

The Utility of Digital Aerial Surveys in Censusing
Dipteryx panamensis, the Key Food and Nesting Tree of the
Endangered Great Green Macaw (*Ara ambigua*) in Costa Rica

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy in the University Program in Ecology
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ABSTRACT

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Abstract

Remote sensing technologies offer an innovative way to study tropical forests and complement research from forest inventory plots. From a logistic standpoint, remote sensing mitigates some of the physical, political, and economic challenges that complicate terrestrial studies of tropical forests. From a biological standpoint, remotely sensed data can elucidate ecological phenomena and dynamics of tropical forests that may be challenging to observe on the ground. I conducted a digital aerial survey during the peak blooming period for *Dipteryx panamensis*. *D. panamensis* is a canopy-emergent, keystone tree species within the lowland Atlantic forests of Costa Rica. The aerial survey occurred over Maquenque National Wildlife Refuge, which is situated in the proposed San Juan-La Selva Biological Corridor. Maquenque was decreed in 2005 to protect the last breeding habitat for the endangered Great Green Macaw (*Ara ambigua*) in Costa Rica. The Great Green Macaw depends on *D. panamensis* as its primary food and nesting resource. However, because of Costa Rica's complex deforestation history, the Great Green Macaw remains imperiled due to habitat fragmentation, degradation, and loss. Only 25 to 35 breeding pairs and 250 individuals likely persist in the country. My research had three main objectives. First, I evaluated a classification technique that capitalized on the unique spectral signature of blooming *D. panamensis* in order to detect this species using a pattern recognition approach. Second, I determined the landscape

density and distribution of this tree species using results from the aerial survey and classification. I also noted environmental factors predicting potential *D. panamensis* habitat using a classification and regression tree (CART) model, and I subsequently calculated how much potential habitat exists in Costa Rica. Third, I identified environmental conditions that indicate potential breeding habitat for the Great Green Macaw using a CART model, and I calculated how much potential breeding habitat exists in Costa Rica. Results of the classification work indicate that *D. panamensis* can be identified based on its unique spectral signature. In particular, the IHS (intensity, hue, saturation) color space was effective at resolving this tree. Results of the density analysis suggest that canopy-emergent *D. panamensis* trees occur at densities as high as 2 trees/hectare. This work demonstrates that *D. panamensis* exists in denser patches than previously determined from forest inventory plots. Environmental conditions that will support high densities of *D. panamensis* habitat occur between 45 and 125 meters in elevation and on soil with an acid and clay profile. Nearly 240,000 hectares could support high density patches of *D. panamensis* in Costa Rica. Potential Great Green Macaw breeding habitat is defined by the density of *D. panamensis* trees within its 550-hectare breeding territory. Approximately 67,000 hectares of Great Green Macaw breeding territory exist in Costa Rica. Ultimately, the conservation of both *D. panamensis* and the Great Green Macaw in Costa Rica may require a multinational partnership between Costa Rica and Nicaragua.

Dedication

Dedicated to the memories of my grandmothers, Popo Chun and Popo Lee, two women whose own journeys spirited me to where I am today.

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* * *

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Chapter 1. Introduction

1.1 A land of pura vida

In 2007, more than 1.9 million international tourists (Fallas 2007) made their way to the tiny country of Costa Rica, which is nestled within the Central American land bridge between North and South America (Figure 1). Many of these tourists came searching for adventure or sanctuary amongst the country's dramatic volcanoes, lush forests, and picturesque beaches. Whether these visitors identified themselves as ecotourists¹ or not, most were engaged in some form of nature-based tourism. More than half of all nonresident visitors explored a national park or protected zone during their trip (ICT 2006). And these visitors came to the right place, to a country whose unofficial motto of *pura vida* or "pure life" encapsulates the spirit of a people renowned for their conservation ethic and value of the natural world.

There is ample evidence for why Costa Rica is heralded as an exemplar of how to conduct tropical conservation in a developing country. Though only 51,100 km² (roughly the size of the state of West Virginia), Costa Rica boasts over 150 protected areas such as national parks, biological preserves, and wildlife refuges that cover nearly 25% of its national territory (Sanchez-Azofeifa *et al.* 2003, WRI 2003). Maquenque

¹ While many definitions of *ecotourism* abound, The International Ecotourism Society (2008) has defined it as "responsible travel to natural areas that conserves the environment and improves the wellbeing of local people".

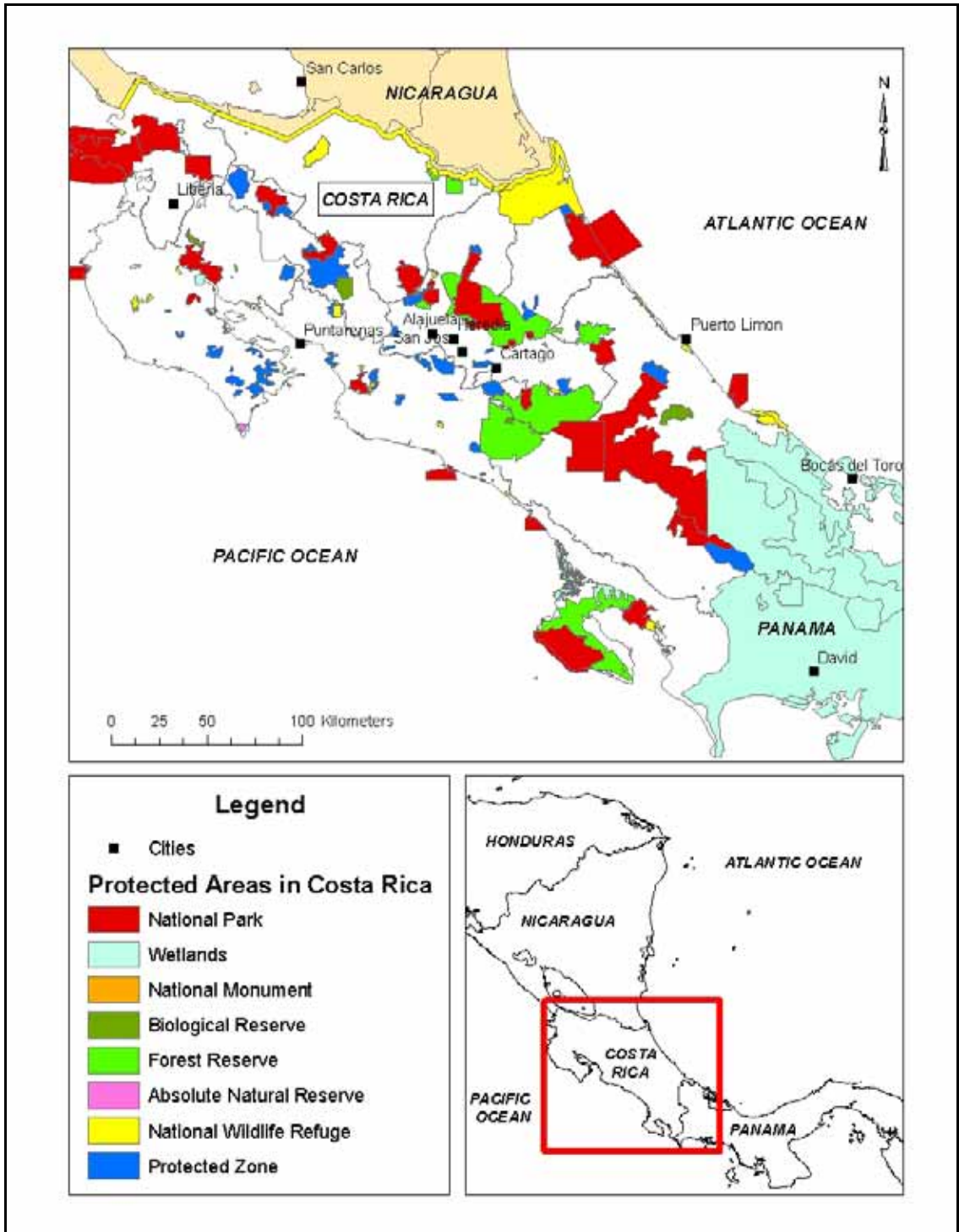


Figure 1: Location of Costa Rica within Central America and protected areas in Costa Rica

National Wildlife Refuge (MNWR), which is embedded within the proposed San Juan-La Selva (SJLS) Biological Corridor (Figure 2), is one of the newest areas to join that list of protected areas. Decreed in 2005, though not yet operational, MNWR may soon draw some of Costa Rica's 1.9 million visitors. If lucky, these tourists may catch a glimpse of the dazzling Great Green Macaw (*Ara ambigua*²), which feeds on and nests in *Dipteryx panamensis*³, a widespread tree of the lowland Atlantic forest.

Yet the story of MNWR and the rest of Costa Rica's protected areas is a complex one. Although this country is a model for tropical conservation and has pioneered innovative strategies like debt-for-nature swaps, bio-prospecting, and payments for ecosystem services, Costa Rica had one of the highest deforestation rates during the 20th century among Latin American countries. While this pattern of land clearing dramatically altered the natural landscape, it also galvanized a cadre of local biologists such as Mario Boza and Alvaro Ulgado (Boza 1993). And this spirit of *pura vida* continues to pave the way for new conservation efforts like MNWR and the SJLS Corridor that will be discussed later.

² *Ara ambiguus* is also an accepted scientific name for the Great Green Macaw. Please see David and Gosselin (2002).

³ Based on a recent nomenclatural ruling, this tree should be referenced as *Dipteryx oleifera* (Stevens *et al.* 2001). However, published studies on this tree in Costa Rica continue to use *Dipteryx panamensis*. Hence, I am following that precedent in this document.

1.2 A bit about Costa Rica's biodiversity

Costa Rica exhibits exceptional biodiversity and a diverse array of ecosystems. Biological inventories have identified over 200 species of mammals, 845 species of birds, 160 species of amphibians, 218 species of reptiles, and 10,000 species of vascular plants comprising 4% of the total number of the world's plant species (Boza 1993). Costa Rica also exhibits a high degree of endemism. For example, Hartshorn and Hammel (1994) estimate that 10% of the plants found in Costa Rica's Atlantic lowlands are endemic to the country. Scientists attribute this disproportionate amount of biodiversity to the fact that Costa Rica is located along the Mesoamerican land bridge that links the continents of North and South America and has facilitated the dispersal of plants and animals over time (Wallace 1997). Costa Rica also has many diverse and unique ecosystems. In fact, this country can be classified into 23 different life zones (Powell *et al.* 2000). The life zone system uses gradients of mean temperature, annual precipitation, and evapotranspiration to predict plant communities (Holdridge 1947, Holdridge *et al.* 1971). Costa Rica is also included in the biodiversity hotspot of Mesoamerica due to this region's high concentration of endemic species yet exceptional loss of habitat overall (Myers *et al.* 2000).

1.3 A pock on the landscape: Costa Rica's history of deforestation

It may seem odd that a country that has protected nearly 25% of its national territory had one of the highest tropical deforestation rates during the 20th century. Yet it is a testament to how far Costa Rica has come in terms of balancing economic growth with natural resource preservation. The arrival of the Spanish in the 1500s marked the beginning of sporadic forest clearing in Costa Rica. This trend accelerated until the mid 1900s as thousands of hectares of forests were cleared for agriculture and cattle pastures (Pfaff and Sanchez-Azofeifa 2004). Many researchers attribute the rise in forest clearing following World War II to various demographic, social, and political factors at both national and international levels that put pressure on the country's natural resources. First, Costa Rica's population expanded four-fold in the two generations following World War II from less than 800,000 to over 3 million people (Rosero-Bixby and Palloni 1998). By the 1960s, Costa Rica had one of the world's fastest population growth rates—a 4% natural increase/year (Rosero-Bixby and Palloni 1998). The annual population growth rate has slowed considerably and is projected to be 1.5% between 2005 and 2010; the total population is about 4.5 million people (United Nations Economic and Social Affairs 2006). Demographers and ecologists have acknowledged a causal link between pressures from population growth and increased natural resource use (Rosero-Bixby and Palloni 1998). The peak in population growth during the 1960s stemmed from

Costa Rica's national policies that prioritized demographic growth and agricultural production (Pfaff and Sanchez-Azofeifa 2004). This ultimately led to forest clearing.

Costa Rica's presence on the international commodities market during the 20th century also affected spatiotemporal patterns of deforestation and influenced which crops were planted in the wake of forest clearing. In the early 1900s, lands that could grow coffee were cleared first (Pfaff and Sanchez-Azofeifa 2004). These areas were concentrated in the central volcanic region of the country. Depending on the shifting prices of various commodities throughout the 20th century, forest was also removed to support crops like banana, sugar cane, pineapple, and cattle. The latter resulted in what Myers (1981) termed the "hamburger connection", as foreign appetite for cheap beef resulted in the widespread clearing of tropical forests in Central and South America in order to raise cattle.

So how have these demographic and economic factors affected land-use patterns, and how much forest was lost during the peak of Costa Rica's land clearing? Ultimately, there have been numerous studies tracking Costa Rica's deforestation trends, and new remote sensing technologies have afforded a more precise documentation of land-use patterns. Joyce (2006) has prepared a comprehensive resource that summarizes land-use change in Costa Rica from 1966 to 2006. Here, I will just highlight some major trends regarding deforestation rates. Based on aerial photos and Landsat Multispectral Scanner data collected from five individual years between 1940 and 1983, Sader and Joyce (1988)

note that the total primary forest remaining in 1940, 1950, 1961, 1977, and 1983 was 67%, 56%, 45%, 32%, and 17%, respectively. Furthermore, deforestation occurred primarily in tropical dry and moist life zones during the early period. Between 1977 and 1983, the annual forest clearing rate was 8.8% in tropical wet forest, and over 78% of the primary forest in this life zone had been lost. During this same period, tropical moist forest was lost at an average annual rate of 16.4% and almost no primary forest in this life zone remained by 1983. Many scientists concur that Costa Rica's deforestation rate peaked in the 1970s. In fact, Costa Rica had the fifth highest deforestation rate in the world from 1976 to 1980 as calculated by the United Nations Food and Agricultural Organization (Sanchez-Azofeifa *et al.* 2001). The annual deforestation rate remained high between 1986 and 1991 as forests were cleared annually at 4.2%/year (Sanchez-Azofeifa *et al.* 2001). By the end of this period, almost all forest within the tropical moist forest and premontane moist forest life zones had been eliminated.

In addition, Costa Rica's social and political history may also be inextricably linked to its deforestation record. Costa Rica managed to avoid most of the strife, civil wars, and economic turmoil that plagued many of its Mesoamerican neighbors like Nicaragua. In fact, Costa Rica suffered only one short civil war in 1948 after which the army was disbanded; to this day, Costa Rica has no standing army (Campbell 2002). This enlightened view of the military enabled the country to focus its spending on social programs that benefit its populace. Costa Rica's universal healthcare system is one of

the best in Latin America and comparable to industrialized nations (Rosero-Bixby and Palloni 1998). For example, life expectancy is on par with the United States at 79.7 and 75.0 years for females and males, respectively. In addition, this country has a well-developed educational system and boasts one of the most educated citizenry with a 98% literacy rate for youth between 15 and 24 years of age according to WRI (2003). Such progressive national policies have resulted in a populace accustomed to a standard of living akin to developed countries, putting pressure on Costa Rica's natural resources.

However, these economic and social successes have put this country in the position to support and nurture national conservation efforts. The 1970s were the inception of Costa Rica's national parks system as a cadre of conservation-minded people decided to do something about Costa Rica's rampant loss of primary forest. Deforestation has slowed in the last two decades. Coupled with reforestation efforts largely begun after 1979 as well as widespread secondary forest regeneration, some of the damage done to Costa Rica's forests has been mitigated (Butterfield 1994, Chazdon 2003). Foreign tourists are now flocking to this country that offers the political stability and amenities not present in many Latin American countries. In addition, new economies like ecotourism offer a way to bridge economic development with sustainable natural resource use.

1.4 Costa Rica's system of protected areas

Costa Rica's nascent conservation movement was borne out of a desire to protect areas of natural beauty in the wake of high deforestation in the 1960s. Boza (1993) acknowledges that the first national parks were created in areas of stunning scenic beauty, on historic sites of national significance, or in areas of demonstrated conservation importance. Thus, the first national parks were created in the early 1970s and included Poás, Cahuita, and Santa Rosa National Parks. At this time, the early conservationists had just five guards and a vehicle, but little experience and no administrative support (Boza 1993). From these humble beginnings, Costa Rica now boasts over 150 protected areas that include not only national parks but wildlife refuges and national monuments that attract some of the 1.9 million annual visitors. These protected areas are now managed under the National System of Conservation Areas known as SINAC, which is part of the government's Ministry of Environment and Energy (MINAE). Even though over 25% of the country's national territory is designated as some type of protected area, only 12 of Costa Rica's 23 life zones are adequately represented with more than 5,000 ha under conservation (Powell *et al.* 2000). Those 12 life zones account for 98% of the total area protected in the country. The remaining 11 life zones are represented in just 2% of the total area protected in the country, or not represented at all. The majority of the protected areas are concentrated along higher elevation regions running along Costa Rica's volcanic backbone. Life zones

in lowland areas are less well represented as these areas were settled by humans and were more susceptible to forest clearing. For example, only 9% of the tropical wet forest life zone is protected (Powell *et al.* 2000). Not only do Powell *et al.* (2000) advocate the expansion of existing protected areas in order to target underrepresented life zones, but they also champion the establishment of corridors in order to facilitate the movement of organisms with large habitat needs and foster genetic flow. Corridors have long been proposed by conservation biologists as a means to link species, habitats, or processes that operate at multiple spatial and temporal scales (Noss 1991). Despite Costa Rica's impressive conservation achievements, it is apparent that more can still be done.

1.5 New conservation directions

With all that Costa Rica has achieved, it is not resting on its laurels. Decreed in 2005, Maquenque National Wildlife Refuge (MNWR) represents the newest addition to Costa Rica's network of protected areas. Because MNWR is located within lowland Atlantic rain forest, it fills some of the gaps missing in the system of protected zones. In addition, it represents the core area within a larger biological corridor effort known as the San Juan-La Selva (SJLS) Biological Corridor that would link protected areas in southern Nicaragua to Costa Rica's Central Volcanic Range reserve. MNWR and the greater SJLS Corridor are the setting for the research contained in this dissertation.

1.5.1 Background on Maquenque National Wildlife Refuge and the proposed San Juan-La Selva Biological Corridor

The SJLS Corridor originated in March 2001 when the SJLS Executive Committee was formed to implement the vision of the Mesoamerican Biological Corridor (MBC) project within Costa Rica. The MBC is a transnational effort among Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama, as well as the five southern states of Mexico (Kaiser 2001). Established in 1997, the purpose of the MBC project is to unite protected areas throughout the Central American isthmus by either expanding extant protected areas or restoring intervening lands. The SJLS Corridor represents one span of the MBC that will link five protected areas in southern Nicaragua (including the 264,000 ha Indio-Maíz Biological Reserve) with Costa Rica's Central Volcanic Range reserve (Chassot *et al.* 2004). It comprises 246,608 ha of fragmented lands and is located in northern Costa Rica within the provinces of Heredia and Alajuela in the Huetar Norte region of the country. The SJLS Corridor takes its name after the San Juan River that forms the border between Costa Rica and Nicaragua and the La Selva Biological Station, a field station operated by the Organization for Tropical Studies in Costa Rica.

1.5.2 Current land use and human dimensions within the San Juan-La Selva Biological Corridor

An estimated 45,000 people live in the SJLS corridor's several towns and smaller population centers (Chassot *et al.* 2004). Approximately, 30,000 people inhabit communities adjacent to the corridor such as Puerto Viejo, La Virgen, and Horquetas de

Sarapiquí. According to official census data from 2000, about 30 inhabitants per square kilometer reside within the proposed corridor region (INEC 2001). The private environmental research firm CEDARENA (Centro de Derecho Ambiental y de los Recursos Naturales) conducted an exhaustive land tenure survey to identify property owners and delineate inholdings within the Huertar Norte region. They ultimately identified over 700 private farms with a registered title within MNWR. As the refuge is developed, compensation and relocation of land owners will be a significant challenge.

Land use within the proposed corridor is varied and includes primary forest, secondary forest, deforested areas, and agricultural zones. Much of the non-forested areas comprise a matrix of abandoned cattle pastures, tree plantations, and various agricultural crops. This region's land conversion can be attributed to government incentives that encouraged the expansion of the agricultural frontier and the clearance of forest for cattle pasture (Butterfield 1994). With the advent of numerous forestry laws as well as a payments for ecosystem services program, much of this previously cleared land is either regenerating naturally or being reforested. Landowners who maintain their land in ways that promote the following services—mitigation of greenhouse gas emissions; water use for domestic purposes, irrigation, and hydroelectricity; biodiversity conservation; or ecotourist and recreational purposes—are allowed to apply to the payments for ecosystem services program for financial remuneration (Snider *et al.* 2003).

1.5.3 San Juan-La Selva Biological Corridor design

The SJLS Executive Committee has outlined a strategy to consolidate the matrix of public and private lands and implement the SJLS Corridor (Chassot *et al.* 2004). Lands will be purchased, and the property rights transferred to SINAC. The initial design for the SJLS Corridor integrates three land-use levels with increasing levels of biodiversity protection and ecosystem integrity within the core (Figure 2). These levels include 1) Core Protected Area, 2) Corridor Nuclei, and 3) Corridor Matrix. The goal of the SJLS corridor initiative is to protect 100% of the core protected area and nuclei and 50% of the matrix (Chassot *et al.* 2004). A more detailed description of each region follows.

MNWR forms the heart of the SJLS Corridor, as it constitutes the Core Protected Area. It was officially decreed in 2005. Totalling approximately 59,700 ha or 24% of the corridor, MNWR is situated just south of the Nicaraguan border. Its boundaries are roughly circumscribed by three rivers, the Río San Juan to the north and the Río Toro and Río Sarapiquí to the southeast. The Río San Carlos flows through the reserve and divides it into two sections. MNWR comprises intact lowland Atlantic forest dominated by a high density of the tree, *D. panamensis*. Lowland Atlantic forest is an ecosystem type that is poorly represented in Costa Rica's suite of protected areas. In addition to safeguarding a unique habitat assemblage, one of the primary purposes of MNWR is to protect the dwindling population of the Great Green Macaw, which depends on *D.*

panamensis as a food resource and nesting substrate. MNWR forms the core of the proposed SJLS Corridor by uniting other wildlands and protected areas throughout Costa Rica and Nicaragua such as Barra del Colorado Wildlife Refuge to the east, La Selva Biological Station and Braulio Carrillo National Park to the south, and the Indio-Maíz Biological Reserve to the north in Nicaragua.

The Corridor Nuclei consist of three blocks of habitat constituting about 41,150 ha or about 17% of the SJLS Corridor (Chassot *et al.* 2004). Tirícias-Crucitas, the largest of the nuclear patches, totals 27,273 ha and would buffer protected areas in adjoining Nicaragua. The Cerros Astilleros-Lomas de Sardinal nuclear area encompasses 9,043 ha, while the Cerros Arrepentidos nuclear area comprises 3,838 ha. While these nuclei have been identified, none has officially been protected. Nor have any of the blocks been prioritized for acquisition.

The remainder of the SJLS Corridor that does not comprise MNWR or the Corridor Nuclei is designated as Corridor Matrix. Currently, the matrix is the most fragmented and degraded portion of the corridor and includes the highest degree of human habitation and varied land uses. This region presents the highest opportunities for restoration or natural forest regeneration.

1.6 Research opportunities within the San Juan-La Selva Biological Corridor

The development of MNWR and the SJLS Corridor adds an exciting chapter to Costa Rica's complex yet extraordinary conservation story. Borne as a reaction to the troubling patterns of deforestation during the 20th century, Costa Rica's conservation movement now has coalesced to consider the visionary SJLS Corridor project, which has ecological ramifications beyond the country's borders. This ongoing conservation project has provided numerous opportunities for scientific research, and I am grateful for the opportunity to participate in and contribute to the ongoing SJLS corridor efforts. It has been an exciting process to observe! While the doctoral research contained in this dissertation addresses broad ecological questions, it is my hope that this research may also assist the ongoing conservation efforts in the proposed SJLS Corridor.

1.7 Synopses of dissertation chapters

Chapter 2 is entitled "An evaluation of digital aerial photography as a means to survey *Dipteryx panamensis*, a canopy-emergent tree species, during its peak blooming in Costa Rica". Here, I examine the utility of digital aerial surveys that coincided with the unique phenological period for *D. panamensis* to analyze this tree species' distribution and density across the SJLS Corridor. The primary purpose of this research was to develop a semi-automated classification approach that keyed in on the unique spectral signature of blooming *D. panamensis* trees. This tree species is a keystone species and an

important nesting and food resource for the Great Green Macaw, the flagship organism around which MNWR was created. Ultimately, this chapter highlights advances in remote sensing technologies. In addition, it justifies the use of digital aerial photography as a cost-effective means of surveying tropical forests.

In Chapter 3, which is titled “Density distribution, habitat description, and fragmentation of a population of *Dipteryx panamensis* in northern Costa Rica”, I utilize the density estimates distilled from the aerial photography methods described in Chapter 2 to create an interpolated surface showing the distribution of *D. panamensis* throughout the SJLS Corridor. In addition, I identify environmental factors that predict hotspots of high *D. panamensis* density by using a classification and regression tree (CART) model. Finally, I examine whether patches of *D. panamensis* are disconnected from each other based on measured pollen dispersal distances.

In the final chapter entitled “Determination and description of potential nesting habitat for the Great Green Macaw (*Ara ambigua*) in northern Costa Rica using a classification and regression tree model”, I examine what environmental factors predict optimal Great Green Macaw nesting habitat. Because the Great Green Macaw relies on mature *D. panamensis* trees as a nesting substrate, I use the interpolated surface showing the distribution and density of *D. panamensis* to guide this analysis. In addition, I quantify how much potential nesting habitat exists within the vicinity of the SJLS

Corridor. Finally, I note if there are any nesting habitat patches that should be prioritized and targeted in the ongoing conservation efforts.

Chapter 2. An evaluation of digital aerial photography as a means to survey *Dipteryx panamensis*, a canopy-emergent tree species, during its peak blooming in Costa Rica

2.1 Introduction

2.1.1 Remote sensing studies of tropical forests compared to forest inventory plots

Tropical forests are widely considered one of the most diverse and productive terrestrial ecosystems. Though they cover less than 7% of Earth's terrestrial surface (they are restricted between 23.5° north and south latitudes), they may harbor nearly half of the world's biodiversity (Reid and Miller 1989). Incredible accounts of species richness have been reported for tropical forests worldwide. For example, Gentry (1988) found that one hectare (ha) of rain forest near Iquitos, Perú contained 283 species of trees > 10 cm dbh (diameter at breast height), while Whitmore *et al.* (1985) counted 233 vascular plant species on just 0.01 ha of lowland tropical rain forest in Costa Rica. Compare this to the fact that Europe, north of the Alps and west of Russia, has only 50 indigenous tree species while eastern North America has but 171 (Whitmore 1998). Tropical regions also exhibit high degrees of endemism. Gentry (1992) noted that the greatest numbers of endemic species occur in Amazonia, Central America (including subtropical Mexico), coastal Brazil, and the northern Andes. In addition, tropical ecosystems are considered to be crucial sinks for CO₂ and may play an important role in

sequestering carbon and mitigating the effects of global climate change. Yet tropical regions are threatened from a variety of anthropogenic forces such as deforestation, agricultural intensification, pasture expansion, and urbanization (Lambin *et al.* 2003). Achard *et al.* (2002) determined that the pace of tropical deforestation and forest degradation from 1990 to 1997 was much higher than previously thought and could have huge consequences on the ability of these systems to act as carbon sinks.

Sophisticated remote sensing technologies now enable tropical ecologists to track these threats from afar, garner a large spatial perspective of tropical forests, and explore these amazing ecosystems that so beguile scientist and layman alike. Until recently, tropical ecologists have relied on a global network of terrestrial forest inventory plots to study tropical forests. While forest inventory plots have provided invaluable, long-term data on ecological, biological, and physical factors such as tropical biodiversity, forest dynamics, and nutrient cycling (Condit 1995, Sheil 1995, Clark and Clark 1999), they have limitations. Clark *et al.* (2004b) note that many forest inventory plots are limited in size, sparsely distributed around the globe, or biased in their placement. In addition, forest inventory plots are relatively small; the mean size of the 17 forest dynamics plots run by the Smithsonian's Center for Tropical Forest Science is 32.3 ha (CTFS 2008). Thus, they tend to poorly sample the large trees generally defined as those > 60 cm diameter above buttress (Clark *et al.* 2004b). These large, canopy-emergent trees have crowns that soar many meters high making them difficult to study from the ground due

to obscuration by the intermediate foliage (Clark *et al.* 2004b, Trichon and Julien 2006). Canopy studies using cranes, walkways, or tree-climbing equipment were initiated largely in the 1980s and enabled tropical ecologists to access the tree crown (Parker *et al.* 1992, Nadkarni 1994). However, these canopy studies only provide a localized glimpse of ecological processes and afford limited detail at landscape scales.

Tropical ecologists have long recognized the potential of remote sensing technologies to complement research in forest inventory plots and enhance the study of tropical forests in general. Remote sensing refers to the acquisition of information on an object, area, or phenomenon by a device that is not in contact with the object, area, or phenomenon under study (Lillesand *et al.* 2004). From a logistic standpoint, remote sensing mitigates some of the physical, political, and economic challenges that complicate terrestrial studies of tropical forests. Tropical ecologists can access remote landscapes via a “bird’s-eye view” of the landscape. These areas could be otherwise challenging to reach because of physical barriers, or dangerous to enter due to political unrest. Economically, the use of computer-assisted interpretation of remotely sensed data may reduce time and costs of traditional field methods (Trichon 2001).

From a biological standpoint, remotely sensed data can elucidate ecological phenomena and dynamics of tropical forests. Trichon (2001) asserts that aerial photos may be used to identify particular trees of interest such as commercially important, rare, endemic, or keystone species. Tree crown architecture and phenology can be studied

(Trichon 2001) as well as forest dynamics such as tree mortality, survivorship, and growth (Clark *et al.* 2004b). Finally, probably the greatest opportunity of remote sensing is the ability to study tropical forests across large spatial or temporal extents.

New remote sensing platforms and the availability of multispectral and hyperspectral data are bringing us closer to conducting automated, individual tree species recognition. As noted above, forest inventory plots tend to undersample very large, canopy-emergent trees. The advances in individual tree species recognition and finer sensors may elucidate this important structural guild over much larger study areas (Clark *et al.* 2004b).

2.1.2 Overview of remote sensing platforms used to identify individual tree crowns in the tropics

Turner *et al.* (2003) describe the multitude of remote sensing platforms and sensors used for biological conservation studies. Here, I will discuss those that have been specifically used to examine tropical forests and highlight some that may enable the study of individual tree crowns. In addition, I will detail the applications of high-resolution, digital aerial surveys as they are the remote sensing method used for the work detailed in this chapter.

Previously, most studies in the tropics relied on remote sensing data coming from spaceborne, satellite platforms such as Landsat Thematic Mapper sensors with a spatial resolution of 30 m. This platform produces medium spatial resolution imagery

that is relatively inexpensive and has been useful in efforts to identify broad land-use/land-cover classifications as well as to detect hotspots of deforested or fragmented zones (Skole and Tucker 1993, Sanchez-Azofeifa *et al.* 2003, Van Laake and Sanchez-Azofeifa 2004). These sensors can resolve aspects of tropical forest structure such as differences between young secondary forest and primary forest. However, due to their coarse spatial resolution, these sensors are unable to differentiate older secondary growth or selectively logged forest from primary forest (Steininger 2000). In addition, medium spatial resolution imagery such as Landsat Thematic Mapper cannot detect features such as individual tree crowns.

High resolution, spaceborne, multispectral sensors such as the commercial IKONOS, SPOT, and QuickBird satellites have provided new insight into tropical forest dynamics and may even enable the discrimination of individual tree crowns. The most recent SPOT satellite was launched in May 2002 and provides multispectral and panchromatic imagery. QuickBird is a commercial satellite that was launched in 2001 and provides multispectral imagery at 2.4 and 2.8 meter resolutions, and panchromatic imagery at 60 and 70 centimeter resolutions. IKONOS is another commercial satellite launched in 1999 that collects high-resolution imagery at 1 and 4 meter resolution and offers both multispectral and panchromatic imagery. Palace *et al.* (2008) and Asner *et al.* (2002) have had some success in estimating crown widths of individual trees and examining forest canopy structure within the Brazilian Amazon using IKONOS

imagery. However, they found it difficult to separate adjacent, intermingled tree crowns. Clark *et al.* (2004b) were able to detect individual tree crowns from IKONOS images within the La Selva Biological Station and accurately measure crown area. They also had moderate success differentiating secondary forests and selectively logged forests from primary forests. Clark *et al.* (2004a) also were able discern individual, emergent tree crowns using QuickBird imagery over the La Selva Biological Station in Costa Rica. Researchers in the temperate zone, specifically Canada, have had more success in conducting semi-automated, individual tree crown recognition using a new generation of high resolution, multispectral imagery known as CASI (Compact Airborne Spectral Imager) (Leckie *et al.* 2003, Leckie *et al.* 2005). However, tree diversity at their Canadian study site was much lower and comprised three dominant coniferous species, each with distinctive crown architecture. Thus, the application of this work may be limited in tropical forests where the tree diversity is so much higher and crown structure more heterogeneous.

While these multispectral sensors provide limited ability to distinguish individual tree crowns and identify species, Clark *et al.* (2005) were able to use airborne, hyperspectral sensor data from the HYDICE (HYperspectral Digital Imagery Collection Experiment) sensor to differentiate seven canopy-emergent trees in Costa Rica at the leaf, pixel, and crown levels. Hyperspectral sensors are passive sensors that acquire simultaneous images in many relatively narrow, contiguous and/or non-contiguous

spectral bands through the ultraviolet, visible, and infrared portions of the electromagnetic spectrum. This study was the first published report on automated tropical forest tree classification using high resolution, hyperspectral imagery. It is a significant advance in using remote sensing to identify individual tree crowns and species in the tropics.

Despite the advances in these high-tech multispectral and hyperspectral sensors and the progress in automated tree crown recognition, aerial photography still offers many advantages in identifying and studying individual tree crowns within tropical forests. Tropical ecologists have long recognized the usefulness of large-scale aerial photography in tropical species identification (Myers 1982). Now, traditional film-based cameras have given way to digital cameras that have resolutions in the megapixel range. Digital cameras can be mounted on helicopters or small planes thereby giving the tropical ecologist flexibility to time flights depending on the season in order to capture specific phenological events. The flying altitude can be controlled, making the identification of individual tree crowns more assured compared to present airborne or spaceborne imagery. In addition, with the widespread availability of digital cameras, aerial photography may be an affordable complement to more expensive airborne or spaceborne imagery. In the tropics, where funding can be limited and conservation is frequently conducted on a “shoe-string” budget, digital aerial photography may provide a cost-effective, accessible, and large-scale method to tropical forest conservation.

Recent work by tropical ecologists in Central and South America have successfully showed that human photo-interpreters had an 87% success rate in identifying tropical forest trees in French Guiana in large-scale aerial photographs (Trichon and Julien 2006). Jansen *et al.* (2008) timed aerial overflights to coincide with fruiting of several palm species on Barro Colorado Island, Panama in order to ascertain if fruit abundance based on photogrammetric analysis correlated with direct fruit counts. Both of these studies, however, relied on manual photo interpretation of images. In addition, aerial photographs captured a small spatial extent of less than 25 ha. Foody *et al.* (2005) stress that while visually interpreting aerial photographs may produce accurate maps, it is an inherently subjective method. Instead, digital image classification techniques should be further investigated. Few studies have explored image classification methods using digital aerial photographs capturing a large spatial extent to systematically identify individual tree crowns within a GIS framework.

2.1.3 Objectives

In this study, I examine the feasibility, cost-effectiveness, and practicality of censusing and discriminating *Dipteryx panamensis* using high resolution digital aerial surveys timed to its peak blooming. *D. panamensis* is an ecologically and economically important tree species. This work was conducted over the lowland Atlantic rain forests of Costa Rica. My main objectives were to:

1. Evaluate the feasibility of using digital aerial surveys timed with the unique phenological period for *D. panamensis* to analyze this tree species' density across a large spatial extent;
2. Develop an image enhancement, classification, and machine learning approach for the computer-automated discrimination of this canopy-emergent tropical tree species;
3. Identify high density areas where *D. panamensis* trees are distributed;
4. Assess the advantages and disadvantages of this classification approach.

2.2 Materials and methods

2.2.1 Study site: San Juan-La Selva Biological Corridor

The digital aerial surveys were conducted over a portion of the proposed San Juan-La Selva Biological Corridor (SJLS) located within northeastern Costa Rica (Figure 2). The SJLS Corridor is situated in northern Costa Rica within the provinces of Heredia and Alajuela within the Huetar Norte region. The SJLS Corridor spans approximately 246,608 hectares and comprises a matrix of land uses including primary forest, secondary forest, agriculture, pasture, and human settlements. The predominant forest type within the SJLS Corridor is lowland Atlantic rain forest dominated by the tree species *D. panamensis*. The creation of the SJLS corridor is the vision of Costa Rica's Ministry of the Environment as well as several, local non-governmental organizations

(NGOs). The SJLS Corridor forms one link of the regional Mesoamerican Biological Corridor effort that aims to restore habitat to promote the movement of organisms with large habitat needs and link protected areas within the seven Central American countries and the four states of southern Mexico (Kaiser 2001). In 2001, the SJLS Corridor executive committee (comprised of NGOs, government agencies, and research groups) was charged with implementing the SJLS Corridor effort within Costa Rica. The executive committee has outlined a strategy to consolidate the matrix of public and private lands within the proposed corridor. The design of the SJLS corridor integrates three land-use levels with increasing levels of biodiversity protection and ecosystem integrity (Chassot *et al.* 2004). These levels include the Corridor Matrix, the Corridor Nuclei, and the Core Protected Area (Figure 2). Maquenque National Wildlife Refuge (MNWR) forms the Core Protected Area within the SJLS Corridor. In 2005, MNWR was officially decreed by Costa Rica's Ministry of the Environment and was allotted conservation funding and protection. MNWR was selected as the Core Protected Area because it represents one of the last breeding habitats for the endangered Great Green Macaw (*Ara ambigua*) in Costa Rica. Studies by Powell *et al.* (1999) indicate that the Great Green Macaw depends on *D. panamensis* for food and nesting. The conservation implications of the Great Green Macaw will be addressed within Chapter 4 of this dissertation.

2.2.2 Aerial survey technique

From July 4-8, 2005, I conducted an extensive aerial survey over 140,178 hectares or 57% of the SJLS Corridor ¹. I chartered a Cessna 206 airplane from AeroBell, a local Costa Rican airplane company, to fly transects over the SJLS Corridor. In general, flights took off at 7 a.m. and lasted until 4 p.m. Costa Rica time. A total of 21 hours were flown. I timed the overflights to coincide with the peak blooming for *D. panamensis*, and I selected the flight dates based on published descriptions of *D. panamensis* flowering patterns and personal observations by tropical ecologists at La Selva Biological Station. Phenological studies conducted by Frankie *et al.* (1974) indicate that adult *D. panamensis* trees begin blooming about one month into the Caribbean rainy season in Costa Rica. Although the trigger for the blooming event varies annually, this event generally begins in late May and continues into early August. After the onset of flowering, individual adult *D. panamensis* trees flower asynchronously over a six-week period with peak blooming occurring in mid-July (Perry and Starrett 1980). Flowers are a bright purple. A more detailed description of the phenological patterns of *D. panamensis* follows in Chapter 3 of this dissertation.

Jacaranda copaia is a less common tree species in the project area. However, it can reach the canopy and produces purple flowers. Thus, this tree could potentially be

¹ As an interesting side note, my aerial surveys did not go unnoticed by the locals living in northern Costa Rica. For more information, please see Appendix A.

confused for flowering *D. panamensis* in the digital images. However, Wright and van Schaik (1994) note an offset in the flowering periods for *J. copaia* and *D. panamensis* in the tropical moist forest of Barro Colorado Island, Panama, and James *et al.* (1998) observe that *J. copaia* flowers in the late dry season in the Coto Brus Valley of Costa Rica. Because *D. panamensis* begins to flower at the start of the rainy season, I was confident that I was photographing this species and not *J. copaia*.

I employed a Nikon D1X digital camera with an image sensor of 5.3 megapixels to photograph the SJLS Corridor and capture blooming, canopy-emergent *D. panamensis* trees. The Nikon camera was mounted outside of the Cessna airplane via a stable platform. Figure 3 depicts the digital camera platform. A test flight was performed to ascertain the highest elevation that could be flown and still resolve individual, blooming *D. panamensis* crowns. Although the pilot had to adjust the flying altitude at times due to the presence of clouds, the Cessna maintained an average flying altitude of about 1371 meters above sea level (4500 feet) during the overflights. A cable connected the Nikon camera to a laptop computer located inside the Cessna cabin. The digital photographs were stored on the laptop as they were taken. In addition, a GPS unit captured continuous positional information of the Cessna's flight path. These positional data were also recorded onto the laptop that was running the program Garmin MapSource. The positional information was subsequently related to each digital photograph.



Figure 3: Digital camera platform and airplane used in aerial surveys

The aerial survey required 21 flight hours to complete. A total of 63 flight transects were flown. Figure 4 depicts the flight lines of the aerial survey. Forty-four of the flight transects were oriented east-west. These transects were generally located over the southern portion of the SJLS Corridor as well as MNWR. Nineteen flight transects traversed the northwestern section of the SJLS corridor and were oriented north-south. In general, adjacent flight transects were separated a distance of 1 kilometer. Photographs within the same flight transect were the most similar in terms of flying elevation, time of day flown, and sun angle. Ultimately, 2,626 digital images were collected that spanned about 140,178 hectares of the 246,608-hectare SJLS Corridor. Some transects were flown a second time because clouds obscured the first pass. Thus, there were 2,550 images in the final image count without duplicates.

2.2.3 Digital photographs

The Nikon camera's shutter speed was adjusted based upon the flying altitude so that adjacent photos within transects overlapped approximately 20%. In addition, photographs between transects overlapped about 20%. The raw, unprocessed digital photographs were collected in the Nikon Electronic Format (.nef) which is the proprietary digital image format used by Nikon digital cameras. All digital images contained a red, green, and blue (RGB) spectral band. The images did not contain an infrared band. The raw images were unreferenced and lacked a geographic coordinate system. However, general positional information could be ascertained for each photo by

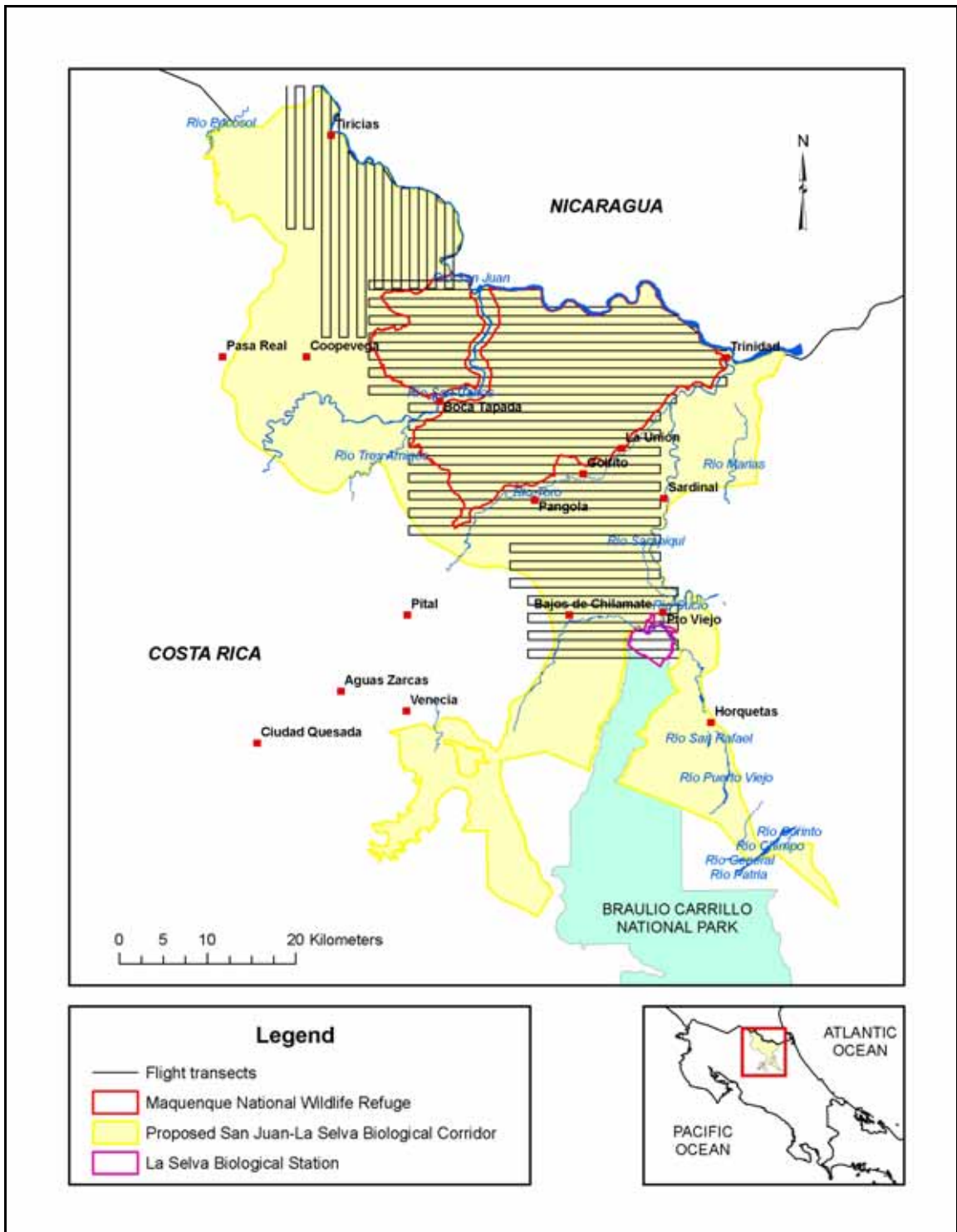


Figure 4: Location of aerial surveys over the proposed San Juan-La Selva Biological Corridor

matching the data from the onboard GPS unit to time/date information collected with each photograph. Based on an average flying altitude of 4500 ft., the digital images contained an average field of view (FOV) of 120 hectares and a resolution of about 0.3 meters/pixel.

2.2.4 Image enhancement: contrast stretch

After the digital photographs were acquired, I converted the photographs to a format suitable for analysis in a remote sensing platform. I used the Nikon Capture 4 program to convert the digital photographs from the .nef format to .tiff format. At this stage, I rotated the images so that the images were oriented with north at the top. Next, I converted the .tiff images to .img files (Erdas Imagine proprietary file format) using the remote sensing program, Erdas Imagine 8.7. Images were retained as unsigned 8-bit.

Because I undertook this remote sensing effort to census only one canopy-emergent tropical tree species, I enhanced my images in order to unpack and accentuate the spectral detail of the blooming, purple *D. panamensis* crowns. The original, digital images contained red, green, and blue bands. When displaying digital images on a computer monitor, the appropriate bands are assigned to a red, blue, and green channel. Here, every pixel within a composite, digital image can be represented within a 3-dimensional coordinate space, or color cube, where the three primary colors comprise the three axes (Lillesand *et al.* 2004). In a visual monitor using an 8-bit-per-pixel data encoding, each pixel can be depicted by a “digital number” that ranges from 0-255. The

RGB color cube is defined by the *brightness* values of each of the three primary colors.

As a technical term, brightness refers to the strength or intensity of a color.

A digital image's spectral histogram depicts the distribution of the number of pixels and the range of digital numbers (DN) for each channel. In the histogram, the x-axis contains the DNs ranging from 0 to 255, while the y-axis represents the number of pixels within the image containing a particular DN. Pixels with a smaller DN will appear darker on-screen, while those with a larger DN appear brighter. During exploratory testing of the digital images, it was apparent that the histograms for each of the three color bands were tightly clumped, thus underutilizing the full range of DN values available for display and analysis. In order to unpack the spectral data contained within the digital images, I performed a *contrast stretch*. The purpose of a contrast stretch is to expand the narrow range of brightness values typically present in the spectral bands of an input image over a wider range of DN values. The result is an output image that has been accentuated in order to enhance the contrast between features of interest making the image more interpretable to an image analyst (Lillesand *et al.* 2004). Standard contrast stretches exist such as a *linear stretch* or a *histogram equalization stretch*. However, the specific contrast stretch that was performed on all the digital images was a Percentage Look-Up Table (LUT) Stretch. This type of contrast stretch clips off a specified percentage of pixels at the low and high ends of the histogram and then allocates the remaining pixels linearly across the DN values, from 0-

255. The purpose of such a stretch is to trim away “noise” at the ends of the histogram that correspond to features that are not of interest to the image analyst.

I performed a contrast stretch first on one candidate image within each of the 63 flight transects and then applied these enhancements to images across the remainder of the same flight transect. Images within the same flight transect were more similar in terms of scene conditions compared with images within different flight transects. Because flying elevation, flight time, and flight direction varied more across flight transects and affected the digital scene within photographs, I performed subsequent image enhancements and transformations based on the unit of the flight transect. For each candidate image, I clipped 10% off the left end of the histogram and 2.5% off the right end of the histogram. Finally, the contrast was adjusted across the image by 60%. These contrast enhancements were performed on the RGB-format, digital images using the Contrast Tool in Erdas Imagine 8.7. The Percentage LUT Stretch accentuated the contrast of the blooming *D. panamensis* trees within the digital images and unpacked the spectral data for this specific feature of interest. Finally, I matched the remaining images within a particular flight transect to the candidate image’s histogram using the batch function. This procedure known as a *histogram matching*, converts the histogram of one image to resemble the histogram of another (LeicaGeosystems 2003).

2.2.5 Image enhancement: conversion to intensity, hue, and saturation color space

Following the contrast stretch, I performed another image enhancement to all of the digital images. At this step, the digital images were still within the original RGB color space. I converted the contrast-stretched, RGB images to an alternate color space known as intensity, hue, and saturation (IHS). This color space uses intensity, hue, and saturation as the three positional parameters instead of red, green, and blue and is based on a color sphere rather than a cube (Jenson 2005). *Intensity* is the overall brightness of a color, and values range between 0 and 1. *Hue* is the principal wavelength of the pixel, or dominant color, and values extend between 0 and 360. *Saturation* refers to the purity of the color relative to gray, and values range between 0 and 1. Gillespie *et al.* (1986) assert that the three color bands, RGB, tend to be highly correlated amongst each other.

Conversion of images in RGB color space to IHS color space serves to extract intensity, hue, and saturation values from each of the red, green, and blue bands and reduce band intercorrelation. In addition, this technique has proven quite effective in differentiating green and senescent plant materials in digital imagery having only three bands and lacking a near infrared band such as the imagery used in my study (Laliberte *et al.* 2006).

2.2.6 Supervised classification

The purpose of the classification step was to extract spectral patterns contained within the IHS band data of the digital images. Computer processors are able to

recognize and sort patterns present in the pixels of digital images and provide meaningful interpretation of features within the scene. In this next step, I extracted spectral patterns contained within the IHS band data of the enhanced digital images. I capitalized on the unique spectral signature of blooming *D. panamensis* trees in order to identify individuals across my digital images. All pixels within the digital images were used for the supervised classification.

I collected spectral signatures on the IHS-converted image in preparation for a supervised classification. Spectral signatures were contained in a single signature file. I used the same candidate image selected for the contrast stretch step to collect the signatures. Spectral signatures are sample pixels that represent a certain feature of interest that the classification algorithm can then use to classify other pixels in the image. Examples of common features could be water, urban areas, bare ground, or vegetation. Signatures are based on training samples collected within the image to be classified. I collected training samples using the Region Growing Tool, which is a more conservative method than a user-defined Area of Interest (AOI). The Region Growing Tool defines training samples based on specified user parameters such as a maximum training sample size or a maximum distance that candidate pixels can be to each other spectrally. Although I was most interested in defining tight signatures representing blooming *D. panamensis* trees, I also collected signatures for other land features. This enabled the supervised classification to allocate pixels for features besides blooming *D. panamensis*

into other classes. Some examples of additional classes included vegetation, water, agriculture, dark regions, bare ground, roads, and clouds. I examined the distribution of classes using the signature mean plot paying particular attention to the *D. panamensis* classes. In addition, I examined the separability of the *D. panamensis* signatures compared to the other signature classes by constructing a separability matrix. A separability matrix compares if training classes are spectrally distinct from each other, and separability is based on the transformed divergence metric. The maximum possible divergence value is 2,000, and values less than 1,500 indicate spectrally similar classes.

I also examined the classification error rates by using a Contingency Matrix. In all, a total of 64 signature files were collected to classify images in each flight transect. The number of signature files is slightly higher than the number of flight transects (63) due to the fact that some transects had to be flown at two different times due to the presence of clouds. Thus, these transects were analyzed separately.

I used the training sample for each candidate image to perform a supervised classification for the rest of the IHS-transformed images within each transect. This is a very unconventional classification method, as normally images are classified using their unique signature file. However, I considered this method to be appropriate, expedient, and effective in my analyses for several reasons. From a practicality standpoint, because I had several thousand digital images to analyze, I needed an efficient way to classify my images without collecting signature files for each image. As mentioned earlier, I

selected a candidate image from each flight image to conduct the initial image enhancements and then gather training signatures because images within transects were more similar to each other due to the flight elevation, time/day flown, and sun angle. Thus, I considered it appropriate to use a single signature file for a candidate image as a proxy for the rest of the images within a flight transect. Finally, I was only interested in resolving blooming *D. panamensis* trees throughout all of the images. Thus, I did not require such a precise classification level accuracy for signatures other than *D. panamensis*.

I initially performed a few “test-runs” of the supervised classification approach on the images. Based on these test-runs, it was apparent that the classification technique performed the best in so-called ideal conditions where the image scene contained mostly forest as well as blooming *D. panamensis*. Other image scenes that contained a lot of bare ground, various types of agriculture such as pineapple plantations, or non-forested areas tended to confuse the classifier. Based on this information, I applied the classification technique on 801 of the 2,550 images. These images represented 31% of the total images flown and were the ones that contained the most contiguous forest/vegetation cover.

Ultimately, I used a pixel-by-pixel classification approach using a maximum likelihood classifier. A maximum likelihood classifier is based on the probability that a pixel belongs to a particular class. The basic equation assumes that these probabilities are equal for all classes, and that the input bands have normal distributions

(LeicaGeosystems 2003). The maximum likelihood classifier is the oft-cited classifier approach used in remote sensing of forest trees (McGraw *et al.* 1998).

2.2.7 Post-classification image processing: recode

Following the supervised classification, I conducted a series of processing steps in order to prepare the images for analysis to determine how well the automated classification approach had identified blooming *D. panamensis* crowns.

The classified images were all *recoded* to identify pixels classified as blooming *D. panamensis* trees. All other pixels that had been aggregated into another signature file that was not designated as *D. panamensis* were recorded as background. A *clump* function was then run to aggregate these contiguous pixels as a unit. Finally, two *sieve* threshold functions were performed to remove pixel clumps smaller than 150 m² and larger than 2100 m². I selected these lower and upper sieve thresholds to target and remove small and large clumps erroneously classified as *D. panamensis*. Running the smaller sieve threshold removed the “salt-and-pepper” effect present in the images and eliminated small clumps that did not correspond to *D. panamensis*. This sieve level did remove some clumps that corresponded to actual *D. panamensis* trees. However, a sensitivity analysis revealed that the sieve level of 150 m² minimized the error of non *D. panamensis* clumps being included as this species. The upper sieve level of 2100 m² was selected after analyzing a subsample of 35 images and determining the largest *D. panamensis* clump in these images as well as the smallest and largest clumps erroneously

identified as *D. panamensis*. The large sieve level of 2100 m² effectively removed large clumps that were not *D. panamensis*. In my analyses, few *D. panamensis* trees actually achieve a crown area greater than 2100 m². Thus, few *D. panamensis* trees were removed due to this sieve function. These sieve thresholds also corresponded to the biology of *D. panamensis* and represented lower and upper crown areas of canopy-emergent *D. panamensis* trees.

2.2.8 *D. panamensis* clump density determination

Following the sieve step, the number of clumps within each image was quantified. In the majority of cases, a “clump” represents an individual *D. panamensis* tree. However, it is possible that a “clump” could represent several, neighboring trees with adjoining crowns. This is because the maximum likelihood classifier is unable to discern discrete objects. Therefore, adjacent *D. panamensis* trees are perceived as a single “clump” in the final classification output. There have been recent breakthroughs in computer assisted pattern recognition techniques that use segmentation in addition to traditional pixel-based classification approaches. This new approach, known as object-oriented classification, first segments a landscape into “objects” based on similarity criteria such as texture (Meinel and Neubert 2004). Thus, a tree crown would be more easily separated from other landscape features and potentially separable from other adjacent tree crowns. I briefly considered using an object-oriented classification approach to classify my images, and I evaluated several programs including eCognition.

However, due to price considerations and software availability, I ultimately opted for the pixel-by-pixel classification approach in Erdas Imagine. Indeed, the fact that some clumps represent multiple *D. panamensis* trees is trivial considering the number of *D. panamensis* stems across the 140,178-ha study area. In addition, from a macro-biological standpoint, most organisms that depend on *D. panamensis* for resources would be unlikely to perceive two, comingled tree crowns as separate entities.

D. panamensis density per image was then determined by dividing the number of *D. panamensis* clumps identified in the classified image by the image's area. The area for each image was calculated based on the field of view (FOV) represented in each image. The FOV calculation incorporated the focal length of the digital camera, the height above the landscape at which the image was taken, as well as the pixel dimensions of the image.

2.2.9 Classification error assessment

I performed a post-classification error assessment to determine various types of errors associated with the supervised classification. The purpose of an error assessment is to examine the different types of classification errors known as omission and commission. For a thorough overview of assessing error in classifications of remotely sensed data, please see Congalton (1991). Error of omission, also known as producer's or exclusion error, reflects the probability of a pixel being correctly classified into the target category. Error of commission, also known as user's or inclusion error, reflects

the probability that a pixel classified into a given category actually represents that category on the ground. An error assessment is most often represented by an error matrix.

Because the supervised classification that I performed was unconventional, I performed a nontraditional error assessment based solely on the ability of the classifier to distinguish *D. panamensis* clumps. I performed a manual error assessment on the classified images following the sieve step. I divided the images into two sets based primarily on the direction in which the aerial surveys were flown. The purpose of aggregating the images into two sets prior to conducting the error assessment was to organize images that were collected under similar flying conditions. The two image sets were named MNWR (Maquenque National Wildlife Refuge) and NZ (Northern Zone) after the regions over which they were flown. Table 1 summarizes the number of photos sampled for the error assessment for the images in the MNWR and NZ regions.

Table 1: Number of photos sampled for the classification error assessment

Region	Number of photos sampled for error	Total number of classified images	Percentage of images sampled for error
MNWR	25	633	3.9%
NZ	12	168	7.0%
Total	37	801	4.6%

The error assessment itself consisted of a manual assessment of how well the classifier identified *D. panamensis* clumps. First, I manually identified and counted the

number of *D. panamensis* clumps within a candidate image from either the MNWR or NZ Region. Next, I compared the *D. panamensis* clumps that I manually identified with the *D. panamensis* clumps the classifier identified. Based on the manually identified *D. panamensis* clumps, I quantified the number of *D. panamensis* clumps correctly identified by the classifier that also corresponded to the *D. panamensis* clumps identified manually. In addition, I quantified the number of tree clumps the classifier missed as well as the number of non *D. panamensis* clumps that the classifier misidentified. The former reflects the error of omission for the classifier while the latter reflects the error of commission for the classifier. Because I was only interested in the classifier's success in identifying *D. panamensis* and because I trained the original classifier to identify *D. panamensis* and not other landscape features, this error assessment did not include other landscape categories. A traditional accuracy assessment would include errors of omission and commission for multiple landscape categories. Hence, a complex error matrix could be generated. Ultimately, my classified images reflect a binary world—*D. panamensis* or non *D. panamensis*.

2.3 Results

2.3.1 Comparison of image enhancement transformations

The image enhancement transformations were an appropriate method to analyze digital photography that contained RGB bands but lacked an infrared band. Figure 5 shows the sequence of image enhancements and transformations for one image.

2.3.2 Signature separability

Sixty-four separate signature files were collected in preparation for performing the supervised classification. At least one candidate signature file was collected per flight transect, and the same signature file was used to classify images within a particular transect. I examined the specific training samples collected for blooming *D. panamensis* within each signature file to ensure separability. Because of the sheer number of signature files, I present the results of the separability analysis from one signature file. Training classes collected for blooming *D. panamensis* crowns were distinct compared to other landscape features such as vegetation, bare ground, water, or shadow areas. Figure 6 is a graph of the mean plot for each of the training samples in this candidate signature file. The graph shows the value for each of the three bands in the IHS color space for each training class. In general, *D. panamensis* training samples were the most distinct within the hue band of the IHS color space. The mean value for this band was 47.4 and ranged from 24.2 to 60.9 indicating that this region of the hue band correlated with the spectral signature for blooming *D. panamensis*.

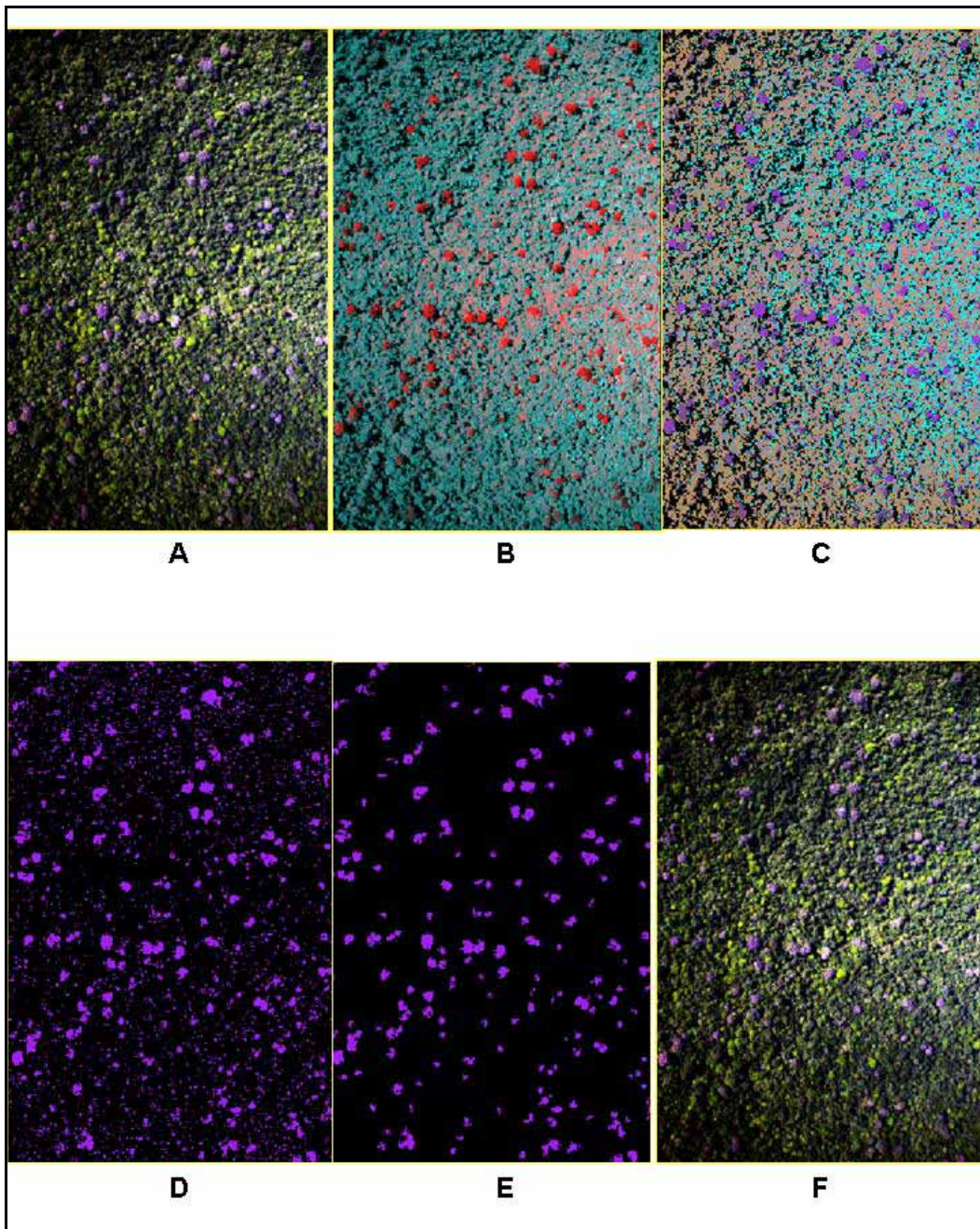


Figure 5: Sequence of image enhancement steps

A) Original RGB image that has been contrast stretched; B) Image that has been converted to IHS; C) Output from supervised classification; D) Image that has been recoded for just *D. panamensis*; E) Image that has been sieved to remove small and large tree clumps; F) Original RGB image for comparison.

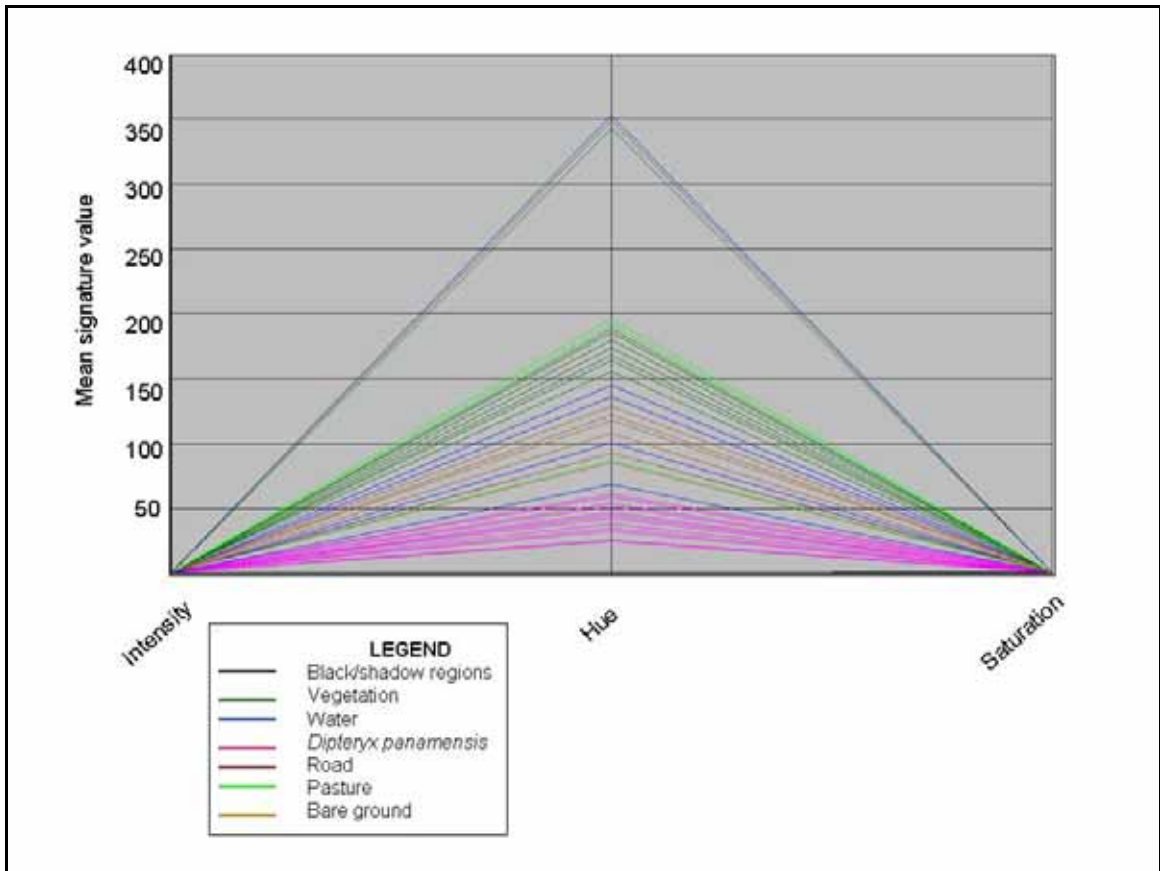


Figure 6: Sample signature separability plot

Results from the signature separability matrix are shown in Appendix B. All of the training classes gathered for this candidate signature are shown, and multiple training classes were collected to capture the spectral signature of blooming *D. panamensis* crowns. What is notable is that all of the *D. panamensis* training classes are separate and distinct from the other training classes, as no value is less than 1,500. This would indicate that training samples are spectrally similar. Some of the *D. panamensis* training classes are spectrally similar to each other as evidenced by values less than 1,500, which is acceptable considering that these classes are sampling the same environmental feature.

2.3.3 Classification error assessment

An error assessment was performed to determine the errors of omission and errors of commission over the entire project area. Errors were also determined separately for the MNWR and NZ regions. Together, the MNWR and NZ regions form the entire project area. The overall error of commission was 22.2% while the overall error of omission was 11.9%. The error of commission was acceptable based on other published studies (Lunetta *et al.* 2004, Foody *et al.* 2005). Table 2 summarizes the errors based on the classification error assessment.

Table 2: Results of the classification error assessment

Region	Percent Error of Omission	Percent Error of Commission
MNWR	6.7%	27.1%
NZ	22.7%	11.9%
Overall (adjusted to account for # of photos in each region)	11.9%	22.2%

2.3.4 High density images

The automated classification technique was successful in classifying high density areas of *D. panamensis*. The classifier worked especially well when applied to image scenes containing the most intact, contiguous forest. Examples of high density regions are shown in Figure 7. These images display densities of 2.0 trees/ha and 1.83 trees/ha.

2.4 Discussion

This study underscores that digital aerial photography still has a place amongst high-tech airborne and spaceborne remote sensing technologies. This technique can be used across a large spatial extent to investigate canopy-emergent trees. Canopy-emergent trees are one of the least studied tropical tree guilds due to their soaring crowns that often make them challenging to study from the ground (Clark *et al.* 2004b). In addition, high resolution digital photography can be analyzed *en masse* in a GIS platform by using a semi-automated classification approach to identify individual tree crowns. While an infrared band may increase the spectral separability of features,

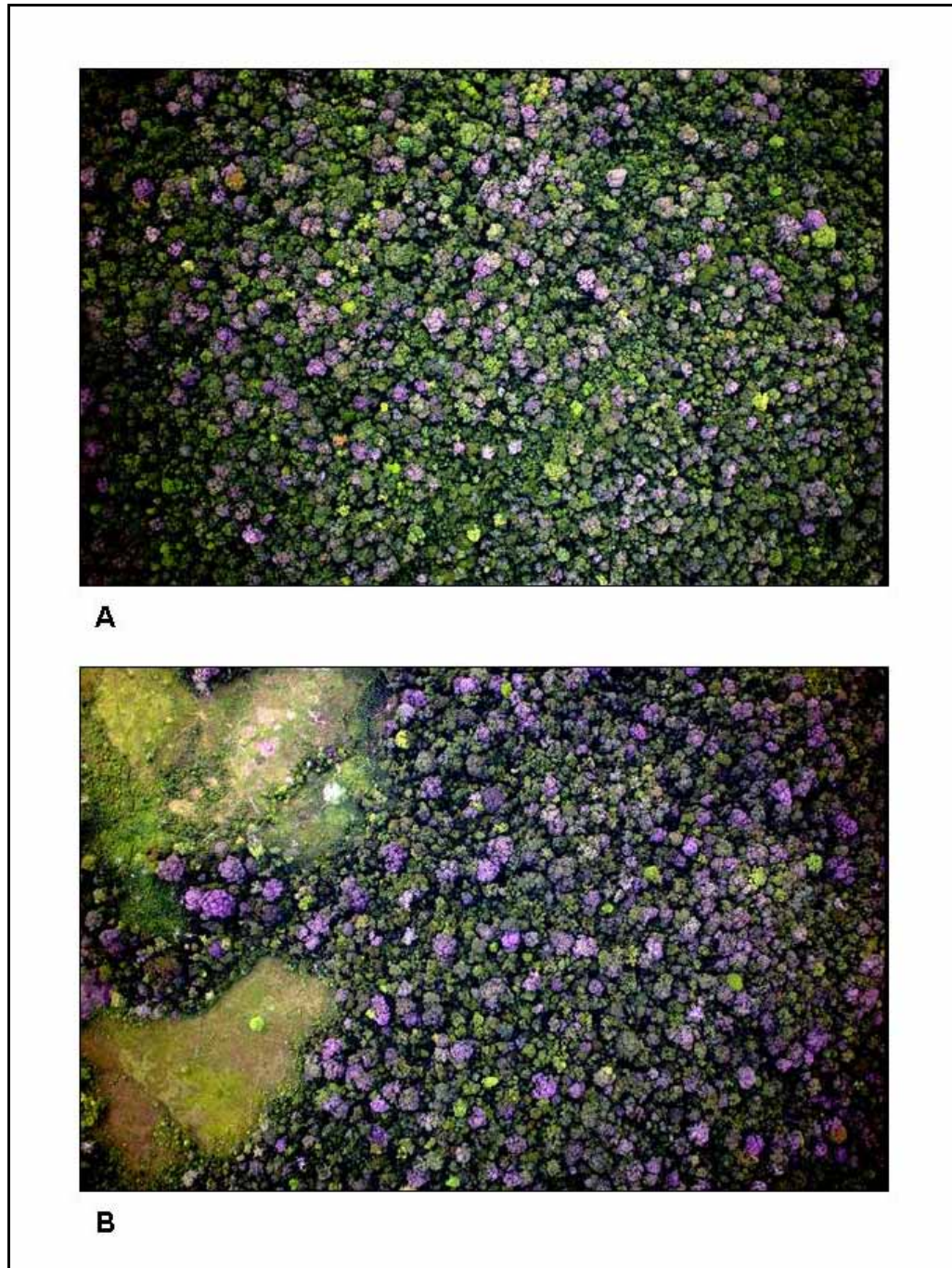


Figure 7: Sample images with high densities of *D. panamensis* trees

Blooming, canopy-emergent *D. panamensis* trees are identifiable from their purple crowns. Image A (97.8 ha) has a density of 1.83 trees/ha. Image B (95.2 ha) has a density of 2.0 trees/ha.

alternative color spaces such as IHS and other image enhancements may help resolve standard RGB digital images. Timing the overflights during a particular phenological period for the focal species—such as a peak blooming event—may also boost the success rate of the classifier. *D. panamensis* is a unique species, however. Fortuitously, this study species has a distinct peak blooming event when other canopy-emergent tree species have only green foliage, making it a prime candidate to calibrate a classification technique. However, this technique may need to be adjusted for species without a clear phenological signal.

Although this classification approach represents a semi-automated approach to identifying and analyzing the spatial distribution of a particular tropical tree species, this method does have some limitations. While a classification algorithm was developed to extract the spectral signature of blooming *D. panamensis* trees, the classification approach worked in ideal conditions when the image scene contained contiguous forest cover. The classifier had a difficult time differentiating spectral differences of blooming *D. panamensis* with bare ground and water present. Thus, only a limited number of the total images could be analyzed using the classifier.

Despite some of these limitations, digital aerial photography may offer some advantages in terms of time and money compared to spaceborne sensors. At this point, image scenes captured from high resolution spaceborne sensors such as SPOT, Quickbird, or IKONOS may be prohibitively expensive for large-scale surveys such as

this project that extended over 100,000 ha. If the digital camera is in hand, the main expense for an aerial survey will be the rental of the airplane or helicopter. In this study, the cost of renting the plane was less than \$5,000.

Ultimately, digital aerial surveys may complement more expensive remote sensing imagery. This approach may be particularly handy in augmenting the spatial extent of field plots, overcoming physical barriers, and sampling sites that may be dangerous or difficult to enter on the ground. In the field of tropical ecology and conservation, practitioners often look for creative ways to conduct research in light of limited funding. Digital aerial photography may be one way to surmount such challenges.

Chapter 3. Density distribution, habitat description, and fragmentation of a population of *Dipteryx panamensis* in northern Costa Rica

3.1 Introduction

Dipteryx panamensis is a large tree that occurs in lowland tropical moist and tropical wet forests along the Atlantic coast from Nicaragua to Colombia (Bonaccorso *et al.* 1980, Flores 1992). Along with several other tree species, *D. panamensis* comprises an important component of the emergent canopy layer. Canopy-emergent trees are defined as having crowns that extend above the mean canopy layer (Clark and Clark 1987). Tropical ecologists have struggled to accurately document the distribution and population densities of tropical emergent trees using forest inventory plots. Although forest inventory plots have long been used to examine biogeographic patterns of floristic species richness, density, and distribution in the tropics (Condit 1995), small field plots may poorly sample large trees. These are generally defined as > 60 cm diameter at breast height (Clark *et al.* 2004b). Because large, canopy-emergent tree species like *D. panamensis* are frequently distributed at densities of less than one adult/ha (Clark and Clark 1987), the size or placement of forest inventory plots may skew their density or distribution values at a landscape level. However, remote sensing techniques present new opportunities to examine the distribution of canopy-emergent trees across a larger spatial extent and present a more accurate representation of biogeographic patterns.

3.1.1 Objectives

I sought to document the landscape distribution and density of *D. panamensis* in the lowland Atlantic forests of Costa Rica. This tree plays an important role as a keystone species in this region and is particularly important as a nesting and food resource for the endangered Great Green Macaw (*Ara ambigua*). Specifically, I used digital aerial surveys to census this tree species across 140,178 ha and augment the coverage of traditional terrestrial plots. In addition, I used the results of this work to examine the connectivity of subpopulations based on pollen dispersal distances. In particular, I address the following specific questions in this chapter:

1. What is the distribution of *D. panamensis* across the study landscape?
2. What are the density trends for this species across the study landscape and over forested areas?
3. What environmental factors predict locations of high *D. panamensis* density?
4. How much potential habitat exists within the study area?
5. Are subpopulations of *D. panamensis* fragmented or connected based upon measured pollen dispersal distances?

3.2 Background

3.2.1 Overview of biogeographic studies in the tropics

The renowned English naturalist, Alfred Russel Wallace who lived from 1823-1913 is often considered the father of biogeography. Wallace (1876) is famous for his studies on the distributions of animals and plants of the Malay Archipelago which are documented in numerous books, most notably in the two-volume work “The Geographical Distribution of Animals”. Biogeography, the discipline that Wallace pioneered, is the scientific field that examines the spatial, distributional, and abundance patterns of biological diversity, both past and present (Lomolino *et al.* 2005). Tropical ecologists have long been curious about patterns of species distribution. For example, a central question driving ongoing studies in the tropics has been what abiotic and biotic factors promote the latitudinal gradient in species diversity (Pianka 1966, Stevens 1989). In other words, why do so many species’ distributions intersect at the tropics and how do these species coexist?

3.2.1.1 Limitations of terrestrial forest inventory plots

Examining the spatial distribution and abundance of any organism is constrained by the ability to census a large enough geographic area to garner an accurate signal. Early tropical ecologists sought to explore patterns of tree species richness through small plot-based studies. For example, Black *et al.* (1950) conducted an early

examination of floristic diversity and population density of trees in Amazonian forests within three 1-ha plots. However, because of the rarity of many tropical tree species, small plot studies may distort or all together miss uncommon species thereby belying their true spatial abundance and distribution. Even in their pioneering study, Black *et al.* (1950) cautioned against drawing conclusions on species diversity and abundance based on a small sample area. A network of 50-hectare plots throughout the tropics has sought to augment the spatial area of study as well as compare forests throughout different regions of the tropics (Condit 1995). These plots afford detailed study of floristic richness, composition, and distribution as every individual ≥ 1 cm in diameter is mapped and identified. While these plots are larger, Clark *et al.* (2004b) note that tropical inventory plots are often subjectively located, too small to capture processes of interest, or rarely sited using a statistical design.

3.2.1.2 The importance of documenting the distribution of keystone species

While tropical ecologists are often interested in documenting the spatial distribution and abundance of rare tree species as these species may contribute to high levels of both alpha and beta diversity (Pitman *et al.* 1999), attention should be given to the distribution and biogeographic patterns of more common tropical tree species at intermediate to large scales. In a study of 21 forest plots distributed across 40,000 ha of the Peruvian Amazon, Pitman *et al.* (1999) determined that while the rarest species occurred at a density of 1 stem/36.375 ha, 88% of tree species occurred at densities <1

individual/ha and at least half occurred somewhere at densities > 1.5 stems/ha. This work suggests that most tree species in tropical regions may be habitat generalists that occur at low densities but large absolute population size. Unlike rarer species, these ubiquitous tree species may actually be the linchpin in an ecosystem and an important keystone resource (Terborgh 1986, Mills *et al.* 1993, Nason *et al.* 1998). Much like a keystone in an arch, a keystone species plays a disproportionate role in an ecosystem's functioning, and the loss or removal of a keystone species could cause a dramatic shift in that ecosystem. Documenting the biogeographic ranges and habitat preferences of common, keystone trees can also assist conservation endeavors aimed at protecting these species and others that depend on them.

3.2.2 Background on study species: *D. panamensis*

3.2.2.1 Conservation status and keystone species designation

Because of *D. panamensis*' keystone status and importance in an ongoing conservation project, I documented the distribution and density of flowering, canopy-emergent individuals across 140,178 ha. This work occurred over Costa Rica's lowland Atlantic forest and employed digital aerial surveys. While relatively ubiquitous, this species is currently listed as a Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix III species (CITES 2008). Appendix III species are those that are regulated within the jurisdiction of a particular country to

prevent or restrict exploitation. The country has also identified the need for cooperation by other countries in order to control trade of this species.

In the lowland Atlantic forests of Costa Rica, *D. panamensis* and about a half dozen other tree species form an important component of the emergent canopy layer. Clark and Clark (1987) assert that the demography of tropical emergent species like *D. panamensis* remains poorly known due to the low density of post-seedling individuals and the fact that most adults occur at densities less than 1 tree/ha. Adult *D. panamensis* trees may reach 50 m in height and close to 1.5 m diameter at breast height (Flores 1992); reproductive maturity is likely attained at about 30 m in height (Perry and Starrett 1980). Based on tree ring counts and ¹⁴C dating, individuals may live close to 300 years with a theoretical maximum age of 645 years (Fichtler *et al.* 2003).

Like the fig tree (Nason *et al.* 1998), *D. panamensis* is considered another keystone tree resource in the tropics. The fruits of *D. panamensis* mature at the onset of the dry season, a time when the fewest tree species present edible, ripe fruits (Frankie *et al.* 1974, Bonaccorso *et al.* 1980). In a given year, a large adult *D. panamensis* tree may produce an estimated 10,000 fruits (Bonaccorso *et al.* 1980). However, individual trees may oscillate between years of high and low fruit production.

3.2.2.2 Phenological patterns

The phenological pattern of *D. panamensis* has been well studied. *D. panamensis* trees flower annually, and the timing of the first flowers occurs immediately after the

months with highest light and lowest rainfall (O'Brien *et al.* 2008). Thus, flowering generally commences around May prior to the onset of the rainy season in northeastern Costa Rica. Individuals of *D. panamensis* bloom asynchronously with overlapping 6-week flowering periods (Perry and Starrett 1980). Flowering generally peaks in July and declines by August. However, O'Brien (2008) observed some *D. panamensis* trees still flowering into October. Flowers, which are arranged along lateral or terminal panicles, generally last for one day before falling to the ground. The presentation of relatively few flowers each day by an individual tree and the asynchronous overlap of blooming individuals seem to encourage inter-tree pollinator movement and favor out-crossing (Perry and Starrett 1980). While it has been long thought that this species is an obligate out-crosser (Perry and Starrett 1980), recent genetic work by Hanson *et al.* (2008) reveals instances of self-pollination.

Immature fruits first appear in early July, and mature fruits are present on the trees from November to March (Bonaccorso *et al.* 1980). The fruits are elliptical drupes that comprise a thin exocarp, a fleshy mesocarp, and a hard endocarp that protects a single seed (De Steven 1988). As fruit production ceases, *D. panamensis* trees exhibit moderate deciduousness. Individuals shed their leaves synchronously during the driest months from February to May (O'Brien *et al.* 2008). A new flush of leaves soon emerges.

3.2.2.3 Interactions with other organisms

In keeping with *D. panamensis*' designation as a keystone tree resource, this species participates in a complex web of interactions with other organisms. Not only does it require other species for critical services like pollination and seed dispersal, but it also supports a host of other species. The prime pollinators include at least 13 species of medium-to-large bees (Perry and Starrett 1980). Bonaccorso *et al.* (1980) observed at least 16 species of mammals that will eat the fruit. Seed commensals that only consume the fleshy mesocarp, do not penetrate the endocarp, and leave the seed intact include primates, bats, marsupials, rodents, and carnivores. Some of these species may even disperse seeds away from the parent tree. Fruit bats, particularly in the genus *Artibeus* are notable dispersers of *D. panamensis* fruit and will often carry the drupes considerable distances until they reach a feeding roost often in a palm. Seed predators that damage the stony endocarp and frequently consume the seed include many rodents such as red-tailed squirrel (*Sciurus granatensis*), agouti (*Dasyprocta punctata*), paca (*Agouti paca*), and spiny rat (*Proechimys semispinosus*) (Bonaccorso *et al.* 1980). Hundreds of migratory or resident birds may frequent *D. panamensis* trees to forage. A notable species includes the endangered Great Green Macaw (*Ara ambigua*). Powell *et al.* (1999) noted that *D. panamensis* accounted for 85% of Great Green Macaw feeding observations during the month of January. In addition, 86% of Great Green Macaw nests occur in the hollows of this tree (Chassot *et al.* 2002, Monge *et al.* 2003).

3.2.2.4 Threats and conservation measures

Although *D. panamensis* is relatively abundant within the lowland Atlantic forests of Costa Rica, it is threatened primarily from logging since its wood is used to make plywood. However, due to the density, weight, and crystalline deposit content of *D. panamensis* wood, this species was extremely difficult to fell with axes and manual saws (Flores 1992). Until recently, solitary individuals stood in pastures cleared of more pliable tree species. Only with the advent of steel chain saws could this tree be targeted. Because of this species' keystone status within the lowland Atlantic forest ecosystem as well as its significance to the Great Green Macaw, Costa Rica's Ministry of the Environment enacted a series of forestry laws that restrict logging of *D. panamensis* by 50%. However, enforcement still remains a challenge. In 2005, a new national wildlife refuge known as Maquenque was decreed (refer to material in Chapter 1). Situated in the larger San Juan-La Selva (SJLS) Biological Corridor, the primary purpose of this 59,700-ha refuge is to protect breeding and nesting habitat of the Great Green Macaw. This mandate effectively affords protection to *D. panamensis* populations.

3.2.2.5 Habitat requirements, distribution, and abundance

Although aspects of *D. panamensis*' phenology are well-studied, specific details about its habitat requirements, distribution, and abundance across a larger spatial extent are still needed. Information about those factors could assist the ongoing conservation efforts while augmenting basic biological data on the species. The following broad

habitat conditions were described by Flores (1992). *D. panamensis* is generally found on humid plateaus with alluvial or sandy soils and sometimes acid and clay soils at elevations between 20-1300 meters above sea level. What is known about the densities of *D. panamensis* seedlings, saplings, and adult trees come from relatively small plot studies. As noted earlier, plot size and the delineation of plot boundaries may skew density values. The few estimates of adult *D. panamensis* densities within intact forest come from plots established at the La Selva Biological Station and include trees that are being followed for a long-term demographic project. Reported density measurements range from 0.45 trees/ha (85 ha plot) to 0.97 trees/ha (65-ha plot) (Hanson *et al.* 2006, Hanson *et al.* 2008). However, these density estimates are difficult to interpret as the plots substantially overlap and are relatively small making them susceptible to skew. Nonetheless, Clark and Clark (1987) assert that tropical emergent species like *D. panamensis* are frequently distributed at densities of less than 1 adult/ha challenging our abilities to study their demographics, abundances, or distribution across large spatial scales. However, remote sensing techniques present new opportunities to examine this species, especially large adults, from an aerial vantage point.

3.2.2.6 Pollen dispersal patterns for *D. panamensis*

A recent study by Hanson *et al.* (2008) examined the effects of varying levels of habitat fragmentation on the genetic structure, genetic diversity, and pollen dispersal distances of adult and progeny populations of *D. panamensis* within four different

habitats—continuous forest, forest fragments, pastures adjacent to fragments, and isolated pastures. Using genetic techniques to analyze parentage, Hanson *et al.* (2008) determined that *D. panamensis* progeny located in isolated pastures were the results of the longest pollination dispersal distances compared to the other three habitats. Pollen traveled a mean of 557 m with the furthest distance being 2.3 km for these offspring in isolated pasture. This is compared to the shortest pollen dispersal distance among continuous forest trees of 240 m. While pollen tended to travel farther amongst trees in pastures, these trees exhibited lower outcrossing rates compared to trees in continuous forest or forests fragments. This suggests that long distance pollen movement is possible for these pasture trees, but the frequency is a lot lower due to higher rates of self-pollination. Thus, these tree populations could be at risk of long-term genetic erosion due to the fragmented landscape.

While this study by Hanson *et al.* (2008) elucidates the effect of habitat loss on the genetic structure of *D. panamensis*, it focused on the southern extent of the proposed SJLS Corridor and was conducted at a relatively small spatial scale. The study sites were separated by a mean distance of 18.4 km, and the largest study site was 65 ha. Results from the work by Hanson *et al.* (2008) could be used to scale up to a landscape level in order to study the separation of *D. panamensis* stands based on pollen dispersal distances.

3.3 Materials and methods

3.3.1 Study Site: San Juan-La Selva Biological Corridor

Patterns of *D. panamensis* distribution, density, and fragmentation were discerned at a landscape level across 140,178 hectares within the proposed San Juan-La Selva Biological Corridor (SJLS) located in northeastern Costa Rica (Figure 2) (refer to material in Chapter 1).

3.3.2 Landscape distribution of *D. panamensis*

3.3.2.1 Digital aerial surveys

The landscape distribution of canopy-emergent *D. panamensis* trees was based on a digital aerial survey from July 4-8, 2005. The survey was timed to coincide with this species' peak blooming. For a detailed description of the aerial survey methods as well as the post-flight image processing, please refer to Chapter 2.

3.2.2.2 *D. panamensis* density determinations: semi-automated supervised classification and manual density approach

After the digital images were captured, the images were adjusted and classified using a supervised approach (Chapter 2). The purpose of these steps was to spectrally enhance the images in preparation for a supervised classification. The supervised classification then identified blooming *D. panamensis* trees in an automated fashion. Of the original 2,550 digital images that were gathered during the aerial survey, 801 were

analyzed using the automated, supervised classification approach. Thus, only about 31% of the digital images collected were analyzed using the classification approach. The classifier performed well on images such as these that contained contiguous forest or vegetation cover. Based on the error assessment (Chapter 2) that identified the errors of omission and commission for the classification within the two survey areas termed MNWR (Maquenque National Wildlife Refuge) and NZ (Northern Zone), I systematically adjusted the number of tree clumps identified within each image scene by a uniform percentage. Although the error within all images was not uniform, this approach addressed the average error throughout. The adjustment value was based on the manual error assessment and represented:

$$\frac{\text{Number of } D. \textit{panamensis} \text{ clumps manually identified within each image}}{\text{Number of } D. \textit{panamensis} \text{ clumps identified by the classifier}}$$

Here, the numerator of this equation represents the actual number of blooming *D. panamensis* within each image scene, while the denominator reflects the number of blooming *D. panamensis* as determined by the classifier. In general, the classifier tended to overestimate the number of *D. panamensis* clumps within each scene. All images within the MNWR region were adjusted by 79%. However, the NZ images did not require adjustment. There is a reason for the difference in adjustment values between the two sites. Images within the NZ were captured on the same day and mostly possessed scenes of contiguous, uninterrupted forests. These were ideal conditions for the application of the classifier. Images within MNWR were captured over several days

and possessed more variable scene conditions like agriculture, pastures, towns, or water. The classifier was less successful over these scenes and tended to overestimate the number of *D. panamensis* tree clumps within the MNWR study area. Although I applied a systematic adjustment for these images, this does not completely remove all error from the images. However, the degree of error remaining within these images regarding the number of *D. panamensis* tree clumps is acceptable compared to the number of trees that are being surveyed over the entire 140,178-hectare study area.

The classified images likely contained a higher density of *D. panamensis* due to the preponderance of intact forest within the scene. Thus, I selected a spatially stratified subset of the remaining images to perform a manual count of *D. panamensis* within each scene. These images had not been analyzed via the supervised classification. A total of 503 images were selected for the manual count representing about 20% of the total digital images collected. Because these images contained less contiguous forest and more human altered landscapes, the manual count was not exceptionally time intensive and provided a more accurate assessment of *D. panamensis* trees than the supervised classification approach. However, the supervised classification was appropriate for image scenes with contiguous vegetation and a lot of blooming *D. panamensis* as the classifier provided a more automated, systematic, and complete approach. A manual effort for these particular images would have been prohibitively time consuming.

Following either the classifier or manual approach, *D. panamensis* density within each image was determined by dividing the total number of *D. panamensis* tree clumps within each image by the image's area. The area for each image was calculated based on the field of view (FOV) represented in each image. The FOV calculation incorporated the focal length of the digital camera, the height above the landscape that the image was taken, and the pixel dimensions of the image. The average FOV for all classifier and manual images was 113.45 ha (SD 24.01). Because the locations of all images had been recorded with an onboard GPS unit during the original aerial survey, the density value for each image could be spatially depicted within a GIS framework.

3.2.2.3 Creation of a *D. panamensis* density map using the IDW interpolation method

In order to depict the spatial variation in *D. panamensis* density across the study area, I created an interpolated surface within a GIS framework of all of the *D. panamensis* densities garnered from individual images. Interpolation is a technique that enables the creation of a continuous raster surface from sampled data. Because it is often impossible to perform a complete census of an area due to financial or time constraints, interpolation is a method by which intervening, non-sampled locations are estimated from sampled values (Theobald 2003).

Numerous interpolation methods exist such as spline, kriging, natural neighbor, and inverse distance weighting (IDW). Selecting the appropriate technique depends on the type of data to be displayed, data accuracy, and the spatial distribution of the data

points. Interpolators like IDW and spline are deterministic because they assign values to unsampled locations based on the surrounding measured values and mathematical formulas that determine the smoothness of the resulting surface. Kriging is considered a geostatistical method and the resulting interpolation is based on a statistical model that includes autocorrelation. In addition, interpolators can be exact or inexact. Exact interpolators preserve the original input value at the sample location. Exact interpolators are suitable for data that can be measured reliably and contain a lot of certainty. With inexact interpolators, however, input values may vary from their original value in order to achieve a better fit in the resulting interpolation.

Because the *D. panamensis* density values covered the project area in an evenly spaced fashion, I utilized the IDW interpolation method using the Geostatistical Analyst tool in ArcGIS 9.1 to create a continuous map of *D. panamensis* density. The IDW method was appropriate because as an exact interpolator, it preserved the original density input values. The IDW interpolation also explicitly assumes that closer things are more similar to one another than things that are farther apart. The IDW method estimates new cell values in the output raster surface by averaging the values of the sample data points in the vicinity of each cell (ESRI 2005). The closer an input point is to the cell being estimated, the more weight it has in determining the value of that cell. Thus, the weight of a measured point diminishes with distance—hence the term “inverse distance weighting”. The power parameter in the IDW method affects how fast

the weights decrease. If the power parameter equals 0, there is no decrease with distance. As the power parameter rises above 0, the weights of distant points decrease rapidly. The Geostatistical Analyst tool in ArcGIS 9.1 has a way to optimize the power parameter. In general, the power parameter should be calibrated depending on the ecological phenomena being modeled. For example, a larger power parameter should be used to model phenomena that have a more localized effect.

A total of 1,304 *D. panamensis* density inputs were used for the interpolation. These density inputs were distilled from the same number of images. The image sample represents 51% of the total number of images gathered and covers approximately 147,856 ha. This area exceeds the size of the area originally flown (140,178 ha) as some images overlap in coverage. An optimized power function of 1.24 was used in the IDW interpolation model. The sample window was an ellipsoid shape and included at least 4 neighboring input points. A cross-validation was performed on the data set in order to determine how well the model performed. The cross-validation step systematically omits a point and compares its predicted value to its true value. The deviation from the predicted to the true value is expressed by the root mean square error (RMSE) given below:

$$\text{RMSE} = \sqrt{(\sum x - x_0)^2 / n}$$

The RMSE is the square root of the average squared difference between the predicted value (x) and the "true" value (x₀) where n is the number of points. The RMSE

for the interpolation model was 0.18. The optimized power parameter of 1.24 produced the lowest RMSE compared to power parameters of other values.

Based on the interpolation, I produced a density map showing the distribution of *D. panamensis* across the study area. The map displayed the densities based on increments of 0.1.

3.3.3 Density trends over the study landscape and forested areas

I used the interpolated density map to analyze density trends across the study landscape. I was specifically interested in locations where high densities of *D. panamensis* were predicted. In particular, I examined the distribution of *D. panamensis* densities across the total landscape as well as over only forested area. The forested areas were derived from a land-use classification of a satellite image over the northeastern part of Costa Rica. The satellite classification shows land use from 1997-2000 (Figure 8). This satellite classification was conducted by the Earth Observation Systems Lab, University of Alberta, Canada. The satellite classification's extent is cropped and does not cover the entire area of the aerial survey. Thus, some of the analyses had to be abridged.

3.3.4 Environmental factors predicting high density locations of *D. panamensis*: a classification tree approach

I used the *D. panamensis* density map as well as other GIS data to identify environmental conditions that have the potential to support regions of high *D.*

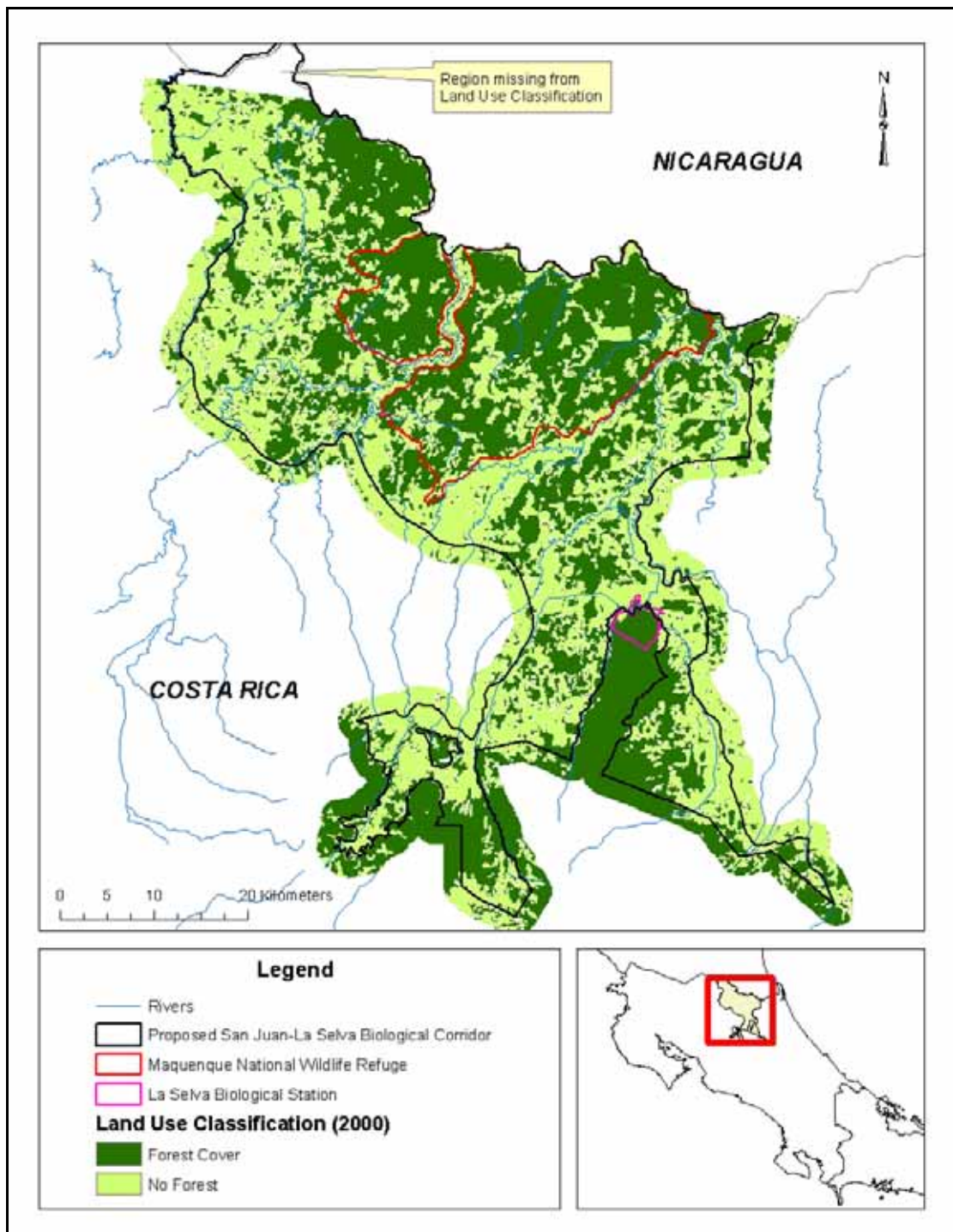


Figure 8: Land use classification within proposed San Juan-La Selva Biological Corridor

panamensis density. For this analysis, I used a classification and regression tree (CART) model. CART models are one of many methods that can be used to predict species-habitat distributions and identify potential habitat (Guisan and Zimmermann 2000). However, CART models offer several advantages over traditional methods such as linear discriminant analysis or cluster analysis due to their flexibility. De'ath and Fabricius (2000) note that CART models are uniquely equipped to deal with ecological data that are often complex, unbalanced, or missing values. They are a nonparametric approach to distinguishing differences among groups (Breiman *et al.* 1984, Vayssieres *et al.* 2000). In addition, because CART models are graphical in nature, each conditional path can easily be executed in a GIS platform in order to display habitat distributions (Urban *et al.* 2002).

The response variable in a CART model can either be categorical or continuous. If it is the former, a classification tree is produced; if it is the latter, a regression tree is obtained. The explanatory variables may be categorical, continuous, or a mix of both. CART models produce a decision tree by recursively partitioning the data. At each split, data are aggregated into two mutually exclusive groups, each of which is as homogeneous as possible. The subgroups are then partitioned further until the data cannot be split anymore or a stopping criterion is met. The objective is to partition the response variable into homogeneous groups but also keep the tree reasonably small (De'ath and Fabricius 2000). Because CART models attempt to partition all the data,

they can often over-fit the data. Large decision trees may actually be meaningless. Thus, these decision trees are then pruned back to the desired size in order to avoid over-fitting the data.

Decision trees are presented graphically with a root node at the top, which represents the undivided data, and branches and leaves toward the bottom. Terminal leaves represent homogeneous data that no longer can be partitioned. The pathway to each terminal leaf in the decision tree defines a set of environmental conditions under which the splitting rule associated with that leaf will apply (Moore *et al.* 1991). It is this set of conditions that can be entered into a GIS platform and used to graphically display potential habitat.

In order to identify potential habitat that can support high density *D. panamensis* stands, I utilized a CART model. The response variable was *D. panamensis* density, which was binned into different density categories making the model output a classification tree. Environmental predictor variables were a mixture of categorical and continuous. Predictor variables were selected based on an *a priori* knowledge of environmental factors that could be important in determining *D. panamensis* occurrences and potential habitat. These were gleaned from the literature and included information on soil, elevation, and rivers. Descriptions of the specific response and predictor variables that were considered in the model are summarized in Table 3.

Table 3: Response and predictor variables used in CART model to predict potential *D. panamensis* habitat

Name	Description	Variable Type
<i>Response variable:</i>		
DENSITY	Values of <i>D. panamensis</i> density binned in 4 increments	Categorical
<i>Predictor variable:</i>		
SOILOR	Soil order	Categorical
SOILSUB	Soil suborder	Categorical
SOILGG	Soil great group	Categorical
SOILTOPO	Soil topography	Categorical
ELEV	Elevation of terrain	Continuous
RIV	Distance to nearest river	Continuous

Data for the response and predictor variables were contained within GIS rasters or shapefiles that were standardized to the same spatial extent and geographic projection. GIS data were projected to WGS 1984 UTM Zone 16N. All GIS analyses were conducted using ArcGIS 9.1. Data for the response variable, DENSITY, consisted of 1,265 observations representing a particular *D. panamensis* density bin. Hence, the response variable was categorical. These density bins were distilled from the original *D. panamensis* density values originating from the digital images covering the SJLS Corridor. Density values were obtained using both an automated pattern recognition technique as well as a manual assessment of blooming *D. panamensis* crowns (Section 3.2.2). Each density value was geographically referenced to the location in which the original photograph was taken and all points were contained in a GIS shapefile. The density bins are summarized in Table 4.

Table 4: Summary of response variable bins

Bin Name	<i>D. panamensis</i> density range	Number of observations
Bin #1	0.00 trees/hectare	85
Bin #2	0.01-0.20 trees/hectare	404
Bin #3	0.21-0.40 trees/hectare	251
Bin #4	>0.41 trees/hectare	525
Total Observations		1,265

The predictor variables were obtained by using the *D. panamensis* shapefile and intersecting the point locations with the raster files for each predictor variable in order to extract the underlying data values. GIS data for the environmental predictor variables originated from the Organization for Tropical Studies.

The CART analysis was performed in the R Statistical Program using the “tree” package (R Development Core Team 2008). I tested several classification trees to determine which predictor variables were relevant in identifying potential habitat that could support high *D. panamensis* density. Predictor variables that did not produce a logical split in the classification tree were removed from consideration. The “tree” settings were customized for the analysis. For example, the minimum required number of observations per node was changed from 20 to 10. Classification trees were run utilizing the cross-validation tool and with it disabled. The final classification tree was run using the following environmental variables: SOILSUB and ELEV. This classification tree required no pruning.

3.3.5 Delineation of potential *D. panamensis* habitat

I was specifically interested in the environmental conditions that could support *D. panamensis* populations at densities > 0.4 trees/ha. Thus, I used the parameters from the classification tree in order to produce a map depicting potential *D. panamensis* habitat.

3.3.6 Fragmentation analysis of moderate density *D. panamensis* patches

I utilized the *D. panamensis* density map developed in Section 3.2.3 to analyze how habitat patches of this species were connected throughout the landscape. Hanson *et al.* (2008) observed that *D. panamensis* progeny located in isolated pastures were the results of the longest pollination dispersal distances, with the farthest distance being 2.3 km. Thus, I used this distance as a threshold. Distances below this value would indicate that two discrete patches were connected based on pollen flow between them. Distances above this value would denote that two patches were disconnected. I delineated *D. panamensis* patches by categorizing the density map into four different density bins. These density bins roughly corresponded to habitat quality. Regions without any *D. panamensis* trees had densities between 0 and 0.1 trees/ha. Low density regions had densities between 0.1 and 0.2 trees/ha. Moderate density areas exhibited densities between 0.2 and 0.5 trees/ha. Finally, high density regions possessed densities > 0.5 trees/ha. These bins are detailed in Table 5. The purpose of this analysis was to gauge

one aspect of habitat fragmentation based on pollen dispersal. Examining seed dispersal patterns could have provided a glimpse of seedling recruitment, the effectiveness of animal seed dispersers, or another aspect of habitat fragmentation. However, only data on pollen movement were available.

Table 5: Description of bins for fragmentation analysis

Name	Density bin (<i>D. panamensis</i> tree clumps/ha)	% of Area
No <i>D. panamensis</i>	0-0.1	32%
Low density	0.1-0.2	15%
Moderate density	0.2-0.5	32%
High density	>0.5	21%

I used the program FRAGSTATS to analyze how moderate density patches of *D. panamensis* were connected throughout the landscape based on the pollen dispersal distance of 2.3 km. FRAGSTATS was developed by McGarigal *et al.* (2002), and it is designed to compute a wide variety of landscape metrics at patch, class, and landscape scales. In particular, I examined the connectivity of moderate density patches to other moderate or high density patches. Only patches that were over 20 ha and were contained entirely within the bounds of the study area were included. I also determined the mean patch size and the mean Euclidean distance of each moderate density patch to its nearest neighbor. The latter metric provided a measure of habitat patch isolation across the landscape.

I also computed the connectance index between these moderate density *D. panamensis* patches. In FRAGSTATS, connectance measures the number of functional joinings between patches of the same class that are within a specified distance of each other. It assesses whether each patch is connected to every other patch in the landscape based on the distance threshold. Here, I used the value of 2.3 km based on the longest pollen dispersal distance measured by Hanson *et al.* (2008).

The fragmentation analysis described above was primarily a heuristic exercise and employed several simplifying assumptions about the landscape and the ecology of pollen and gene flow. First, this analysis examined whether *direct* pollination events could occur among trees located in a discrete moderate-density patch to trees located in another moderate-density patch. I utilized the distance threshold of 2.3 km, which represents the maximum pollination dispersal distance between *D. panamensis* trees measured by (Hanson *et al.* 2008). The analysis ignores the potential contribution of isolated trees within the intervening areas between patches that are located in either low or no-density regions. Thus, I am not claiming that moderate-density patches within the landscape are genetically isolated from each other, nor am I maintaining that gene flow does not occur between these patches. I am merely examining whether direct pollination events could occur. In addition, I am not specifically examining gene flow as my analysis is not occurring at the individual tree level—rather the patch level.

Ultimately, the purpose of this analysis is to apply Hanson *et al.*'s (2008) results based on a localized study and scale up to a landscape level.

3.4 Results and discussion

3.4.1 Landscape distribution of *D. panamensis*

Figure 9 shows the distribution of *D. panamensis* density across the 140,178-ha study area. Densities are binned into increments of 0.1 tree clumps/ha. The northwestern part of the study area contains the highest densities with, canopy-emergent trees reaching 2 tree clumps/ha. This high-density region borders Nicaragua.

3.4.2 Density trends over the study landscape and forested areas

Table 6 summarizes the percentage of the *total* landscape surveyed that is represented in each *D. panamensis* density bin. Table 6 also shows the distribution of *D. panamensis* density over only forested areas. The satellite classification that was used to identify forested areas does not cover the entire extent of the density map. In particular, the satellite classification does not extend into the extreme northern part of the study area where *D. panamensis* densities are the highest. Hence, approximately 3,388 ha of the original *D. panamensis* density map are not included in this analysis which is why these values are missing. Figure 10 represents the percentage of the *total* landscape represented in each *D. panamensis* density bin. Figure 11 represents the percentage of the *forested* landscape represented in each *D. panamensis* density bin.

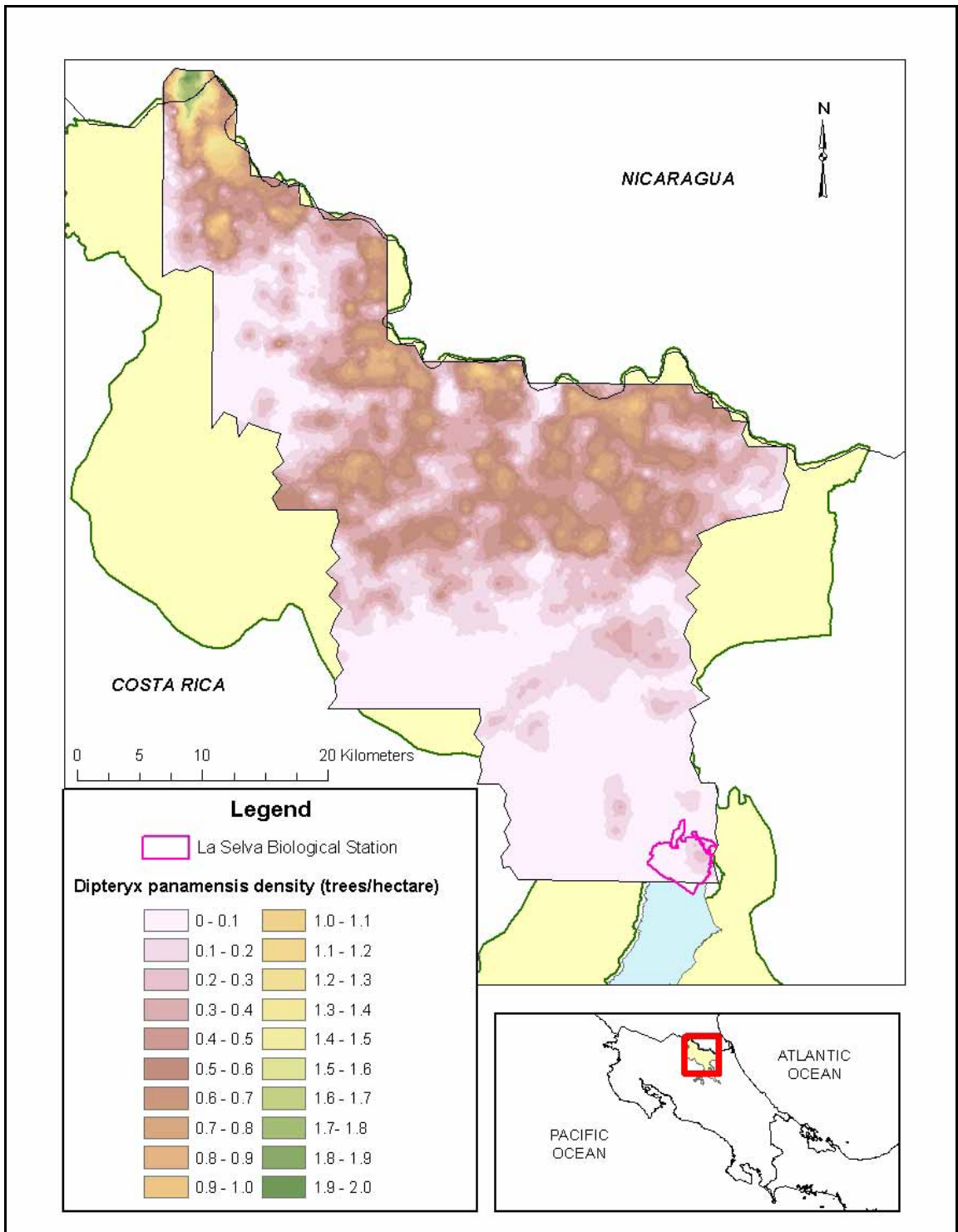


Figure 9: Density distribution of *D. panamensis*

Table 6: Percentage of the total and forested landscape represented by each *D. panamensis* density bin

Density Bin Range (trees/hectare)	Area (ha) (over total landscape)	Percentage (over total landscape)	Area (ha) (over forest cover)	Percentage (over forest cover)
0-0.1	44095.05	31.45%	18870.84	21.72%
0.1-0.2	21574.89	15.39%	13539.24	15.59%
0.2-0.3	16135.74	11.51%	10550.79	12.15%
0.3-0.4	14922.72	10.64%	10261.08	11.81%
0.4-0.5	13531.32	9.65%	10139.22	11.67%
0.5-0.6	12820.05	9.14%	10661.13	12.27%
0.6-0.7	8317.89	5.93%	7143.57	8.22%
0.7-0.8	4600.44	3.28%	3956.04	4.55%
0.8-0.9	1617.48	1.15%	1192.95	1.37%
0.9-1.0	676.35	0.48%	384.48	0.44%
1.0-1.1	503.46	0.36%	156.33	0.18%
1.1-1.2	284.58	0.20%	11.7	0.01%
1.2-1.3	204.84	0.15%	Data Missing	Data Missing
1.3-1.4	200.61	0.14%	Data Missing	Data Missing
1.4-1.5	100.89	0.07%	Data Missing	Data Missing
1.5-1.6	119.88	0.09%	Data Missing	Data Missing
1.6-1.7	170.91	0.12%	Data Missing	Data Missing
1.7-1.8	215.37	0.15%	Data Missing	Data Missing
1.8-1.9	82.98	0.06%	Data Missing	Data Missing
1.9-2.0	18.63	0.01%	Data Missing	Data Missing
Total	140,194.08	100%	86,867.37	100%

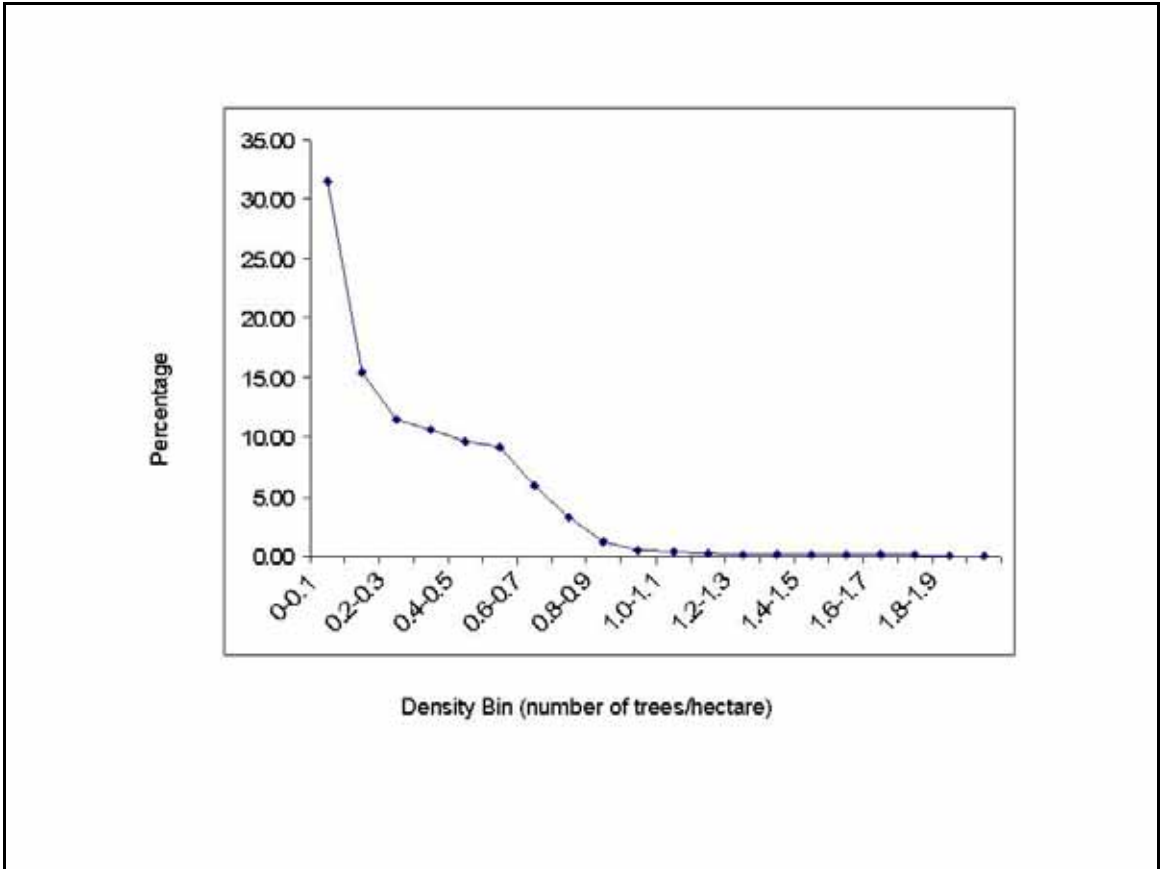


Figure 10: Percentage of the total landscape represented in various *D. panamensis* density bins

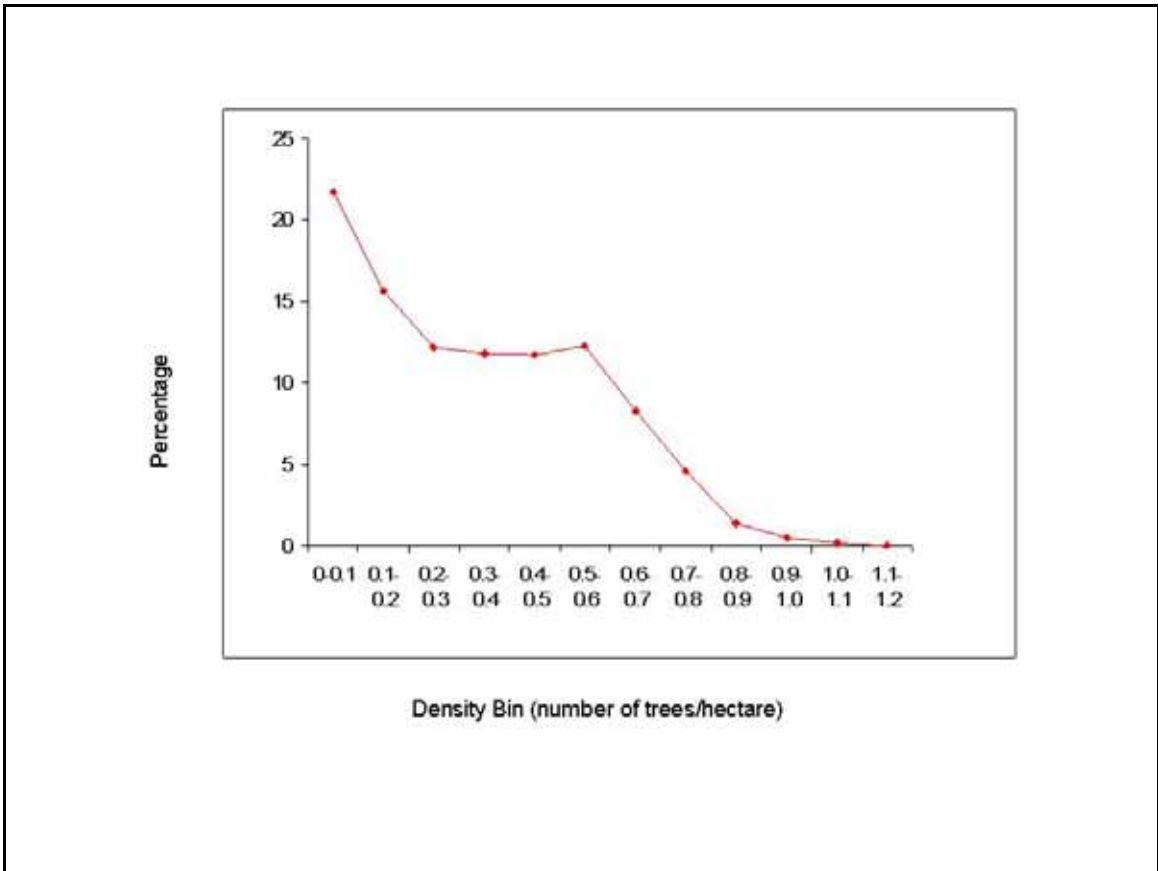


Figure 11: Percentage of forested landscape represented in various *D. panamensis* density bins

This research highlights that canopy-emergent *D. panamensis* trees can occur at densities as high as 2 trees/ha. Nearly 20 ha were identified that support this density level. In addition, nearly 600 ha contain densities over 1.5 trees/ha, and 1,900 ha contain densities over 1.0 tree/ha. The aerial survey could only detect individual trees that protruded from the canopy and those that were in flower. Thus, the total density of this species would be higher if other life-history stages like understory trees or non-flowering individuals were included.

Density patterns within the La Selva Biological Station are also worth noting. La Selva, which is operated by the Organization for Tropical Studies, comprises about 1,600 ha of tropical wet forests. Only 413 ha of La Selva (25%) contained densities between 0.1-0.2, and 96 ha of La Selva (6%) contained densities between 0.2-0.3 ha. The remainder of the field station had densities less than 0.1 tree clumps/ha.

While it is often thought that canopy-emergent tree species like *D. panamensis* exist at densities less than 1 adult-tree/ha (Clark and Clark 1987), this work clearly shows that this species can occur at much higher densities. However, the distribution of this species throughout the entire study area averages between 0.3 and 0.4 trees/ha. Thus, over a large spatial area, the relative densities are more moderate. Nonetheless, the results of this work may assist in ongoing conservation endeavors such as MNWR and the SJLS Corridor aimed at protecting this keystone tree and other species within the lowland Atlantic rain forest of Costa Rica.

3.4.3 Environmental factors that predict locations of high *D. panamensis* density

Results from the classification tree model indicated the environmental conditions predicted to support *D. panamensis* stands with a density of 0.4 tree clumps/ha or greater. These environmental conditions occur between elevations of 45-125 meters and on the Humult, Aquent, and Tropept-Aquept soil suborders.

3.4.4 Delineation of potential *D. panamensis* habitat

Figure 12 shows the distribution of potential habitat predicted to support *D. panamensis* at densities of 0.4 tree clumps/ha and above. The map highlights the greater SJLS Corridor vicinity. Potential habitat covers about 236,568 hectares and is the result of the classification tree model. Although the potential habitat includes the Humult, Aquent and Tropept-Aquept soil suborders, 96% of the potential habitat occurs on the Humult suborder. Humult soils are soils with high organic matter content (humus) that are generally found on high ground (*tierra firme*). They belong to the Ultisol soil order. Soils belonging to this order are normally found on old land surfaces and are formed from the processes of clay mineral weathering (Brady and Weil 2002). They are low in bases and have subsurface horizons of illuvial clay accumulations.

Ultimately, the classification tree model predicts that *D. panamensis* will occur within a much narrower elevation range than a previous habitat description by Flores (1992). She stated that the elevation distribution of this species is between 20 and 1300

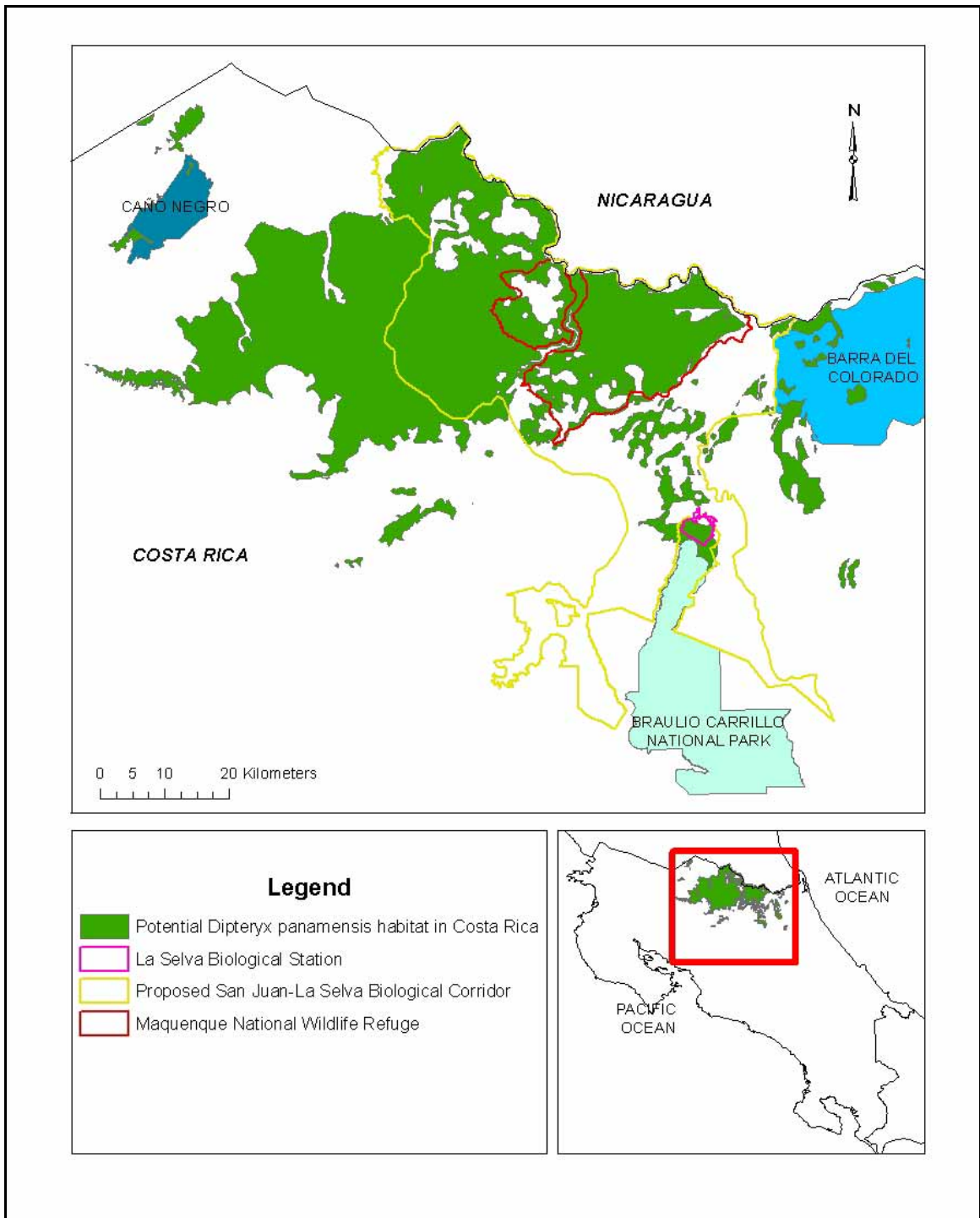


Figure 12: Potential habitat that can support *D. panamensis* > 0.4 trees/hectare

meters. This species is much more restricted to lowland habitat than previously described as it is predicted to occur between 45 and 125 meters in elevation. The soil conditions predicted to support densities of this species >0.4 tree clumps/ha generally fit prior published reports. Flores (1992) stated that this species is found on alluvial or sandy soils and sometimes in acid and clay soils. The Humult soil suborder fits this soil profile because it is derived from clay mineral weathering, is low in bases, and has a high organic content.

Elevation emerged as an important environmental predictor variable in the CART model because it likely serves as a proxy for other edaphic conditions that can support *D. panamensis*. For instance, soils between 45 and 125 meters in elevation may exhibit appropriate soil texture or drainage conditions for this species.

Based on the habitat analysis, 236,568 ha have the potential to support this species at densities over 0.4 trees/ha. This area represents less than 5% of the country. Thus, despite this species' designation as a common, generalist tree, conservation measures that prohibit its removal should be renewed and strengthened. In addition, potential habitat should be protected and/or restored.

3.4.5 Degree of fragmentation of moderate density *D. panamensis* patches

Thirteen patches with moderate *D. panamensis* densities were analyzed for whether direct pollination events could occur between trees within each discrete patch.

These 13 patches are indicated in Figure 13. These patches were derived from the *D. panamensis* density map by applying a threshold to identify density regions between 0.2 and 0.5 tree-clumps/ha. I considered patches *connected* if 2.3 km or less separated them. Patches were *fragmented* if they were separated by over 2.3 km. Basic metrics were also collected for these 13 patches including patch size and Euclidean distance to the nearest patch. Results for these metrics are summarized in Table 7. The mean patch size was 263 ha while the mean Euclidean distance was 1.52 km.

Table 7: Summary of FRAGSTATS metrics

Metric	Mean	Lowest	Highest
Patch Size	263 ha	32 ha	1843 ha
Euclidean Distance	1.52 km	0.16 km	6.15 km

The connectance index for these 13 patches was 12.1%. The connectance index is a measure of the functional joinings between patches where each pair of patches is either connected or not based on a specific distance threshold. It is reported as a percentage of the maximum possible connections given the number of patches. The distance threshold for this landscape was 2.3 km based on the longest pollen dispersal distance measured by Hanson *et al.* (2008). This connectance index indicates that of the maximum possible connections between the 13 patches, only 12.1% of the potential connections are less than 2.3 km.

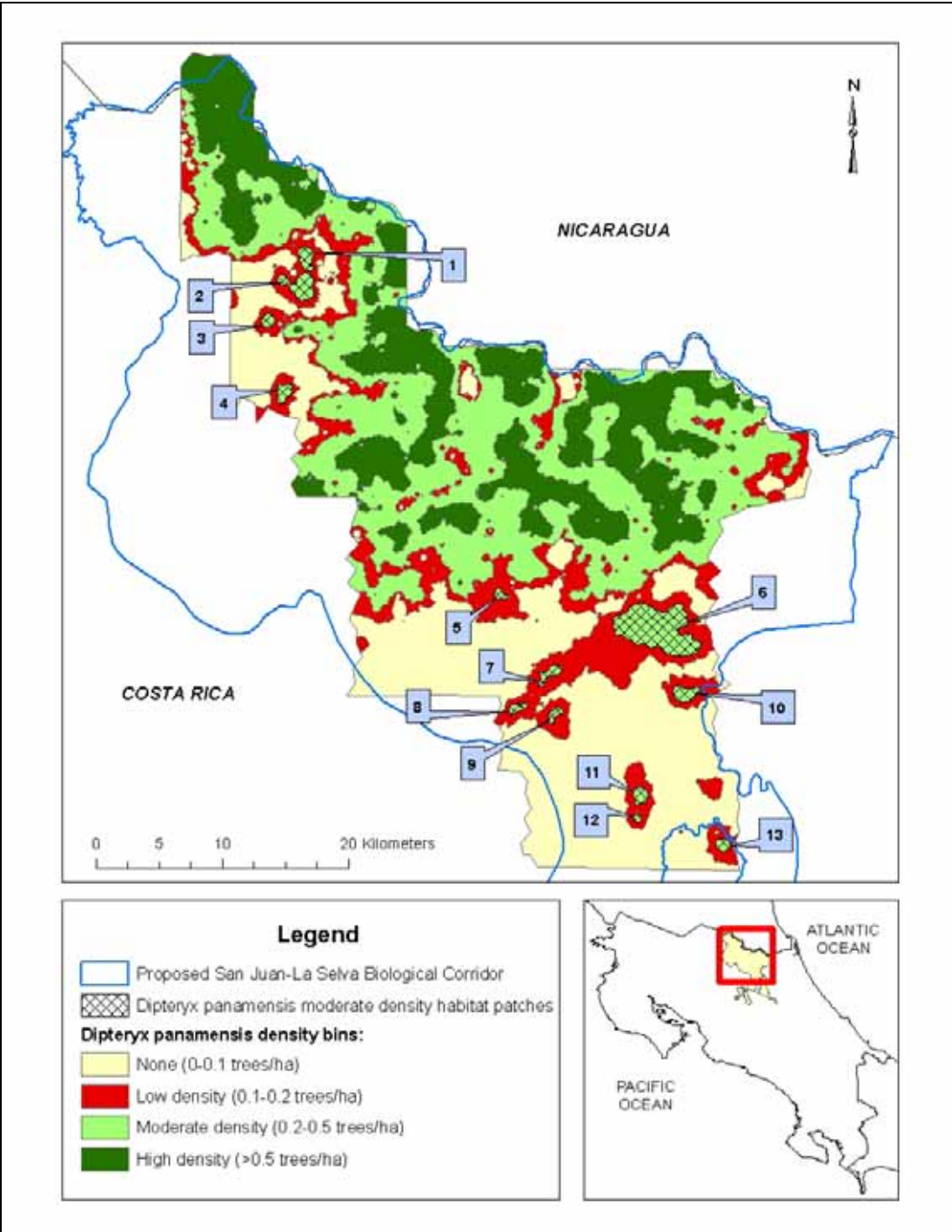


Figure 13: Distribution of 13 subpopulation patches with moderate *D. panamensis* density

Figure 14 illustrates the connectivity and fragmentation of the 13 moderate density patches based on a pollen dispersal distance of 2.3 km. Connected patches are shaded the same color. Based on this analysis, there are four separate subpopulations. It is unlikely that *direct* pollination events can occur between subpopulations of different colors. Seven of the patches (shaded dark blue) are connected to a larger habitat patch. One subpopulation (shaded light green) is located within the La Selva Biological Station. Based on the extent of this study area, direct pollination events are unlikely between this patch and the other 12 moderate density patches.

The purpose of this analysis was to gauge one aspect of fragmentation based on pollen dispersal distances across patches of *D. panamensis*. This study does not suggest that the four subpopulations are genetically isolated from each other as there are intervening *D. panamensis* trees in the low or no density regions. However, what this work implies is that there are certain moderate density patches that have direct pollen flow between patches and are hence more connected. These patches may be more disconnected to other moderate density patches that occur over 2.3 km away. Thus, trees within a linked subpopulation may be more genetically similar to each other compared to trees in patches farther afield. Based on the scope of this work, the trees located within the subpopulation at the La Selva Biological Station may be genetically more similar to each other than trees in the other subpopulations. Pollen from these trees may not be flowing to other clusters of moderate density patches.

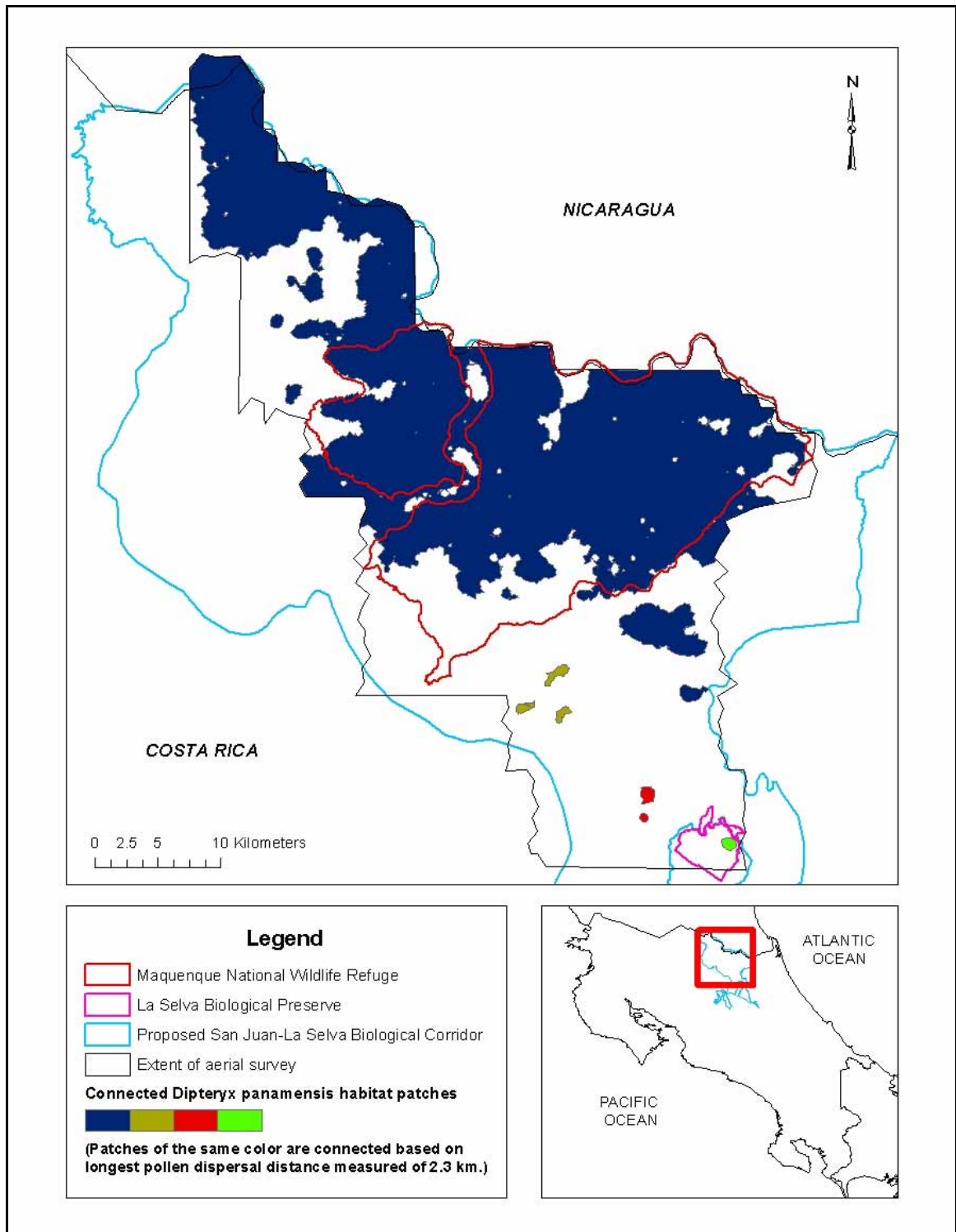


Figure 14: Connected moderate density *D. panamensis* patches

3.5 Conclusions

This study indicates that canopy-emergent *D. panamensis* trees have the potential to exist at densities approaching 2 adult trees/ha. This density is much higher than previous measurements which ranged from 0.45 trees/ha to 0.97 trees/ha (Hanson *et al.* 2006, Hanson *et al.* 2008). Elevation and soil suborder are also important conditions that predict appropriate habitat that can support *D. panamensis*. In particular, elevation may serve as a proxy for other important edaphic conditions such as drainage or soil texture. In addition, this work examines the landscape distribution of an important keystone species across 140,178 ha. Because this area lies within a proposed biological corridor, results from this work may inform the ongoing conservation endeavors.

The FOV of the digital images that were used to determine the density estimates averaged 113 ha. The FOV is analogous to the size of a very large terrestrial forest inventory plot. However, these sampling units that comprised the overall density map were much larger than most forest inventory plots in the tropics. As Clark *et al.* (2004b) stress, remote sensing provides a way to increase the size of areas sampled and improve the statistical sampling design. Because the crowns of adult *D. panamensis* often extend above the canopy, the aerial survey method also permitted the study of a species that can be difficult to track from the ground.

Because *D. panamensis* was censused during its peak blooming, the results suggest that there is a sizable reproductive population. Although a copious crown of

flowers may not necessarily translate into an abundant fruit crop, this work does indicate that dense areas may experience high reproductive output. Many animals, including the endangered Great Green Macaw, consume *D. panamensis* fruits. Thus, a healthy, reproductive population is crucial to sustain the organisms dependent on this keystone resource. However, the results of the fragmentation analysis indicate that the landscape contains some *D. panamensis* subpopulations where pollen may not be moving directly. This could affect the long-term genetic diversity of certain regions. An interesting complement to this work would be to study patterns of *D. panamensis* gene flow through seed dispersal. Patterns of seed dispersal could provide another glimpse of habitat fragmentation based on movement of seeds by mammalian seed dispersers as well as recruitment of seedlings. This work could elucidate new habitat opportunities for the Great Green Macaw.

Finally, this work suggests that similarly dense regions of *D. panamensis* exist across Costa Rica's border. The highest densities of this species were located in the northern part of the aerial survey right at the border with Nicaragua's Indio-Maíz Biological Reserve (Figure 15). This region likely has similar, high densities of *D. panamensis* but distributed over a much larger geographic area. Indio-Maíz Biological Reserve is one of Nicaragua's largest protected areas covering 264,000 ha. Despite the fact that many local inhabitants still extract natural resources here due to the country's tumultuous history, this reserve is one of the largest remaining stands of primary rain

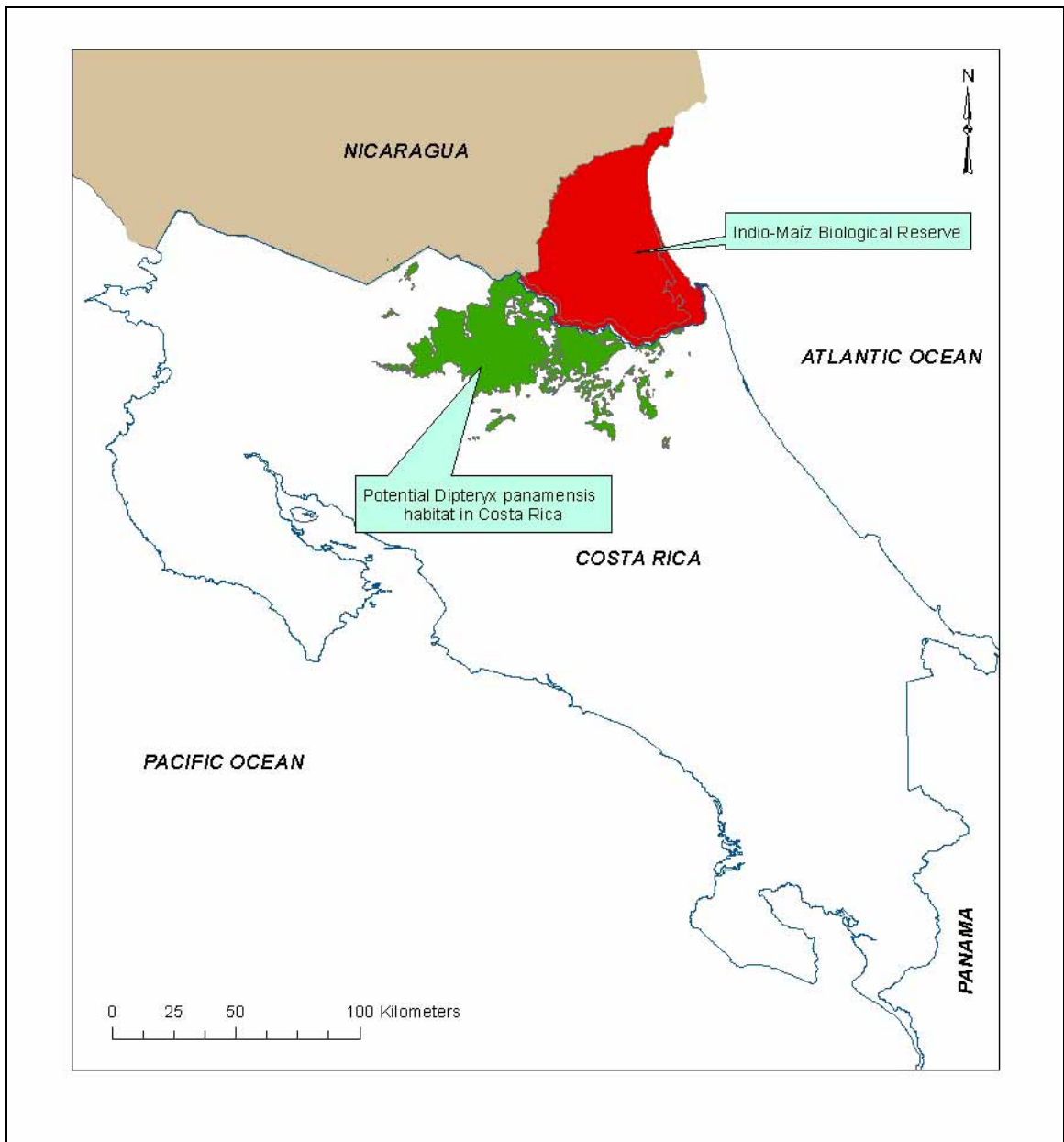


Figure 15: Location of Indio-Maíz Biological Reserve, Nicaragua in relation to potential *D. panamensis* habitat in Costa Rica

forest in all of Central America (Nygren 2004). Thus, the Indio-Maíz Biological Reserve is an important piece in the larger landscape. Subsequent research on *D. panamensis* should occur in the Indio-Maíz Biological Reserve in order to extend the biogeographic study of this species. In addition, future conservation efforts should promote multinational partnerships that protect biodiversity spanning both countries.

Chapter 4. Determination and description of potential nesting habitat for the Great Green Macaw (*Ara ambigua*) in northern Costa Rica using a classification and regression tree model

4.1 Introduction

The Great Green Macaw (*Ara ambigua*) is the second largest New World macaw and one of only two macaw species native to Costa Rica. Because this species is threatened by habitat loss and degradation, nest-robbing and trapping for the international bird trade¹, as well as persecution via hunting (Guedes 2004), the Great Green Macaw is listed as endangered on the International Union for Conservation of Nature's (IUCN) Red List (EN A2cd+3cd) (BirdLife International 2005). In addition, the Convention on International Trade in Endangered Species of Wild Fauna and Flora has designated the Great Green Macaw as an Appendix I species (CITES 2008). Appendix I species are threatened with extinction, and all international trade in commercial specimens is prohibited.

In northeastern Costa Rica, Powell *et al.* (1999) estimate that only 35 Great Green Macaw breeding pairs and 200 individuals remain. A follow-up to this study suggests that the overall population may have expanded slightly to 250 individuals (Vargas M. 2008). While habitat fragmentation and degradation are affecting the persistence of this

¹ Great Green Macaw nestlings have fetched \$300 apiece in Costa Rica (Bjork and Powell 1999).

species in Costa Rica, scientists contend that the loss of breeding habitat and removal of its nesting trees are having the greatest impact on this species (Powell *et al.* 1999). Like most other macaw species, the Great Green Macaw is a secondary cavity nester. Breeding pairs rely on large hollows in mature trees to lay eggs and raise their young. In particular, Great Green Macaw breeding pairs have an affinity for one particular tree species. A census of Great Green Macaw nests that occurred between 1994 and 2003 identified that nearly 90% were located in large *Dipteryx panamensis* trees (Powell *et al.* 1999, Chassot *et al.* 2002). Not only is this tree species important as a nesting substrate for the Great Green Macaw, but its fruits are an important food resource throughout the breeding season. Although *D. panamensis* is a relatively common, canopy-emergent species within the lowland Atlantic forest of Costa Rica, it has been logged extensively in the past.

The creation of Maquenque National Wildlife Refuge (MNWR) in 2005 represents a positive first step in the protection of potential nesting and breeding habitat for the Great Green Macaw in northern Costa Rica (Figure 2). This region was targeted because it contains several large nesting trees used by Great Green Macaw breeding pairs. In addition, MNWR protects foraging habitat that may be critical during the Great Green Macaw's breeding season. MNWR is also embedded within the larger San Juan-La Selva (SJLS) Biological Corridor effort that aims to connect protected areas in southern Nicaragua to those in central Costa Rica (Chapter 1).

4.1.1 Objectives

To complement this conservation project, I conducted research to further elucidate the ecology of the Great Green Macaw's nesting and breeding habitat. I utilized the results of an aerial survey that I performed in 2005 documenting the distribution and density of *D. panamensis* trees across 140,178 ha in northern Costa Rica (Chapters 2 and 3). I synthesized the biogeographic distribution of *D. panamensis* with the locations of known nesting trees used by the Great Green Macaw in order to assess the quantity and quality of nesting habitat for this species. In particular, I addressed the following questions:

1. What environmental factors predict optimal Great Green Macaw nesting habitat?
2. Based on these environmental factors, how much potential habitat exists within northern Costa Rica?
3. What areas should be targeted as conservation priorities?

4.2 Background

4.2.1 General description and ecology of the Great Green Macaw in Costa Rica

The Great Green Macaw belongs to the family *Psittacidae*. It is one of 17 species of macaws, of which one is extinct, another is extinct in the wild, and seven other species are endangered (Texas A&M University 2006). In general, macaws are characterized by

a long tail, large beak, and bare facial patch (Abramson 1999). Adult Great Green Macaws are mostly yellowish-green with a scarlet forehead. This species approaches 31 inches in length and can weigh up to 1.3 kg (Stiles and Skutch 1989). The Great Green Macaw occurs as two sub-species. The nominate race occurs in humid, lowland forests of the Atlantic/Caribbean lowlands of eastern Honduras, Nicaragua, and Costa Rica, both slopes of Panama, and in northwestern Colombia; the race *guayaquilensis* occurs on the Pacific slopes of Western Ecuador (Snyder *et al.* 2000, BirdLife International 2005). According to Snyder *et al.* (2000), the Central American populations are restricted to four isolated subpopulations that are confined to lowland Atlantic forest. The subpopulation that is the focus of this chapter occurs from southeastern Nicaragua to northeastern Costa Rica. (Hereinafter, I will use *population* to refer to the Costa Rican portion of the Nicaraguan/Costa Rican subpopulation.)

Until recently, very little was known about the Great Green Macaw's food, nesting, and habitat requirements. As of 1989, its nest was still undescribed (Stiles and Skutch 1989). One of the first extensive examinations of ecological, behavioral, and demographic dynamics of Costa Rica's Great Green Macaw population was initiated in 1994 by the Great Green Macaw Research and Conservation Project, which is now affiliated with the Centro Científico Tropical (CCT) in San José, Costa Rica. This research by Powell *et al.* (1999) comprised radio-telemetry efforts to determine Great Green Macaw home ranges, monitoring and data collection on all known nest sites, and

phenological studies of tree species that constituted its diet. During the study period, Powell *et al.* (1999) estimated that Costa Rica's population of Great Green Macaw averaged around 200 individuals with no more than 35 reproductively active pairs. A follow-up to this study was conducted in 2008, and it indicated that the overall population may have increased to 250 Great Green Macaw individuals (Vargas M. 2008). In northern Costa Rica, the breeding range has shrunk by 90% and is restricted to about 1,120 km². This area abuts southern Nicaragua and the San Juan River to the north and is bordered by the Sarapiquí and San Carlos Rivers to the east and west, respectively. In 2005, part of this region was decreed MNWR.

The Great Green Macaw is dependent on *D. panamensis* trees for food and nesting. As secondary cavity nesters, Great Green Macaw breeding pairs select large *D. panamensis* trees with hollows in order to construct nests. This tree is subject to numerous threats that may cascade and affect the Great Green Macaw's long-term viability (Chapter 3). The scarcity of natural nest sites may be one of the major factors limiting the number of adult macaws—including the Great Green—that can reproduce during a breeding season (Munn 1992). Cavities take a long time to form since the process is initiated by decomposition when water or moisture enters the wood, drains down the inside of the trunk or branch, and empties out of the tree through fissures and cracks (Mawson and Long 1994). While macaws will clean and maintain cavities, they do not form them on their own, hence the designation as secondary cavity nesters.

Because macaws may use the same nesting tree year after year, the removal of a single nesting tree represents a reduction in reproductive output over the life of the tree, since hundreds of macaw chicks may be reared from a single tree during its lifetime (Brightsmith 2005). In addition, the fact that most wild macaw species have a naturally low reproductive rate only compounds these anthropogenic threats and underscores the importance of identifying and protecting their nesting and breeding habitat (Nycander *et al.* 1999).

Between 1994 and 2002, 66 active Great Green Macaw nests located in northern Costa Rica were tracked by CCT scientists. Of these, 57 (86%) were located in large *D. panamensis* trees (Powell *et al.* 1999, Chassot *et al.* 2002). The remaining nests were located in large trees of the following species: *Carapa nicaraguensis*, *Goethalsia meiantha*, and *Vochysia ferruginea* (Powell *et al.* 1999). In northern Costa Rica, nesting occurs between December and June with egg-laying occurring in late January. Nests contain eggs in January or February and nestlings between February and April. Most chicks fledge by late April.

The Great Green Macaw closely tracks fruit production of a variety of tree species and may forage on fruit from over 30 species as they move between Costa Rica's lowlands and higher volcanic regions. Great Green Macaws consume *D. panamensis* fruit from about September to April (Chapter 3). During peak *D. panamensis* fruit production in January, this resource may account for 85% of the Great Green Macaw's

diet (Powell *et al.* 1999). January is also a crucial time in the Great Green Macaw's reproductive cycle as this month coincides with its egg-laying period and precedes hatching and nestling development. Around June, the birds disperse from lowland, Atlantic forests to higher elevations of Costa Rica's volcanic ranges and drier forests in Nicaragua. This seasonal migration correlates with the cessation of fruiting for *D. panamensis*, and the birds are likely searching for alternative food sources at higher elevations. Between April and August when *D. panamensis* fruit are scarce, Great Green Macaws will switch to fruit from *Sacoglottis trichogyna*. Powell *et al.* (1999) reported that *D. panamensis* and *S. trichogyna* accounted for between 65% and 95% of foraging trees between October and July. A study of Great Green Macaws in Ecuador also noted this population's seasonal movements coupled with changes in food availability (Berg *et al.* 2007).

4.3 Materials and methods

4.3.1 Determination of Great Green Macaw nesting habitat

Snyder *et al.* (2000) conjectured that it is the loss of the large nesting trees, specifically *D. panamensis* in Costa Rica that may jeopardize the long-term viability of this species. Results from work that I conducted regarding the distribution of *D. panamensis* density across 140,178 ha in northern Costa Rica indicate that this tree species still exists in relatively high densities (Chapter 3). Reproductive, adult *D. panamensis* can

reach densities as high as 2 trees/ha. Nearly 20% of the land surveyed exhibits densities of 0.5 trees/ha and higher, and over 50% exhibits densities of 0.2 trees/ha and higher. However, an analysis of landscape connectivity and fragmentation indicated that moderate density patches of *D. panamensis* exhibit a very small average patch size. Direct pollen flow may also be lacking between these patches as they are separated by distances greater than the maximum pollen dispersal distance measured for this species (Chapter 3).

Because the quantity and quality of nesting habitat is critical for the Great Green Macaw, I investigated whether there are environmental factors that predict optimal Great Green Macaw nesting habitat, how much potential habitat exists within northern Costa Rica, and if there are any habitat patches that should be prioritized for conservation. To address these points, I developed a habitat model to identify critical habitat variables that predict optimal Great Green Macaw nesting habitat. I then used these variables as well as existing GIS base layers in order to create a map of potential GGM nesting habitat. This work occurred in the vicinity of MNWR within the proposed SJLS Corridor.

4.3.2 Existing Great Green Macaw nesting data

I used data documenting the locations of existing Great Green Macaw nest sites and information regarding habitat requirements during the breeding season. These data were collected as part of a larger effort by the CCT to detail the Great Green Macaw's

ecology (Powell *et al.* 1999). Based on telemetry studies, CCT scientists identified that breeding pairs utilize a home range of 550 ha on average. This territory does not overlap with the breeding habitat of other pairs. In addition, CCT researchers identified active Great Green Macaw nests as well as formerly active nests that had been cut. Nests were located based on extensive field surveys and interviews with local residents, and the nest locations were then recorded using a GPS. These data are maintained as a GIS point file, which I used in my analyses. CCT scientists identified 66 trees that the Great Green Macaw had used from 1994 to 2003 as nesting sites. Nest sites were not always active in consecutive years because nesting pairs often skip a nest site that had been active the previous breeding season. Of the 66 sites identified, 57 (86%) were located in large *D. panamensis* trees (Chassot *et al.* 2002). Because of data availability, I utilized the locations of 51 nest sites that had been identified from 1994-2003. Of these 51 nest sites, 10 trees had been cut by the end of the survey period. In some cases, the nests had been cut deliberately even after the tree had been protected and demarcated as a nesting tree. In these instances, it is likely that the Great Green Macaw chicks were being targeted. In other cases, some nest trees had been removed unwittingly.

4.3.3 Development of Great Green Macaw nesting habitat model: a classification tree approach

I used environmental variables that are important components in delineating Great Green Macaw nesting habitat. These environmental variables were contained in

GIS raster data that covered the project area. All GIS data were projected to WGS 1984 UTM Zone 16N, and raster data had the same grid cell size of 30 m.

I modeled potential Great Green Macaw nesting habitat by using a Classification and Regression Tree (CART) approach (Chapter 3). The CART analysis was performed in the R Statistical Program using the “tree” package (R Development Core Team 2008). For background on CART models, please see Chapter 3. I considered the locations of the Great Green Macaw nest sites as *presences*. I intersected the presence points with the raster surfaces for each environmental variable in order to extract the underlying data values and create a spreadsheet with the resulting data values. Because five of the original 51 nest points fell outside of the extent of the environmental layers, I removed these points from my analysis. Thus, the 46 nests represented presences.

In order to create a complementary portrait of the landscape as a whole, I generated 50 points and randomly arrayed them spatially across the project area. The random points were at least 1 km away from each other in distance, and they were restricted from a 550 ha buffer around each of the nest points, which corresponded to the breeding territory of a Great Green Macaw pair. Ultimately, one of the random points fell outside the extent of the environmental layers resulting in 49 points. These 49 points reflect average *background* conditions across the project area. Similar to the presence points, I intersected the background points with the raster surfaces for each environmental variable in order to extract the underlying data values and create a

spreadsheet with the resulting background values. The *presence* and *background* points represented the response variable in the CART model. Because the response variable was categorical, the model was run as a classification tree. I evaluated several classification tree models that included various combinations of the environmental predictor variables. Predictor variables that did not produce a logical split in the classification tree were removed from consideration. A description of the response and predictor variables appears in Table 8.

Table 8: Response and predictor variables used in the CART model to predict potential Great Green Macaw habitat

Name	Description	Variable Type
<i>Response variable:</i>		
NEST_PRESENCE	This file represented either point locations of known Great Green Macaw nest locations or random points representing habitat “background”.	Categorical
<i>Predictor variable:</i>		
DENSITY	Raster surface depicting <i>D. panamensis</i> density distribution throughout the project area.	Continuous
DENS_550HA	Mean <i>D. panamensis</i> density within a 550 ha buffer. <i>D. panamensis</i> density was characterized in this way because Great Green Macaw breeding pairs utilize 550 ha of non-overlapping territory during the breeding season to forage.	Continuous
FOREST_COV	Mean forest cover within a 100 ha region ranging from no forest cover (0) to high forest cover (1).	Continuous
LANDUSE	Land use type: forest cover, deforested, no forest, or water.	Categorical
RIVERS_DIST	This raster surface represented the distance to the nearest river.	Continuous
ROADS_DIST	This raster surface represented the distance to the nearest road.	Continuous
ELEV	Elevation of the terrain.	Continuous

4.4 Results and discussion

4.4.1 Classification tree model

The final classification tree included two environmental predictor variables (DENS_550HA and ELEV) and was calibrated with 11 terminal nodes. This classification tree was pruned based on “misclassification” and produced a final classification tree containing three terminal nodes. A confusion matrix was constructed to determine the classification success in assigning group membership of the “presence” samples. The classification success for this group was 91%. Thus, only 4 of the 46 known nest “presence” points did not occur in areas satisfied by environmental conditions predicted by the CART model.

4.4.2 Environmental conditions predicting Great Green Macaw habitat

Results from the classification tree model indicate that Great Green Macaw pairs nest in habitat where adult, reproductive *D. panamensis* trees occur in densities of 0.2 trees/ha or greater within a 550 ha buffer around the nesting tree and where the ground elevation is less than 132 meters. *D. panamensis* density within the breeding territory is the most important environmental condition predicting potential Great Green Macaw nesting habitat. If this condition is satisfied, then the overall quality of the surrounding forest is insignificant. Thus, if the mean density of adult, reproductive *D. panamensis* trees meets or exceeds 0.2 trees/ha, Great Green Macaw pairs may nest in habitat with a

range of forest cover. Results from the classification tree indicate that there is no relationship between the distance of nesting trees to rivers or roads.

The results of this study underscore the importance of large, reproductive *D. panamensis* trees in delineating potential Great Green Macaw nesting habitat. Breeding habitat occurs in lowland areas (<132 m) where *D. panamensis* trees grow at densities that meet or exceed 0.2 trees/ha within the 550-ha breeding territory. *D. panamensis* trees are a critical resource for this bird during all phases of the breeding season—from the time it selects a nesting tree in late December to when juveniles fledge in June. Nearly 90% of all Great Green Macaw nests identified in northern Costa Rica are located within hollowed cavities of large *D. panamensis* trees. Results of the habitat analysis suggest that Great Green Macaw pairs select nesting trees that are surrounded by relatively dense stands of reproductive *D. panamensis* trees. *D. panamensis* fruit likely sustain the adults, chicks, nestlings, and fledglings over the course of the breeding season. Fortuitously, the Great Green Macaw breeding season coincides with the peak production of *D. panamensis* fruit. During the nest-building period in late December, adults are likely foraging for food in the vicinity of the nest tree. Once the eggs are laid, the female remains on the nest while the male forages within the breeding territory; when nestling are present, both parents will forage for food (Powell *et al.* 1999). Because breeding Great Green Macaw pairs will utilize a 550-ha swathe of forest around the nest

tree in order to forage for food, the quality and quantity of *D. panamensis* trees in the vicinity are crucial.

4.4.3 Location of potential Great Green Macaw nesting habitat

Figure 16 shows the distribution of potential Great Green Macaw nesting habitat within the lowland Atlantic rain forest of northern Costa Rica. Approximately 67,271 ha of potential Great Green Macaw nesting habitat exists within the northern reaches of the study area. Assuming that Great Green Macaw breeding pairs require 550 ha of non-overlapping habitat during the breeding habitat, northern Costa Rica could support about 120 breeding macaw pairs. It is estimated that only 35 breeding pairs currently utilize this area (Powell *et al.* 1999). The “holes” in the map, where non-habitat occurs within predicted nesting habitat, are regions that generally occur above the elevation threshold predicted by the CART model. Many of these regions do meet the criteria for *D. panamensis* density within the breeding territory. While these regions would most likely be able to support Great Green Macaw nests, these regions were excluded from predicted habitat since the CART model was influenced by the locations of the known nest trees. These trees generally occurred in lowland areas.

The habitat analysis did not identify forest cover as a primary indicator of Great Green Macaw habitat. This study suggests that as long as adequate *D. panamensis* stands exist within the breeding territory, Great Green Macaw may be willing to nest within a

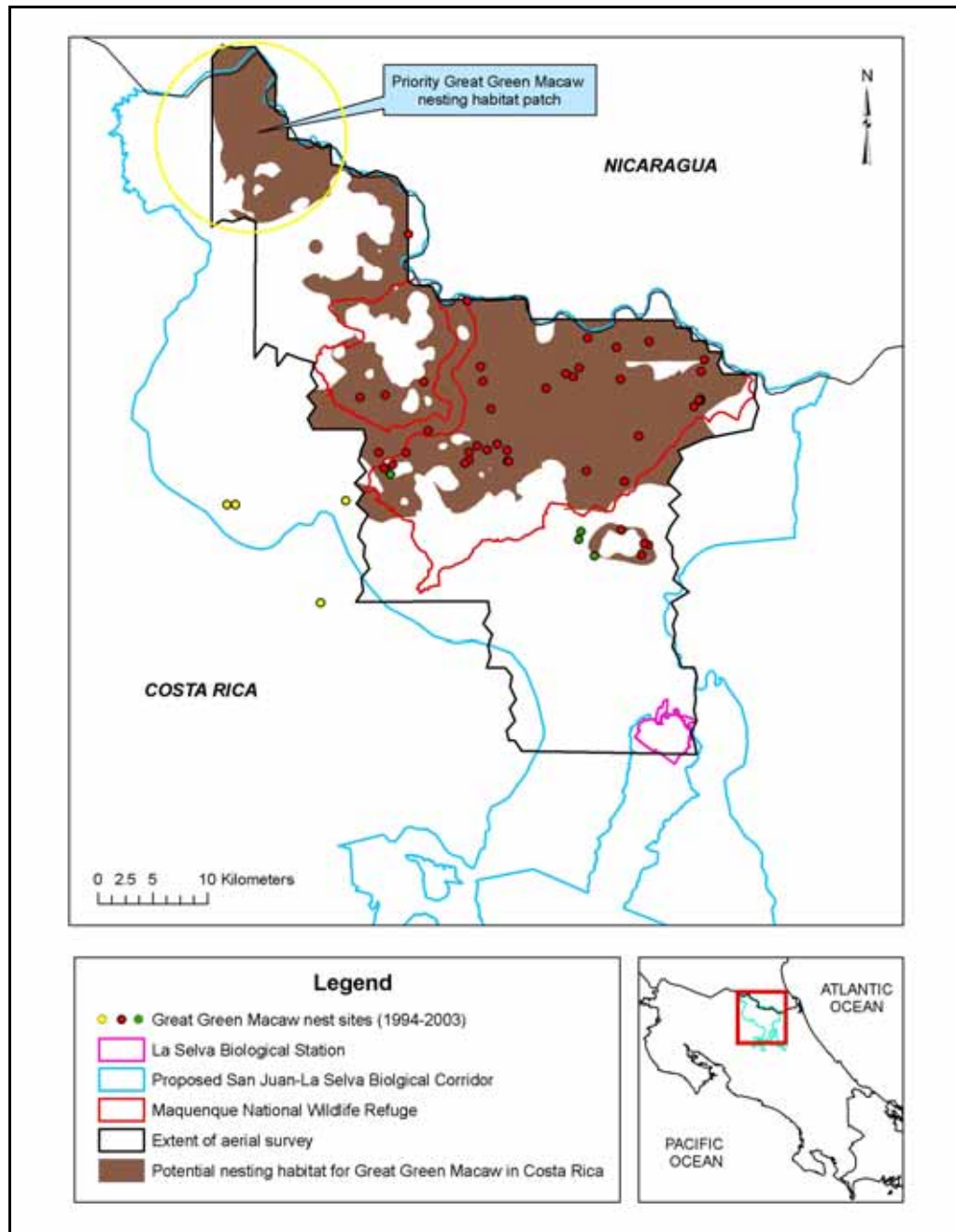


Figure 16: Potential Great Green Macaw nesting habitat within Costa Rica

Yellow nest sites were excluded from the CART model since they fell outside of the study area. Green nest sites did not occur in areas predicted by the CART model to be potential Great Green Macaw nesting habitat. The area circled in yellow was identified as a conservation priority as it contains the highest densities of *D. panamensis*.

mosaic of landscapes such as pastures, forest fragments, or secondary forests. Of course, relatively dense stands of *D. panamensis* are likely correlated with forest cover, and of the 67,271 ha of potential Great Green Macaw nesting habitat identified, nearly 76% occurs in areas with forest cover greater than 50%. However, the possibility that Great Green Macaw may nest in areas of varying forest cover may represent an opportunity for those working to expand Costa Rica's Great Green Macaw population. In fact, Bjork and Powell (1999) noted that several Great Green Macaw nesting trees were located in cattle pastures.

4.5 Conclusions

The landscape within the lowland Atlantic forests of northeastern Costa Rica represents a patchwork of primary forest surrounded by a network of pastures, agricultural zones, and regenerating forests. This network of multiple land uses is a reminder of a time when Costa Rica had one of the highest deforestation rates, averaging around 3.7% from the early 1970s to the early 1990s (Sanchez-Azofeifa *et al.* 2003). However, many ecologists suggest that tropical forest restoration may undo some of the damage done by prior anthropogenic degradation (Lamb *et al.* 2005, Chazdon 2008). Targeted restoration of *D. panamensis* trees within abandoned pasture may jumpstart the recovery of land that is currently not viable for Great Green Macaw nesting or foraging. Such actions may ensure the long-term presence and viability of this species within Costa Rica's forests.

However, while targeted habitat restoration and forest regeneration may represent one solution to maintaining Costa Rica's Great Green Macaw population, habitat protection must be the first step, and existing nesting trees should be safeguarded. In fact, a recent decision by Costa Rica's 4th Chamber of the Supreme Court on September 16, 2008 states that MINAE must abstain from the continuation or initiation of the use, exploitation, or extraction of *D. panamensis* (Fallas 2007) (Appendix C). This is a very positive development.

Understanding what environmental conditions predict potential Great Green Macaw habitat is also essential in developing or fine-tuning any conservation program for this species. MNWR was established in 2005, and one of its primary purposes is to protect breeding habitat for the Great Green Macaw in Costa Rica. Approximately 43,700 ha of land identified as potential Great Green Macaw breeding habitat lies within the boundaries of MNWR. This covers nearly 75% of the new wildlife refuge. However, an important region of potential breeding habitat that is currently unprotected is located in the northwestern part of the study area (Figure 16). My selection of this patch as a conservation priority is based on the following criteria. Not only does this area meet the minimum requirements of *D. panamensis* density within a 550-ha breeding territory, but this zone possesses some of the highest measured densities of adult *D. panamensis* trees on record of nearly 2 adult trees/ha (Chapter 3). Thus, I am basing my recommendation on the extent of *D. panamensis* density in this region. In addition, I do not believe that

surveys have been conducted in this region for Great Green Macaw nests. This region would benefit from extensive ground studies of this bird species. Future efforts to preserve Great Green Macaw breeding habitat need to prioritize this habitat patch. At the very least, the logging moratorium against removing large *D. panamensis* trees should be strictly enforced in this area.

Despite emerging information about the Great Green Macaw's breeding habitat and current conservation efforts to preserve habitat, Costa Rica's population of Great Green Macaw may never reach the potential of 120 breeding pairs predicted here. Habitat fragmentation and other anthropogenic threats may simply be too widespread. Although this research indicates that there is more than enough foraging habitat during the breeding season because *D. panamensis* densities are high, the number of suitable nesting trees may be limited. Even with adequate food during the breeding season as represented by high densities of reproductive *D. panamensis* trees, it is the scarcity of natural nest sites that may be limiting the number of adult Great Green Macaws that reproduce annually (Munn 1992).

While Costa Rica's Great Green Macaw may remain on the brink, a note of hope lies across the San Juan River and over the border in Nicaragua. The Indio-Maíz Biological Reserve is located just across Costa Rica's northeastern border (Figure 17). It comprises nearly 264,000 ha of lowland Atlantic forest, the same type of forest where Great Green Macaw pairs breed in Costa Rica. Because of Nicaragua's recent political

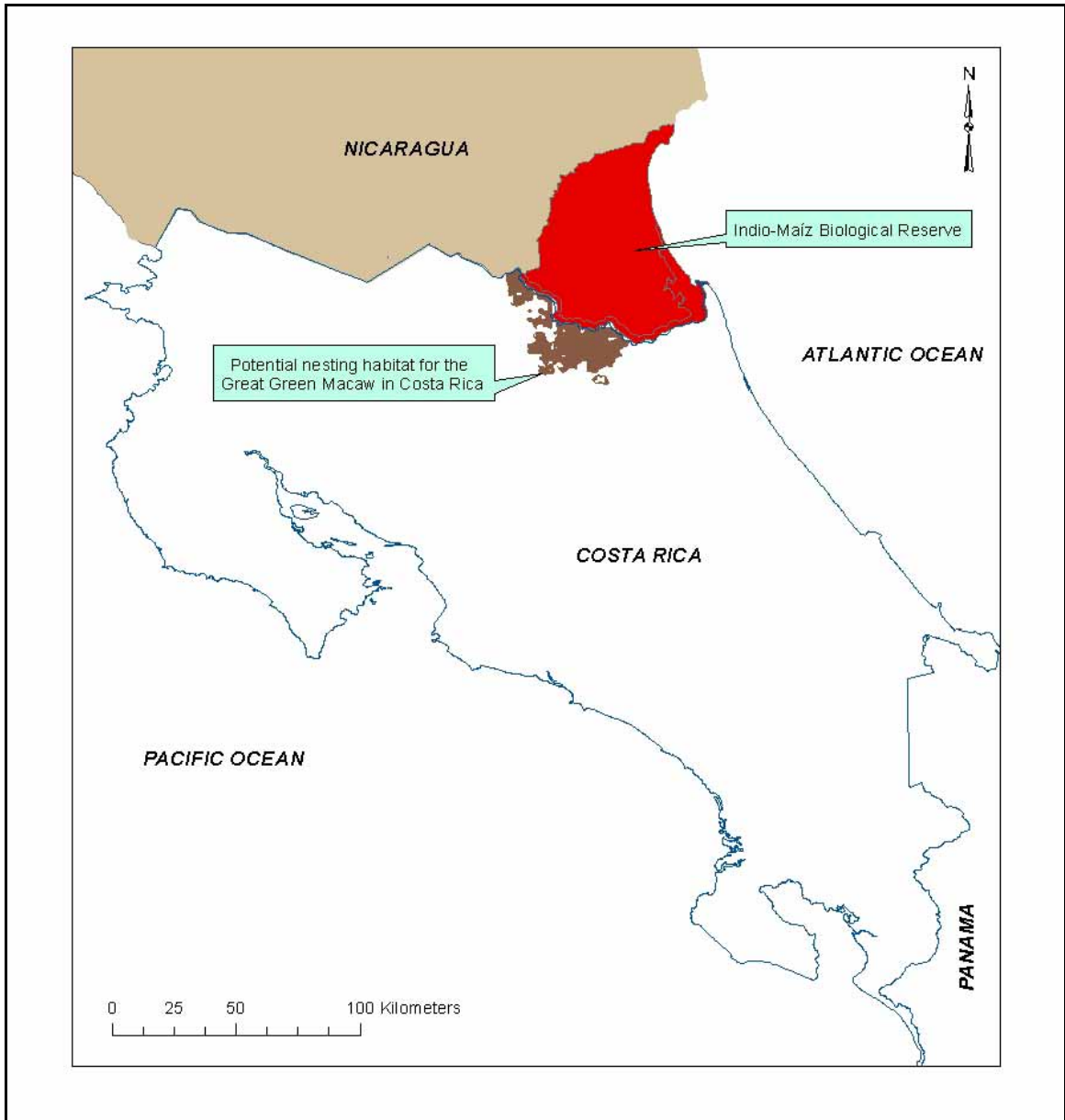


Figure 17: Location of Indio-Maíz Biological Reserve, Nicaragua in relation to potential Great Green Macaw nesting habitat in Costa Rica

history, much of the Indio-Maíz Biological Reserve remains intact and unlogged. While extensive field surveys of Great Green Macaw in Nicaragua remain scarce, it is estimated that the Nicaraguan population is nearly ten times the size of the population south of the border and that the Costa Rican population is merely a subpopulation of the much larger Nicaraguan population (Powell *et al.* 1999). Most likely, the Indio-Maíz Biological Reserve contains extensive forest swathes with extremely high densities of *D. panamensis* trees only seen in a few patches in northern Costa Rica. Likely, many areas exceed the minimum Great Green Macaw nesting requirement of 0.2 trees/ha within the breeding territory. Thus, to maintain the Great Green Macaw within Costa Rica, ongoing efforts to protect the habitat in Nicaragua need to be funded. In addition, the level of research that has been conducted in Costa Rica should be extended north. For example, known nesting trees should be identified and protected and the breeding population should be more accurately censused. If appropriate GIS and remote sensing data exist, a similar study could be initiated to identify potential Great Green Macaw nesting habitat in the Indio-Maíz Biological Reserve based on the parameters from the present work.

Chapter 5. General conclusions

This dissertation provides new insights into the utility of digital aerial surveys in censusing an ecologically and economically important tropical tree species across a large spatial extent. I demonstrate that digital aerial surveys can be timed to capture the unique blooming pattern for the canopy-emergent tree, *Dipteryx panamensis*. In particular, I developed a semi-automated, pattern recognition technique that capitalized on the distinct spectral signature of blooming *D. panamensis* trees. Specifically, the alternate color space, IHS (intensity, hue, and saturation), enhanced the images and enabled *D. panamensis* to be identifiable by the computer classifier. The aerial survey occurred in Costa Rica over a portion of two new protected areas—the proposed San Juan-La Selva Biological Corridor and Maquenque National Wildlife Refuge. It covered over 140,000 ha. Results of this work suggest that digital aerial surveys may provide a cost effective and efficient approach to studying tropical landscapes that may be dangerous or challenging to enter on the ground. This approach is especially effective in studying the distribution of large, canopy-emergent tree species, like *D. panamensis*, which are often difficult to study from the ground. In addition, digital aerial surveys may augment the size of traditional forest inventory plots. Due to biases in placement, terrestrial plots often misrepresent the abundance or density of large, infrequently distributed trees.

Besides testing a novel remote sensing technique, this dissertation also examined the landscape distribution and conservation implications of *D. panamensis*. I created a raster surface depicting the density of *D. panamensis* across the entire aerial survey extent using the output from the digital photographs. This work provided basic, ecological information regarding *D. panamensis*, and indicated that reproductive, canopy-emergent trees can exist in densities as high as 2 adult trees/ha. An analysis of the environmental conditions that can support *D. panamensis* showed that this tree species is restricted to regions between 45 and 125 meters in elevation on soil with an acid and clay profile.

Finally, the distributional work on *D. panamensis* provided the basis for an analysis on the environmental factors that predict nesting habitat for the endangered Great Green Macaw (*Ara ambigua*). Because *D. panamensis* is a critical food and nesting resource for the Great Green Macaw, this dissertation highlighted important conservation implications and priorities for both *D. panamensis* and the Great Green Macaw. Results from this dissertation underscored that Great Green Macaw breeding pairs nest in habitat where adult, reproductive *D. panamensis* trees occur in densities of 0.2 trees/ha or greater within a 550 ha buffer around the nesting tree.

Ultimately, the future of the Great Green Macaw may rely on the conservation of the Indio-Maíz Biological Reserve in Nicaragua. This protected area is one of the largest remaining stands of primary rain forest in Central America. It is likely that *D. panamensis* occurs in high densities in Nicaragua similar to or greater than those

identified in Costa Rica. In addition, Costa Rica's population of Great Green Macaw, which numbers only around 250 individuals, is likely a mere subpopulation of the larger population that exists over the border in Nicaragua. Subsequent research and conservation efforts of both *D. panamensis* and the Great Green Macaw in Costa Rica should include a bi-national partnership with Nicaragua. Such a visionary collaboration may ensure the survival of the Great Green Macaw for many more generations!

**Appendix A: Newspaper article published in *La Nación*
describing “suspicious” overflights**

BOCA SAN CARLOS

Vecinos reportan otro vuelo sospechoso en la zona norte

Carlos Hernández

Corresponsal de La Nación

CIUDAD QUESADA. - En los últimos tres días una aeronave sin matrícula sobrevoló el caserío de Boca San Carlos, en la margen tica del río San Juan, según vecinos del lugar.

Esta vez se trató de una avioneta blanca, cuyo último vuelo fue ayer cerca de las 9:30 a. m., el cual coinci-

dió con el paso por el río de una embarcación nicaragüense, dijeron.

Los vecinos precisaron que el aparato pasó sobre el cauce del río, recorrió la reserva biológica nicaragüense Indio Maíz y se enrumbo hacia Sarapiquí. Para la Policía tica, la presencia de avionetas sospechosas por ese sector podría tener relación con el narcotráfico. ■

I had the dubious distinction of having my aerial survey work written up in the July 7, 2005 issue of Costa Rica's national newspaper, La Nación (Hernández 2005). While the aerial surveys were conducted for research purposes, the last sentence of this article suggests an alternative purpose of the overflights!

Appendix B: Results of the signature separability matrix

Results of the Signature Separability matrix*

Training Sample Names	Black_1	Black_2	Black_3	Vegetation_1	Vegetation_2	Vegetation_3	Vegetation_4
Black_1	0						
Black_2	977	0					
Black_3	1443	290	0				
Vegetation_1	2000	2000	2000	0			
Vegetation_2	2000	2000	2000	1073	0		
Vegetation_3	2000	2000	2000	2000	2000	0	
Vegetation_4	2000	2000	2000	2000	2000	1960	0
Vegetation_5	2000	2000	2000	2000	2000	719	1644
Vegetation_6	2000	2000	2000	2000	2000	593	1989
Vegetation_7	2000	2000	2000	2000	2000	1785	425
Vegetation_8	2000	2000	2000	2000	2000	2000	2000
Vegetation_9	2000	2000	2000	2000	2000	1752	1547
Dipteryx panamensis_1	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_2	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_3	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_4	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_5	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_6	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_7	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_8	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_9	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_10	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_11	2000	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_12	2000	2000	2000	2000	2000	2000	2000
Water_1	2000	2000	2000	2000	1999	2000	2000
Water_2	2000	2000	2000	2000	2000	2000	2000
Bare_Ground_1	2000	2000	2000	2000	2000	2000	2000
Bare_Ground_2	2000	2000	2000	2000	2000	2000	2000
Road_1	2000	2000	2000	2000	2000	2000	2000
Road_2	2000	2000	2000	2000	2000	2000	2000
Pasture_1	2000	2000	2000	2000	2000	1130	1993
Pasture_2	2000	2000	2000	2000	2000	2000	2000
Pasture_3	2000	2000	2000	2000	2000	1921	2000
Bare_Ground_3	2000	2000	2000	2000	2000	2000	2000
Road_3	2000	2000	2000	2000	2000	2000	2000

*Numbers after the name indicate that multiple training samples were collected to describe a training class. Training samples are distinct if values are greater than 1,500.

Results of the Signature Separability matrix, cont.

Names of Training Classes	Vegetation_5	Vegetation_6	Vegetation_7	Vegetation_8	Vegetation_9	Dipteryx panamensis_1
Black_1						
Black_2						
Black_3						
Vegetation_1						
Vegetation_2						
Vegetation_3						
Vegetation_4						
Vegetation_5	0					
Vegetation_6	1408	0				
Vegetation_7	1005	1938				
Vegetation_8	2000	2000	2000	0		
Vegetation_9	1035	1956	943	2000	0	
Dipteryx panamensis_1	2000	2000	2000	2000	2000	0
Dipteryx panamensis_2	2000	2000	2000	2000	2000	664
Dipteryx panamensis_3	2000	2000	2000	2000	2000	1870
Dipteryx panamensis_4	2000	2000	2000	2000	2000	1835
Dipteryx panamensis_5	2000	2000	2000	2000	2000	640
Dipteryx panamensis_6	2000	2000	2000	2000	2000	1158
Dipteryx panamensis_7	2000	2000	2000	2000	2000	1851
Dipteryx panamensis_8	2000	2000	2000	2000	2000	1832
Dipteryx panamensis_9	2000	2000	2000	2000	2000	1883
Dipteryx panamensis_10	2000	2000	2000	2000	2000	1998
Dipteryx panamensis_11	2000	2000	2000	2000	2000	2000
Dipteryx panamensis_12	2000	2000	2000	2000	2000	1982
Water_1	2000	2000	2000	2000	2000	2000
Water_2	2000	2000	2000	2000	2000	2000
Bare_Ground_1	2000	2000	2000	2000	2000	2000
Bare_Ground_2	2000	2000	2000	2000	2000	2000
Road_1	2000	2000	2000	2000	2000	2000
Road_2	2000	2000	2000	2000	2000	2000
Pasture_1	1727	1694	1945	2000	1981	2000
Pasture_2	2000	2000	2000	2000	2000	2000
Pasture_3	1999	1761	2000	2000	2000	2000
Bare_Ground_3	2000	2000	2000	2000	2000	2000
Road_3	2000	2000	2000	2000	2000	2000

Results of the Signature Separability matrix, cont.

Names of Training Classes	Dipteryx panamensis 2	Dipteryx panamensis 3	Dipteryx panamensis 4	Dipteryx panamensis 5	Dipteryx panamensis 6	Dipteryx panamensis 7
Black_1						
Black_2						
Black_3						
Vegetation_1						
Vegetation_2						
Vegetation_3						
Vegetation_4						
Vegetation_5						
Vegetation_6						
Vegetation_7						
Vegetation_8						
Vegetation_9						
Dipteryx panamensis_1						
Dipteryx panamensis_2	0					
Dipteryx panamensis_3	1672	0				
Dipteryx panamensis_4	1358	943	0			
Dipteryx panamensis_5	1286	1817	1854	0		
Dipteryx panamensis_6	1671	1652	1813	232	0	
Dipteryx panamensis_7	1568	597	960	1875	1837	0
Dipteryx panamensis_8	1516	1995	1907	1977	1995	1993
Dipteryx panamensis_9	1147	1801	869	1977	1990	1505
Dipteryx panamensis_10	1993	1997	1774	2000	2000	1998
Dipteryx panamensis_11	2000	2000	2000	2000	1999	2000
Dipteryx panamensis_12	1676	1997	1955	1998	2000	1975
Water_1	2000	2000	2000	2000	2000	2000
Water_2	2000	2000	2000	2000	2000	2000
Bare_Ground_1	2000	2000	2000	2000	2000	2000
Bare_Ground_2	2000	2000	2000	2000	2000	2000
Road_1	2000	2000	2000	2000	2000	2000
Road_2	2000	2000	2000	2000	2000	2000
Pasture_1	2000	2000	2000	2000	2000	2000
Pasture_2	2000	2000	2000	1997	1982	2000
Pasture_3	2000	2000	2000	2000	2000	2000
Bare_Ground_3	2000	1999	2000	1995	1966	2000
Road_3	2000	2000	2000	2000	2000	2000

Results of the Signature Separability matrix, cont.

Names of Training Classes	Dipteryx panamensis 8	Dipteryx panamensis 9	Dipteryx panamensis 10	Dipteryx panamensis 11	Dipteryx panamensis 12	Water_1	Water_2
Black_1							
Black_2							
Black_3							
Vegetation_1							
Vegetation_2							
Vegetation_3							
Vegetation_4							
Vegetation_5							
Vegetation_6							
Vegetation_7							
Vegetation_8							
Vegetation_9							
Dipteryx panamensis_1							
Dipteryx panamensis_2							
Dipteryx panamensis_3							
Dipteryx panamensis_4							
Dipteryx panamensis_5							
Dipteryx panamensis_6							
Dipteryx panamensis_7							
Dipteryx panamensis_8	0						
Dipteryx panamensis_9	1700	0					
Dipteryx panamensis_10	1882	1903	0				
Dipteryx panamensis_11	2000	2000	2000	0			
Dipteryx panamensis_12	1724	1457	2000	2000	0		
Water_1	2000	2000	2000	2000	2000	0	
Water_2	2000	2000	2000	2000	2000	2000	0
Bare_Ground_1	2000	2000	2000	2000	2000	2000	1999
Bare_Ground_2	2000	2000	2000	2000	2000	2000	2000
Road_1	2000	2000	2000	2000	2000	2000	2000
Road_2	2000	2000	2000	2000	2000	2000	2000
Pasture_1	2000	2000	2000	2000	2000	2000	2000
Pasture_2	2000	2000	2000	2000	2000	2000	2000
Pasture_3	2000	2000	2000	2000	2000	2000	2000
Bare_Ground_3	2000	2000	2000	2000	2000	2000	2000
Road_3	2000	2000	2000	2000	2000	2000	2000

Results of the Signature Separability matrix, cont.

Names of Training Classes	Bare_Ground_1	Bare_Ground_2	Road_1	Road_2	Pasture_1	Pasture_2	Pasture_3	Bare_Ground_3	Road_3
Black_1									
Black_2									
Black_3									
Vegetation_1									
Vegetation_2									
Vegetation_3									
Vegetation_4									
Vegetation_5									
Vegetation_6									
Vegetation_7									
Vegetation_8									
Vegetation_9									
Dipteryx panamensis_1									
Dipteryx panamensis_2									
Dipteryx panamensis_3									
Dipteryx panamensis_4									
Dipteryx panamensis_5									
Dipteryx panamensis_6									
Dipteryx panamensis_7									
Dipteryx panamensis_8									
Dipteryx panamensis_9									
Dipteryx panamensis_10									
Dipteryx panamensis_11									
Dipteryx panamensis_12									
Water_1									
Water_2									
Bare_Ground_1	0								
Bare_Ground_2	2000	0							
Road_1	2000	2000	0						
Road_2	2000	1994	2000	0					
Pasture_1	2000	2000	2000	2000	0				
Pasture_2	2000	2000	1867	2000	2000	0			
Pasture_3	2000	2000	2000	2000	1991	2000	0		
Bare_Ground_3	2000	1999	1992	2000	2000	940	2000	0	
Road_3	2000	1996	2000	1273	2000	2000	2000	2000	0

**Appendix C: Recent ruling that bans the use,
exploitation, or extraction of *D. panamensis***

Costa Rica, Martes 16 de septiembre de 2008

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PORTADA **EL PAÍS** DEPORTES SUCESOS ECONOMÍA ALDEA GLOBAL EL MUNDO OPINIÓN
Sociedad Política Su cantón

Sala IV prohíbe explotación del almendro amarillo

ÁNGELA ÁVALOS R. | 09:06 AM | aavalos@nacion.com

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San José (Redacción) Un voto de la Sala Constitucional prohibió la explotación del almendro amarillo en el país. Este árbol es vital para la supervivencia de la lapa verde, una especie en peligro de extinción.

La sentencia 2008-13426 la acaba de dar a conocer la oficina de prensa de la Corte.

Según el comunicado de prensa, "las autoridades del Ministerio de Ambiente y Energía (MINA E) deben de abstenerse de continuar o iniciar con cualquier procedimiento tendiente al aprovechamiento, explotación o extracción del almendro amarillo (*dipteryx panamensis*) mientras este árbol y la lapa verde se encuentren en la lista de especies amenazadas o en peligro de extinción".

"... se anula la resolución administrativa ACAHN-HN-DR-002-07, dictada por el Director del Área de Conservación Arenal Huetar Norte a las 14:44 horas del 26 de febrero de 2007.

"Se ordena a Alberto Delgado Artavia, Director a.i. del Área de Conservación Arenal Huetar Norte, o a quien ocupe ese cargo, proceder a archivar cualquier diligencia o procedimiento destinado al aprovechamiento, explotación o extracción del almendro amarillo (*dipteryx panamensis*).

"Se prohíbe a ese funcionario dar inicio o continuar cualquier procedimiento tendiente al aprovechamiento, explotación o extracción del almendro amarillo (*dipteryx panamensis*) mientras este árbol y la lapa verde (*ara ambigua*) se encuentren en la lista de especies amenazadas o en peligro de extinción, sin que esa prohibición exima al servidor indicado de resolver y notificar lo correspondiente a quienes hubieran planteado alguna gestión en ese sentido, esto último de acuerdo con el contenido del artículo 41 de la Constitución Política", dice la sentencia de la Sala IV.

El fallo ordena la realización de inspecciones periódicas en el Área de Conservación Arenal Huetar Norte para verificar que no se está extrayendo el almendro amarillo y con ello afectando el hábitat y alimento de la lapa verde.

El recurso de amparo lo interpuso un hombre de apellido Carmiol Ulloa a favor de la Asociación Red Costarricense de Reservas Naturales contra las autoridades del Ministerio.

Para los recurrentes, existen cerca de 100 especies leñosas como opciones de comercialización.

This article describes the recent ruling on *D. panamensis* and was published in Costa Rica's national newspaper, La Nación (Ávalos R. 2008).

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Biography

Sara L. M. Chun was born in 1976. She grew up in Mountain View, California. In 1998, she graduated from Harvard College with a bachelor's degree in Biology. During her college years, Sara made several research trips to the tropical countries of Costa Rica, Malaysia, and Indonesia. These trips piqued Sara's curiosity of tropical systems. After college, Sara spent three years working as a restoration ecologist at H. T. Harvey & Associates, an environmental consulting firm based in San Jose, California. Some of her job duties included designing and monitoring riparian and wetland restoration sites, writing environmental reports such as Mitigation and Monitoring Plans, and drafting scopes and budgets for project proposals. In the fall of 2001, Sara began the doctoral program in the University Program in Ecology at Duke University.

Sara is committed to balancing academic research with teaching and professional development. As a doctoral student at Duke University, Sara participated in the Preparing Future Faculty (PFF) program. The PFF program matches doctoral students with a faculty mentor at a local teaching college so that participants can observe and experience faculty responsibilities at a variety of academic institutions. In the fall of 2007, Sara taught her own graduate course entitled, "Ecosystem Science and Management" to 23 master's students. This course was conducted through the Duke Environmental Leadership program, which is an online executive master's program.

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