of environmental services.

### Our Research Question

Within the context of retaining biodiversity and guaranteeing the continuity of ecosystem services that tropical forests provide to human societies, there is great value in understanding forest archipelago dynamics that come hand in hand with landscape fragmentation. This project in particular examined the edge effect theory along the *Sendero Panamá* of the Parque Natural Metropolitano. Our research question asked if a significant difference in species richness could be observed between edge quadrats and non-edge quadrats along said trail. In accordance with the theory presented above, we conducted this experiment with the hypothesis that edge quadrats would present a significantly poorer species richness than non-edge, forest interior quadrats. This study is important because it adds to the knowledge that is being accumulated on the consequences of habitat fragmentation and thus contributes to the future conception of efficient conservation strategies.

## METHODS

Throughout our research we fully respected McGill's Code of Ethics for Research. We never harmed or altered the environment we were working with.

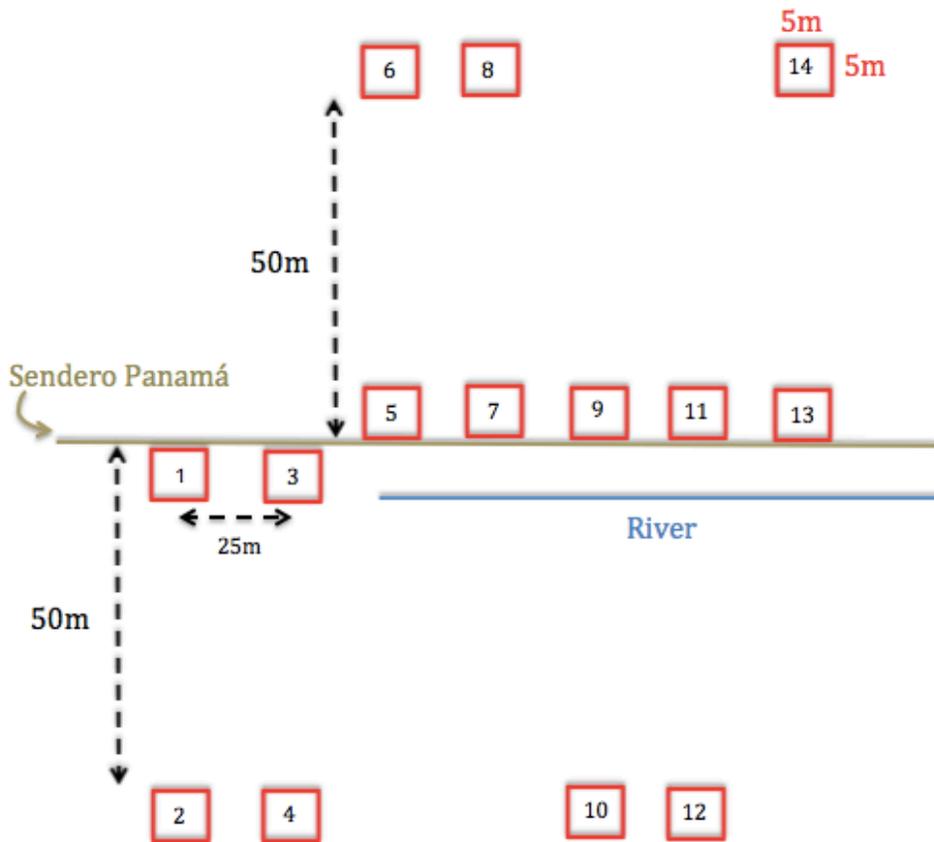
### Study area and sampling

The study site was located at the southern end of the Panama Canal watershed, in the Parque Natural Metropolitano (PNM). The PNM is located in the Panamá province at a latitude of 8°58'N and a longitude of 79°35' W, and has an average altitude of 50m above sea level. The mean temperature is 28°C with an average of 1740mm of annual precipitation (Tosi, 1971), making it a zone of humid tropical forest.

Sampling was carried out along the *Sendero Panamá*, a 225m-long path reopened specifically for the purpose of this study after six years of disuse. The *Sendero Panamá* was considered to be an appropriate edge as it was previously travelled extensively, particularly during the time of US occupation of the area (from the early 20<sup>th</sup> century up to 1999). Given that an edge has long lasting influence on the forest it impacts, we considered the forest alongside the path to have been under continuous edge effect since the creation of the *Sendero Panamá*.

Over the course of our project, we sampled two different habitats: (1) forest interior (or non-edge) and (2) forest edge along the path. To do so, between February 4<sup>th</sup> and April 4<sup>th</sup> 2016 we established seven 5m by 5m quadrats every 25m along the edge of the *Sendero Panamá*. Each edge quadrat was paired with a non-edge quadrat of the same size installed 50m into the forest perpendicular from the path, beyond the extent of edge disturbance (Sizer and Tanner 1999). Every two quadrats, we alternated the side of the path along which they were established,

except in instances where the topography of the terrain prevented us from installing a quadrat (due to a river running along the path for example), in which case the quadrat was established on the opposite side of the path (see Figure 1).



**Figure 1.** *Map of the quadrats established along the sendero Panamá (not to scale)*

In each 25m<sup>2</sup> quadrat, we measured tree (woody and palm) abundance by counting the number of stems with diameters at breast height (DBH) superior to 5cm. The species of the tree was then identified on site if possible. Nonetheless, due to the difficulty associated with identifying species with a naked eye, we also photographed the trees' respective trunk and leaves to later confirm their identity using reference books.

In addition, three abiotic variables were studied to explore their influence on species richness along the edge. We measured temperature, dew point (from which we inferred relative humidity) and amount of incoming radiation at zenith. The amount of incoming radiation was classified into a four level ordinal scale (with categories ranging from 0%-25%, 25%-50%, 50%-75% and 75%-100% of sunlight). All abiotic factors were measured at the same time of day (in the morning between 9:00 am and 12:00 pm) to reduce time-of-day effects. It is important to note that these measurements were taken during a particularly dry season in Panama and hence are not indicative of the region's climate for other months.

## **Data analysis**

### Species accumulation curve

We designed our methodology to estimate as accurately as possible tree species richness in edge and non-edge environments so as to later compare the diversity between these two habitat types. In order to do so, we verified that our estimate of species richness in both environments was adequate using a species accumulation curve.

In theory, finding out how many species are present in a habitat implies sampling more and more individuals until no new species is discovered. This can be explained graphically through a **species accumulation curve**, which records the cumulative number of new species discovered as additional quadrats are sampled (Gotelli and Colwell, 2001). The sampling curve rises rapidly at first, and then slows down as fewer and rarer species are added, eventually plateauing at an asymptote once all the species in the studied area have been sampled.

According to Thompson and colleagues (2003), species accumulation curves can be calculated in two different ways: either plotting all the data points, or using only the data points

where new species were found (and the cumulative number of species found increased). In this analysis, we chose to follow Thompson and colleagues' (2003) methodology and use all of the data collected, as it would provide a more precise estimation of the species richness in each habitat. In addition, we plotted the number of species as a function of the accumulated number of individuals (not of quadrats), since this technique enables density to be taken into account (Gotelli and Colwell, 2001). The mean individual-based species-accumulation curve was therefore plotted for both sets of data collected (edge and non-edge habitat) to evaluate our measure of biodiversity and assess whether our data are representative of the biodiversity present in the studied habitats.

#### Edge effect on species richness

After numerically testing for the normality assumption using Shapiro-Wilk  $W$ , we carried out a t-test to evaluate the significance of the difference in tree species richness between the two habitats sampled. Since our two datasets exhibited unequal variances, we chose to carry out a heteroscedastic t-test.

In addition, we used Jaccard's coefficient of similarity (JI) to determine the percent similarity of species composition between edge and non-edge quadrats (Benítez-Malvido and Martínez-Ramos, 2003). To do so, we applied the following equation to our data:

$$J_{E,N} = \frac{a}{a + b + c}$$

where  $J_{E,N}$  is the Jaccard coefficient of similarity between edge and non-edge quadrats,  $a$  = number of species present in both habitats,  $b$  = number of species present only in edge habitat, and  $c$  = number of species present only in non-edge habitat (Jaccard, 1912). This therefore

measures the ratio of shared species to unique species in two habitats, based on species presence-absence data (Magurran, 1988).

To further test the difference in species composition between edge and non-edge quadrats, we constructed a non-metric multidimensional scaling (NMDS) basing our ordination on the Jaccard index of percent similarity. To do so, we chose to use the MASAME NMDS package (<http://mb3is.megx.net/eatme/NMDS/>). NMDS has the advantage of being very flexible in both the definition and conversion of dissimilarity distance, and it does not require that the data meet the usual parametric assumptions of other ordination techniques (Carr, 1997).

### Species diversity

In the field, we collected data not only on species richness but also on their relative abundance in edge and non-edge habitats. Species richness (R) quantifies the total number of species found in a sample. Readily measured and analyzed, it is a popular index in ecological research (Currie and Paquin, 1987; Hubbell et al. 1999; Ugland et al. 2003). Richness does not however take abundance into account, and as such does not measure diversity (a concept which also encompasses evenness, defined as the relative abundance of species).

To calculate the species diversity present in the two habitats sampled, we used Simpson's Diversity index:

$$D = \frac{\sum_{i=1}^R n_i (n_i - 1)}{N(N - 1)}$$

where  $n$  is the total number of individuals of a particular species that have been sampled, and  $N$  the total number of individuals of all species sampled.

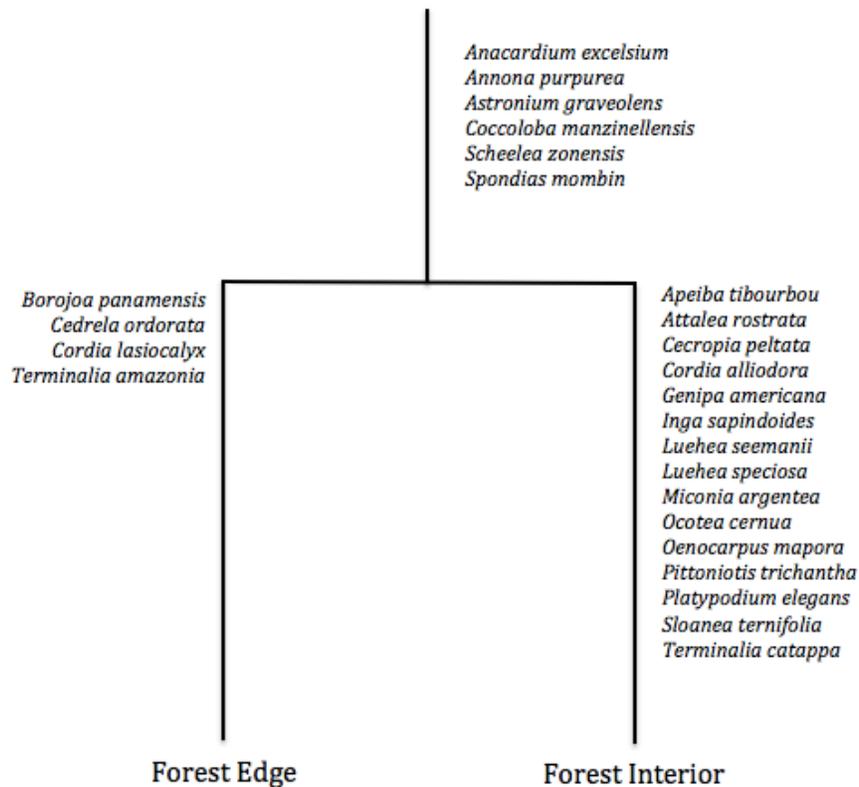
Since this index gives 0 as infinite diversity and 1 as no diversity, it is often considered counter-intuitive. For this reason we used the Simpson's Reciprocal Index (equal to  $1/D$ ) in our data analysis, where the higher the value is, the greater the diversity. Although the diversity index used does not take into account the area sampled, we disregarded this as both sets of quadrats are of equivalent size.

### The influence of abiotic factors

Finally, we used a series of t-tests to determine whether the abiotic variables measured in the field were significantly different between edge and non-edge habitats.

## RESULTS

Over the course of our three-month research, we sampled 250m<sup>2</sup> of forest (half in an edge habitat and the other half in a non-edge habitat). A total of 51 individuals were sampled, belonging to 25 different tree species. Six species were classified as dominant since the number of collected individuals represented more than 5% of the total sample (Magura, 2002): *Anacardium excelsium*, *Annona purpurea*, *Astronium graveolens*, *Coccoloba manzinellensis*, *Luehea speciosa* and *Spondias mombin*. The dominant species showed very little habitat preference, as five of them (all except *L. speciosa*) were found in both edge and forest interior (Figure 2).



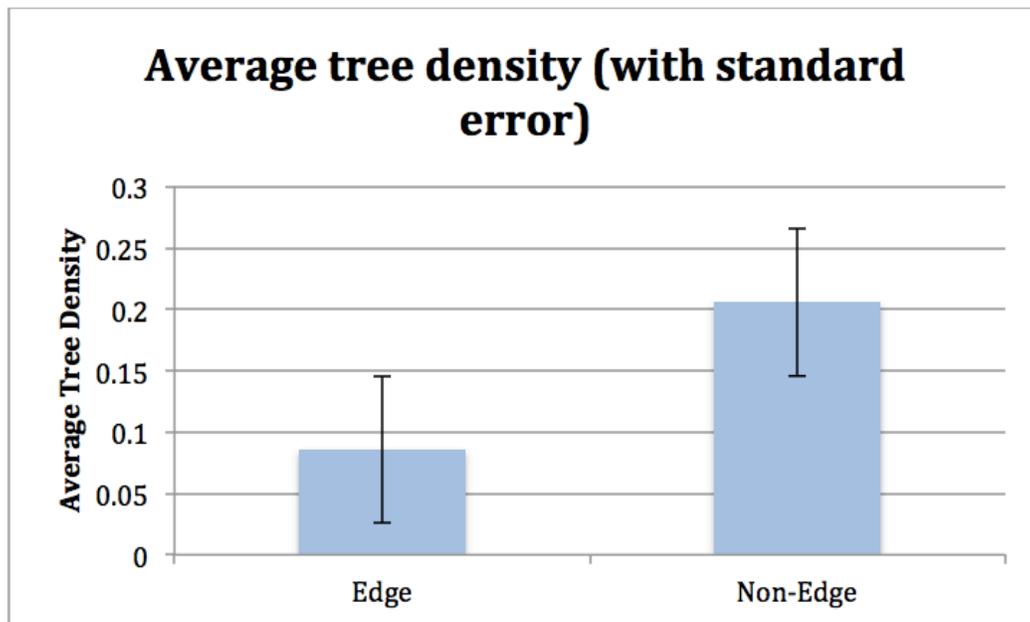
**Figure 2.** Dendrogram showing the distribution of trees species among the studied habitats.

This dendrogram shows that there is a difference in edge-tolerance between the species sampled, with certain species being edge sensitive (such as *Apeiba tibourbou* or *Attalea rostrata* amongst others), and others edge-preferring (such as *Borojoa panamensis* or *Cedrela Ordonata* for example).

### Tree Density

We recorded lower average tree density in edge quadrats (Figure 3). On average, edge habitats had a density of 0.086 tree.m<sup>-1</sup> and non-edge a density of 0.21 tree.m<sup>-1</sup>.

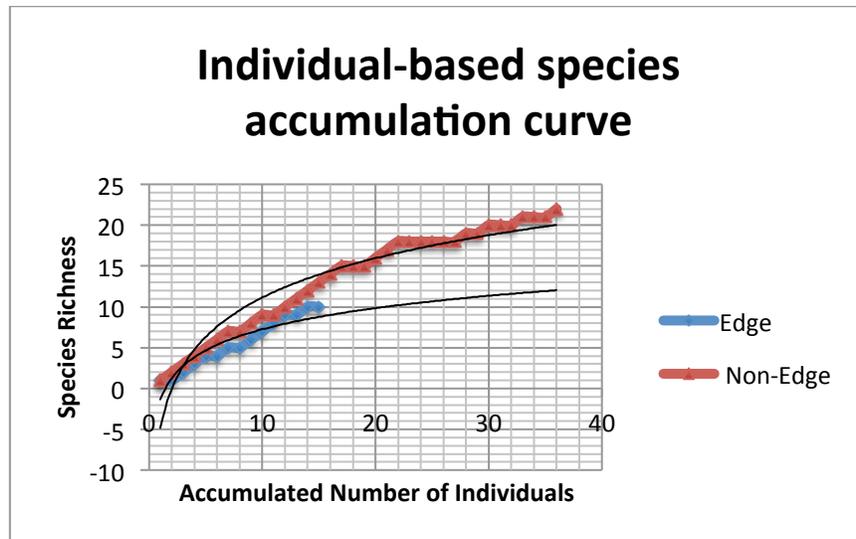
It is important to remember here that only woody and palm trees with a DBH above 5cm were sampled. This means that all shrubs, grasses and seedling were discarded, which could explain the observed difference in density.



**Figure 3.** Chart comparing the average tree density found in both habitats studied, with standard error. A difference in tree density can be observed.

### Species accumulation curve

The species accumulation curve (Figure 4) has been adjusted to individuals rather than quadrats, enabling us to take into account the observed difference in tree density (Gotelli and Colwell, 2001). Despite our extensive sampling efforts, neither of the two species accumulation curves reached an asymptote for our sampling sites, and the curves continued increasing, albeit at a slower rate. This shows that species richness was not entirely recorded in the habitats studied.

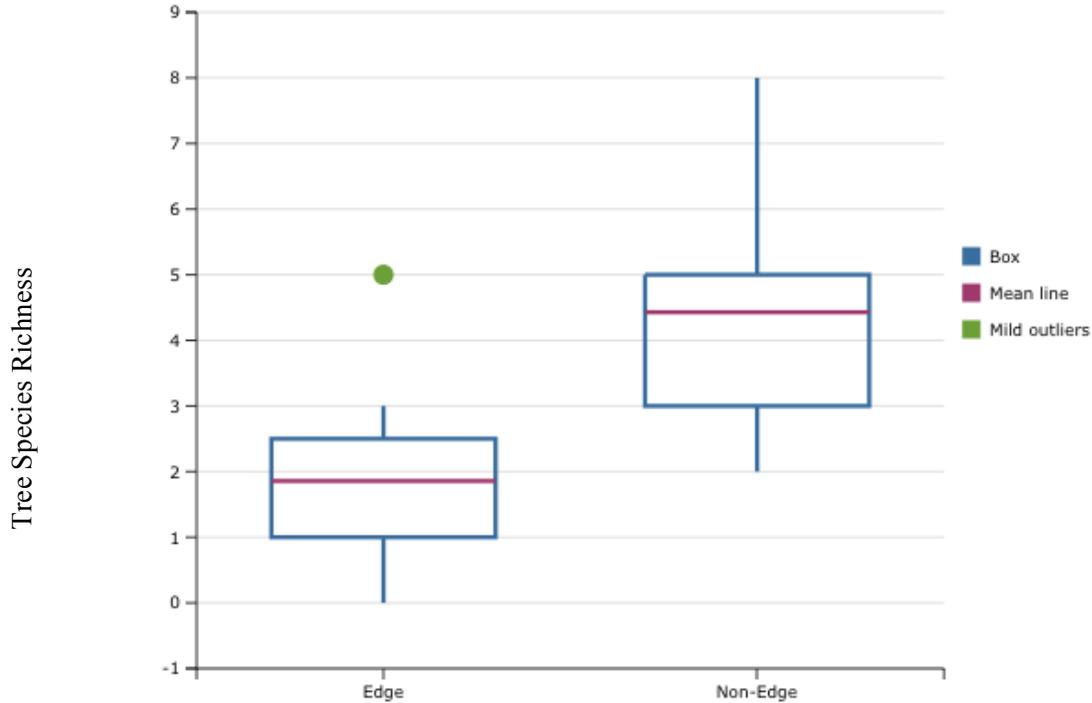


**Figure 4.** The individual-based accumulation curve for our species inventory of edge and non-edge habitats.

### Species richness

In order to carry out a t-test we first tested for data normality using the Shapiro-Wilk W test. In both edge ( $W=0.88511$ ,  $p\text{-level}=0.25012$ ) and non-edge ( $W= 0.89183$ ,  $p\text{-level}= 0.8437$ ) habitats, the p-level was superior to the chosen alpha level of 0.05, leading us to accept the null hypothesis that the data is normally distributed.

A t-test indicated a significant difference ( $p < 0.05$ ) in tree species richness between edge and non-edge habitats (Figure 5,  $df=12$ ,  $p\text{-level}=0.02527$ ), as can be seen in Figure 5.



**Figure 5.** Boxplot indicating the tree species richness sampled in edge and non-edge habitats. The mean richness in edge habitat is 1.85714 tree species per quadrat, whereas it is equal to 4.42857 in non-edge habitats. The mild outlier observed in the edge habitat is quadrat 5, where we sampled 5 different species of trees.

Once we had established that along the *Sendero Panamá*, the sampled tree diversity was lower than in the forest interior, we asked ourselves whether there was an important difference in the composition of the trees species sampled, or in other words whether the edge and non-edge habitats harboured significantly different tree assemblages.

The Jaccard coefficient of similarity showed that edge and non-edge habitats are only 16.22% similar (Table 1). They thus have quite a different composition when it comes to tree species.

**Table 1.** Presence-absence data on tree species in studied habitats.

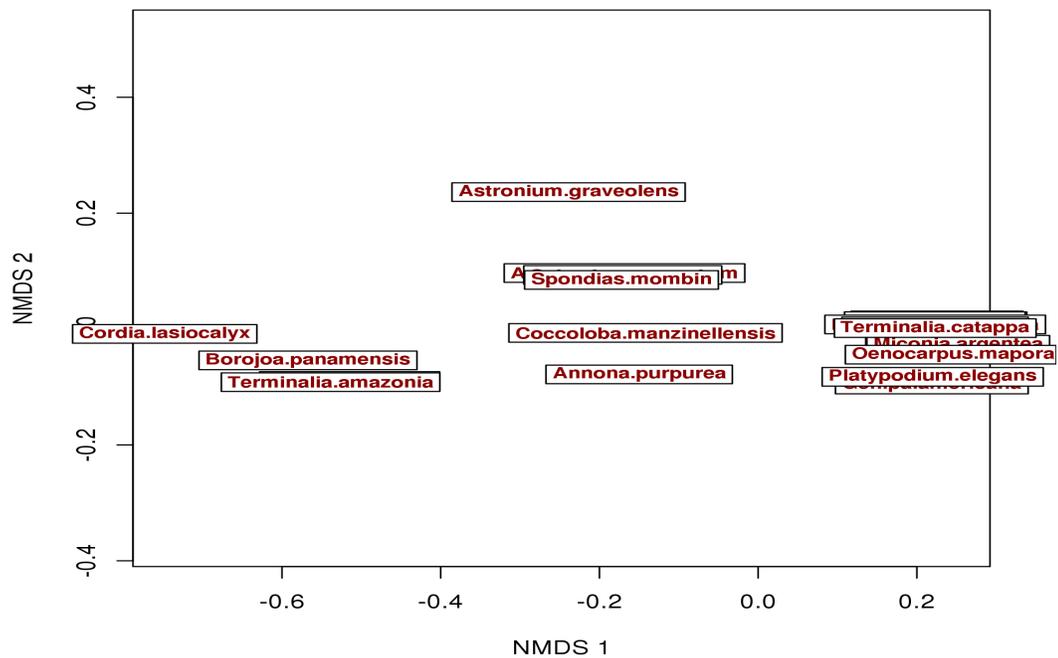
Species	Edge	Non-Edge	Common to both
<i>Anacardium excelsium</i>	1	1	1
<i>Annona purpurea</i>	1	1	1
<i>Apeiba tibourbou</i>	0	1	0
<i>Astronium graveolens</i>	1	1	1
<i>Attalea rostrate</i>	0	1	0
<i>Borojoa panamensis</i>	1	0	0
<i>Cecropia peltata</i>	0	1	0
<i>Cedrela odorata</i>	1	0	0
<i>Coccoloba manzinellensis</i>	1	1	1
<i>Cordia alliodora</i>	0	1	0
<i>Cordia lasiocalyx</i>	1	0	0
<i>Genipa Americana</i>	0	1	0
<i>Inga sapindoides</i>	0	1	0
<i>Luehea seemanii</i>	0	1	0
<i>Luehea speciose</i>	0	1	0
<i>Miconia argentea</i>	0	1	0
<i>Ocotea cernua</i>	0	1	0
<i>Oenocarpus mapora</i>	0	1	0
<i>Pittoniotis trichantha</i>	0	1	0

<i>Platypodium elegans</i>	0	1	0
<i>Scheelea zonensis</i>	1	1	1
<i>Sloanea ternifolia</i>	0	1	0
<i>Spondias mombin</i>	1	1	1
<i>Terminalia Amazonia</i>	1	0	0
<i>Terminalia catappa</i>	0	1	0
<b>Total</b>	<b>10</b>	<b>21</b>	<b>6</b>

Jaccard's Coefficient	0.162162162
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**Notes.** In this table, 1 represents presence of the species in the sample and 0 that the species is absent. From this table, the Jaccard coefficient of similarity was calculated.

In addition, the NMDS ordination shows that the tree species samples from the non-edge habitat and the edge are separated from each other, with the exception of a cluster of species common to both habitats (Figure 6).



**Figure 6.** Ordination of the species sampled based on the Jaccard similarity index. The cluster to the left represents the species found in edge quadrats, the cluster to the right the species found in the non-edge quadrats, and the middle cluster represents the species that are common to both.

### Species diversity

In addition to analyzing species richness, we computed species diversity to account for stem density using Simpson's index. We found that non-edge habitats had significantly higher species diversity than edge habitats (Table 2).

**Table 2.** Simpson's index and reciprocal index calculated for edge and non-edge habitats.

	Edge	Non-Edge
<b>Simpson's index (D)</b>	0.066666667	0.042857143
<b>Simpson's Reciprocal Index (1 / D)</b>	15	23.33333333

### Environmental variables

No significant differences in abiotic variables were found between the edge and the edge habitats. As we can see in table 3, none of the p-values computed are below  $\alpha = 0.05$ , and so no significant difference in neither temperature, relative humidity or incoming radiation can be observed between edge and non-edge habitats.

**Table 3.** Results of *t*-tests carried out on abiotic variables of the studied habitats

	Edge		Non-Edge		<i>t</i>	<i>df</i>	<i>p</i> - value
	M	SD	M	SD			
<i>Temperature</i>	31.43	0.98	30.71	0.76	1.53	12	0.15171
<i>Relative Humidity</i>	62	6.23	63.21	3.88	0.44	12	0.66946
<i>Incoming Radiation</i>	3.29	0.49	3.57	0.79	0.82	12	0.43013

**Note.** M = Mean, SD = Standard Deviation. P-value is given for two-tailed distribution. The *t*-value is the value of a *t* test comparing the mean abundance of individual tree species within edge and non-edge habitats.

## DISCUSSION

### Discussion of the main findings

The main aim of this research project was to test the influence of edges on tree species richness in the forest surrounding the *Sendero Panamá*. We hypothesized that tree species richness observed in the forest interior would be higher than the one observed at the forest edge. Indeed, studies have shown that fragment edges lead to a homogenization of tree species composition by promoting the proliferation of pioneer species at the expense of shade-tolerant longer-lived species (Laurance et al. 1998, Benitez-Malvido, 1998).

The species accumulation curve that we plotted using our inventory of sampled species failed to reach an asymptote and continued increasing, albeit at a decreasing rate (Figure 4), indicating that additional species would have been found with further sampling efforts. It is important, however, to recognize that tropical forests worldwide harbour an incredibly high diversity of tree species; possibly more than 53,000 different species (Ferry Slik et al. 2015). Given that sampling efforts for this project were limited in time, it is not surprising that our results do not represent a complete inventory of all the species present. Despite these shortfalls, we consider our data to be meaningful on the scale of the *Sendero Panamá* as the exact same sampling method was used in both habitats studied.

As hypothesized, we found a significant difference ( $p < 0.05$ ) between the tree species richness of forest interior ( $M = 4.428$ ,  $SD = 2.07$ ) and forest edge ( $M = 1.857$ ,  $SD = 1.68$ ) conditions ( $t(12) = 2.55$ ,  $p = 0.02527$ ). These results suggest that edge does have a strong effect on tree species richness along the *Sendero Panamá*, decreasing the diversity of woody and palm tree species within the edge environment. This could be due to the edge-provoked changes in abiotic factors,

which previous studies have shown to trigger an increase in tree mortality rates and a reduction in seedling abundance (Laurance et al. 1998, Benitez-Malvido, 1998). Because environmental conditions are harsher at the forest edges, seedling recruitment of certain tree species is hindered and increased light availability causes the proliferation of pioneer tree species. Our results are in accordance with the findings from Benitez et al.'s study (2003) where the more edges a fragment displayed, the poorest the species richness was. More importantly, their results also indicated that central forest blocks in the forest interior with no edges had higher species richness.

In addition, our results show tree density to be substantially higher in non-edge quadrats (Figure 3). On average, edge habitats had a tree density of 0.086 tree.m<sup>-1</sup> whilst non-edge habitats displayed an average of 0.21 tree.m<sup>-1</sup>. It is important to remember here that our study only considered woody and palm tree species with a DBH above 5cm, disregarding a number of other bushes, seedlings, and grasses that had too small of a diameter for consideration. This difference in density of trees with DBH above 5 cm highlights that, on average, our non-edge quadrats harboured a higher number of tree individuals than edge quadrats. In addition, edge effect theory explains that trees tend to be larger and older in forest interior than in forest edge. Combining the previous statement with the results we obtained, higher density of assumed larger trees suggests higher tree biomass in the forest interior. Once again, this is in accordance with edge effect theory: a proliferation of pioneer species at the edges at the expense of old-growth flora inevitably causes collapse in the overall forest biomass (Nascimento et al.2005).

When analysing the respective tree species composition of each of the habitats studied using the Jaccard coefficient, we found only 16.2% of species similarity between edge quadrats and non-edge quadrats (Table 1). Previous studies have shown that forest interior harbours a greater richness of shade-tolerant species, which invest highly in secondary growth as opposed to

short-lived fast-growing pioneer species. Indeed, one of the observed effects of edges has been a decline in tree diversity due to the elimination or rarefication of many large-seeded, old-growth tree species (Santos et al. 2008). This is caused by a higher mortality of large trees near forest edges that get outcompeted by light-intensive pioneer species (Tabarelli et al. 2008). Furthermore, Capers and colleagues (2005) have found that the most common or abundant tree species in mature forests tend to be much less abundant or even absent in the early-successional forests created by disturbances such as edges. This might help explain why we found such a different tree species composition in both habitats.

When we analyzed species composition, we found that tree species along the trail had a clear habitat preference. Only 24% (or a total of six species) of the 25 species identified in this study were common to both edge and non-edge habitats (Figure 2; Table 1), with the rest being site-specific. Of the six species that were identified as dominant because they represented more than 5% of the total individuals sampled (Magura 2002), five species (*Anacardium excelsium*, *Annona purpurea*, *Astronium graveolens*, *Coccoloba manzinellensis* and *Spondias mombin*) were found in both forest edge and forest interior, thus showing the least habitat preference. The NMDS ordination plot (Figure 6) further confirmed these data by grouping the identified species into three clusters: edge-preferring, generalist and edge-avoiding species. In addition, it is interesting to note that the only sampled individual of *Cecropia peltata* – one of the principal pioneer species in the studied environment – was found in a non-edge habitat. We do not draw any significant conclusion from this finding. Nonetheless, we take this opportunity to discuss gap theory which predicts presence of pioneer species within disturbed areas of the forest interior. This theory explains that areas experiencing intermediate disturbance, such as gaps in the forest interior, harbour higher species diversity than undisturbed areas (Hubbell et al. 1999). At first

glance, light gap theory seems to contradict edge effect theory, but a closer look at both hypotheses reveals that gaps and edges are not quite the same. Indeed, according to Hubbell and colleagues (1999), disturbances in the forest interior increase the habitat's species richness by allowing the temporary establishment of certain pioneer trees. This sounds like a direct contradiction to the edge effect theory, where the zones that exhibit poorest species richness are actually the disturbed edges. Moreover and most importantly, edges are often permanent (next to roads or settlements) and hence they differ by their very nature from natural gaps which regenerate over time. We believe that this subtle difference explains why edge and gap theories differ in their predictions. While edges are artificially maintained in a state of "disturbance" (overall harsher environmental conditions) by human activity, gaps have the opportunity to, over long periods of time, regenerate and return to a composition dominated by shade-tolerant old-growth trees (Hubbell et al. 1999). Whereas edges trigger homogenization of the flora through sustained disturbances, temporary disturbance induced by gaps actually promotes species richness. In relation to the pioneer tree we observed in the forest interior, it is important to remember that in the case of this research project, the habitats we studied were not isolated from each other, allowing some level of exchange between them. This could further explain the presence of certain generalist species common to both edge and non-edge habitats.

In addition to having different tree species composition, forest edge and forest interior have been found to influence their microenvironment in different ways. Our results did show that forest interior have on average lower temperatures and incoming radiation than forest edge, as well as higher relative humidity (Table 3). By decreasing the amount of incoming solar radiation to the forest ground through their extensive canopy cover, mature trees modify their environment's moisture regime amongst other things, leading to lower soil temperatures and

higher relative humidity (Vetaas 1992). It must be noted however that the differences between the above abiotic factors were not found to be significant. Nonetheless, a lower temperature observed at the forest interior agrees with edge effect theory since edges are known to be hotter harsher environments.

### **Limitations of our study**

A study by Didham and Lawton (1999) found that edge effects can sometimes penetrate as deeply as 100m into the forest interior. Though another source argues that penetrating 50 m into the forest is sufficient to avoid edge effects (Sizer and Tanner, 1999), we understand that the extent and magnitude of edge effects must be case specific. Our study site did not permit us to move deeper into the interior since the forested fragment where the *Sendero Panamá* is located contains another trail: *Sendero Momotides*. In our research design, the depth to which we entered the forest was limited by the point at which propagating edge effects from the Momotides trail risked contaminating our data. If this research were to be repeated, an initial assessment of the extent to which edge effects penetrate into the forest interior should be conducted so as to know exactly how deeply sampling efforts need to go to avoid said effects. Nonetheless, our data still confirmed our hypothesis with significance.

As our species accumulation curve pointed out, the cumulative number of tree species sampled did not correspond to the total diversity present in the Parque's forest. The physical length of the Sendero Panamá can be considered a limitation to this study. Its short extent and the size of our quadrats constrained the number of sampling sites we could establish without them being too close to each other. For future research, we recommend using a trail longer than ~225

m so that more quadrats can be established; this would give a better estimate of the number of species that would be discovered if sampling efforts were infinite.

Moreover, our study was conducted in a specific region of the world, and thus any conclusions drawn from it should limit themselves in their application to this region. Though theory and other experimental evidence link our findings to many other tropical forests around the world, our results apply to the lowland tropical forest of the Pacific coast of the Panama Canal watershed.

### **Implications of the study and future research**

The findings of this study confirm the edge effect theory and hence the pervasive consequences that habitat fragmentation has on forest structure and species composition. It is evident from our study that tree species richness is affected negatively by forest edges. The rapid spread of pioneer species combined with the fact that edges remain environmentally adverse habitats for shade-tolerant species cause a radical shift in tree species composition. As a consequence, the structure, life-history traits and functionality of forests is at risk of being significantly altered by fragmentation. Similarly to what we observed along the Sendero Panamá, edge effects are driving Neotropical fragmented forests worldwide to a permanent state of early-successional systems. This has serious implications because it limits the value of tropical forests in terms of biodiversity conservation and provision of environmental services. In other words, our study confirms that any efficient conservation strategy must guarantee the safeguard of large cores of primary forests because they have been shown to fulfill an irreplaceable role in conservation (Gascon et al. 2000).

For our host, the Parque Natural Metropolitano, the research we conducted is of particular interest to their arboretum. The purpose of their project is to provide visitors with an educative tour through which a walk along the Sendero Panamá will allow them to see and identify many trees native to Panama. Taking this requirement into consideration, they will have to plant many different trees within eyesight of the path and hence within edge-affected zones. However, as highlighted by the results of the present study, special attention will have to be paid to the life-history traits of each tree to find out whether they are shade-tolerant or pioneer species. Indeed, if edges are too adverse of environments for certain shade-tolerant species, there is a risk that some of the trees planted for the arboretum might not survive in the edges of the Sendero Panama. Perhaps special care will be needed to guarantee the survival of some of the Arboretum's trees and we hope that the Parque takes our findings into consideration when their project concretizes itself.

For further research on the subject, we suggest that an investigation of seedling mortality rates be undertaken. An underlying assumption of edge theory and the effects it has on the forest is that edge creation differentially affects mortality and recruitment of various tree species. Tracking these mortality rates over a longer time frame can help better understand the dynamics triggered by habitat fragmentation and how it affects pioneer and shade-tolerant trees. Moreover, such a study would provide a more holistic understanding of edge effects, allowing us to better predict the future state, composition and functions of fragmented landscapes. Similarly, biomass comparisons between the interior and the edges of forest could be conducted. We believe that this would provide great insight as to how fragmentation is affecting the carbon sequestration and storage capacities of tropical forests. This is of extreme relevance in the contemporary context of global warming and of attempts to halt it.

## **ACKNOWLEDGMENTS**

We would like to offer our gratitude to all the staff at Parque Natural Metropolitano for receiving us and providing us with advice and help whenever needed. Special thanks to the Director, Señora Vísquez, for allowing us to participate in their arboretum project and for making this internship possible. To Yarabí Vega, our coordinator at the park, for her speed in communicating with us and for always welcoming us into her office with a smile. Thank you to Señor Sixto Mequizama whose knowledge of the forest significantly helped us in our tree identifications; we truly appreciated walking through the jungle with this fascinating man.

At the Smithsonian Tropical Research Institute, we would like to thank Lady Mancilla for organizing our stay in Panama, always going above and beyond to facilitate our lives. We are very grateful of Dr. Diana Sharpe's supervision. Thank you for providing us with guidance and advice throughout this research.

Thank you to our friends and peers of the PFSS program for always providing us with moral and sometimes technical support.

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